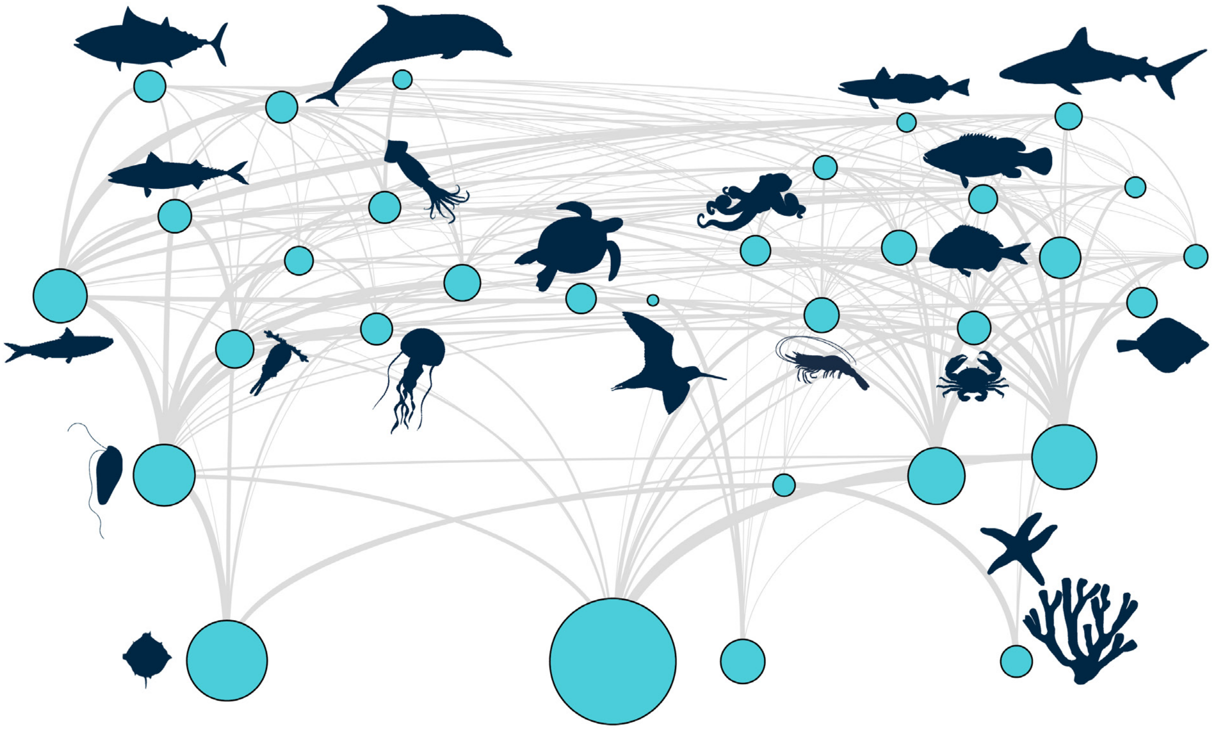
חקר ימים ואגמים לישראל
Israel Oceanographic & Limnological Research

UPC

ICM Institute of Marine Sciences

Ecosystem modelling in the Eastern Mediterranean Sea: the cumulative impact of alien species, fishing and climate change on the Israeli marine ecosystem



PhD Thesis 2019
Xavier Corrales Ribas

Ecosystem modelling in the Eastern Mediterranean Sea: the cumulative impact of alien species, fishing and climate change on the Israeli marine ecosystem

Modelización ecológica en el Mediterráneo oriental: el impacto acumulado de las especies invasoras, la pesca y el cambio climático en el ecosistema marino de Israel

Memoria presentada por
Xavier Corrales Ribas
para optar al título de Doctor por la Universidad Politécnica de Cataluña (UPC) dentro del
Programa de Doctorado de Ciencias del Mar

Supervisores de tesis:

Dr. Marta Coll Montón. Instituto de Ciencias del Mar (ICM-CSIC), Barcelona, España

Dr. Gideon Gal. Centro de Investigación Oceanográfica y Limnológica de Israel (IOLR), Migdal, Israel

Tutor:

Dr. Manuel Espino Infantes. Universidad Politécnica de Cataluña (UPC), Barcelona, España

Enero 2019

This PhD thesis has been framed within the project DESSIM (*A Decision Support system for the management of Israel's Mediterranean Exclusive Economic Zone*) through a grant from the *Israel Oceanographic and Limnological Research Institute* (IORL). The PhD has been carried out at the Kinneret Limnological Laboratory (IOLR) (Migdal, Israel) and the Institute of Marine Science (ICM-CSIC) (Barcelona, Spain).

The project team included Gideon Gal (Kinneret Limnological Laboratory, IORL, Israel) who was the project coordinator and co-director of this thesis, Marta Coll (ICM-CSIC, Spain), who was co-director of this thesis, Sheila Heymans (Scottish Association for Marine Science, UK), Jeroen Steenbeek (Ecopath International Initiative research association, Spain), Eyal Ofir (Kinneret Limnological Laboratory, IORL, Israel) and Menachem Goren and Daphna DiSegni (Tel Aviv University, Israel).

“In nature there are no rewards or punishments, there are consequences”

“En la naturaleza no hay recompensas ni castigos, hay consecuencias”

Bob Ingersoll

ACKNOWLEDGEMENTS

I would like to think about this thesis as a race, with accelerated and decelerated moments. It has been a quite long trip (5 years). During this time I lived in 4 different places, I worked in 4 research institutes, I met a lot of people and I made good friends. During all this time I have felt accompanied and I would like to thank to all the people that during one part of the trip or even all of it have contributed to the fact that today I am able to write this part of the thesis. I would like to mention all the people, so I apologize if I forget someone. Here it is my short tribute to all of them.

First and foremost, this thesis would has not been possible without the opportunity that my supervisors, Dr. Marta Coll and Dr. Gideon Gal, gave me quite a long time ago. Thank you for all your support, guidance, encouragement and patience, allowing me to take a valuable experience in terms of research and personal enrichment.

Thanks also to the members of the project team as well as co-authors on the different chapters of my thesis. Thank you for your time and advice on my work. Many thanks to Dr. Eyal Ofir for all the help during my stay in Israel, for all the discussions, for all the conversations, for all the trips, etc. Definitively, for being a friend. Many thanks extended also to Jeroen Steenbeek, who helped a lot during the thesis, especially for all the discussions and fixing Ecopath/Ecosim bugs. A special thanks to Dr. Sheila Heymans, who helped me on model development and kindly received in Oban. I am grateful to Dr. Stelios Katsanevakis, for the opportunity to participate in a European project, for my stay in Lesbos and for all your help and support in one of the chapters of the thesis. Many thanks to Dr. Dor Edelist and Dr. Menachem Goren for all the data on the study area and all the discussions, contributions, insightful comments and confidence they had in me. I want to warmly thank Dr. Chiara Piroddi, for all your lessons, valuable comments and discussions about Ecopath and ecological aspects.

At the same time, I would like to thanks all the people who during my scientific training have brought some contribution, especially Dr. Josep Lloret and Dr. Isabel Palomera. Thanks for your advice, support, encouragement and your friendship.

During the PhD, I had the fortune to meet many people. Thanks very much to my colleagues from the Kinneret Limnological Laboratory, especially Noam, Ruthy, Peleg, Yaron and Yohi. Many thanks to the colleagues and friends from Renewable Marine

Resources Department from the Institute of Marine Science (ICM-CSIC). Firstly, a special thanks to my office mates: Marc F., Morane and John. Thanks for your patience with your chatterbox office mate and all your help. A special thanks to Daniel Vilas, for our friendship, support, help, valuable comments… I also would like to thanks Marc B., Mariona and Cristina, for our smoking breaks, your friendship and great (and bad) moments in front of the ICM. I would like to express many thanks to Alejandro, Marta Albo, Ivan, Marta Carretón, Carol, Claudio, Núria, Dafni, Susana, Anabel, Vanesa, Amalia, Federico, Elena Lloret, Elena Fernández, Fernando, Joan Navarro, Lucia, David, Joan Mir, Alizée, Javi, and Diego. I am also deeply thankful to Natalia Serpetti for your help while I was in Oban and to Athanasios Evagelopoulus, Maria Sini and Vasilis Trygonis for your warm reception during my stay in Mytilene.

A really warm thanks to all my friends. Per la nostre amistat, per tots els bons moments i sobretot pel vostre suport en els moments dolents. En primer lloc a la colla d’amics de tota la vida de Portbou. Sempre aprop (tot i la distancia), actuant com a vàlvules d’escapament i desconexió en aquest petit racó de la Costa Brava. Moltes gràcies Pedro, Carlos (i els teus fills Leo i Enzo), Natalia, Eric, Paula, Anna, Didi, Davinia, Antonio, Laura, Joel, Carrillo, Edgar, Borja, Saida, Abraham, Manel, ... També m’agradaria donar les gràcies als companys de pis que he tingut a Barcelona. Moltes gràcies Andreu, Pablo, Marta, Janire i Elena. A totes les amistats barcelonines que hem continuat mantenint la amistat: Jordi, Virginia, Jenifer, Miquel, Uriol, David, Nuria, Gemma, Iris, Salva, Anna, Nuria ... I com no, un agraïment especial també al grup “Bailones”. Per tots el moments compartits, riures, balls, sortides, activitats, ... Heu sigut una via d’escapament molt important durant la última part de la tesis. Moltes gràcies Roberto, Eli, Alba, Eva, Mel, Mónica, David, Oscar, Laia, Elena, Laura, Paula, Joan, Robert, Toni, …

I would like to conclude thanking my family. Especialment als meus pares, al meu germà i a la meva àvia. Moltes gràcies per tot: per fer-me la persona que soc ara, per tots els valors que m’heu inculcat, pel vostre amor, confiança i recolzament incondicional. Per aprendre a lluitar, a créixer. Gràcies per estar sempre al meu costat. A vosaltres us ho dec tot! Mil gràcies!

ABSTRACT

The ecosystems of the Eastern Mediterranean Sea have undergone significant ecological changes caused by multiple human stressors, including the impact of invasive alien species (IAS), overfishing and sea warming. Firstly, I reviewed modelling approaches that have been used to assess the impact of IAS in aquatic ecosystems. According to the review, multispecies/ecosystem mechanistic models dominated the applications, with dynamic and non-spatial models being the most prevalent. Most of the models included an additional human stressor, mainly fisheries, climate change and/or nutrient loading. In the review, I summarised the main features of these applications and analysed their capabilities and limitations. Based on my conclusions, I reflected on future directions of development and applications of suitable modelling tools.

In the review, I found that the Ecopath with Ecosim (EwE) approach had been frequently used to assess the impacts of already established IAS. In addition, the review highlighted EwE capabilities to forecast existing, emerging and potential new IAS. Other available literature reviews had shown EwE capabilities in assessing impacts of fishing and climate change, the other two stressors included in this thesis.

Therefore, as a second step in the thesis, I first developed two static Ecopath ecosystem models from EwE approach representing the food web of the Israeli Mediterranean coast in 1990s and 2010s to characterize the structure and functioning of the ecosystem and assess past and current impacts of IAS and fishing. I then used the time-dynamic Ecosim module of EwE to fit the 1990s model to available time series of observations between both periods and to explore the historical dynamics of the ecosystem considering the effects of IAS, fishing dynamics and sea warming. Finally, the time-dynamic ecosystem model was used to perform future simulations of ecosystem change. Particularly, and after interacting with key stakeholders, I assessed the effects of a new set of fishing regulations currently being implemented in Israel, future changes in sea temperature following IPCC (Intergovernmental Panel on Climate Change) scenario projections and the potential increases in IAS biomass in the future. Firstly, I investigated the impacts of the stressors separately, and then I combined them to evaluate their cumulative effects.

Results from the static Ecopath models highlighted that the Israeli marine ecosystem, despite productivity differences, shared some structural and functional traits with other Mediterranean ecosystems such as the dominance of the pelagic domain in term of flows, the important role of detritus through low trophic levels and the importance of the benthic-pelagic coupling. In both time periods investigated, the same keystone groups were identified with the exception of hake in 2010s, which showed a decline in its keystone role, and may indicate that hake had lost its ecological role due to population declines. Most of the functional groups identified as keystone species had been previously identified as keystones in other Mediterranean ecosystems, such as dolphins, large pelagic fishes, sharks and squids.

The temporal dynamic Ecosim model indicated that trophic interactions, ocean warming and fishing were important drivers of the ecosystem dynamics. In general, temporal biomass trends revealed that native demersal predators (e.g. hake) and native medium trophic level fishes (e.g. mullets) largely declined over time, while an increase over time of alien species was observed. Results from selected ecological indicators suggested a degradation pattern of the ecosystem over time.

Future scenarios using the temporal dynamic Ecosim model showed overall potential benefits of fishing effort reductions, and detrimental impacts of increasing sea temperature and increasing biomass of alien species. Cumulative scenarios highlighted that the beneficial effects of fisheries reduction could be dampened by the impact of increasing sea temperature and alien species when acting together. These results support the need for reducing local and regional stressors, such as fishing and biological invasions, to retain marine ecosystems within a “safe operating space (SOS)” and ensure ecosystem resilience in an ongoing warming and impacted sea.

RESUMEN

Los ecosistemas marinos del Mediterráneo oriental han sufrido cambios ecológicos importantes debido a múltiples presiones antropogénicas, incluido el impacto de especies invasoras, la sobrepesca y el calentamiento del mar. En primer lugar, he revisado los modelos que se han utilizado para evaluar el impacto de las especies invasoras en los ecosistemas acuáticos. De acuerdo con esta revisión, predominan los modelos mecanísticos de carácter multiespecífico/ecosistémico, siendo los modelos dinámicos y no espaciales los más frecuentes. La mayoría de los modelos incluyen un impacto antropogénico adicional, principalmente la pesca, el cambio climático y el aporte de nutrientes. Además, he resumido las principales características de estos modelos y he analizado sus capacidades y limitaciones. En base a las conclusiones de esta revisión, se han mostrado posibles direcciones para futuros desarrollos de los modelos y la aplicación de modelos adecuados.

En esta revisión, he observado que el modelo Ecopath with Ecosim (EwE) ha sido utilizado frecuentemente para evaluar los impactos de las especies invasoras ya establecidas. Además, la revisión ha destacado las capacidades de EwE de pronosticar los futuros impactos de las especies invasoras establecidas, emergentes y potenciales. Otras revisiones disponibles en la literatura han demostrado las capacidades de EwE para evaluar los impactos de la pesca y el cambio climático.

Por lo tanto, he desarrollado dos modelos estáticos Ecopath que representan la red trófica de la costa Mediterránea de Israel en los años 1990 y 2010 para caracterizar la estructura y funcionamiento del ecosistema y evaluar los impactos de las especies invasoras y la pesca en el pasado y en el presente. Después he utilizado el módulo dinámico-temporal Ecosim para ajustar el modelo de 1990 a series temporales de datos disponibles entre ambos periodos y para explorar la dinámica histórica del ecosistema considerando el efecto de las especies invasoras, la dinámica de la flota pesquera y el calentamiento del mar. Finalmente, el módulo dinámico-temporal ha sido utilizado para realizar simulaciones futuras de cambios en el ecosistema. En particular, he evaluado los efectos de un nuevo conjunto de regulaciones de pesca que se están implementando actualmente en Israel, futuros cambios en la temperatura del mar siguiendo las proyecciones del Panel Intergubernamental sobre el Cambio Climático (IPCC por sus

siglas en inglés) y posibles aumentos de la biomasa de las especies invasoras. Primero he investigado los diferentes impactos por separado y, luego, los he combinado para evaluar sus efectos acumulativos.

Los resultados de los modelos estáticos Ecopath han destacado que el ecosistema marino israelí, a pesar de un patrón de productividad diferente, comparte algunas características estructurales y funcionales con otros ecosistemas mediterráneos como el dominio del hábitat pelágico en términos de flujos tróficos, el importante papel del detritus a través de niveles tróficos bajos y la importancia del acoplamiento bentónico-pelágico. Los mismos grupos funcionales clave fueron identificados en ambos periodos investigados, a excepción de la merluza en 2010, lo que puede indicar que la merluza ha perdido su papel ecológico debido al declive de su población. La mayoría de los grupos funcionales identificados como especies clave ya han sido identificados previamente como tales en otros ecosistemas mediterráneos como por ejemplo los delfines, los grandes peces pelágicos, los tiburones y los calamares.

El módulo dinámico-temporal Ecosim indicó que las interacciones tróficas, el aumento de la temperatura del mar y la pesca jugaron un papel clave en la dinámica del ecosistema. En general, las tendencias temporales de la biomasa revelaron que los depredadores demersales nativos (por ejemplo, la merluza) y los peces demersal nativos de nivel trófico medio (por ejemplo, los salmonetes) disminuyeron en gran medida con el tiempo, mientras que se observó un aumento de las especies invasoras con el tiempo. Los resultados de los indicadores ecológicos sugirieron un patrón de degradación del ecosistema con el tiempo.

Los escenarios futuros utilizando el módulo dinámico-temporal Ecosim mostraron los beneficios potenciales generales de las reducciones del esfuerzo pesquero y los impactos negativos del aumento de la temperatura del mar y el aumento de la biomasa de las especies invasoras. Los escenarios acumulativos resaltaron que los efectos beneficiosos de la reducción de la pesca pueden verse disminuidos por el impacto del aumento de la temperatura del mar y las especies invasoras cuando actúan al mismo tiempo. Estos resultados respaldan la necesidad de reducir los impactos antropogénicos locales y regionales como la pesca y las especies invasoras, para mantener los ecosistemas marinos dentro de un “espacio operativo seguro (SOS por sus siglas en

inglés)” y promover la resiliencia de los ecosistemas en un mar en continuo calentamiento y altamente impactado.

RESUM

Els ecosistemes marins de la Mediterrànea oriental han patit canvis ecológics importants a causa de múltiples pressions antropogèniques, inclòs l'impacte d'especies invasores, la sobrepesca i el calentament del mar. En primer lloc, he revisat els models que s'han utilitzat per avaluar l'impacte de les espècies invasores en ecosistemes aquàtics. D'acord amb aquesta revisió, predominen els models mecanístics de caràcter multiespecífic/ecosistèmic, sent els models dinàmics i no espacials els més freqüents. La majoria dels models inclouen un impacte antropogènic adicional, principalment la pesca, el canvi climàtic i l'aport de nutrients. A més, he resumit les principals característiques d'aquest models i he analitzat les seves capacitats i limitacions. En base a les conclusions d'aquesta revisió, s'han exposat possibles direccions per futurs desenvolupaments dels models i l'aplicació de models adecuats.

En aquesta revisió he observat que el model Ecopath with Ecosim (EwE) ha estat utilitzat freqüentment per avaluar els impactes de les espècies invasores ja establertes. A més, la revisió ha destacat les capacitats d'EwE de pronosticar els futurs impactes de les espècies establertes, emergents i potencials. Altres revisions disponibles a la literatura han demostrat les capacitats d'EwE per avaluar els impactes de la pesca i el canvi climàtic.

Per tant, he desencolupat dos models estàtics Ecopath que representen la xarxa tròfica de la costa Mediterrànea d'Israel en els anys 1990 y 2010 per caracteritzar l'estructura i funcionament de l'ecosistema i avaluar els impactes de les espècies invasores i la pesca en el passat i el present. Després he utilitzat el mòdul dinàmic-temporal per ajustar el model de 1990 a sèries temporals de dades disponibles considerant l'efecte de les espècies invasores, la dinàmica de la flota pesquera i l'escalfament del mar. Finalment, el mòdul dinamic-temporal ha estat utilitzat per realitzar simulacions futures de canvis en l'ecosistema. En particular, he avaluat els efectes d'un nou conjunt de regulacions de pesca que s'estan implementant actualment a Israel, canvis en la temperatura del mar seguint les projeccions del panell intergovernamental sobre el Canvi Climàtic (IPCC per les seves sigles en anglès) i possibles augments de la biomass de les espècies invasores. Primer he investigat els diferents impactes per separat i, després, els he combinat per avaluar els seus efectes acumulatius.

Els resultats dels models estàtics Ecopath han destacat que l’ecostema marí d’Israel, malgrat un patró de productivitat diferent, comparteix algunes característiques estructurals i de funcionals amd altres ecosistemes marins mediterrànis com el domini de l’hàbitat pelàgic en termes de fluxes tròfics, l’important paper del detritus a través de nivells tròfics baixos i la importància de l’acoplament bentònic-pelàgic. Els mateixos grups funcionals clau van ser identificats en els dos períodes investigats, a excepció del lluç en el 2010, que pot indicar que el lluç ha perdut el seus paper ecològic a causa del declivi de la seva població. La majoria del grups funcionals identificats com a espècies claus ja han estat identificats com a tals en altres ecosistemes mediterranis com ara els dofins, els gran peixos pelàgics, els taurons i els calamars.

El mòdul dinàmic-temporal Ecosim ha indicat que les interaccions tròfiques, l’augment de la temperatura del mar i la pesca van jugar un paper clau en la dinàmic de l’ecosistema. En general, les tendències temporals de la biomasa van revelar que els depredadors demersals natius (per exemple, el lluç) i els peixos dersals natius de nivell tròfic mitjà (per exemple, els rogers) van disminuir en gran mesura amb el temps, mentre que es va observar un augment de les espècies invasores amb el temps. Els resultats dels indicadors ecològics van suggerir un patrò de degradació de l’ecosistema amb el temps.

Els escenaris futurs van mostrar els beneficis potencials generals de les reduccions de l’esforç pesquer i els impactes negatius de l’augment de la temperatura del mar i l’augment de la biomasa de les espècies invasores. Els escenaris acumulatius van ressaltar que els efectes beneficiosos de la reducció de la pesca poden ser reduïts per l’impacte de l’augment de la temperatura del mar i les espècies invasores quan actuen al mateix temps. Aquests resultats recolzen la necessitat de reduir els impactes antropogènics locals i regionals com la pesca i les espècies invasores, per mantenir els ecosistems marins dins d’un “espai operatiu segur (SOS per les seves sigles en anglès)” i promoure la resiliència dels ecosistemes en un mar en continu escalfament i altament impactat.

HEBREW ABSTRACT

המערכות האקולוגיות של מזרח ים התיכון עברו שינויים מהותיים בעקבות גורמי עקה שונים הכוללים בין השאר כניסה והתבססות של מינים פולשים, דיג יתר והתחממות הים. תחילה, ערכתי סקירה ספרותית מקיפה שבה בחנתי את הגישות השונות לשימוש במודלים אקולוגיים לבחינת השלכות האפשריות של התבססות של מינים פולשים על מערכות אקולוגיות אקווטיות. מתוך הסקירה עולה כי מודלים תהליכיים, רב-מיניים, ולא מרחביים הם הנפוצים ביותר. רוב המודלים כללו מרכיב עקה אנתרופוגני נוסף כגון דיג יתר, שינויים אקלימיים ועומס נוטריינטים. בנוסף, סיכמתי את השימושים במודלים, היכולות והמגבלות. על בסיס המסקנות, הצעתי כיווני פיתוח ומחקר עתידיים לצורך הרחבת כלי המידול שיעמדו לרשות חוקרים בתחום.

בסקירה הספרותית שערכתי, מצאתי שנעשה שימוש תדיר במודלים מהסוג Ecopath with Ecosim (EwE) לצורך הערכת ההשלכות של התבססות של מינים פולשים על מערכות אקולוגיות. בנוסף, נמצא כי מודלים מהסוג הזה יכולים לחזות את ההשלכות של כניסה של מינים פולשים חדשים ומינים שעלולים לפלוש. סקירות נוספות שנערכו בעבר הצביעו על האפשרות להערכת ההשפעות של דיג ושינויי אקלים על מערכות אקולוגיות אקווטיות בעזרת מודלים מהסוג EwE.

בעקבות ממצאי הסקירות בניתי שני מודלים סטטיסטים מהסוג Ecopath שייצגו את המערכת האקולוגית של מדף היבשת הישראלי בתחילת שנות ה-90 וכן ב-2010 על מנת לאפיין את מבנה מארג המזון ותפקוד המערכת ולבחון את ההשפעות של מינים פולשים ודיג. בהמשך, בניתי מודל דינמי בזמן מהסוג Ecosim על מנת להרחיב את המודל הסטטי משנות ה-90 ולשחזר את התצפיות בין שתי התקופות לצורך בחינת התהליכים שהתרחשו בתקופה זאת , וחשיבותם. במיוחד, בחנתי את ההשלכות של המינים הפולשים, הדיג ושינויי האקלים על מארג המזון. בנוסף, השתמשתי במודל הדינמי על מנת להריץ תרחישים של שינויים במערכת האקולוגית. בתרחישים בחנתי את ההשלכות של השינויים בתקנות הדיג, שינויים אקלימיים על בסיס התחזיות של הועדה בין-ממשלתית בנושא שינויי אקלים (IPCC) וכן את הפוטנציאל לעליה בביומסה של מינים פולשים בעתיד. תחילה בחנתי את ההשפעות של כל גורם בנפרד ובהמשך את ההשלכות המצטברות של שלושת הגורמים יחדיו.

מתוצאות המודלים הסטטיים עולה כי, למרות התנאים הייחודים של מזרח ים התיכון, למערכת האקולוגית של מדף היבשת הישראלי מאפיינים דומים, מבחינת מבנה ותפקוד, למערכות אחרות בים תיכון. לדוגמא, החשיבות של המרכיב הפלגי במערכת מבחינת מעברי האנרגיה, משמעות חומרי הרקב ברמות הטרופיות הנמוכות וערך הצימוד שבין המערכות הפלגית והבנתית. בשתי התקופות שנבחנו, מיני המפתח היו דומים למעט הבקלה (Hake) שאיבד מחשיבותו במודל של 2010 כנראה לאור הירידה בגודל האוכלוסייה. מרבית הקבוצות שזוהו כמיני מפתח זוהו ככאלה במודלים אחרים של ים תיכון כדוגמאת הדולפינים, הכרישים, והדיונונים. המודל הדינמי בזמן הצביע על חשיבות האינטראקציות בין מרכיבי מארג המזון השונים, התחממות הים ודיג כגורמים המשפיעים על תהליכים אקולוגיים. באופן כללי, הביומסה של קבוצות

הטורפים הדמרסליים, כגון הבקלה, וכן דגים מקומיים מרמות טרופיות ביניים, כגון המולית, הצטמצמה במקביל לעליה בביומסה של מינים פולשים עם הזמן. תוצאות המדדים האקולוגיים מצביעים על התדרדרות מצב המערכת האקולוגית לאורך זמן.

תוצאות התרחישים העתידיים רמזו על התועלות שבצמצום היקף הדיג וההשלכות השליליות שיתלוו לעלייה בטמפרטורה המים ולעליה בביומסה של מינים פולשים. תוצאות ההרצות שבהם נבחנו שלושת הגורמים בו זמנית הדגישו את צמצום התועלות שבהגבלות מאמץ הדיג בעקבות העלייה בטמפרטורה ובמינים הפולשים. תוצאות אלו מצביעות על הצורך בצמצום גורמי עקה מקומיים ואזוריים כגון דיג והדירה של מינים פולשים כדי לשמר את המערכת האקולוגית בתוך תחום תפקוד בטוח ולהגברת העמידות של המערכת האקולוגית לאור השינויים הסביבתיים הצפויים.

FIGURES AND TABLES

General Introduction

Figures

Chapter 1: Advances and challenges when modelling the impacts of invasive alien species

Figures

Tables

Chapter 2: Modelling the role and impact of alien species and fisheries on the Israeli marine continental shelf ecosystem

Figures

Tables

Chapter 3: Hindcasting the dynamics of an Eastern Mediterranean marine ecosystem under the impacts of multiple stressors

Figures

Tables

Chapter 4: Future scenarios of marine resources and ecosystem conditions in the Eastern Mediterranean under the impacts of fishing, alien species and sea warming.

Figures

Tables

CHAPTER 1: INTRODUCTION

1.1. Human impacts on the marine environment

1.1.1. Historical and emergent impacts on marine ecosystems

The ocean covers two-thirds of the planet and holds a broader phylogenetic biodiversity of life than terrestrial ecosystems (Mora et al., 2011). Since ancient times, oceans have been an important source of food, employment and other economic benefits for humanity (Jackson et al., 2001, Lotze et al., 2006). In particular, coastal areas have provided advantages for human settlement because marine environment facilitates certain activities such as fishing, industry, trade and tourism (Barragán and de Andrés, 2015). Nearly 40% of the world's population lives within 100 km of the coast and this percentage is increasing (Agardy et al., 2005).

The ocean productivity seemed unlimited (Christy and Scott, 1965, Costanza et al., 1999). However, as human population grows, the use of marine resources and the impacts of anthropogenic activities on marine ecosystems have intensified, spread and diversified (Halpern et al., 2008b, Halpern et al., 2015a).

During the last few decades, marine ecosystems have been altered at surprising rates in a global context as a result of escalating pressure from the cumulative impact of global, regional and local stressors, including climate change, biological invasions and direct human pressures such as overexploitation, pollution and habitat modification (Costello et al., 2010, Halpern et al., 2015a). Given the range of human activities, stressors often co-occur in time and space. Thus most marine ecosystems are exposed to the impacts of multiple stressors (Breitburg and Riedel, 2005, Halpern et al., 2015a, Ramírez et al., 2018). In fact, no area of the world's oceans is unaffected by anthropogenic activities and 40% of marine areas in 2015 was strongly affected by multiple human activities (Halpern et al., 2008b, Halpern et al., 2015a).

Overexploitation is one of the major threats to marine ecosystems worldwide, causing biodiversity loss, profound and significant ecological changes and the loss of ecosystem services (Pauly et al., 1998, Worm et al., 2006). Specifically, since the Industrial Revolution, and especially after the Second World War, fishing was developed due to the implementation of new technologies, the geographic and bathymetric expansion of fishing and the capture of less accessible and initially less valuable species (Pauly et al., 2002, Swartz et al., 2010, Anticamara et al., 2011, Watson et al., 2013, Watson and

Morato, 2013). Marine catches increased between 1950 and 1996, when they peaked at a maximum of 130 million tonnes and then started a steady decline (Fig. 1) (Pauly and Zeller, 2016). This decline occurred despite increased fishing effort and efficiency, and the geographic and bathymetric expansion of fishing activities (Swartz et al., 2010, Watson et al., 2013). Therefore, it seems that the overall limits of sustainable exploitation was long exceeded (Worm and Branch, 2012, Pitcher and Cheung, 2013).

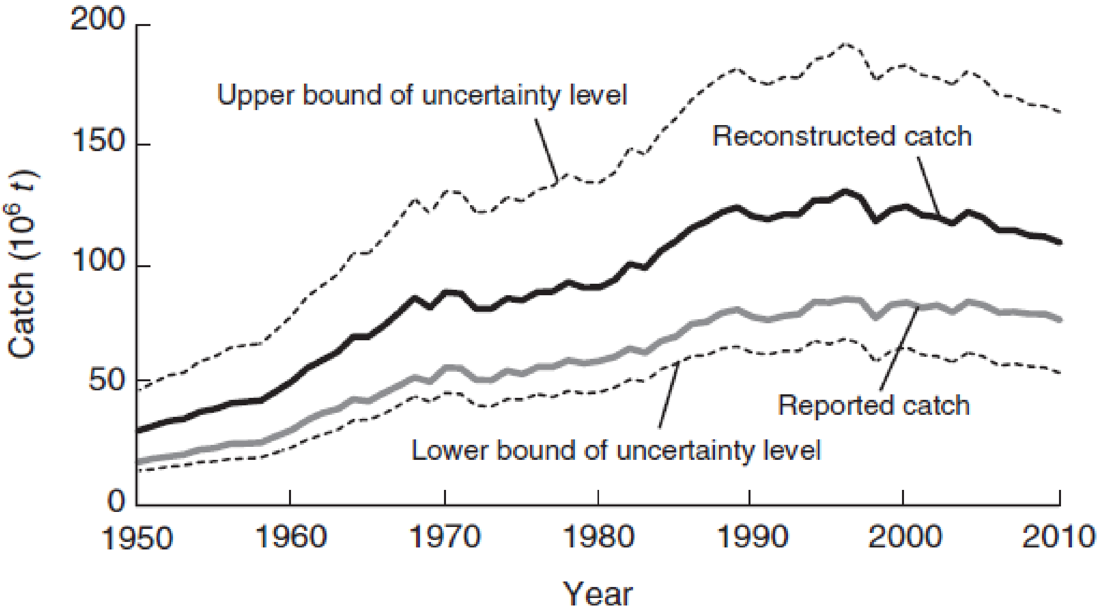


Fig. 1. Trajectories of reported and reconstructed catches from 1950 to 2010. Uncertainty of reconstructed catches is also shown. Source: Pauly and Zeller (2016).

Fishing has a variety of direct and indirect effects on marine ecosystems (Crowder et al., 2008). Direct impacts of fishing include the reduction, and even the local or regional extinction, of commercial and non-commercial species (Pauly et al., 2002, Worm et al., 2009), the loss of genetic diversity (Allendorf et al., 2008, Pinsky and Palumbi, 2014) and changes in population structure (Barnett et al., 2017, Robinson et al., 2017). Indirect impacts include habitat degradation, mainly through the destruction of the seabed (Turner et al., 1999, Grabowski et al., 2014, Hiddink et al., 2017), the generation of a large amount of discards (Kelleher, 2005, Zeller et al., 2018), incidental capture of large marine vertebrates or bycatch (Lewison et al., 2004, Lewison et al., 2014) and changes in the structure and functioning of marine ecosystems (Frank et al., 2005, Daskalov et al., 2007).

Overfishing transforms an original stable, mature and efficient ecosystem into one that is immature and stressed (Odum, 1969, Garcia et al., 2003). Organism and ecosystems already stressed by fishing are more vulnerable to emergent impacts of stressors such as climate change and biological invasions (Occhipinti-Ambrogi and Savini, 2003, Poloczanska et al., 2016).

With the increasing emissions of greenhouse gases, humans have triggered multiple negative effects on the planet, which include, among others, a global warming, ocean acidification, deoxygenation and changes in primary productivity (Fig. 2) (Walther et al., 2002, Caldeira and Wickett, 2003, Bopp et al., 2013). Oceans have absorbed a large part of the additional temperature and carbon dioxide produced by human activities (Sabine et al., 2004, Feely et al., 2009). As a result, climate change is modifying ocean biogeochemistry by promoting acidification, increasing temperatures and deoxygenation (the loss of dissolved oxygen from the ocean) (Hoegh-Guldberg and Bruno, 2010, Doney et al., 2012). Acidification is altering the seawater chemistry of the world's oceans with consequences for marine organism, especially those that produce calcareous skeletal structures (Fabry et al., 2008). Marine biota respond to ocean warming through changes in distributions and abundances (Poloczanska et al., 2016), in phenology (Edwards and Richardson, 2004) and in body size (Cheung et al., 2013a). All these impacts have already altered the structure and function of marine ecosystems by decreasing ocean productivity, changes in ocean circulation and stratification, oxygen supply, reducing abundance of habitat-forming species, coastal habitat loss due to increasing sea level and altering food-web dynamics (Hoegh-Guldberg and Bruno, 2010, Doney et al., 2012). In addition, climate change is affecting global fisheries and societies that depend on them (Cheung et al., 2013b, Barange et al., 2014) and is favouring the invasion and spread of alien species (Occhipinti-Ambrogi, 2007, Walther et al., 2009, Sorte et al., 2010).

1.1.2. The invasion of marine species

Biological invasions are among the major components of global change in marine ecosystems (Fig. 3) (Grosholz, 2002, Bax et al., 2003). In the marine environment, most alien species are reported in bays and estuaries, which are focal points of human population and trade (Ruiz et al., 2000). However, open ocean areas could also be critically altered by alien species (for example, the Mediterranean Sea) (Edelist et al., 2013a). Alien species (also known as exotic, introduced, allochthonous, non-indigenous or non-native species) are any taxa that are introduced outside their natural past or present distribution, including any part, gamete seeds, eggs, or propagules that might survive and subsequently reproduce. Invasive alien species (IAS) are defined as those alien species whose introduction or spread threaten biological diversity (CBD, 2002). Many organisations and states, e.g. the European Union (Regulation 1143/2014), include in the definition of IAS not only impacts on biodiversity but also on ecosystem services.

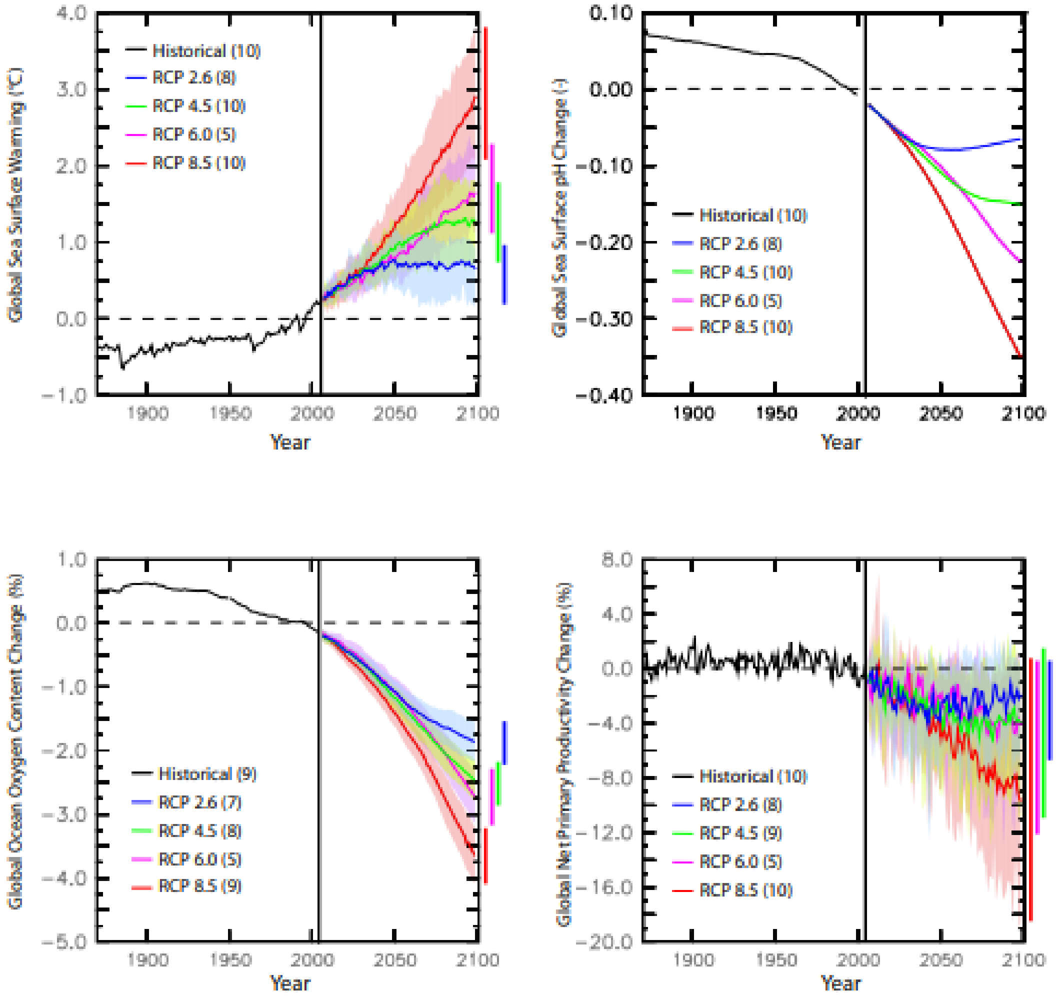


Fig. 2. Time series of global sea surface temperature (ºC), surface pH change (pH unit), ocean O_2 content change (%), and global net primary productivity change (%) over 1870-2100. Shadows represent standard deviation. All variables are plotted relative to 1990-1999. Source: Bopp et al. (2013).

Once alien species become established in marine ecosystems, it is nearly impossible to eliminate them (Thresher and Kuris, 2004). Therefore, prevention through managing vectors and pathways have been recognized as the most effective policy (CBD, 2002).

The study of alien species in marine ecosystems has, historically, lagged behind that of terrestrial and freshwater ecosystems (Grosholz, 2002). However, during the last decades, there has been increasing research on this topic that has provided insights into their ecological consequences (Grosholz, 2002, Katsanevakis et al., 2014c). The impacts of IAS can be detected at any biological level, ranging from the loss of native genotypes, changes in community composition, changes in habitat conditions, effects on food web properties, ecosystem processes and functioning, and impacts on ecosystem services (Levin and Crooks, 2011, Katsanevakis et al., 2014c).

Humans have traded and, intentionally or unintentionally, transported alien species for millennia, but the rate of new introductions of alien species have been accelerated in recent decades by the rapid globalisation of human activities and increases in trade and transport capacity, despite growing national and international efforts to reduce invasion risk (Hulme, 2009, Katsanevakis et al., 2013, Nunes et al., 2015, Seebens et al., 2017). Therefore, marine ecosystems are experiencing unpreceded rates of species extinctions and introductions (Byrnes et al., 2007, Hulme, 2009), leading to a biotic homogenization (Sala and Knowlton, 2006). Moreover, their impacts are expected to further increase, especially due to climate change (Walther et al., 2009, Raitsos et al., 2010).

In marine ecosystems, there are many examples of large-scale and dramatic impacts of IAS (Fig. 3). An increasing number of alien species are currently dominating many habitats, which contribute strongly to changes in community structure and the ecosystem structure (Cohen and Carlton, 1998, Grosholz, 2002, Jimenez et al., 2018). In the Black Sea, overfishing, eutrophication and the invasion of the comb jelly, *Mnemiopsis leidy*, profoundly impacted the structure and functioning of the ecosystem, with important effect on fisheries, including the collapse of the European anchovy (*Engraulis encrasicolus*) fishery (Shiganova, 1998, Oguz et al., 2008a). The Mediterranean Sea, which is the study area of the present thesis, is one of the marine ecosystems most affected by biological invasions (Molnar et al., 2008, Costello et al., 2010).

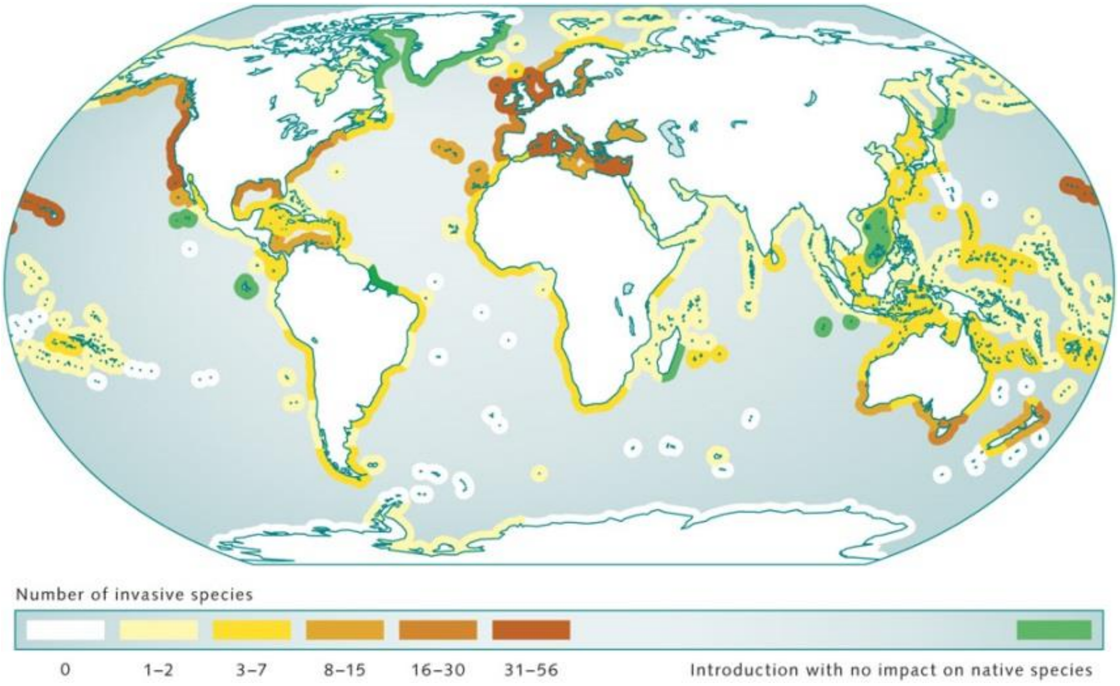


Fig. 3. Map showing the number of harmful invasive species by coastal ecoregion. Source: Early et al. (2016) and https://pipap.sprep.org

1.2. The ecosystem-based approach

Managing coastal and marine resources is becoming increasingly complex as interacting and cumulative anthropogenic impacts are rapidly increasing. These anthropogenic impacts come from the activities of multiple sectors such as fisheries, oil and gas extraction, shipping, sea bed mining, marine renewable energy, desalination plants, tourism, and urban and coastal development (Vierros et al., 2015). Since most activities do interact, managing each activity largely in isolation will be insufficient to conserve marine ecosystems (Breitburg and Riedel, 2005, Halpern et al., 2008a).

The appreciation of the interconnectedness between the environment, species populations and the cumulative impacts of human activities illustrates the pressing need to move towards a more comprehensive management of human activities such as an ecosystem-based management (EBM) (Rosenberg and McLeod, 2005, Leslie and McLeod, 2007). While there are a number of differing definitions for EBM or even different approaches or conceptual frameworks (e.g., integrated coastal management) and definitions vary across them, they have similar core principles and they agree about the need to move towards a more holistic management approach that recognizes the interaction of activities within the ecosystem (McLeod et al., 2005, Link, 2010a). EBM applied to the marine environment calls for a shift in ocean management policies from management of individual sectoral activities such as fisheries, towards an integrated approach that considers the interdependence of the entire ecosystem, including humans and the environments in which they live (Rosenberg and McLeod, 2005, Leslie and McLeod, 2007). EBM aims to maintain ecosystems in healthy, productive and resilient conditions so they can provide needed ecosystem services (McLeod et al., 2005).

EBM is now widely recognized as the best way to manage marine ecosystems and has been a prominent topic in science based management for several decades (Long et al., 2015, Smith et al., 2017). However, progress towards implementing and operationalizing it has been slow (Levin et al., 2013, Cochrane et al., 2014). Despite this, several efforts have been made to implement the EBM. For example, EBM is a key element to NOAA’s Integrated Ecosystem Assessments (Levin et al., 2009), Fisheries and Oceans Canada has implemented aspects of EBM (Curran et al., 2012) and there has been a strong shift towards EBM in Australia (Smith et al., 2007, Smith et al., 2017). In Europe, the Marine Strategy Framework Directive (MSFD), following the EBM approach, aims to achieve “clean, healthy and productive” oceans (Good Environmental Status) by 2020, focusing on 11 descriptors related to ecosystem features, human drivers and pressures (Berg et al., 2015, Marshall et al., 2018).

1.3. Ecosystem models as tools to assess the impacts of human activities

Humans have always used models, defined as a simplified representation of some real-world entity, as tools to solve problems. Models allow us to increase understanding of processes, drivers and responses of organism and ecosystem to human pressures, identify gaps in our knowledge and allow making predictions about future dynamics. However, models will never be able to represent all the features of the real system due to the complexity of ecosystems, but they may contain qualitative or quantitative descriptions of key components and processes of the system essential in the context of the problem to be solved or described, and the relationships between those components.

Intense research and our increasing understanding of aquatic ecosystems, together with the development of computing technology, which has enabled us to handle very complex mathematical models, has allowed the development of a large variety of models during the last decades (Whipple et al., 2000, Wonham and Lewis, 2009, Fulton, 2010, Koenigstein et al., 2016).

A desirable model would be one that maximizes generality (the applicability of a model to different ecosystems, data sets and questions), realism (the model includes detailed processes through mathematical equations) and precision (the degree of exactness in measurements or predictions) (Levins, 1966). However, in practice, modelling is essentially a trade-off between generality, realism and precision (Levins, 1966). While some models sacrifice realism (mostly statistical models), others sacrifice generality or precision (mostly mechanistic models) (Levins, 1966). The main difference between these models is related to their internal structure. In mechanistic models, the relationship between the variables is specified in terms of the biological process, while statistical models look for patterns and relationships in the observed data, regardless of the causative processes involved (Hilborn and Mangel, 1997, Whipple et al., 2000, Robson, 2014b). Therefore, mechanistic models can offer a deeper understanding of the system than a statistical analysis, but generally require additional data or deeper understanding of studied processes (Kendall et al., 1999, Jørgensen and Fath, 2011, Robson, 2014b).

Mechanistic models could be categorized into qualitative and quantitative models. Qualitative models such as loops analysis provide a framework for formulating qualitative relationships between variables within a particular system using signed diagraphs to represent community interactions and predict system stability and perturbations (Puccia and Levins, 1985, Dambacher et al., 2002). The high mathematical rigor of the analyses and their high generality and realism (Levins, 1966, Whipple et al., 2000) make them a powerful tool for applied ecology (Dambacher et al., 2002, Dambacher et al., 2009). However, they have low precision and high uncertainty, as the magnitude of the interactions are not included (Dambacher et al., 2002). Therefore, within the EBM framework, the development and implementation of mechanistic models has mainly focused on quantitative models (Fulton, 2010).

The EBM approach has generated a great interest among the scientific community and therefore several new tools have been developed in recent decades, which include the development and application of multispecies and ecosystem models (Plagányi, 2007, Link, 2010a, Christensen and Maclean, 2011). These have been recognized as powerful tools to examine the interactions between marine resources and ecosystems and human activities within an ecosystem context, estimate the impact of human activities, assess impacts of the environment, evaluate the effect of management measures and provide support to the decision-making process (Plagányi, 2007, Collie et al., 2014, Acosta et al., 2016).

In these approaches, model complexity reflects a trade-off between simplicity and accuracy (Levins, 1966, Fulton et al., 2003). Simple models often ignore important components, processes and interactions and can thus have large model bias. However, increasing model complexity to improve biological processes representation can lead to an associated increase in scientific uncertainty, as a result of (1) incomplete knowledge about components, processes and interactions, which could lead the user to make assumptions, (2) large data demands and (3) the imprecision of parameters estimates (Fulton et al., 2003, Plagányi, 2007). Therefore, it has been recommended to include essential processes and components in a balanced way to address the question under consideration while capturing the complexity of aquatic systems (FAO, 2008, Hannon and Ruth, 2014).

There are different types of multispecies and ecosystem modelling approaches (Plagányi, 2007, Fulton, 2010, Peck et al., 2016, Tittensor et al., 2018), which can be generally divided into: 1) Minimum realistic models (MRM) and models of intermediate complexity (MICE), which include a limited number of species that have important interactions with the target species (Punt and Butterworth, 1995, Plagányi et al., 2014); 2) Multispecies individual-based models (IBM) such as OSMOSE (Shin and Cury, 2004), which is a two-dimensional dynamic IBM representing the whole life cycle of several fish species and 3) aggregate biomass, food web and network models such as Ecopath with Ecosim (Christensen and Walters, 2004a), which attempt to take into account all trophic levels, from primary producers to top predators, and the interactions within the ecosystem. Finally, end-to-end models or whole ecosystem models such as Atlantis (Fulton et al., 2004b) are the last generation of marine ecosystem models and attempt to represent all the ecosystem components (from nutrients, biogeochemical cycling and primary producers to top predators) and the anthropogenic and natural drivers of the systems (Travers et al., 2007, Fulton, 2010, Rose et al., 2010).

1.3.1. The Ecopath with Ecosim approach

The ecosystem modeling approach using the Ecopath with Ecosim (EwE) model was initially developed by Polovina (1984) to characterize the trophic relationships in the coral reef ecosystem of the "French Frigate Shoals" island (Northwestern Hawaii) by developing the static module Ecopath. Subsequently, the Ecopath module was adapted by Dr. Daniel Pauly, Dr. Villy Christensen and Dr. Carl Walters from the University of British Columbia (Vancouver, Canada) (Christensen and Pauly, 1992, Christensen and Pauly, 1993), and the temporal (Ecosim) and spatial (Ecospace) dynamic modules were developed (Walters et al., 1997, Walters et al., 1999). Currently, these modules are integrated into a modeling package called Ecopath with Ecosim (EwE) and Ecospace (Christensen and Walters, 2004a, Christensen et al., 2008, Heymans et al., 2016).

The EwE modelling approach is considered the most widely used aquatic ecological model (Coll et al., 2015, Colléter et al., 2015) and was recognized by the National Oceanographic and Atmospheric Administration (NOAA) as one of the 10 biggest scientist breakthroughs in the organization's 200-year history (http://celebrating200years.noaa.gov/breakthroughs/ecopath/). Its application has allowed, among others, to characterize exploited ecosystems, identify the role of fishing, evaluate the importance of trophic configuration and environmental factors in the dynamics of exploited resources, assess the location and size of Marine Protected Areas (MPA) and analyze management options in an ecosystem context (Christensen and Walters, 2004a, Coll et al., 2008b, Heymans et al., 2012, Colléter et al., 2015).

The Ecopath mass-balance approach

Ecopath models provide a quantitative representation of the studied ecosystem, or a "snapshot", in terms of trophic flows, for a defined period of time. The key principle of the Ecopath model is the mass balance: for each group represented in the model, the energy removed from that group, for example by predation or fishing, must be balanced by the energy consumed, i.e. consumption, and the energy incorporated to the system, i.e. through migration. This principle is achieved through the two master equations: one describing the biological production and the other describing the consumption for each functional group or "box" in the model.

A functional group in an Ecopath model consists of an onthogenic fractions of a species, a single species or a group of species that share common biological and ecological traits such as habitat, feeding and depth distribution (Christensen and Walters, 2004a, Christensen et al., 2008). This definition depends on the objectives of the model and data availability (especially biomass, diet and catch).

The first equation that describes the production of each functional group (P_i) is as follows:

$$P_i = \sum_j B_j \cdot M2_{ij} + Y_i + E_i + BA_i + P_i \cdot (1 - EE_i) \qquad \text{Eq. (1)}$$

where $M2_{ij}$ is the predation mortality caused by the biomass of the predators (B_j); Y_i is the export from the system due to fishing activity; E_i represents other exports; BA_i is the biomass accumulation in the ecosystem and ($1\text{-}EE_i$) is the other mortality factor, where *EE* is the Ecotrophic Efficiency that represents the degree of production of each functional group (*i*) which is utilized by higher trophic levels or is exported due to catch or migration (Christensen and Walters, 2004a, Christensen et al., 2008).

Eq. (1) can be re-expressed as:

$$B_i \cdot \left(\frac{P}{B}\right)_i = \sum_j B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} + Y_i + E_i + BA_i + B_i \cdot \left(\frac{P}{B}\right)_i \cdot (1 - EE_i) \quad \text{Eq. (2)}$$

where $(P/B)_i$ is the production of group (*i*) per unit biomass and is equivalent to total mortality, or *Z*, under steady-state condition (Allen, 1971); $(Q/B)_i$ is the consumption of group (*i*) per unit biomass; and (DC_{ij}) is the proportion of group (*i*) in the diet composition of predator (*j*) in terms of biomass.

The energy balance within each group is ensured when the consumption by group (i) equals the sum of its production and unassimilated food. This is represented by the second master equation of the approach:

$$Consumption\ (Q) = production\ (P) + respiration\ (R) + unassimilated\ food\ (U) \qquad \text{Eq. (3)}$$

Further details on the algorithms and equations, in addition to limitations and challenges of the approach are described in Christensen and Walters (2004a), Christensen et al. (2008), Ainsworth and Walters (2015) and Heymans et al. (2016).

Ecopath parameterizes the model by describing a system of linear equations for all the functional groups in the model. For each functional group, three of the four basic parameters (B_i, $(P/B)_i$, $(Q/B)_i$, EE_i) are required, in addition to the catch by fleet and functional group (Y_j) and the diet composition (DC_{ij}) of all groups.

The Ecosim time-dynamic model

Ecosim is the time-varying expression of the Ecopath model and consists of the analysis of biomass dynamics expressed through a series of differential equations (Walters et al., 1997, Christensen and Walters, 2004a). These equations are derived from the first Ecopath master equation (Eq. 1), and are defined as:

$$\frac{dB_i}{dt} = \left(\frac{P}{Q}\right)_i \cdot \sum Q_{ji} - \sum Q_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i \qquad \text{Eq. (4)}$$

Where dB_i/dt is the growth rate of group (i) during time t in terms of its biomass B_i; $(P/Q)_i$ is the net growth efficiency of group (i); M_i is the non-predation mortality rate; F_i is the fishing mortality rate; e_i is the emigration; and I_i is the immigration rate (Christensen et al., 2008).

$\sum Q_{ji}$ expresses the total consumption by functional group (i) and is calculated based on the foraging arena concept, that assumes that the prey is not 100% available for predators in aquatic systems (Walters et al., 1997, Walters and Martell, 2004, Ahrens et al., 2012). This theory assumes that different behavioral traits make prey vulnerable or not to predation (depending on whether they hide or not, how they distribute, how they school, etc.). Thus, the biomass of a prey (i) is divided into a vulnerable and a non-vulnerable fraction and the transfer rate or vulnerability (v_{ij}) between the two fractions determines the trophic flow control between the predator and prey (Fig. 4 and 5). The vulnerability concept incorporates density-dependency and expresses how far a group is from its carrying capacity (Christensen and Walters, 2004a, Christensen et al., 2008). Default values of vulnerability ($v_{ij} = 2$) represent a mixed trophic flow, a low value ($v_{ij} < 2$) indicates a “bottom-up” flow and a situation closer to carrying capacity, while a high value ($v_{ij} > 2$) indicates a “top-down” flow and a situation further away from carrying capacity (Walters and Martell, 2004, Ahrens et al., 2012).

For each predator-prey interaction, the consumption rate is calculated by:

$$Q_{ij} = \frac{a_{ij} \cdot v_{ij} \cdot B_i \cdot B_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot {}^{M_{ij}}\!/_{D_j}}{v_{ij} + v_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot B_j \cdot S_{ij} \cdot {}^{T_j}\!/_{D_j}} \cdot f(Env_{function}, t) \qquad \text{Eq. (5)}$$

Where a_{ij} is the rate of effective search for prey (i) by predator (j), T_i represents prey relative feeding time, T_j is the predator relative feeding time, S_{ij} is the user-defined seasonal or long term forcing effects, M_{ij} is the mediation forcing effects and D_j represents effects of handing time as a limit to consumption rate (Walters et al., 1997, Christensen and Walters, 2004a, Christensen et al., 2008). Environmental response functions ($f(Env_{function}, t)$) can be used to account for external drivers that change overtime, such as temperature. In particular, the intercept between the environmental response function and the environmental driver is used to calculate a multiplier factor (Eq. 5), which then modifies the consumption rates of the functional group with a maximum value of 1 and declining value as the environmental driver deviates from the optimum values (Christensen et al., 2014b, Serpetti et al., 2017).

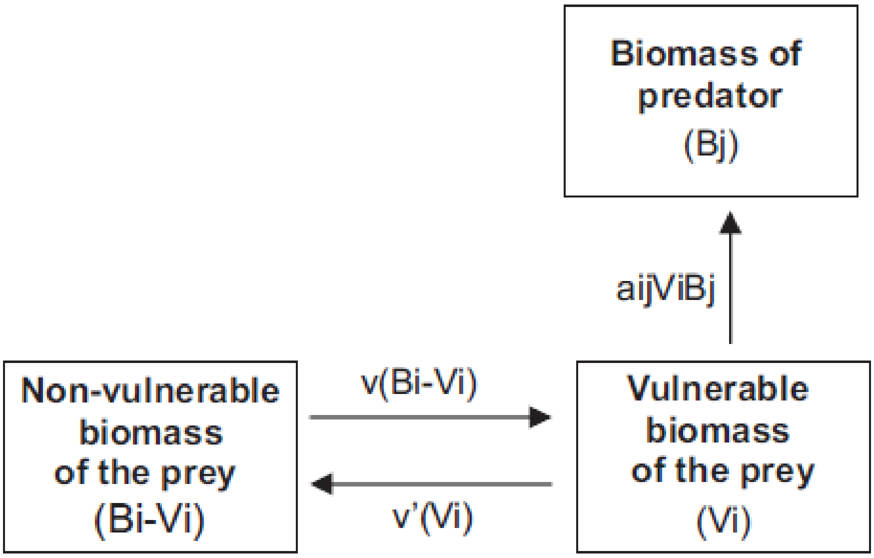


Fig. 4. Representation of the foraging arena theory that represents the biomass flow between unavailable biomass of prey ($B_i – V_i$), available biomass of prey (V_i) and flow to predator (j) with biomass B_j. Adapted from Walters et al. (1997).

In order to explain historical changes in a marine ecosystem, a model should (at least) consider food-web effects, environmental change and human impacts. During this thesis I have included the more important drivers of the Israeli Mediterranean marine ecosystem. Specifically, I have included food-web effects through trophic interactions (prey-predator interactions and the vulnerability parameter), environmental change through the inclusion of sea warming (also an anthropogenic impact) and changes in primary production, and impacts of human activities by including specific groups of alien species and the effects of fishing. These are the current major drivers in the Levantine Sea (Edelist et al., 2013a, Givan et al., 2017a, Rilov et al., 2018).

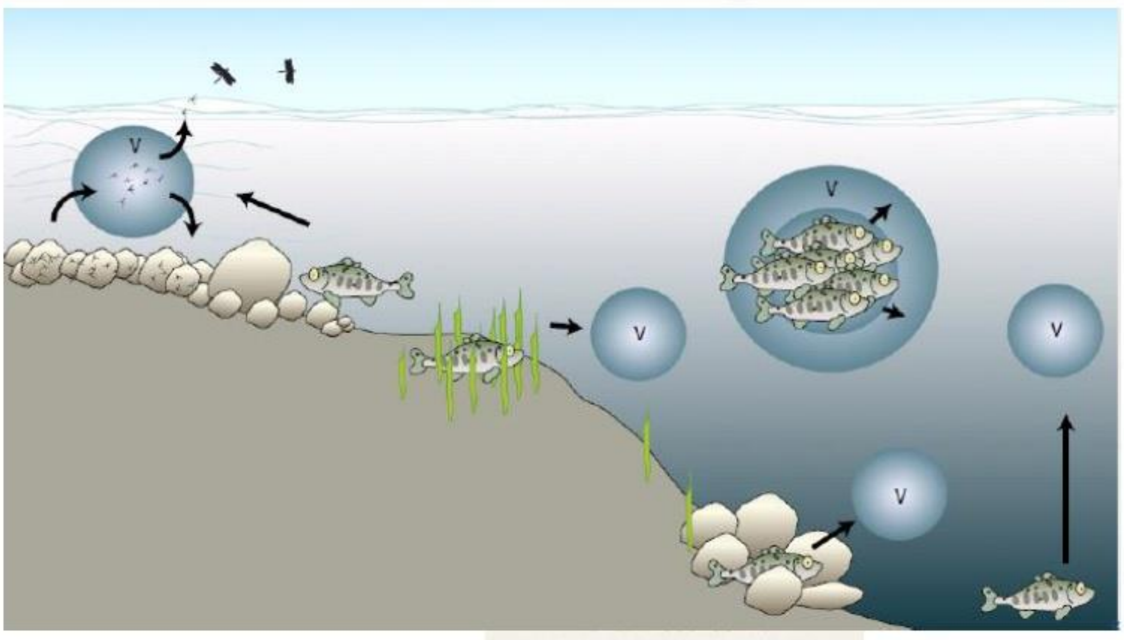


Fig. 5. Schematic representation of the foraging arena theory that represents several behaviors of aquatic organism that limit their exposure to predation risk (v is the vulnerable biomass of prey). Source: Ahrens et al. (2012).

1.3.2. Ecological indicators

Ecological indicators are important within the EBM framework because (1) they serve as proxies for several complex ecological processes, (2) are quantitative representations of ecosystem status, which means they can provide an indication of the condition of the ecosystem, its components or its functioning, and (3) provide a means for evaluating the impact of human activities in marine ecosystems and the effectiveness of management measures (Cury et al., 2005, Shin et al., 2010, Tam et al., 2017). Ecological indicators are increasingly used to document ecosystem status and to track the effects of anthropogenic and environmental stressors on marine ecosystems (Rice, 2003, Fulton et al., 2005, Fu et al., 2015). In fact, there have been international initiatives, such as IndiSeas initiative (“Indicators for the Seas), which has developed and assessed ecological indicators to evaluate the impact of fishing on marine ecosystems worldwide (Shin and Shannon, 2010, Shannon et al., 2014, Coll et al., 2016) or the Ocean Health Index, a comprehensive framework used to assess the health and benefits of the ocean from global to local scales based on ten societal goals, ranging from food provision to job, tourism and coastal protection (Halpern et al., 2012, Halpern et al., 2015b).

Ecosystem models can be used to derive useful indicators to describe ecosystem properties (Christensen and Walters, 2004a, Piroddi et al., 2015b, Coll and Steenbeek, 2017). For example, ecosystem models can provide useful indicators described under the attributes of the Marine Strategy Framework Directive of the EU (Lassen et al., 2013, Rombouts et al., 2013, Piroddi et al., 2015b). In particular, EwE provides indicators to describe five descriptors (1: Biological diversity, 2: Non-indigenous species, 3: Commercially exploited fish and shellfish, 4: Marine food webs, and 6: Sea floor integrity) (Piroddi et al., 2015b) and, particularly, it can be very informative for descriptor 4 (Rombouts et al., 2013, Piroddi et al., 2015b).

However, not all the indicators are equally robust, defined as the consistency of performance across alternative ecosystem types, levels of perturbation and uncertainty (Fulton et al., 2005, Heymans et al., 2014). A key aspect of robustness is that indicators should respond specifically to changes in the pressures they are designed to represent (e.g., fishing) rather than changes in other drivers (e.g., environment) (Shin et al., 2018). In fact, an ecological indicator that has been selected to track fishing impacts could also respond to other drivers such as environmental change (Large et al., 2013, Fu et al., 2015). In addition, ecological indicators vary with ecosystem traits (depth, size, latitude, etc.), highlighting that the features of the ecosystem need to be accounted for when setting reference levels and thresholds for conservation and management (Heymans et al., 2014).

1.3.3. Scenario testing

Scenarios are defined as plausible descriptions of alternative futures for direct or indirect drivers based on a coherent and consistent set of assumptions. Good scenarios could help us to understand how key drivers may interact and affect the plausible future. The consequences of these drivers are usually assessed using models (Ferrier et al., 2016).

In the EBM context, when models are able to satisfactorily replicate the past, we can start thinking of using them to make predictions and evaluate “what if” questions (Christensen, 2013). Although ecosystem models and ecological forecasts face several obstacles linked to ecosystems characteristics and include high uncertainty (Link et al., 2012, Payne et al., 2015, Maris et al., 2017), they have the potential to contribute significantly to achieve goals in marine conservation by offering guidance to decision-makers (Fulton et al., 2015, Hyder et al., 2015). Their use in assessments, policy support and decision making can provide insights about how the ecosystem could respond to plausible future stressors, enabling the development of adaptive management strategies, and allows for exploring the implications of alternative managements options (Acosta et al., 2016, Ferrier et al., 2016, Merrie et al., 2017). The use of scenarios and models for assessing biodiversity and ecosystem services has been well supported by the International Science-Policy Platform on Biodiversity and Ecosystem services (IPBES) process (Acosta et al., 2016, Brotons et al., 2016).

EwE applications have been used to forecast future human impacts on marine ecosystems, especially fishing (Christensen and Walters, 2011). In fact, the Institute for European Environmental Policy concluded that, among available models of marine ecosystems, EwE was the most suitable for the development of scenarios for exploring future trends of marine biodiversity and changes in ecosystem services (Sukhdev, 2008). For example, EwE has been applied to maximize ecosystem considerations and economic yield (Christensen and Walters, 2004b), applying MSY (Maximum Sustainable Yield) policies from single-species assessments (Walters et al., 2005), reduce fishing mortality due to bycatch reduction (Criales-Hernandez et al., 2006), impose effort restrictions to recreational fishery (Cisneros-Montemayor et al., 2012), explore the potential ecosystem effects of improved selectivity (Coll et al., 2008a) and spatial optimization of protected areas (Christensen et al., 2009). In addition, during the last decade it has been increasingly used to assess the impact of other stressors such as climate change (Ainsworth et al., 2011, Serpetti et al., 2017) and biological invasions (Pinnegar et al., 2014, Libralato et al., 2015).

1.4. The study area: The Mediterranean Sea and the Israeli Mediterranean coast

The Mediterranean Sea is a semi-enclosed sea located at the crossroad of Africa, Europe and Asia. It connects with the Atlantic Ocean through the Strait of Gibraltar, with the Sea of Marmara and the Black Sea through the Bosporus Strait and with the Red Sea and the Indian Ocean through the Suez Canal (Fig. 6). The Strait of Sicily divides the Mediterranean Sea into the western and eastern basin. The Mediterranean Sea is the largest (2,969,000 km^2) and deepest (with an average depth of 1,400 m and a maximum depth of 5,267 m) enclosed sea. Although it covers only 0.82% of the whole oceanic surface, it hosts about 7% of the known marine biodiversity, highlighting its high biodiversity, and it has a high endemism (Bianchi and Morri, 2000, Coll et al., 2010).

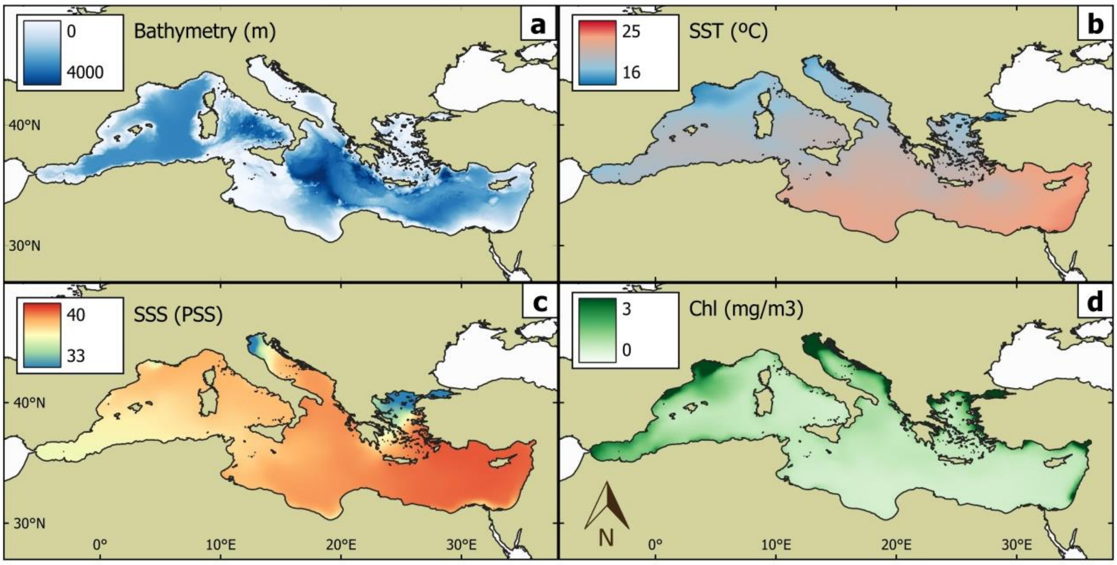


Fig. 6. The Mediterranean Sea with (a) the bathymetric profile, (b) mean sea surface temperature (ºC), (c) sea surface salinity (practical Salinity Scale (PSS)), and (d) chlorophyll concentration (mg/m^3) in 2017. Source: Tyberghein et al. (2012) and Assis et al. (2018).

Although the Mediterranean Sea is considered as a Large Marine Ecosystem (Sherman and Duda, 1999), environmental and biodiversity patterns show that it is highly heterogeneous. Overall, the Mediterranean Sea is considered oligotrophic (Bosc et al., 2004) with some local regions of enhanced productivity (Siokou-Frangou et al., 2010). Biological productivity decreases from north to south and from west to east (Fig. 6), while salinity and temperature increase from west to east (Fig 6) (Brasseur et al., 1996, Bosc et al., 2004, Coll et al., 2010, Siokou-Frangou et al., 2010). The annual mean sea surface temperature shows a high seasonality, which induce a seasonal stratification of the waters and determines a maximum primary production in autumn and spring and a minimum in summer (Bosc et al., 2004).

In addition, biodiversity decreases from west to east (Coll et al., 2010). This has been attributed to: 1) the Messinian salinity crisis, which caused a massive extinction and the subsequent colonization of the Mediterranean Sea by species from the Atlantic Ocean; 2) hydrological changes during the Pleistocene that made the Eastern Mediterranean Sea and especially the Levantine Sea an isolated part of the whole Mediterranean, 3) unfavourable environmental conditions (primary production, temperature and salinity) in the eastern area, and 4) less intensive biological sampling effort (Coll et al., 2010, Por, 2012).

The Mediterranean Sea has a long history of human disturbance and exploitation (Margalef, 1985, Coll et al., 2010, Lotze et al., 2011a). However, several studies have shown that the Mediterranean Sea ecosystems have changed dramatically during the last 50 years (Azzurro et al., 2011, Maynou et al., 2011, Fortibuoni et al., 2017, Piroddi et al., 2017), mainly due to technological improvements of fishing industry, demographic explosion in the coastal areas, the impacts of climate change and the introduction of alien species (Golani and Appelbaum-Golani, 2010, Lejeusne et al., 2010, Lotze et al., 2011a). In addition, the Mediterranean Sea is being altered through habitat loss and degradation, pollution, eutrophication, and aquaculture (Coll et al., 2010, Coll et al., 2012, Micheli et al., 2013, Ramírez et al., 2018). Because of such intense pressure, the Mediterranean Sea is characterized as a sea “under siege”, and classified among the most impacted ecoregions of the world (Coll et al., 2012, Halpern et al., 2015a).

There is evidence of the high impact of fishing on the Mediterranean Sea based on several analyses, indicating that many demersal and pelagic stocks are fully exploited or overexploited (Fig. 7) (Vasilakopoulos et al., 2014, Tsikliras et al., 2015, Cardinale and Scarcella, 2017, Fernandes et al., 2017). To date, 90% of assessed Mediterranean European stocks are overfished (Colloca et al., 2017), while the situation in non-EU countries, although data limitations, might be critical (Goren et al., 2013, GFCM, 2016a, GFCM, 2016b). The actual situation of Mediterranean stocks is due to a diversity of factors: fleet overcapacity, ineffectiveness of current effort system to control fishing mortality, illegal and unreported catches, unselective harvesting, lack of coordination between Mediterranean countries, and the continuous non-adherence to the scientific advice and inadequacies of existing national management plans (Lleonart, 2015, Stergiou et al., 2016, Cardinale and Scarcella, 2017). In addition, recreational fisheries are playing an important role due to its popularity as a leisure activity in coastal areas by inhabitants and the increasing numbers of tourist (Gaudin and De Young, 2007, Font and Lloret, 2014).

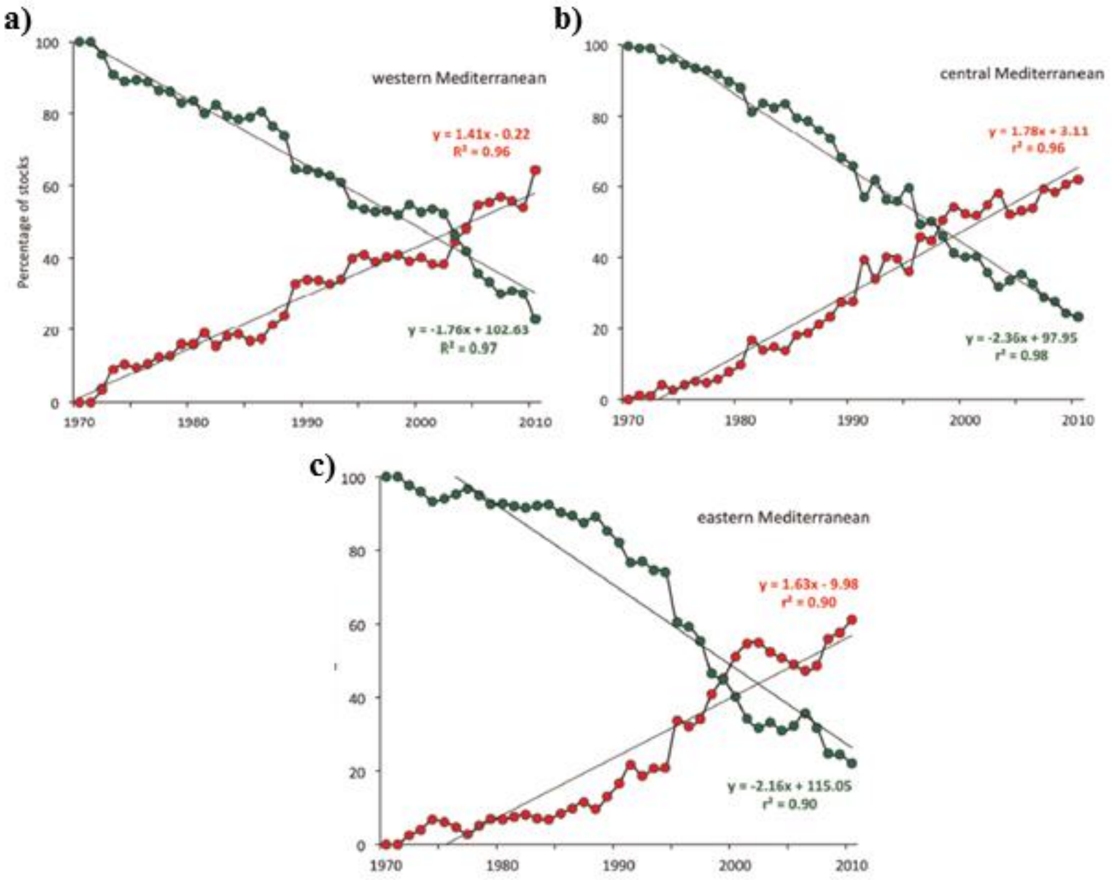


Fig. 7. Percentage of overfished and collapsed stocks (red) and percentage of developing and fully exploited (green dots) for the (a) western, (b) central, and (c) eastern Mediterranean Sea. Source: Stergiou et al. (2016).

In addition, the Mediterranean Sea is one of the most severely affected marine ecosystems by biological invasions (Galil, 2000, Molnar et al., 2008, Costello et al., 2010), especially its eastern basin (Fig. 8) (Katsanevakis et al., 2014b, Galil et al., 2016). The main vectors of biological invasions into the Mediterranean Sea are the Suez Canal, shipping (commercial and recreational) aquaculture and aquarium trade (Katsanevakis et al., 2013, Galil et al., 2014a). The Suez Canal was opened in 1989 to shorten the trade route between the Mediterranean and Indian Ocean. The length of the Suez Canal is 162.5 km, and nearly 70 km were excavated through dry land while the remainder crosses several lakes. The Red Sea is higher than the Eastern Mediterranean Sea, so the canal serves as a tidal strait that pours water from the Red Sea into the Mediterranean (Golani, 2010). The Bitter Lakes, which were hypersaline natural lakes forming part of the Canal, blocked the migration of many species from the Red Sea into the Mediterranean Sea (known as Lessepsian migration) for many decades. However, as the salinity of the lakes gradually equalized with that of the Red Sea, the ability of species to spread northwards increased (Hewitt et al., 2006). In addition, the construction of the Aswan High Dam across the Nile River in the 1960s reduced the inflow of freshwater and nutrient-rich silt from the Nile, making environmental conditions between the Eastern Mediterranean Sea and the Red Sea more similar and eliminating a barrier (especially during the Nile floods) for larvae of species sensitives to low salinities at the northern mouth of the Canal (Hewitt et al., 2006, Rilov and Galil, 2009).

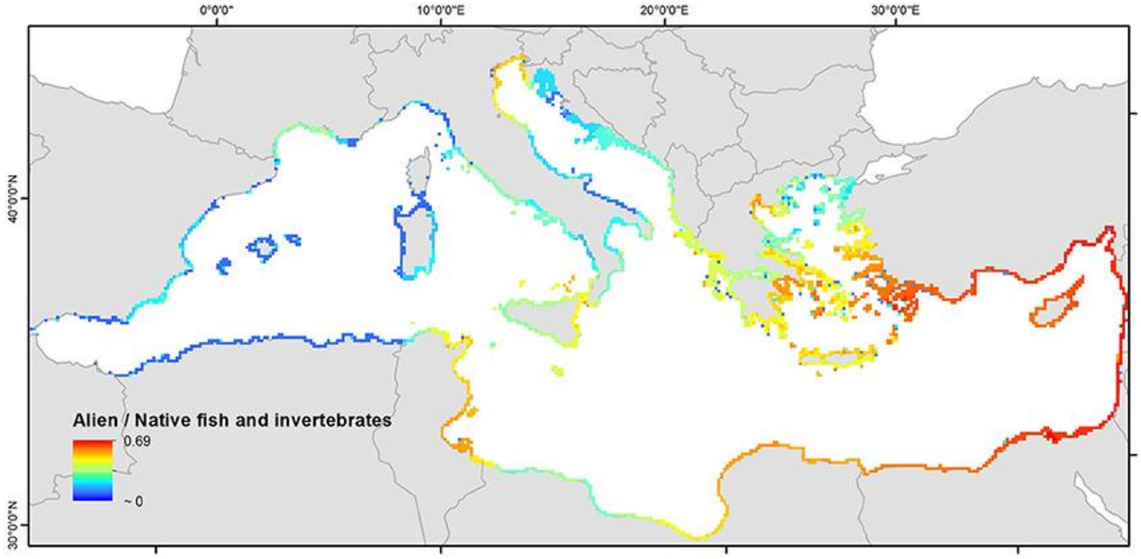


Fig. 8. Alien-native ratio of fish and invertebrate richness in the coastal areas of the Mediterranean Sea. Source: Katsanevakis et al. (2014b).

Until 1960s, the rate of new introductions followed a steady increase (Fig. 9) (Rilov and Galil, 2009, Galil et al., 2014a). However, this rate has been increased in recent decades, especially since 1990s, mainly due to the increasing role of the Mediterranean as a trade hub, the continued enlargement of the Suez Canal and sea warming (Fig. 9) (Raitsos et al., 2010, Galil et al., 2014a). Currently, there are 821 alien macro species recorded to date in the Mediterranean Sea (Galil et al., 2014a, Zenetos et al., 2017), of which more than half are considered to be established and spreading (Zenetos et al., 2012), profoundly modifying biodiversity patterns in the Mediterranean Sea (Katsanevakis et al., 2014b).

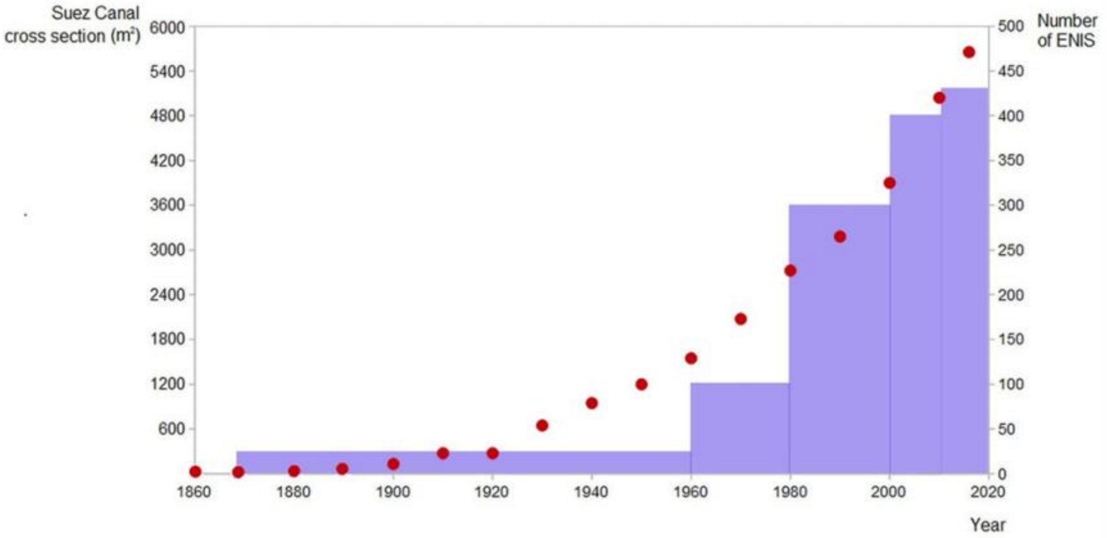


Fig. 9. The enlargement of the Suez Canal (cross section, m^2) and the number of species introduced through the Suez Canal (red dots). Source: Galil et al. (2017).

Although so far there are no recorded basin-wide extinctions of native species in the Mediterranean due to these invasions, there are many examples of local extirpations and range shifts concurrent with the spread of alien species (Galil, 2007a, Edelist et al., 2013a, Katsanevakis et al., 2014a). For example, currently the number of Lessepsian fishes has exceeded 100 species, which constitutes nearly a quarter of teleost species inhabiting the area (Golani, 2010, Zenetos et al., 2012, Fricke et al., 2015). Currently they constitute the dominant part of coastal fish in terms of biomass and abundance (Edelist et al., 2013a, Goren et al., 2016, Mavruk et al., 2017). Therefore, alien species have dramatically altered Mediterranean ecosystems as well as other human activities (Golani, 1998, Galil and Goren, 2014, Katsanevakis et al., 2014c, Goren et al., 2016). Two species of rabbitfish, *Siganus rivulatus* and *S. luridus*, have altered the rocky community structure of the rocky infralittoral (Sala et al., 2011, Vergés et al., 2014) since the role of native herbivores were negligible. In addition, some alien species pose substantial health hazards and have negative impacts on fisheries. For example, the invasive pufferfish *Lagocephalus sceleratus* has a significant impact on the artisanal fisheries as often they damages both fishing gear and the catch, and also presents a potential risk to humans as it contains tetrodotoxin, which may cause poisoning and even death (Nader et al., 2012, Katsanevakis et al., 2014c).

Global warming is already impacting the Mediterranean Sea, mainly through changes in species distributions and mortality events of native species with cold-temperate affinities (Lejeusne et al., 2010, Moullec et al., 2016). Following the sea warming registered during the last 30 years (Nykjaer, 2009, Shaltout and Omstedt, 2014), the Mediterranean Sea is under a process of "meridionalization" and "tropicalization" of the northern and southern sectors, respectively. The term "meridionalization" refers to the northward extension of native thermophilic species and the rarefaction of "cold" stenothermal species; while the term "tropicalization" refers to the introduction and increasing abundance of (sub)tropical species, which is obvious in the south-eastern sectors of the basin, through the Suez Canal and the Strait of Gibraltar (Bianchi, 2007, Bianchi et al., 2013)

Moreover, the Mediterranean Sea is predicted to be one of the regions most affected by climate change (Giorgi, 2006), with sea surface temperature expected to warm by an average of 2.8 °C by 2080-2099 (Somot et al., 2006). Fish assemblages are expected to be deeply modified as a result of climate change (Ben Rais Lasram et al., 2010, Albouy et al., 2012, Albouy et al., 2013), with potential effects on marine food-webs and ecosystem structure (Albouy et al., 2014).

1.5. Objectives

Taking into account the above context, the main objective of this thesis was to assess the cumulative impacts of alien species, fishing and climate change on the eastern Mediterranean Sea, specifically in the Israeli Mediterranean continental shelf ecosystem, through the application of an ecosystem modelling approach.

The specific objectives of this thesis were:

a) To achieve a general overview about available modelling tools to investigate the impacts of alien species in aquatic ecosystem, and critically assess their advantages, limitations and challenges;

b) To characterize the structure and functioning of the marine ecosystem in the Israeli Mediterranean continental shelf ecosystem during the early 1990's and 2008-2010 developing two ecosystem models;

c) To assess the past and current impact of alien species and fishing activity in the Israeli Mediterranean continental shelf ecosystem using an ecosystem approach;

d) To compare the above results with other food-web models developed in several areas of the Mediterranean Sea to put the results in a wider basin context;

e) To explore the historical dynamics of the marine resources of the Israeli Mediterranean continental shelf ecosystem considering the impact of alien species, fishing and climate change as the main external drivers of the ecosystem using a dynamic temporal modeling approach;

f) To assess potential ecological impacts of future conditions of different stressors (first, separately, and, secondly, in a combined way to evaluate their cumulative effects) on the Israeli Mediterranean continental shelf ecosystem using a dynamic temporal modeling approach;

g) To acknowledge uncertainty during modelling development and to take into account the impact of the lack of information on modelling results.

The first objective of the thesis was achieved with the development of a systematic literature review (Chapter 2.1), which is currently under review in the peer review journal *Biological Invasions*. The second, third and fourth objectives were achieved through the development of two food-web ecosystem models representing two time periods (1990’s and 2010’s) (Chapter 2.2). This chapter has been published in the peer review journal *Journal of Marine Systems, 170, 88-102 (2017).* The fifth objective was achieved by fitting and validating the 1990’s to time series of observations until 2010 using the temporal dynamic module of the EwE approach (Chapter 2.3). This chapter has been published in the peer review journal *Marine Ecology Progress Series, 580, 17-36 (2017).* The sixth objective was achieved using the temporal-dynamic calibrated model and the development of previously defined scenarios of change. This chapter has been published in the peer review journal *Scientific Reports, 8 (2018).* The seventh objective was achieved by using the Monte Carlo routine and the Ecosampler plug-in in chapters 2.3 and 2.4. With this work, I participated in the development of the Ecosampler plug-in by testing the tool with the Israeli’s case study. This tool has been published in the peer review journal *SoftwareX, 7, 198-204 (2018)* (Annexes of this thesis).

CHAPTER 2:

RESULTS

2.1. Advances and challenges when modelling the impacts of invasive alien species

Corrales, X.[1,2]; Katsanevakis, S.[3]; Coll, M.[2,4]; Heymans, J.J.[5,6]; Piroddi, C.[2,7]; Ofir, E.[1]; Gal, G.[1]

1. Kinneret Limnological Laboratory, Israel Oceanographic & Limnological Research. PO Box 447. Migdal, Israel.
2. Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta, nº 37-49. 08003. Barcelona, Spain.
3. Department of Marine Sciences, University of the Aegean, University Hill. Mytiliene 81100, Greece.
4. Ecopath International Initiative Research Association, Barcelona, Spain
5. Scottish Association for Marine Science, Scottish Marine Institute. Oban, PA37 1QA, Scotland.
6. European Marine Board, Wandelaarkaai 7, Oostende 8400, Belgium.
7. European Commission, Joint Research Center (JRC), Directorate D-Sustainable Resources, Water and Marine Resources Unit. 21027, Ispra (VA), Italy.

Submitted to Biological Invasions

Abstract

Invasive alien species (IAS) have become an important driver of biodiversity change and have exerted severe pressure on natural ecosystems. The development of modelling approaches to assess and predict their impacts and evaluate management options has increased substantially.

We reviewed these modelling approaches, applied in aquatic ecosystems, using a systematic review approach in line with the Preferred Reporting Items for Systematic Reviews and Meta-analyses (PRISMA). Multispecies/ecosystem models dominated, with dynamic and non-spatial models being the most prevalent. Most of the models included an additional human stressor, mainly fisheries, climate change or nutrient loading. The impacts on biota focused on predation, but also on competition and ecosystem functions, while the impacts on ecosystem services focused on food provisions and water purification.

We reflect on the ability of models to assess different impacts of IAS populations and highlight the need to advance their capabilities to predict future impacts.

Keywords: Invasive alien species; impacts; modelling; marine ecosystems; freshwater ecosystems; PRISMA.

1. Introduction

Biological invasions are currently one of the most important drivers of biodiversity change and exert severe pressure on terrestrial, freshwater and marine ecosystems, with both ecological and economic impacts (Bax et al., 2003, Simberloff et al., 2013, Gallardo et al., 2016). Alien species (also known as exotic, introduced, allochthonous, non-indigenous or non-native species) are any taxa that are introduced outside their natural past or present distribution, including any part, gamete seeds, eggs, or propagules that might survive and subsequently reproduce. Invasive alien species (IAS) are defined as those alien species whose introduction or spread threaten biological diversity (CBD, 2002). Many organisations and states, e.g. the European Union (Regulation 1143/2014), include in the definition of IAS not only impacts on biodiversity but also on ecosystem services. The impacts of IAS can be detected at any biological level, ranging from changes in the genetic diversity of native species to species extinction and alterations of an entire ecosystem (Grosholz, 2002, Strayer, 2010, Levin and Crooks, 2011), and include impacts on ecosystem services (Pejchar and Mooney, 2009, Katsanevakis et al., 2014c).

Humans have traded and, intentionally or unintentionally, transported alien species for millennia, but the rapid globalisation and increases in trade and transport capacity in recent decades have accelerated biological invasions, despite growing national and international efforts to reduce invasion risk (Hulme, 2009, Katsanevakis et al., 2013, Nunes et al., 2015, Seebens et al., 2017). In addition, biological invasions interact with other stressors such as climate change, habitat degradation and loss, overexploitation and pollution, which compromise the integrity of aquatic ecosystems (Dudgeon et al., 2006, Halpern et al., 2015a). Because disturbance is generally thought to favour invasions, stressed ecosystems may more easily be colonised by alien species (Occhipinti-Ambrogi and Savini, 2003, Strayer, 2010). This can explain the unprecedented rates of species extinctions and introductions observed in aquatic ecosystems (Miller et al., 1989, Byrnes et al., 2007). This, in turn, is leading to a general biotic homogenisation (Rahel, 2002, Sala and Knowlton, 2006). Moreover, the impacts of IAS are projected to further increase, especially due to climate change (Walther et al., 2009, Raitsos et al., 2010).

There are many examples of large-scale and dramatic effects of IAS in aquatic ecosystems. For example, 821 alien species have been recorded to date in the Mediterranean Sea, of which more than half are considered established and spreading (Galil et al., 2014a, Katsanevakis et al., 2014b, Zenetos et al., 2017). The Mediterranean Sea, in fact, is one of the most invaded regions in the world (Molnar et al., 2008, Costello et al., 2010) and its ecosystems have been significantly impacted, with declines in abundance, modifications of biodiversity patterns and local extirpations concurrent with IAS (e.g., Galil, 2007a, Sala et al., 2011, Edelist et al., 2013a, Katsanevakis et al., 2014b). The Laurentian Great Lakes, in North America, are among the most highly invaded freshwater ecosystems in the world with over 180 IAS (Ricciardi, 2006). These invasions have altered biodiversity, habitat structure, productivity, water quality, contaminant cycling and ecosystem services (Kelly et al., 2009). The introduction of the Nile perch (*Lates niloticus*) in Lake Victoria, located in Africa, to stimulate fisheries resulted in a dramatic regime shift, where the very diverse and complex haplochromine-based ecosystem was replaced by a system dominated by only a few species (Goudswaard et al., 2008).

Studying the impacts of IAS in aquatic ecosystems is a challenge due to: (1) the dynamic nature of natural ecosystems; (2) limitations of methodological tools; and (3) a general lack of knowledge about IAS and invading processes, which include, among others, a time lag between the invasion and the discovery of IAS, errors in species inventories and alien status, and uncertainties in field surveys, environmental preferences and trophic interactions (potential preys and predators) of IAS in the new environment (Crooks, 2005, Azzurro et al., 2016, Katsanevakis and Moustakas, 2018). These have all led to great uncertainties in marine invasion science (Katsanevakis and Moustakas, 2018).

However, our growing understanding of aquatic ecosystems and the improvement of approaches has allowed the development of new insights into the ecological consequences of IAS. Approaches range from documenting invaders and examining interactions between invaders and native species to assess the ecological and economic impacts of invasion by using a large variety of modelling techniques (Wonham and Lewis, 2009). Modelling tools, in fact, can provide a means for increasing understanding of processes, drivers and responses of organisms and ecosystems to human pressures; identifying gaps in available knowledge and allowing the development of predictions about possible future dynamics.

The principal aim of this study is to map and review available modelling approaches used to evaluate the impacts of IAS in aquatic systems to date. We summarise the main features of these applications and analyse their capabilities and limitations. Based on the conclusions of this review, we reflect on future directions of development and applications of suitable modelling tools.

2. Methods

We followed a systematic review approach in line with PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) (Moher et al., 2010). This approach consists of three steps: (1) systematic article selection using a search engine; (2) article screening; and (3) a review of relevant articles and extraction of the information.

We performed the bibliographic search using Elsevier’s Scopus database (www.scopus.com). Eligibility criteria included any article, review, or book chapter published between 1990 and the cut-off date, 8th February 2017, with the following terms in the title, abstract or keywords:

1. “model” or “modelling” or “modeling”; and
2. “impact” or “impacts” or “effect” or “effects”; and
3. “invasive species” or “alien species” or “allochthonous species” or “introduced species” or “non-indigenous species” or “non-native species” or "invasion" or "exotic"; and
4. “marine” or “sea” or “coast” or “coastal” or “estuarine” or “bay” or “freshwater” or “lake” or “river” or “reservoir” or "lagoon".

The search was limited to relevant subject areas (Agricultural and Biological Science, Environmental Science, Earth and Planetary Sciences and multidisciplinary) and to English and Spanish publications. The search resulted in 1306 publications.

In addition, we manually included relevant papers from other sources that were not found in the previous search, which included (1) a bibliographic search (Corrales et al., 2014) of the Ecopath with Ecosim modelling tool that assessed impacts of IAS (e.g., Kitchell et al., 2000, Downing et al., 2012, Kao et al., 2016); (2) papers cited in review papers such as Wonham and Lewis (2009), Thompson et al. (2013) and Piroddi et al. (2015b); (3) papers from the personal files of the authors (e.g., Padilla et al., 1996); and (4) relevant papers found in selected articles during the third step of the systematic review (extraction of the information). With these additional articles, the total number of papers increased to 1382 (Fig. S1 in the Annex 1).

Article screening started with these 1382 articles and consisted of a two-stage process: the first screening of articles was based on the title and the abstract, and the second on the full article. During this process, articles were excluded if they: (1) did not apply or develop a model to evaluate the impact of IAS, or (2) were related only to terrestrial habitat/species. After the first selection process, 389 articles (28.3% of the original papers) were selected. After the second selection process, 189 articles (see Annex 1 for the final list of articles and their full references) were included in the analysis (13.8% of the original papers). Species distribution models (SDMs) and studies based on stable isotope analysis passed the first screening process but were excluded in the second if they did not include, qualitatively or quantitatively, the study of IAS impacts.

The following information was extracted from each selected article (see Table S1 in Annex 1):

(1) Year of publication;

(2) Realm of the study (freshwater, estuarine or marine);

(3) Biogeographic region, based on Olson et al. (2001) (freshwater) and Spalding et al. (2007) (marine);

(3) Ecosystem type (e.g., lake, river, bay);

(4) Information related to the IAS included in the model: number of IAS, scientific and common name/s, type of organism/s (e.g., fish, invertebrates), habitat/s (demersal or pelagic) and trophic level/s (TL). The TL concept identifies the position of organisms within food webs by identifying the source of energy of each organism, with TL 1 for producers and higher values for consumers (Lindeman, 1942). We classified TL as low ($TL<3$), medium ($3\leq TL\geq 3.5$) and high ($TL>3.5$) based on outputs from models or databases such as FishBase (Froese and Pauly, 2017) and SeaLifeBase (Palomares and Pauly, 2017);

(5) Information related to the model: modelling level (species or multispecies/ecosystem level), type of model (statistical versus mechanistic), model category (e.g., bioenergetics and biogeochemical model), data type (time and spatial scales), if other external stressors were included (for example, fisheries, climate change and nutrient loading), if the model was validated and how it was validated, if uncertainty was evaluated, and if the model was used to provide management recommendations; and

(6) Information related to the impacts of alien species: number and types of impacts on ecosystem services (based on the classification by Liquete et al. (2013)) and/or on biota (for example, predation, competition and ecosystem processes/function); if the impact was positive or negative; and which indicators were used to evaluate the impact (number of indicators, type and units).

To summarise categorical variables and test pair-wise potential dependences, we applied a crosstabulation analysis and Chi-square test of independence, using the statistical software Statgraphics (Statgraphics-Centurion, 2009).

3. Results

3.1. Temporal development, ecosystem coverage and species included

Since 1992, there has been an increase in the number of publications of models that assessed the impacts of IAS in aquatic ecosystems (Fig. 1a). From 1992 to 2004 the average rate of publications was 3.1 papers per year, while from 2005 to 2016 the rate increased to 12.2 papers per year. Most papers studied freshwater ecosystems (75%), especially lakes, followed by marine (22%) and estuarine (3%) ecosystems (Fig. 1b).

The studies covered most of the marine and freshwater biogeographic regions (Fig. 2). In the freshwater realm, most of the models were developed in the Nearctic biogeographic region (75%), followed by the Palearctic (10%) and Afrotropical (8%). We did not find studies in the Oceanian and Antarctic biogeographic regions. In the marine realm, the Temperate Northern Atlantic (64%), the Tropical Atlantic (11%) and the Temperate Northern Pacific (9%) biogeographic regions represented most of the studies, while no studies were conducted in the Western and Central Indo-Pacific, Tropical Eastern Indo-Pacific, Arctic and Southern Ocean biogeographic regions.

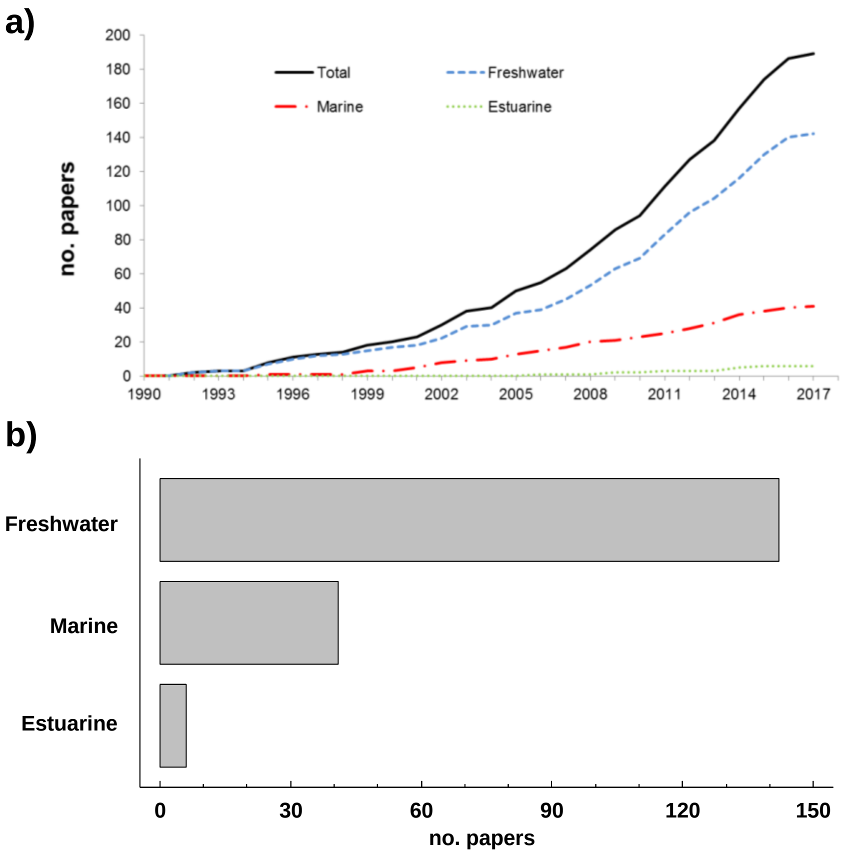


Figure 1. (a) Cumulative number of publications over time found in the systematic review (the year 2017 covers January 1st to 8th February); and (b) number of publications per ecosystem type.

The studies covered most of the marine and freshwater biogeographic regions (Fig. 2). In the freshwater realm, most of the models were developed in the Nearctic biogeographic region (75%), followed by the Palearctic (10%) and Afrotropical (8%). We did not find studies in the Oceanian and Antarctic biogeographic regions. In the marine realm, the Temperate Northern Atlantic (64%), the Tropical Atlantic (11%) and the Temperate Northern Pacific (9%) biogeographic regions represented most of the studies, while no studies were conducted in the Western and Central Indo-Pacific, Tropical Eastern Indo-Pacific, Arctic and Southern Ocean biogeographic regions.

The IAS modelled included many taxonomic groups (Table 1). In freshwater and marine ecosystems, fishes (58 % and 31%, respectively) and molluscs (mainly bivalves) (29% and 20%, respectively) were the most frequently studied groups in the selected models, while in estuarine ecosystems, zooplankton (50%) and molluscs (31%) were the main groups (Table 1). Most of the studies focused on low trophic level species, especially in estuarine (71.4% of the species) and freshwater (54.5% of the species) ecosystems (Fig. 3a) (Chi-square: $p. < 0.005$; i.e. trophic level differed significantly between type of environment). Pelagic and demersal species were equally represented (Fig 3b).

Table 1. Number and percentage of IAS found in the selected models per taxonomic group and ecosystem type.

	Freshwater		Marine		Estuarine		Total	
	Number	**%**	**Number**	**%**	**Number**	**%**	**Number**	**%**
Plants	6	2.2	16	9.3	1	7.1	6	5
Parasites	5	1.8	0	0	0	0	5	1.1
Phytoplankton	3	1.1	3	1.7	0	0	6	1.3
Zooplankton	13	4.7	4	2.3	7	50	24	5.2
Bryozoan	0	0	2	1.2	0	0	2	0.4
Polychaetes	0	0	9	5.2	0	0	9	1.9
Barnacles	0	0	3	1.7	0	0	3	0.7
Molluscs	80	28.9	34	19.7	3	21.4	117	25.2
Ascidians	0	0	2	1.2	0	0	2	0.4
Ctenophores	0	0	16	9.3	0	0	16	3.5
Cnidarians	0	0	7	4.1	0	0	7	1.5
Shrimps	0	0	12	6.9	1	7.1	13	2.8
Crabs	3	1.1	11	6.4	0	0	14	3
Other benthic crustaceans	2	0.7	0	0	0	0	2	0.4
Fishes	161	58.1	54	31.2	2	14.29	217	46.8
Birds	4	1.4	0	0	0	0	4	0.9
Total	277	100	173	100	14	100	464	100

3.2. Overview of the main modelling approaches

We found a large variety of statistical and mechanistic models used to study the impacts of IAS (Table 2). Multispecies/ecosystem level models were more prevalent than species/population level models in all ecosystem types (Fig. 4a) (Chi-square: $p = 0.1$; i.e. no significant differences of modelling level among ecosystems). At the species/population modelling level, a similar number of studies developed statistical and mechanistic models, while at the multispecies/ecosystem level, most studies used mechanistic models (Fig. 4b) (Chi-square: $p < 0.005$; i.e. type of model differed by modelling level). Of the statistical models reported in this review, we found a similar diversity of models at the species/population and multispecies/ecosystem levels (Table 2). On the contrary, a higher diversity of mechanistic models was found at the multispecies/ecosystem level (Table 2).

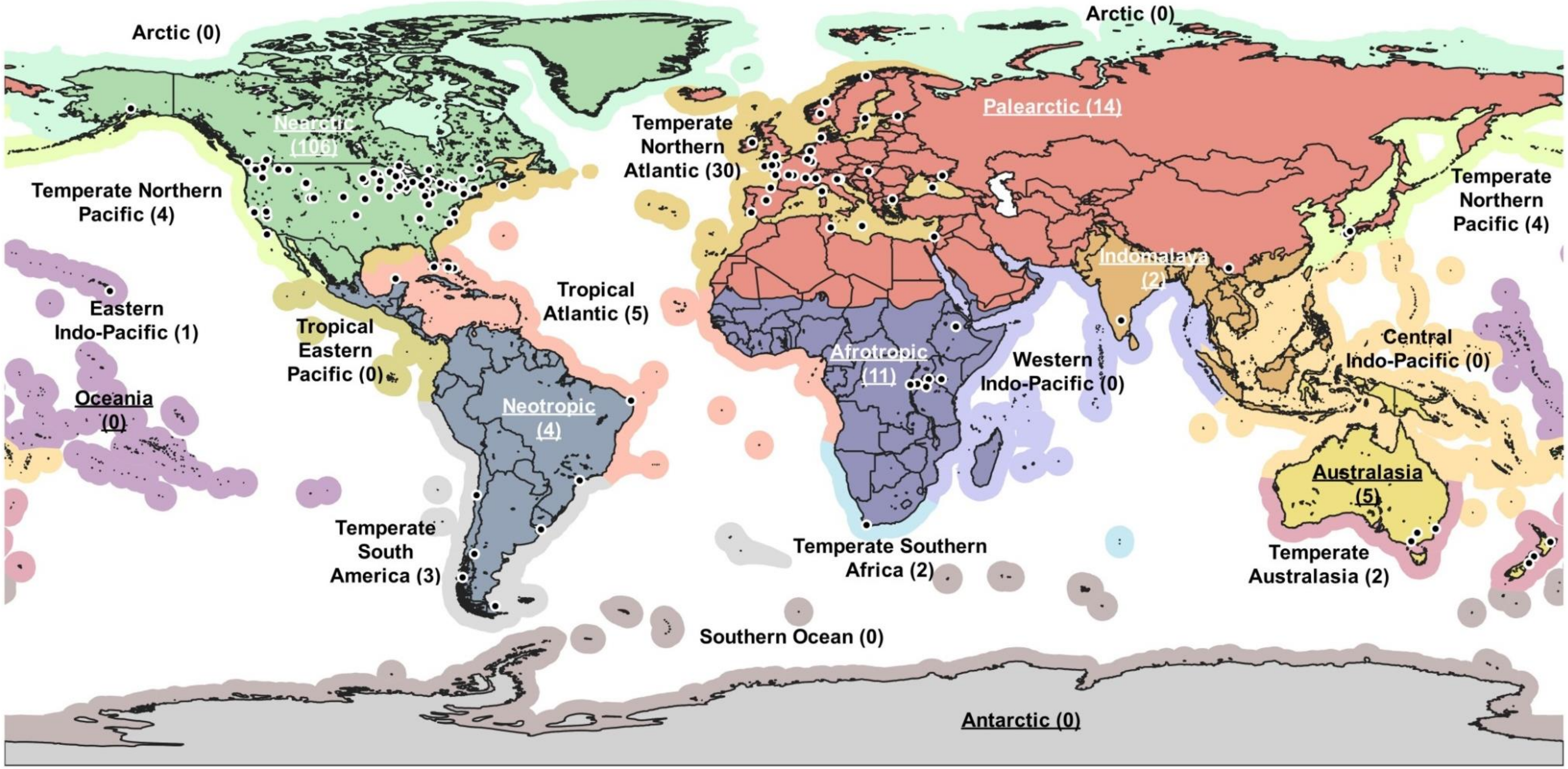


Figure 2. Distribution of the studies included in the systematic review. Different realms (marine and terrestrial biogeographic regions) are presented with different colours. Realms were based on Spalding et al. (2007) and Olson et al. (2001). Numbers in brackets indicate the total number of studies for each biogeographic region.

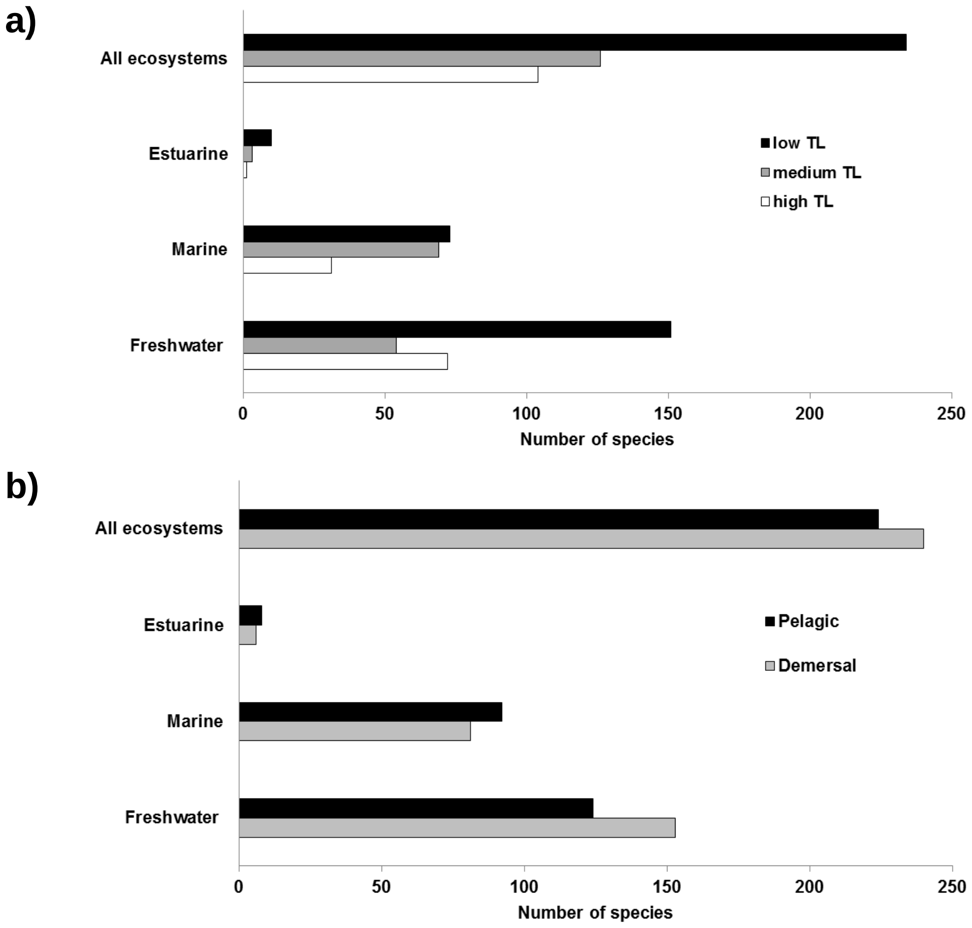


Figure 3. Number of species included in the models found in the systematic review per (a) trophic level (TL) and (b) habitat in each ecosystem type.

The average number of IAS included in the species/population level models was smaller (1.2 ± 0.4 SD) than the average number in multispecies/ecosystem level models (2.9 ± 6.7 SD) (Fig. 4c). Some species/population level models encompassed two alien species but their impacts were assessed together as they played the same ecological role, for example, zebra mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) filtering phytoplankton (e.g., Cha et al., 2013, Rowe et al., 2015b).

The temporal and spatial scales over which the models operated varied greatly. We found static studies that included a model representing a specific time period, models comparing different periods, and dynamic models of all modelling types. Dynamic models were most frequently developed, both at the single species and multi-species level (Fig. 5a) (Chi-square: p =0.2). Non-spatial models dominated, with model comparison between study sites and spatial models being less prevalent (Fig. 5b) (Chi-square: p =0.5).

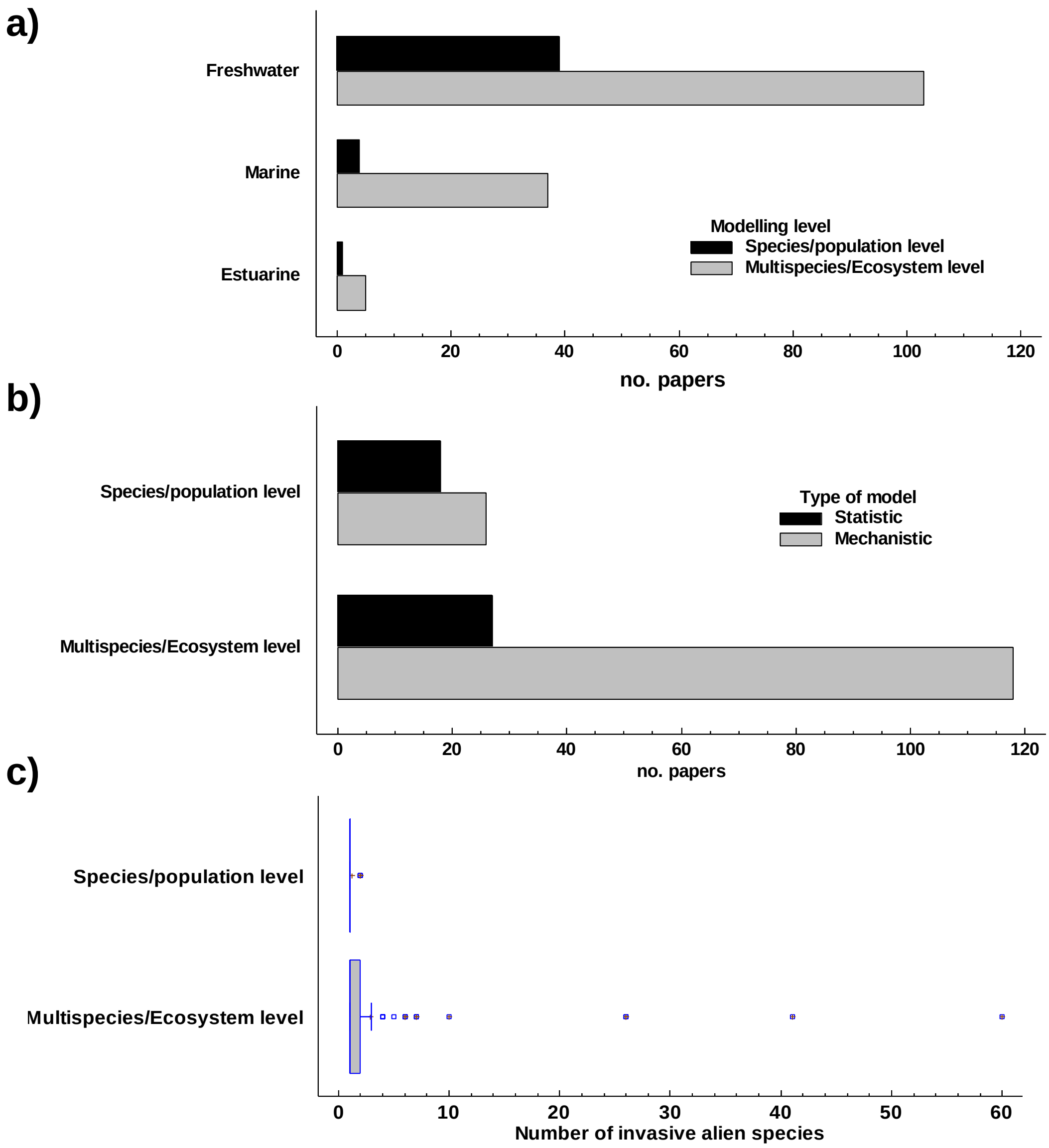


Figure 4. (a) Number of studies of each modelling level found in the systematic review per ecosystem type; (b) number of studies of each type of model per modelling level; and (c) number of IAS included per modelling level.

Since 1992, there has been a progressive increase in the number of models that included an additional stressor, especially since 2001. From 1992 to 2001, the average rate of publications that included additional stressors aside from IAS was 1.1 papers per year, while from 2002 to 2016 the rate increased to 6.3 papers per year (Fig. 6a). Most of the multispecies/ecosystem models were driven by additional stressors, while most of models at the species level did not incorporate an additional stressor aside from the IAS (Fig 6b) (Chi-square: $p < 0.005$). The most frequently included additional stressors were fisheries (45%), followed by nutrient loading (25%) and climate change (through changes in water temperature and primary production) (21%) (Fig. 6c).

Table 2. Summary table of models found in the systematic review showing the model name, model category, a representative reference and if the modelling approach was coupled with other models (yes or not), temporal scale (ST: static; DY: dynamic; CP: comparative between periods), spatial scale (NS: non-spatial; CS: comparative between study sites; SP: spatial), if the model included other human stressors as drivers and which ones, and if the uncertainty was evaluated (yes or no).

	Model name	Model category	Representative reference	Coupled	Temporal scale	Spatial scale	Other stressor	Which stressor	Uncertainty
Species/population level									
Statistic									
1	ANCOVA	Single-species	Gribben and Wright (2006)	no	DY	CS	no		no
2	Linear models and structural equation modelling	Single-species	Correa and Hendry (2012)	no	ST	CS	no		no
3	Multiple regression model	Single-species	Van Zuiden et al. (2016)	no	DY	NS	yes	Temperature	no
4	Quantile regression models	Single-species	Crane et al. (2015)	no	CP	NS	yes	Temperature	no
5	Behavioural choice model	Single-species	Beville et al. (2012)	no	ST	NS	yes	Fishing	no
6	Bayesian hierarchical model	Single-species	Cha et al. (2013)	no	CP	CS	no		yes
7	Poisson model and linear regression model	Single-species	Ricciardi et al. (1995)	no	DY	CS	no		no
8	Generalised linear model (GLM)	Single-species	Onikura et al. (2013)	no	ST	SP	no		no
9	Two-tiered modelling approach	Single-species	Stapanian et al. (2009)	no	DY	NS	no		no
10	GIS-based spatial model	Single-species	Woodford et al. (2011)	no	ST	SP	no		no
11	Species distribution model	Single-species	Olden et al. (2011)	no	DY	SP	yes	Recreational users of lakes	no
12	Geostatistical model	Single-species	Rowe et al. (2015b)	no	DY	SP	no		yes
Mechanistic									
13	Von Bertalanffy growth model	Single-species	Crane and Einhouse (2016)	no	CP	NS	no		no
14	Bioeconomic model	Single-species and economic activity	Liu et al. (2014)	no	DY	NS	yes	Fishing	yes
15	Hedonic price	Economic activity	Olden and Tamayo (2014b)	no	ST	NS	no		no
16	Schaefer model	Single-species	Kateregga and Sterner (2009a)	no	DY	NS	yes	Fishing	no
17	Individuals-based models	Single-species	Caldow et al. (2007)	no	DY	NS	no		no
18	Stage and age-structured models	Single-species	Ferguson et al. (2012)	no	ST	NS	no		no

Multispecies/ecosystem level									
Statistic									
19	Linear model	Community	Bajer et al. (2016)	no	ST	CS	no		no
20	Least-squares regression	Community	Ricciardi (2003)	no	CP	CS	no		no
21	Multiple regression model	Community	Clavero et al. (2013)	no	ST	NS	yes	Footprint	no
22	Hierarchical Bayesian model	Community	Nilsson et al. (2012)	no	ST	CS	no		yes
23	Generalised linear model (GLM)	Community	De Amorim et al. (2015)	no	ST	CS	no		no
24	Generalised additive model (GAM)	Community	Knapp (2005)	no	CP	CS	no		no
25	Species occupancy models, boosted regression trees and linear and logistic regression models	Community	Macdonald et al. (2012)	no	ST	CS	no		no
26	Partial least square path model	Community	Jellyman and Harding (2016)	no	ST	NS	no		no
27	MARSS model	Community	Kratina et al. (2014)	no	CP	CS	yes	Temperature	no
28	Intervention time series model	Community	Pace et al. (1998)	no	DY	CS	no		yes
29	Structural equation modelling	Community	Pagnucco and Ricciardi (2015)	no	ST	CS	no		no
30	Transfer function (TF) models	Community	Aravena et al. (2009)	no	DY	CS	yes	River discharge and temperature	no
31	Species distribution model	Community	Wenger et al. (2011)	no	DY	SP	yes	Temperature	no
Mechanistic									
32	Size-structured model	Community	Green et al. (2014)	no	DY	NS	yes	Fishing	yes
33	Bioenergetic model	Bioenergetics model	Walrath et al. (2015)	no	DY	NS	no		no
34	Age-structured model with bioenergetic model	Bioenergetics model	Stewart et al. (2010)	yes	DY	NS	yes	Temperature	no
35	Bioenergetic model coupled with phytoplankton growth model	Bioenergetics model	Reed-Andersen et al. (2000)	yes	DY	NS	no		yes
36	Integrated ecological-economic model for the Black Sea anchovy fishery	Bioeconomic model	Knowler (2005)	yes	DY	NS	yes	Fishing and nutrients	no
37	Integrated economic-biological model	Bioeconomic model	Settle and Shogren (2002)	yes	DY	NS	yes	Fishing	no
38	Ecological and economic model	Bioeconomic model	Grosholz et al. (2011)	yes	DY	CS	yes	Fishing	yes
39	Social-ecological model	Bioeconomic model	Roy et al. (2011)	yes	DY	NS	yes	Temperature and nutrient loading	yes
40	Mathematical model of the food web	Biogeochemical model	Fontaine and Stewart (1992)	yes	DY	NS	yes	Nutrient loading and pollution	no
41	Lake autotrophic model	Biogeochemical model	Higgins et al. (2014)	no	DY	NS	yes	Nutrient loading	no

42	Bioenergetic model coupled with eutrophication model	Biogeochemical model	Bierman et al. (2005)	yes	DY	SP	yes	Temperature and nutrient loading	yes
43	Coupled model of bioenergetic-based anchovy population dynamics and lower trophic food web structure	Biogeochemical model	Oguz et al. (2008b)	yes	DY	NS	yes	Fishing and nutrient loading	no
44	Reactive-transport model	Biogeochemical model	Norkko et al. (2012)	no	DY	NS	no		no
45	Total phosphorous mass model	Biogeochemical model	Gudimov et al. (2015)	no	DY	SP	yes	Nutrient loading	yes
46	Simplified lake ecosystem mathematical model	Biogeochemical model	Magnea et al. (2013)	no	DY	NS	yes	Nutrient loading	no
47	Biophysical model	Biophysical model	Rowe et al. (2015a)	yes	DY	SP	no		yes
48	Ecosystem model developed for the Port Phillip Bay Environmental Study	Hydrodynamic-biogeochemical model	Murray and Parslow (1999)	yes	DY	SP	yes	Nutrient loading	no
49	Hydrodynamic model	Hydrodynamic-biogeochemical model	Macisaac et al. (1999)	yes	DY	SP	no		yes
50	ELCOM-CAEDYM	Hydrodynamic-biogeochemical model	Schwalb et al. (2014)	yes	DY	SP	yes	Temperature and nutrient loading	yes
51	3D SPBEM	Hydrodynamic-biogeochemical model	Isaev et al. (2016)	yes	DY	SP	yes	Temperature and nutrient loading	no
52	Lake Michigan ecosystem model (LM-Eco)	Hydrodynamic-biogeochemical model	Miller et al. (2010)	yes	DY	SP	yes	Temperature and nutrient loading	no
53	Two-dimensional hydrodynamic and water quality model (CE-QUAL-W2)	Hydrodynamic-biogeochemical model	Zhang et al. (2011)	yes	DY	SP	yes	Nutrient loading	no
54	2-dimensional physical and biological/reactive-transport model	Hydrodynamic-biogeochemical model	Laruelle et al. (2009)	yes	DY	SP	yes	Nutrient loading	no
55	PEGASE with POTAMON model	Hydrodynamic-biogeochemical model	Pigneur et al. (2014)	yes	DY	SP	yes	Temperature, nutrient loading and hydrodynamic	no
56	Dynamic ecosystem model of the lower trophic levels	Hydrodynamic-biogeochemical model	Fishman et al. (2009)	yes	DY	SP	yes	Temperature and nutrient loading	no
57	Ecological model BIOGEN	Hydrodynamic-biogeochemical model	Lancelot et al. (2002)	yes	DY	SP	yes	Temperature and nutrient loading	yes
58	Dynamic water quality model	Hydrodynamic-biogeochemical model	Glaser et al. (2009)	yes	DY	SP	yes	Nutrient loading	no

59	One-dimensional physical-biological ecosystem model	Hydrodynamic-biogeochemical model	Oguz et al. (2001)	yes	DY	SP	yes	Nutrient loading	no
60	Ecological-mathematical model	Hydrodynamic-biogeochemical model	Volovik et al. (1995)	no	DY	SP	yes	Temperature	no
61	CIMPAL	Conservative additive model	Katsanevakis et al. (2016)	no	ST	SP	no		
62	DPSER	Conceptual integrated model	Cook et al. (2014)	no	ST	NS	yes	Fisheries and temperature	
63	Loop models of ecological and socio-economic systems	Qualitative model	Ortiz and Stotz (2007)	no	DY	NS	yes	Fisheries	
64	Mathematical model of trophic interactions	Food-web model	Padilla et al. (1996)	no	DY	CS	no		yes
65	Pelagic food web	Food-web model	Amundsen et al. (2013)	no	CP	NS	no		no
66	Intermediate complexity for ecosystem assessments (MICE)	Food-web model	Blamey et al. (2014)	no	DY	NS	yes	Fishing	yes
67	Ecological Network Analysis	Food-web model	Miehls et al. (2009)	no	CP	CS	no		no
68	Ecopath with Ecosim (static)	Food-web model	Downing et al. (2012)	no	CP	NS	yes	Fishing	no
69	Ecopath with Ecosim (dynamic)	Food-web model	Kao et al. (2014b)	no	DY	NS	yes	Fisheries and nutrient loading	no
70	Atlantis	End to end model	Nyamweya et al. (2016)	no	DY	SP	yes	Fisheries, nutrient loading and temperature	no

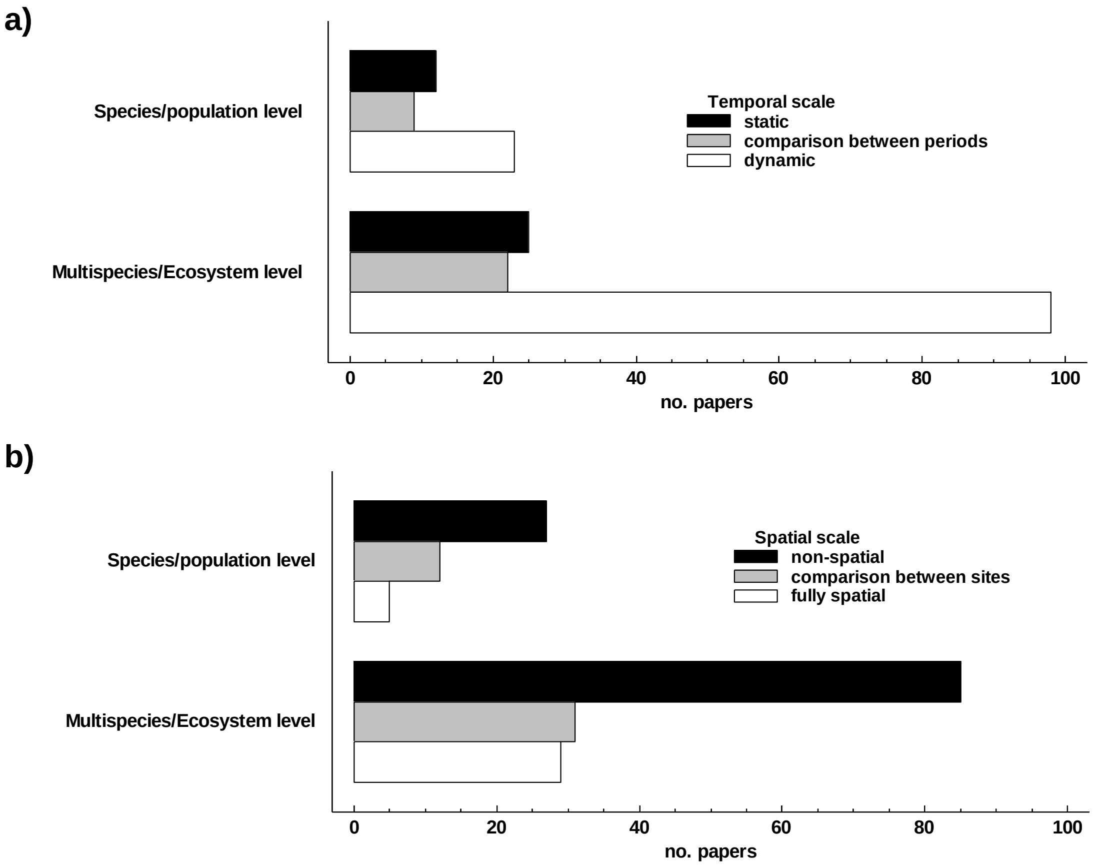


Figure 5. (a) Number of studies found in the systematic review by temporal and (b) spatial scale per modelling level.

Most studies (70%) did not evaluate uncertainty, with a similar percentage in species/population and multispecies/ecosystem models (Fig. 7) (Chi-square: $p = 0.5$). For models that assessed uncertainty we found studies that manually changed different input parameters using literature ranges (e.g., Jiang et al., 2015), estimated a degree of increase or decrease based on expected changes (Johnson et al., 2005, Van Guilder and Seefelt, 2013), assessed effects of different initial IAS biomass values (Zhang et al., 2008, Schwalb et al., 2014) or used Monte Carlo routines (Yurista and Schulz, 1995, Cha et al., 2011).

3.3. Modelling impacts of IAS

3.3.1. At the species/population level

Several statistical models that focused on the species/population level were used to assess the impact of IAS (Table 2). For example, Onikura et al. (2013) used a generalised linear model to predict potential inter-sub-specific hybridisation and to identify important areas of conservation. To evaluate the impact of competition for resource, Van Zuiden et al. (2016) used multiple regression models to assess the impact of smallmouth bass (*Micropterus dolomeiu*) and climate change on native walleye (*Sander vitreus*). Olden et al. (2011) used a SDM to assess impacts of invasive rusty crayfish (*Orconectes rusticus*) on two native congeners (*O. virilis* and *O propinquus*), while Woodford et al. (2011) used a GIS-based spatial model to predict whether two invasive trout species (*Salmo trutta* and *Oncorhynchus mykis*) would exclude the native *Galaxias vulgaris* due to predation.

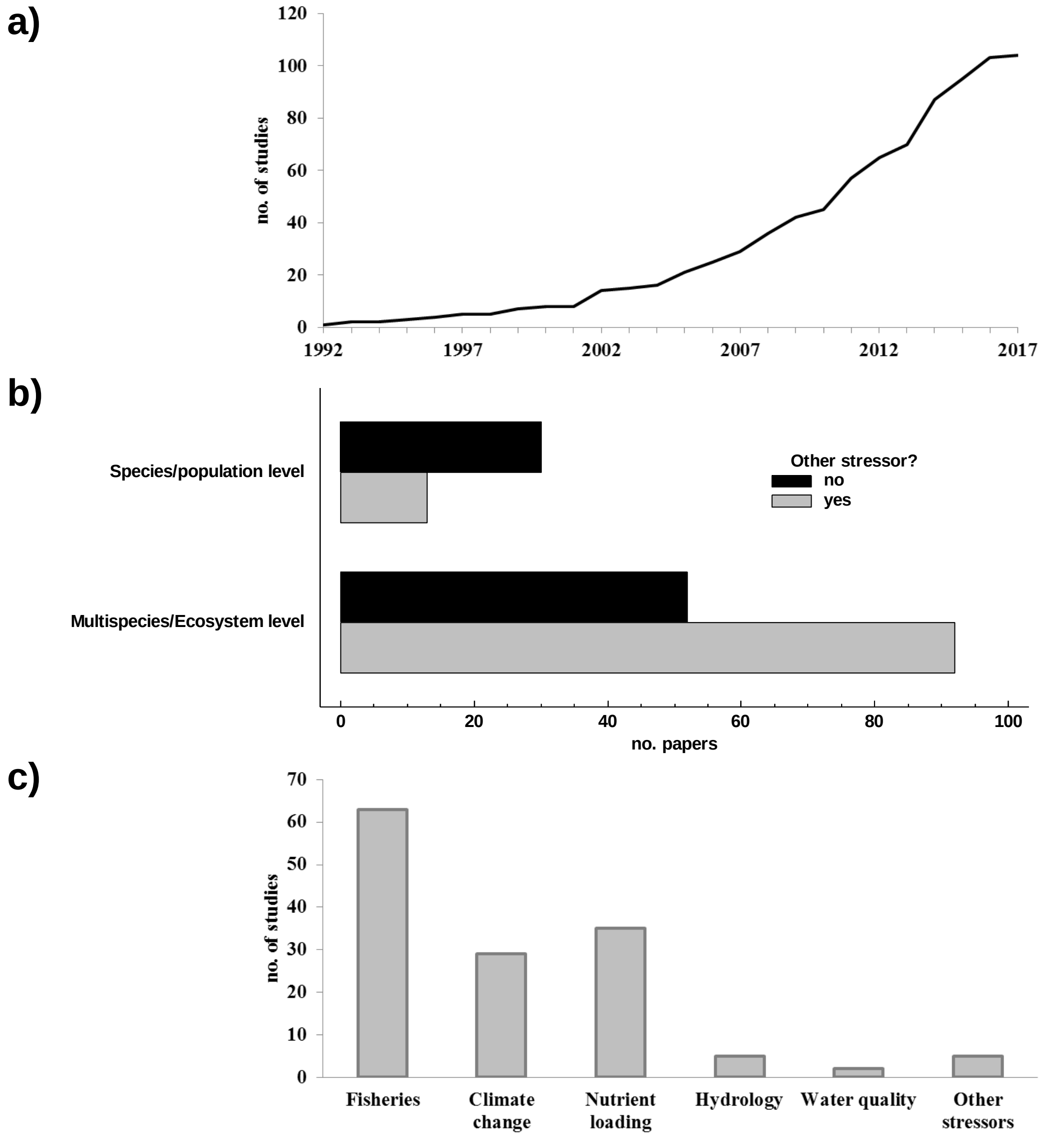


Figure 6. (a) Number of models that were driven by additional stressors found in the systematic review; (b) cumulative number of models that included other stressors over time; and (c) number of models that include each stressor.

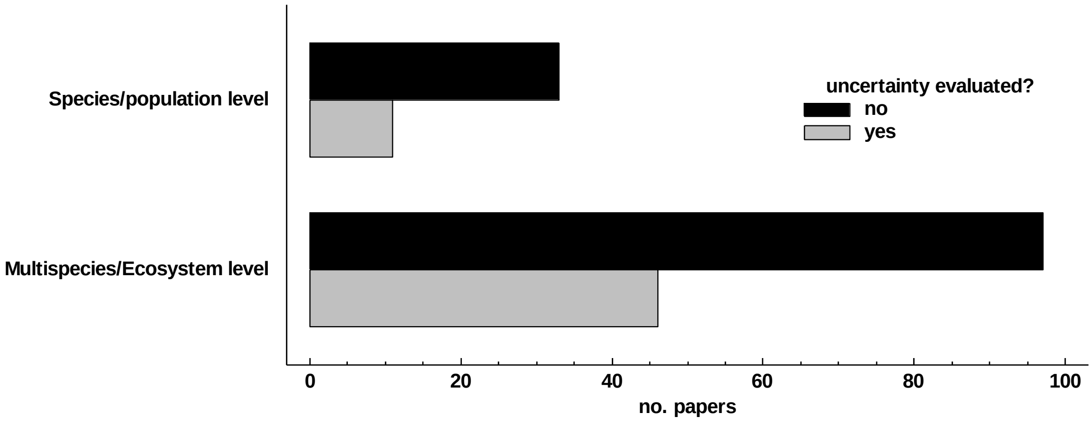


Figure 7. Number of studies found in the systematic review that evaluated uncertainty.

In addition, a variety of mechanistic models were used to assess the impact of IAS at the species level. For example, Liu et al. (2014) developed a bioeconomic model to capture the effects of invasive farmed fish on native stocks (growth and stock size) and harvest. Caldow et al. (2007) developed an individual-based model to evaluate the positive effects of the Manila clam (*Tapes philippinarum*) on the Eurasian oystercatcher (*Haematopus ostralegus*), providing more food and therefore reducing their winter mortality.

3.3.2. At the multispecies/ecosystem level

A large variety of statistical models that focused on the multispecies/ecosystem level were used to assess the impact of IAS (Table 2). For example, Bajer et al. (2016) fitted multivariate linear models to quantify the effects of the common carp (*Cyprinus carpio*) on plant cover and species richness, as well as additional effects of water quality and total phosphorous. De Amorim et al. (2015) assessed the impacts of the invasive African signalgrass (*Urochloa arrecta*) on a macrophyte community using a generalised linear model, while Knapp (2005) used a generalised additive model to assess the effects of invasive trout and habitat characteristics on lentic herpetofauna. Wenger et al. (2011) assessed the effect of flow regime, temperature and biotic interactions on the distribution of four trout species (of which three were IAS) under climate change using a SDM.

A large variety of mechanistic models were used to assess the impact of IAS at the multispecies/ecosystem level (Table 2). Within these model types, approaches ranged from simple to more complex, including coupled models, where models were integrated (with or without dynamic feedbacks) and outputs of one model provided inputs to the other (Travers et al., 2007).

A common method for assessing the impacts of IAS at the multispecies/ecosystem level was the development of bioenergetics models. For example, Walrath et al. (2015) used a bioenergetics model to estimate predation of the northern Pike (*Esox lucius*) on westslope cutthroat trout (*Oncorhynchus clarkia lewisi*) and other prey taxa. Reed-Andersen et al. (2000) coupled a zebra mussel bioenergetics model with an empirical phytoplankton growth model to predict the impacts of zebra mussels on water clarity.

Some ecological models were coupled with economic models. For example, Knowler (2005) assessed the economic consequences of the comb jelly (*Mnemiopsis leidy*) on the Black Sea anchovy (*Engraulis encrasicolus*) fishery using an integrated ecological-economic approach. This model combined a Ricker stock-recruitment model of the anchovy population with a balance model of *Mnemiopsis* biomass and an economic model. Grosholz et al. (2011) assessed the economic impacts of the invasive European green crab (*Carcinus maenas*) on commercial shell-fisheries along the West Coast of the United States using a combination of ecological and economic models.

Biochemical models, which were mainly developed to represent chemical fluxes (mainly nitrogen and phosphorus) affecting low trophic level groups (e.g. phytoplankton and zooplankton), were also used to assess impacts of IAS. For example, Magnea et al. (2013) developed a dynamic model for alpine lake ecosystems to describe phosphorous (the limiting nutrient), phytoplankton, three zooplankton compartments and fish. Bierman et al. (2005) used an ecosystem model in Saginaw Bay (Lake Huron, US) in which zebra mussel bioenergetics were integrated with an eutrophication model that represented nutrients and multiple functional groups of phytoplankton and zooplankton.

The coupling of biogeochemical models with hydrodynamic models allowed the inclusion of spatial and temporal variability of the environment, mainly represented by variables such as temperature, irradiance, salinity and currents. For example, Schwalb et al. (2014) and Bocaniov et al. (2014) used a three-dimensional (3D) hydrodynamic model (ELCOM) coupled with a biogeochemical model (CAEDYM). The CAEDYM included a mussel sub-model that allowed the authors to assess impacts of invasive dreissenids on phytoplankton. Isaev et al. (2016) used a 3D ecosystem model (SPBEM), that coupled a transport module with a biogeochemical module, to assess the impact of bioirrigation activity of the invasive alien polychaetes *Marenzelleria* spp. in the Gulf of Finland. In addition, Zhang et al. (2011) used a coupled 2D-hydrodynamic model and a water quality model (CE-QUAL-W2) to evaluate effects of dreissenids and zooplankton on phytoplankton in Lake Erie, USA.

Food-web models, which represent a description of species interactions within the ecosystem, were also frequently used. These models ranged from those that included only some species or functional groups to the inclusion of the entire food web. For example, Blamey et al. (2014) used a Model of Intermediate Complexity for Ecosystem assessments (MICE) (also called Minimally Realistic Model or MRM), to evaluate if overfishing of predatory fish may have caused a regime shift following the invasion of West Coast rock lobster (*Jasus lalandii*). Miehls et al. (2009) used an Ecological Network Analysis (ENA) to assess the effects of zebra mussel within and between two invaded ecosystems and compare food web characteristics before and after the invasion. In addition, the Ecopath with Ecosim (EwE) approach (Christensen and Walters, 2004a, Heymans et al., 2016) was frequently used to assess impacts of IAS. For example, Lercari and Bergamino (2011) quantified the impacts of two IAS (the gastropod, *Rapana venosa*, and the bivalve, *Corbicula fluminea*) in Río de la Plata estuary (Argentina and Uruguay) during a specific time period by developing an Ecopath model, while Downing et al. (2012) assessed impacts of IAS and fishing in Lake Victoria through three Ecopath models representing the before, during and after periods of the Nile perch bloom. In addition, Kao et al. (2014b) developed a time dynamic (Ecosim) model to evaluate relative impacts of changes in nutrient loads, fishing and two invasive groups (dreissenids and the alewife *Alosa pseudoharengus*).

Other types of models were employed to assess impacts of IAS. For example, Cook et al. (2014) used an integrated conceptual ecosystem model (Driver-Pressure-State-Ecosystem Service-Response or DPSER) to explore the direct and indirect relative impact of 12 ecosystem pressures on 11 ecosystem state variables and 11 ecosystem services in southern Florida. Ortiz and Stotz (2007) used qualitative (loop) models of ecological and socio-economic systems to analyse and predict the impact of a possible accidental introduction of the abalone (*Haliotis discuss hannai*) into the benthic community of north-central Chile. A conservative additive model was developed to assess the spatial cumulative impacts of IAS on marine habitats in the Mediterranean Sea (Katsanevakis et al., 2016).

Finally, there has been a growing interest in recent years to develop models that attempt to represent the entire ecosystem. These models are called end-to-end (E2E) or whole-of-system models and represent ecosystem components from nutrients, biogeochemical cycling and primary producers to top predators (including human components) linked through trophic interactions and the associated abiotic environment (e.g., currents and water column properties such as temperature and salinity) (Travers et al., 2007, Fulton, 2010). However, only one example of end-to-end models dealing with IAS was found. Nyamweya et al. (2016) developed an Atlantis model for Lake Victoria to assess impacts of overfishing, IAS such as Nile perch and Nile tilapia (*Oreochromis niloticus*), eutrophication and climate change.

3.4. Predicted impacts of IAS at species and ecosystem levels and the utility of models in impact management

Quantified impacts of IAS varied according to the type of model used (Fig. 8). Interestingly, at the species/population level, most of the studies reported negative impacts of the IAS on ecosystem compartments and/or ecosystem services, while at the multispecies/ecosystem level, negative and both negative and positive impacts were similarly represented (Fig. 8a) (Chi-square: $p < 0.005$). We found only a limited number of cases of only positive impacts in the results of both single species and multispecies models (Fig. 8a).

Most studies reported impacts on biota rather than on ecosystem services, and on multiple-species than single-species (Fig. 8b and c). Most of these impacts (single and multispecies) were due to ecological interactions involving predation and/or competition for resources. In addition, some models were used to assess impacts on ecosystem processes and function (Fig. 8b) such as biodiversity, biogeochemical fluxes, energy flows and ecosystem stability, and impacts on other ecosystem services (Fig. 8c). Water purification (39%) and food provision (from fisheries or aquaculture) (36%) were the most assessed ecosystem services, followed by recreation and tourism (for example, recreational fisheries) (15.8%) (Fig. 8c).

Most of the studies (around 90%) did not provide management recommendations, regardless of modelling level (Fig. 9a) (Chi-square: p = 0.6) or type of environment (Fig. 9b) (Chi-square: p = 0.7). In studies that provided management recommendations, these were too general, although some studies provided specific management advice (Online Supplementary Information B). For example, Stapp and Hayward (2002), based on a stage-structured matrix model, suggested the development of control programs to reduce survival of all age classes of lake trout (*Salvelinus namaycush*) in addition to focusing on adults. Using an EwE model, Arias-González et al. (2011) and Pine et al. (2007) assessed, through different scenarios of fishing exploitation, how to eradicate invasive alien top predators.

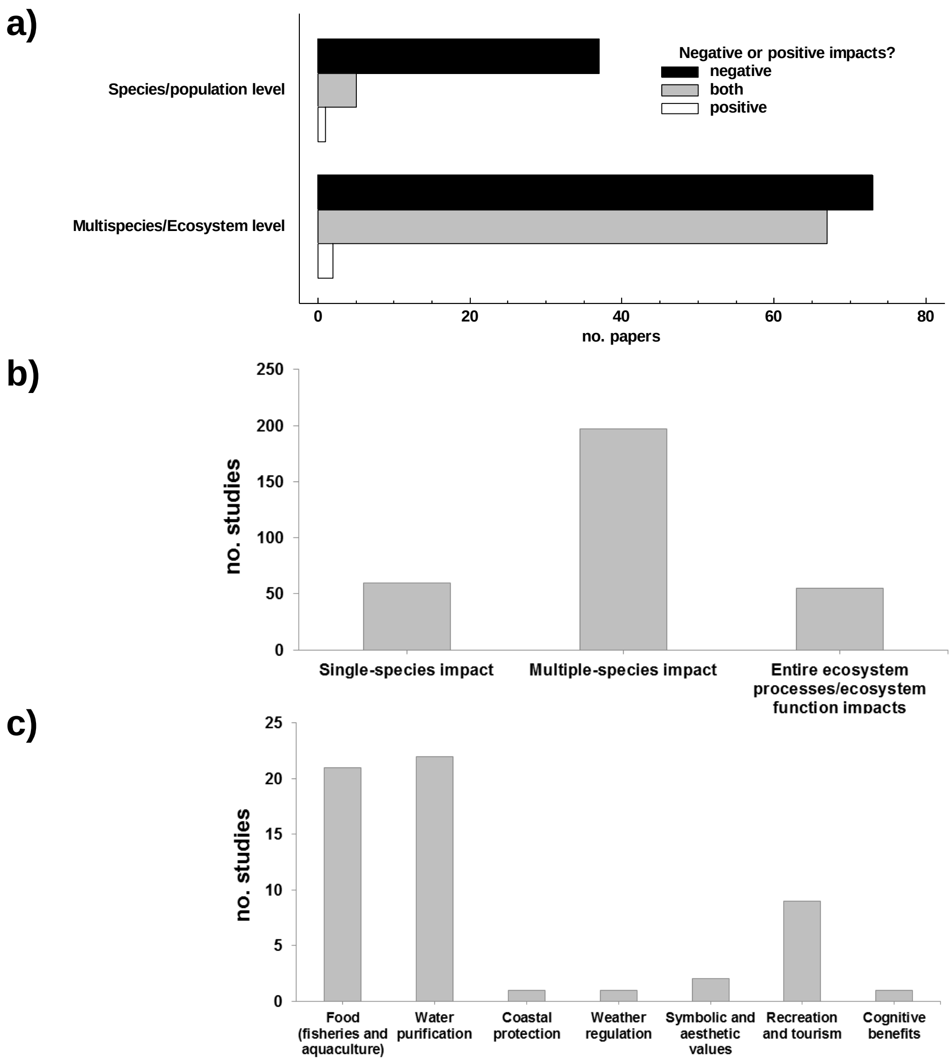


Figure 8. (a) Number of studies that assessed negative, positive or both negative and positive impacts; and overview of the number of studies that reported impacts on (b) biota and (c) ecosystem services.

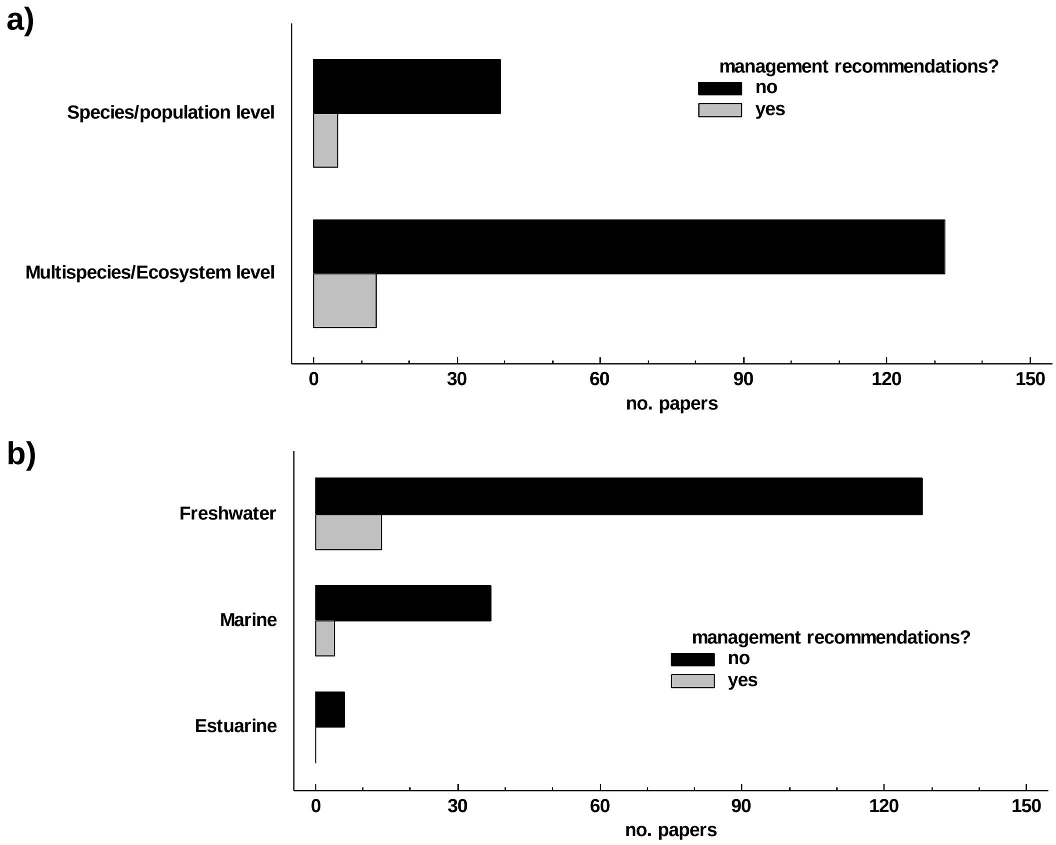


Figure 9. Number of studies whose outputs have been used to provide management recommendations by (a) modelling level and (b) environment.

4. Discussion

4.1. Making progress in modelling impacts of IAS on aquatic ecosystems

In recent decades, the rate of human-mediated introductions have increased (Hulme, 2009, Seebens et al., 2017) and some have had great impact on native species and recipient ecosystems and their services (Simberloff et al., 2013, Gallardo et al., 2016). In parallel, considerable research has been conducted to understand and predict invasions and assess their ecological impacts (Ricciardi et al., 2013, Chan and Briski, 2017), highlighting the growing concern over this issue. Therefore, evaluating IAS impacts is essential to developing strategies to prevent and manage their effects (Pyšek and Richardson, 2010, Ojaveer et al., 2015).

According to our results, while there has been an exponential growth of modelling approaches, this growth has not been consistent across ecosystem and biogeographic regions. Most of the studies were concentrated in freshwater ecosystems, followed by marine and estuarine ecosystems. This is in line with a review of hypotheses for causes of biological invasions and their impacts, which showed that most studies were carried out in terrestrial ecosystems, followed by freshwater, marine and estuarine ecosystems (Lowry et al., 2013).

The results of our review highlight geographic differences in IAS modelling efforts. While models have been developed for most biogeographic regions (freshwater and marine realms) they have mainly focused on particular areas, namely North America but also Europe, in agreement with Lowry et al. (2013), Pyšek et al. (2008) and Buchadas et al. (2017). This geographic distribution of models can be largely explained by different funding opportunities for research and research priorities across countries, although there may have been some bias in our findings due to the exclusion of non-English and non-Spanish publications in our review.

According to our results, most available studies focused on species occupying low trophic levels. Lowry et al. (2013) and Pyšek et al. (2008) also found that most of the research on biological invasions focused on low trophic levels. However, in their reviews most of the species were primary producers (mainly terrestrial plants), while most of the species we identified were fishes and molluscs (mainly bivalves). It is likely that this taxonomic composition indicates research priorities over the last few decades and, in some regions, also reflects the proportion of IAS in the studied ecosystems. In fact, impacts have been described for a small proportion of IAS, which tend to be those with the greatest impact on organisms and ecosystems and their services (Vilà et al., 2009, Pyšek and Richardson, 2010). For example, dreissenids (freshwater mussels) have been largely studied and modelled due to their wide distribution and dramatic ecological and economic impacts, especially in North America (Pyšek et al., 2008, Higgins and Vander Zanden, 2010).

Most models were used to assess the detrimental effects of IAS (Pyšek et al., 2008, Katsanevakis et al., 2014c). However, IAS can have positive effects on native species and ecosystems, as well (e.g., Caldow et al., 2007, Norkko et al., 2012). This is highlighted in multispecies/ecosystem level models, which incorporate interactions among many species, and therefore indirect effects that can cause both positive and negative impacts. Most of these impacts are related to the effect of an invasive alien predator on native preys, but research has also focused on competition for resources and ecosystem processes and function. In fact, effects of invasive alien prey on native predators have been less studied (Carlsson et al., 2009), and according to the trophic position hypothesis, we could expect negative impacts of IAS on biodiversity within a trophic level but positive effects on the biodiversity of higher trophic levels through community-wide antagonism (competition and consumption) and facilitation (habitat and food provisioning) interactions, respectively (Thomsen et al., 2014).

Ecological processes operate at different spatial and temporal scales, and thus the choice of scales is very important (Jørgensen and Fath, 2011). These choices affect model complexity, as finer temporal and spatial resolution need more detailed data and require increased computation power and effort, while exacerbating uncertainty (Rose et al., 2010, Plagányi et al., 2014). Therefore, the spatial and temporal scales should be modelled to the degree required to address the question under consideration (FAO, 2008, Fulton, 2010). In the context of modelling the impacts of IAS in aquatic ecosystems, suitable modelling frameworks need to allow the incorporation of several IAS with different ecological and trophic roles and, therefore, with different temporal and spatial requirements, especially in highly invaded areas. Connecting these parts of the model or even "sub-models" is a challenging task (Rose et al., 2010).

According to our review, dynamic models were the most frequently developed, followed by static and comparative static models. This is probably due to the fact that assessing the impact of IAS in aquatic ecosystems is a complex undertaking, which is time dependent. It may also be due to the need for tools to manage aquatic ecosystems (Cuddington et al., 2013, Buchadas et al., 2017). Model comparison between periods provides a means of assessing the impact over time. This modelling technique presents some advantages over developing a single static model, especially if comparison includes models before and after invasion, as it allows the assessment of the overall impact of IAS on the invaded ecosystem. Non-spatial models were more frequent than spatial ones. This is due to the challenges of spatial modelling and the large data requirements (Fulton et al., 2004b, Jørgensen, 2008). In non-spatial models, comparisons between invaded and non-invaded areas are interesting and have provided insights into the impacts of IAS (e.g., Rowe, 2007, Blamey et al., 2013).

4.2. Advantages and disadvantages of existing modelling approaches

A desirable model is one that maximizes generality (the applicability of a model to different ecosystems, data sets and questions), realism (the model includes detailed processes through mathematical equations) and precision (the degree of exactness in measurement or predictions) (Levins, 1966). However, in practice, modelling is essentially a trade-off among these desirable attributes (Levins, 1966). A main difference between statistical and mechanistic models is related to their internal structure. In mechanistic models, the relationship between the variables is specified in terms of the biological process, while statistical models look for patterns and relationships in the observed data, regardless of the causative processes involved (Hilborn and Mangel, 1997, Robson, 2014b).

Statistical and single-species models offer a simplistic view of the ecosystem, ignoring processes and interactions, but they are easily constructed and can highlight ecosystem characteristics. Large complex models, on the other hand, can provide a more comprehensive picture of the ecosystem but they have large data demands, can represent processes poorly and can have a large degree of uncertainty due to errors in model structure and parameter values (Fulton et al., 2003, Link et al., 2012, Gal et al., 2014). Therefore, it has been recommended to include essential processes and components in a balanced way to address the question under consideration while capturing the complexity of aquatic systems (FAO, 2008, Hannon and Ruth, 2014).

Statistical models have been widely used to study the impacts of IAS in aquatic ecosystems. These models have been shown to be useful to assess impacts of IAS on native species (e.g., Stapanian et al., 2009, De Amorim et al., 2015) and also to predict potential spatial exclusion (e.g., Sharma et al., 2011, Wenger et al., 2011). In addition, they are used to disentangle the relative importance of IAS and other stressors in native species declines (e.g., Light and Marchetti, 2007, Hermoso et al., 2011, Bajer et al., 2016), as well as changes in abiotic factors such as dissolved oxygen, pH, turbidity, temperature, conductivity, river width, calcium concentration and substrate (e.g., Macdonald et al., 2012, Pagnucco and Ricciardi, 2015). Such analyses can improve our understanding of broad patterns in biodiversity changes and provide insight into processes that may be responsible for the patterns observed in the data (Whipple et al., 2000, Light and Marchetti, 2007). However, statistical models incorporate low levels of realism as they treat the data largely ignoring the ecological processes that generate them (Levins, 1966, Jørgensen and Fath, 2011).

A large number of mechanistic models have been used to study the impacts of IAS, ranging from simple to very complex. At the species level, models assess impacts of IAS on populations. These impacts include effects on growth (Liu et al., 2014, Crane and Einhouse, 2016), catchability (Kateregga and Sterner, 2009b), mortality (Caldow et al., 2007), predation (Green et al., 2014, Rowe et al., 2015b) and competition (Liu et al., 2014), as well as economic impacts on property values (Olden and Tamayo, 2014a) and fisheries (Liu et al., 2014). However, aquatic ecosystems are dynamic and complex, with interactions between species (trophic and non-trophic), which generally involve competition and predation, and should incorporate environmental elements and human stressors (Garcia et al., 2003, Thoms, 2006). An understanding of the functional interactions and processes in aquatic ecosystems, as well as the cumulative impacts of human activities, requires a shift to more comprehensive analysis, as is emphasized by ecosystem-based management (Rosenberg and McLeod, 2005).

Most of the mechanistic models at the multispecies/ecosystem level that we found were quantitative, with only one qualitative model (loop analysis) found applied to the study of the impacts of IAS on aquatic ecosystems (Ortiz and Stotz, 2007). Within the context of modelling impacts of IAS, with data limitations in many cases, loop analysis could become a valuable tool (Metcalf, 2010), as precise model predictions and estimates of the magnitude of the impacts are not always necessary to inform management questions (Ramsey and Veltman, 2005).

The development and application of bioenergetics models have increased in recent years (Chipps and Wahl, 2008, Hartman and Kitchell, 2008) due to their user-friendly software, reasonable time and effort to develop, ease of interpretation and ability to make predictions (Chipps and Wahl, 2008, Jørgensen, 2008). In invasion ecology, these models are particularly useful because they provide a means of evaluating the trophic impacts (amount of prey eaten) of IAS and assessing the suitability of an ecosystem for invasion considering their energy requirements and food availability (e.g., Anderson et al., 2015, Foley et al., 2017). However, the use of these models presents some disadvantages, including the requirement of good data, associated with intense sampling, and they can be difficult to calibrate (Chipps and Wahl, 2008, Hartman and Kitchell, 2008, Jørgensen, 2008)

Biogeochemical models (which may or may not be coupled with hydrodynamic models) have been widely used over the last few decades as a research and management tool due to the increasing power of computers, the development of more robust and detailed processes and increasing data availability, and user-friendly software (Jørgensen, 2008, Fulton, 2010, Ganju et al., 2016). Coupling biogeochemical models with hydrodynamic models represented an important and necessary step, and considerable progress has been made in the spatial resolution of the hydrodynamic models (Ganju et al., 2016). In invasion ecology, these models (coupled or not) have proved to be a useful tool to assess: (1) the role of top-down (grazing by native species, i.e. zooplankton, and IAS, i.e. dreissenids) and bottom-up (nutrient availability) forces on primary productivity and changes to energy pathways due to IAS (Higgins et al., 2014), (2) the competition between native and invasive alien grazers (Zhang et al., 2011), (3) the role of IAS (i.e. dreissenids) on nutrient (i.e. phosphorous) and native community (i.e. macrophytes) dynamics (Gudimov et al., 2015), (4) the role of IAS in the proliferation of toxic algae blooms (Bierman et al., 2005), and (5) the role of IAS in the recovery of hypoxic regions due to the impacts of bioirrigation on biogeochemical cycles within sediments (Norkko et al., 2012). Despite these advantages, hydrodynamic-biogeochemical models are very time consuming, and can be difficult to calibrate and validate due to the large amount of data and processes (Fulton et al., 2003, Arhonditsis and Brett, 2004, Jørgensen and Fath, 2011). In addition, some key processes are excluded or are represented with a weak mechanistic basis (Doney, 1999, Robson, 2014a, Ganju et al., 2016).

The study of food webs presents important challenges due to data availability, quantification of interactions and the need to represent ecosystem processes and dynamics (Dunne, 2006). Food-web models have also been increasingly used over the last few decades, and one example is the wide application of the Ecopath with Ecosim (EwE) approach (Heymans et al., 2014, Colléter et al., 2015). Assessing the impacts of IAS in a food web context is a challenging task. For example, within the EwE framework, all species must have a positive biomass in the baseline static Ecopath model when using the temporal dynamic module Ecosim, presenting a challenge for species that invaded the ecosystem after the baseline Ecopath model. Some applications have addressed this by developing two Ecopath models, one representing the food web before the invasion and one after the invasion (e.g., Downing et al., 2012, Corrales et al., 2017b). However, this approach impedes the study of the expansion process and their impact over time. Several strategies have been successfully applied to simulate IAS and their temporal impacts using the temporal dynamic model of EwE, Ecosim (e.g., Langseth et al., 2012, Kao et al., 2016, Corrales et al., 2017a). In addition, Ecosim has been used to evaluate the eradication and resilience of IAS and the potential effects of its removal on the ecosystem (e.g., Pine et al., 2007, Arias-González et al., 2011), as well as the possible impacts that a new IAS might have on the ecosystem (Pinnegar et al., 2014), and their possible future cumulative effect with fishing and climate change (Libralato et al., 2015). At the same time, there has been a growing interest in MICE (Plagányi et al., 2014), which, unlike whole food-web models (e.g., EwE), represents a limited number of species believed to have the most important interactions with target species. MICE can be an especially valuable tool for areas where available data for the whole ecosystem are lacking.

Despite the growing development of a variety of end-to-end models in aquatic ecosystems (Fulton, 2010, Rose et al., 2010), we only found one study using end-to-end modelling (within the Atlantis framework (Fulton et al., 2004a)) to study impacts of IAS on aquatic ecosystems. This may reflect the current challenges of implementing end-to-end modelling within the context of invasion ecology.

4.3. Moving forward

Some of the main limitations in model development are data availability, accessibility and quality. Due to uncertainties in field surveys (Katsanevakis et al., 2012), effective monitoring is needed, as it provides essential information to develop modelling applications. Within the context of IAS, there is an urgent need to deal with uncertainties in alien status and IAS inventories (McGeoch et al., 2012, Katsanevakis and Moustakas, 2018). We need to improve our knowledge of their population dynamics, biological traits, ecology, such as trophism and behaviour, and environmental affinities. This is especially important due to the fact that climate change may favour the establishment and spread of IAS while native species may be forced out of their tolerance limits (Walther et al., 2009, Rilov, 2016). The improvement of data availability and better collaboration between data collectors and modellers is needed to enhance model development and validation and the interpretation of model outputs.

Calibration, validation and uncertainty analyses are critical processes for evaluating model performance and testing the validity of the assumptions included in the model, especially in complex models (FAO, 2008, Jørgensen and Fath, 2011, Grüss et al., 2017). Our review highlights that most models used to evaluate impacts of IAS on aquatic systems did not assess uncertainties, in line with previous research (Katsanevakis and Moustakas, 2018, Stelzenmüller et al., 2018). This is an important shortcoming that needs further research and development in the field.

We have shown the capabilities of models to assess the impacts of already established IAS. However, since IAS are increasing in aquatic ecosystems and this increase is likely to continue into the future, there is a need for predictive methodologies that allow the forecasting of plausible scenarios that include existing, emerging and potential new IAS (Dick et al., 2014). However, making predictions about future impacts of IAS presents several obstacles linked to the high uncertainties of ecological forecasting (Maris et al., 2017), in addition to intrinsic features of IAS (Havel et al., 2015), especially related to the unknown population dynamics in current and future invaded ecosystems. Predicting potentially new IAS and their impact on the invaded ecosystem is a challenging task. The invasion process includes the phases of arrival, establishment and naturalisation and, therefore, depends on the combination of dynamic interspecific relationships (with native species or even other IAS), habitats, environmental effects and other anthropogenic activities. A modelling approach dealing with these phases is needed, and could require the coupling of different models that are able to predict the probability of a species to arrive and, once it invades the ecosystem, to model species interactions and the effect of multiple environmental factors and human activities.

Several tools are available to predict potential IAS and their spread (Kolar and Lodge, 2001, Wonham and Lewis, 2009), such as risk assessments (Kolar and Lodge, 2002, Townhill et al., 2017), vector-based models (Seebens et al., 2016), species distribution models (SDMs) (Jiménez-Valverde et al., 2011, Larson et al., 2014), or studies that identify characteristics of species likely to invade, such as environmental affinity and ecological traits (Belmaker et al., 2013). Within this context, Romanuk et al. (2009) simulated invasions by integrating models of network structure and nonlinear population dynamics. In addition, SDMs are increasingly used to forecast potential distributions of species, although the climate niche could be different between the native and invaded ecosystem (Mainali et al., 2015, Parravicini et al., 2015) and despite dispersal limitations (Václavík and Meentemeyer, 2009). Current research of SDM is focusing on incorporating the effects of species interactions (Wisz et al., 2013, Albouy et al., 2014). Within this context, the new habitat capacity model and the spatial-temporal module of EwE, Ecospace (Steenbeek et al., 2013, Christensen et al., 2014b), provides a step forward for temporal-spatial modelling, as it combines food-web modelling with SDMs and could be a valuable tool for predicting the future spread of IAS.

Future scenarios of biological invasions are rarely developed due to the challenges of invasion biology (Courchamp et al., 2017). Despite these constraints, there have been attempts to predict impacts of already established IAS, particularly in aquatic ecosystems (Ricciardi, 2003) but also on marine ecosystems (Corrales et al., 2018). For example, Pinnegar et al. (2014) used a Rank Proportion Algorithm (RPA) (Link, 2004) to predict the diet composition of a potential new IAS based on its diet on an already invaded ecosystem (the Eastern Mediterranean Sea). The authors of this study then used this new diet as input to an EwE model representing an ecosystem of the Western Mediterranean Sea. Finally, Pinnegar et al. (2014) used the EwE model to assess possible impacts of the IAS on the new ecosystem assuming different expansion rates. In fact, the RPA model, or similar approaches, could be a valuable tool to predict diet composition for recent or even possible future invaders. The incorporation of RPA or related methods into ecosystem models could be a promising future development to enable the inclusion of IAS in future scenarios of global change.

Models, especially multi-species/ecosystem models, have become an essential decision-making tool, although they are generally not used to manage ecosystems (Collie et al., 2014). Within IAS management, models are rarely used to provide management recommendations. A possible reason is that there is a mismatch between research outputs and decision-makers priorities (N'Guyen et al., 2016, Piria et al., 2017). While researcher outputs have been focused on IAS impacts, decision-makers prioritize IAS prevention. In fact, prevention of new introductions through managing vectors and pathways is a priority in the development of effective policies (CBD, 2002) and as such, risk assessment has been widely used in IAS management (Pyšek and Richardson, 2010). Future collaboration between researchers, decision-makers and other stakeholders is essential to move this aspect forward and promote the use of modelling techniques for management advice in the context of biological invasions (N'Guyen et al., 2016, Novoa et al., 2018).

Acknowledgments

XC and EO were supported by an IOLR scholarship under the DESSIM project ("A Decision Support System for the management of Israel's Mediterranean Exclusive Economic Zone"). MC was partially funded by the European Commission through the Marie Curie Career Integration Grant Fellowships – PCIG10-GA-2011-303534 - to the BIOWEB project and the European Union´s Horizon research program grant agreement No 689518 for the MERCES project. This study was partially funded by COST (European Cooperation in Science and Technology) Action 15121 "Advancing marine conservation in the European and contiguous seas" (MarCons - http://www.marcons-cost.eu/; Katsanevakis et al. (2017)) - supported by the Horizon 2020 Framework Programme for research and innovation**.** XC thanks Daniel Vilas for help with Figure 2.

2.2. Modelling the role and impact of alien species and fisheries on the Israeli marine continental shelf ecosystem

Corrales, X.[1,2]*; Ofir, E.[1]; Coll, M.[2,3]; Goren, M.[4]; Edelist, D.[5]; Heymans, J.J.[6]; Gal, G.[1]

1. Kinneret Limnological Laboratory, Israel Oceanographic & Limnological Research. PO Box 447, Migdal, Israel;
2. Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta, nº 37-49. 08003. Barcelona, Spain;
3. Ecopath International Initiative Research Association, Barcelona, Spain
4. Department of Zoology and The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv 69978, Israel;
5. Tel-Shikmona, Israel Oceanographic & Limnological Research. PO Box 8030, Haifa 31080, Israel;
6. Scottish Association for Marine Science, Scottish Marine Institute, Oban, PA 371QA, Scotland.

Journal of Marine Systems 170 (2017), 88-102

https://doi.org/10.1016/j.jmarsys.2017.02.004

See original publication in Annex 2

Abstract

The ecosystems of the Israeli Mediterranean coast have undergone significant changes in recent decades mainly due to species invasions and fishing. In order to characterize the structure and functioning of the marine continental shelf of the Israeli Mediterranean coast and assess temporal changes, we developed a food web model representing two time periods: 1990-1994 and 2008-2012.

The 1990-1994 and 2008-2012 food web models were composed of 39 and 41 functional groups, respectively. Functional groups ranged from primary producers to top predators, and included six and eight alien functional groups, respectively, encompassing several crustacean and fish species. Input data included local surveys and fishery statistics, published data on stomach content analyses, and the application of empirical equations to estimate consumption and production rates.

Results of the competitive interactions between alien and native species and changes in trophic flows between food web components highlight the increasing impact of alien species over time. Fishing had noticeable impacts in both time periods and played an important role in the ecosystem. Despite different productivity rates and other environmental differences, the Israeli marine ecosystem shared common structural and functional traits with other Mediterranean marine ecosystems. This is the first attempt to study the ecosystem of the Levant region using mass-balance models and to integrate such a large amount of alien species into food web analyses.

Keywords: Eastern Mediterranean Sea; food web; Ecopath model; alien species; fishing.

1. Introduction

Biological invasions are currently considered as one of the most important direct drivers of biodiversity change and pose a major threat on marine ecosystems, with both ecological and economic impacts (Bax et al., 2003, Molnar et al., 2008, Rilov and Crooks, 2009). These impacts include changes in the genetic diversity of native species, local species extinctions and alterations of entire food webs (Grosholz, 2002, Levin and Crooks, 2011).

The Mediterranean Sea, specifically its eastern basin (Rilov and Galil, 2009, Edelist et al., 2013a, Katsanevakis et al., 2014b), is one of the marine ecosystem most affected by alien species (Molnar et al., 2008, Costello et al., 2010). Currently, there are nearly 700 alien species described in the Mediterranean Sea, of which more than half are considered to be established and spreading (Zenetos et al., 2010, Galil et al., 2014a, Galil et al., 2016). Although no complete extinctions, due to alien species, have been recorded in the Mediterranean Sea, sudden declines in abundance and local extirpations of native species concurrent with the proliferation of alien species have been documented (Galil, 2007a, Golani, 2010, Edelist et al., 2013a).

The Mediterranean Sea is currently classified among the most impacted ecoregions of the world (Costello et al., 2010, Halpern et al., 2015a). The increasing impact of fishing in the Mediterranean Sea is evident. Many demersal and pelagic stocks are fully exploited or overexploited (Vasilakopoulos et al., 2014, Tsikliras et al., 2015). In addition, the Mediterranean Sea is being altered by other anthropogenic activities posing impacts, such as habitat loss and degradation, pollution, eutrophication and climate change (Coll et al., 2010, Coll et al., 2012).

Within this context, the marine ecosystem of the Israeli Mediterranean coast, located within the Levantine Sea in the eastern part of the Mediterranean basin, has undergone significant changes in recent decades caused primarily by species invasion, fishing, river damming and climate change (Edelist et al., 2013a, Goren et al., 2013, Edelist et al., 2014, Sternberg et al., 2015).

The Levantine Sea has the hottest, most saline and most oligotrophic waters in the Mediterranean Sea (Azov, 1991, Brasseur et al., 1996), as a result of high evaporation rates, very low riverine inputs and limited vertical mixing. These characteristics are the main factors influencing several faunistic phenomena such as “Levantine nanism" (Sonin et al., 2007) and general faunal impoverishment compared to other Mediterranean Sea regions (Coll et al., 2010).

Multiple empty niches in the Levant due to the low regional biodiversity and the existence of the native species in a habitat at the limits of their tolerance levels (Golani, 1998, Galil, 2008, Rilov and Galil, 2009) can be potentially utilized by alien species. In addition, the opening of the Suez Canal in 1869, its continuous enlargement and the similar temperature and salinity regimes in the Levantine Sea and the Red Sea allowed for the progressive introduction of many Indo-Pacific species into the eastern Mediterranean Sea (known as Lessepsian immigrants) (Rilov and Galil, 2009). This phenomenon is almost entirely unidirectional, i.e. into the Mediterranean , and it was accelerated during the second half of the 20th century and the first decade of the 21th century (Rilov and Galil, 2009, Golani, 2010).

The environment of the eastern Mediterranean Sea has become more extreme to its native species due to climate change, favouring the establishment and spread of thermophilic species, such as most of the Lessepsian immigrants (Ben Rais Lasram et al., 2010, Lejeusne et al., 2010, Bianchi et al., 2013). Currently, the Levantine Sea is the world's most invaded marine ecoregion and the ecosystem has shifted considerably due to the collapse of several native species and the increasing dominance of alien species (Edelist et al., 2013a).

The study of biological invasions and their impacts on the marine environment has increased in the last few decades and it is providing new insights into their ecological consequences (Wonham and Lewis, 2009). Most studies of alien species on marine ecosystems have focused on population level questions, such as population establishment, spread, impacts, invasion control and spatial distributions (e.g., Ruesink and Collado-Vides, 2006, Azzurro et al., 2013). In addition, several tools of different complexity have been employed to examine the impact of alien species (Wonham and Lewis, 2009). These applications range from analyses that include a number of groups within the pelagic compartment to modelling applications that include entire food webs (e.g.,Berdnikov et al., 1999, Oguz et al., 2001, Arias-González et al., 2011, Libralato et al., 2015).

Given the interconnectedness between populations, environment and human activities, a shift towards a more comprehensive analysis and management of human activities is required, as it is emphasized by the ecosystem-based management (EBM) approach (Rosenberg and McLeod, 2005, Link, 2010a). Within this context, ecosystem modelling tools are particularly useful because they allow the study of marine ecosystems as a whole, integrating available information to study direct and indirect interactions among ecosystem compartments, i.e. trophic interactions and the impact of fishing activity on marine resources (Plagányi, 2007, Fulton, 2010). One popular modelling approach used to study marine food webs is the Ecopath with Ecosim (EwE) approach (Christensen and Walters, 2004a), widely applied to describe the structure and functioning of aquatic food webs and to assess the impacts of human activities and environmental changes (Christensen and Walters, 2011, Heymans et al., 2014, Colléter et al., 2015, Heymans et al., 2016).

Several Ecopath models have been built over the last decade in the Mediterranean Sea (Coll and Libralato, 2012). However, all available ecosystem models (with the exception of the Gulf of Gabes (Hattab et al., 2013), in Tunis) were developed for the northern Mediterranean Sea, and mostly in the western basin. In addition, the EwE approach has been used to study the impacts of alien species in several aquatic systems but typically, these studies have included only one or two alien functional groups (Corrales et al., 2014).

In this study we developed a food web Ecopath model of the Israeli Mediterranean continental shelf for two time periods (1990-1994 and 2008-2010). The models were constructed in order to characterize the structure and functioning of the food web and to assess the past and current impact of several alien species and fishing on the Israeli continental shelf food web. Due to the large number of alien species in the region, this represents a major modeling challenge and an important step forward in modeling alien species with EwE, generally, and the Mediterranean Sea in particular.

2. Material and methods

2.1. Study area and time periods

The Israeli Mediterranean continental shelf ecosystem (thereafter referred to ICS) (Fig. 1) food web models cover an area of 3725 km^2 between 0 to 200 m depth. The bathymetric extension of the models is constrained by biology and fisheries as the study area includes the entire continental shelf, where the alien species live, and where the fishery mainly operates. Two time periods were modelled: 1990-1994 (thereafter referred to 1990s) and 2008-2012 (thereafter referred to 2010s). These two time periods were chosen due to the availability of data, the increase in the extent of occurrence of alien species, and the decline in fishing from 1990 to present (Edelist et al., 2013a, Goren et al., 2013).

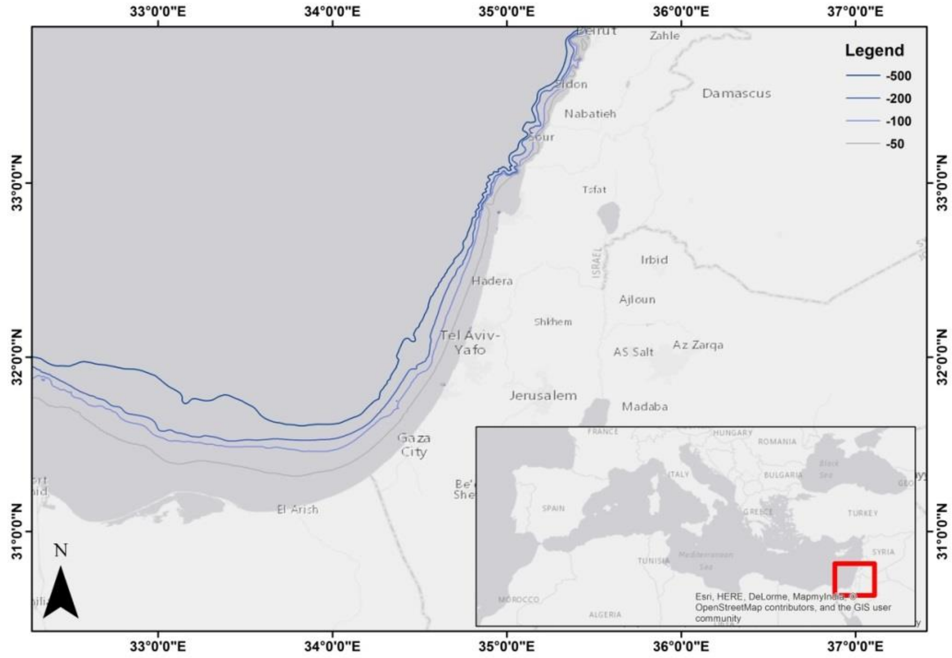


Fig. 1. The study area encompassing the Israeli EEZ and depth contours.

Israel's Mediterranean fisheries include a small semi-industrial trawl fleet, a small artisanal sector of gill and trammel-netters and longliners, a small purse seine fleet and a growing recreational sector (Edelist et al., 2013b, Goren et al., 2013). They are all multi-species fleets (Edelist et al., 2013b), that fish on the continental shelf, mainly near the coast (Edelist et al., 2011).

2.2. Ecopath modeling approach

Ecopath with Ecosim (EwE) version 6.4.3 (Christensen and Walters, 2004a, Christensen et al., 2008) was used to describe ICS food web. We used the static Ecopath model, to provide a quantitative representation of the food web as a "snapshot" in terms of flows and biomasses for a defined period of time. The food web is modelled by using functional groups, which can consist of ontogenetic fractions of a species, single species or groups of species sharing common ecological traits. These groups are linked through their trophic interactions.

Ecopath is based on two master equations describing the production (Eq. 1) and consumption (Eq. 2) of each functional group (Christensen and Walters, 2004a, Christensen et al., 2008).

Production = predation mortality + fishing mortality + other mortality + biomass accumulation + net migration (Eq. 1)

Consumption = production + respiration + unassimilated food (Eq. 2)

For each functional group, three of the four basic parameters (biomass (B), production (P/B) and consumption (Q/B) rates, and ecotrophic efficiency (EE)) are required and the forth is estimated. In addition, for each functional group the diet composition is required as well as the catch by fleet. A detailed explanation of the algorithms and equations of the approach and its main advantages and limitations are described in Christensen and Walters (2004a) and Heymans et al. (2016).

2.3. Functional groups and input data

To represent the ICS food web, we defined the functional groups based on biological and ecological features of species such as habitat, depth distribution, diets, and data availability. We followed a similar food web structure and parametrization to other Ecopath models developed for the Mediterranean Sea (Coll et al., 2006, Tsagarakis et al., 2010, Corrales et al., 2015) (Table 1). The data of the two models, 1990s and 2010s, are shown in Table 1 and a detailed description of these inputs is provided in the Table S1 in Annex 2.

To assess the impact of alien species in the ecosystem we included specific alien functional groups. Due to the large number of alien species and differences in time of settlement in the ecosystem, we included the most abundant species (33 species in 1990s and 41 species in 2010s), for which sufficient data were available, including crustaceans and fish species (see Table S2 in Annex 2). At present, sufficient information for other alien groups such as cephalopods, molluscs, polychaetes and jellyfish is not available.

In addition to ecological traits (feeding habitats and habitat type), we combined alien species into functional groups based on their arrival in the ecosystem. Crustacean species invaded the ecosystem prior to 1990 and were grouped into alien shrimps and alien crabs. Fish species invaded, and continue to invade, the ecosystem both before and after 1990. In the demersal habitat, we defined the following alien fish groups: goatfishes (*Upeneus sp.*), alien herbivores (*Siganus sp.*), alien lizardfish (*Saurida lessepsianus*), earlier alien demersal fishes (demersal fishes that invaded the ecosystem before 1990) and new alien demersal fishes (demersal fishes that invaded the ecosystem after 1990). Small, medium and large pelagic fishes invaded the ecosystem before 1990. However, due to lack of information, these groups had to be combined with native species, creating three groups: small pelagic fishes, native medium pelagic fishes and large pelagic fishes. An additional group of new alien medium pelagic fishes were created for new species that arrived post 1990.

In total, 39 functional groups were used in the ICS model for the 1990s period, including 2 primary producers, 12 groups of invertebrates, 20 groups of fishes, 1 group of sea turtles, 1 group of seabirds, 1 group of dolphins and 2 groups of detritus (natural detritus or "marine snow" and discards) (Table 1). Two alien fish groups were added to the 2010s model to account for the new arrivals (Table 1).

Input parameters for the species and functional groups were mainly obtained from published literature and unpublished information from Israel Oceanographic and Limnological Research (IOLR) and Tel-Aviv University. The data were collected from the study area or surrounding areas (see Table S1 in Annex 2 for details on parameterization of each functional group).

Biomass estimates were obtained from fishery dependent bottom trawl survey (swept-area method), visual surveys conducted in the area, and additional information from the literature. Biomass estimates for pelagic species were not available and therefore we used realistic EE values to estimate the biomass of 10 functional groups (Heymans et al., 2016). Production and consumption rates were either estimated using empirical equations (Heymans et al., 2016) accounting for changes in water temperature between both time periods, or taken from literature or from other models and corrected for temperature changes following Opitz (1996). Diet information was compiled using published and unpublished data on stomach content analyses, giving preference to local or similar areas. To date, limited information on the diet of alien species is available. In the absence of information from the Mediterranean Sea, we assumed the same diet composition for alien crustaceans (shrimps and crabs) as for the native groups. For migratory species (large pelagic fishes, sea birds, turtles and dolphins), we set a fraction of the diet composition as import based on the time that these species feed outside the system (Christensen et al., 2008, Heymans et al., 2016).

Fisheries data were obtained from a reconstruction of Israeli catches including both commercial and discards, the recreational fishery and unregulated and unreported catch (Edelist et al., 2013b). We considered three commercial fishing fleets: bottom trawl, purse seine and artisanal fisheries (including gillnets and longliners).

2.4. Pre-balancing and balancing analyses

An Ecopath model is considered ecologically and thermodynamically balanced under the following conditions: (1) estimated EE < 1 for all functional groups, (2) values of P/Q (production/consumption rate or gross efficiency of food conversion, GE) are between 0.1 and 0.35 with the exception of some fast growing groups, (3) R/A (respiration/food assimilation) < 1, (4) R/B (respiration/biomass) are between 1 and 10 for fishes and higher values for small organisms, (5) NE (net efficiency of food conversion) > GE and (6) P/R (production/respiration) < 1 (Christensen et al., 2008, Heymans et al., 2016) (Table 1 and Table S3 in Annex 2).

Initial results of the ICS models showed that the EE > 1 for 16 (1990s) and 15 (2010s) demersal groups (fish, cephalopods and crustaceans). To achieve mass-balance, we applied a manual mass-balanced procedure following a top-down approach modifying appropriate input parameters (starting from the groups with higher trophic levels) and following the best practice guidelines provided in the literature (Heymans et al., 2016).

In order to ensure that the model parameters obeyed general ecologic principles and to guide the balancing procedure we used the PREBAL analysis (Link, 2010b). This analysis highlighted that some P/B and Q/B values had to be adjusted since they were too low or too high based on their trophic levels. For additional information on the application of the PREBAL procedure see Annex 2.

Table 1. Initial (in bold) and modified input data of the Israeli Mediterranean continental shelf model for 1990-1994 (1990s) and 2008-2012 (2010s) time periods. B = final biomass (t·km^{-2}); P/B = production/biomass (year^{-1}); Q/B = consumption/biomass (year^{-1}); EE = ecotrophic efficiency; P/Q = production/consumption ratio; landings and discards (t·km^{-2}·year^{-1}). (*) indicates groups that were considered within the pelagic compartment.

	Functional group	B		P/B		Q/B		EE		P/Q		Landings		Discards	
		1990s	2010s	1990s	2010s	1990s	2010s	1990s	2010s	1990s	2010s	1990s	2010s	1990s	2010s
1	Phytoplankton*	**2.78**	**3.04**	**88.42**	**78.90**	-	-	0.24	0.23			-	-	-	-
2	Benthic primary producers	0.08	0.07	**5.50**	**5.50**	-	-	**0.50**	**0.70**			-	-	-	-
3	Micro and Mesozooplankton*	1.15	1.05	**22.82**	**23.19**	69.15	70.27	**0.95**	**0.95**	**0.33**	**0.33**	-	-	-	-
4	Macrozooplankton*	0.16	0.15	17.15	17.43	**57.17**	**58.09**	**0.95**	**0.95**	**0.30**	**0.30**	-	-	-	-
5	Gelatinous plankton*	0.07	0.06	**15.56**	**15.82**	**56.65**	**57.57**	**0.30**	**0.30**	0.27	0.27	-	-	-	-
6	Polychaetes	0.70	0.72	**5.28**	**5.37**	**22.80**	**23.17**	**0.80**	**0.80**	0.23	0.23	-	-	-	-
7	Suprabenthos	0.21	0.23	**11.84**	**11.88**	**57.12**	**57.31**	**0.80**	**0.80**	0.21	0.21	-	-	-	-
8	Native shrimps	0.12	0.08	**3.10**	**3.11**	**9.76**	**9.80**	0.95	0.95	0.32	0.32	**0.04**	**0.00**	**0.01**	**0.03**
9	Alien shrimps	0.07	0.10	**3.10**	**3.11**	**10.12**	**10.16**	0.95	0.95	0.31	0.31	**0.03**	**0.04**	-	-
10	Native crabs	0.05	0.02	**2.80**	**2.81**	**9.25**	**9.29**	0.95	0.95	0.30	0.30	**0.00**	**0.00**	-	-
11	Alien crabs	0.02	0.09	**2.80**	**2.81**	**9.55**	**9.59**	0.95	0.95	0.29	0.29	-	**0.02**	**0.01**	**0.05**
12	Benthic invertebrates	1.13	1.21	3.27	3.28	**10.90**	**10.94**	**0.80**	**0.80**	**0.30**	**0.30**	-	-	-	
13	Benthic cephalopods	0.04	0.05	**1.90**	**1.91**	**6.80**	**6.82**	0.95	0.95	0.28	0.28	**0.01**	**0.01**	-	-
14	Benthopelagic cephalopods*	0.06	0.07	**2.50**	**2.51**	**26.47**	**26.56**	0.95	0.95	0.09	0.09	**0.01**	**0.02**	-	-
15	Mullets	0.05	0.01	**1.86**	**1.87**	**8.32**	**8.37**	0.96	0.98	0.22	0.22	**0.05**	**0.01**	**0.00**	-
16	Goatfishes	0.03	0.03	**1.88**	**1.89**	**8.54**	**8.60**	0.99	0.99	0.22	0.22	**0.02**	**0.03**	**0.00**	**0.01**
17	Hake	0.05	0.01	**0.89**	**0.89**	**5.80**	**5.84**	0.99	0.97	0.15	0.15	**0.02**	**0.00**	-	
18	Flatfishes	0.02	0.02	**1.52**	**1.53**	**8.23**	**8.26**	0.98	0.96	0.18	0.18	**0.00**	**0.00**	**0.01**	**0.01**
19	Rocky fishes	0.06	0.05	**1.73**	**1.74**	**7.18**	**7.20**	0.95	0.98	0.24	0.24	**0.02**	**0.02**	-	-
20	Small native dem. fishes	0.24	0.21	**1.49**	**1.50**	**6.62**	**6.67**	0.98	0.96	0.23	0.22	**0.12**	**0.13**	**0.03**	**0.04**
21	Large native dem. fishes	0.11	0.02	**1.10**	**1.10**	**6.08**	**6.10**	0.97	0.97	0.18	0.18	**0.08**	**0.01**	**0.00**	**0.00**

22	Alien herbivores	0.01	0.02	**1.72**	**1.73**	6.90	6.92	0.95	0.95	**0.25**	**0.25**	**0.00**	**0.01**	-	-
23	Earlier alien dem. fishes	0.03	0.10	**1.58**	**1.59**	**6.79**	**6.81**	0.99	0.97	0.23	0.23	**0.00**	**0.01**	**0.01**	**0.06**
24	New alien dem. fishes	**-**	0.11	**-**	**1.49**	**-**	**6.67**	-	0.95	-	0.22	**-**	**0.03**	-	**0.04**
25	Alien lizardfish	0.07	0.03	**1.18**	**1.18**	**7.01**	**7.04**	0.93	0.93	0.17	0.17	**0.05**	**0.03**	**0.00**	-
26	Demersal fishes (upper slope)	0.01	0.01	1.01	1.01	**5.92**	**5.94**	0.96	0.93	**0.17**	**0.17**	-	-	**0.00**	**0.00**
27	Benthopelagic fishes*	0.15	0.13	2.03	2.06	**10.14**	**10.28**	**0.95**	**0.95**	**0.20**	**0.20**	**0.03**	**0.02**	**0.02**	**0.03**
28	Mesopelagic fishes*	0.06	0.05	1.74	1.75	**8.70**	**8.73**	**0.95**	**0.95**	**0.20**	**0.20**	-	-	-	-
29	Demersal sharks	0.02	0.04	**0.70**	**0.70**	4.67	4.68	0.64	0.70	0.15	0.15	**0.01**	**0.02**	**0.00**	**0.00**
30	Rays and skates	0.03	0.05	**0.94**	**0.94**	**5.70**	**5.72**	0.87	0.89	0.16	0.16	**0.01**	**0.03**	**0.01**	**0.00**
31	Small pelagic fishes*	0.70	0.58	2.40	2.45	**11.98**	**12.27**	**0.95**	**0.95**	**0.20**	**0.20**	**0.12**	**0.04**	**0.00**	**0.01**
32	Horse mackerel*	0.13	0.09	1.44	1.46	**8.02**	**8.13**	**0.95**	**0.95**	**0.18**	**0.18**	**0.06**	**0.04**	**0.00**	**0.01**
33	Mackerel*	0.07	0.08	1.42	1.44	**7.88**	**7.99**	**0.95**	**0.95**	**0.18**	**0.18**	**0.02**	**0.02**	-	-
34	Native medium pelagic fishes*	0.10	0.07	0.85	0.86	**7.07**	**7.09**	**0.90**	**0.90**	**0.12**	**0.12**	**0.04**	**0.04**	-	-
35	Alien medium pelagic fishes*	**-**	0.02	-	0.85	**-**	**7.11**	-	**0.90**	**-**	**0.12**	**-**	**0.01**	-	**0.00**
36	Large pelagic fishes*	**0.06**	**0.06**	**0.90**	**0.90**	**5.35**	**5.38**	0.98	0.99	0.17	0.17	**0.05**	**0.06**	-	-
37	Turtles	0.06	0.06	**0.17**	**0.17**	**2.78**	**2.83**	**0.50**	**0.50**	0.06	0.06	-	-	**0.00**	**0.00**
38	Sea birds	**0.00**	**0.00**	**5.10**	**5.10**	**75.23**	**75.23**	0.01	0.01	0.07	0.07	-	-	**0.00**	**0.00**
39	Dolphins*	**0.01**	**0.01**	**0.09**	**0.09**	**10.95**	**10.95**	0.48	0.48	0.01	0.01	-	-	**0.00**	**0.00**
40	Detritus	**17.81**	**17.95**	-	-	-	-	0.23	0.24	-	-	-	-	-	-
41	Discards	**0.17**	**0.29**	-	-	-	-	0.97	0.49	-	-	-	-	-	-

After testing the model parameters with PREBAL, biomass and diets were readjusted where needed, as in other Ecopath models developed in the Mediterranean Sea (Coll et al., 2006, Tsagarakis et al., 2010, Corrales et al., 2015). We estimated biomass by calculating the average and maximum value for each species and year from the bottom surveys. In the absence of catchability coefficients to correct biomass estimates, maximum values were used to ensure mass-balance. We also adjusted the biomass inputs taking into account the fishing mortality patterns in other Mediterranean areas (demersal fish groups) and using a reasonable value of EE (EE values close but lower than 1) (Heymans et al., 2016), leaving the model to calculate the biomass for some groups (e.g. for crustacean and cephalopods groups). Finally, the diet matrix was slightly adjusted to take into account the abundances of species in the ecosystem (see Table S4 and S5 in Annex 2).

2.5. Pedigree index and quality of the model

The pedigree routine (Christensen and Walters, 2004a) was used to quantify the uncertainty associated with the input parameters and the quality of the models and to validate choices made in balancing the model. For each input datum, we assigned pedigree values to record the degree of confidence associated with the data. With the information for each functional group, the pedigree index was calculated for the overall model. The pedigree index ranges between 0 (low quality) and 1 (high quality), allowing a description of the quality of the model that can be compared to other models. The confidence intervals for the pedigree analysis and index values used are described in Table S6 in Annex 2.

To evaluate the quality of the model we also compared some model outputs to the results of independent data. The trophic levels (TL) estimated for the 2010s Ecopath model were compared to the δ^{15}N values (‰) estimated by Stable Isotope Analysis (SIA) conducted on the Lebanese coast during 2011-2012 (Fanelli et al., 2015). For those functional groups from the model with several δ^{15}N values, the values were weighted using biomass proportions of these species in each functional group. TLs estimated by the Ecopath model were plotted against the δ^{15}N values and the correlation was tested using the Spearman-rank non-parametric correlation coefficient test (Zar, 1984).

2.6. Model analyses and ecological indicators

In order to assess the changes between the two models and the possible role and impact of alien species and fisheries a number of key food web indicators were analyzed and compared between time periods. In addition, we compared our results with those of the south Catalan Sea (Coll et al., 2006), the northern and central Adriatic Sea (Coll et al., 2007) and the north Aegean Sea (Tsagarakis et al., 2010).

Although the topology (number of functional groups, distribution of the species, area modeled and depth range included) of the model affects many food web indicators (Heymans et al., 2014, Heymans et al., 2016), we assumed that the comparison was possible as both ICS models (1990s and 2010s) represent the same ecosystem with the same model structure with the exception of two new functional groups that invaded the ecosystem during the time (comparison between ICS models). Comparison with other Mediterranean models included only robust indicators following previous studies (Heymans et al., 2014, Corrales et al., 2015). The ICS models were developed following similar criteria to other Mediterranean models (number of functional groups, distribution of the species and parameterization) and included similar depth ranges.

a) Ecosystem structural and functioning traits

To represent the biomasses, trophic flows and trophic levels (TL), we used a flow diagram and a Lindeman spine representation (Lindeman, 1942). In the Lindeman spine, the flows and biomasses are aggregated for each discrete trophic level and the detritus box is separated from the primary producers to show the amount of energy that flows through it.

The Ecopath model outputs a variety of indicators related to the development and maturity of ecosystems according to Odum (1969). In this study, the following indicators were included: (1) Total system throughput (TST, $t\cdot km^{-2}\cdot year^{-1}$), estimated as the total flows in the ecosystem (sum of all consumption exports, respiration and flow to detritus; (2) total biomass (TB, $t\cdot km^{-2}$); (3) total primary production/total respiration (Pp/R); (4) total primary production/ total biomass (Pp/B, $t\cdot km^{-2}\cdot year^{-1}$); (5) system omnivory index (SOI), (6) Finn's cycling index (FCI, %) and (7) Finn's mean path length (PL) (Odum, 1969, Finn, 1976, Christensen, 1995, Christensen et al., 2008, Heymans et al., 2014). We also included the transfer efficiency (TE), the fraction of total flows of each discrete trophic level that are either exported out of the ecosystem (e.g., by the fishing activity) or transferred to higher trophic levels through consumption. TE summarizes the inefficiency or energy dissipation between discrete trophic levels that is produced along the food web due to respiration, excretion, egestion, natural mortality and exports. The mean trophic level of the community (mTLco), calculated by weighting the TL of each functional group by its biomass was also used to compare the models.

b) Ecological roles of functional groups

Trophic level (TL) was used to analyze the ecological position of the functional groups of the ICS model (Lindeman, 1942, Stergiou and Karpouzi, 2001).

The Mixed Trophic Impact (MTI) analysis was used to quantify the direct and indirect impact in the food web that a hypothetical increase in the biomass of one functional group would have on the biomasses of all the other functional groups in the food web, including the fishing fleets (Ulanowicz and Puccia, 1990, Christensen et al., 2008).

The keystoneness index developed by Valls et al. (2015) was used to identify the keystone species. A keystone species is defined as a predator species with a high and wide impact on the food web despite its low biomass (Paine, 1966, Paine, 1969, Valls et al., 2015). The index is calculated as:

$$\mathrm{KS} = \mathrm{IC} \text{ x } \mathrm{BC} \qquad \text{(Eq. 3)}$$

where IC is the impact component and BC is the biomass component. The IC represents the overall effect of group (i) on all other groups in the food web excluding the impact on (i) itself and the impacts on dead groups and fleets (Libralato et al., 2006). The BC is defined as the rank of the group according to their biomass values in descending order (Valls et al., 2015).

c) Impacts and role of alien species

To evaluate the impact of alien species on the ecosystem, the changes in the contribution of alien species to the biomass and catch, and changes to flows related to alien species between the two time periods were calculated. For the changes to flows related to alien species, the consumption by alien groups on their prey and the predation on alien groups by their predators for both time periods were estimated.

d) Impacts of fishing on the food web

The impacts of fishing on the food web were assessed using the mean trophic level of the catch (mTLc) (Christensen, 1996) and the primary production required to sustain the fisheries (% PPR) (Pauly and Christensen, 1995), taking into account both primary and detritus production. The MTI analysis was also used to quantify the direct and indirect impact of each fleet on the functional groups and the exploitation rate (fishing mortality/total mortality, F/Z) was calculated for the functional groups that were exploited.

3. Results

3.1. Ecosystem structural and functioning traits

The overall trophic flows among functional groups and TLs show that in the 1990s most of the flows to detritus (93.3%), consumption (69%) and production (95.8%) were related to the pelagic compartment (Table 1 and 2) due to the contribution of planktonic groups. Similar contributions (92.8%, 66.1% and 95.4%, respectively) were found in the 2010 model. The flow diagram indicates an important bento-pelagic coupling (Fig. 2), with 23.4% (1990s) and 27% (2010s) of flows from the pelagic compartment transferred to the demersal habitat through consumption when predation of planktonic groups on their prey were excluded (results not shown). Results also emphasized the important role of small pelagic fishes (functional group or F.G. 31) in linking TL II from the pelagic compartment with higher trophic levels from the pelagic and demersal habitat. Of this group’s biomass, 74.6% and 83.5% was transferred to the pelagic higher trophic levels and 25.4% and 16.5% to the demersal higher trophic levels in 1990s and 2010s, respectively (results not shown).

Most of the energy flows were between TL I, II and III (Fig. 3a and b). Exports, primarily represented by catches, were mainly focused on TL III and IV. An important link between detritus and TL II was found, as flows from the detritus and from the primary producers to TL II were similar in both time periods. The Transfer Efficiencies

(TE), decreased with the increasing TL (Fig. 3). The mean TE was 18.9% and 19% for the two time periods, respectively (Table 3).

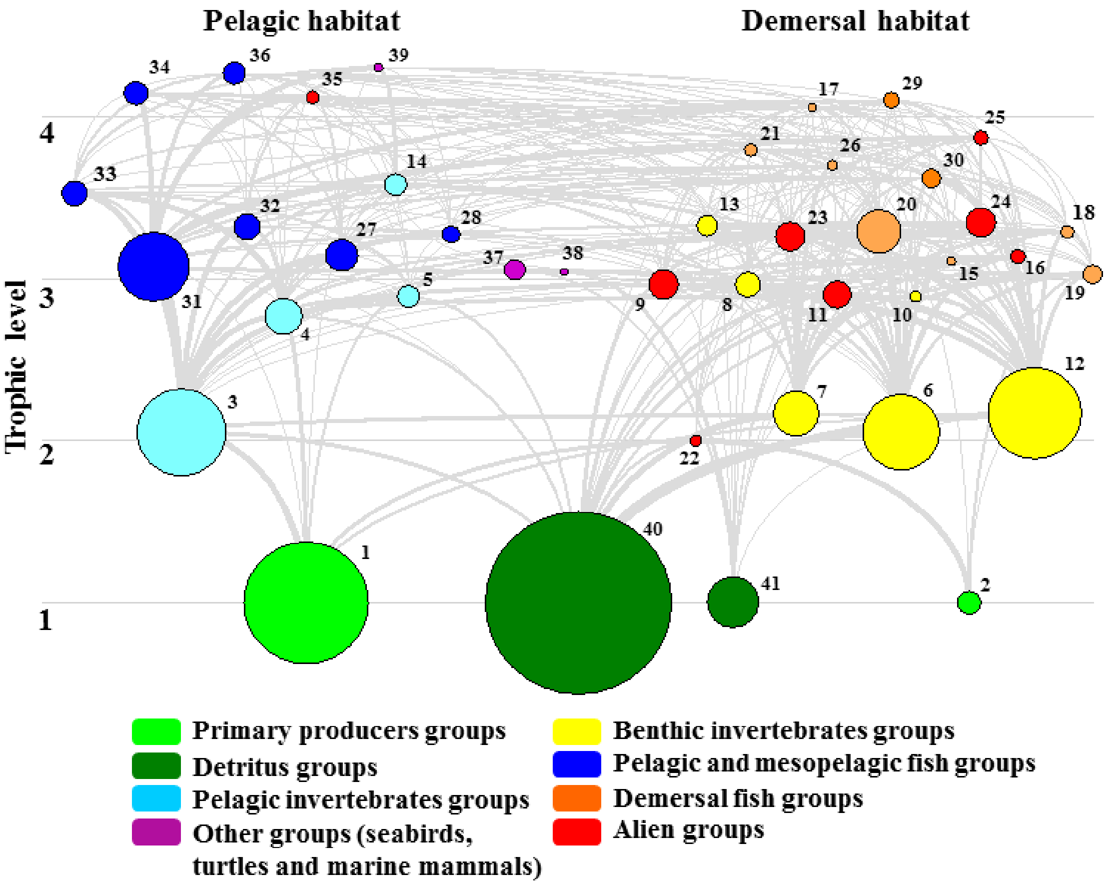


Fig. 2. Flow diagram of the Israeli Mediterranean continental shelf model representing the 2008-2012 period. The size of each circle is proportional to the biomass of the functional group. The numbers identify the functional groups of the model (listed in Table 1). The thickness of the connecting lines is proportional to the magnitude of their trophic flows.

Analyses of flows in terms of the Lindeman spine for both time periods indicated similar patterns when studying the overall food web (Fig. 3a and b). However, results from different habitats (pelagic *versus* demersal), highlight a change in the food web over time (Fig. 4): biomass, production and consumption of pelagic groups located in TL III decreased between the two time periods while values for TL IV remained constant. In contrast, the biomass, production and consumption of demersal groups located in TL III increased between the two time periods while values at TL IV decreased (Fig. 4).

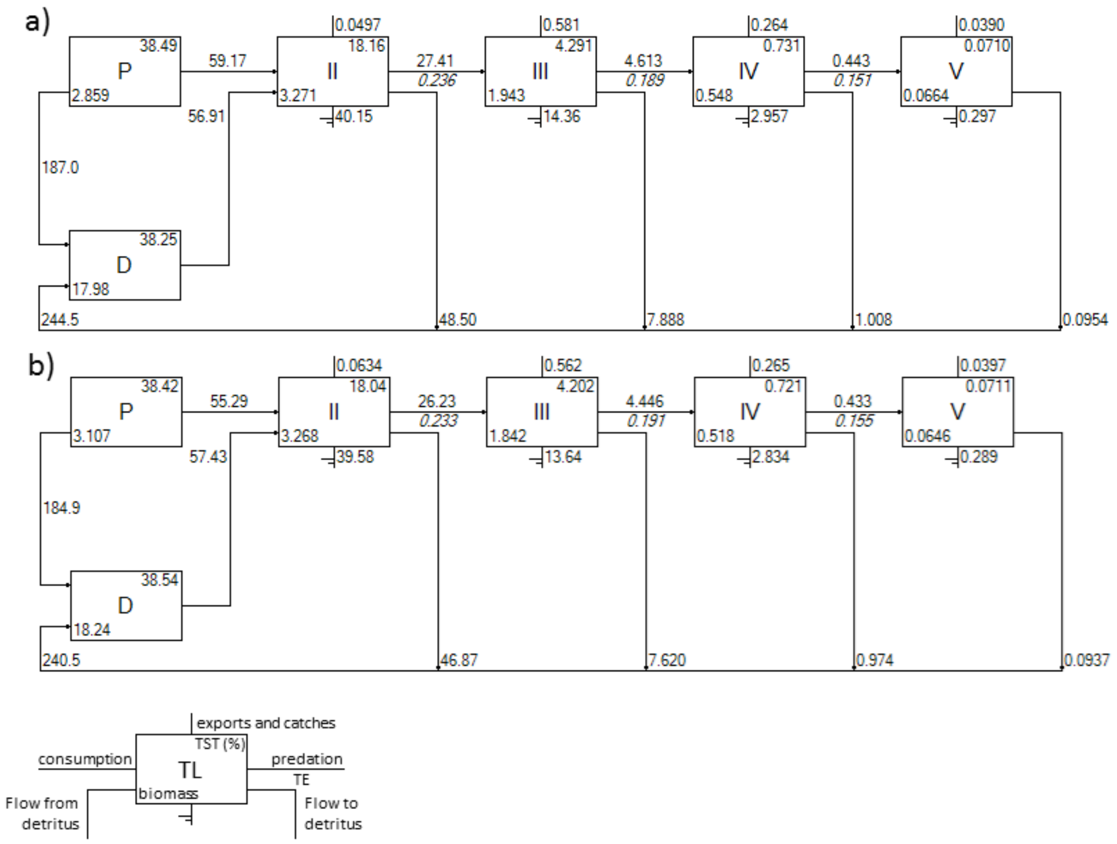


Fig. 3. Lindeman spine representation of the Israeli Mediterranean continental shelf ecosystem for the 1990-1994 (a) and the 2008-2012 (b) time periods. Trophic level (TL) I is split into primary producers (P) and detritus (D). Flows are represented in t·km^{-2}·year^{-1} and biomass in t·km^{-2}.

3.2. Ecological roles of functional groups

In the 1990s, functional groups ranged from TL = 1 for primary producers (F.G. 1 and 2) and detritus (F.G. 40-41) to TL = 4.33 for dolphins (F.G. 39) (Table 2). The highest TLs (>4) corresponded to dolphins (F.G. 39), hake (F.G. 17), demersal sharks (F.G. 29), native and alien medium pelagic fishes (F.G. 34 and 35) and large pelagic fishes (F.G. 36). Invertebrates were classified with a TL between 2.05 and 2.97, with cephalopods (F.G. 13 and 14) showing higher TLs. Fish had TLs between 3.02 and 4.25, with the exception of the alien herbivores (F.G. 22), which had a lower TL (TL = 2). Similar TLs were found for the 2010s model. TLs estimated from the 2010s model were highly and positively correlated with the δ^{15}N values from Lebanon (Fig. 5, Spearman-rank correlation coefficient, $R_s = 0.90$, $n = 12$, $p < 0.0001$). These results showed that an increase of δ^{15}N values calculated from SIA coincided with an increase of TLs estimated by the Ecopath model.

Table 2. Output estimates of the Israeli Mediterranean continental shelf model for 1990-1994 (1990s) and 2008-2012 (2010s) time periods. TL = Trophic Level; F = fishing mortality (year^{-1}); M2= predation mortality (year^{-1}); M0 = other natural mortality (year^{-1}); F/Z = exploitation rate (fishing mortality (F) / total mortality (Z)); FD = flow to detritus (t·km^{-2}·year^{-1}).

	Functional groups	TL		F		M2		MO		F/Z		FD	
		1990s	2010s	1990s	2010s	1990s	2010s	1990s	2010s	1990s	2010s	1990s	2010s
1	Phytoplankton	1.00	1.00	-	-	21.21	18.10	67.21	60.79	0.00	0.00	186.77	184.78
2	Benthic primary producers	1.00	1.00	-	-	2.75	3.85	2.75	1.65	0.00	0.00	0.22	0.11
3	Micro and Mesozooplankton	2.05	2.05	-	-	21.68	22.03	1.14	1.16	0.00	0.00	33.06	30.72
4	Macrozooplankton	2.77	2.77	-	-	16.29	16.56	0.86	0.87	0.00	0.00	3.74	3.66
5	Gelatinous plankton	2.89	2.89	-	-	4.67	4.75	10.89	11.07	0.00	0.00	1.53	1.46
6	Polychaetes	2.05	2.05	-	-	4.23	4.30	1.06	1.07	0.00	0.00	7.10	7.41
7	Suprabenthos	2.16	2.16	-	-	9.47	9.50	2.37	2.38	0.00	0.00	4.13	4.41
8	Native shrimps	2.97	2.97	0.43	0.44	2.52	2.51	0.16	0.16	0.14	0.14	0.25	0.17
9	Alien shrimps	2.96	2.96	0.39	0.41	2.55	2.55	0.16	0.16	0.13	0.13	0.14	0.23
10	Native crabs	2.89	2.89	0.01	0.01	2.65	2.66	0.14	0.14	0.00	0.00	0.09	0.04
11	Alien crabs	2.89	2.90	0.56	0.72	2.10	1.95	0.14	0.14	0.20	0.26	0.05	0.19
12	Benthic invertebrates	2.15	2.16	-	-	2.62	2.62	0.65	0.66	0.00	0.00	3.20	3.44
13	Benthic cephalopods	3.29	3.33	0.12	0.15	1.69	1.66	0.09	0.10	0.06	0.08	0.04	0.05
14	Benthopelagic cephalopods	3.57	3.58	0.23	0.31	2.14	2.07	0.13	0.13	0.09	0.12	0.35	0.36
15	Mullets	3.10	3.11	1.02	0.89	0.76	0.95	0.08	0.03	0.55	0.48	0.09	0.01
16	Goatfishes	3.11	3.14	1.01	0.98	0.86	0.88	0.02	0.02	0.54	0.52	0.05	0.05
17	Hake	4.05	4.06	0.47	0.26	0.42	0.61	0.00	0.02	0.53	0.29	0.05	0.01
18	Flatfishes	3.28	3.29	0.69	0.65	0.79	0.81	0.04	0.06	0.45	0.43	0.03	0.04
19	Rocky fishes	3.02	3.03	0.26	0.41	1.38	1.28	0.08	0.04	0.15	0.23	0.09	0.08
20	Small native dem. fishes	3.25	3.29	0.66	0.78	0.80	0.65	0.03	0.07	0.44	0.52	0.32	0.30
21	Large native dem. fishes	3.70	3.80	0.80	0.78	0.27	0.29	0.04	0.04	0.72	0.71	0.13	0.03

22	Alien herbivores	2.00	2.00	0.24	0.36	1.40	1.28	0.09	0.09	0.14	0.21	0.01	0.03
23	Earlier alien dem. fishes	3.25	3.26	0.58	0.61	0.99	0.93	0.01	0.05	0.37	0.38	0.04	0.15
24	New alien dem. fishes	-	3.35	-	0.64	-	0.77	-	0.08	-	0.43	-	0.15
25	Alien lizardfish	3.78	3.87	0.78	0.78	0.32	0.31	0.09	0.08	0.66	0.66	0.10	0.05
26	Demersal fishes (upper slope)	3.70	3.70	0.11	0.09	0.86	0.84	0.04	0.08	0.11	0.09	0.01	0.02
27	Benthopelagic fishes	3.14	3.14	0.31	0.43	1.62	1.52	0.10	0.10	0.15	0.21	0.32	0.28
28	Mesopelagic fishes	3.27	3.27	0.00	-	1.65	1.66	0.09	0.09	0.00	0.00	0.11	0.08
29	Demersal sharks	4.04	4.10	0.36	0.46	0.08	0.03	0.25	0.21	0.52	0.66	0.02	0.04
30	Rays and skates	3.59	3.62	0.70	0.74	0.12	0.09	0.12	0.11	0.75	0.79	0.03	0.06
31	Small pelagic fishes	3.07	3.07	0.18	0.08	2.09	2.25	0.12	0.12	0.08	0.03	1.76	1.49
32	Horse mackerel	3.30	3.32	0.48	0.46	0.89	0.93	0.07	0.07	0.33	0.31	0.22	0.15
33	Mackerel	3.53	3.53	0.26	0.31	1.09	1.06	0.07	0.07	0.18	0.22	0.12	0.13
34	Native medium pelagic fishes	4.13	4.15	0.41	0.58	0.35	0.20	0.09	0.09	0.49	0.67	0.15	0.11
35	Alien medium pelagic fishes	-	4.12	-	0.46	-	0.31	-	0.09	-	0.54	-	0.04
36	Large pelagic fishes	4.25	4.26	0.83	0.86	0.05	0.04	0.01	0.00	0.92	0.95	0.07	0.07
37	Turtles	3.05	3.05	0.08	0.09	0.00	0.00	0.08	0.09	0.50	0.50	0.04	0.04
38	Sea birds	3.04	3.05	0.04	0.04	0.00	0.00	5.06	5.06	0.01	0.01	0.02	0.02
39	Dolphins	4.33	4.30	0.04	0.04	0.00	0.00	0.05	0.05	0.48	0.48	0.02	0.02
40	Detritus	1.00	1.00	-	-	-	-	-	-	-	-	0.00	0.00
41	Discards	1.00	1.00	-	-	-	-	-	-	-	-	0.00	0.15

Table 3. Characteristics, statistics and ecological indicators for the Israeli Mediterranean continental shelf model (ICS) in the two time periods.

Indicators	1990-1994	2008-2012	Units
Number of functional groups	39	41	
Number of primary producers	2	2	
Number of alive functional groups	37	39	
Total system throughput (TST)	646.36	631.89	$t \cdot km^{-2} \cdot year^{-1}$
Total primary production/Total respiration (Pp/R)	4.26	4.26	
Total primary production/Total biomass (Pp/B)	28.32	27.28	
System omnivory index (SOI)	0.19	0.19	
Finn's cycling index (of total throughput) (FCI)	5.72	5.78	% of TST
Finn's mean path length (PL)	2.62	2.63	
Total biomass (excluding detritus) (TB)	8.69	8.80	$t \cdot km^{-2}$
Mean trophic level of the community (mTLco)	1.35	1.34	
mTLco (excluding TL=1)	2.62	2.60	
Total catches (TC)	0.94	0.93	$t \cdot km^{-2} \cdot year^{-1}$
Total landings	0.80	0.64	$t \cdot km^{-2} \cdot year^{-1}$
Total discards	0.14	0.29	$t \cdot km^{-2} \cdot year^{-1}$
Mean trophic level of the catch (mTLc)	3.38	3.37	
Primary production required to sustain the fisheries (PPR, considering PP + detritus)	10.36	11.34	%
Mean transfer efficiency (TE)	18.90	19.00	%
Ecopath pedigree index	0.54	0.54	

The MTI analysis showed that most of the groups had a negative impact on themselves as a result of competition for the resources within the group and had a direct negative impact on their main prey through predation (Fig. 6a and 6b). Results highlighted some indirect effects between groups through competition for resources. For example, between benthic invertebrates (F.G. 12) and alien herbivores (F.G. 22), and between small native demersal fishes (F.G. 20), earlier alien demersal fishes (F.G. 23) and new alien demersal fishes (F.G. 24). An important impact of small pelagic fishes (F.G. 31) and small native demersal fishes (F.G. 20) on higher and lower trophic levels was also observed. A comparison between time periods highlighted the increasing impact of demersal sharks (F.G. 29), rays and skates (F.G. 30) and alien groups: earlier alien dem. fishes (F.G. 23), new alien dem. fishes (F.G. 24) and alien medium pelagic fishes (F.G. 35). By contrast there was a decreasing impact of mullets (F.G. 15), hake (F.G. 17), large native demersal fishes (F.G. 21), alien lizardfish (F.G. 25) and native medium pelagic fishes (F.G. 34) due to changes in biomass composition.

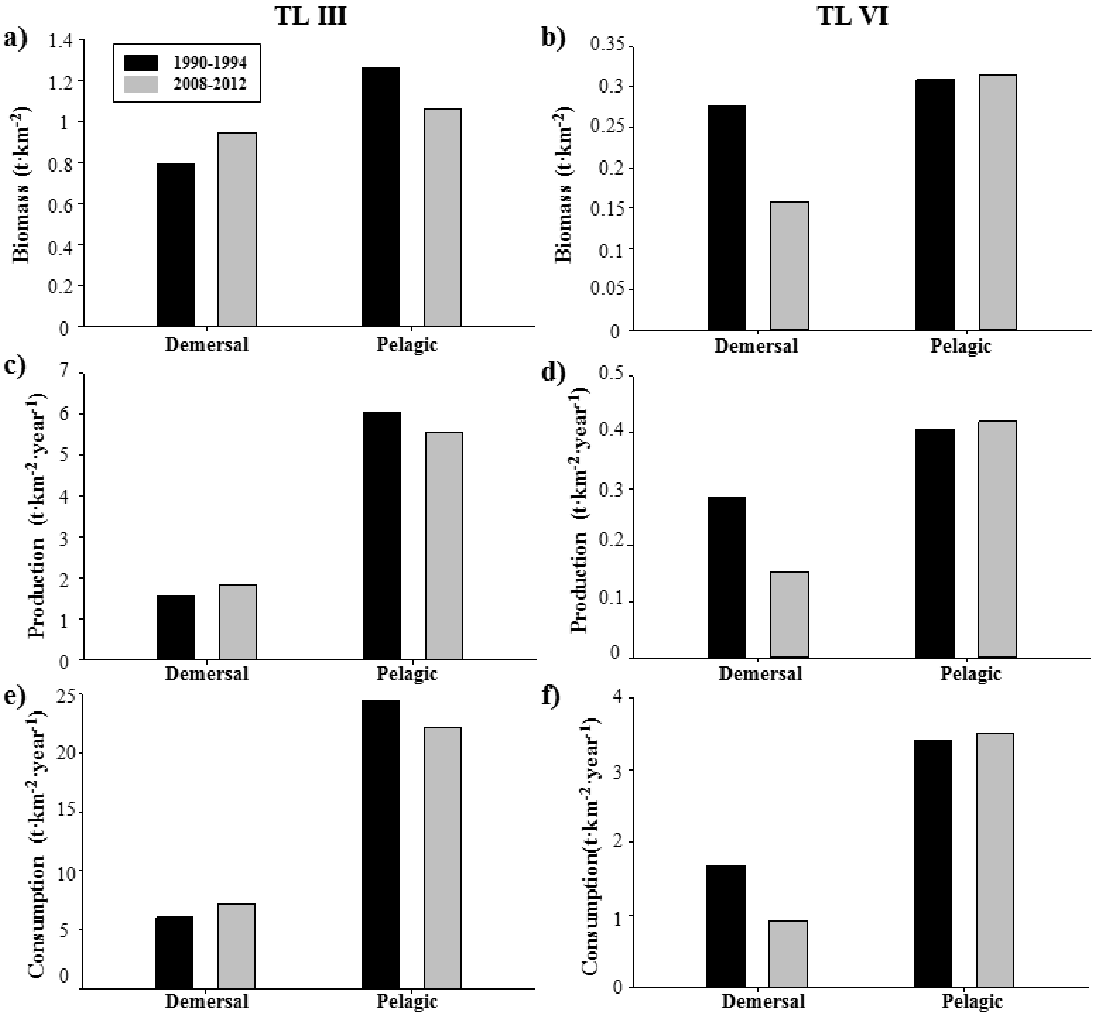


Fig. 4. Biomass (t·km^{-2}), production (t·km^{-2}·year^{-1}) and consumption (t·km^{-2}·year^{-1}) by discrete trophic levels (TL) and habitat in both time periods. Left hand panels are TL III and right panels are TL IV. Top row is biomass (a and b), middle row is production (c and d) and bottom row is consumption (e and f).

Native medium pelagic fishes (F.G. 34), dolphins (F.G. 39), demersal sharks (F.G. 29), large pelagic fishes (F.G 36), alien lizardfish (F.G. 25) and squids (F.G. 14) may have been potential keystone species in the ICS in both time periods (Fig. 7a and 7b). Hake (F.G. 17) was identified as a potential keystone species during the 1990s but not in the 2010s. This result indicates that the keystone role of hake in the ICS ecosystem disappeared in the latter period.

3.3. Impacts and role of alien species

The contribution of alien groups to the total biomass increased from 9.5% in 1990s to 23.3% in 2010s (Fig. 8a). For crustaceans (shrimps and crabs) and demersal fishes the alien species increased from 35.1% and 20.2% to 66.3% and 47.5%, respectively (Fig.

8a). For example, alien shrimps (F.G. 9) and earlier alien demersal fishes (F.G. 23) increased their biomass by 55.5% and 256.6%, respectively (Table 1). A remarkable result is the large biomass of new alien demersal fishes (F.G. 24) achieved within a decade of the invasion of the first species of this group, with a rate of increase of 0.01 t·km^{-2}·year^{-1}. The biomass of alien pelagic fish species increased from 0% to 2.6% between the 1990s and 2010s (Fig. 8a).

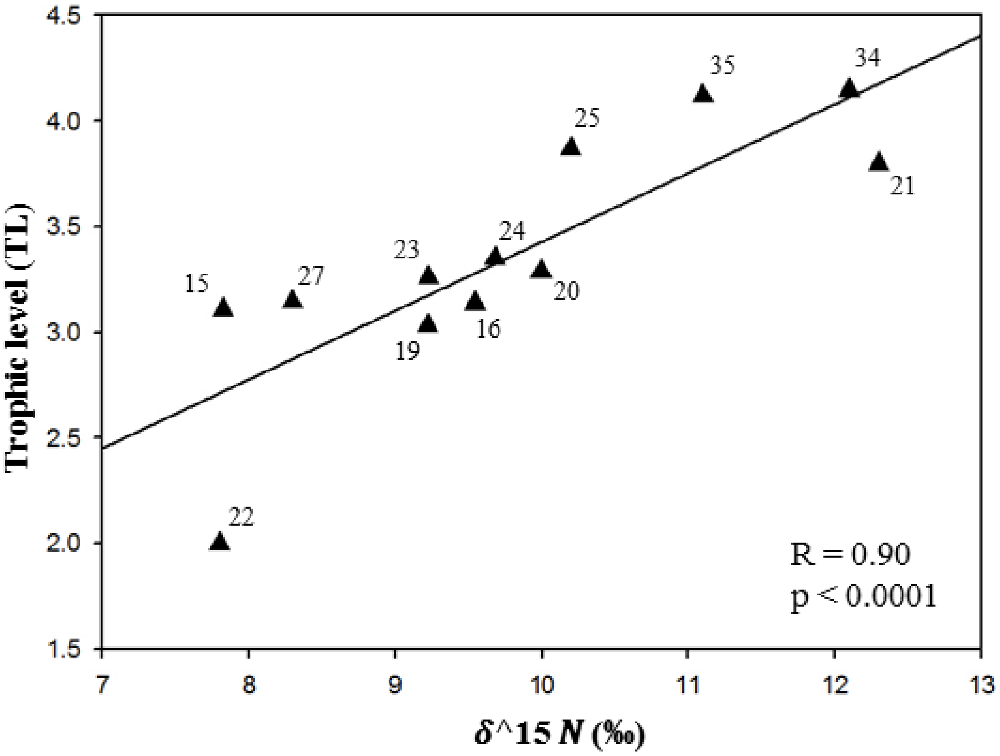
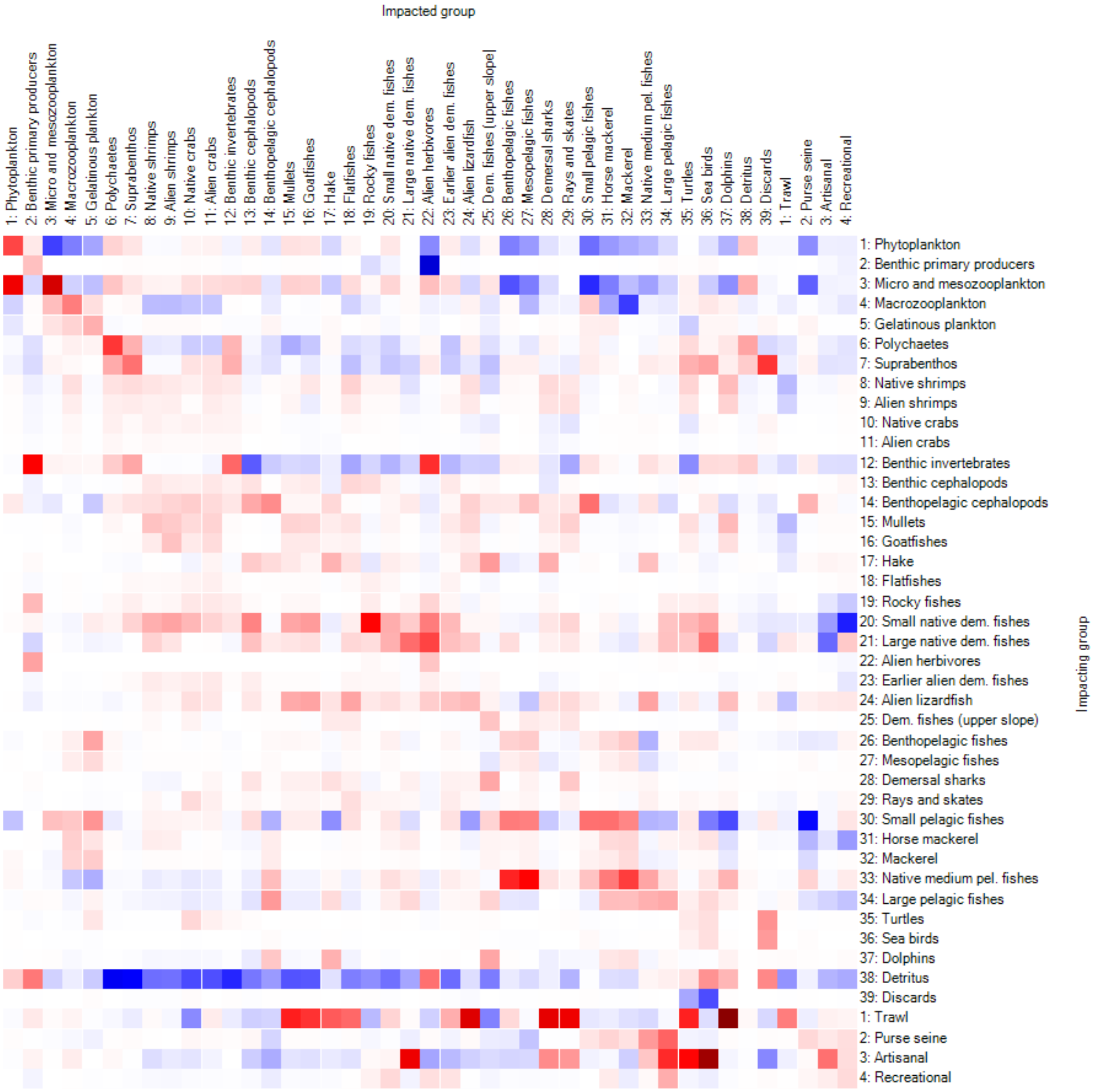


Fig. 5. Correlation between trophic level (TL) calculated with the 2008-2012 Ecopath model (2008-2012 period) and the δ^{15}N values calculated from stable isotope analysis conducted along the Lebanese coast (Fanelli et al., 2015). The numbers in the figure identify the functional groups of the model (listed in Table 1).

The analysis of the catch showed similar patterns to those observed in the biomass. The contribution of alien groups to the total catch increased from 14.9% in 1990s to 34.1% in 2010s (Figure 8b). This increase was from 43.1%, 22.2% and 0% to 75.4%, 46.1% and 4.9% for crustaceans, demersal fishes and pelagic fishes, respectively (Figure 8b). The catch of alien crabs (F.G. 11) and alien herbivores (F.G. 22) increased 399.1% and 224.3%, respectively (Table 1). The analysis of the percent contribution of alien species to the catch for each fleet showed that the largest increases corresponded to the trawl and the recreational fleet, with increases from 30.1% and 6.2% to 48% and 18.2% from 1990s to 2010s, respectively (Figure 8c).

a)



b)

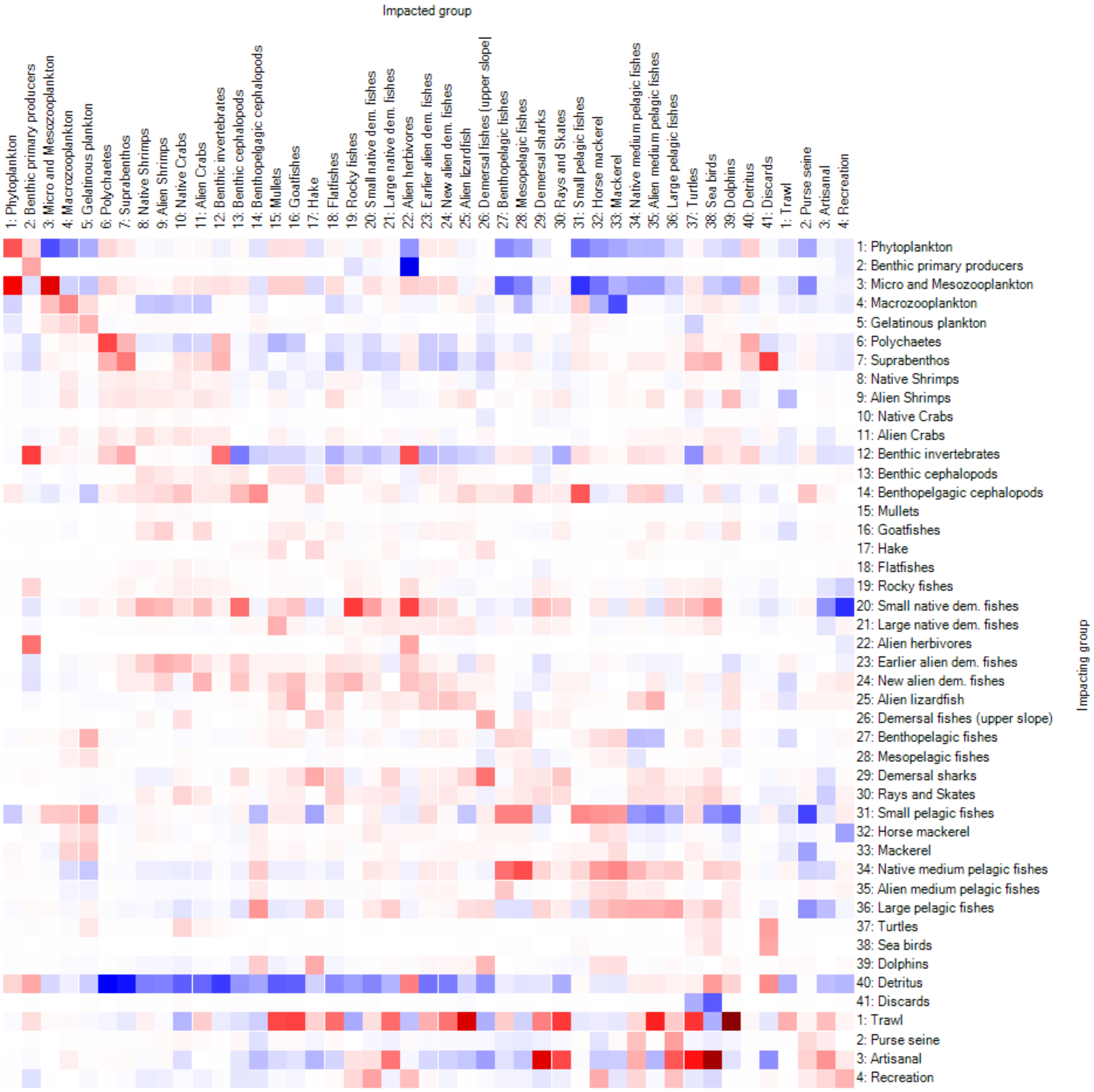


Fig. 6. Mixed Trophic Impact (MTI) analysis of the Israeli Mediterranean continental shelf ecosystem for 1990-1994 (a) and 2008-2012 (b) time periods. Negative (red) and positive (blue) impacts are represented.

The analysis of predation and consumption (Fig. 9a and 9b), as well as the MTI analysis, showed the increasing importance of alien groups between the two time periods. Results highlight that the predation by alien species on their prey increased slightly more than their consumption by their predators (Fig. 9a and 9b). For example, the grazing of alien herbivores (F.G. 22) on primary producers increased 109.8% while the predation on alien herbivores by their predators increased 90.6%.

The keystoneness index analysis showed that alien lizardfish (F.G. 25) was identified as a potential keystone species in both time periods (Fig. 7a and 7b). It also showed the possibility of alien medium pelagic fish (F.G. 35) to become a keystone group in the future, as this group had a high keystoneness index despite its recent invasion (Fig. 7b).

3.4. Impacts of fishing on the food web

Total catch in 1990s was 0.94 $t \cdot km^{-2} \cdot year^{-1}$, and did not differ considerably between both time periods, suggesting stable catch production (Table 3). Exploitation rates (F/Z) (Table 2) were high for many of the exploited demersal groups, including, mullets (F.G. 15), goatfishes (F.G. 16), large native demersal fishes (F.G. 21), alien lizardfish (F.G. 25), demersal sharks (F.G. 29), rays and skates (F.G. 30); and medium (F.G. 34 and 35) and large pelagic fishes groups (F.G. 36) (Table 2).

The percentage of primary production required to sustain the fisheries (%PPR) was 10.36% and 11.34% for the 1990s and 2010 time periods, respectively (Table 3).

The MTI analysis applied to the fishing fleets showed that the four fleets included in the ICS models had negative impacts on themselves and to a lesser extent on the other fleets, indicating direct and indirect competition for marine resources (Fig. 6a and 6b). Most fleets had expected impacts on target species. The trawl fleet had the highest impact on many demersal and pelagic groups and also had a high impact on turtles (F.G. 37) via direct mortality, and on dolphins (F.G. 39) via direct mortality and competition for resources. The artisanal fleet had a high impact on turtles (F.G. 37) and seabirds (F.G. 38) via direct mortality.

4. Discussion

These are the first published food web models of the Israeli Mediterranean continental shelf (ICS) ecosystem. After parameterization, data quality analysis and balancing the model, results showed the important role of alien fish, shrimps and crabs on the southeastern Mediterranean Sea and their increased impact from the 1990s to 2010s. Fishing also had notable impacts on the ecosystem, already in the 1990s as well as in the 2010s.

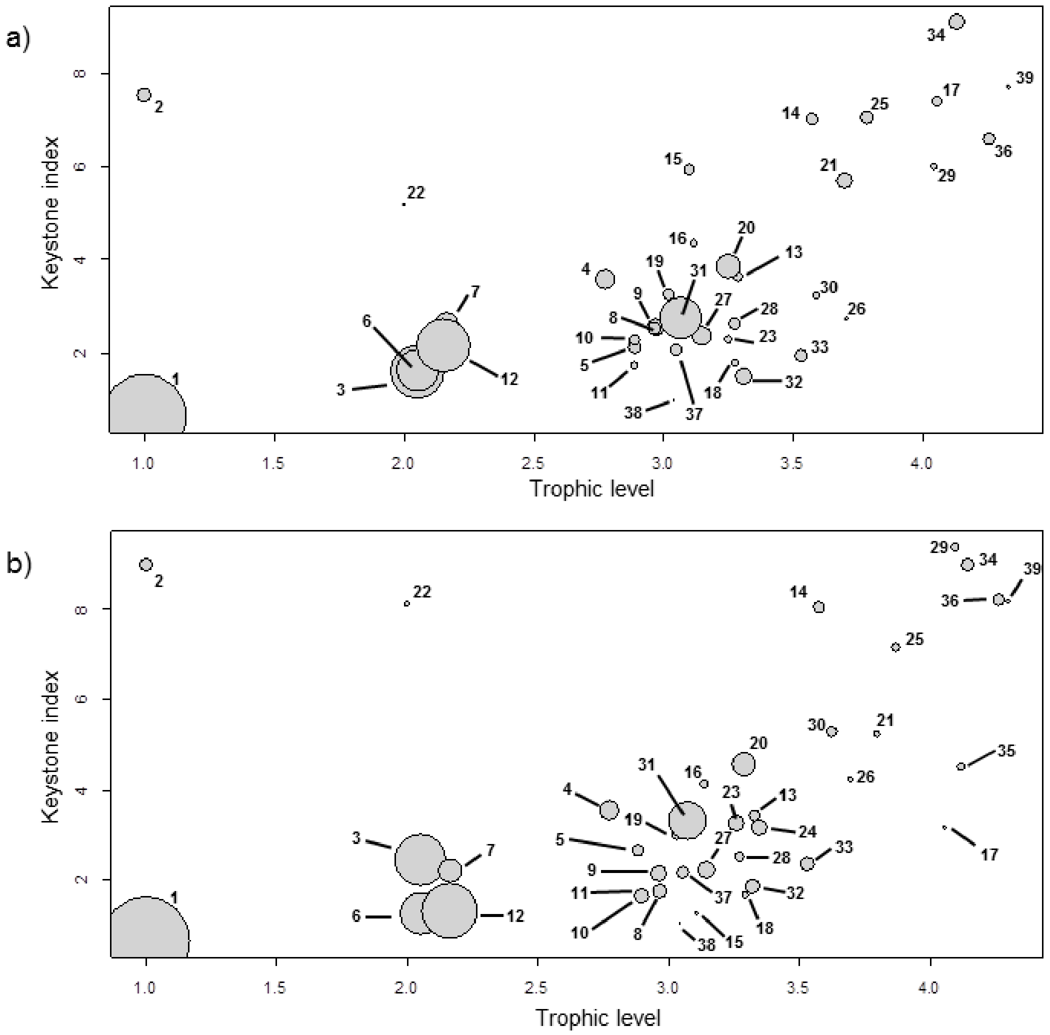


Fig. 7. Functional groups plotted against keystone index and trophic level for 1990-1994 (a) and 2008-2012 (b) time periods. The numbers identify the functional groups of the model (listed in Table 1). The size of each circle is proportional to the biomass of the functional group.

This study represents an important step forward in evaluating the past and current impacts of alien species and fishing activities in the ICS. One of the main advantages of undertaking such a study is the identification of information gaps. The pedigree index obtained for both ICS models (1990s and 2010s) indicated an acceptable quality of the models (Morissette, 2007, Lassalle et al., 2014) although they are among the lowest values in the Mediterranean Sea (Corrales et al., 2015). There are many information gaps, specifically in the pelagic habitat and benthic invertebrates groups. Population assessments of small and medium pelagic fishes and plankton sampling in the study area would greatly improve the parameter estimates of these groups. A fisheries independent annual trawl survey would improve the available data and increase the understanding and quantification of changes in the Levantine Sea. Detailed stomach content analyses are needed for alien species to complement available information and our understanding of the impact of alien species in this area.

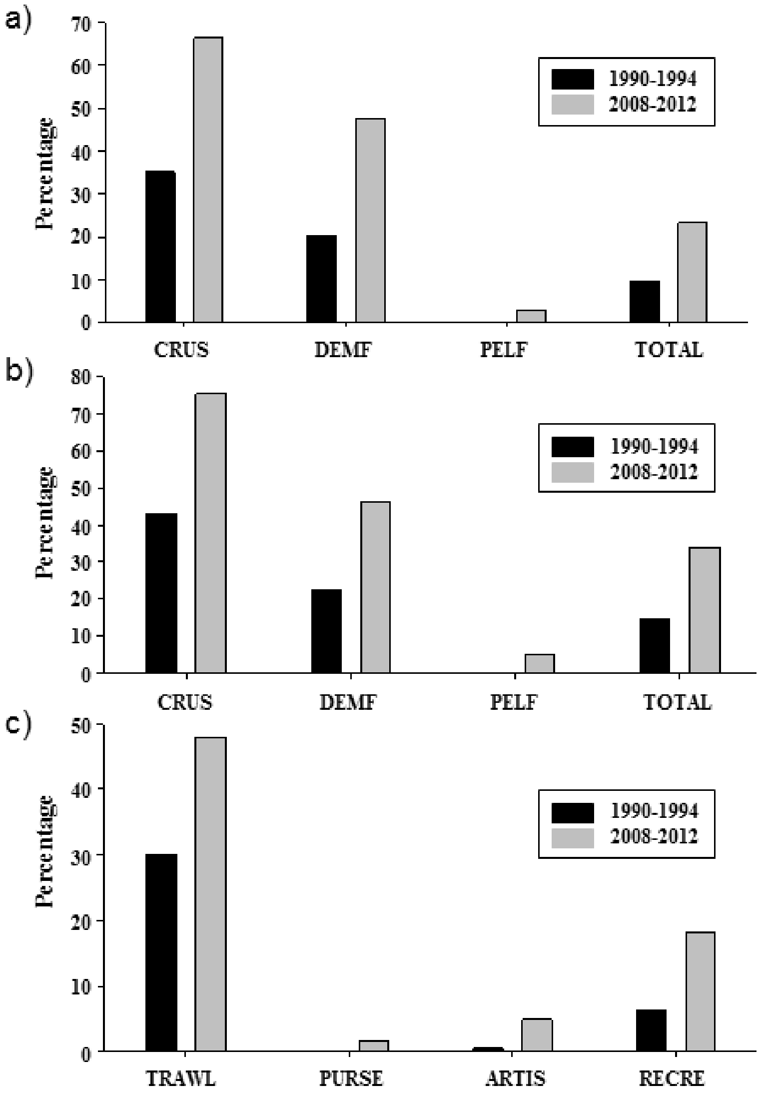


Fig. 8. Contribution (%) of alien species to the total biomass (a), to the catch of different groups (b) and to the total catch of the various fleets (c). Total biomass includes all the groups with sufficient information to split between native and alien species (fish, cephalopods and crustaceans (shrimps and crabs)). Planktonic groups, suprabenthos, polychaetes and benthic invertebrates are excluded for the analysis. CRUS = Crustaceans (shrimps and crabs); DEMF = Demersal fishes; PELF = Pelagic fishes; PURSE = Purse seine; ARTIS = Artisanal; RECRE = Recreational.

Obtaining good estimates of total catch (both official and Illegal, Unregulated and Unreported (IUU)) (Edelist et al., 2013b) was challenging but the reconstruction used in this study offered a more complete estimation than the official data available. However, as Edelist et al. (2013b) indicated, the catch data of the artisanal fleet and the purse seine were less reliable than the trawl catch due to the large number of vessels and landing sites. In addition, the recreational sector requires detailed examination due to its actual importance and its potential growth, as in other Mediterranean regions (Gaudin and De Young, 2007, Pauly et al., 2014).

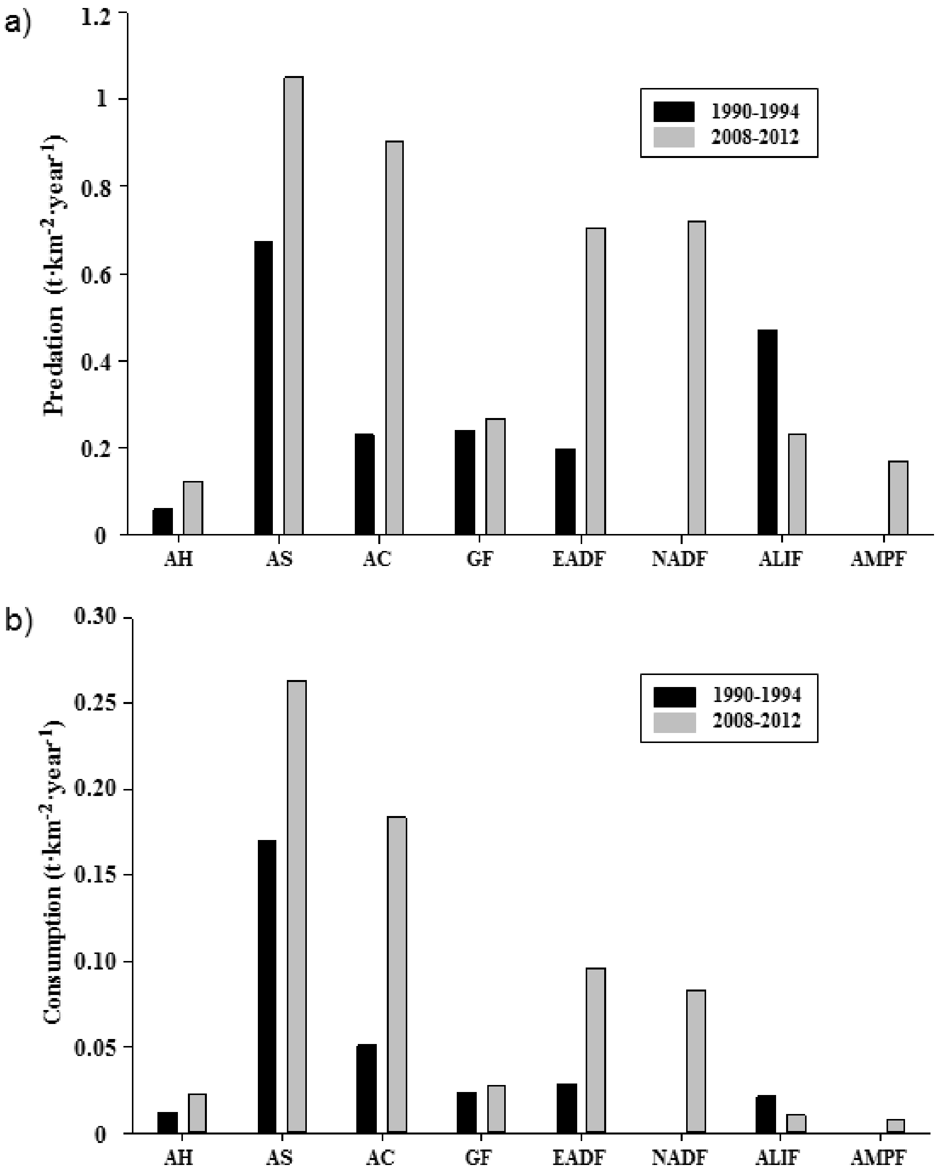


Fig. 9. Predation (t·km^{-2}·year^{-1}) by alien species on their prey (a) and consumption (t·km^{-2}·year^{-1}) of alien species by their predators (b) for the two time periods (1990-1994 and 2008-2012). AH = Alien herbivores; AS = Alien shrimps; AC = Alien crabs; GF = Goatfishes; EADF = Earlier alien demersal fishes; NADF = New alien demersal fishes; ALIF = Alien lizardfish; AMPF = Alien medium pelagic fishes.

Comparison and calibration of model outputs are part of the model validation process. Here we used information from Stable Isotope Analysis (SIA) from a neighboring area to compare outputs with trophic levels estimates from the model. Our results showed a high correlation with the SIA estimates obtained for the Lebanese coast (Fanelli et al., 2015), highlighting that the diet information used here represent the trophic relationships reasonably well. Although the stomach content analysis and SIA were not performed in the same area, they are from the Levantine Sea and could be used here to parameterize and validate our models. Future work should include more independent analysis to validate the models (i.e. information on fishing mortalities from stock assessment) while the 1990s model should be calibrated to available time series of historical data using the temporal modeling approach Ecosim (Walters et al., 1997).

4.1.Ecosystem structural and functioning traits and ecological role of functional groups

In agreement with the oligotrophic nature of the Levantine Sea, TST and TB estimates, were much lower in our models than in other Mediterranean models set up in the western and central basin (Corrales et al., 2015). These features had been also observed on a larger scale Mediterranean Sea food web model (Piroddi et al., 2015a). The TEs of both time periods were higher (almost double) than the average value of 10% reported worldwide (Pauly and Christensen, 1995). These values were also higher than in other Mediterranean Sea areas (Corrales et al., 2015) and for the Mediterranean Sea as a whole (Piroddi et al., 2015a). Such high values highlight the nutrient-poor waters of the Israeli Mediterranean coast.

Results related with ecosystem development theory (Odum, 1969, Odum, 1971), suggest that the Israeli ecosystem was at a developing stage in both time periods. For example, the Pp/R values were higher than 1, indicating that more energy was produced than respired within the system. The Pp/B values were high, indicating low levels of biomass accumulation within the system compared with productivity; and the FCI values, which represents the proportion of throughput cycled within the ecosystem, was low, indicating an immature system. Food web complexity indices such as the SOI and PL were low, suggesting that the ICS models look more chain-like than web-like. All of these indicators presented similar values in both time periods, suggesting that the functioning of the whole ecosystem did not change significantly over time, and could indicate that the ecosystem was already highly impacted in the 1990s.

Results from the Lindeman spine suggest food web changes in different habitats. The increasing flows in the demersal habitat in TL III can be due to the increasing impact of alien species on the ecosystem. This could be related to the empty niches left by the native species that the alien species occupied or as a result of a potential trophic cascade due to the overexploitation of top predators like hake (F.G. 17), large native demersal fishes (F.G. 21) and alien lizardfish (F.G. 25). However, the decreasing flows in TL III of the pelagic habitat were not clear and should be interpreted carefully since (1) there is a lack of pelagic data and (2) increasing water temperature and river damming were postulated to play an important role in these declines (Edelist et al., 2013b).

The Israeli marine ecosystem was found to share some common features in structure and functioning with other Mediterranean ecosystems such as the important role of detritus via TL II; the dominance of the pelagic fraction in term of flows; and the importance of the benthic-pelagic coupling. For example, the contribution of planktonic groups to the detritus and the relationship between detritus and organisms at TL II (mainly benthic invertebrate groups) was identified as a key process in the Mediterranean Sea (Coll et al., 2006, Tsagarakis et al., 2010, Corrales et al., 2015).

In both time periods the same keystone groups were identified with the exception of hake in 2010s. Most of these groups were also keystones in other Mediterranean areas (Coll and Libralato, 2012, Corrales et al., 2015). Hake (F.G. 17) was not identified as a keystone species in the 2010s model, and could therefore be a native top predator that may have lost its ecological role. The decline of hake has been attributed to overfishing, oceanographic changes, increased temperature and the competition for resources with the alien lizardfish (F.G. 25) (Galil, 2007a, Gucu and Bingel, 2011, Halim and Rizkalla, 2011, Edelist, 2012).

4.2. The role and impact of alien species

Our results show that alien species has become an important part of the ecosystem. Their increasing biomass, catch and flows within the ecosystem, have altered the structure of the food web. Higher percentages of alien species have been found in the catch than in the biomass, as most of the fishing effort has been redirected to the shallow waters (Edelist et al., 2013b), where most of the commercial demersal biomass is now attributed to alien species (Edelist et al., 2013a).

A high proportion of alien demersal species has been found in other parts of the eastern Mediterranean Sea as well (Gücü and Bingel, 1994, Taşkavak et al., 1998, Harmelin-Vivien et al., 2005, Carpentieri et al., 2009, Gücü et al., 2010). The rapid expansion of the new alien demersal fishes (F.G. 24) is in line with studies that indicated that the most recent wave of invasion has established large populations along the eastern Mediterranean Sea (Edelist et al., 2012, Nader et al., 2012, Edelist et al., 2013a, Stern et al., 2014). The trawl fleet and recreational fishers caught the highest percentages of alien species because most of the trawl fishing effort are focused on shallow soft bottoms; and the recreational fishers catch on hard coastal bottoms, where alien herbivores (F.G. 22) constitute an important part of the total biomass (Goren and Galil, 2001). Except alien herbivores, alien species appear to be poorly established in the rocky littoral zone (Golani et al., 2007). However, the importance of alien species in the catch of all the fleets might be underestimated, especially in the artisanal and the purse seine, as an important part of the catch includes groups that were not sufficiently separate into specific functional groups in the model due to lack of data (e.g. small pelagic fishes and native medium pelagic fishes).

Trophic flows related to alien species increased as a result of their biomass expansion and impacted the ecosystem. The rapid growth of the alien herbivores population altered the community structure of the rocky infralittoral (Sala et al., 2011, Vergés et al., 2014). Prior to their arrival, the role of native herbivorous fishes were negligible, and therefore, the alien herbivores increased the rate of algal recycling and provided more food to potential predators (Galil, 2007b). Moreover, some competition for resources has been found in the demersal habitat. Our results highlighted that the consumption of prey by alien species increased more than the consumption on alien species by their predators. This may be due to the increasing importance of alien species in the catch, preventing energy transfer to higher trophic levels.

Several hypotheses have been proposed to explain the impact that alien species have on the marine ecosystem of the eastern Mediterranean Sea and the decline of native species. Trophic interactions between native and alien species may cause native species to be outcompeted or partially displaced by the invaders (Galil, 2000, Galil, 2007a). Several authors indicated the success of some alien species could be related to the existence of underexploited niches in the ecosystem that could be exploited by the alien species (Golani, 1998, Galil, 2008, Rilov and Galil, 2009). In addition, the impact of fishing activity could facilitate the establishment and spread of alien species as a result of the overexploitation of native species (Galil, 2008) and the possible better adaptation and competitiveness of alien species to proliferate in the highly impacted trawled areas (Edelist et al., 2011). Moreover, environmental conditions (specially temperature but also salinity) might have become more suitable for thermophilic species like most of the Lessepsian migrants, providing various advantages when competing with temperate native species (Golani, 1998, Galil, 2007a).

4.3. Impacts of fishing on the food web

Results of this study showed that fishing activity played an important role over time on the ecosystem and had noticeable impacts. For example, some groups had higher exploitation rates than the general reference point of 0.5 proposed by Rochet and Trenkel (2003), suggesting the overexploitation of several marine resources.

However, the primary production required to sustain the fisheries (%PPR) showed a lower value than the 24.2% estimated for non-tropical shelves worldwide (Pauly and Christensen, 1995). It was lower than the northern and central Adriatic Sea model (Coll et al., 2007), and higher than the south Catalan Sea model (Coll et al., 2006) and the north Aegean Sea model (Tsagarakis et al., 2010). The total catch was stable between both periods, but landings decreased around 20% from 1990s to 2010s while discards increased dramatically, corroborating the unsustainability of the Israeli fisheries (Goren et al., 2013, Edelist et al., 2014). There are reasons for this: The trawl fleet refocused the effort to the shallow waters, where many fish species are characterized by small size and where many nursery habitats are found; and many of the new alien species, found mainly in shallow waters, are discarded as they are small or are venomous/poisonous or for cultural reasons (Edelist et al., 2013b).

The mTLc and mTLco values in the ICS models were higher than models developed in the western and central Mediterranean Sea, and similar to the north Aegean Sea model (Tsagarakis et al., 2010, Coll and Libralato, 2012, Corrales et al., 2015). This could be related to the oligotrophic nature of the eastern Mediterranean Sea and therefore the lower proportion of low TL organisms such as small pelagic fishes in the total catch and the ecosystem , as also seen in the Aegean Sea (Tsagarakis et al., 2010). Moreover, the mTLc and mTLco in the Israeli model are similar during both time periods as the biomass and catch of top predators (i.e., hake (F.G. 17), large native demersal fishes (F.G. 21) alien lizardfish (F.G. 25)) and low trophic levels (like small pelagic fishes (F.G. 31)) decrease while the biomass and catch of medium trophic levels (i.e. earlier (F.G. 23) and new alien demersal fishes (F.G. 24)) increased. In fact, Edelist et al. (2013a) suggested that alien species have masked changes to the mTLco in the demersal fish community by replacing native by alien fishes with similar ecological position in the food web.

4.4.Concluding remarks

This study presents the first attempt to develop a food web model of the Israeli Mediterranean ecosystem. Furthermore it demonstrates the large changes that have occurred to the food web structure and functioning since 1990s. These changes are a consequence of fishing and the increasing number and biomass of alien species.

The current state of the ICS ecosystem is a result of the cumulative impacts of alien species, overfishing and climate change superimposed on the geological history and environmental conditions of the eastern Mediterranean Sea (Galil, 2008, Bianchi et al., 2014). It is difficult to quantify the contribution of each of these factors (Galil, 2007b) but they could be amplified by their cumulative effects. The nature of these effects (additive, synergistic or antagonist) is unknown, although some authors suggested synergistic effects between alien species, fishing and climate change (Galil, 2008, Goren et al., 2013).

Future work including the calibration and fitting of the 1990s model to historical time series data (Walters et al., 1997, Christensen and Walters, 2004a) should be used to continue this analysis and evaluate both historical and potential future cumulative impacts of multiple stressors to the ecosystem dynamics of the southeastern Mediterranean Sea.

Acknowledgements

The authors would like to acknowledge the scientific researchers from Israel Oceanographic and Limnological Research and Tel Aviv University for providing information and advice, with special mention to Jonathan Belmaker and his research team, Menachem Goren research team and Noam Shachar. We also address special thanks to the Department of Fisheries in the Ministry of Agriculture and particularly to James Shapiro and Oren Sonin, for their continuous contributions with advice and data, and to Yaniv Levi and Dani Kerem for providing data on sea turtles and dolphins. Xavier Corrales would like to address a special thanks to Isabel Palomera, Chiara Piroddi, Jeroen Steenbeek, Ismet Saygu and Audrey Valls for their advice and to Federico Quattrocchi for help with R software and Fig. 1. XC and EO were supported by an IOLR scholarship under the DESSIM project (“A Decission Support System for the management of Israel’s Mediterranean Exclusive Economic Zone”). MC was partially funded by the European Commission through the Marie Curie Career Integration Grant Fellowships – PCIG10-GA-2011-303534 - to the BIOWEB project.

2.3. Hindcasting the dynamics of an Eastern Mediterranean marine ecosystem under the impacts of multiple stressors

Corrales, X.[1,2]*; Coll, M.[2,3]; Ofir, E.[1]; Piroddi, C.[2]; Goren, M.[4]; Edelist, D.[5]; Heymans, J.J.[6]; Steenbeek, J.[2,3], Christensen, V.[7]; Gal, G.[1]

1. Kinneret Limnological Laboratory, Israel Oceanographic & Limnological Research. PO Box 447, Migdal, Israel.
2. Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta, nº 37-49. 08003. Barcelona, Spain.
3. Ecopath International Initiative Research Association, Barcelona, Spain
4. Department of Zoology and The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv 69978, Israel.
5. Department of Maritime Civilizations, University of Haifa, Mount Carmel, Haifa 31905, Israel.
6. Scottish Association for Marine Science, Scottish Marine Institute, Oban, PA 371QA, Scotland.
7. University of British Columbia, Institute of Ocean and Fisheries, Vancouver, Canada.

Marine Ecology Progress Series 580 (2017), 17-36

DOI: https://doi.org/10.3354/meps12271

See original publication in Annex 3

Abstract

An important challenge for conserving and managing marine ecosystems is to advance our understanding of how multiple human stressors, environmental factors and marine resources interact and influence each other. The ecosystems of the Israeli Mediterranean coast have undergone significant ecological changes in recent decades, caused primarily by the introduction of alien species, fishing and the warming of the waters.

Here we used a food-web model representing the continental shelf of the Israeli Mediterranean coast to explore the historical dynamics of the area considering the combined effect of alien species, fishing activities and changes in sea surface temperature and primary productivity. The food-web model was fitted to available time series of data from the early 1990s to 2010 using the temporal dynamic module of the Ecopath with Ecosim (EwE) modeling approach. An important challenge was to model the numerous alien species inhabiting the Eastern Mediterranean Sea, one of the most invaded marine ecosystems of the world.

Historical model simulations satisfactorily matched observed data, especially regarding alien groups. However, lack of data from the pelagic environment limited our ability to compare model output with historical observations. Trophic interactions, climate change and fishing were important factors explaining the historical dynamics of the ecosystem, which showed a degradation pattern over time. Results also highlighted an increasing proportion of alien species in biomass and catch over time with important effects on the food web.

This study represents an important step forward in understanding the changes that are occurring in the Israeli continental shelf ecosystem and the Levantine Sea.

Keywords: Eastern Mediterranean Sea, food-web model, Ecopath with Ecosim, cumulative impacts, alien species, climate change, fishing impact.

1. Introduction

During the last decades marine ecosystems have changed at surprising rates under the impacts of global, regional and local stressors, including climate change, biological invasions and direct human pressures such as overexploitation, pollution and habitat modification (Costello et al., 2010, Halpern et al., 2015a). Variations in the abundance of marine species and their distributions have been documented (Carlton and Ruiz, 2005, Perry et al., 2005, Lotze et al., 2006), affecting the structure and functioning of marine ecosystems (Byrnes et al., 2007, Doney et al., 2012, Christensen et al., 2014a) and the ecosystem services provided to humans (Worm et al., 2006, Katsanevakis et al., 2014c).

Given the range of human activities, stressors often co-occur in time and space. Thus most marine ecosystems are exposed to the impacts of multiple stressors (Breitburg and Riedel, 2005, Halpern et al., 2015a), in addition to the effects of environmental fluctuations (Ravier and Fromentin, 2004, Cury et al., 2008). The ability to understand how human activities, environmental factors and marine organisms interact and influence each other is an issue of pressing importance.

A shift towards more comprehensive management of human activities following an ecosystem-based management (EBM) approach requires means to evaluate their interactive and cumulative impacts (Leslie and McLeod, 2007, Giakoumi et al., 2015). Thus, studying cumulative impacts has become one of the most important challenges in ecology, conservation and management (Crain et al., 2009, Parsons et al., 2014).

Within this context, ecosystem modeling approaches have increasingly been adopted as useful tools to study marine ecosystems as a whole (Piroddi et al., 2015b). They integrate available information to consider direct and indirect interactions among ecosystem compartments and stressors, e.g. trophic interactions and the impact of fishing activity (Plagányi, 2007, Fulton, 2010). One of the most used approaches is the Ecopath with Ecosim (EwE) modeling toolbox, which has been widely applied to model aquatic food webs (Heymans et al., 2014, Colléter et al., 2015).

The EwE approach has been mainly used to assess the impacts of fishing activities on marine ecosystems and investigate management options (Cury et al., 2005, Heymans et al., 2014). In addition, it is increasingly being used to assess the impact of cumulative stressors such as climate change, habitat modification and other stressors that are becoming more important in the marine environment (Coll et al., 2015, Colléter et al., 2015). One of these increasingly important stressors is the invasion of non-native species (e.g., Arias-González et al., 2011, Libralato et al., 2015).

Modeling species invasions using EwE models and evaluating their expansion and effects in the food web is a challenging task (Langseth et al., 2012, Corrales et al., 2014). For example, the time of arrival and important ecological traits of alien species need to be known in advance before their dynamics can be modeled. One solution has been to develop two food webs, one representing the ecosystem before the invasion and one after the invasion (e.g., Downing et al., 2012, Akoglu et al., 2014). However, this approach impedes the study of the expansion process and the impact of alien species on the food web during the intermediate period. Several alternative approaches have been used to simulate alien species and their temporal impacts (e.g., Arias-González et al., 2011, Langseth et al., 2012), which are briefly explained in “Materials and methods: Incorporating the impact of alien species”.

The marine ecosystem of the Eastern Mediterranean Sea has undergone significant changes in recent decades, caused primarily by the introduction of alien species through the Suez Canal (known as Lessepsian migration), intense fishing activity and the effects of climate change (Lejeusne et al., 2010, Katsanevakis et al., 2014b, Tsikliras et al., 2015).

In this study, a food-web model representing the Israeli Mediterranean continental shelf (ICS model) in the early 1990s (Corrales et al., 2017b) was fitted to available time series of data from the early 1990s to 2010 using the temporal dynamic module Ecosim (Walters et al., 1997, Christensen and Walters, 2004a). The specific objectives of this study were to: (1) explore the historical dynamics of marine resources of the ICS model considering the effect of alien species, fishing activities and climate change (through historical changes in temperature) as the main ecosystem drivers, and (2) quantify ecological changes during this period using selected ecological indicators.

This study represents the first development of a temporal dynamic food-web model that quantifies the impact of multiple stressors in the Eastern Mediterranean Sea. We reviewed previous attempts to model species invasions in EwE and we developed a strategy that satisfied the amount of available data and alien species in the study area. Given the large number of alien species inhabiting the Eastern Mediterranean Sea and the lack of temporal quantitative analysis on the impact of alien species in the region in addition to other human impacts, the present study represents an important step forward in modeling alien species, generally, and in the Mediterranean Sea in particular (Corrales et al., 2014).

2. Materials and methods

2.1. Study area

The study area comprises the Israeli Mediterranean continental shelf (hereafter referred as ICS) (Fig. 1), in the Levantine Sea. The ecosystem modeled covers an area of 3725 km^2, including depths from 0 to 200 m. The Levantine Sea has the hottest, saltiest and most nutrient poor waters in the Mediterranean Sea (Azov, 1991, Brasseur et al., 1996). Its circulation is characterized by a dominant northward current along with the general counterclockwise current gyre of the Eastern Mediterranean Sea (Hamad et al., 2006). The ecosystem along the Israeli Mediterranean coast has changed over recent decades due to direct anthropogenic impacts, in addition to the increasing water temperature (Edelist et al., 2013a, Goren et al., 2013, Sternberg et al., 2015). Currently, the Levantine Sea is the world's most invaded marine ecoregion (with a current ratio of alien to native species richness of 0.69) (Katsanevakis et al., 2014b) and the invasions have profoundly altered the ecosystem (Edelist et al., 2013a). The impact of fishing is also high, although overall commercial fishing effort has decreased in the past 20 year (Fig. 2a) (Goren et al., 2013, Edelist et al., 2014). In addition, mean sea surface temperature has risen (1.26ºC between 1994 and 2010) (Mediterranean Forecasting System COPERNICUS; http://marine.copernicus.eu/) (Fig. 2b), facilitating the establishment and spread of thermophilic species over time (Fig. 2c,d), which are mostly Lessepsian migrants. This has also negatively impacted native species (mainly cold-water species) by placing them at the edge of their thermal ranges (Ben Rais Lasram et al., 2010, Raitsos et al., 2010).

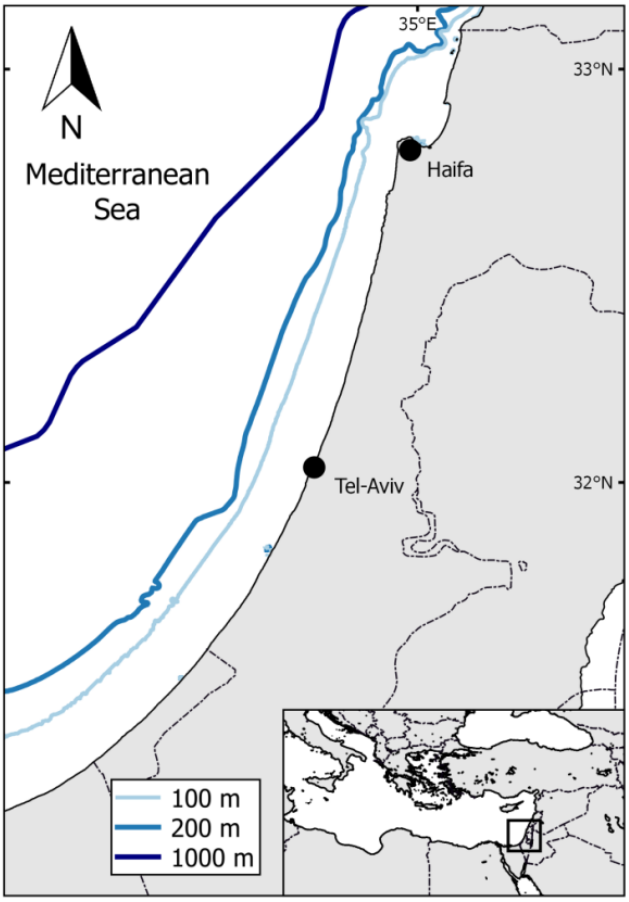


Fig. 1. The study area encompassing the Israeli Mediterranean continental shelf ecosystem and selected depth contours. Modeled area includes depths from 0 to 200 m.

2.2. Modeling approach

2.2.1. Ecopath with Ecosim framework

An Ecosim model representing the ICS ecosystem during the 1994-2010 period was fitted to time series of historical data. The Ecosim simulated the period between two Ecopath models representing the 1990-1994 and 2008-2010 time periods (Corrales et al., 2017b). The original model representing the 1990-1994 period comprised 39 functional groups, including the main trophic components of the food web from primary producers to top predators (see Table S1 in Annex 3). The model included six alien groups encompassing several crustacean and fish species located at various trophic positions in the food web. The main fishing fleets acting in the ecosystem were also considered: bottom trawl fleet, artisanal gear consisting of longlines and gillnets, purse seine and recreational fishers.

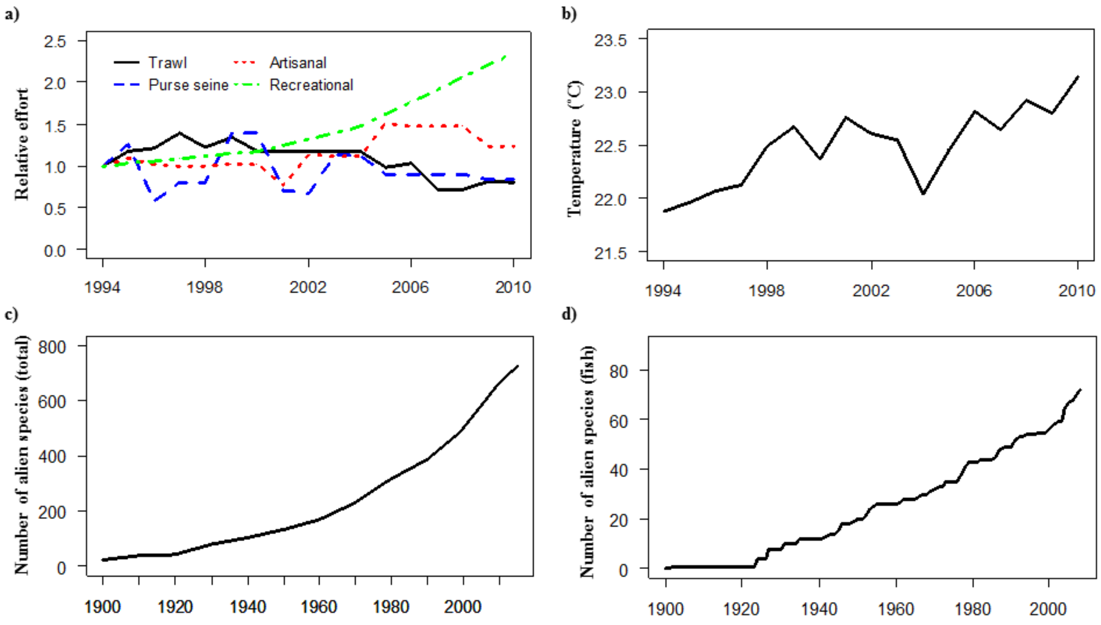


Fig. 2. Ecosystem drivers of the Israeli Mediterranean continental shelf ecosystem considered in this study: (a) relative fishing effort by fleet, (b) annual sea surface temperature, (c) number of alien species in the Mediterranean Sea (adapted from (Galil et al., 2014a)) and (d) number of alien fish species in the Mediterranean Sea (adapted from Golani (2010)).

Two multispecies alien groups (new alien demersal fish and alien medium pelagic fish, new alien groups, hereafter), which incorporate alien species with different times of settlement, were absent in the previous version of the model (1990-1994) (Corrales et al., 2017b). Thus they were added to the baseline Ecopath model (see “Incorporating the impact of alien species”). Input parameters of the baseline model are fully described in Corrales et al. (2017b) and the new input parameters are shown in Table S1 in Annex 3.

Ecosim is the time-dynamic module of the EwE framework and describes the temporal dynamics of species biomass and flows over time by accounting for changes in predation, consumption rate, fishing and the environment (Walters et al., 1997, Christensen and Walters, 2004a).

Ecosim uses a set of differential equations to describe biomass dynamics, expressed as:

$$\frac{dB_i}{dt} = \left(\frac{P}{Q}\right)_i \cdot \sum Q_{ji} - \sum Q_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i \qquad \text{(Eq. 1)}$$

where dB_i/dt is the growth rate of group (i) during time t in terms of its biomass B_i; $(P/Q)_i$ is the net growth efficiency of group (i); M_i is the non-predation mortality rate;

F_i is the fishing mortality rate; e_i is the emigration; and I_i is the immigration rate (Christensen and Walters, 2004a).

Consumption rates (Q_{ij}) are calculated based on the "foraging arena" theory, which divides the biomass of a prey into a vulnerable and a non-vulnerable fraction and the transfer rate or vulnerability between the two fractions determines the trophic flow between the predator and the prey. The vulnerability concept incorporates density-dependency and expresses how far a group is from its carrying capacity (Christensen and Walters, 2004a, Christensen et al., 2008). Default values of vulnerability ($v_{ij} = 2$) represents a mixed trophic flow, a low value ($v_{ij} < 2$) indicates a "bottom-up" flow and a situation closer to carrying capacity, while a high value ($v_{ij} > 2$) indicates a "top-down" flow and a situation further away from carrying capacity (Walters and Martell, 2004, Ahrens et al., 2012). For each predator-prey interaction, consumption rates are calculated as:

$$Qij = \frac{a_{ij} * v_{ij} * B_i * P_j * T_i * T_j * M_{ij} / D_j}{v_{ij} + v_{ij} * T_i * M_{ij} + a_{ij} * M_{ij} * P_i * T_j / D_j} * f(Env_{function}, t) \qquad \text{(Eq. 2)}$$

where a_{ij} is the rate of effective search for prey (i) by predator (j), T_i represents prey relative feeding time, T_j is the predator relative feeding time, B_i is prey biomass, P_j is predator abundance, M_{ij} is the mediation forcing effects, and D_j represents effects of handing time as a limit to consumption rate (Christensen et al., 2008, Ahrens et al., 2012). Environmental response functions ($f(Env_{function}, t)$) can be used to account for external drivers that change overtime, such as temperature (see "Incorporating the impact of climate change"). In particular, the intercept between the environmental response function and the environmental driver is used to calculate a multiplier factor (Eq. 2), which then modifies the consumption rates of the functional group with a maximum value of 1 and declining value as the environmental driver deviates from the optimum values (Serpetti et al., 2017).

A detailed explanation of the algorithms and equations of the EwE approach are given in Christensen and Walters (2004a) and Heymans et al. (2016). A summary of the Ecosim fitting procedure followed in this study is provided in Fig 3 and explained in detail below.

2.2.2. Incorporating the impact of alien species

We reviewed the main strategies that have been used to simulate species invasion and their impact using EwE and specially using Ecosim modeling and the fitting procedure (Table 1). These strategies ranged from using time series of data of alien species to force their biomass (e.g., Arias-González et al., 2011) to fitting the models based mainly on three approaches: (1) initial biomass of alien species were set at low levels and their population increase was controlled by applying an artificial fishing mortality (e.g., Langseth et al., 2012); (2) alien species were set up with a high initial biomass and then were constrained by applying a high artificial fishing pressure (e.g., Kumar et al., 2016); and, (3) using forcing functions to remove the effect of alien species on their preys and predators until the year of invasion (e.g., Kao et al., 2016). In addition, other approaches to assess the impact of alien species without a fitting procedure were available and were also considered (e.g., Pinnegar et al., 2014, Libralato et al., 2015).

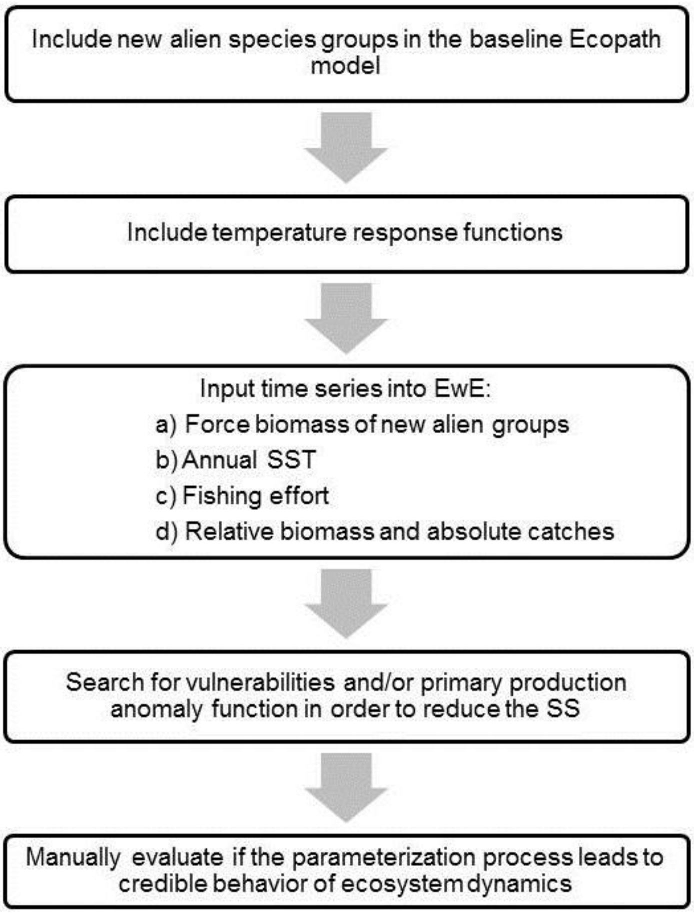


Fig. 3. Main steps followed to fit the Ecosim model to the time series.

We adopted and modified one of the approaches proposed by Langseth et al. (2012). Under this strategy, we set the initial Ecopath biomass of new alien groups at the beginning of the temporal simulations with values equal to the 2008-2010 Ecopath model values (Corrales et al., 2017b). This resulted in an unbalanced flow of biomass in the 1990-1994 Ecopath model due to the additional predation mortality of the new alien groups. To correct for this, we applied a negative biomass accumulation to their prey equal to the amount of prey consumed by these new alien groups in the 1990-1994 Ecopath model (see Table S1 in Annex 3). For predators that prey on these new alien groups, we used post-invasion contributions (as in the 2008-2010 period) of their diet to calculate appropriate levels of natural mortalities (M0) of the new alien groups. Contributions of the other groups to the diet of these predators were proportionally reduced so the total standardized diet was maintained at the same level.

Table 1. Summary of methods used to maintain "low" levels and release "high" levels of new alien species in Ecosim time dynamics food-web models. New alien groups represent groups that invaded the ecosystem after the period of the Ecopath baseline model. Only models fitted to time series are included.

Method	Number of new alien groups	Time series of alien species	Ecopath biomass of alien species	Reference
Force time series	3	Forced	High	Langseth et al. (2012)
Artificial fishery	1	Forced	Low	Arias-González et al. (2011)
Force time series	2	Forced	Low	Rogers et al. (2014)
Artificial fishery	3	Fit	Low	Langseth et al. (2012)
Artificial fishery	3	Fit	High	Langseth et al. (2012)
Changes in vulnerabilities	3	Fit	High	Langseth et al. (2012)
Changes in vulnerabilities	2	Fit	Low	Kao et al. (2014a)
Changes in vulnerabilities	3	Fit	Low	Kao et al. (2016)
Artificial fishery	3	Fit	High	Cox and Kitchell (2004)
Artificial fishery	1	Fit	High	Kumar et al. (2016)
Artificial fishery	2	Fit	Low	Zhang et al. (2016)
Force time series	2	Forced and fit	High	Present study

In Ecosim, biomasses of these two new alien groups were forced to zero until four years before the invasion (2001 for new alien demersal fishes and 2000 for alien medium pelagic fishes) (Galil, 2007b)) (Table 2). This was done to account for the lag between the invasion and the discovery of the alien species, as there is a tendency to determine the presence of the alien species only after they have become established, especially in small and non-commercial species in poorly monitored areas (Azzurro et al., 2016).

2.2.3. Incorporating the impact of climate change

The effect of climate change has been incorporated in Ecosim using forcing functions affecting the Q/B (Consumption/Biomass) ratio of selected functional groups, either by directly modifying their predation search rates (e.g.,Ainsworth et al., 2011, Alva-Basurto and Arias-González, 2014, Guénette et al., 2014) or modifying production, consumption and mortality values (Cornwall and Eddy, 2015).

The most recent version of the EwE software (version 6.5) allows incorporating and linking environmental preferences of functional groups to any number of environmental drivers (e.g., temperature, salinity and oxygen) as has been previously described for Ecospace (Christensen et al., 2014b).

In our study, a time series of the annual sea surface temperature (SST, upper 30 m) from 1994 to 2010 (Fig. 2b, Table 2), obtained from the Mediterranean Forecasting System COPERNICUS (http://marine.copernicus.eu/), was used to drive the temporal dynamics of sensitive functional groups with available information (mostly crustaceans and fish groups) (see Table S2 in online supplementary information).

The environmental response functions ($f(Env_{function}, t)$ in Eq. 2) that link the species or functional groups dynamics with the environmental drivers were first obtained from AQUAMAPS (www.aquamaps.org) (Kaschner et al., 2006), which is a global database on species distribution. These environmental response functions are given as curves showing minimum and maximum tolerance levels and 10^{th} and 90^{th} preferable quintiles to the environmental parameters (in our case, temperature). As a second step, these functions were modified using expert opinion from scientists working in the Israeli Mediterranean ecosystem (mainly from Tel Aviv University) to incorporate local knowledge. The final environmental preferences for each functional group were obtained by weighting the values of the species included in a functional group to their relative biomass contribution to that group (see Table S2 in Annex 3).

Although salinity also affects the marine resources in the Eastern Mediterranean Sea (Mavruk and Avsar, 2008), this factor was not considered in this study as data on the environmental responses of many species was lacking.

Table 2. Information on the time series used to fit the Israeli Mediterranean continental shelf ecosystem model to data. Data are organized by (see 3 rightmost columns) drivers, biomass forcing data and reference data for evaluating model fit. Dem: demersal.

Functional group	Time series of data	Coverage	To drive the model	To force the biomass	To compare predicted results
1. Phytoplankton	Relative Biomass	1998-2010			x
8. Native shrimp; 9. Alien shrimp; 11. Alien crabs; 13. Benthic cephalopods; 14. Benthopelagic cephalopods, 17. Hake; 18. Flatfishes; 25. Alien lizardfish; Demersal fishes (upper slope)	Relative Biomass	1994, 2000, 2010			x
	Total Catch	1994-2010			x
15. Mullets; 16. Goatfishes	Relative Biomass	1994, 2000, 2010			x
	Total Catch	1994, 2000, 2008, 2009, 2010			
19. Rocky fishes, 20. Small native dem. fishes; 21. Large native dem. fishes; 22. Alien herbivorous; 23. Earlier alien dem. fishes; 27. Benthopelagic fishes; 29. Demersal sharks; 30. Rays and skates	Relative Biomass	1994, 2000, 2010			x
	Total Catch	1994-2010 (except 2008)			x
24. New alien dem. fishes	Absolute Biomass	1994-1997			
	Relative Biomass	1994, 2000, 2010			x
	Total Catch	2002-2010			x
31. Small pelagic fishes; 32. Horse mackerel; 33. Mackerel, 34. Native medium pelagic fishes; 36. Large pelagic fishes	Total Catch	1994-2010 (except 2008)			x
35. Alien medium pelagic fishes	Absolute Biomass	1994-1996		x	
	Total Catch	2005-2010 (except 2008)			x
	Relative effort (all fleets)	1994-2010	x		
	Environmental driver (temperature)	1994-2010	x		

2.2.4. Time series of fishing and the fitting to time series

In addition to alien species and SST changes, we compiled available time series of fishing activities to drive fisheries in the model (Table 2). These included data on nominal fishing effort, expressed in number of days at sea, obtained for trawls, purse seine and artisanal fleets (Fig. 2a). Data were obtained from the Fisheries Department of the Ministry of Agriculture and Rural Development of Israel. Fishing effort for the recreational fishers was estimated based on catch reconstruction efforts (Edelist et al., 2013b), as no data were available from official sources (Fig. 2a).

Available relative observed biomass and absolute observed catch data were used to compare model outputs (Table 2). Ecosim allows the incorporation of biomass and catch data as absolute or relative values (Christensen et al., 2008). When these data are introduced as relative values, Ecosim tries to fit the trends rather than absolute values. Relative observed biomass data for most of the demersal groups were obtained from fishery dependent trawl surveys (swept-area method) conducted in the study area during three time periods (1990-1994, 2000 and 2008-2010) (Edelist et al., 2011, Edelist et al., 2013a). In relation to the 1990-1994 and 2008-2010 biomass dataset, we used average values due to the large variability in the data and the uncertainty of the fishery dependent survey. Absolute observed catch data were obtained from a reconstruction of Israeli catches, which included both commercial fleet and discards, the recreational fleet and the Illegal, Unregulated and Unreported catch (IUU) (Edelist et al., 2013b).

To fit the Ecosim model to these time series of observed data for the 1994-2010 period, we used the Stepwise Fitting Procedure (Scott et al., 2016), which automates the model fitting procedure described by Mackinson et al. (2009a) and Heymans et al. (2016). The fitting procedure tests alternative hypotheses related to the impact of fishing, changes in predator-prey dynamics (vulnerabilities), changes in primary production (production anomalies) or all of the above together (Table 3) (Mackinson et al., 2009a, Heymans et al., 2016). A primary production anomaly is a forcing function applied to the primary production rate (in our study both phytoplankton and benthic primary producers) that may represent historical productivity changes impacting biomasses through the ecosystem. During the fitting procedure, vulnerabilities and production anomalies were estimated to improve model fits by comparing model predictions to observed data using the sum of squares (SS) statistics. The fitting procedure finds the statistically “best fit” model based on Akaike’s Information Criterion (AIC), which penalizes for estimating too many parameters based on the number of time series available for estimating the SS (Mackinson et al., 2009a, Heymans et al., 2016):

$$\text{AIC} = n \cdot \log(\text{minSS}/n) + 2k \qquad (3)$$

where *n* is the number of observations, *minSS* is the minimum sum of squares calculated by the algorithm as a result of comparing predicted versus observed values, and *k* is the number of parameters. This number can include changes in vulnerabilities (Vs), changes on primary production anomaly (expressed as number of spline points (PPsp), which smooth the time series of the PP anomaly) or changes in both (Mackinson et al., 2009a, Heymans et al., 2016). The maximum total number of parameters that can be estimated (Vs, PPsp or Vs + PPsp) is *k-1,* where *k* is the number of observed time series (in this case biomass and catch time series) (Mackinson et al., 2009a, Heymans et al., 2016). In this study, the maximum number of parameters that could be estimated was 47 (there were 48 time series of biomass and catch). We used the corrected Akaike's Information Criterion (AICc), calculated as follows:

$$AICc = AIC + 2k \cdot (k-1)/(n-k-1) \qquad (4)$$

To choose the best final model, the last step is to manually evaluate whether if the parameterization process leads to credible and sensible behavior (Heymans et al., 2016).

Table 3. Fitting procedure applied to the Israeli Mediterranean continental shelf model. The procedure follows the methodology suggested by Mackinson et al. (2009a) and Heymans et al. (2016).

Step	Description
1. Baseline	No environmental or fishery data are used to drive the model. All vulnerabilities with default values (vij=2)
2. Baseline and trophic interactions	No environmental or fishery data are used to drive the model. Vulnerabilities are estimated using the "fit to time series" module
3. Baseline and environment	No fishery data is used to drive the model. All vulnerabilities with default values (vij=2). The "PP anomaly" is estimated using the "fit to time series" module
4. Baseline, trophic interactions and environment	No fishery data is used to drive the model. Vulnerabilities and the "PP anomaly" are estimated using the "fit to time series" module
5. Fishery	Fishing effort is included to drive the model. No environmental data is used to drive the model. All vulnerabilities with default values (vij=2)
6. Fishery and trophic interactions	Fishing effort is included to drive the model. No environmental data is used to drive the model. Vulnerabilities are estimated using the "fit to time series" module
7. Fishery and environment	Fishing effort is included to drive the model. All vulnerabilities with default values (vij=2). The "PP anomaly" is estimated using the "fit to time series" module
8. Fishery, trophic interactions and environment	Fishing effort is included to drive the model. Vulnerabilities and the "PP anomaly" are estimated using the "fit to time series" module

2.2.5. Importance of the drivers in historical biomass dynamics

To evaluate the importance of predator-prey interactions (vulnerabilities), climate change and fishing on the dynamics of functional groups, we ran the fitted Ecosim model three times, each time minimizing the effect of: (1) trophic interactions, which were set to the initial default value (vulnerability = 2); (2) temperature, which was kept constant over time; and, (3) fishing effort for all the fleets, which was kept constant over time.

2.3. Ecological indicators and uncertainty

Once the fitting procedure was completed, we used the best fit model to examine biomass and catch time series predicted by the model to explore the dynamics of functional groups, especially those related to alien species.

In addition, a selection of ecological indicators was used to describe ecological changes in the ecosystem over time. To calculate the ecological indicators we used the recently developed ECOIND plug-in (Coll and Steenbeek, 2017) and the Ecological Network Analysis (ENA) module in EwE. The indicators selected for this analysis were:

(1) Total biomass (excluding detritus) ($t \cdot km^{-2}$), which includes biomass of all the functional groups excluding detritus (detritus and discards). This indicator was used to quantify changes at the whole ecosystem level (Heymans et al., 2014).

(2) Forage fish biomass ($t \cdot km^{-2}$), which includes the biomass of benthopelagic and small pelagic fishes, mackerel and horse mackerel. This indicator was analyzed to quantify changes in the pelagic compartment (Hilborn and Walters, 1992).

(3) Predatory biomass ($t \cdot km^{-2}$), which includes biomass of all the groups with trophic level (TL) ≥ 4 and tends to decrease with increasing fishing impact in marine ecosystems (Rochet and Trenkel, 2003).

(4) Invertebrate biomass ($t \cdot km^{-2}$), which includes biomass of benthic invertebrates groups. This indicator was used to assess the dynamics of benthic invertebrates in the ecosystem, which tend to benefit from reductions of fish and predator biomass (Pauly et al., 1998).

(5) Demersal fish biomass ($t \cdot km^{-2}$), which includes biomass of all the fish groups in the demersal compartment. This indicator was analyzed in order to quantify changes to the demersal compartment (Hilborn and Walters, 1992).

(6) Kempton's index, which expresses biomass diversity by considering those organism with TL ≥ 3 and tends to decrease with ecosystem degradation (Kempton and Taylor, 1976).

(7) Mean TL of the community (mTLco), which expresses the TL of the whole ecosystem, reflects the structure of the ecosystem and is used to quantify the impact of fishing (Rochet and Trenkel, 2003) .

(8) Mean TL of the catch (mTLc), which expresses the TL of the catch, reflects the fishing strategy of the fleet and is used to quantify the impact of fishing (Pauly et al., 1998).

(9) Total catch ($t \cdot km^{-2} \cdot year^{-1}$), which includes the annual catches of the different fleets and provides an idea of total fisheries removals (Hilborn and Walters, 1992).

(10) Total System Throughput ($t \cdot km^{-2} \cdot year^{-1}$) (TST), which estimates the total flows in the ecosystem and is a measure of ecosystem size (Ulanowicz, 1986).

(11) Finn's Cycling Index (FCI, %), which represents the proportion of the TST that is recycled in the system and is an indicator of stress and structural differences (Finn, 1976).

(12) Path length (PL), defined as the average number of groups that flows through, which is an indicator of stress (Christensen, 1995).

We addressed the uncertainty in Ecopath input parameters on Ecosim outputs (biomass and catch trends, and ecological indicators) by using the Monte Carlo (MC) uncertainty routine (Heymans et al., 2016, Coll and Steenbeek, 2017). We ran 1000 MC simulations based on the coefficient of variation obtained from the pedigree routine, which assesses the quality of the input data (Corrales et al., 2017b). Results from the MC simulations were used to plot the 5th and 95th percentile confidence intervals for the fitted biomass and catch trends and for ecological indicators. For ENA indicators (TST, FCI and PL), we used the recently developed ECOSAMPLER plug-in (Steenbeek et al., 2018), which creates a number of alternative balanced Ecopath models from MC runs, to assess uncertainty analyses in EwE results. Finally, we used Spearman's rank correlation to evaluate the correlation between model results (time series of biomass, catch and ecological indicators) with time.

3. Results

3.1. Fitting of the model and final model configuration

The best fit model was obtained when trophic interactions, fishing and primary production anomaly were included in the model configuration (Step 8 in Table 4). The parameterization with 23 vulnerabilities (trophic interactions between predators and their prey) and 2 spline points was identified as the best model based on the AICc test criteria (Step 8 in Table 4). However, this model was not able to reproduce the trends of alien shrimps and earlier alien demersal fishes satisfactorily, which are target groups of the study.

Therefore, we moved through the fitting procedure analysis to find the model that was able to reproduce the trends of most of the groups and still showed credible statistical behavior. We finally choose a model fit with 32 vulnerabilities and 2 spline points as the best fit model although the improvement of the model fits was reduced (Step 8 in Table 4).

Table 4. Results of the fitting procedure of the Israeli Mediterranean continental shelf ecosystem fitted to time series of data from 1994 to 2010. The table shows the statistically "best" model for each step. Vs is the number of vulnerabilities estimated, PPsp is the number of primary production spline points, k is the number of parameters (Vs + PPsp) and %IF is the improved fit compared to the baseline AICc. The "best" model chosen in this study is highlighted in bold.

Step	Vs	PPsp	k	SS	AICc	%IF
1. Baseline	0	0	0	229.8	-309.1	
2. Baseline and trophic interactions	12	0	12	151.9	-471.7	52.6
3. Baseline and environment	0	3	3	224.9	-312.7	1.2
4. Baseline, trophic interactions and environment	36	3	39	119.5	-513.2	66.0
5. Fishery	0	0	0	220.5	-327.8	6.1
6. Fishery and trophic interactions	22	0	22	133.6	-506.8	64.0
7. Fishery and environment	0	3	3	215.2	-332.9	7.7
8. Fishery, trophic interactions and environment						
	23	2	25	114.9	-568.0	83.8
	32	**2**	**34**	**121.9**	**-517.9**	**67.6**

3.2. Importance of ecosystem drivers

The best fit model improved the fit by 67.6% over the baseline model (Step 8 in Table 4). Our results showed that trophic interactions were the main factor explaining the historical dynamics (1994-2010) of marine resources (an average of 28.1% of the variability, ± 11.6%), followed by climate change (12.1%), fishing (8.1 ±7.7%) and changes in primary production (4.7 ±4.1%) (Fig. 4).

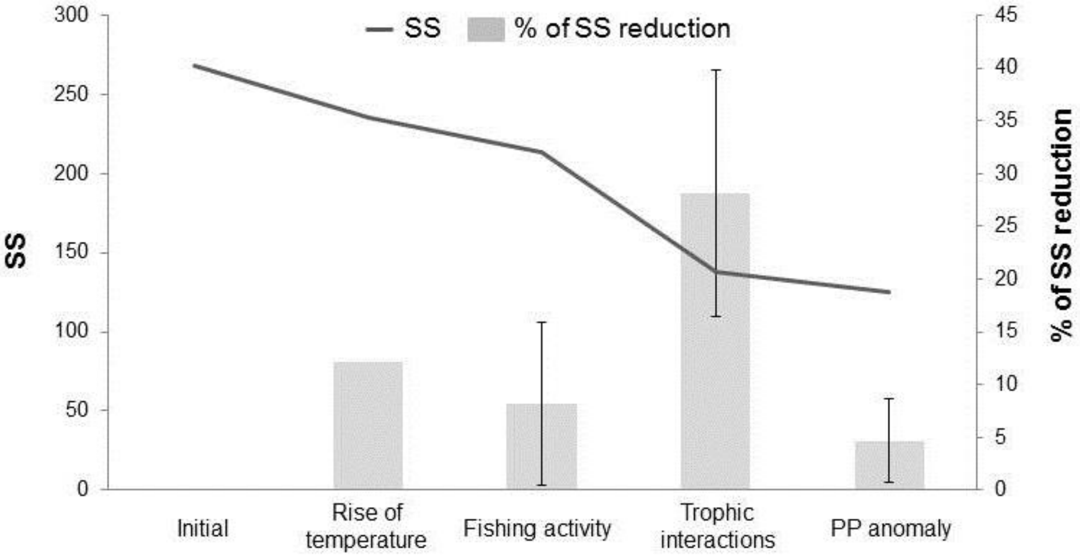


Fig. 4. Diagnostic of the model fitting process. Each step on the x-axis represents a step in the model fitting process (including the effects of the rise in temperature, Table 4) to minimize the sum of squares (SS, left y-axis) and their contribution (% SS reduction, right Y axis) and standard deviation. Standard deviation was calculated based on the different order according to which the drivers were included to reduce SS during the fitting process. Rise in temperature does not have a standard deviation because it was included before the fitting process. PP: primary production.

3.3. Historical biomass and catch trends by species and group

Observed biomass and catch time series were satisfactorily reproduced by model predictions (Fig. 5 and 6) when using the best fit model (32 vulnerabilities and 2 spline points). Overall, alien shrimps (Fig. 5b and 6b), hake (Fig. 5f and 6f), small native demersal fishes (Fig. 5h and 6h), earlier alien demersal fishes (Fig. 5j and 6j), new alien demersal fishes (Fig. 5k and 6k) and alien lizardfish (Fig. 5l and 6l) showed the best fits, while benthic cephalopods, benthopelagic cephalopods, demersal fishes (upper slope), benthopelagic fishes, mackerel and horse mackerel were the least well fitted (Fig. S1 and S2 in Annex 3).

The model also provided predicted biomass trends for 17 functional groups (Fig. 5o-r and Fig. S1b-g,i,o-u in online supplementary information) that lacked historical observations to be used in the fitting. However, we had catch data for 7 of these 17 functional groups (Fig. 6 and Fig. S2 in Annex 3). In these cases, model predictions satisfactorily matched observed catch data except for large pelagic fishes, where the catches were underestimated (Fig. 6r), attesting to the migratory nature of these species and the "hit or miss" nature of pelagic fisheries.

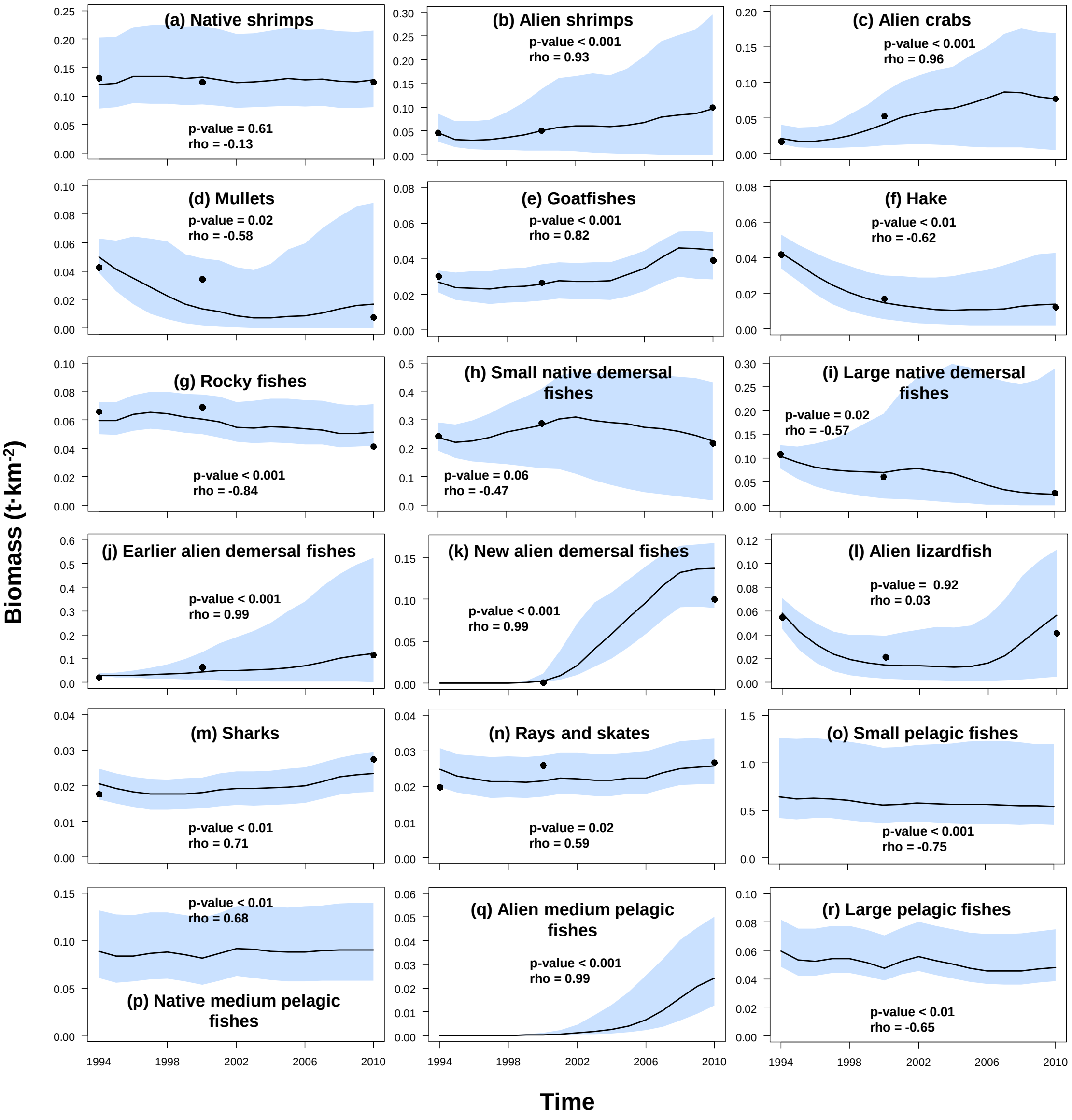


Fig. 5. Predicted (solid lines) versus observed (dots) biomass (t·km^{-2}) for the groups with available data for the Israeli Mediterranean continental shelf ecosystem model for the period 1994-2010. No data are available for the last 4 groups related to pelagic species. Grey shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

The model showed a decreasing historical pattern for the biomasses of several groups (Fig. 5). For example, mullets (Fig. 5d), hake (Fig. 5f) and large native demersal fishes (Fig. 5i) showed a large and significant decline. Small native demersal fishes did not showed a significant decreasing trend, decreasing at the beginning of the simulation, followed by an increase from 1997 to 2001 and a decrease from 2002 to 2010 (Fig. 5h). On the contrary, alien shrimps (Fig. 5b), alien crabs (Fig. 5c), goatfishes (Fig. 5e), earlier alien demersal fishes (Fig. 5j), new alien demersal fishes (Fig. 5k) and alien medium pelagic fishes (Fig. 5q) showed significant increasing biomass trends.

Catch time series estimated by Ecosim showed similar trends as those observed for biomass (Fig. 6 and see Fig. S2 in Annex 3). For example, we observed significant large declines for mullets (Fig. 6d), hake (Fig. 6f) and large native demersal fishes (Fig. 6i), while all alien groups showed significant increasing trends (Fig. 6b,c,e,j,k,q) except alien lizardfish (Fig. 6l). For rocky fishes, although biomass trends showed a significant decrease (Fig. 5g), catches increased significantly (Fig. 6g) due to the growing impact of recreational fishers (Fig. 2a). Overall, catches predicted by the model satisfactorily matched observed data (Fig. 6). Despite this, the model at times overestimated (e.g. small pelagic fishes) (Fig. 6o) or underestimated (e.g. demersal sharks) (Fig. 6m) catches.

Trends in dynamics of alien groups were well reproduced (Fig. 5b,c,e,j,k,l,q and 6b,c,e,j,k,l,q). Remarkably, the model was able to simulate the invasion and population dynamics of the new alien groups: new alien demersal fishes and alien medium pelagic fishes relatively well (Figs. 5k,q and 6k,q). The predicted biomass of new alien demersal fishes was slightly higher than the observed biomass although not enough data were available to establish a clear pattern (Fig. 5k). The predicted catch of this group satisfactorily matched observed data, although a clear overestimation occurred in 2006 (Fig. 6k). We were not able to compare predicted biomass of alien medium pelagic fishes to observed data as no data were available (Fig. 5q). The predicted catch of this group was reproduced relatively well although it was slightly underestimated (Fig. 6q). Moreover, although the catch time series started at 2005, the first species of this group that invaded the ecosystem was recorded in 2000.

In most cases, the main driver of population dynamics was trophic interactions (Fig. 7). In addition, results showed that the rise in temperature and fishing played an important role in the dynamics of small native demersal fishes, alien lizardfish and earlier alien demersal fishes. For mullets, the rise in temperature was the main driver while it also played an important role for hake. Fishing was an important driver for large native demersal fishes (Fig. 7).

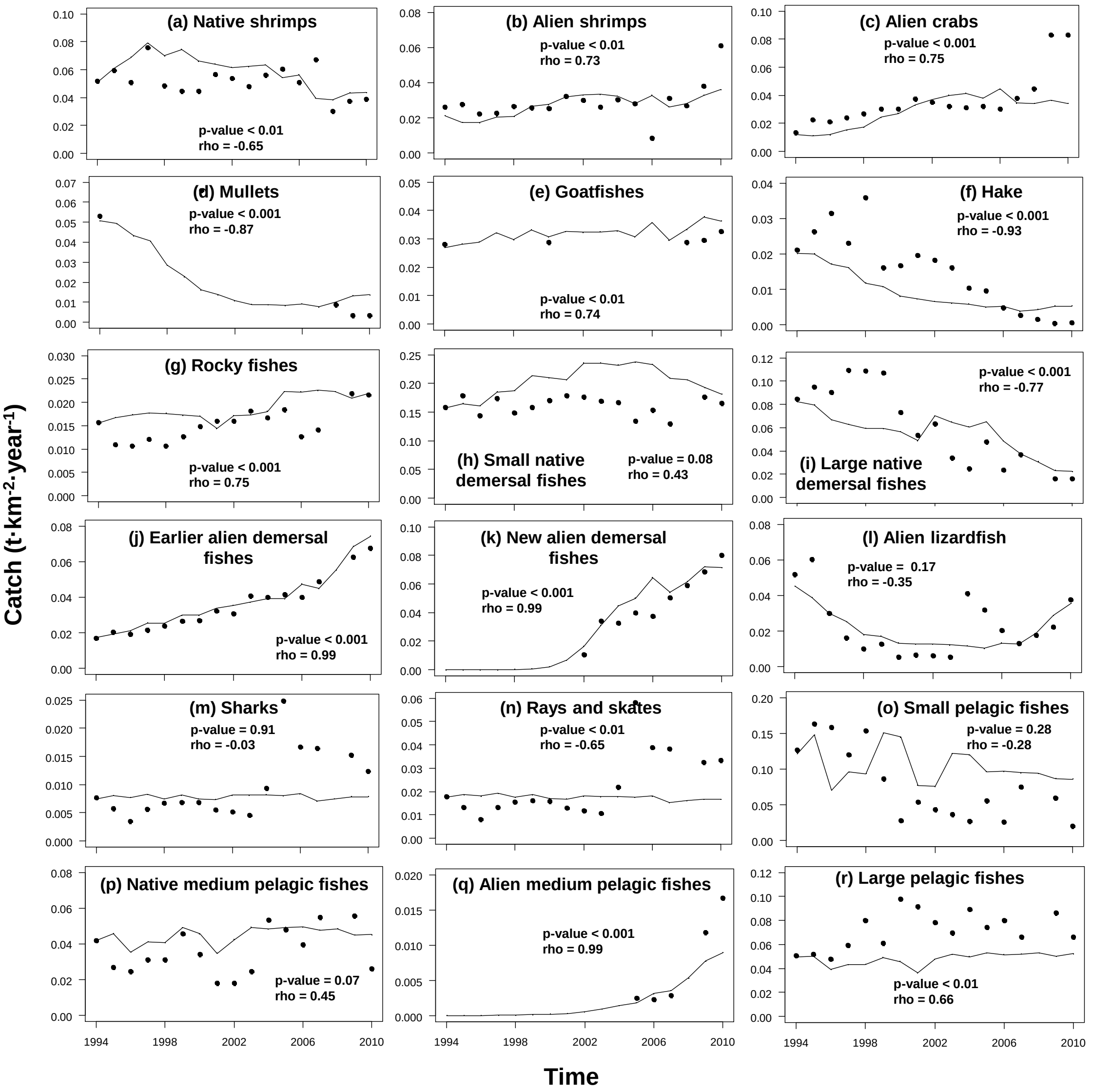


Fig. 6. Predicted (solid lines) versus observed (dots) catches (t·km^{-2}·yr^{-1}) for the groups with available data for the Israeli Mediterranean continental shelf ecosystem model for the period 1994-2010.

3.4. Ecological indicators

Indicators related to alien species showed the growing impact of these groups in the ecosystem. For example, total biomass of alien species increased from 0.19 to 0.59 t·km^{-2} (Fig. 8a), representing 8.9% and 25.2% of the total biomass, respectively, if we include all the groups with sufficient information to split between native and alien species (shrimps, crabs, cephalopods and fishes). Biomass of alien invertebrates and demersal fish groups increased from 0.07 and 0.12 to 0.20 and 0.37 t·km^{-2}, respectively

(Fig. 8a), which represents an increase from 29.3% and 19.2% to 51.4% and 52.3% of the biomass of crustaceans (shrimps and crabs) and fishes, respectively. The analysis of the catch showed similar patterns to those observed in the biomass (Fig. 8b). Total catch of alien groups increased from 0.12 to 0.31 t·km^{-2}·year^{-1} (Fig. 8b), which represents an increase from 14.2% to 33.1%. By groups, this increase was from 0.03, 0.09 and 0 to 0.08, 0.22 and 0.01 t·km^{-2}·year^{-1} for invertebrates, demersal fishes and pelagic fishes, respectively (Fig. 8b), that represents an increase from 39.5%, 21.1% and 0% to 62.7%, 47.3% and 3.5% for invertebrates, demersal fishes and pelagic fishes, respectively (Fig. 8b).

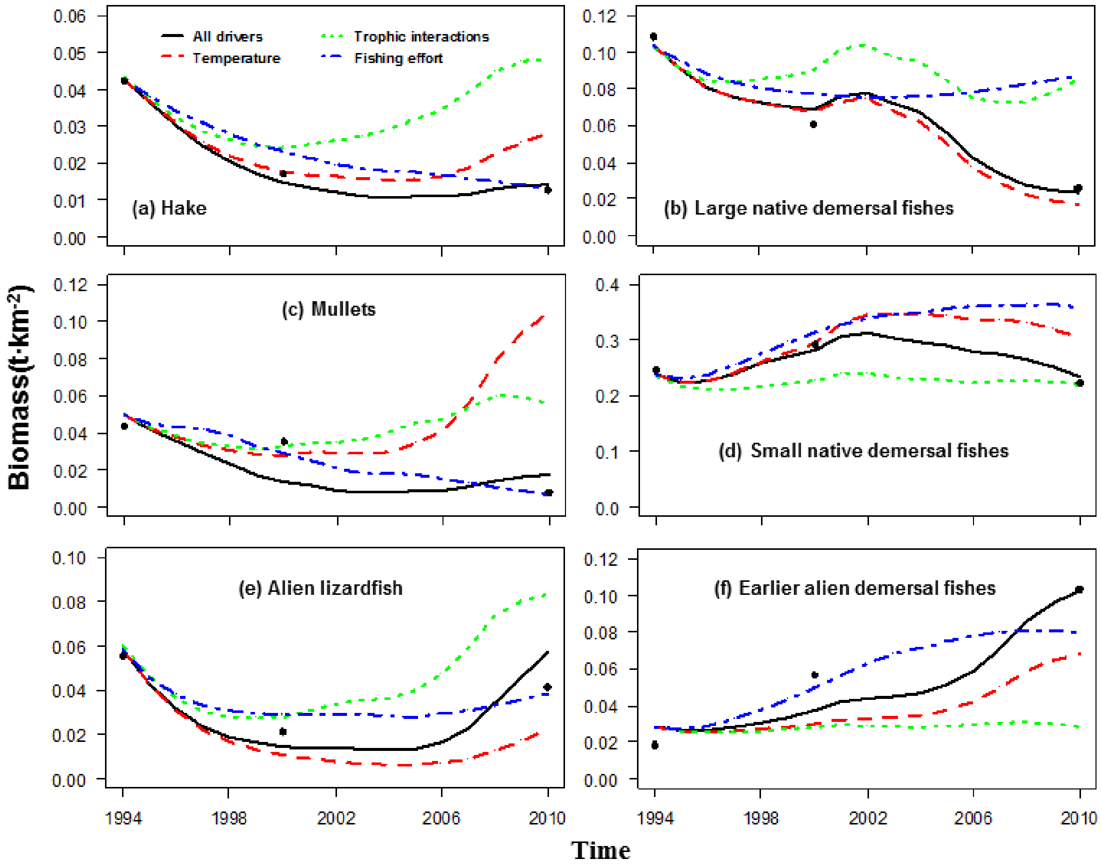


Fig. 7. Predicted (solid lines) versus observed (dots) biomass (t·km^{-2}) for (a) hake, (b) large native demersal fishes, (c) mullets, (d) small native demersal fishes, (e) alien lizardfish and (f) earlier alien demersal fishes, when one of the drivers (trophic interactions, temperature, or fishing effort) were maintained constant in the Ecosim module, for the period 1994-2010.

Other ecological indicators also showed that the ecosystem changed from 1994 to 2010 (Fig. 9). For example, we observed a significant increasing trend of total biomass (excluding detritus) (Fig. 9a) and a non-significant decreasing trend of forage fish biomass (Fig. 9b). Predatory biomass did not show a significant trend although it showed a decreasing trend at the beginning of the simulation followed by an increasing trend at the end (Fig. 9c). Invertebrate biomass and demersal fish biomass showed a significant increasing trend (Fig. 9d,e). The Kempton's index fluctuated in time with a non-significant decreasing pattern (Fig. 9f). The mTLco showed a non-significant decreasing trend (Fig. 9g), while the mTLc showed an overall significant increasing pattern, firstly decreasing and later increasing with time (Fig. 9h). Total catch presented several strong fluctuations in time with an overall significant increasing trend (Fig. 9i). TST showed a significant increasing trend (Fig. 9j), in line with total biomass (excluding detritus). FCI and PL presented a significant decreasing pattern (Fig. 9l).

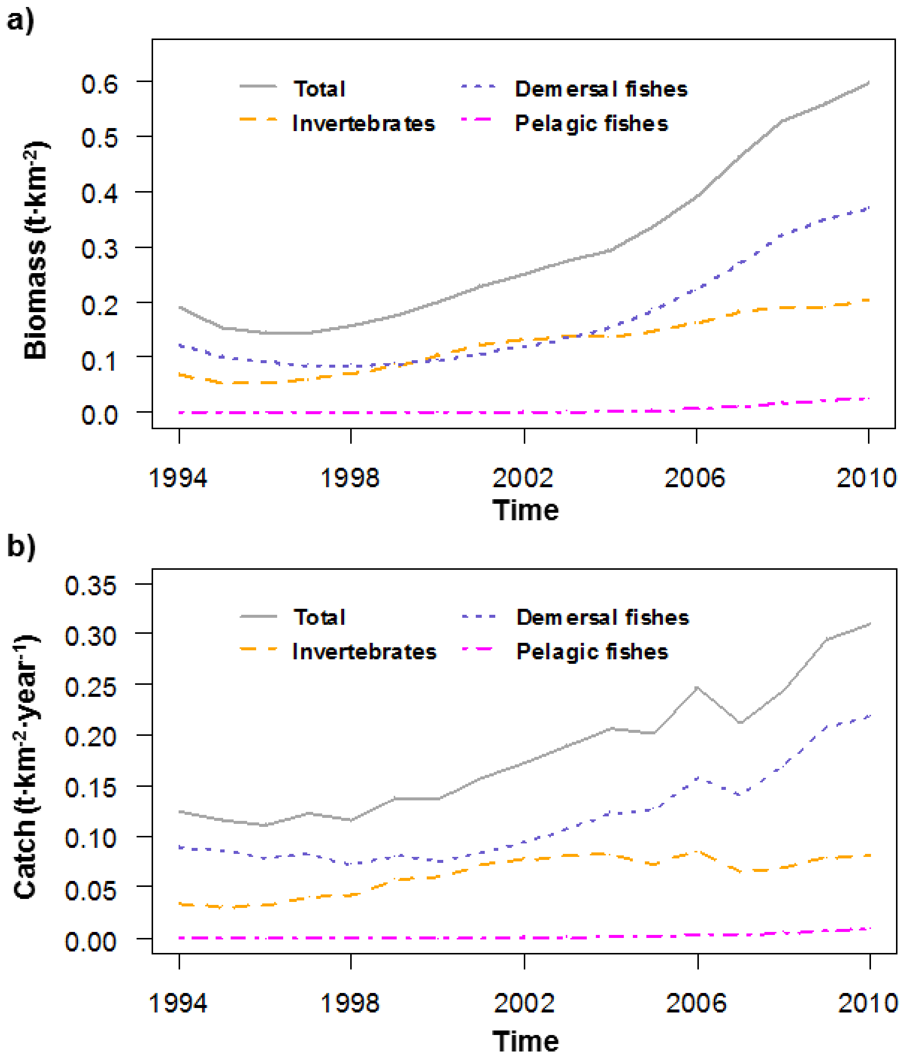


Fig. 8. Simulated (a) total biomass (t·km^{-2}) and (b) catch (t·km^{-2}·yr^{-1}) (b) of different groups of alien species for the period 1994-2010 for the Israel Mediterranean continental shelf ecosystem.

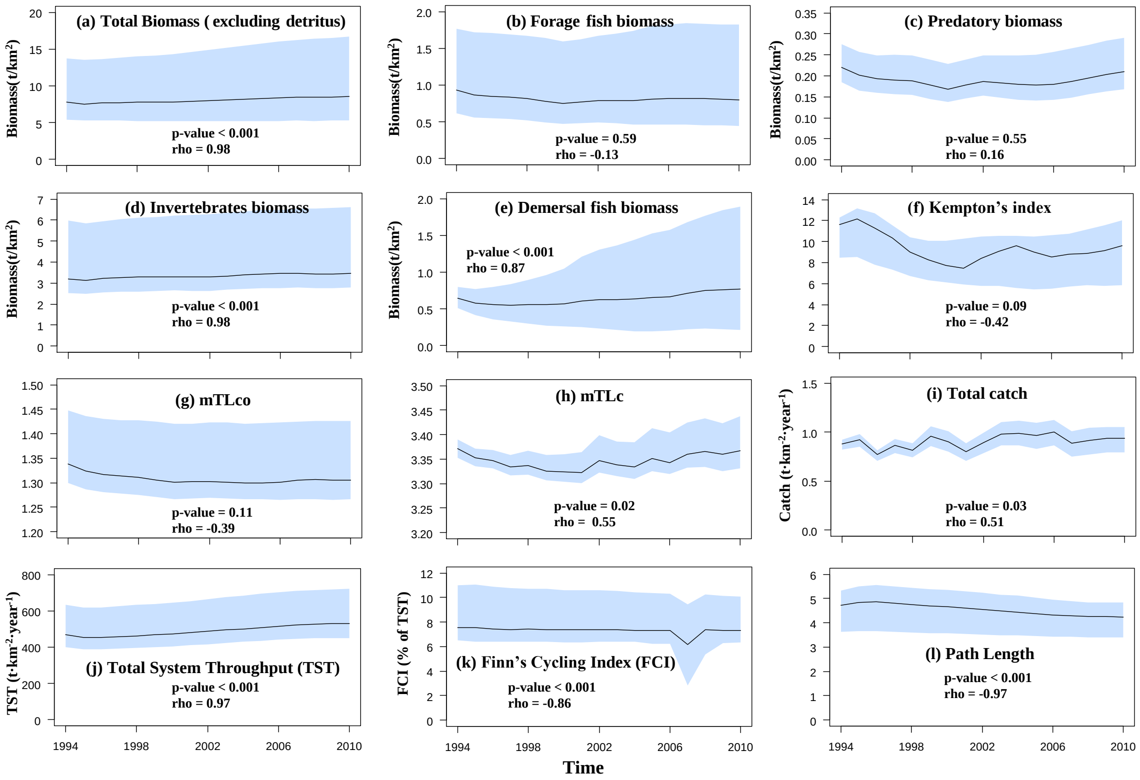


Fig. 9. Ecological indicators estimated for the period 1994-2010 from the Israel Mediterranean continental shelf ecosystem. mTLco: mean trophic level of the community; mTLc: mean trophic level of the catch; TST: Total System Throughput; FCI: Finn's Cycling Index; PL: Path length. Grey shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

4. Discussion

4.1. Ecosystem drivers of the Israeli Mediterranean continental shelf ecosystem

Our model explained a large proportion of the variability of available time series from 1994 to 2010 when trophic interactions, fishing and primary production anomaly were considered. Our results showed that trophic interactions explained the highest variability, highlighting the importance of trophic interactions in marine food web dynamics, as previously documented (Shannon et al., 2004, Coll et al., 2008c, Coll et al., 2009).

In addition, climate change (included as an increase in sea surface temperature) explained a large proportion of the variability, indicating its impacts on the Israeli Mediterranean marine ecosystem. This is in line with the fact that climate change is strongly impacting marine ecosystems worldwide (Harley et al., 2006, Hoegh-Guldberg and Bruno, 2010) and particularly the Mediterranean Sea (Ben Rais Lasram et al., 2010, Lejeusne et al., 2010, Moullec et al., 2016). Currently, the Mediterranean Sea is under a process of “meridionalization” and “tropicalization” of the northern and southern sectors, respectively, mainly due to the northward extension of native thermophilic species and the introduction of alien species through the Suez Canal and the Strait of Gibraltar (Bianchi, 2007, Bianchi et al., 2013). Fish assemblages are expected to be significantly modified as a result of climate change (Ben Rais Lasram et al., 2010, Albouy et al., 2012), with potential effects on marine food webs and ecosystem structure (Albouy et al., 2014), especially in the Levantine Sea due to its “naturally” extreme environmental conditions and the current rise in temperature.

Results also highlighted that fishing was an important historical driver of the ecosystem, especially for the exploited invertebrate and fish populations. It is noteworthy, however, that the fishing effort of the Israeli fleet has declined over the past two decades (Edelist et al., 2013b).

Changes in primary production, captured in our model with the primary production anomaly (PP anomaly), represent the temporal variation of the primary productivity of the system and explained a smaller proportion of data variability. The PP anomaly predicted by the model showed an increasing trend (see Fig. S3 in online supplementary material). This might be related to the nutrient enrichment from anthropogenic sources during the last decades in Egypt and Israel (Nixon, 2003, Suari and Brenner, 2015). This enrichment followed the drastic reduction in PP in the 1970s, when the flow of nutrient-rich Nile waters was substantially reduced by the construction of the Aswan High Dam (Nixon, 2004). The south eastern Mediterranean is characterized by extreme oligotrophic conditions (Azov, 1991), so local nutrient enrichment from land origins could play an important role as it may significantly enhance primary productivity at local scales (Barale et al., 2008, Macias et al., 2014, Suari and Brenner, 2015). Yet, in our ecosystem and as shown in the results, changes in PP seemed to have only marginally explained the variation of observed biomass and catch data.

4.2. Biomass and catch trends

Our results showed changes in the temporal dynamics of marine resources from 1994 to 2010. Even though hundreds of species have invaded the Mediterranean Sea (Galil et al., 2014a), causing the collapse of several native species (Edelist et al., 2013a) and rising concerns about dire consequences for Mediterranean marine ecosystems (Galil et al., 2015), quantitative studies that explain these changes and impacts of alien species are scarce (Rilov and Galil, 2009, Golani, 2010). For example, little is known about the dependency of population dynamics on environmental factors and the trophic interactions between alien and native species. Despite this, individual cases and general knowledge can be used to support and explain our results.

In general, our study revealed three main patterns: (1) native demersal predators, such as hake and large native demersal fishes decreased over time; (2) native medium trophic level fishes largely decreased (mullets) or slightly decreased with time (rocky fishes and small native demersal fishes); and (3) an increase over time of alien species, mainly low and medium trophic levels (alien crabs and shrimps, alien herbivores, earlier alien demersal fishes and new alien demersal fishes), but also high trophic levels (medium alien pelagic fishes). This was especially obvious at the end of the analyzed time period.

The first pattern (a decreasing trend for native demersal predators) is related to the impact of fishing activity, due to the high fishing mortalities, but could also be due to the negative impact of increasing temperatures and trophic interactions. In the current study we have shown that an important driver for the decline in large native demersal fishes was fishing. The decline of predators due to overfishing has been observed worldwide (Pauly et al., 1998, Jackson et al., 2001) and also in the Mediterranean (Ferretti et al., 2008, Maynou et al., 2011). This is in line with studies at sub-regional levels, as e.g., the Catalan (Coll et al., 2008c), Adriatic (Coll et al., 2009) and Ionian Seas (Piroddi et al., 2010); and at regional level, as e.g., the whole Mediterranean Sea (Piroddi et al., 2017). For hake, we observed that the rise in temperature and trophic interactions were the main drivers. This is in line with studies that showed that the decline in hake in the Levantine Sea can be attributed to oceanographic changes, overfishing, increase in temperature and the competition for resources with the alien lizardfish. These have led to its bathymetric displacement to deeper waters (Galil, 2007a, Gucu and Bingel, 2011, Halim and Rizkalla, 2011, Edelist, 2012).

The second pattern (a decreasing trend for native medium TL fishes) may be related to the cumulative impacts of fishing, climate change and competition for resources. For example, the large decrease in mullets in Israel has been attributed to competition for resources with their alien competitor (goatfishes) and the warming of the waters. This could have caused a bathymetric separation of these groups (Golani, 1994), as goatfishes currently dominate shallow strata (0 to 100 m) while mullets occupy deeper waters, although it seems that goatfishes have recently extended their bathymetric distribution (Edelist et al., 2013a). In addition, mullets have suffered high fishing mortality. Other native groups such as rocky fishes and small native demersal fishes decreased slightly over time. For these groups, we observed increasing fishing mortalities, mainly related to the increasing impact of recreational fishers, as in other Mediterranean areas (Pauly et al., 2014). Moreover, reductions in abundance and catches, and the displacement to deeper waters of native species that coincided with the explosion of alien species have been documented (Edelist et al., 2013a). For example, the native porgy *Pagellus erythinus* has been displaced by the alien *Nemipterus randalli*. The reasons are poorly studied but a competitive exclusion between species related to the rise in temperature and trophic interactions have been suggested (Golani, 1998, Galil, 2008).

The third pattern (an increasing trend for invasive species) may be related to the combination of several factors such as the existence of underexploited niches in the ecosystem, overexploitation of native species, possible better adaptation and competitive properties of invaders and more favorable environmental conditions in the Eastern Mediterranean Sea as a result of climate change (Galil, 2008, Rilov and Galil, 2009, Edelist et al., 2011). In addition, the large increase in alien species (of low and medium trophic levels) could be attributed to the increase in primary production and the decrease in some top predators, which implies more food supply and could lead to increases in their prey species, respectively. In our study we observed an increase in invertebrate biomass (the main prey for these groups), a decrease in top predators and the importance of the rise in temperature for their dynamics.

4.3. Ecological indicators

Trends in ecological indicators documented ecological changes in the ICS ecosystem as a whole. For example, along the Israeli Mediterranean coast, alien species have become an important part of the ecosystem, as biomass and catches of alien species have increased with time, altering the structure of the food web.

We observed a large decrease in predators at the beginning of the period due to the decline in hake, large native demersal fishes and alien lizardfish. Since 2007, predatory biomass has increased due to the recovery of alien lizardfish and the explosion of medium alien pelagic fishes. This result is in line with the Kempton's index, which includes species or groups with TL ≥ 3. In addition, demersal fish biomass increased due to the explosion of demersal alien species, mainly medium trophic level species.

The decline in mTLco and mTLc observed in our study coincides with more general trends observed in many marine ecosystems that are caused mainly by overfishing (Pauly et al., 1998). The depletion of top predators and biological invasions, predominantly by organisms with low TL, have caused a decrease in the TL of many marine ecosystems (Byrnes et al., 2007). Our results show that mTLco has decreased slightly over time with a stable trend at the end of the period. However, in our study, we observed that mTLc has decreased and later increased. This is due to the depletion of top predators at the beginning of the period, the recovery of alien lizardfish afterwards and the increasing importance of alien species (medium and high trophic levels) in the catch. Indeed, alien medium trophic level species (earlier alien demersal fishes and new alien demersal fishes) have higher trophic levels than native medium trophic level species (rocky fishes and small native demersal fishes), as highlighted by Fanelli et al. (2015) and Goren et al. (2016).

Our results indicate a small but significant increase in TST with time. Finn (1976) suggested that an increase or decline in the TST could be a sensitive indicator of the state of the ecosystem, as it indicates if the ecosystem is in equilibrium. The increase in TST indicates that the ecosystem is not at equilibrium and may be a result of higher primary productivity with time that leads to an increase in the total production of the system, especially at low trophic levels, and of the increasing importance of alien species in the ecosystem. The FCI and PL showed a moderate decreasing trend. Odum (1969) found that cycling increases as systems mature (and thus FCI increases) and PL increases with maturity, with the opposite trends expected in stressed ecosystems (Odum, 1985). Therefore, our results suggest a degradation trend of the food web during the simulated period.

4.4. Model assumptions and limitations

Modeling marine food webs is challenging due to their complexity, significant data requirements and high uncertainty, which requires the setting of different assumptions (Plagányi, 2007, Fulton, 2010, Rose et al., 2010). In addition, our understanding of the impact of individual stressors is limited and we have less understanding of the cumulative impact that different stressors would have on marine organisms and ecosystems. However, during the last decades, the data available for marine ecosystems has increased substantially and models have made considerable progress.

Several information gaps about the ecosystem of the Eastern Mediterranean Sea were identified by Corrales et al. (2017b), which are mainly related to the pelagic compartment, benthic invertebrates and the reliability of catch data. In addition, the current study highlights a lack of historical biomass time series, as only a few data points were available through the analysis of three surveys conducted in the study area. This limited our knowledge of historical trends in marine resources and therefore, the capability of the model to capture these patterns.

Temperature responses/preferences are key components for understanding the impact of climate change on marine ecosystems and therefore, marine organisms (Madeira et al., 2012). However, temperature responses of organisms are subject to uncertainty. In this study, the baseline information came from a general database (AQUAMAPS) (Kaschner et al., 2006). This is a very comprehensive database; however, it does not account for regional or sub-regional differences/preferences of species environmental responses, implying high uncertainty. To compensate for this somewhat we incorporated expert local knowledge and corrected the general information. Although temperature is the most important environmental factor in driving population dynamics (Por, 1978a), salinity has been suggested to be an important factor to consider (Mavruk and Avsar, 2008). However, this factor was not considered in the study due to the lack of data regarding the response of organisms to changes in salinity. This represents a limitation of the model, which should be addressed in the future.

In addition, this study only included fish and crustacean (shrimps and crabs) alien species. At present, reliable information on ecological characteristics such as reproduction, habitat, trophic position and depth is available for most introduced fish species and some crustaceans species (Rilov and Galil, 2009), but not for other groups, such as polychaetes, mollusks and jellyfish. Since biological invasions of other groups seems to be of the same magnitude or even larger (Rilov and Galil, 2009, Galil et al., 2014a), this limits our ability to assess the overall impact of alien species on this ecosystem and our estimation is likely conservative.

In order to assess the effect of uncertainty of the model parameters we applied a MC sampling routine. Our results show that uncertainty was generally high and varied among the functional groups. This is due to the high uncertainty of the initial Ecopath inputs and highlights the need of additional and accurate data. Recognizing this uncertainty is essential if this information is used for management advice.

Despite these limitations, this study included the best available data and thus is the best available representation of historical trends of the ICS ecosystem and a step forward in understanding its functioning. As new information is generated, the model should be updated and its quality improved.

5. Concluding remarks

This study represents the first example of a food-web model fitted to time series in the Eastern Mediterranean Sea to quantify the impact of multiple stressors. Our results show that trophic interactions, fishing activities and environmental factors (rise in temperature and primary production anomaly) played an important role in the historical dynamics of the Israeli Mediterranean continental shelf ecosystem from 1994 to 2010.

Our results highlight important changes in the biomass of several functional groups and species, such as a decrease in native top predators, a decrease in native medium trophic levels and an explosion of alien species, mainly medium trophic level organisms. Results from ecological indicators show a trend of ecosystem degradation over time.

Future work may include the development of forecasting scenarios in order to evaluate future cumulative impacts of multiple stressors to the Israeli Mediterranean continental shelf ecosystem. These scenarios can include different fishing management options, rise in temperature following Intergovernmental Panel on Climate Change (IPCC) projections and prognoses of increasing impact of alien species.

6. Acknowledgments

The authors acknowledge the scientific researchers from Israel Oceanographic and Limnological Research and Tel Aviv University for providing information and advice, with special mention to Jonathan Belmaker and his research team and M. Goren's research team. We also address special thanks to the Department of Fisheries in the Ministry of Agriculture and Rural Development of Israel and particularly to James Shapiro and Oren Sonin, for their continuous contributions with advice and data. X.C. would like to thanks Federico Quattrocchi and Morane Clavel for help with R and Daniel Vilas for help with the Fig. 1. XC was supported by an IOLR scholarship under the DESSIM project ("A Decision Support System for the management of Israel's Mediterranean Exclusive Economic Zone"). MC was partially funded by the European Commission through the Marie Curie Career Integration Grant Fellowship No. PCIG10-GA-2011-303534 to the BIOWEB project. M.C. and J.S. were partially funded by the European Union's Horizon research program grant agreement No. 689518 for the MERCES project.

2.4. Future scenarios of marine resources and ecosystem conditions in the Eastern Mediterranean under the impacts of fishing, alien species and sea warming.

Corrales, X.[1,2*], Coll, M.[2,3], Ofir, E.[1], Heymans, J.J.[4,5], Steenbeek, J.[2,3], Goren, M.[6], Edelist, D.[7], Gal, G[1].

1. Kinneret Limnological Laboratory, Israel Oceanographic & Limnological Research. PO Box 447, Migdal, Israel.
2. Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta, nº 37-49. 08003. Barcelona, Spain.
3. Ecopath International Initiative Research Association, Barcelona, Spain.
4. Scottish Association for Marine Science, Scottish Marine Institute, Oban, PA 371QA, Scotland.
5. European Marine Board, Wandelaarkaai 7, Oostende 8400, Belgium.
6. Department of Zoology and The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv 69978, Israel.
7. Leon Recanati Institute for Marine Studies, Charney School for Marine Sciences, Faculty of Natural Sciences, University of Haifa, Mont Carmel, Haifa 31905, Israel.

Scientific Reports 8 (2018)

DOI: 10.1038/s441598-018-32666-x

See original publication in Annex 4

Abstract

Using a temporal-dynamic calibrated Ecosim food web model, we assess the effects of future changes on marine resources and ecosystem conditions of the Israeli Mediterranean continental shelf. This region has been intensely invaded by Indo-Pacific species. The region is exposed to extreme environmental conditions, is subjected to high rates of climate change and has experienced intense fishing pressure. We test the impacts of a new set of fishing regulations currently being implemented, a continued increase in sea temperatures following IPCC projections, and a continued increase in alien species biomass. We first investigate the impacts of the stressors separately, and then we combine them to evaluate their cumulative effects.

Our results show overall potential future benefits of fishing effort reductions, and detrimental impacts of increasing sea temperature and increasing biomass of alien species. Cumulative scenarios suggest that the beneficial effects of fisheries reduction may be dampened by the impact of increasing sea temperature and alien species when acting together. These results illustrate the importance of including stressors other than fisheries, such as climate change and biological invasions, in an ecosystem-based management approach. These results support the need for reducing local and regional stressors, such as fishing and biological invasions, in order to promote resilience to sea warming.

Keywords: Food web model, Eastern Mediterranean Sea, cumulative impacts, future scenarios.

1. Introduction

Marine ecosystems have been increasingly altered worldwide by a diversity of global, regional and local anthropogenic stressors. These stressors include climate change, biological invasions, overexploitation, pollution and habitat destruction and often co-occur in time and space and have cumulative effects (Costello et al., 2010, Halpern et al., 2015a). Such ecosystem changes can have large consequences on species abundance and distributions, marine biodiversity, and ecosystem functioning and services (Worm et al., 2006, Pereira et al., 2010, McCauley et al., 2015).

Despite increasing knowledge about the impacts of single stressors on marine populations, habitats and ecosystems, the cumulative effect of multiple stressors remains largely unknown (Crain et al., 2008, Côté et al., 2016). In addition, marine populations, habitats, and their ecosystems are affected by environmental fluctuations (Cury et al., 2008, Link et al., 2010). Therefore, understanding how multiple human threats, marine organisms, and ecosystems interact and influence each other is an issue of pressing importance. To address this challenge, a shift towards a more comprehensive analysis and management of human activities is required, as emphasised by the ecosystem-based management (EBM) approach (Rosenberg and McLeod, 2005, Leslie and McLeod, 2007).

The EBM approach has sparked great interest among the scientific community and new tools have been developed in recent decades. Within this context, ecosystem modelling approaches have increasingly been adopted as useful tools to study marine ecosystems as a whole and to forecast ecosystem dynamics and develop and test future scenarios for marine ecosystems (Fulton et al., 2011, Christensen, 2013, Acosta et al., 2016).

Ecosystem models and ecological forecasts face several obstacles linked to ecosystem characteristics and include high uncertainty (Link et al., 2012, Maris et al., 2017). Nevertheless, they have the potential to contribute significantly to achieving goals in marine conservation and management by offering guidance to decision-makers (Hyder et al., 2015). Their use in assessments, policy support, and decision-making can provide insights into how the ecosystem could respond to plausible future stressors, enabling the development of adaptive management strategies, and allowing for exploration of the implications of alternative management options (Acosta et al., 2016, Ferrier et al., 2016, Merrie et al., 2017).

One of the most commonly used ecosystem modelling software is Ecopath with Ecosim (EwE), which has been widely applied to model aquatic food webs (Heymans et al., 2014, Colléter et al., 2015). This approach has been used to hindcast and forecast future human impacts on aquatic food webs, such as fishing (Christensen and Walters, 2011), and increasingly other stressors like climate change (Ainsworth et al., 2011) and biological invasions (Pinnegar et al., 2014). EwE has been applied within the scope of evaluating cumulative impacts of human activities (Coll et al., 2015). For example, Serpetti et al. (2017) assessed the cumulative impact of sea warming and sustainable levels of fishing pressure in the West Coast of Scotland. In addition, Libralato et al. (2015) developed temporal simulations to explore the effects of the arrival of invasive species, changes in primary production and sea warming in the Adriatic Sea.

The Mediterranean Sea is a semi-enclosed sea that is highly impacted by anthropogenic activities (Costello et al., 2010, Halpern et al., 2015a). The Mediterranean is a global hotspot of alien species (Molnar et al., 2008, Costello et al., 2010, Edelist et al., 2013a), especially its eastern basin due to the opening and continuous enlargement of the Suez Canal (Katsanevakis et al., 2014b, Galil et al., 2016). Currently, 821 species are described as established alien species in the Mediterranean Sea (Zenetos et al., 2017). In addition, the high impact of fishing in the area has been shown by several analyses, indicating that most of the stocks are fully exploited or overexploited (Vasilakopoulos et al., 2014, Tsikliras et al., 2015). Climate change is also strongly affecting Mediterranean marine biota and ecosystems (Lejeusne et al., 2010, Givan et al., 2017a), mainly due to substantial temperature increases (Nykjaer, 2009, Shaltout and Omstedt, 2014). In fact, the Mediterranean is under a process of “meridionalization” and “tropicalization” of the northern and southern sectors, respectively, mainly due to the northward expansion of native thermophilic species and the introduction of (mainly tropical) alien species through the Suez Canal and the Strait of Gibraltar (Bianchi, 2007, Bianchi et al., 2013). In addition, the Mediterranean is being altered by other anthropogenic activities such as habitat loss and degradation, pollution, and eutrophication, making the Mediterranean Sea a hotspot of global change (Coll et al., 2010, Coll et al., 2012).

Within this context, the marine ecosystem of the Israeli Mediterranean coast, located in the eastern part of the basin, has been altered in recent decades mainly due to species invasions, unsustainable fishing activities, and increasing water temperature (Edelist et al., 2013a, Goren et al., 2013, Sternberg et al., 2015). As a result, great changes in its biodiversity and functioning have occurred (Edelist et al., 2013a, Galil and Goren, 2014, Katsanevakis et al., 2014b, Corrales et al., 2017a). The importance of each stressor has rarely been investigated, and available studies suggest a general strong impact of increasing sea water temperature and more specific impacts of fishing activities and alien species (Corrales et al., 2017a, Givan et al., 2017a).

Recently, new fishing regulations took effect in the Israeli Mediterranean continental shelf (hereafter referred to as ICS), which includes a reduction in fishing effort for several fleets with the aim of recovering fish stocks. However, it is expected that the rate of invasion and the impact of alien species and climate change will increase in the future due to the recent enlargement of the Suez Canal and sea warming (Albouy et al., 2013, Galil et al., 2017).

In this study, we used a temporally dynamic food web model of the ICS ecosystem (Corrales et al., 2017b), previously constructed and fitted to available time series of observational data from 1994 to 2010 (Corrales et al., 2017a), to assess potential future ecological effects of different global change scenarios. These scenarios included different fisheries management alternatives, sea warming following IPCC (Intergovernmental Panel on Climate Change) projections and projected increases in the biomass of alien species over the next 50 years (2010-2060).

2. Material and methods

2.1. Study area

The Israeli Mediterranean continental shelf (ICS) ecosystem (Fig. S1 in Annex 4) is located in the Eastern Mediterranean Sea, also known as the Levantine Sea. The Levantine Sea has the hottest, most saline and most oligotrophic waters in the Mediterranean Sea (Azov, 1991, Brasseur et al., 1996) as a result of high evaporation rates, very low riverine inputs and limited vertical mixing.

Currently, the Levantine Sea is the world’s most invaded marine ecoregion, with important effects on the food web (Edelist et al., 2013a, Goren et al., 2016). In addition, it has been suggested that intense fishing pressure has jeopardized the sustainability of fishing activities (Edelist et al., 2011). Finally, the waters of the Levantine Sea are warming at higher rates than the global average (Belkin, 2009, Nykjaer, 2009), with important effects on marine biota (Rilov, 2016, Givan et al., 2017a).

2.2.Overview of the modelling approach

The ecological modelling approach Ecopath with Ecosim (EwE) (Christensen and Walters, 2004a) was used to model the study area. The EwE approach consists of three main modules: the mass-balance routine Ecopath, the time dynamic routine Ecosim and the spatial-temporal dynamic module Ecospace. For an extensive review of EwE principles, basic concepts, capabilities and limitations, see Christensen and Walters (2004a) and Heymans et al. (2016).

The Ecopath mass-balance model was developed using EwE version 6.5 (www.ecopath.org) to characterise the structure and functioning of the ICS and to assess the past and current impact of alien species and fishing (Corrales et al., 2017b). The model covered an area of 3,725 km^2, with coastal waters up to 200 m in depth. It represented two time periods (1990-1994 and 2008-2010), including 39 and 41 functional groups, respectively, from primary producers to top predators and considers specific groups for alien species (Figure S2a; Table S1 in Annex 4) (Corrales et al., 2017b). This model took into account the main fleets operating in the area, including bottom trawl, purse seine and artisanal fisheries, and recreational fishers. Direct and indirect trophic impacts between functional groups and fleets are shown in Figure S2b in Annex 4.

Based on the Ecopath model, the time dynamic module Ecosim (Walters et al., 1997) was constructed and fitted to time series of data from 1994 to 2010. The model was used to consider the combined effect of alien species, fishing activities and changes in sea surface temperature and primary productivity (Corrales et al., 2017a). Ecosim uses a set of differential equations to describe biomass dynamics, expressed as:

$$\frac{dB_i}{dt} = \left(\frac{P}{Q}\right)_i \cdot \sum Q_{ji} - \sum Q_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i \qquad \text{(Eq. 1)}$$

where dB_i/dt is the growth rate of group (i) during time t in terms of its biomass B_i; $(P/Q)_i$ is the net growth efficiency of group (i); M_i is the non-predation mortality rate;

F_i is the fishing mortality rate; e_i is the emigration; and I_i is the immigration rate (Christensen and Walters, 2004a). Consumption rates (Q_{ij}) are calculated based on the “foraging arena” theory (Ahrens et al., 2012), which divides the biomass of a prey into a vulnerable and a non-vulnerable fraction and the transfer rate or vulnerability between the two fractions determines the trophic flow between the predator and the prey. The vulnerability concept incorporates density-dependency and expresses how far a group is from its carrying capacity (Christensen and Walters, 2004a, Christensen et al., 2008). For each predator-prey interaction, consumption rates are calculated as:

$$Qij = \frac{a_{ij} * v_{ij} * B_i * P_j * T_i * T_j * M_{ij} / D_j}{v_{ij} + v_{ij} * T_i * M_{ij} + a_{ij} * M_{ij} * P_i * T_j / D_j} * f(Env_{function}, t) \qquad \text{(Eq. 2)}$$

where a_{ij} is the rate of effective search for prey (i) by predator (j), v_{ij} is the vulnerability parameter, Ti represents prey relative feeding time, T_j is the predator relative feeding time, B_i is prey biomass, P_j is predator abundance, M_{ij} is the mediation forcing effects, and D_j represents effects of handing time as a limit to consumption rate (Christensen et al., 2008, Ahrens et al., 2012). Environmental response functions ($Env_{function}$, t), which represents the tolerance relationship of a species to an environmental parameter (here defined with a minimum and maximum levels and the 10th and 90th preferable quantiles), can be used to account for environmental drivers that change overtime, such as temperature. The intercept between the environmental response function and the environmental driver is used to calculate a multiplier factor (f) (Eq. 2), which then modifies the consumption rates of a species, or functional group, with a maximum value of 1 and declining values (and thus limiting the foraging capacity of a group) when the environmental driver deviates from the optimum values (Christensen et al., 2014b, Serpetti et al., 2017).

A time series of nominal fishing effort from the Fisheries Department of the Ministry of Agriculture and Rural Development of Israel was used to drive the model by modifying fishing mortality on targeted groups. A time series of annual sea surface temperature (SST, upper 30 meters) from 1994 to 2010 and temperature response functions were used to drive the temporal dynamics of sensitive functional groups with available information (mostly crustaceans and fish groups) (Corrales et al., 2017a). Time series of SST were obtained from the Mediterranean Forecasting System Copernicus (http://marine.copernicus.eu/). Environmental response functions, which here determine optimum temperatures and thermal tolerance, were obtained initially from AquaMaps (Kaschner et al., 2006) and were modified incorporating expert local knowledge (see Corrales et al. (2017a) and Table S2 in Annex 4 for further details).

2.3. Simulation of future scenarios

We used the temporal dynamic module Ecosim to evaluate the effect of plausible future scenarios for major stressors in the area (Table 1). With the exception of the two new alien groups (new alien demersal fishes and alien medium pelagic fishes), we used the original Ecosim configuration that was fitted to the time series of data (Corrales et al., 2017a). For these two new alien groups, low vulnerability values had been estimated by the model in the fitting procedure, impeding a further increase in biomass of these groups in the future. As a continuous increase in biomass of these groups is expected, we applied a high vulnerability value (v = 10) to them to allow a larger change in the baseline predation mortality. All future scenarios were run for 50 years, from 2010 to 2060, and included variations of different stressors (Table 1). Primary production, in the absence of information about projected potential changes, was kept constant in all the scenarios from 2010 to 2060.

Table 1. List of scenarios and stressor conditions.

Scenario	Name	Fishing	Temperature	Alien species
1	BAU (business as usual)	Kept at 2010 levels	Kept at 2010 level	Model predicts
2	Israeli regulation	New Israeli regulations	Kept at 2010 level	Model predicts
3	Stop trawl	New Israeli regulations + stop trawl in 3 years	Kept at 2010 level	Model predicts
4	Israeli regulation (alien spp. constant)	New Israeli regulations	Kept at 2010 level	Force (kept at 2010 levels)
5	RCP2.6	Kept at 2010 levels	Best-case	Model predicts
6	RCP4.5	Kept at 2010 levels	Intermediate	Model predicts
7	RCP8.5	Kept at 2010 levels	Worst-case	Model predicts
8	Increase alien species	Kept at 2010 levels	Kept at 2010 level	Force (increase)
9	Combination (no forcing of alien spp.)	New Israeli regulations	Intermediate	Model predicts
10	Combination (forcing of alien spp.)	New Israeli regulations	Intermediate	Force (increase)
11	Combination (forcing alien spp. constant)	New Israeli regulations	Intermediate	Force (kept at 2010 levels)

The original configuration of the dynamic model was used as a baseline simulation (Business as usual (BAU)) (**Scn1**). We then assessed the impact of various fisheries management strategies while keeping constant temperature levels from 2010 to 2060. **Scn2** included the new fishing regulations approved by the Fisheries Department of the

Ministry of Agriculture and Rural Development of Israel in 2016. These regulations, among other components, consist of a reduction in fishing efforts for the trawling and artisanal sectors and impose restrictions on the recreational fishers. For the trawl fleet, a complete cessation of its activity between April and June was implemented. In addition, the trawl fleet in the northern part of the country is to be mostly eliminated. These two regulations were implemented in our scenario and represented a reduction in trawl effort of nearly 50% (Fig. 1a). For the artisanal fleet, a ban between April and May was implemented and implied a reduction in fishing effort of nearly 15% (Fig. 1a). For recreational fishers, the new regulation restricted their capacity to a maximum catch of 5 kg per day. In the absence of detailed data about recreational effort and being conservative, a reduction of 20% of the effort was applied (Fig. 1a). In addition, some sectors of the Israeli society have called for a ban of trawling altogether. Therefore, we ran a scenario that applies the new fishing regulations with trawling eliminated within the first 3 years of the simulation (Fig. 1b) (**Scn3**). In addition, to quantify only the effects of these new fishing regulations, we ran a scenario keeping the biomass of alien species and temperature constant from their 2010 levels to 2060 (**Scn4**).

To predict the impact of sea warming on the ICS ecosystem, future SST projections of the study area were obtained from the Royal Netherlands Meteorological Institute Climate explorer (http://climexp.knmi.nl). We calculated SST projections under the four scenarios of greenhouse emissions (RCP2.6, RCP4.5, RCP6 and RCP8.5). As SST from this explorer did not match the SST from COPERNICUS, we calculated SST anomalies for the 2010-2060 period and these SST anomalies were applied to the COPERNICUS time series (Fig. 1c). Due to similar trends of the intermediate scenarios (RCP4.5 and RCP6), we applied only the RCP4.5 scenario. Therefore, the scenarios conducted to simulate potential impacts of sea warming were RCP2.6 (**Scn5**), RCP4.5 (**Scn6**) and RCP8.5 (**Scn7**). In these scenarios, fishing effort was kept constant from its 2010 levels to 2060.

To forecast future impacts of alien species, we forced the biomass of alien groups to follow current trends (Fig. S3 in Annex 4), while keeping fishing effort and SST constant from their 2010 levels to 2060 (**Scn8**).

In addition, we evaluated the combined impacts of the stressors simultaneously through three scenarios. In **Scn9** (combination without forcing alien species), we merged scenarios 2 and 6, thus combining the new fishing regulations with an intermediate increase in SST, and we left alien species to change through the time (we did not force their biomass). In **Scn10** (combination with forcing alien species), we merged scenarios 2, 6 and 8, thus combining the new fishing regulations, the intermediate increase in SST and an increase in the biomass of alien species following current trends. In **Scn11** (combination with forcing alien species constant), we merged scenarios 2 and 6, thus combining the new fishing regulations, the intermediate increase in SST, and we force alien species to keep them at 2010 levels.

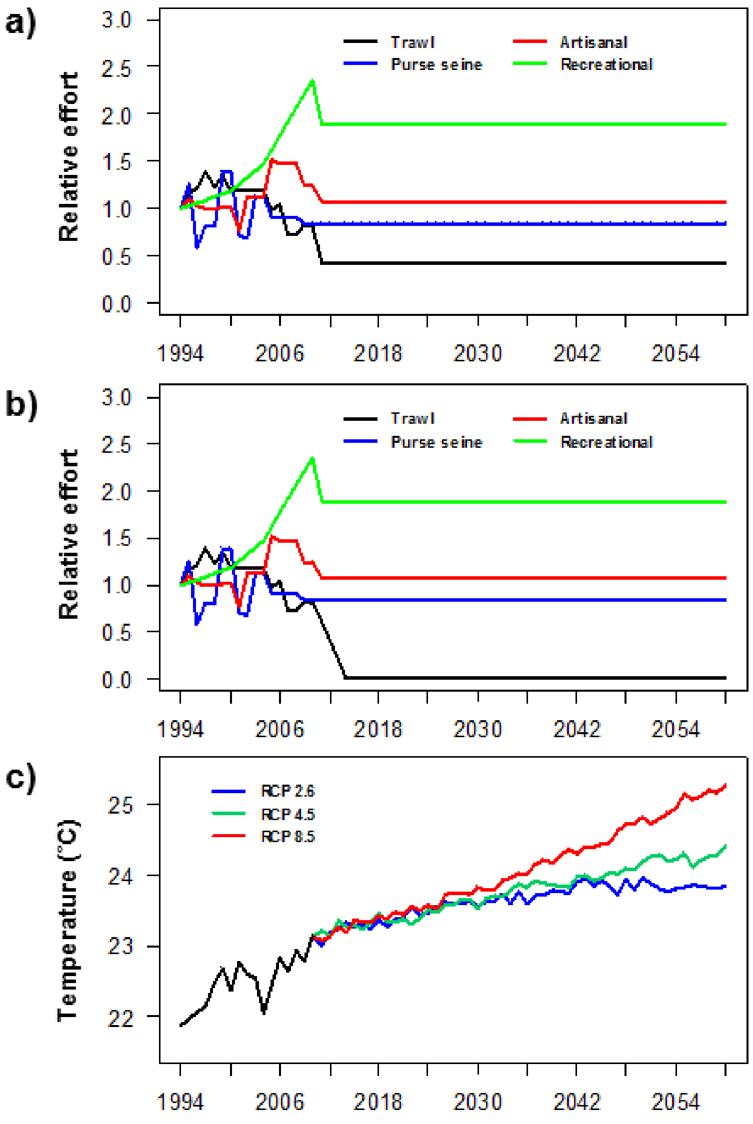


Fig. 1. Stressors in the Israeli Mediterranean continental shelf (ICS) ecosystem for the period 1994-2060 considered in this study: (a) relative fishing effort by fleet as a result of the application of the new Israeli law starting in 2010 in the simulations; (b) relative fishing effort by fleet as a result of the application of the new Israeli law with the closure of the trawl fleet after three years of reduction from 2010; and (c) historical annual sea surface temperature (black line) and its projection under the three scenarios of IPCC projections.

2.4. Analysis

We analysed changes in the biomass of selected functional groups. These groups were chosen taking into account their inclusion in the time series fitting (see Corrales et al. (2017a)) and considering their importance (economic and ecological importance, such as commercial species and vulnerable species). In addition, functional groups were aggregated taking into account their ecological role, taxonomy, habitat and between alien and native functional groups. Therefore, we defined separate groups as primary producers, zooplanktonic species, invertebrates, fishes and vulnerable species (which included sea turtles, sea birds and dolphins). Invertebrates and fishes were split into native and alien groups, and fishes were also divided between demersal and pelagic.

In addition, a selection of ecological indicators was used to evaluate the impacts of ecological changes on the ecosystem over time:

(13) Total biomass (excluding detritus) ($t{\cdot}km^{-2}$), which included biomass of all the functional groups excluding detritus (detritus and discards). This indicator was used to quantify changes at the whole ecosystem level (Heymans et al., 2014).

(14) Forage fish biomass ($t{\cdot}km^{-2}$), which included the biomass of benthopelagic fishes, small pelagic fishes, mackerel and horse mackerel. This indicator was analysed to quantify changes in the pelagic compartment (Hilborn and Walters, 1992).

(15) Invertebrate biomass ($t{\cdot}km^{-2}$), which included biomass of benthic invertebrate groups. This indicator was used to assess the dynamics of benthic invertebrates in the ecosystem, which tends to benefit from reductions in fish and predator biomass (Pauly et al., 1998).

(16) Predatory biomass ($t{\cdot}km^{-2}$), which included biomass of all the groups with $TL \geq 4$ and tends to decrease with increasing fishing impact in marine ecosystems (Rochet and Trenkel, 2003).

(17) Kempton’s index, which expresses biomass diversity by considering those organisms with trophic levels ≥ 3 and tends to decrease with ecosystem degradation (Kempton and Taylor, 1976).

(18) Total catch (t·km^{-2}·year^{-1}), which includes the annual catches of the different fleets and provides an idea of total fisheries removals (Hilborn and Walters, 1992).

(19) Mean Trophic Level of the catch (mTLc), which expresses the TL of the catch, reflects the fishing strategy of the fleet and is used to quantify the impact of fishing (Pauly et al., 1998).

(20) Mean Trophic Level of the community (mTLco), which expresses the Trophic Level (TL) of the whole ecosystem, reflects the structure of the ecosystem and is used to quantify the impact of fishing (Rochet and Trenkel, 2003) .

(21) Total System Throughput (t·km^{-2}·year^{-1}) (TST), which estimates the total flows in the ecosystem and is a measure of ecosystem size (Ulanowicz, 1986).

(22) Finn’s Cycling Index (FCI, %), which represents the proportion of the TST that is recycled in the system and is an indicator of stress and structural differences (Finn, 1976).

(23) Path length (PL), defined as the average number of compartments through which a unit of inflow passes, which is an indicator of stress (Christensen, 1995).

2.5. Assessing uncertainty

Monte Carlo simulations and the Ecosampler plug-in were used to evaluate the impact of uncertainty in Ecopath input parameters (biomass, production and consumption rates) on Ecosim outputs (biomass and catch trends, and ecological indicators) (Heymans et al., 2016, Coll and Steenbeek, 2017, Steenbeek et al., 2018). We ran 500 Monte Carlo simulations for each scenario based on input parameter pedigree, which documents the quality of the input data (see Table S3 in Annex 4 for confidence intervals of all input parameter), to determine the 5% and 95% confidence intervals for Ecosim outputs. Finally, a Spearman’s rank correlation test implemented in R software v 3.4.2 was used to assess the correlation between model outputs (predicted results without uncertainty analysis) with time.

3. Results

3.1. Baseline scenario

Under the baseline simulation (Scn1), the model predicted a decreasing biomass trend over time for the biomass of several groups (Fig. 2 and 3). Alien invertebrates significantly decreased (Fig. 3), due to the depletion of alien crabs and shrimps (Fig. 2). Other medium trophic level organisms, such as goatfishes and small native demersal fishes, suffered significant large declines (Fig. 2). These decreases were due to the increase of various predators and competitors (for trophic interactions, see Fig. S2b in Annex 4 (hereafter referenced only as Fig. S2b)) and current negative impacts of sea warming. For example, small native demersal fishes decreased due to the increase of competitors such as earlier and new alien demersal fishes (Fig. S2b and 2), the increasing predation of alien lizardfish (Fig. 4f) and the negative impact of current SST. The model also showed a significant large decline of large demersal native fishes due to their overexploitation (Fig. 4d). In addition, vulnerable species such as turtles and seabirds were projected to significantly decrease (Fig. 2 and 3), due to the notable impact of fishing activities on their populations (Fig. S2b).

In contrast, the model predicted significant large increases in alien fishes (both demersal and pelagic) (Fig. 3), such as earlier and new alien demersal fishes, alien lizardfish and alien medium pelagic fishes (Fig. 2 and 4e). This may be due to their earlier overexploitation prior to the reduction in fishing effort between 2007 and 2010, which is mainly due to a recent decreasing activity of trawl fleet (the most important fleet in the area). This follows current biomass increases due to possible empty niches and the depletion of native competitors (Fig. S2b). Mullets (Fig. 4a), sharks and rays (Fig. 2) significantly increased over time. This may be due to the decline in the fishing effort between 2007 and 2010.

Within this scenario, forage fish and invertebrate biomass decreased significantly with time while predatory biomass and total catch significantly increased over time (Fig. 5). Community indicators, such as mTLco and mTLc, and indicators related to ecosystem development theory such as TST and FCI significantly decreased with time, while PL significantly increased (Fig. 5).

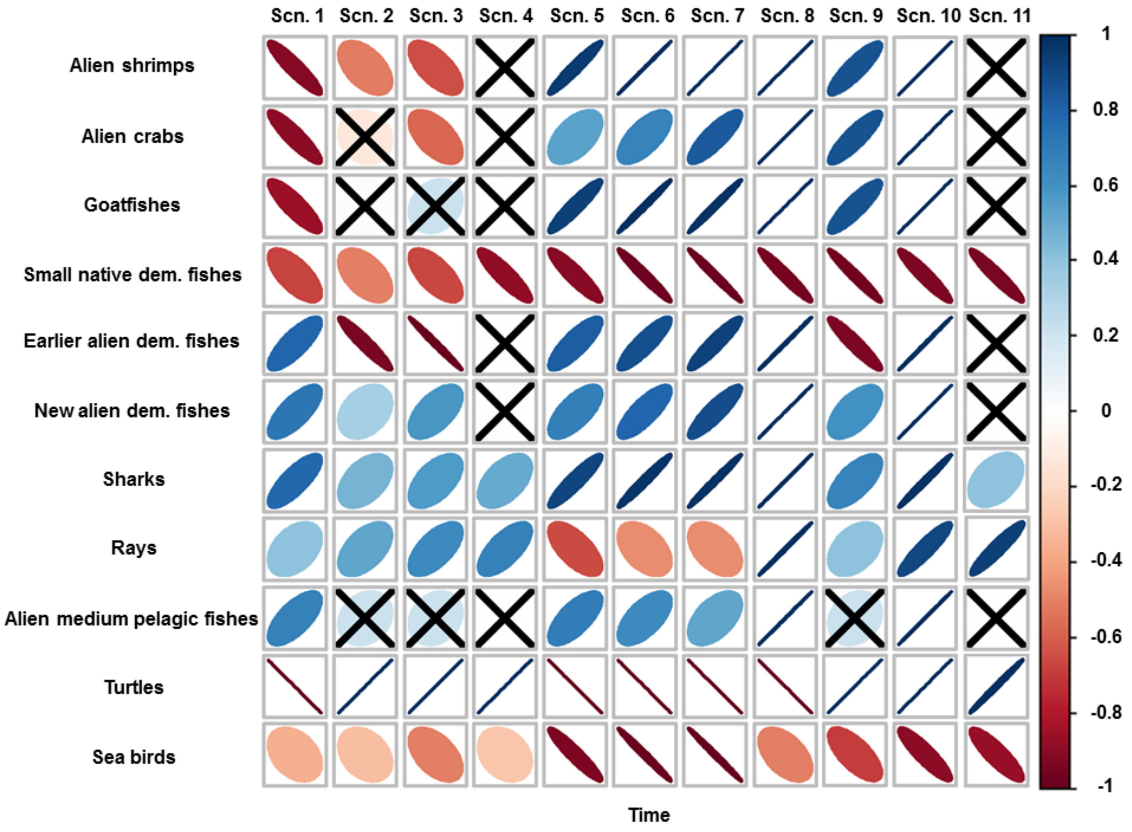


Fig. 2. Spearman's rank correlation between selected biomasses of functional groups and time for the ten future scenarios (Table 1). Positive correlations are in blue and negative correlations in red. Legend colour shows the correlation coefficient and its correspondent colour gradient. Colour intensity and the size of the ellipses are proportional to the correlation coefficients, with more diffused and wider ellipses representing lower correlation strengths. When the indicator is non-significant (>0.05), it is represented with an "X" symbol.

3.2.Fishing scenarios

Under scenarios that only included changes (decreases) in fishing effort (Scn2 and Scn3), the model predicted mixed trends with both significant large decreases and increases in medium trophic level groups and significant large increases in high trophic level groups (Fig. 2). For example, alien invertebrates significantly decreased while vulnerable species significantly increased (Fig. 3). Alien shrimps, small native demersal fishes, earlier alien demersal fishes and alien herbivores significantly decreased over time (Fig. 2 and 4e). This is due to the increasing predation mortality as a consequence of the recovery of top predators (Fig. S2b) and also, in some cases, a result of negative impacts of sea warming. In addition, the model predicted a significant decrease of sea birds due to the fewer discards caused by the reduction of the trawl fleet (Fig. 2). In contrast, the model predicted significant large increases of top predators, such as hake, large native demersal fishes, alien lizardfish, demersal sharks and rays and skates (Fig. 2 and Fig. 4b,d,f). The model also showed increasing trends for mullets, new alien demersal fishes and turtles (Fig. 2 and Fig. 4a), due to the reduction in fishing effort. Most of these trends were exacerbated in Scn3, with the closure of the trawl fleet. For example, the model predicted major and faster recoveries for mullets, hake, large native demersal fishes and alien lizardfish (Fig. 4a,b,d,f), while alien shrimps, small native demersal fishes, earlier alien demersal fishes and sea birds had stronger negative impacts (Fig. 2).

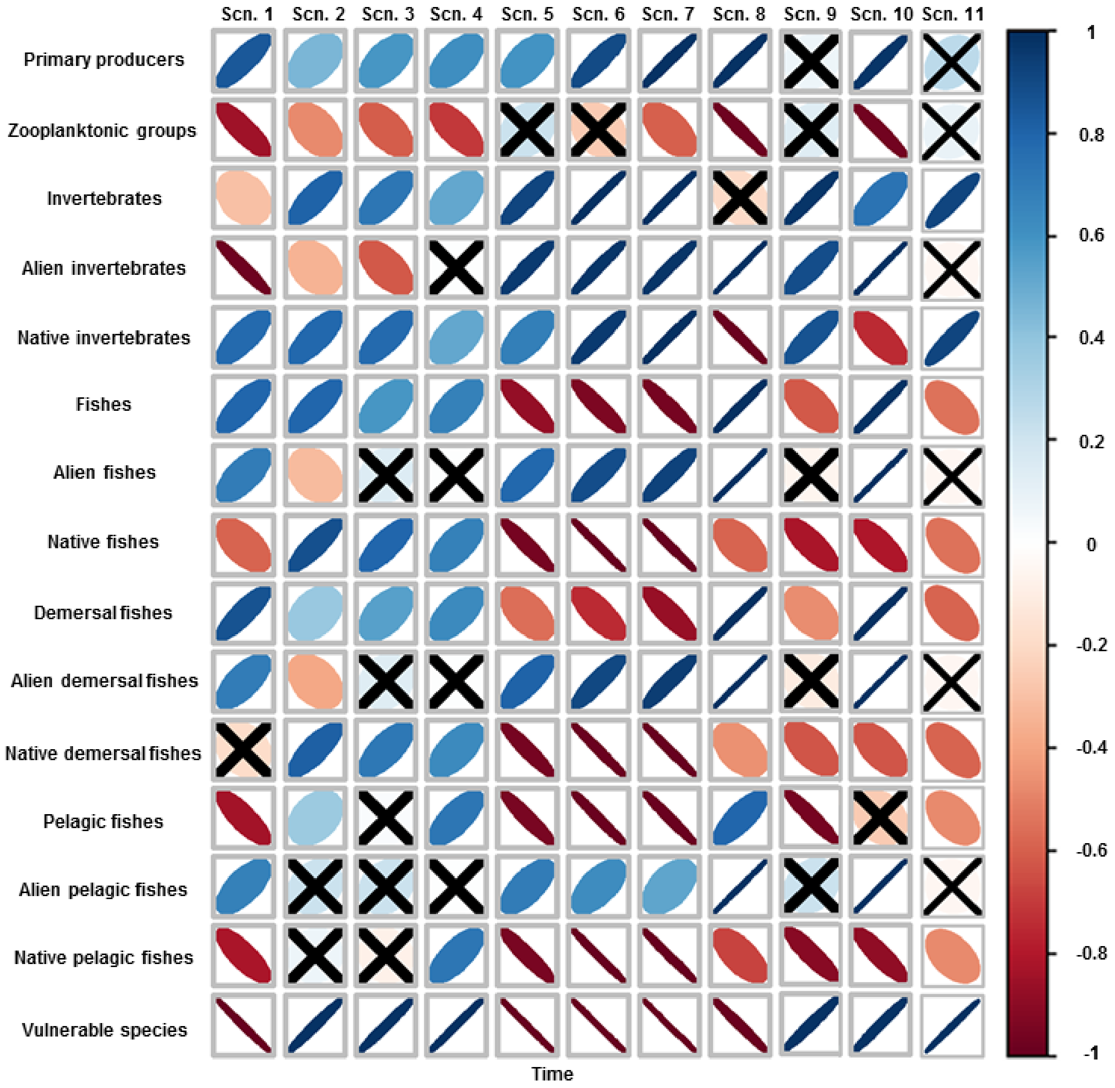


Fig. 3. Spearman's rank correlation between the biomass of aggregated groups and time for the ten future scenarios (Table 1). Positive correlations are in blue and negative correlations in red. Legend colour shows the correlation coefficient and its correspondent colour gradient. Colour intensity and the size of the ellipses are proportional to the correlation coefficients, with more diffused and wider ellipses representing lower correlation strengths. When the indicator is non-significant (>0.05), it is represented with an "X" symbol.

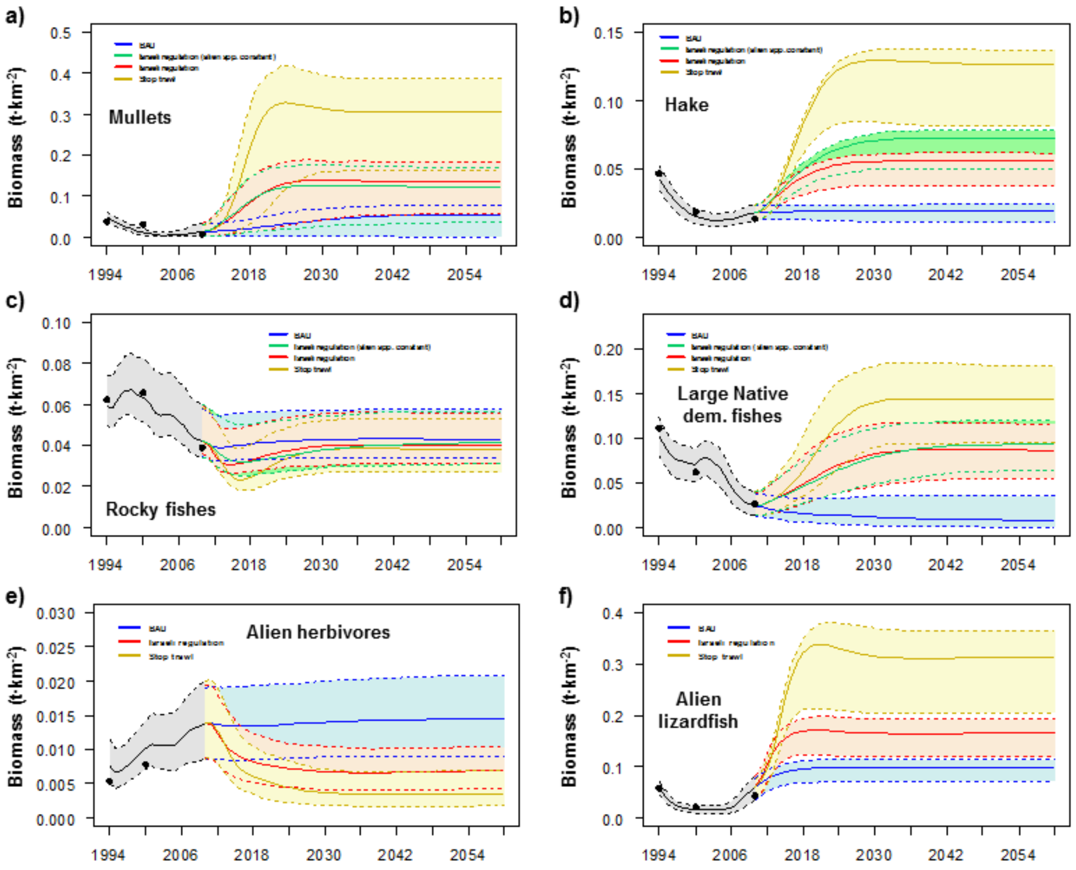


Fig. 4. Comparison between the predicted (solid lines) and observed (dots) time series of biomass (t·km^2), and scenarios results for (a) mullets, (b) hake, (c) rocky fishes, (d) large native demersal fishes, (e) alien herbivores and (f) alien lizardfish under different future scenarios of fishing for the Israeli Mediterranean continental shelf (ICS) ecosystem model for the period 1994-2060. Black line represents historical model predictions and coloured lines represent different scenarios. Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

Under Scn4, which assessed the impacts of the new fishing regulations while keeping the biomass of alien species constant, the model showed important effects of alien species. For example, hake and large native demersal fish presented better recoveries than in Scn2 (Fig. 4b, d). For hake, this may be due to competition for resources with alien lizardfish, while for large native demersal fishes it may be due to a higher abundance of their key prey, such as rocky fishes, small native demersal fishes and earlier alien demersal fishes.

Within these three scenarios (Scn2, Scn3 and Scn4), most of the ecological indicators presented significant increasing trends (Fig. 5). For example, total biomass, invertebrate biomass, predatory biomass and total catch showed significant increasing trends (Fig. 5). In addition, mTLco and mTLc significantly increased (Fig. 4). FCI significantly increased in all scenarios while PL had non-significant trends in Scn2 and Scn3 and decreased in Scn4 (Fig. 5).

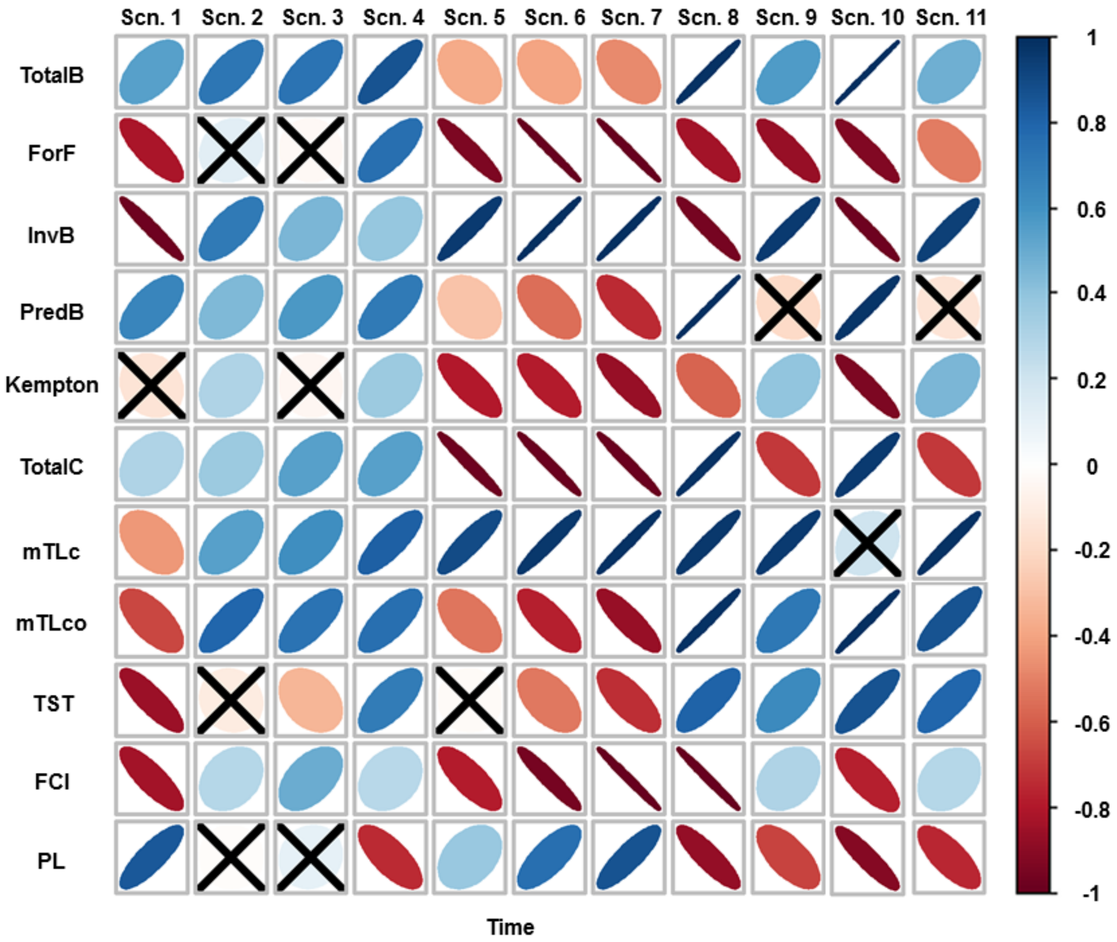


Fig. 5. Spearman's rank correlation between the ecological indicators analysed and time for the ten scenarios (Table 1). Positive correlations are in blue and negative correlations in red. Legend colour shows the correlation coefficient and its correspondent colour gradient. Colour intensity and the size of the ellipses are proportional to the correlation coefficients, with more diffused and wider ellipses representing lower correlation strengths. When the indicator is non-significant (>0.05), it is represented with an "X" symbol. TotalB= Total biomass (t·km^{-2}); ForF = Forage fish (t·km^{-2}); InvB = Invertebrate biomass (t·km^{-2}); PredB = Predatory biomass (t·km^{-2}); Kempton = Kempton's index; TotalC = Total catch (t·km^{-2}·year^{-1}); mTLco = mean Trophic Level of the community; mTLc = mean Trophic Level of the catches; TST = Total System Throughput (t·km^{-2}·year^{-1}); FCI = Finn's Cycling Index (%); PL = Path length.

3.3.Sea warming scenarios

Under scenarios of sea warming (Scn5, Scn6 and Scn7), the model predicted different responses of species to rising SST (Fig. 2). The model showed significant increases of alien invertebrates and alien fishes (both demersal and pelagic), while native fishes (both demersal and pelagic) and vulnerable species decreased (Fig. 3). These trends were exacerbated as temperature increased (Fig. 2 and 3).

For specific groups, the model predicted significant increasing trends for alien shrimps, alien crabs, goatfishes, earlier and new alien demersal fishes and sharks (Fig. 2). These increases may be due to the depletion of competitors and predators (Fig. S2b). In contrast, small native demersal fishes declined due to unfavourable thermal conditions, and rays and skates were projected to strongly decline (Fig. 2). A total collapse of mullets was predicted under the intermediate and worst IPCC projections (Fig. 6a), while hake and rocky fishes were predicted to be almost depleted in the worst case of sea warming (Fig. 6b, c). Large native demersal fishes were projected to be positively impacted as temperature increases (Fig. 6d), although they showed negative trends due to their overexploitation. Alien herbivores and alien lizardfish biomass significantly increased in all climate scenarios, with major increases as temperature rose except for the alien lizardfish in the worst-case scenario (Fig. 6e, f)

Within these scenarios, we observed significant decreasing trends for most of the ecological indicators, with stronger correlations as temperature increased (Fig. 5). However, invertebrate biomass, mTLc and PL showed increasing trends (Fig. 5).

3.4.Alien species scenario

Under the scenario that assessed the impact of alien species forced to follow current biomass trends (Scn8), the model predicted strong impacts on the food web (Fig. 2 and 3). Within this scenario, native invertebrates, native fishes (both demersal and pelagic) and vulnerable species declined significantly (Figure 3).

For specific groups, the model predicted significant decreases of small native demersal fishes due to current thermal conditions and increasing predation mortality and competition (Fig. S2b). Similarly, turtles and sea birds declined due to a decline of their main prey (Fig. S2b and 2). Mullets were predicted to be slightly negatively impacted, due to their initial recovery as a result of the decreasing fishing effort in 2007-2010 and the negative impacts of alien species (Fig. S2b and 7a). Rocky fishes declined significantly, due to a higher abundance of competitors and predators (Fig S2b and 7c). In contrast, hake and large native demersal fishes (Fig. 7b, d) as well as demersal sharks and rays and skates (Fig. 2) significantly increased. This may be due to reduced fishing activities and a higher abundance of alien prey (Fig. S2b), although native prey exhibited opposite trends (Fig. 3).

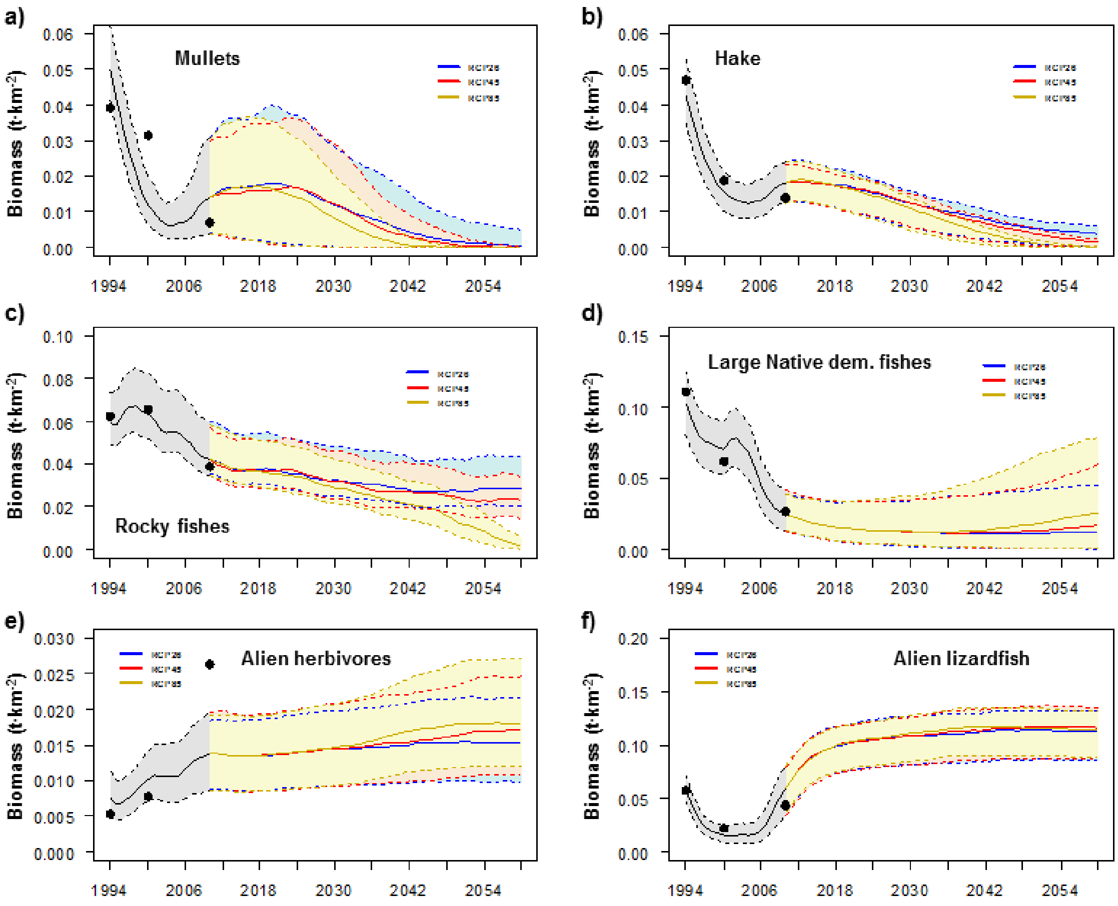


Fig. 6. Comparison between the predicted (solid lines) and observed (dots) time series of biomass (t·km^2), and scenarios results for (a) mullets, (b) hake, (c) rocky fishes, (d) large native demersal fishes, (e) alien herbivores and (f) alien lizardfish under different future scenarios of climate change for the Israeli Mediterranean continental shelf (ICS) ecosystem model for the period 1994-2060. Black line represents historical model predictions and coloured lines represent different scenarios. Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

Under this scenario, total biomass, predatory biomass and total catch significantly increased (Fig. 5). In contrast, forage fish, invertebrate biomass and Kempton's index significantly decreased (Fig. 5). FCI and PL were projected to decline significantly, while TST increased (Fig. 5).

3.5.Cumulative scenarios

When assessing the cumulative effects of new Israeli fishing regulations and an intermediate scenario of an increase in SST, while alien species biomass was not forced (Scn9), the model projected biomass increases for native invertebrates, alien groups (both invertebrates and fishes) and vulnerable species, while the biomass of native fishes (both demersal and pelagic) significantly decreased (Fig. 3). For specific groups, the biomass of some significantly increased such as alien shrimps and crabs, goatfishes, new alien demersal fishes, demersal sharks, rays and skates, and turtles (Fig. 2). In addition, significant increases were observed for hake, large demersal fishes and alien lizardfish, but their recoveries were of a lower magnitude than Scn10 due to the limitation of alien prey (Fig. 8b, d, f). In fact, hake declined at the end of the simulation due to sea warming (Fig. 8b). In contrast, the biomass of small native demersal fishes, earlier alien demersal fishes and sea birds significantly decreased (Fig. 2). In addition, the model predicted significant declines in mullets and rocky fishes (Fig. 8a, c), although they showed better trajectories than Scn10, due to lower impacts of alien species. Alien herbivores also declined (Fig. 8e), due to recoveries of predators (both native and alien) (Fig. S2b).

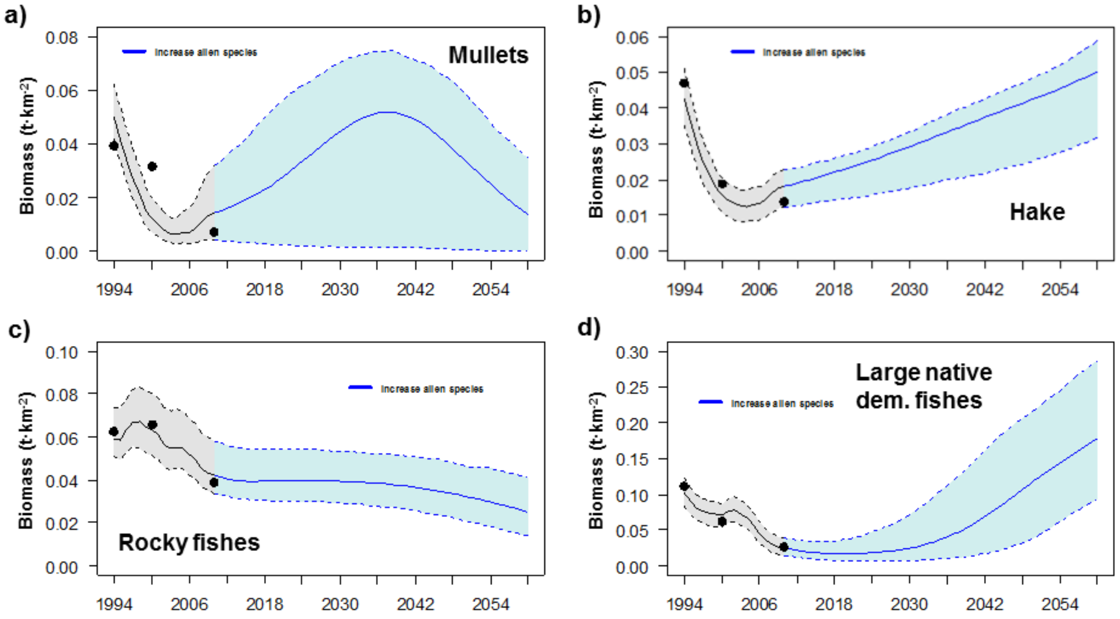


Fig. 7. Comparison between the predicted (solid lines) and observed (dots) time series of biomass (t·km^2), and scenarios results for (a) mullets, (b) hake, (c) rocky fishes (or small native demersal fishes) and (d) large native demersal fishes under the future scenario of increasing the biomass of alien species for the Israeli Mediterranean continental shelf (ICS) ecosystem model for the period 1994-2060. Black line represents historical model predictions and coloured lines represent different scenarios. Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

Under this scenario, total biomass, invertebrate biomass, mTLc and mTLco significantly increased, while forage fish and total catch significantly declined (Fig. 5). TST and FCI were projected to increase, while PL declined (Fig. 5).

When assessing the cumulative effects of the new Israeli fishing regulations, the intermediate scenario of sea warming and an increase in alien biomass following current trends (Scn10), the model predicted a significant decreasing pattern of native invertebrates and native fishes (both demersal and pelagic), while vulnerable species significantly increased (Fig. 3). Several groups that were negatively affected included small native demersal fishes and sea birds (Fig. 2). In addition, the model predicted a near collapse of mullets (Fig. 8a), despite the reduction of fishing effort, and a significant decline of rocky fishes (Fig. 8c). In contrast, demersal sharks, rays and skates and turtles significantly increased (Fig. 2). In addition, hake and large native demersal fishes were predicted to increase (Fig. 8b, d), mainly due to reduced fishing effort and a higher abundance of alien prey (Fig. S2b), although native prey significantly declined and there was negative impact of SST on hake.

Within this scenario, forage fish, invertebrate biomass and Kempton’s index significantly decreased, while predatory biomass, total catch and mTLco significantly increased (Fig. 5). FCI and PL were projected to decline significantly, while TST increased (Fig. 5).

Finally, under the assessment of the cumulative impact of the new Israeli fishing regulations and the intermediate scenario of sea warming, while keeping the biomass of alien species constant (Scn11), the model highlighted the important effects of alien species. For example, native invertebrates increased more than in Scn9 and native fishes decreased less than Scn9 and Scn10 (Fig. 3). For specific groups, small native demersal fishes decreased less than Scn9 and Scn10 (Fig. 2). Hake presented a better trajectory than Scn9 (Fig. 8b). This could be due to a less competition for resources with alien lizardfish, which biomass was kept at constant population levels. However, it presented a worst trajectory than Scn10 (Fig. 8), which could be due less prey availability. On the other hand, large native demersal fishes presented a worse trajectory than Scn9 and Scn10 (Fig. 8d), which could be also due to less prey availability. Mullets and rocky fishes presented similar trajectories than Scn9 (Fig. 8a,c), which may be related to similar predation rates and competition for resources in both scenarios.

Within this scenario, ecological indicators presented similar trends to Scn9 (Fig. 5). In several cases slightly better trends than Scn9 were observed, such as in forage fish, Kempton's index, mTLc and mTLco, while total catch and PL presented slightly worse trends than Scn9 (Fig. 5).

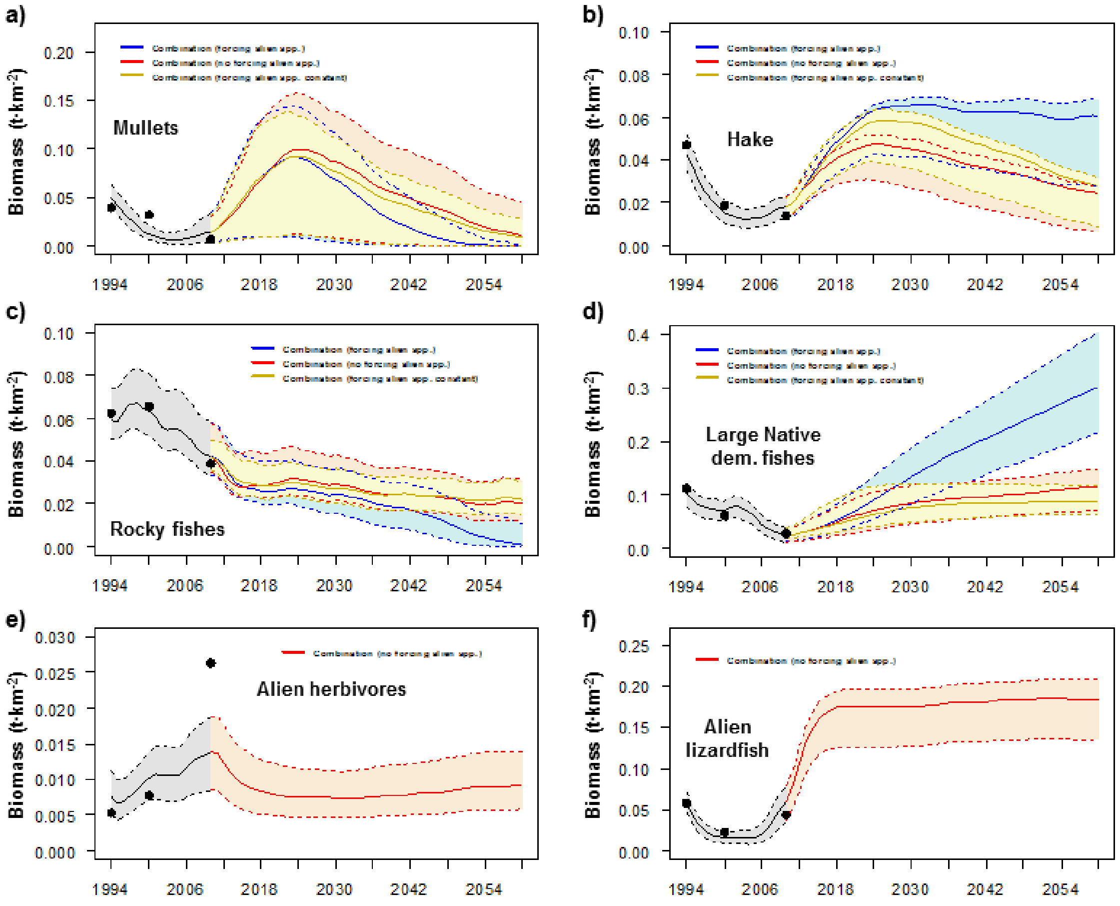


Fig. 8. Comparison between the predicted (solid lines) and observed (dots) time series of biomass (t·km^2), and scenarios results for (a) mullets, (b) hake, (c) rocky fishes, (d) large native demersal fishes, (e) alien herbivores and (f) alien lizardfish under different future scenarios of a combination of stressors for the Israeli Mediterranean continental shelf (ICS) ecosystem model for the period 1994-2060. Black line represents historical model predictions and coloured lines represent different scenarios. Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine. Scenarios that include forcing of the biomass are not shown.

3.6.Common patterns of future scenarios

In general, primary producers increased in most of the scenarios (Fig. 3). This can be attributed to the decrease of zooplanktonic groups in most of the scenarios (Fig. 3), which is due to increased predation on these groups. Alien invertebrates decreased in scenarios that only fishing reductions were applied while increasing in the other scenarios (Fig. 3). This can be attributed to increasing predation and decreasing predation and competition, respectively. Alien fishes increased in all scenarios due to reductions of competition and predators except in Scn2 (Fig. 3), where there is a large decrease in earlier alien demersal fishes attributed to higher predation rates (Fig. 2). New alien demersal fishes increased in all the scenarios, which may due to fishing reductions and/or the decrease of competition (both native and alien groups). Native fishes decreased in all scenarios except those scenarios where only fishing reductions were applied (Fig. 2). Specifically, small native demersal fishes decreased in all scenarios. This general pattern is due to unfavorable thermal conditions, while for specific scenarios we can add increasing predation (fishing reductions) and competition for resources (alien species scenarios) or both (cumulative scenarios) as the main drivers of the ecological patterns. Vulnerable species increased in all scenarios that implied reductions in fishing activities (Fig. 3), although sea birds decreased in all scenarios (Fig. 2).

4. Discussion

In the current context of global change and ecological crisis, there is an increasing demand for approaches that can forecast potential impacts of human stressors, in addition to environmental pressures (Maris et al., 2017). In this study, we used a temporal dynamic food web model for the Israeli Mediterranean continental shelf that accounted for different environmental and human impacts, such as sea warming, fisheries and alien species, to assess potential futures of marine resources and ecosystem conditions of the Eastern Mediterranean Sea. Despite several limitations, this study represents to our knowledge the first attempt to evaluate potential impacts of future conditions in the Eastern Mediterranean Sea in an ecosystem context combining different global change stressors.

Our results highlight that under current conditions (the baseline scenario) several species will remain depleted or even greatly decline, due to unfavourable thermal conditions, increasing impacts of alien species, and unsustainable fishing activities. Meanwhile, alien groups will continue to increase in abundance, as many of these species have higher thermal tolerances. This general degradation of the system is also captured by the decline of ecological indicators linked with ecosystem condition, such as mTLc, mTLco and FCI. These results are in line with Corrales et al. (2017a), where results indicated a historical degradation pattern of the food web over the last two decades (1990-2010) due to the impacts of alien species, climate change and fishing. However, other ecological indicators increased, such as total biomass, predatory biomass and PL. This could be due to the fact that reductions of native species in terms of biomass and path lengths are compensated by the increase of alien species.

In contrast, when fishing effort for several fleets was reduced, our results highlighted a potential restoration of several exploited groups including commercially important species such as hake, mullets and large native demersal fishes, and some vulnerable species such as sharks and rays and skates. Alien groups (fish and crustaceans) were negatively impacted, mainly due to the recovery of predators, while native groups were positively affected. This overall improvement of some marine resources was captured by several ecological indicators that showed a trend of increasing values, such as the predatory biomass, Kempton’s Index, mTLc, mTLco and FCI.

Fishing has been identified as one of the main stressors on marine ecosystems (Jackson et al., 2001, Lotze et al., 2006), and studies have shown the potential benefits of fishing reduction (Worm et al., 2009, Lotze et al., 2011b). Our results highlighted the benefits of reducing fishing activities on the exploited marine organisms and ecosystem in the Eastern Mediterranean Sea, and support the call for a reduction in fishing capacity and exploitation levels worldwide if marine resources are to recover (Pauly et al., 2002, Worm et al., 2009).

The scenarios of sea warming showed potential detrimental impacts on the food web, with the impacts becoming greater as temperature increased. Within these scenarios, native species were negatively impacted, and we observed some collapses, while alien species were favoured. In line with this, several ecological indicators, including Kempton’s Index, mTLco and FCI suggested a potential degradation of the ecosystem. Predicted collapses of some native species in this study may not indicate a total collapse of the species in the Eastern Mediterranean Sea, but may indicate that if these species are to persist in the ecosystem, they may have to migrate to northern areas or to deeper and cooler waters outside of the modelled area, or they will have to adapt. Shifts in species distributions (latitudinal and bathymetric) in relation to climate change have been observed and predicted in many areas of the world (Pörtner and Peck, 2010, Stuart-Smith et al., 2015, Poloczanska et al., 2016). Bathymetric shifts and species collapses have been observed recently in the study area associated with sea warming and the proliferation of alien species (Edelist et al., 2013a, Rilov, 2016). In addition, several studies have predicted important changes in species distributions due to sea warming in the Mediterranean Sea (Ben Rais Lasram et al., 2010, Albouy et al., 2013). In fact, the increasing importance of alien species (thermophilic biota) concurrent with sea warming has led to the tropicalization of the Mediterranean biota (Bianchi, 2007).

Our projections of the impact of sea warming present some limitations. For example, the temperature response/preferences used in our study are subject to uncertainty, as they came from a global database (AquaMaps) (Kaschner et al., 2006), although we did incorporate local knowledge to adapt the global responses to local conditions (see Corrales et al. (2017a) for more details). In addition, due to the lack of information on the responses to the explanatory variable change, our model did not incorporate salinity, which has been suggested as an important environmental factor in the study area (Mavruk and Avsar, 2008). Also, other impacts of climate change were not considered. For example, ocean acidification, which mainly acts on invertebrates and basal species, can have strong impacts on the food web (Orr et al., 2005, Fabry et al., 2008). Furthermore, our model does not account for the possible acclimatization, selection, and adaptation of species to climate change. Correctly predicting the impacts of climate change on marine organisms and ecosystems remains challenging due to a general lack of knowledge about the capacity of organisms to adapt to rapid climate change (Munday et al., 2013). In addition, our model is a temporal-dynamic representation of the ecosystem and does not explicitly incorporate spatial dynamics (such as movement of species) and therefore the potential movement of species to deeper waters or latitudinal (northward) shifts are not captured. Within this context, the new habitat foraging capacity model of the spatial-temporal module of EwE, Ecospace (Steenbeek et al., 2013, Christensen et al., 2014b), has provided a step forward for temporal-spatial modelling by combining species distribution and food web models. As new information becomes available, our modelling exercise should be updated and improved, so model predictions would become increasingly valuable for understanding cumulative impacts within a spatial-temporal dynamic framework.

Our results highlighted the potential negative impacts of alien species on marine species and food webs, either when extrapolating current trends to the future, or when allowing EwE to predict their future abundance. Alien species proliferation causes the collapse of small native demersal fishes and a degradation pattern in the food web, as shown by different ecological indicators (i.e., predatory biomass, Kempton’s index, mTLco, FCI and PL). Biological invasions are considered a major threat to local biodiversity (Molnar et al., 2008, Katsanevakis et al., 2014c). Although no complete extinctions have yet been reported in the Mediterranean Sea as a direct result of alien species, there are many examples of sudden declines and local extirpations of native species concurrent with the proliferation of alien species (Galil, 2007a, Edelist et al., 2013a).

It is important to note that our model has a limited capacity to assess the impacts of alien species. Our study only considers alien fish and crustacean (shrimps and crabs) species, since for other groups no information was available to be considered within our temporal modelling approach (Rilov and Galil, 2009). However, the invasion of other organisms seems to be of the same magnitude or even greater (Rilov and Galil, 2009, Galil et al., 2014a). In addition, the information about pelagic fishes were limited and the definition of small and medium pelagic fishes groups within the model includes both native and alien species (Corrales et al., 2017a). Finally, several new alien species have invaded the Eastern Mediterranean Sea in recent years and were not included in the model (Galil et al., 2016, Zenetos et al., 2017). One of these species, the lionfish (*Pterois miles*), has alarmed the scientific community, arriving in the Mediterranean Sea in 1991 (Golani and Sonin, 1992) but not recorded again until 2012 (Bariche et al., 2013). This species has had detrimental effects on invaded ecosystems, such as the Caribbean Sea (Green et al., 2012). It is expected that the current and future enlargement of the Suez Canal and future sea warming will allow the invasion of more species (Galil et al., 2014b), and that the Eastern Mediterranean Sea can become an extension of the Red Sea in terms of species composition, even including reef building corals (Por, 2009, Givan et al., 2017b).

Under cumulative stressor scenarios, our study showed that the beneficial effects of fisheries reduction could be dampened by the combined impacts of sea warming and alien species. For example, mullets, hake and predators in general may not recover if sea warming and alien species impacts are also at play. These results highlight the need to include stressors other than fisheries, such as climate change and biological invasions, in the assessment of risk and the implementation of an ecosystem-based management approach to correctly assess the future of marine ecosystems. Serpetti et al. (2017), using an EwE model on the west coast of Scotland, highlighted that ocean warming could jeopardize sustainable fisheries practices in the future. Our results are complementary to this study and suggest that regional and global scale impacts such as biological invasions and sea warming can impair, or at least limit, the outputs of local fisheries management measures.

There is an increasing need to identify and quantify the biophysical thresholds that must not be exceeded, so as to prevent catastrophic shifts in ecosystems. Catastrophic shifts can be defined as persistent and substantial reorganizations of the structure and functioning of ecosystems and from which their recovery is difficult or impossible (Scheffer et al., 2001, Rockström et al., 2009). The boundaries of several processes (e.g., climate change and biodiversity loss) define the “safe operating space” for humanity (Rockström et al., 2009). However, crossing certain boundaries may take the ecosystem beyond its “safe operating space”, where the risk of unpredictable and damaging change is very high. Our results highlighted the fact that a reduction in fishing activities promotes the resilience of some species to climate change and the impacts of alien species in the Eastern Mediterranean Sea, with resilience defined as the capacity of species and ecosystems to resist and absorb disturbance and their ability to recover (Levin and Lubchenco, 2008, Côté and Darling, 2010). In addition, some native species reacted better to reduced fishing activities when alien species were maintained at constant levels in the absence and presence of sea warming. However, once a boundary is crossed, a species can collapse. In our study, this is the case for mullets and hake. These species have been severely impacted in recent decades by fishing activities, alien species (goatfishes and alien lizardfish, respectively), and sea warming (Galil, 2007a, Gucu and Bingel, 2011, Halim and Rizkalla, 2011, Edelist, 2012, Corrales et al., 2017a). In the cumulative impact scenarios, these functional groups initially benefited from reduced fishing effort. However, once the boundary of thermal tolerance was crossed, mullets and hake decreased notably. When we forced an increase in alien species biomass, in addition to sea warming, mullets collapsed due to the additional effects of predation and competition, while hake biomass remained almost constant due to the higher abundance of prey. Our study illustrates that complex dynamics between environmental and ecological processes may interact in the future and it is essential to take them into account.

In recent decades, human activities have exponentially increased (Halpern et al., 2015a). These include local stressors such as overfishing, habitat destruction and pollution, and regional and global stressors, such as biological invasions and climate change. Such anthropogenic effects impose large impacts on marine organisms and ecosystems, affecting ecosystem structure and services (Worm et al., 2006, Doney et al., 2012, Katsanevakis et al., 2014c). Organisms and ecosystems already stressed by fishing are more vulnerable to further impacts such as climate change and biological invasions (Occhipinti-Ambrogi and Savini, 2003, Poloczanska et al., 2016). As temperature will increase in the future and options for the management of ocean warming are limited at the local and regional scale, reducing local and regional threats such as overexploitation and biological invasions, may be one of the solutions to promoting resilience to climate change, ensuring the capacity to exploit marine resources safely and preserving ecosystem functions and services (Scheffer et al., 2015, Stuart-Smith et al., 2015).

Different management actions have been used for reducing the impacts of fisheries, including, among others, the establishment of catch limits, fishing effort reductions, increasing gear selectivity and the implementation of Marine Protected Areas (MPAs) (FAO, 2007). MPAs have been suggested as an effective tool to mitigate impacts of climate change and alien species (Francour et al., 2010, Roberts et al., 2017), although biological invasions have been largely disregarded in marine conservation plans (Giakoumi et al., 2016) and the effectiveness of MPAs in preventing invasions has been questioned (Simberloff, 2000). The prevention of new introductions should be a priority in the development of effective policies, followed by early detection, rapid response and possible eradication of alien species (CBD, 2002). In the context of our study area, some authors have suggested installing an environmental barrier in the Suez Canal, such as an hypersaline lock, since it may “reduce the likelihood of species migration through canals” (Hewitt et al., 2006). In fact, “the Suez Canal had, for nearly a century, a natural salinity barrier in the form of the high salinity Bitter Lakes” (Hewitt et al., 2006). In addition, although eradication is challenging, some countries have initiated eradication programs to minimize the impacts of alien species in the marine environment. For example, in Cyprus, governmental authorities encouraged fishermen to catch alien poisonous pufferfish (*Lagocephalus sceleratus*) (Rousou et al., 2014), which have detrimental effects on native biota and fisheries (Nader et al., 2012).

Ecological indicators are quantitative measurements that provide information about key ecosystem characteristics. They are increasingly used to document ecosystem status and to track the effects of anthropogenic and environmental stressors on marine ecosystems, as well as the effectiveness of management measures; making them a valuable tool within the EBM framework (Fulton et al., 2005, Shin and Shannon, 2010, Shin et al., 2010). We showed that trophic level-based indicators (mTLc and mTLco) were informative about the effects of fishing pressure, as they decreased in the baseline scenario (high fishing pressure) while increasing in all scenarios where fishing reductions were implemented. However, they exhibited opposite trends in sea warming scenarios. The predatory biomass indicator also indicated potential benefits of fishing restrictions, as well as detrimental impacts of sea warming. In addition, Kempton's index successfully tracked fishing pressure, sea warming and impacts of alien species. Therefore, our study illustrates how several ecological indicators obtained from EwE models can be useful to assess ecosystem status(Lassen et al., 2013, Piroddi et al., 2015b), but they may show complex trends to interpret as additional pressures to marine ecosystems are investigated.

Acknowledgements

XC was supported by an IOLR scholarship under the DESSIM project ("A Decision Support System for the management of Israel's Mediterranean Exclusive Economic Zone"). MC was partially funded by the European Commission through the Marie Curie Career Integration Grant Fellowships – PCIG10-GA-2011-303534 - to the BIOWEB project. MC and JS were partially funded by the European Union´s Horizon research program grant agreement No 689518 for the MERCES project.

Authors contributions:

XC, MC, EO, JH, JS, MG, DE and GG designed the study and analyses. XC, MC, JH and GG analysed data. JS and MC contributed with new methods. XC wrote the manuscript with assistance from MC and GG and input from JH, EO, JS, MG and DE.

CHAPTER 3: GENERAL DISCUSSION

The purposes for developing a quantitative model is to gain understanding of the natural world by organizing data and synthesizing information, corroborating hypotheses, identifying gaps in available knowledge and to develop predictive tools (Oreskes, 2003). In this thesis, I investigated the past, current and possible future effects of multiple anthropogenic activities on the Israeli Mediterranean continental shelf ecosystem through the application of an ecosystem modelling approach. The application of an ecosystem modelling approach implied the collection, analysis and integration of a large amount of data to parameterize the models and validate results. This study represents, to my knowledge, the first attempt to fit to time series and validate an ecosystem model in the Eastern Mediterranean Sea to assess the impact of multiple stressors. In addition, it also represents the first attempt to evaluate potential impacts of future conditions in the Eastern Mediterranean Sea within an ecosystem context combining global, regional and local stressors.

The first task of the thesis was to conduct a systematic and critical review of available modelling approaches that have been used to date to assess and predict impacts of invasive alien species (IAS) on aquatic ecosystems (Chapter 2.1). The review represents the first attempt to map available modelling approaches to assess impacts of IAS in aquatics ecosystems. The other two impacts included in this PhD thesis, fishing and climate change, have been widely studied and a number of literature reviews of modelling approaches are available (Whipple et al., 2000, Plagányi, 2007, Fulton, 2010, Koenigstein et al., 2016). Therefore, the review allowed me to learn and summarize the main features of the most applied approaches and analyze their capabilities and limitations.

Although no single model is able to capture all the processes, the review highlighted the Ecopath with Ecosim (EwE) modelling approach as a common tool for assessing impacts of already established IAS within an ecosystem context and its capabilities to forecast existing, emerging and potential new IAS. However, I found that most of the EwE applications assessing the impact of biological invasions included one or two alien species. In this PhD the scope of modelling alien species was far more extensive as it entailed the modelling of a large amount of alien species located at all trophic levels of the food web that have settled over a continuous period of time. Results from the review guided the methodological approach I used during the model development, especially in developing a new strategy when using the temporal dynamic EwE module, Ecosim (Walters et al., 1997).

In Chapter 2.2 I developed two food-web Ecopath models of the Israeli Mediterranean continental shelf representing two time periods (1990-1994 and 2008-2012). These models were built in order to characterize the structure and functioning of the ecosystem and assess the past and current impacts of alien species and fishing activities. In Chapter 2.3 the food web model representing early 1990s was fitted to available time series of observations from 1994 to 2010 using the temporal dynamic module Ecosim with the aim to explore the historical dynamics of the ecosystem considering the combined effect of alien species, fishing activities and changes in sea surface temperature. I took advantage of previous modelling efforts using EwE to assess the impact of alien species (Chapter 2.1) and I adopted and modified one of the strategies that had been previously used (Langseth et al., 2012). The new modelling strategy allowed the model to satisfactory reproduce the invasion and expansion of these two new alien groups. I also used a new capability of the approach by using environmental response functions, which allows to link species, or functional groups dynamics, with environmental drivers (Christensen et al., 2014b, Serpetti et al., 2017). These functions enabled environmental drivers, such as sea surface temperatures, to be included in the model as an ecosystem driver to assess the impact of climate change.

Finally, in Chapter 2.4 I used the temporal-dynamic calibrated food web model to analyze the potential ecosystem impacts of future conditions in the ecosystem through the development of previously defined future scenarios of change. These scenarios were defined jointly between scientists and local stakeholders. Particularly, I evaluated the effects of a new set of fishing regulations currently being implemented, changes in sea surface temperature (SST) following IPCC (Intergovernmental Panel on Climate Change) scenario projections and the potential increases in alien species biomass. I first investigated the impacts of stressors separately, and I then combined them to evaluate their cumulative effects. This was done with the aim of informing local and regional stakeholders about plausible futures of the eastern Mediterranean Sea, specifically the Israeli Mediterranean ecosystem.

3.1. Synthesis of the main findings

3.1.1. Ecosystem structure and functioning of the Israeli Mediterranean continental shelf ecosystem

Several ecological indicators investigated (e.g., transfer efficiency (TE), total system throughput (TST) and total biomass (TB)) using the two Ecopath models highlighted the ultra-oligotrophic nature of the Israeli Mediterranean marine ecosystem compared to other Mediterranean Ecopath models (Corrales et al., 2015). In fact, the Levantine Sea has the most oligotrophic waters of the Mediterranean Sea (Azov, 1991). In addition, the high values of TEs obtained in the Israeli models (almost double the average value reported worldwide (Christensen, 1995); and higher than other Mediterranean Sea areas (Corrales et al., 2015, Piroddi et al., 2015a)) indicated a high efficiency of the ecosystem in transferring energy between trophic levels. In fact, it has been suggested that in the Mediterranean Sea there is relatively abundant fish production (and also fisheries yields) despite the oligotrophic nature of the basin (called the “Mediterranean paradox”) (Sournia, 1973, Macias et al., 2014). The higher rates of TE could be partially related to this paradox.

The Lindeman spine, which is a representation of the biomass and fluxes between discrete trophic levels (Lindeman, 1942), presented similar patterns in both periods for the overall food web. However, the analysis of the different habitats (pelagic and demersal/benthic) highlighted a change in the food web between the two periods. While in the demersal compartment flows of medium trophic levels (TL III) increased between both periods, the values at higher trophic levels (TL IV) decreased. In line with the previous results, the temporal dynamic model highlighted three main temporal patterns: (1) native demersal predators decreased over time, (2) native demersal medium trophic levels fishes decreased over time; and (3) alien species, mainly low and medium trophic levels, increased over time. Therefore, the increasing flows in the demersal habitat in trophic levels III were due to the increasing abundance of alien species, despite declines of some native populations.

In the pelagic compartment, the static models suggested that flows of medium trophic levels (TL III) decreased between both periods while values at higher trophic levels remained constant. The reasons for the decreasing flows of medium trophic levels of the pelagic habitat are not clear and should be interpreted carefully due to the lack of data from the pelagic compartment. In fact, in Chapter 2.3 (temporal dynamic model) this statement was not confirmed, as forage fish (which include benthopelagic and small pelagic fishes, mackerel and horse mackerel) showed a non-significant temporal trend. Therefore, this thesis highlighted the importance of calibration and fitting models in order to validate and improve Ecopath models (the baseline) and to confirm (or not) different hypothesis from the static models.

Most of the groups identified as a keystone in the Israeli Mediterranean ecosystem, which are defined as a species with a high and wide impact on the food web despite its low biomass (Paine, 1966, Paine, 1969, Valls et al., 2015), were also identified as such in other Mediterranean areas (Coll and Libralato, 2012, Corrales et al., 2015). The analysis was based on the Mixed Trophic Impact (MTI) analysis which quantifies the direct and indirect impact that a hypothetical increase in the biomass of one functional group would have on the biomass of all other functional groups, including the fishing fleets (Ulanowicz and Puccia, 1990)). The results of the analysis indicated that the ecological role of European hake had been lost in the latter period likely due to overexploitation and sea warming. Both analysis (keystone index and MTI) also highlighted a decreasing role of large native demersal fishes (“groupers”) due to overfishing, while they suggested an increasing role of alien species and demersal sharks. On the contrary, the MTI analysis showed an increasing ecological role of earlier and new alien demersal fishes and alien medium pelagic fishes. The keystoneness index also showed that alien lizardfish is a potential keystone species in both time periods and highlighted the possibility of alien medium pelagic fishes to become a keystone group in the future, due to its high keystoneness index despite its recent invasion. In fact, alien medium pelagic fishes group include one of the most successful invaders of the Mediterranean Sea, the bluespotted cornetfish (*Fistularia commersonii*) (Azzurro et al., 2013). In the Mediterranean Sea, demersal sharks have declined dramatically mainly due to overfishing (Ferretti et al., 2008, Dulvy et al., 2016). However, sightings in the Israeli Mediterranean marine ecosystem have increased during the last 20 years. This could be related to alterations in the behavior of sharks (aggregations near coastal power plants) or an increase in the size of the population (Barash et al., 2018).

Ecological indicators (Chapter 2.3) for the Israeli Mediterranean marine ecosystem confirmed the historical changes in the structure and functioning of the ecosystem. In particular, a large decrease in predators at the beginning of the period was observed (due to overexploitation), followed by an increasing trend at the end of the simulation (mainly due to an overall decrease in fishing effort and the explosion of alien species). TST slightly increased with time, suggesting that the ecosystem is not in equilibrium. This has been related to higher primary productivity and the increasing importance of alien species. FCI and PL presented significant decreasing patterns. Therefore, our results suggested a degradation pattern over time of the ecosystem and an ecosystem in flux due to cumulative impacts of stressors acting on the ecosystem.

3.1.2. Ecosystem drivers of the Israeli Mediterranean continental shelf ecosystem

The temporal dynamic model highlighted that sea warming played an important role in the historical dynamics of the Israeli Mediterranean Sea ecosystem during the last two decades. In fact, climate change is strongly affecting Mediterranean organisms and ecosystems (Lejeusne et al., 2010, Moullec et al., 2016), leading a process of “meridionalization” and “tropicalization” of the northern and southern sectors, respectively (Bianchi, 2007, Bianchi et al., 2013). Particularly, the eastern basin is warming faster than the western (Nykjaer, 2009, Shaltout and Omstedt, 2014). Therefore, since the Levantine Sea represents the southeastern limit of distribution of most of the native species due to a naturally-extreme environment (temperature and salinity) (Sara, 1985, Rilov, 2016) and the environment is becoming more extreme due to climate change, many native species are more vulnerable. This stress could cause declines of populations or even local extirpations as it was showed in the present thesis and other studies (Rilov, 2016, Givan et al., 2017a). For example, sea warming played an important role in the dynamics of mullets, European hake and small native demersal fishes (see below). These results are in line with Givan et al. (2017a), who indicated a large decrease in biomass of native species with an affinity to cold waters while species with an affinity to warm waters (most of the alien species) increased.

This thesis also highlighted that fishing was an important driver affecting the dynamics of the ecosystem and especially for the exploited invertebrate and fish populations. High fishing mortalities and exploitation rates were found for several groups. This is in line with previous studies in the Mediterranean Sea that highlighted an overexploitation of its marine resources (Tsikliras et al., 2015, Colloca et al., 2017) and also at the ecosystem level (Coll et al., 2008c, Libralato et al., 2008, Coll et al., 2009). Predators (such as European hake and large native demersal fishes) have declined through time due to the impact of human activities, mainly due to overfishing but also could be due to sea warming and alien species (see below). The decline of predators due to overfishing has been already observed worldwide (Pauly et al., 1998, Myers and Worm, 2003) and also in the Mediterranean Sea (Ferretti et al., 2008, Azzurro et al., 2011, Maynou et al., 2011).

It is worth mentioning that fishing effort of the Israeli fleet declined over the past 2 decades (Edelist et al., 2013b). However, official statistics of fishing effort may not be able to capture real trends due to biases and data deficiencies (Anticamara et al., 2011, Gorelli et al., 2016, Bell et al., 2017). In fact, our time series of fishing effort included data on nominal effort (expressed as days at sea) for professional fisheries, while data from recreational fishers was estimated based on catch reconstruction efforts. This is an important shortcoming of the model developed in this thesis that needs further research. Good estimates of fishing effort are critically important for understanding impacts of fishing in marine resources and ecosystems and for effective fisheries management (Hilborn and Walters, 1992).

While fishing effort declined, total catch fluctuated over time with an overall increasing trend. This could be related to the depletion of native top predators (e.g., European hake and large native demersal fishes) and the explosion of alien species (both medium and high trophic levels). In line with this trend, the mean trophic level of the catch indicator (mTLc) first decreased and later increased. However, total landings decreased around 20% from 1990s to 2010s, while discards increased dramatically, from around 15% to 31% of the total catch between both periods. In fact, discard proportions in the Mediterranean are large, especially for the trawl fleet (Tsagarakis et al., 2013). This is mainly due to the catch of species of low commercial value, the use of small mesh size (which implies the catch of small individuals) and market influence (i.e. to avoid low prices of landings (especially for small pelagic fishes), fishermen increase discards when catches are high) (Machias et al., 2001, Tsagarakis et al., 2013). In the case of the Israeli fleet, the following features should be considered: the “Levantine nanism” (smaller size of organisms in the Levantine Sea) (Sonin et al., 2007), the modification of trawling grounds (in recent years their effort has been constrained to shallow waters), and the increasing abundance of alien species (many of them are discarded as they are small or are venomous/poisonous or for cultural reasons) (Edelist et al., 2011, Edelist et al., 2013b). The high fishing mortalities of some species/groups, the depletion of top predators and the high discard rates indicate the unsustainability of the Israeli fisheries, in line with previous studies in the area (Edelist et al., 2013b, Goren et al., 2013).

The temporal model also highlighted the increasing importance of alien species in the ecosystem, with important effects on species and on the structure of the food web. Several hypotheses have been proposed to explain the establishment and spread of alien species in the area. One hypothesis emphasizes the nature of the Levant Sea, where alien species can potentially utilize multiple empty niches in the area due to lower regional biodiversity and the existence of native species in a habitat at the limits of their tolerance levels (Por, 1978b, Golani, 1998, Galil, 2008, Rilov and Galil, 2009, Givan et al., 2017b). Another hypothesis suggests that alien species, originated from a rich and diverse tropical or sub-tropical ecosystem, have a superior competitive advantage over indigenous Mediterranean species from a poorer temperate region (Golani, 2010). Also, potential predators may be scarce (Edelist et al., 2012), while the presence of certain alien species may increase the probability of other alien species to establish a viable population (“invasion meltdown” theory) (Simberloff and Von Holle, 1999, Rilov and Galil, 2009). In addition, environmental conditions have become more suitable for alien species, providing various advantages when competing with native species (Golani, 1998, Galil, 2007a). Also, it has been suggested that the impact of fishing activity may have facilitated the establishment and spread of alien species (mostly fast-growing species) due to the overexploitation of native species (Galil, 2008) and the possible better adaptation and competitiveness of alien species to proliferate in the highly impacted trawl grounds (Edelist et al., 2011).

Whatever the exact mechanism (probably a synergy of factors), the declines and bathymetric shifts of native species concurrent with the proliferation of alien species are well documented in the study area (Golani, 1993, Golani, 1994, Galil, 2007b, Edelist et al., 2013a). However, there is a lack of studies supporting a competitive displacement of native species by alien species (Golani, 2010). At present, only few studies have attempted to investigate it (e.g., Golani, 1994, Bariche et al., 2004, Sala et al., 2011). It has been highlighted that these declines may not be disentangled from other anthropogenic impacts such as overexploitation, habitat destruction, pollution and sea warming (Galil, 2007b, Galil, 2008). The positive impacts of sea warming and overfishing on alien species were highlighted in Chapters 2.3 and 2.4.

According to the results presented in this thesis, primary production (PP) changes played a minor role in describing the historical dynamics of the Israeli Mediterranean coast ecosystem. However, it has been suggested that changes in PP could be an important driver acting upon the Mediterranean Sea ecosystems (Macias et al., 2014, Piroddi et al., 2017). The lower role of bottom-up processes in the Israeli Mediterranean coast (as well the Levantine Sea) could be explained by the reduction of nutrient-rich Nile waters (water discharge dropped to about 10% of its previous level) by the construction of Aswan High Dam in 1964 (Nixon, 2003). In fact, prior to the Aswan High Dam, the annual Nile flood produced phytoplankton blooms that supported a productive fishery (Azov, 1991, Nixon, 2003). Although the minor role of PP changes in this study, the model predicted an increasing trend of PP, which may be related to nutrient enrichment from anthropogenic sources during the last decades in Egypt, the Gaza Strip and Israel (Oczkowski et al., 2009, Suari and Brenner, 2015). This nutrient enrichment could play an important role in the extreme oligotrophic conditions of the area. Therefore, future work should be dedicated to further investigate the impact of anthropogenic enrichment in the area.

While ecological changes in the Eastern Mediterranean Sea, especially regarding the fish community, are well documented (e.g., Sala et al., 2011, Edelist et al., 2013a), the driving forces are not completely understood. For example, a strong impact of alien species has been widely suggested, but rarely evaluated (Golani, 2010, Katsanevakis et al., 2014c). The importance of each stressor has been debated, although there is a general lack of empirical estimates (Galil, 2008, Golani, 2010, Galil et al., 2018). This is due to the challenge of understanding the interactive effects of multiple stressors (Crain et al., 2008, Côté et al., 2016). Although most of the studies highlighted the cumulative impact of overfishing, alien species and sea warming, different studies highlighted different roles. For example, Edelist et al. (2013a) suggested alien species as the current main driver of the ecosystem, while Arndt et al. (2018) highlighted that most of the declines of native species are not associated with competition with alien species. On the other hand, Givan et al. (2017a) indicated a major role of sea warming.

The results of the present thesis suggest a general strong impact on the ecosystem of sea warming and more specific impacts of fishing and alien species. Therefore, the results of the temporal dynamic model are in line with Givan et al. (2017a), who suggested sea warming as the most important driver, followed by fishing. For example, the temporal dynamic model showed that fishing played a major role in the decline of large native demersal fishes. For European hake, the model highlighted that sea warming and trophic interactions played a key role, with an additional effect of fishing. In fact, the decline of European hake has been related to sea warming, overexploitation, competition with alien lizardfish and oceanographic changes (Gucu and Bingel, 2011, Halim and Rizkalla, 2011, Edelist, 2012). Edelist (2012) showed how European hake and alien lizardfish are inversely represented in catches and described niche partitioning (alien species dominate the shallow waters while native species remain into deeper and cooler waters) between both species. Results from this thesis also highlighted an important role of temperature and trophic interactions in the dynamics of mullets. The large decline of native mullets has been associated with sea warming and competition with alien goatfishes. The niche partitioning pattern has also been described between native mullets and alien goatfishes (Golani, 1994), although goatfishes has extended its bathymetric distribution in recent years (Edelist, 2012). Regarding alien species groups, the model highlighted a key role of sea warming and trophic interactions, highlighting the more favorable environmental conditions in the Eastern Mediterranean Sea to alien species and suggesting possible better competitive properties of invaders (Galil, 2008, Rilov and Galil, 2009, Edelist et al., 2011).

3.1.3. Future ecosystem conditions

Although modelling scenarios of future conditions is a challenging task due to high uncertainties and complex ecosystem characteristics (Link et al., 2012, Maris et al., 2017), they can provide considerable benefits. For example, they allow understanding possible future impacts on marine ecosystem and can offer guidance to decision-makers by evaluating the tradeoff between different management measures and identify those measures that have the potential to meet preferred objectives. In this study, information provided by local stakeholders was used to define a set of plausible future scenarios.

The participation of stakeholders in these definitions ensures the interest that they may have for the results.

The results of the baseline scenario ("business as usual") showed that under current conditions biomass of several species or functional groups will strongly decrease and several ecological indicators will indicate ecosystem degradation. This is due to increasing impacts of alien species, strong negative impact of current thermal conditions on native species and overfishing. This ecosystem degradation is in line with results of Chapter 2.3, which highlighted a historical degradation pattern of the system over the last two decades (1990-2010); and also with other independent studies in the area (Goren et al., 2013).

Under scenarios of fishing reductions, the model highlighted potential future benefits of fishing effort reductions, at species/functional group level as well as at food-web/ecosystem level through the restoration of several exploited groups and thus the improvement of several ecological indicators. In addition, our results revealed that sustainable fisheries management can improve the overall catch of the fishing fleets. Fishing is considered one of the greatest pressures on marine ecosystems (Jackson et al., 2001, Costello et al., 2010) and several studies have indicated potential benefits of fishing reductions (Lotze et al., 2011b, Costello et al., 2016). The results of these scenarios highlighted the need for a reduction in fishing capacity, in line with other studies in the area (Edelist, 2012, Goren et al., 2013) and at a global scale (Worm et al., 2009).

The scenarios of sea warming indicated potential detrimental impacts on marine resources, especially for sensitive native species, and ecosystem state. Within this context, results highlighted potential collapses or large decreases of several native species/functional groups. These collapses may not indicate a total collapse of the species in the Levantine Sea, although mass mortality events have been recorded in the northwestern Mediterranean (Rivetti et al., 2014, Marbà et al., 2015) and in the study area (Rilov, 2016). Results could also indicate that species may migrate to northern areas or move to deeper and cooler waters (which are not considered in the modelling framework used in this study). In fact, bathymetric shifts have been already observed in the study area, which have been related to sea warming and competition with alien species (Golani, 1994, Edelist et al., 2013a). In addition, a northwards extension of native species due to sea warming have been observed in the Mediterranean Sea (Sabates et al., 2006, Moullec et al., 2016). Species distribution models have predicted that future sea warming would deeply modify fish assemblages by the end of the 21st century, including the contraction of suitable habitat of some species to the coldest parts of the basin or even species extinctions (Ben Rais Lasram et al., 2010, Albouy et al., 2012, Albouy et al., 2013), with potential effects on marine food webs and ecosystem structure (Albouy et al., 2014).

In Chapter 2.4 I also showed how increasing alien species biomass may contribute to several declines or even collapses of native species and a degradation pattern of the system. Although the impact of alien species has been widely discussed (Rilov and Galil, 2009, Edelist et al., 2013a), empirical evidence is lacking (Golani, 2010, Katsanevakis et al., 2014c). Therefore, this scenario, which only includes changes to alien species biomass (following current trends) while maintaining fishing effort and sea warming at 2010 levels, provides a means to theoretically analyze the future impacts of alien species on native species through competition and predation interactions. For example, small native demersal fishes were projected to collapse. This could be related to increasing competition (earlier and new alien demersal fishes) and predation (mainly alien lizardfish, large native demersal fishes and alien medium pelagic fishes).

Under the cumulative stressors scenarios, results highlighted that sea warming and alien species can impair, or at least limit, the impacts of better fishing practices. For example, mullets and European hake may not recover despite fishing reductions due to the negative impact of sea warming and alien species. However, the impact of alien species could be different for specific cases. For example, alien species exacerbated the negative impact of sea warming in the dynamics of mullets due to competition with goatfishes and higher predation rates. In contrast, alien species could mitigate partially the negative impact of sea warming on European hake due to higher abundance of prey. Since scenarios of sea warming and alien species simulated increasing effects of these stressors, the application of fisheries reductions in the combined scenarios did not allow analyzing the cumulative effect of stronger negative impacts of the three stressors. However, as the beneficial effects of fisheries reduction were dampened by the impact of sea warming and alien species, one can hypothesize possible synergies of all the stressors if they increase at the same time.

3.2. Implications for management

Driven by the need to assess how tropic interactions, the environment and multiple human activities interact and influence each other, multispecies/ecosystem models have become an essential analytical and decision-making tool (Collie et al., 2014). However, few are currently used to implement management decisions, mainly due their complexity and large uncertainties and the challenge of translating complex results to management decisions (Fogarty, 2013, Collie et al., 2014, Lehuta et al., 2016). An exception is the calibrated EwE model of the North Sea (Mackinson et al., 2009b) that was used to explore the interactions between fisheries for cod, haddock and whiting. This model was recently used by the ICES Working Group on Multispecies Assessment Methods (WGSAM) to establish a "key run" to analyse the dynamics of marine resources within an ecosystem context (ICES, 2016). In addition, the new habitat foraging capacity model implemented in Ecospace, the spatial-temporal module of EwE, was part of an assessment of potential environmental impacts associated with the proposed expansion of the Port of Metro Vancouver (Vancouver, 2015).

The main objective of the DESSIM project, in which this thesis was conceived and performed, was to develop a tool for examining possible management policies in order to inform governmental agencies and stakeholders in the Eastern Mediterranean Sea. Modelling exercises such as this can provide information that could help managers in resource planning. However, the model presented here cannot be used for tactical decisions and should be considered from a conceptual level of "what if?" questions about what will happen to the Israeli Mediterranean coast ecosystem. This is due to large uncertainties of the model (see section 3.3). Despite this, it would be useful within the EBM context to inform decision-makers about possible future trends in biomass and catches under different future scenarios of global change.

For example, results of the present thesis have highlighted the importance of including stressors other than fisheries, such as climate change and biological invasions, in an ecosystem-based management approach to correctly hindcast, and to provide informative forecast dynamics of marine ecosystems. These results are in line with other studies. For example, Mackinson (2013) showed the importance of including environmental drivers such as changes in temperature and nutrient levels in addition to fishing to explain the ecosystem dynamics of the North Sea. Serpetti et al. (2017)

highlighted the improvement of model performance with the addition of sea warming to fishing and primary production anomaly (in this case related to the Atlantic Multidecadal Oscillation (AMO)) along the West Coast of Scotland ecosystem. Serpetti et al. (2017) also highlighted that ocean warming could jeopardize in the future sustainable fisheries practice on the West Coast of Scotland.

Marine ecosystems are increasingly impacted worldwide by a diversity of global, regional and local anthropogenic stressors (Halpern et al., 2015a). While the impacts of single stressors has been widely assessed, research of the cumulative impact of multiple stressors is less common (Crain et al., 2009). In fact, understanding the consequences of multiple anthropogenic impacts has become a key issue and one of the main challenges in ecology, conservation and management (Crain et al., 2009, Parsons et al., 2014, Côté et al., 2016). Within this context, there is an increasing need to identify and quantify the boundaries of several stressors that define the “safe operating space” for humanity (Rockström et al., 2009, Steffen et al., 2015, Carpenter et al., 2017) that must not be transgressed to prevent catastrophic shifts in marine ecosystems. In Chapter 2.4 results emphasized the way in which better fishing practices promote resilience to impacts of sea warming and alien species. This is in line with different studies that highlighted how improved fisheries management could mitigate the negative impacts of climate change (Cheung et al., 2018, Gaines et al., 2018), also in the Mediterranean Sea (Ramírez et al., 2018). In addition, results highlighted how native species reacted better to reduced fishing activities when alien species were kept at 2010 levels (in both absent and presence of sea warming). Furthermore, results illustrated how ocean warming may cause the collapse of several sensitive native species or functional groups (e.g., European hake and mullets) with the current fishing regulations. All these results provide valuable information for decision-makers to effectively impede catastrophic shifts in the Israeli Mediterranean continental shelf ecosystem.

Under the historical ecosystem degradation and possible future impacts on the Israeli Mediterranean continental shelf ecosystem showed in the present thesis, conservation management should focus on mitigating local and regional stressors in order to promote resilience to climate change (Ramírez et al., 2018). Although reducing global greenhouse gas emissions is critical, options for the management of ocean warming are limited at national scale. The impact of fishing can be mitigated through better fishing regulations at local scales, although it is recognized that managing multi-species and multi-fleet fisheries is a challenging task. Different management actions have been used worldwide for reducing the impacts of fisheries (FAO, 2007) and in Chapter 2.4 I presented the potential benefits of some fishing regulations that recently took effect in the area when other stressors were kept constant. Therefore, results of the scenarios highlighted the need for a reduction in fishing capacity, in line with other studies in the area (Edelist, 2012, Goren et al., 2013). In addition, a sustainable fisheries management option could be enhanced by the implementation of different management measures such as improving fishing selectivity, the implementation of temporal closures, and the establishment of MPAs (Edelist, 2012, Goren et al., 2013). Within this context, the spatial-temporal module of EwE, Ecospace, has been developed within the DESSIM project using the new habitat capacity model of Ecospace (Christensen et al., 2014b) and the spatial-temporal data framework (Steenbeek et al., 2013), to spatially describe the study area. This module can allow the assessment of the establishment of MPAs, providing essential information for marine spatial planning (Shabtay et al., 2018) in the area to effectively manage the Israeli marine ecosystem, complementing the results of this thesis.

The management of impacts of regional stressors, such as biological invasions, need the coordination between different countries although national measures are possible. Prevention of new introductions through managing vectors and pathways is a priority in the development of effective policies (CBD, 2002). Within this context, installing an environmental barrier in the Suez Canal have been suggested (Hewitt et al., 2006, Katsanevakis et al., 2013). In addition, although extirpation is almost impossible, eradication programs could mitigate the impacts of alien species. For example, governmental authorities in Cyprus have encouraged fishermen to catch alien poisonous pufferfish (*Lagocephalus sceleratus*) (Nader et al., 2012). The protection of native predators (mainly groupers) and the active removal of alien herbivores have been proposed to control the dramatic impacts of alien herbivores (Rilov et al., 2018).

From a biogeographic perspective, with the recent expansion of the Suez Canal (Galil et al., 2015) and ongoing sea warming, a continuous invasion of Lessepsian migrants and declines in native populations are expected (Galil et al., 2014b), causing further transformation (tropicalization and meridionalization) of the ecosystems in the Eastern

Mediterranean Sea, as well as a spread of these changes to the rest of the Mediterranean Sea. In fact, it is possible that over time the Eastern Mediterranean Sea shall become an extension of the Red Sea in terms of species composition, even including reef building corals (Por, 2012, Givan et al., 2017b). Impacts of sea warming could cause local extinctions of several native species (Ben Rais Lasram et al., 2010), with important effects on Mediterranean ecosystems (Albouy et al., 2014). Within this context, alien species could play an important role in supporting ecosystem functioning in largely degraded ecosystems by serving as functional substitutes for extinct taxa (Walther et al., 2009, Schlaepfer et al., 2011). In fact, Edelist et al. (2013a) suggested that changes in trophic level and biodiversity in the demersal fish community in Israel have been masked by replacing native by alien species with similar ecological positions. Several alien species could be ecologically benign as they are occupying unutilized ecological niches (Givan et al., 2017a), while other alien species can have detrimental impacts such as alien herbivores (Sala et al., 2011). Therefore, a realistic conservation target could be the restoration and preservation of ecosystem functions rather than to preserve the native biodiversity (Rilov et al., 2018). This topic needs further research in the study area.

3.3. Data gaps/limitations and uncertainties

One of the main limitations of ecosystem models is data availability and quality. Deficiencies in both aspects can lead to great uncertainties in model results. Although the models developed in the present thesis presented a reasonable quality when compared to a global assessment (Morissette, 2007), they had the lowest pedigree index values for the Mediterranean Sea EwE models (Corrales et al., 2015). In fact, Coll et al. (2010) highlighted a lack of data in several eastern and southern regions of the Mediterranean Sea, which is confirmed in this thesis. It is evident from the input data of the models developed in this thesis that there are many information gaps, especially for the Ecopath model representing the 1990s. In this study the major obstacles encountered were related to the diet composition, biomass estimates and fisheries data.

The models presented in the current thesis included fish and crustacean (shrimp and crabs) alien species. At the time the models were developed, reliable information on ecological features and biomass estimates were available for most of introduced fish species and some crustacean species, but not for other groups such as cephalopods, mollusks, polychaetes and jellyfish (Rilov and Galil, 2009, Galil and Goren, 2014), and they, therefore, were not included as separate groups. In addition, most of the alien pelagic fish species (except medium pelagic fishes that invaded the ecosystem after 1990s) had to be combined with native species due to the lack of information. Finally, since 2010 (the last year of the calibrated model) several alien species have invaded the Eastern Mediterranean Sea (Galil et al., 2016, Zenetos et al., 2017) and were not included in the model. An enigmatic example is the invasion of the lionfish (*Pterois volitans*). These deficiencies limited the ability of the present study to comprehensively evaluate the overall impact of alien species on the ecosystem.

Currently, comprehensive datasets on the feeding ecology of many species are insufficient even with the increasing number of studies in recent decades. In general, species at low trophic levels (i.e., zooplanktonic and invertebrates groups), and alien species in our particular case are poorly studied. For example, diet composition of zooplanktonic and invertebrate groups in the models developed during this thesis came from studies in the Western Mediterranean Sea, while the diet composition of alien crustaceans was assumed to be the same as the native groups. Since alien species are playing an increasingly role in the ecosystem and due to the limited knowledge about their trophic interactions, there is an urgent need for studies on this topic. As stomach content analyses may be complex, time-consuming and expensive to collect (Link, 2004, Albouy et al., 2011), alternative methods may be necessary. In Chapter 2.1, I highlighted how the Rank Proportion Algorithm could be a valuable tool to predict diet composition for recent or even possible new invaders (Link, 2004, Pinnegar et al., 2014). Diet composition should ideally be expressed in weight or volume, as trophic relationships may be determined in energetic terms (Stobberup et al., 2009). However, the method used to study the feeding ecology of some species was different (i.e., frequency of occurrence and numerical percentage) and therefore, in this work some assumptions were made to convert the available data in weight, increasing uncertainties related to the diet matrix. In this study, although many of the available studies were from the Eastern Mediterranean Sea, sometimes they did not overlap with the studied periods (1990-1994 and 2008-2012). This represented a limitation since diet composition could change over time due to changes in prey abundance, changes in predator abundance, change in environmental factors such as water clarity, and changes in predator search tactics (Christensen and Walters, 2004a). This is especially relevant in the present study since abundance of alien species has largely increased (so, their importance as a prey may have increased), and particularly for new invaders, as the studies may not include these species as preys as they did not invade the ecosystem during the sampling period. For all these reasons, among others, diet composition is usually one of the most poorly estimated parameters in quantitative food-web analyses (Link, 2004) and efforts to increase our knowledge about the trophic ecology of species should continue.

There is a lack of biomass estimates for most of the pelagic species and benthic invertebrates groups. Therefore, future biomass studies and monitoring should emphasize small pelagic fishes due to their important ecological role in Mediterranean ecosystems (Coll et al., 2006, Palomera et al., 2007, Corrales et al., 2015, Piroddi et al., 2015a). To correct this, population assessments of small and medium pelagic fishes, and acoustic surveys, as well as plankton sampling, are needed in the study area (Chapter 2.2). In addition, biomass estimates of crustacean and demersal fish groups came from fishery dependent trawl surveys (swept-area method), which present several problems because they tend to underestimate biomasses. Furthermore, as highlighted in Chapter 2.3, there was a lack of historical biomass time series, as only 3 data points were available through the analysis of 3 surveys conducted in the study area. This constraint has limited the capability of the model to capture temporal patterns. Although a fishery independent survey, such as the scientific demersal MEDITS campaign (Bertrand et al., 2002), is often expensive and/or difficult to conduct, it would improve the available data and its quality. The ability of ecosystem models to replicate trends and project credible forecast increases with data availability, quality, and the length of historical data provided (Giron-Nava et al., 2017).

Obtaining realistic estimates of total catch, both official catches and Illegal, Unregulated and Unreported (IUU), is a challenging task worldwide (Pauly and Zeller, 2016). In the Mediterranean Sea several studies have shown that fisheries statistics are generally incomplete and unreliable (Coll et al., 2014, Moutopoulos and Koutsikopoulos, 2014, Pauly et al., 2014, Ulman et al., 2015a, Ulman et al., 2015b). In Chapter 2.2 and 2.3 I used data from a reconstruction of the Israeli catches (Edelist et al., 2013b), conducted as a part of a project (Sea Around Us) with the aim to reconstruct global fisheries catches (Pauly and Zeller, 2016). Although this catch reconstruction present several limitations, particularly for the artisanal fleet, purse seiners and the recreational fishery, it represents a more complete and realistic estimation than the official data available.

The application of environmental response functions, used to link species responses to environmental parameters, were incorporated with the recent habitat capacity model of the spatial-temporal module Ecospace (Christensen et al., 2014b). Later on, they were incorporated into the temporal dynamic model Ecosim and this thesis is one of the first applications of this capability of the approach. In this thesis, temperature response functions, in absence of local data from literature, were obtained from the AquaMaps database, which is a global comprehensive database of marine species distributions (Kaschner et al., 2006). However, AquaMaps does not account for regional differences/preferences of species environmental responses. For example, fish have the capacity to adjust their preferred temperatures through acclimation (Johnson and Kelsch, 1998) and therefore the temperature range could be overestimated or underestimated in local regions if global data is used. To consider this, I modified the available functions from AquaMaps using expert opinion from scientists working in the study area to incorporate local knowledge. Maximum tolerance levels were increased for several functional groups (crustacean and fish groups) for which we applied response functions. In fact, the Eastern Mediterranean Sea, and especially the Levantine Sea, represents the southern limit of most of the native species and they could be “naturally” close to their physiological tolerance limits (Rilov, 2016). Organisms could respond to environmental stress through different mechanism, from biochemical buffering through gene expression and physiological (or phenotypic) flexibility to behavioural responses, change in gene frequency (selection), evolutionary gene modification and speciation and ecological responses (migration and ecological interactions) (Peck, 2011). The possible mechanism depends on the extent (from nanometer to global regions), the time scale (from seconds to decades) and the magnitude of the applied stress (Peck, 2011). Through an acclimation mechanism, native species in the Levantine Sea may have slightly changed their environmental affinities following a long-term exposure to higher temperatures.

The model did not incorporate salinity, although it has been suggested to be an important factor to consider (Mavruk and Avsar, 2008). Response functions to salinity were available from AquaMaps but experts from the study area were not able to help modify these functions due to the lack of information. This additional information should be added to future iterations of the models. In addition, other impacts of climate change, such as ocean acidification and changes in primary productivity (Hoegh-Guldberg and Bruno, 2010), were not included though they may also be important. In addition, the model does not fully account for possible adaptive capabilities of species to climate change and ontogenetic variations of environmental affinities (Pörtner and Peck, 2010).

Calibration, validation and uncertainty analysis are critical processes for evaluating model performance and testing the validity of the assumptions included in the model, especially if the objective of the model is to be used for management purposes (Fulton et al., 2003, FAO, 2008, Jørgensen and Fath, 2011, Heymans et al., 2016). During this PhD, I followed the best practices for creating and calibrating EwE models provided by Heymans et al. (2016) to enhance the quality and confidence of the model. In Chapter 2.2, I used the PREBAL analysis (Link, 2010b) to ensure the coherency of the basic input parameters with respect to general ecological rules/principles and to guide the balancing procedure. I also validated the Ecopath models using independent data from stable isotope estimates. Specifically, tropic levels estimated for the 2010s model were validated using information from stable isotope analysis from a neighbouring area (Fanelli et al., 2015). This analysis highlighted that the diet information used in this model represented the trophic interactions reasonably well. However, I only validated one of the models due to the lack of data. In addition, there is a need for other independent analysis to validate model outputs such as information on mortalities (both natural and fishing) from stock assessments. However, stock assessment analyses were not available in the study area. These analyses have been proved to be useful to validate Ecopath models in other areas of the Mediterranean Sea (Coll et al., 2006, Torres et al., 2013, Corrales et al., 2015).

In Chapter 2.3 I fitted the model to time series of observations following the model-fitting procedure described by Mackinson et al. (2009a), Heymans et al. (2016) and Scott et al. (2016), and I evaluated whether the parameterization lead to credible and sensible behaviour. Within this context, the best fitted model was not able to reproduce the trends of several target groups and therefore, I moved through the fitting procedure analysis to find the model that was able to reproduce the trends of most of the groups (with special emphasis on target groups) and still retains credible statistical behaviour. Finally, in Chapter 2.3 and 2.4 I assessed uncertainties in model outputs (both biomass and catch trends, and ecological indicators) by using the Monte Carlo routine and ECOIND plug-in (Heymans et al., 2016, Coll and Steenbeek, 2017) and the recently developed EcoSampler plug-in (Steenbeek et al., 2018), to which I contributed with a case study (Annex 5).

Because of the caveats explained above, uncertainties in model outputs are high. Despite these limitations, the models developed in this thesis include the best available information and follow the best practices in ecosystem modelling development. As such, the model of the Israeli Mediterranean continental shelf represents the best approximation to date to assess historical, current, and future dynamics of the ecosystem. As new information is generated, the present models can be updated and further developed, improving their quality and becoming increasingly valuable tools for understanding cumulative impacts and evaluating management options for the marine ecosystem of the Israeli Mediterranean continental shelf.

CHAPTER 4: CONCLUSIONS

In this thesis I performed a systematic review of available modelling approaches that have been used to evaluate the impacts of IAS in aquatic systems in the past. Learning from what has been done and the limitations, I developed an ecosystem modelling approach to assess the past, current and future cumulative impacts of alien species, fishing and climate change on the Israeli Mediterranean continental shelf ecosystem, including key marine organisms, from the lowest to highest trophic levels of the ecosystem. This study is the first to provide a basis for understanding the structure and functioning of the ecosystem in the area and for hindcasting and forecasting the dynamics of the ecosystem considering the main drivers. Since human impacts are increasing in the region, this study provides a basis to inform local and regional governmental agencies and stakeholders about conservation and management options of the marine resources and ecosystems.

The main conclusions derived from this study are:

1) Time dynamic models were the mostly frequently developed for assessing the impacts of the IAS, while spatial models were less frequent. This could be related to the fact that assessing the impact of IAS is time dependent. It may also be due to the need for tools to analyze alternative management options of aquatic ecosystems, where time dynamic models are achievable while spatial modelling requires larger and more complex datasets.

2) Despite the fact that no single model is able to capture all the processes within an ecosystem, the Ecopath with Ecosim (EwE) approach can integrate available information into a coherent description of aquatic food webs and account for anthropogenic activities in an ecosystem context.

3) Results from the static food-web models highlighted that, despite differences in productivity patterns and other environmental parameters, the Israeli marine ecosystem shares common structural and functional traits with other Mediterranean ecosystems. For example, the importance of the benthic-pelagic coupling; and the important role of detritus and low trophic level organisms.

4) Native medium pelagic fishes, dolphins, demersal sharks, large pelagic fishes and squids were identified as potential keystone species in the Israeli Mediterranean ecosystem in both time periods analyzed (1990s and 2010s). This analysis also

highlighted that European hake lost its keystone role in the latter period. In addition, alien lizardfish was identified as a potential keystone species while the results also showed the possibility of alien medium pelagic fishes to become a keystone group in the future.

5) Analyzing at the ecosystem dynamics, biomass trends reveled three main patters: (1) native demersal predators decreased with time, (2) native medium trophic level demersal fishes decreased with time; and (3) alien species increased over time. These biomass trends, together with several ecological indicators, such as community biomass, trophic levels, catch and diversity indicators, have shown an overall ecosystem degradation over time.

6) Results from the historical modelling exercise suggested a general strong impact of sea warming on the ecosystem and more specific impacts of fishing and alien species; while changes in primary production played only a minor role in describing historical ecosystem dynamics.

7) Both static and temporal dynamic models highlighted an increasing proportion of alien species in biomass and catch, with important effects on the food web, e.g., specific impacts through competitive and predation interactions and large impacts through changes in trophic flows between food web components.

8) Future scenarios considering changes of one stressor at time showed potential overall future benefits of fishing effort reductions through the restoration of several exploited groups and the improvement of the state of the ecosystem. The scenarios of increasing sea temperature highlighted detrimental impacts on marine resources, especially sensitive native species, and on ecosystem state. The scenario of increasing biomass of alien species showed detrimental impacts on several native groups through competition for resources, also due to the negative impacts of current thermal conditions, and a degradation pattern of the ecosystem.

9) Cumulative scenarios revealed that the beneficial effects of fisheries reduction may be dampened by the combined impacts of sea warming and increasing biomass of alien species. These results support the need for reducing local and regional stressors, such as fishing and biological invasions, to promote resilience in an ongoing warming sea and to retain marine ecosystems within a “safe operating space (SOS)”, ensuring the

capacity to exploit marine resources safely and preventing ecosystem functions and services to degrade.

10) The results of the present thesis showed that uncertainties were high due to data limitations, which were mainly related to the pelagic compartment, benthic invertebrates and the reliability of catch data. Recognizing and assessing the uncertainty of the model is essential if the model is aim to be used to provide informative and robust advice for management. In the present thesis, the impact of uncertainties of input data on model outputs such as biomass predictions and ecological indicators were assessed by using the Monte Carlo routine and the ECOIND, and EcoSampler plug-ins. In addition, the identification of such information should inform future scientific research objectives in the area. Despite main limitations, the models developed in this thesis include the best available information and follow the best practices in ecosystem modelling development. As new information is generated, the present models can be updated and further developed, improving their quality and becoming increasingly valuable tools for understanding cumulative impacts and evaluating management options for the marine resources of the Israeli Mediterranean continental shelf.

REFERENCES

ACOSTA, L. A., WINTLE, B. A., BENEDEK, Z., CHHETRI, P. B., HEYMANS, S. J., ONUR, A. C., PAINTER, R. L., RAZAFIMPAHANANA, A. & SHOYAMA, K. 2016. Using scenarios and models to inform decision making in policy design and implementation. *In:* IPBES (ed.) *Methodological assessment of scenarios and models of biodiversity and ecosystem services [S. Ferrier, K. N. Ninan, P. Leadley, R. Alkemade, L. A. Acosta, H.R. Akçakaya, L. Brotons, W.W.L. Cheung, V. Christensen, K. A. Harhash, J. Kabubo-Mariara, C. Lundquist, M. Obersteiner, H. Pereira, G. Peterson, R. Pichs-Madruga, N. Ravindranath, C. Rondinini and B.A. Wintle (eds.)]*. Bonn, Germany.

AGARDY, T., ALDER, J., DAYTON, P., CURRAN, S., KITCHINGMAN, A., WILSON, M., CATENAZZI, A., RESTREPO, J., BIRKELAND, C. & BLABER, S. 2005. Coastal systems.

AHRENS, R. N., WALTERS, C. J. & CHRISTENSEN, V. 2012. Foraging arena theory. *Fish and Fisheries,* 13**,** 41-59.

AINSWORTH, C., SAMHOURI, J., BUSCH, D., CHEUNG, W. W., DUNNE, J. & OKEY, T. A. 2011. Potential impacts of climate change on Northeast Pacific marine foodwebs and fisheries. *ICES Journal of Marine Science: Journal du Conseil***,** fsr043.

AINSWORTH, C. & WALTERS, C. 2015. Ten common mistakes made in Ecopath with Ecosim modelling. *Ecological Modelling***,** 14-17.

AKOGLU, E., SALIHOGLU, B., LIBRALATO, S., OGUZ, T. & SOLIDORO, C. 2014. An indicator-based evaluation of Black Sea food web dynamics during 1960–2000. *Journal of Marine Systems,* 134**,** 113-125.

ALBOUY, C., GUILHAUMON, F., ARAÚJO, M. B., MOUILLOT, D. & LEPRIEUR, F. 2012. Combining projected changes in species richness and composition reveals climate change impacts on coastal Mediterranean fish assemblages. *Global Change Biology,* 18**,** 2995-3003.

ALBOUY, C., GUILHAUMON, F., LEPRIEUR, F., LASRAM, F. B. R., SOMOT, S., AZNAR, R., VELEZ, L., LOC'H, F. & MOUILLOT, D. 2013. Projected climate change and the changing biogeography of coastal Mediterranean fishes. *Journal of Biogeography,* 40**,** 534-547.

ALBOUY, C., GUILHAUMON, F., VILLÉGER, S., MOUCHET, M., MERCIER, L., CULIOLI, J., TOMASINI, J. & MOUILLOT, D. 2011. Predicting trophic guild and diet overlap from functional traits: statistics, opportunities and limitations for marine ecology. *Marine Ecology Progress Series,* 436**,** 17-28.

ALBOUY, C., VELEZ, L., COLL, M., COLLOCA, F., LOC'H, F., MOUILLOT, D. & GRAVEL, D. 2014. From projected species distribution to food-web structure under climate change. *Global Change Biology,* 20**,** 730-741.

ALVA-BASURTO, J. C. & ARIAS-GONZÁLEZ, J. E. 2014. Modelling the effects of climate change on a Caribbean coral reef food web. *Ecological Modelling,* 289**,** 1-14.

ALLEN, K. R. 1971. Relation between production and biomass. *Journal of the Fisheries Board of Canada,* 28**,** 1573-1581.

ALLENDORF, F. W., ENGLAND, P. R., LUIKART, G., RITCHIE, P. A. & RYMAN, N. 2008. Genetic effects of harvest on wild animal populations. *Trends in Ecology & Evolution,* 23**,** 327-337.

AMUNDSEN, P. A., LAFFERTY, K. D., KNUDSEN, R., PRIMICERIO, R., KRISTOFFERSEN, R., KLEMETSEN, A. & KURIS, A. M. 2013. New parasites and predators follow the introduction of two fish species to a subarctic lake: Implications for food-web structure and functioning. *Oecologia,* 171**,** 993-1002.

ANDERSON, K. R., CHAPMAN, D. C., WYNNE, T. T., MASAGOUNDER, K. & PAUKERT, C. P. 2015. Suitability of Lake Erie for bigheaded carps based on bioenergetic models and remote sensing. *Journal of Great Lakes Research,* 41**,** 358-366.

ANTICAMARA, J., WATSON, R., GELCHU, A. & PAULY, D. 2011. Global fishing effort (1950–2010): trends, gaps, and implications. *Fisheries Research,* 107**,** 131-136.

ARAVENA, G., VILLATE, F., URIARTE, I., IRIARTE, A. & IBÁÑEZ, B. 2009. Response of Acartia populations to environmental variability and effects of invasive congenerics in the estuary of Bilbao, Bay of Biscay. *Estuarine, Coastal and Shelf Science,* 83**,** 621-628.

ARHONDITSIS, G. B. & BRETT, M. T. 2004. Evaluation of the current state of mechanistic aquatic biogeochemical modeling. *Marine Ecology Progress Series,* 271**,** 13-26.

ARIAS-GONZÁLEZ, J. E., GONZÁLEZ-GÁNDARA, C., LUIS CABRERA, J. & CHRISTENSEN, V. 2011. Predicted impact of the invasive lionfish< i> Pterois volitans</i> on the food web of a Caribbean coral reef. *Environmental research,* 111**,** 917-925.

ARNDT, E., GIVAN, O., EDELIST, D., SONIN, O. & BELMAKER, J. 2018. Shifts in Eastern Mediterranean Fish Communities: Abundance Changes, Trait Overlap, and Possible Competition between Native and Non-Native Species. *Fishes,* 3**,** 19.

ASSIS, J., TYBERGHEIN, L., BOSCH, S., VERBRUGGEN, H., SERRÃO, E. A. & DE CLERCK, O. 2018. Bio-ORACLE v2. 0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography,* 27**,** 277-284.

AZOV, Y. 1991. Eastern Mediterranean—a marine desert? *Marine pollution bulletin,* 23**,** 225-232.

AZZURRO, E., MAYNOU, F., BELMAKER, J., GOLANI, D. & CROOKS, J. 2016. Lag times in Lessepsian fish invasion. *Biological Invasions***,** 1-12.

AZZURRO, E., MOSCHELLA, P. & MAYNOU, F. 2011. Tracking signals of change in Mediterranean fish diversity based on local ecological knowledge. *PloS one,* 6**,** e24885.

AZZURRO, E., SOTO, S., GAROFALO, G. & MAYNOU, F. 2013. Fistularia commersonii in the Mediterranean Sea: invasion history and distribution modeling based on presence-only records. *Biological Invasions,* 15**,** 977-990.

BAJER, P. G., BECK, M. W., CROSS, T. K., KOCH, J. D., BARTODZIEJ, W. M. & SORENSEN, P. W. 2016. Biological invasion by a benthivorous fish reduced the cover and species richness of aquatic plants in most lakes of a large North American ecoregion. *Global Change Biology,* 22**,** 3937-3947.

BARALE, V., JAQUET, J.-M. & NDIAYE, M. 2008. Algal blooming patterns and anomalies in the Mediterranean Sea as derived from the SeaWiFS data set (1998–2003). *Remote Sensing of Environment,* 112**,** 3300-3313.

BARANGE, M., MERINO, G., BLANCHARD, J., SCHOLTENS, J., HARLE, J., ALLISON, E., ALLEN, J., HOLT, J. & JENNINGS, S. 2014. Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nature Climate Change,* 4**,** 211.

BARASH, A., PICKHOLTZ, R., PICKHOLTZ, E., BLAUSTEIN, L. & RILOV, G. 2018. Seasonal aggregations of sharks near coastal power plants in Israel: an emerging phenomenon. *Marine Ecology Progress Series,* 590**,** 145-154.

BARICHE, M., LETOURNEUR, Y. & HARMELIN-VIVIEN, M. 2004. Temporal fluctuations and settlement patterns of native and Lessepsian herbivorous fishes on the Lebanese coast (eastern Mediterranean). *Environmental Biology of Fishes,* 70**,** 81-90.

BARICHE, M., TORRES, M. & AZZURRO, E. 2013. The presence of the invasive Lionfish Pterois miles in the Mediterranean Sea. *Mediterranean Marine Science,* 14**,** 292-294.

BARNETT, L. A., BRANCH, T. A., RANASINGHE, R. A. & ESSINGTON, T. E. 2017. Old-growth fishes become scarce under fishing. *Current Biology,* 27**,** 2843-2848. e2.

BARRAGÁN, J. M. & DE ANDRÉS, M. 2015. Analysis and trends of the world's coastal cities and agglomerations. *Ocean & Coastal Management,* 114**,** 11-20.

BAX, N., WILLIAMSON, A., AGUERO, M., GONZALEZ, E. & GEEVES, W. 2003. Marine invasive alien species: a threat to global biodiversity. *Marine Policy,* 27**,** 313-323.

BELKIN, I. M. 2009. Rapid warming of large marine ecosystems. *Progress in Oceanography,* 81**,** 207-213.

BELMAKER, J., PARRAVICINI, V. & KULBICKI, M. 2013. Ecological traits and environmental affinity explain Red Sea fish introduction into the Mediterranean. *Global Change Biology,* 19**,** 1373-1382.

BELL, J. D., WATSON, R. A. & YE, Y. 2017. Global fishing capacity and fishing effort from 1950 to 2012. *Fish and Fisheries,* 18**,** 489-505.

BEN RAIS LASRAM, F., GUILHAUMON, F., ALBOUY, C., SOMOT, S., THUILLER, W. & MOUILLOT, D. 2010. The Mediterranean Sea as a 'cul-de-sac'for endemic fishes facing climate change. *Global Change Biology,* 16**,** 3233-3245.

BERDNIKOV, S., SELYUTIN, V., VASILCHENKO, V. & CADDY, J. 1999. Trophodynamic model of the Black and Azov Sea pelagic ecosystem: consequences of the comb jelly,< i> Mnemiopsis leydei</i>, invasion. *Fisheries Research,* 42**,** 261-289.

BERG, T., FÜRHAUPTER, K., TEIXEIRA, H., UUSITALO, L. & ZAMPOUKAS, N. 2015. The Marine Strategy Framework Directive and the ecosystem-based approach–pitfalls and solutions. *Marine pollution bulletin,* 96**,** 18-28.

BERTRAND, J. A., GIL DE SOLA, L., PAPACONSTANTINOU, C., RELINI, G. & SOUPLET, A. 2002. The general specifications of the MEDITS surveys. *Scientia Marina,* 66**,** 9-17.

BEVILLE, S. T., KERR, G. N. & HUGHEY, K. F. D. 2012. Valuing impacts of the invasive alga Didymosphenia geminata on recreational angling. *Ecological Economics,* 82**,** 1-10.

BIANCHI, C., CORSINI-FOKA, M., MORRI, C. & ZENETOS, A. 2014. Thirty years after-dramatic change in the coastal marine habitats of Kos Island (Greece), 1981-2013. *Mediterranean Marine Science,* 15**,** 482-497.

BIANCHI, C. N. 2007. Biodiversity issues for the forthcoming tropical Mediterranean Sea. *Biodiversity in Enclosed Seas and Artificial Marine Habitats.* Springer.

BIANCHI, C. N., BOUDOURESQUE, C. F., FRANCOUR, P., MORRI, C., PARRAVICINI, V., TEMPLADO, J. & ZENETOS, A. 2013. The changing biogeography of the Mediterranean Sea: from the old frontiers to the new gradients. *Boll. Mus. Ist. Biol. Univ. Genova,* 75**,** 81-84.

BIANCHI, C. N. & MORRI, C. 2000. Marine biodiversity of the Mediterranean Sea: situation, problems and prospects for future research. *Marine pollution bulletin,* 40**,** 367-376.

BIERMAN, V. J., KAUR, J., DEPINTO, J. V., FEIST, T. J. & DILKS, D. W. 2005. Modeling the role of zebra mussels in the proliferation of blue-green algae in Saginaw Bay, Lake Huron. *Journal of Great Lakes Research,* 31**,** 32-55.

BLAMEY, L. K., PLAGÁNYI, É. E. & BRANCH, G. M. 2013. Modeling a regime shift in a kelp forest ecosystem caused by a lobster range expansion. *Bulletin of Marine Science,* 89**,** 347-375.

BLAMEY, L. K., PLAGÁNYI, T. E. & BRANCH, G. M. 2014. Was overfishing of predatory fish responsible for a lobster-induced regime shift in the Benguela? *Ecological Modelling,* 273**,** 140-150.

BOCANIOV, S. A., SMITH, R. E. H., SPILLMAN, C. M., HIPSEY, M. R. & LEON, L. F. 2014. The nearshore shunt and the decline of the phytoplankton spring bloom in the Laurentian Great Lakes: Insights from a three-dimensional lake model. *Hydrobiologia,* 731**,** 151-172.

BOPP, L., RESPLANDY, L., ORR, J. C., DONEY, S. C., DUNNE, J. P., GEHLEN, M., HALLORAN, P., HEINZE, C., ILYINA, T. & SEFERIAN, R. 2013. Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences,* 10**,** 6225-6245.

BOSC, E., BRICAUD, A. & ANTOINE, D. 2004. Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. *Global Biogeochemical Cycles,* 18.

BRASSEUR, P., BECKERS, J.-M., BRANKART, J. & SCHOENAUEN, R. 1996. Seasonal temperature and salinity fields in the Mediterranean Sea: Climatological analyses of a historical data set. *Deep Sea Research Part I: Oceanographic Research Papers,* 43**,** 159-192.

BREITBURG, D. L. & RIEDEL, G. F. 2005. Multiple stressors in marine systems. *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity.* . Washington: Island Press.

BROTONS, L., CHRISTENSEN, V., RAVINDRANATH, N. H., CAO, M., CHUN, J. H., MAURY, O., PERI, P. L., PROENÇA, V., SALIHOGLU, B., CHATURVEDI, R. K., COLL, M., OTTO, S. R., RAO, A. S. & TITEUX, N. 2016. Modelling impacts of drivers on biodiversity and ecosystems. . *In:* IPBES (ed.) *Methodological assessment of scenarios and models of biodiversity and ecosystem services [S. Ferrier, K. N. Ninan, P. Leadley, R. Alkemade, L. A. Acosta, H.R. Akçakaya, L. Brotons, W.W.L. Cheung, V. Christensen, K. A. Harhash, J. Kabubo-Mariara, C. Lundquist, M. Obersteiner, H. Pereira, G. Peterson, R. Pichs-Madruga, N. Ravindranath, C. Rondinini and B.A. Wintle (eds.)].* Bonn, Germany.

BUCHADAS, A., VAZ, A. S., HONRADO, J. P., ALAGADOR, D., BASTOS, R., CABRAL, J. A., SANTOS, M. & VICENTE, J. R. 2017. Dynamic models in research and management of biological invasions. *Journal of Environmental Management,* 196**,** 594-606.

BYRNES, J. E., REYNOLDS, P. L. & STACHOWICZ, J. J. 2007. Invasions and extinctions reshape coastal marine food webs. *PloS one,* 2**,** e295.

CALDEIRA, K. & WICKETT, M. E. 2003. Oceanography: anthropogenic carbon and ocean pH. *Nature,* 425**,** 365.

CALDOW, R. W. G., STILLMAN, R. A., DIT DURELL, S. E. A. L. V., WEST, A. D., MCGRORTY, S., GOSS-CUSTARD, J. D., WOOD, P. J. & HUMPHREYS, J. 2007. Benefits to shorebirds from invasion of a non-native shellfish. *Proceedings of the Royal Society B: Biological Sciences,* 274**,** 1449-1455.

CARDINALE, M. & SCARCELLA, G. 2017. Mediterranean Sea: a failure of the European fisheries management system. *Frontiers in Marine Science,* 4**,** 72.

CARLSSON, N. O., SARNELLE, O. & STRAYER, D. L. 2009. Native predators and exotic prey–an acquired taste? *Frontiers in Ecology and the Environment,* 7**,** 525-532.

CARLTON, J. T. & RUIZ, G. M. 2005. The magnitude and consequences of bioinvasions in marine ecosystems. *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity. Island Press, Washington, DC USA***,** 123-148.

CARPENTER, S. R., BROCK, W. A., HANSEN, G. J., HANSEN, J. F., HENNESSY, J. M., ISERMANN, D. A., PEDERSEN, E. J., PERALES, K. M., RYPEL, A. L. & SASS, G. G. 2017. Defining a Safe Operating Space for inland recreational fisheries. *Fish and Fisheries,* 18**,** 1150-1160.

CARPENTIERI, P., LELLI, S., COLLOCA, F., MOHANNA, C., BARTOLINO, V., MOUBAYED, S. & ARDIZZONE, G. 2009. Incidence of lessepsian migrants on landings of the artisanal fishery of south Lebanon. *Marine Biodiversity Records,* 2**,** e71.

CBD 2002. Sixth Conference of the Parties, the Hague, the Netherlands. 7–19 April 2002: Decision VI/23: Alien Species that Threaten Ecosystems, Habitats or Species to Which is Annexed Guiding Principles for the Prevention, Introduction and Mitigation of Impacts of Alien Species that Threaten Ecosystems, Habitats or Species. http://www.biodiv.org

CISNEROS-MONTEMAYOR, A. M., CHRISTENSEN, V., ARREGUÍN-SÁNCHEZ, F. & SUMAILA, U. R. 2012. Ecosystem models for management advice: An analysis of recreational and commercial fisheries policies in Baja California Sur, Mexico. *Ecological Modelling,* 228**,** 8-16.

CLAVERO, M., HERMOSO, V., APARICIO, E. & GODINHO, F. N. 2013. Biodiversity in heavily modified waterbodies: Native and introduced fish in Iberian reservoirs. *Freshwater Biology,* 58**,** 1190-1201.

COCHRANE, K., BIANCHI, G., FLETCHER, W., FLUHARTY, D., MAHON, R. & MISUND, O. A. 2014. Regulatory and governance frameworks. *The Sea,* 16**,** 77-119.

COHEN, A. N. & CARLTON, J. T. 1998. Accelerating invasion rate in a highly invaded estuary. *science,* 279**,** 555-558.

COLL, M., AKOGLU, E., ARREGUÍN-SÁNCHEZ, F., FULTON, E., GASCUEL, D., HEYMANS, J., LIBRALATO, S., MACKINSON, S., PALOMERA, I. & PIRODDI, C. 2015. Modelling dynamic ecosystems: venturing beyond boundaries with the Ecopath approach. *Reviews in fish biology and fisheries,* 25**,** 413-424.

COLL, M., BAHAMON, N., SARDÀ, F., PALOMERA, I., TUDELA, S. & SUURONEN, P. 2008a. Improved trawl selectivity: effects on ecosystems in the South Catalan Sea (NW Mediterranean). *MARINE ECOLOGY-PROGRESS SERIES-,* 355**,** 131.

COLL, M., BUNDY, A. & SHANNON, L. J. 2008b. Ecosystem modelling using the Ecopath with Ecosim approach. *Computers in Fisheries Research.* New York: Springer-Verlag.

COLL, M., CARRERAS, M., CORNAX, M., MASSUTÍ, E., MOROTE, E., PASTOR, X., QUETGLAS, A., SÁEZ, R., SILVA, L. & SOBRINO, I. 2014. Closer to reality: Reconstructing total removals in mixed fisheries from Southern Europe. *Fisheries Research,* 154**,** 179-194.

COLL, M. & LIBRALATO, S. 2012. Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea. *Fish and Fisheries,* 13**,** 60-88.

COLL, M., PALOMERA, I., TUDELA, S. & DOWD, M. 2008c. Food-web dynamics in the South Catalan Sea ecosystem (NW Mediterranean) for 1978–2003. *Ecological Modelling,* 217**,** 95-116.

COLL, M., PALOMERA, I., TUDELA, S. & SARDÀ, F. 2006. Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. *Journal of Marine Systems,* 59**,** 63-96.

COLL, M., PIRODDI, C., ALBOUY, C., BEN RAIS LASRAM, F., CHEUNG, W. W., CHRISTENSEN, V., KARPOUZI, V. S., GUILHAUMON, F., MOUILLOT, D. & PALECZNY, M. 2012. The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves. *Global Ecology and Biogeography,* 21**,** 465-480.

COLL, M., PIRODDI, C., STEENBEEK, J., KASCHNER, K., LASRAM, F. B. R., AGUZZI, J., BALLESTEROS, E., BIANCHI, C. N., CORBERA, J. & DAILIANIS, T. 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PloS one,* 5**,** e11842.

COLL, M., SANTOJANNI, A., PALOMERA, I. & ARNERI, E. 2009. Food-web changes in the Adriatic Sea over the last three decades. *Marine Ecology Progress Series,* 381**,** 17-37.

COLL, M., SANTOJANNI, A., PALOMERA, I., TUDELA, S. & ARNERI, E. 2007. An ecological model of the Northern and Central Adriatic Sea: analysis of ecosystem structure and fishing impacts. *Journal of Marine Systems,* 67**,** 119-154.

COLL, M., SHANNON, L., KLEISNER, K., JUAN-JORDÁ, M., BUNDY, A., AKOGLU, A., BANARU, D., BOLDT, J., BORGES, M. & COOK, A. 2016. Ecological indicators to capture the effects of fishing on biodiversity and conservation status of marine ecosystems. *Ecological Indicators,* 60**,** 947-962.

COLL, M. & STEENBEEK, J. 2017. Standardized ecological indicators to assess aquatic food webs: The ECOIND software plug-in for Ecopath with Ecosim models. *Environmental Modelling & Software,* 89**,** 120-130.

COLLÉTER, M., VALLS, A., GUITTON, J., GASCUEL, D., PAULY, D. & CHRISTENSEN, V. 2015. Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. *Ecological Modelling,* 302**,** 42-53.

COLLIE, J. S., BOTSFORD, L. W., HASTINGS, A., KAPLAN, I. C., LARGIER, J. L., LIVINGSTON, P. A., PLAGÁNYI, É., ROSE, K. A., WELLS, B. K. & WERNER, F. E. 2014. Ecosystem models for fisheries management: finding the sweet spot. *Fish and Fisheries*.

COLLOCA, F., SCARCELLA, G. & LIBRALATO, S. 2017. Recent trends and impacts of fisheries exploitation on mediterranean stocks and ecosystems. *Frontiers in Marine Science,* 4**,** 244.

COOK, G. S., FLETCHER, P. J. & KELBLE, C. R. 2014. Towards marine ecosystem based management in South Florida: Investigating the connections among ecosystem pressures, states, and services in a complex coastal system. *Ecological Indicators,* 44**,** 26-39.

CORNWALL, C. E. & EDDY, T. D. 2015. Effects of near-future ocean acidification, fishing, and marine protection on a temperate coastal ecosystem. *Conservation Biology,* 29**,** 207-215.

CORRALES, X., COLL, M., OFIR, E., HEYMANS, J. J., STEENBEEK, J., GOREN, M., EDELIST, D. & GAL, G. 2018. Future scenarios of marine resources and ecosystem conditions of the Eastern Mediterranean under impacts of fishing, alien species and ocean warming. *Scientific Reports*.

CORRALES, X., COLL, M., OFIR, E., PIRODDI, C., GOREN, M., EDELIST, D., HEYMANS, J., STEENBEEK, J., CHRISTENSEN, V. & GAL, G. 2017a. Hindcasting the dynamics of an Eastern Mediterranean marine ecosystem under the impacts of multiple stressors. *Marine Ecology Progress Series,* 580**,** 17-36.

CORRALES, X., COLL, M., TECCHIO, S., BELLIDO, J. M., FERNÁNDEZ, Á. M. & PALOMERA, I. 2015. Ecosystem structure and fishing impacts in the northwestern Mediterranean Sea using a food web model within a comparative approach. *Journal of Marine Systems,* 148**,** 183-199.

CORRALES, X., GAL, G. & COLL, M. 2014. Modeling the alien species impacts in marine ecosystems. *Steenbeek, J., Piroddi, C., Coll, M., Heymans, J.J., Villasante, S., Christensen, V. (eds) Ecopath 30 Years conference proceedings: Extended Abstracts. Fisheries Centre Research Reports 22(3) (ISSN 1198-6727). 237 pp.* Vancouver: Fisheries Centre, University of British Columbia.

CORRALES, X., OFIR, E., COLL, M., GOREN, M., EDELIST, D., HEYMANS, J. & GAL, G. 2017b. Modeling the role and impact of alien species and fisheries on the Israeli marine continental shelf ecosystem. *Journal of Marine Systems,* 170**,** 88-102.

CORREA, C. & HENDRY, A. P. 2012. Invasive salmonids and lake order interact in the decline of puye grande Galaxias platei in western Patagonia lakes. *Ecological Applications,* 22**,** 828-842.

COSTANZA, R., ANDRADE, F., ANTUNES, P., VAN DEN BELT, M., BOESCH, D., BOERSMA, D., CATARINO, F., HANNA, S., LIMBURG, K. & LOW, B. 1999. Ecological economics and sustainable governance of the oceans. *Ecological Economics,* 31**,** 171-187.

COSTELLO, C., OVANDO, D., CLAVELLE, T., STRAUSS, C. K., HILBORN, R., MELNYCHUK, M. C., BRANCH, T. A., GAINES, S. D., SZUWALSKI, C. S. & CABRAL, R. B. 2016. Global fishery prospects under contrasting management regimes. *Proceedings of the National Academy of Sciences,* 113**,** 5125-5129.

COSTELLO, M. J., COLL, M., DANOVARO, R., HALPIN, P., OJAVEER, H. & MILOSLAVICH, P. 2010. A census of marine biodiversity knowledge, resources, and future challenges. *PloS one,* 5**,** e12110.

CÔTÉ, I. M. & DARLING, E. S. 2010. Rethinking ecosystem resilience in the face of climate change. *PLoS biology,* 8**,** e1000438.

CÔTÉ, I. M., DARLING, E. S. & BROWN, C. J. 2016. Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society of London B: Biological Sciences,* 283.

COURCHAMP, F., FOURNIER, A., BELLARD, C., BERTELSMEIER, C., BONNAUD, E., JESCHKE, J. M. & RUSSELL, J. C. 2017. Invasion biology: specific problems and possible solutions. *Trends in Ecology & Evolution,* 32**,** 13-22.

COX, S. P. & KITCHELL, J. F. 2004. Lake Superior ecosystem, 1929–1998: simulating alternative hypotheses for recruitment failure of lake herring (Coregonus artedi). *Bulletin of Marine Science,* 74**,** 671-683.

CRAIN, C. M., HALPERN, B. S., BECK, M. W. & KAPPEL, C. V. 2009. Understanding and managing human threats to the coastal marine environment. *Annals of the New York Academy of Sciences,* 1162**,** 39-62.

CRAIN, C. M., KROEKER, K. & HALPERN, B. S. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology letters,* 11**,** 1304-1315.

CRANE, D. P. & EINHOUSE, D. W. 2016. Changes in growth and diet of smallmouth bass following invasion of Lake Erie by the round goby. *Journal of Great Lakes Research,* 42**,** 405-412.

CRANE, D. P., FARRELL, J. M., EINHOUSE, D. W., LANTRY, J. R. & MARKHAM, J. L. 2015. Trends in body condition of native piscivores following invasion of Lakes Erie and Ontario by the round goby. *Freshwater Biology,* 60**,** 111-124.

CRIALES-HERNANDEZ, M. I., DUARTE, L. O., GARCÍA, C. B. & MANJARRÉS, L. 2006. Ecosystem impacts of the introduction of bycatch reduction devices in a tropical shrimp trawl fishery: Insights through simulation. *Fisheries Research,* 77**,** 333-342.

CROOKS, J. A. 2005. Lag times and exotic species: The ecology and management of biological invasions in slow-motion1. *Ecoscience,* 12**,** 316-329.

CROWDER, L. B., HAZEN, E. L., AVISSAR, N., BJORKLAND, R., LATANICH, C. & OGBURN, M. B. 2008. The impacts of fisheries on marine ecosystems and the transition to ecosystem-based management. *Annual Review of Ecology, Evolution, and Systematics,* 39**,** 259-278.

CUDDINGTON, K., FORTIN, M.-J., GERBER, L., HASTINGS, A., LIEBHOLD, A., O'CONNOR, M. & RAY, C. 2013. Process-based models are required to manage ecological systems in a changing world. *Ecosphere,* 4**,** 1-12.

CURRAN, K., BUNDY, A., CRAIG, M., HALL, T., LAWTON, P., QUIGLEY, S., FISHERIES, D. O., OCEANS, O., ON & CANADIAN SCIENCE ADVISORY SECRETARIAT, O., ON 2012. Recommendations for science, management, and an ecosystem approach in fisheries and Oceans Canada, Maritimes Region. DFO, Ottawa, ON(Canada).

CURY, P., SHANNON, L., ROUX, J., DASKALOV, G., JARRE, A., MOLONEY, C. & PAULY, D. 2005. Trophodynamic indicators for an ecosystem approach to fisheries. *ICES Journal of Marine Science: Journal du Conseil,* 62**,** 430-442.

CURY, P. M., SHIN, Y.-J., PLANQUE, B., DURANT, J. M., FROMENTIN, J.-M., KRAMER-SCHADT, S., STENSETH, N. C., TRAVERS, M. & GRIMM, V. 2008. Ecosystem oceanography for global change in fisheries. *Trends in Ecology & Evolution,* 23**,** 338-346.

CHA, Y., STOW, C. A. & BERNHARDT, E. S. 2013. Impacts of dreissenid mussel invasions on chlorophyll and total phosphorus in 25 lakes in the USA. *Freshwater Biology,* 58**,** 192-206.

CHA, Y., STOW, C. A., NALEPA, T. F. & RECKHOW, K. H. 2011. Do invasive mussels restrict offshore phosphorus transport in lake huron? *Environmental Science and Technology,* 45**,** 7226-7231.

CHAN, F. T. & BRISKI, E. 2017. An overview of recent research in marine biological invasions. Springer.

CHEUNG, W. W., JONES, M. C., REYGONDEAU, G. & FRÖLICHER, T. L. 2018. Opportunities for climate-risk reduction through effective fisheries management. *Global Change Biology*.

CHEUNG, W. W., SARMIENTO, J. L., DUNNE, J., FRÖLICHER, T. L., LAM, V. W., PALOMARES, M. D., WATSON, R. & PAULY, D. 2013a. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change,* 3**,** 254-258.

CHEUNG, W. W., WATSON, R. & PAULY, D. 2013b. Signature of ocean warming in global fisheries catch. *Nature,* 497**,** 365.

CHIPPS, S. R. & WAHL, D. H. 2008. Bioenergetics modeling in the 21st century: reviewing new insights and revisiting old constraints. *Transactions of the American Fisheries Society,* 137**,** 298-313.

CHRISTENSEN, V. 1995. Ecosystem maturity—towards quantification. *Ecological Modelling,* 77**,** 3-32.

CHRISTENSEN, V. 1996. Managing fisheries involving predator and prey species. *Reviews in fish biology and fisheries,* 6**,** 417-442.

CHRISTENSEN, V. 2013. Ecological Networks in Fisheries: Predicting the Future? *Fisheries,* 38**,** 76-81.

CHRISTENSEN, V., COLL, M., PIRODDI, C., STEENBEEK, J., BUSZOWSKI, J. & PAULY, D. 2014a. A century of fish biomass decline in the ocean. *Mar Ecol Prog Ser,* 512**,** 155-166.

CHRISTENSEN, V., COLL, M., STEENBEEK, J., BUSZOWSKI, J., CHAGARIS, D. & WALTERS, C. J. 2014b. Representing variable habitat quality in a spatial food web model. *Ecosystems,* 17**,** 1397-1412.

CHRISTENSEN, V., FERDAÑA, Z. & STEENBEEK, J. 2009. Spatial optimization of protected area placement incorporating ecological, social and economical criteria. *Ecological Modelling,* 220**,** 2583-2593.

CHRISTENSEN, V. & MACLEAN, J. 2011. *Ecosystem approaches to fisheries: a global perspective,* Cambridge, Cambridge University Press.

CHRISTENSEN, V. & PAULY, D. 1992. ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling,* 61**,** 169-185.

CHRISTENSEN, V. & PAULY, D. 1993. *Trophic models of aquatic ecosystems,* ICLARM Conference Proceedings.

CHRISTENSEN, V. & WALTERS, C. 2011. Progress in the use of ecosystem models for fisheries management. *Ecosystem approaches to fisheries: a global perspective. Cambridge University Press, Cambridge.* Cambridge: Cambridge University Press.

CHRISTENSEN, V., WALTERS, C., PAULY, D. & FORREST, R. 2008. Ecopath with Ecosim version 6 user guide. *Lenfest Ocean Futures Project, University of British Columbia, Vancouver*.

CHRISTENSEN, V. & WALTERS, C. J. 2004a. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling,* 172**,** 109-139.

CHRISTENSEN, V. & WALTERS, C. J. 2004b. Trade-offs in ecosystem-scale optimization of fisheries management policies. *Bulletin of Marine Science,* 74**,** 549-562.

CHRISTY, F. T. & SCOTT, A. 1965. *The common wealth in ocean fisheries,* The John Hopkins Press. Baltimore.

DAMBACHER, J. M., GAUGHAN, D. J., ROCHET, M. J., ROSSIGNOL, P. A. & TRENKEL, V. M. 2009. Qualitative modelling and indicators of exploited ecosystems. *Fish and Fisheries,* 10**,** 305-322.

DAMBACHER, J. M., LI, H. W. & ROSSIGNOL, P. A. 2002. Relevance of community structure in assessing indeterminacy of ecological predictions. *Ecology,* 83**,** 1372-1385.

DASKALOV, G. M., GRISHIN, A. N., RODIONOV, S. & MIHNEVA, V. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences,* 104**,** 10518-10523.

DE AMORIM, S. R., UMETSU, C. A., TOLEDO, D. & CAMARGO, A. F. M. 2015. Effects of a non native species of Poaceae on aquatic macrophyte community composition: A comparison with a native species. *Journal of Aquatic Plant Management,* 53**,** 191-196.

DICK, J. T., ALEXANDER, M. E., JESCHKE, J. M., RICCIARDI, A., MACISAAC, H. J., ROBINSON, T. B., KUMSCHICK, S., WEYL, O. L., DUNN, A. M. & HATCHER, M. J. 2014. Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biological Invasions,* 16**,** 735-753.

DONEY, S. C. 1999. Major challenges confronting marine biogeochemical modeling. *Global Biogeochemical Cycles,* 13**,** 705-714.

DONEY, S. C., RUCKELSHAUS, M., DUFFY, J. E., BARRY, J. P., CHAN, F., ENGLISH, C. A., GALINDO, H. M., GREBMEIER, J. M., HOLLOWED, A. B. & KNOWLTON, N. 2012. Climate change impacts on marine ecosystems. *Marine Science,* 4.

DOWNING, A. S., VAN NES, E. H., JANSE, J. H., WITTE, F., CORNELISSEN, I. J., SCHEFFER, M. & MOOIJ, W. M. 2012. Collapse and reorganization of a food web of Mwanza Gulf, Lake Victoria. *Ecological applications,* 22**,** 229-239.

DUDGEON, D., ARTHINGTON, A. H., GESSNER, M. O., KAWABATA, Z. I., KNOWLER, D. J., LÉVÊQUE, C., NAIMAN, R. J., PRIEUR-RICHARD, A. H., SOTO, D. & STIASSNY, M. L. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological reviews,* 81**,** 163-182.

DULVY, N., ALLEN, D., RALPH, G. & WALLS, R. 2016. The conservation status of Sharks, Rays and Chimaeras in the Mediterranean Sea [Brochure]. *IUCN, Malaga, Spain*.

DUNNE, J. A. 2006. The network structure of foodwebs. *In:* PASCUAL, M. D., J.A. (ed.) *Ecological networks: linking structure to dynamics in food webs.* Oxford: Oxford University Press.

EARLY, R., BRADLEY, B. A., DUKES, J. S., LAWLER, J. J., OLDEN, J. D., BLUMENTHAL, D. M., GONZALEZ, P., GROSHOLZ, E. D., IBAÑEZ, I. & MILLER, L. P. 2016. Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature communications,* 7**,** 12485.

EDELIST, D. 2012. *Fishery management and marine invasion in Israel.* PhD thesis, University of Haifa, Faculty of Humanities, Department of Maritime Civilizations.

EDELIST, D., GOLANI, D., RILOV, G. & SPANIER, E. 2012. The invasive venomous striped eel catfish Plotosus lineatus in the Levant: possible mechanisms facilitating its rapid invasional success. *Marine Biology,* 159**,** 283-290.

EDELIST, D., GOLANI, D. & SPANIER, E. 2014. First implementation of the Large Fish Index (LFI) in the eastern Mediterranean. *Scientia Marina,* 78**,** 185-192.

EDELIST, D., RILOV, G., GOLANI, D., CARLTON, J. T. & SPANIER, E. 2013a. Restructuring the Sea: profound shifts in the world's most invaded marine ecosystem. *Diversity and Distributions,* 19**,** 69-77.

EDELIST, D., SCHEININ, A., SONIN, O., SHAPIRO, J., SALAMEH, P., RILOV, G., BENAYAHU, Y., SCHULZ, D. & ZELLER, D. 2013b. Israel: Reconstructed estimates of total fisheries removals in the Mediterranean, 1950–2010. *Acta adriatica,* 54.

EDELIST, D., SONIN, O., GOLANI, D., RILOV, G. & SPANIER, E. 2011. Spatiotemporal patterns of catch and discards of the Israeli Mediterranean trawl fishery in the early 1990s: ecological and conservation perspectives. *Scientia Marina,* 75**,** 641-652.

EDWARDS, M. & RICHARDSON, A. J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature,* 430**,** 881.

FABRY, V. J., SEIBEL, B. A., FEELY, R. A. & ORR, J. C. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science,* 65**,** 414-432.

FANELLI, E., AZZURRO, E., BARICHE, M., CARTES, J. E. & MAYNOU, F. 2015. Depicting the novel Eastern Mediterranean food web: a stable isotopes study following Lessepsian fish invasion. *Biological Invasions,* 17**,** 2163-2178.

FAO 2007. Marine Protected Areas as a Tool for Fisheries Management. MPAs, fisheries management and the ecosystem approach. FI Project Websites. 26 April 2007. [12 January 2018].

FAO 2008. Best Practices in Ecosystem Modelling: Modelling Ecosystem Interactions for Informing an Ecosystem Approach to Fisheries. *In:* FAO (ed.) *Fisheries Management — The Ecosystem Approach to Fisheries, FAO Technical Guidelines for Responsible Fisheries.* Rome.

FEELY, R. A., DONEY, S. C. & COOLEY, S. R. 2009. Ocean acidification: Present conditions and future changes in a high-CO_2 world. *Oceanography,* 22**,** 36-47.

FERGUSON, J. M., TAPER, M. L., GUY, C. S. & SYSLO, J. M. 2012. Mechanisms of coexistence between native bull trout (Salvelinus confluentus) and non-native lake trout (Salvelinus namaycush): Inferences from pattern-oriented modeling. *Canadian Journal of Fisheries and Aquatic Sciences,* 69**,** 1-15.

FERNANDES, P. G., RALPH, G. M., NIETO, A., CRIADO, M. G., VASILAKOPOULOS, P., MARAVELIAS, C. D., COOK, R. M., POLLOM, R. A., KOVAČIĆ, M. & POLLARD, D. 2017. Coherent assessments of Europe’s marine fishes show regional divergence and megafauna loss. *Nature Ecology & Evolution,* 1**,** 0170.

FERRETTI, F., MYERS, R. A., SERENA, F. & LOTZE, H. K. 2008. Loss of large predatory sharks from the Mediterranean Sea. *Conservation Biology,* 22**,** 952-964.

FERRIER, S., NINAM, K. N., LEADLEY, P., ALKEMADE, R., KOLOMYTSEV, G., MORAES, M., MOHAMMED, E. Y. & TRISURAT, Y. 2016. Overview and vision. *IPBES, 2016: Methodological assessment of scenarios and models of biodiversity and ecosystem services [S. Ferrier, K. N. Ninan, P. Leadley, R. Alkemade, L. A. Acosta, H.R. Akçakaya, L. Brotons, W.W.L. Cheung, V. Christensen, K. A. Harhash, J. Kabubo-Mariara, C. Lundquist, M. Obersteiner, H. Pereira, G. Peterson, R. Pichs-Madruga, N. Ravindranath, C. Rondinini and B.A. Wintle (eds.)],.* Secretariat of the Intergovernmental Platform for Biodiversity and Ecosystem Services, Bonn, Germany.

FINN, J. T. 1976. Measures of ecosystem structure and function derived from analysis of flows. *Journal of theoretical Biology,* 56**,** 363-380.

FISHMAN, D. B., ADLERSTEIN, S. A., VANDERPLOEG, H. A., FAHNENSTIEL, G. L. & SCAVIA, D. 2009. Causes of phytoplankton changes in Saginaw Bay, Lake Huron, during the zebra mussel invasion. *Journal of Great Lakes Research,* 35**,** 482-495.

FOGARTY, M. J. 2013. The art of ecosystem-based fishery management. *Canadian Journal of Fisheries and Aquatic Sciences,* 71**,** 479-490.

FOLEY, C. J., ANDREE, S. R., POTHOVEN, S. A., NALEPA, T. F. & HÖÖK, T. O. 2017. Quantifying the predatory effect of round goby on Saginaw Bay dreissenids. *Journal of Great Lakes Research,* 43**,** 121-131.

FONT, T. & LLORET, J. 2014. Biological and ecological impacts derived from recreational fishing in Mediterranean coastal areas. *Reviews in Fisheries Science & Aquaculture,* 22**,** 73-85.

FONTAINE, T. D. & STEWART, D. J. 1992. Exploring the effects of multiple management objectives and exotic species on great lakes food webs and contaminant dynamics. *Environmental Management,* 16**,** 225-229.

FORTIBUONI, T., GIOVANARDI, O., PRANOVI, F., RAICEVICH, S., SOLIDORO, C. & LIBRALATO, S. 2017. Analysis of long-term changes in a Mediterranean marine ecosystem based on fishery landings. *Frontiers in Marine Science,* 4**,** 33.

FRANCOUR, P., MANGIALAJO, L. & PASTOR, J. 2010. Mediterranean marine protected areas and non-indigenous fish spreading. *Fish Invasions of the Mediterranean Sea: Change and renewal. D. Golani & B. Appelbaum-Golani eds., Pensoft Publisher, Sofia-Moscow***,** 127-144.

FRANK, K. T., PETRIE, B., CHOI, J. S. & LEGGETT, W. C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *science,* 308**,** 1621-1623.

FRICKE, R., GOLANI, D. & APPELBAUM-GOLANI, B. 2015. First record of the Indian anchovy Stolephorus indicus (van Hasselt, 1823)(Clupeiformes: Engraulidae) in the Mediterranean Sea. *BioInvasions Records,* 4**,** 293-297.

FROESE, R. & PAULY, D. 2017. FishBase. World Wide Web electronic publication. www.fishbase.org, version (06/2017).

FU, C., LARGE, S., KNIGHT, B., RICHARDSON, A. J., BUNDY, A., REYGONDEAU, G., BOLDT, J., VAN DER MEEREN, G. I., TORRES, M. A. & SOBRINO, I. 2015. Relationships among fisheries exploitation, environmental conditions, and ecological indicators across a series of marine ecosystems. *Journal of Marine Systems,* 148**,** 101-111.

FULTON, E. A. 2010. Approaches to end-to-end ecosystem models. *Journal of Marine Systems,* 81**,** 171-183.

FULTON, E. A., BOSCHETTI, F., SPORCIC, M., JONES, T., LITTLE, L. R., DAMBACHER, J. M., GRAY, R., SCOTT, R. & GORTON, R. 2015. A multi-model approach to engaging stakeholder and modellers in complex environmental problems. *Environmental Science & Policy,* 48**,** 44-56.

FULTON, E. A., FULLER, M., SMITH, A. & PUNT, A. 2004a. Ecological indicators of the ecosystem effects of fishing.

FULTON, E. A., LINK, J. S., KAPLAN, I. C., SAVINA-ROLLAND, M., JOHNSON, P., AINSWORTH, C., HORNE, P., GORTON, R., GAMBLE, R. J. & SMITH, A. D. 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish and Fisheries,* 12**,** 171-188.

FULTON, E. A., SMITH, A. D. & JOHNSON, C. R. 2003. *Effect of complexity on marine ecosystem models.*

FULTON, E. A., SMITH, A. D. & JOHNSON, C. R. 2004b. Effects of spatial resolution on the performance and interpretation of marine ecosystem models. *Ecological Modelling,* 176**,** 27-42.

FULTON, E. A., SMITH, A. D. & PUNT, A. E. 2005. Which ecological indicators can robustly detect effects of fishing? *ICES Journal of Marine Science,* 62**,** 540-551.

GAINES, S. D., COSTELLO, C., OWASHI, B., MANGIN, T., BONE, J., MOLINOS, J. G., BURDEN, M., DENNIS, H., HALPERN, B. S. & KAPPEL, C. V. 2018. Improved fisheries management could offset many negative effects of climate change. *Science advances,* 4**,** eaao1378.

GAL, G., MAKLER-PICK, V. & SHACHAR, N. 2014. Dealing with uncertainty in ecosystem model scenarios: application of the single-model ensemble approach. *Environmental Modelling & Software,* 61**,** 360-370.

GALIL, B. 2007a. Loss or gain? Invasive aliens and biodiversity in the Mediterranean Sea. *Marine pollution bulletin,* 55**,** 314-322.

GALIL, B. 2008. Alien species in the Mediterranean Sea—which, when, where, why? *Hydrobiologia,* 606**,** 105-116.

GALIL, B., BOERO, F., FRASCHETTI, S., PIRAINO, S., CAMPBELL, M., HEWITT, C., CARLTON, J., COOK, E., JELMERT, A. & MACPHERSON, E. 2015. The Enlargement of the Suez Canal and Introduction of Non-Indigenous Species to the Mediterranean Sea. *Limnology and Oceanography Bulletin,* 24**,** 41-43.

GALIL, B. & GOREN, M. 2014. Metamorphoses: bioinvasions in the Mediterranean Sea. *The Mediterranean Sea.* Springer.

GALIL, B., MARCHINI, A., OCCHIPINTI-AMBROGI, A., MINCHIN, D., NARŠČIUS, A., OJAVEER, H. & OLENIN, S. 2014a. International arrivals: widespread bioinvasions in European Seas. *Ethology Ecology & Evolution,* 26**,** 152-171.

GALIL, B., MARCHINI, A., OCCHIPINTI-AMBROGI, A. & OJAVEER, H. 2017. The enlargement of the Suez Canal—Erythraean introductions and management challenges. *Management of Biological Invasions,* 8**,** 141-152.

GALIL, B. S. 2000. A sea under siege–alien species in the Mediterranean. *Biological Invasions,* 2**,** 177-186.

GALIL, B. S. 2007b. Seeing Red: Alien species along the Mediterranean coast of Israel. *Aquatic Invasions,* 2**,** 281-312.

GALIL, B. S., BOERO, F., CAMPBELL, M. L., CARLTON, J. T., COOK, E., FRASCHETTI, S., GOLLASCH, S., HEWITT, C. L., JELMERT, A. & MACPHERSON, E. 2014b. 'Double trouble': the expansion of the Suez Canal and marine bioinvasions in the Mediterranean Sea. *Biological Invasions***,** 1-4.

GALIL, B. S., MARCHINI, A. & OCCHIPINTI-AMBROGI, A. 2016. East is east and West is west? Management of marine bioinvasions in the Mediterranean Sea. *Estuarine, Coastal and Shelf Science*.

GALIL, B. S., MARCHINI, A. & OCCHIPINTI-AMBROGI, A. 2018. Mare Nostrum, Mare Quod Invaditur—The History of Bioinvasions in the Mediterranean Sea. *Histories of Bioinvasions in the Mediterranean.* Springer.

GALLARDO, B., CLAVERO, M., SÁNCHEZ, M. I. & VILÀ, M. 2016. Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology,* 22**,** 151-163.

GANJU, N. K., BRUSH, M. J., RASHLEIGH, B., ARETXABALETA, A. L., DEL BARRIO, P., GREAR, J. S., HARRIS, L. A., LAKE, S. J., MCCARDELL, G. & O'DONNELL, J. 2016. Progress and challenges in coupled hydrodynamic-ecological estuarine modeling. *Estuaries and Coasts,* 39**,** 311-332.

GARCIA, S. M., ZERBI, A., ALIAUME, C., DO CHI, T. & LASSERRE, G. 2003. *The ecosystem approach to fisheries: issues, terminology, principles, institutional foundations, implementation and outlook,* Rome, FAO.

GAUDIN, C. & DE YOUNG, C. 2007. *Recreational fisheries in the Mediterranean countries: a review of existing legal frameworks*, Food & Agriculture Org.

GFCM 2016a. Working group on Stock Assessment of Demersal Species (WGSAD). Final Report, GFCM and FAO headquarters. Rome.

GFCM 2016b. Working group on Stock Assessment of Small Pelagic Species (WGSASP). Final Report, GFCM and FAO headquarters. Rome.

GIAKOUMI, S., GUILHAUMON, F., KARK, S., TERLIZZI, A., CLAUDET, J., FELLINE, S., CERRANO, C., COLL, M., DANOVARO, R. & FRASCHETTI, S. 2016. Space invaders; biological invasions in marine conservation planning. *Diversity and Distributions,* 22**,** 1220-1231.

GIAKOUMI, S., HALPERN, B. S., MICHEL, L. N., GOBERT, S., SINI, M., BOUDOURESQUE, C. F., GAMBI, M. C., KATSANEVAKIS, S., LEJEUNE, P. & MONTEFALCONE, M. 2015. Towards a framework for assessment and management of cumulative human impacts on marine food webs. *Conservation Biology,* 29**,** 1228-1234.

GIORGI, F. 2006. Climate change hot-spots. *Geophysical Research Letters,* 33.

GIRON-NAVA, A., JAMES, C. C., JOHNSON, A. F., DANNECKER, D., KOLODY, B., LEE, A., NAGARKAR, M., PAO, G. M., YE, H. & JOHNS, D. G. 2017. Quantitative argument for long-term ecological monitoring. *Marine Ecology Progress Series,* 572**,** 269-274.

GIVAN, O., EDELIST, D., SONIN, O. & BELMAKER, J. 2017a. Thermal affinity as the dominant factor changing Mediterranean fish abundances. *Global Change Biology*.

GIVAN, O., PARRAVICINI, V., KULBICKI, M. & BELMAKER, J. 2017b. Trait structure reveals the processes underlying fish establishment in the Mediterranean. *Global Ecology and Biogeography,* 26**,** 142-153.

GLASER, D., RHEA, J. R., OPDYKE, D. R., RUSSELL, K. T., ZIEGLER, C. K., KU, W., ZHENG, L. & MASTRIANO, J. 2009. Model of zebra mussel growth and water quality impacts in the Seneca River, New York. *Lake and Reservoir Management,* 25**,** 49-72.

GOLANI, D. 1993. The biology of the Red Sea migrant, Saurida undosquamis in the Mediterranean and comparison with the indigenous confamilial Synodus saurus (Teleostei: Synodontidae). *Hydrobiologia,* 271**,** 109-117.

GOLANI, D. 1994. Niche separation between colonizing and indigenous goatfish (Mullidae) along the Mediterranean coast of Israel. *Journal of Fish Biology,* 45**,** 503-513.

GOLANI, D. 1998. Impact of Red Sea fish migrants through the Suez Canal on the aquatic environment of the Eastern Mediterranean. *Bulletin Series Yale School of Forestry and Environmental Studies,* 103**,** 375-387.

GOLANI, D. 2010. Colonization of the Mediterranean by Red Sea fishes via the Suez Canal–Lessepsian migration. *Fish Invasions of the Mediterranean Sea: Change and Renewal. Pensoft Publishers, Sofia-Moscow.*

GOLANI, D., REEF-MOTRO, R., EKSHTEIN, S., BARANES, A. & DIAMANT, A. 2007. Ichthyofauna of the rocky coastal littoral of the Israeli Mediterranean, with reference to the paucity of Red Sea (Lessepsian) migrants in this habitat. *Marine Biology Research,* 3**,** 333-341.

GOLANI, D. & SONIN, O. 1992. New records of the Red Sea fishes, Pterois miles (Scorpaenidae) andPteragogus pelycus (Labridae) from the eastern Mediterranean Sea. *Japanese Journal of Ichthyology,* 39, 167-169.

GOLANI, G. & APPELBAUM-GOLANI, B. 2010. *Fish Invasions of the Mediterranean Sea: Change and Renewal*.

GORELLI, G., SARDÀ, F. & COMPANY, J. B. 2016. Fishing Effort Increase and Resource Status of the Deep-Sea Red Shrimp Aristeus antennatus (Risso 1816) in the Northwest Mediterranean Sea Since the 1950s. *Reviews in Fisheries Science & Aquaculture,* 24, 192-202.

GOREN, M. & GALIL, B. S. 2001. Fish biodiversity in the vermetid reef of Shiqmona (Israel). *Marine Ecology,* 22, 369-378.

GOREN, M., GALIL, B. S., DIAMANT, A. & STERN, N. 2016. Invading up the food web? Invasive fish in the southeastern Mediterranean Sea. *Marine Biology,* 163, 180.

GOREN, M., SHULTS, D. & GAFNI, A. 2013. The Current State of Fish and Israel's Fisheries in the Mediterranean Sea. A special report to the Society for the Protection of Nature in Israel (SPNI). English version. 1-80pp. Tel Aviv. .

GOUDSWAARD, K. P., WITTE, F. & KATUNZI, E. F. 2008. The invasion of an introduced predator, Nile perch (Lates niloticus, L.) in Lake Victoria (East Africa): chronology and causes. *Environmental Biology of Fishes,* 81, 127-139.

GRABOWSKI, J. H., BACHMAN, M., DEMAREST, C., EAYRS, S., HARRIS, B. P., MALKOSKI, V., PACKER, D. & STEVENSON, D. 2014. Assessing the vulnerability of marine benthos to fishing gear impacts. *Reviews in Fisheries Science & Aquaculture,* 22, 142-155.

GREEN, S. J., AKINS, J. L., MALJKOVIĆ, A. & CÔTÉ, I. M. 2012. Invasive lionfish drive Atlantic coral reef fish declines. *PloS one,* 7, e32596.

GREEN, S. J., DULVY, N. K., BROOKS, A. M. L., AKINS, J. L., COOPER, A. B., MILLER, S. & ɤOTÉ, I. M. 2014. Linking removal targets to the ecological effects of invaders: A predictive model and field test. *Ecological Applications,* 24, 1311-1322.

GRIBBEN, P. E. & WRIGHT, J. T. 2006. Sublethal effects on reproduction in native fauna: Are females more vulnerable to biological invasion? *Oecologia,* 149, 352-361.

GROSHOLZ, E. 2002. Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology & Evolution,* 17, 22-27.

GROSHOLZ, E., LOVELL, S., BESEDIN, E. & KATZ, M. 2011. Modeling the impacts of the European green crab on commercial shellfisheries. *Ecological Applications,* 21, 915-924.

GRÜSS, A., ROSE, K. A., SIMONS, J., AINSWORTH, C. H., BABCOCK, E. A., CHAGARIS, D. D., DE MUTSERT, K., FROESCHKE, J., HIMCHAK, P. & KAPLAN, I. C. 2017. Recommendations on the use of ecosystem modeling for informing ecosystem-based fisheries management and restoration outcomes in the Gulf of Mexico. *Marine and Coastal Fisheries*.

GUCU, A. & BINGEL, F. 2011. Hake, Merluccius merluccius L., in the northeastern Mediterranean Sea: a case of disappearance. *Journal of Applied Ichthyology,* 27, 1001-1012.

GÜCÜ, A. C. & BINGEL, F. 1994. Trawlable species assemblages on the continental shelf of the northeastern Levant Sea(Mediterranean) with an emphasis on Lesseptian migration. *Acta adriatica,* 35, 83-100.

GÜCÜ, A. C., OK, M. & SAKINAN, S. 2010. Past and present of fish fauna in the NE Levant Sea and factor facilitating the colonization by Lessepsian fishes. *EastMed (2010) Report of the Sub-Regional Technical meeting on the Lessepsian migration and its impact on Eastern Mediterranean fishery*.

GUDIMOV, A., KIM, D. K., YOUNG, J. D., PALMER, M. E., DITTRICH, M., WINTER, J. G., STAINSBY, E. & ARHONDITSIS, G. B. 2015. Examination of the role of dreissenids and macrophytes in the phosphorus dynamics of Lake Simcoe, Ontario, Canada. *Ecological Informatics,* 26**,** 36-53.

GUÉNETTE, S., ARAÚJO, J. N. & BUNDY, A. 2014. Exploring the potential effects of climate change on the Western Scotian Shelf ecosystem, Canada. *Journal of Marine Systems,* 134**,** 89-100.

HALIM, Y. & RIZKALLA, S. 2011. Aliens in Egyptian Mediterranean waters. A check-list of Erythrean fish with new records. *Mediterranean Marine Science,* 12**,** 479-490.

HALPERN, B. S., FRAZIER, M., POTAPENKO, J., CASEY, K. S., KOENIG, K., LONGO, C., LOWNDES, J. S., ROCKWOOD, R. C., SELIG, E. R. & SELKOE, K. A. 2015a. Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature communications*, 6.

HALPERN, B. S., LONGO, C., HARDY, D., MCLEOD, K. L., SAMHOURI, J. F., KATONA, S. K., KLEISNER, K., LESTER, S. E., O'LEARY, J. & RANELLETTI, M. 2012. An index to assess the health and benefits of the global ocean. *Nature,* 488**,** 615.

HALPERN, B. S., LONGO, C., LOWNDES, J. S. S., BEST, B. D., FRAZIER, M., KATONA, S. K., KLEISNER, K. M., ROSENBERG, A. A., SCARBOROUGH, C. & SELIG, E. R. 2015b. Patterns and emerging trends in global ocean health. *PloS one,* 10**,** e0117863.

HALPERN, B. S., MCLEOD, K. L., ROSENBERG, A. A. & CROWDER, L. B. 2008a. Managing for cumulative impacts in ecosystem-based management through ocean zoning. *Ocean & Coastal Management,* 51**,** 203-211.

HALPERN, B. S., WALBRIDGE, S., SELKOE, K. A., KAPPEL, C. V., MICHELI, F., D'AGROSA, C., BRUNO, J. F., CASEY, K. S., EBERT, C. & FOX, H. E. 2008b. A global map of human impact on marine ecosystems. *science,* 319**,** 948-952.

HAMAD, N., MILLOT, C. & TAUPIER-LETAGE, I. 2006. The surface circulation in the eastern basin of the Mediterranean Sea. *Scientia Marina,* 70**,** 457-503.

HANNON, B. & RUTH, M. 2014. Modeling Dynamic Biological Systems. *Modeling Dynamic Biological Systems.* Cham: Springer International Publishing.

HARLEY, C. D., RANDALL HUGHES, A., HULTGREN, K. M., MINER, B. G., SORTE, C. J., THORNBER, C. S., RODRIGUEZ, L. F., TOMANEK, L. & WILLIAMS, S. L. 2006. The impacts of climate change in coastal marine systems. *Ecology letters,* 9**,** 228-241.

HARMELIN-VIVIEN, M. L., BITAR, G., HARMELIN, J.-G. & MONESTIEZ, P. 2005. The littoral fish community of the Lebanese rocky coast (eastern Mediterranean Sea) with emphasis on Red Sea immigrants. *Biological Invasions,* 7**,** 625-637.

HARTMAN, K. J. & KITCHELL, J. F. 2008. Bioenergetics modeling: progress since the 1992 symposium. *Transactions of the American Fisheries Society,* 137**,** 216-223.

HATTAB, T., BEN RAIS LASRAM, F., ALBOUY, C., ROMDHANE, M. S., JARBOUI, O., HALOUANI, G., CURY, P. & LE LOC'H, F. 2013. An ecosystem model of an exploited southern Mediterranean shelf region (Gulf of Gabes, Tunisia) and a comparison with other Mediterranean ecosystem model properties. *Journal of Marine Systems,* 128**,** 159-174.

HAVEL, J. E., KOVALENKO, K. E., THOMAZ, S. M., AMALFITANO, S. & KATS, L. B. 2015. Aquatic invasive species: challenges for the future. *Hydrobiologia,* 750**,** 147-170.

HERMOSO, V., CLAVERO, M., BLANCO-GARRIDO, F. & PRENDA, J. 2011. Invasive species and habitat degradation in Iberian streams: an analysis of their role in freshwater fish diversity loss. *Ecological applications,* 21**,** 175-188.

HEWITT, C., MINCHIN, D., OLENIN, S. & GOLLASCH, S. 2006. Canals, invasion corridors and Introductions. *Bridging Divides.* Springer.

HEYMANS, J., COLL, M., LIBRALATO, S. & CHRISTENSEN, V. 2012. 9.06 Ecopath theory, modelling and application to coastal ecosystems. *Treatise on Estuarine and Coastal Science.* Elsevier.

HEYMANS, J. J., COLL, M., LIBRALATO, S., MORISSETTE, L. & CHRISTENSEN, V. 2014. Global Patterns in Ecological Indicators of Marine Food Webs: A Modelling Approach. *PloS one,* 9**,** e95845.

HEYMANS, J. J., COLL, M., LINK, J. S., MACKINSON, S., STEENBEEK, J., WALTERS, C. & CHRISTENSEN, V. 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecological Modelling*.

HIDDINK, J. G., JENNINGS, S., SCIBERRAS, M., SZOSTEK, C. L., HUGHES, K. M., ELLIS, N., RIJNSDORP, A. D., MCCONNAUGHEY, R. A., MAZOR, T. & HILBORN, R. 2017. Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proceedings of the National Academy of Sciences***,** 201618858.

HIGGINS, S. & VANDER ZANDEN, M. 2010. What a difference a species makes: a meta–analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecological Monographs,* 80**,** 179-196.

HIGGINS, S. N., ALTHOUSE, B., DEVLIN, S. P., VADEBONCOEUR, Y. & VANDER ZANDEN, M. J. 2014. Potential for large-bodied zooplankton and dreissenids to alter the productivity and autotrophic structure of lakes. *Ecology,* 95**,** 2257-2267.

HILBORN, R. & MANGEL, M. 1997. *The ecological detective: confronting models with data,* Princeton University Press.

HILBORN, R. & WALTERS, C. J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. *Reviews in fish biology and fisheries,* 2**,** 177-178.

HOEGH-GULDBERG, O. & BRUNO, J. F. 2010. The impact of climate change on the world's marine ecosystems. *science,* 328**,** 1523-1528.

HULME, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology,* 46**,** 10-18.

HYDER, K., ROSSBERG, A. G., ALLEN, J. I., AUSTEN, M. C., BARCIELA, R. M., BANNISTER, H. J., BLACKWELL, P. G., BLANCHARD, J. L., BURROWS, M. T. & DEFRIEZ, E. 2015. Making modelling count-increasing the contribution of shelf-seas community and ecosystem models to policy development and management. *Marine Policy,* 61**,** 291-302.

ICES 2016. Report of the Working Group on Multispecies Assessment Methods (WGSAM), 9-13 November, Woods Hole, USA. ICES CM 2015/SSGEPI:20. p. 206.

ISAEV, A. V., EREMINA, T. R., RYABCHENKO, V. A. & SAVCHUK, O. P. 2016. Model estimates of the impact of bioirrigation activity of Marenzelleria spp. on the Gulf of Finland ecosystem in a changing climate. *Journal of Marine Systems*.

JACKSON, J. B., KIRBY, M. X., BERGER, W. H., BJORNDAL, K. A., BOTSFORD, L. W., BOURQUE, B. J., BRADBURY, R. H., COOKE, R., ERLANDSON, J. & ESTES, J. A. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *science,* 293**,** 629-637.

JELLYMAN, P. G. & HARDING, J. S. 2016. Disentangling the stream community impacts of Didymosphenia geminata: How are higher trophic levels affected? *Biological Invasions,* 18**,** 3419-3435.

JIANG, L., XIA, M., LUDSIN, S. A., RUTHERFORD, E. S., MASON, D. M., MARIN JARRIN, J. & PANGLE, K. L. 2015. Biophysical modeling assessment of the drivers for plankton dynamics in dreissenid-colonized western Lake Erie. *Ecological Modelling,* 308**,** 18-33.

JIMÉNEZ-VALVERDE, A., PETERSON, A. T., SOBERÓN, J., OVERTON, J., ARAGÓN, P. & LOBO, J. M. 2011. Use of niche models in invasive species risk assessments. *Biological Invasions,* 13**,** 2785-2797.

JIMENEZ, H., KEPPEL, E., CHANG, A. & RUIZ, G. 2018. Invasions in Marine Communities: Contrasting Species Richness and Community Composition Across Habitats and Salinity. *Estuaries and Coasts,* 41**,** 484-494.

JOHNSON, J. A. & KELSCH, S. W. 1998. Effects of evolutionary thermal environment on temperature-preference relationships in fishes. *Environmental Biology of Fishes,* 53**,** 447-458.

JOHNSON, T. B., BUNNELL, D. B. & KNIGHT, C. T. 2005. A potential new energy pathway in central Lake Erie: the round goby connection. *Journal of Great Lakes Research,* 31**,** 238-251.

JØRGENSEN, S. E. 2008. Overview of the model types available for development of ecological models. *Ecological Modelling,* 215**,** 3-9.

JØRGENSEN, S. E. & FATH, B. 2011. *Fundamentals of Ecological Modelling: Application in Environmental Management and Research*, Elsevier.

KAO, Y.-C., ADLERSTEIN, S. & RUTHERFORD, E. 2014a. The relative impacts of nutrient loads and invasive species on a Great Lakes food web: An Ecopath with Ecosim analysis. *Journal of Great Lakes Research,* 40**,** 35-52.

KAO, Y.-C., ADLERSTEIN, S. A. & RUTHERFORD, E. S. 2016. Assessment of Top-Down and Bottom-Up Controls on the Collapse of Alewives (Alosa pseudoharengus) in Lake Huron. *Ecosystems***,** 1-29.

KAO, Y. C., ADLERSTEIN, S. & RUTHERFORD, E. 2014b. The relative impacts of nutrient loads and invasive species on a Great Lakes food web: An Ecopath with Ecosim analysis. *Journal of Great Lakes Research,* 40**,** 35-52.

KASCHNER, K., WATSON, R., TRITES, A. & PAULY, D. 2006. Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. *Marine Ecology Progress Series,* 316**,** 285-310.

KATEREGGA, E. & STERNER, T. 2009a. Lake victoria fish stocks and the effects of water hyacinth. *Journal of Environment and Development,* 18**,** 62-78.

KATEREGGA, E. & STERNER, T. 2009b. Lake Victoria fish stocks and the effects of water hyacinth. *The Journal of Environment & Development,* 18**,** 62-78.

KATSANEVAKIS, S., COLL, M., PIRODDI, C., STEENBEEK, J., BEN RAIS LASRAM, F., ZENETOS, A. & CARDOSO, A. 2014a. Invading the Mediterranean Sea: biodiversity patterns shaped by human activities. *Frontiers in Marine Science - Marine Ecosystem Ecology*.

KATSANEVAKIS, S., COLL, M., PIRODDI, C., STEENBEEK, J., BEN RAIS LASRAM, F., ZENETOS, A. & CARDOSO, A. C. 2014b. Invading the Mediterranean Sea: biodiversity patterns shaped by human activities. *Marine Ecosystem Ecology,* 1**,** 32.

KATSANEVAKIS, S., MACKELWORTH, P., COLL, M., FRASCHETTI, S., MAČIĆ, V., GIAKOUMI, S., JONES, P., LEVIN, N., ALBANO, P. & BADALAMENTI, F. 2017. Advancing marine conservation in European and contiguous seas with the MarCons Action. *Research Ideas and Outcomes,* 3**,** e11884.

KATSANEVAKIS, S. & MOUSTAKAS, A. A. 2018. Uncertainty in marine invasion science. *Frontiers in Marine Science,* 5**,** 38.

KATSANEVAKIS, S., SMIT, A. W., PIPITONE, C., LEOPOLD, M., CRONIN, M., SCHEIDAT, M., DOYLE, T. K., BUHL-MORTENSEN, L., BUHL-MORTENSEN, P. & D'ANNA, G. 2012. Monitoring marine populations and communities: methods dealing with imperfect detectability.

KATSANEVAKIS, S., TEMPERA, F. & TEIXEIRA, H. 2016. Mapping the impact of alien species on marine ecosystems: The Mediterranean Sea case study. *Diversity and Distributions*, 22**,** 694-707.

KATSANEVAKIS, S., WALLENTINUS, I., ZENETOS, A., LEPPÄKOSKI, E., ÇINAR, M. E., OZTÜRK, B., GRABOWSKI, M., GOLANI, D. & CARDOSO, A. C. 2014c. Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review.

KATSANEVAKIS, S., ZENETOS, A., BELCHIOR, C. & CARDOSO, A. C. 2013. Invading European Seas: Assessing pathways of introduction of marine aliens. *Ocean & Coastal Management,* 76**,** 64-74.

KELLEHER, K. 2005. *Discards in the world's marine fisheries: an update*, Food & Agriculture Org.

KELLY, D. W., LAMBERTI, G. A. & MACISAAC, H. J. 2009. The Laurentian Great Lakes as a case study of biological invasion. *Bioeconomics of Biological Invasions.* Oxford University Press: New York.

KEMPTON, R. & TAYLOR, L. 1976. Models and statistics for species diversity.

KENDALL, B. E., BRIGGS, C. J., MURDOCH, W. W., TURCHIN, P., ELLNER, S. P., MCCAULEY, E., NISBET, R. M. & WOOD, S. N. 1999. Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. *Ecology,* 80**,** 1789-1805.

KITCHELL, J. F., COX, S. P., HARVEY, C. J., JOHNSON, T. B., MASON, D. M., SCHOEN, K. K., AYDIN, K., BRONTE, C., EBENER, M. & HANSEN, M. 2000. Sustainability of the Lake Superior fish community: interactions in a food web context. *Ecosystems,* 3**,** 545-560.

KNAPP, R. A. 2005. Effects of nonnative fish and habitat characteristics on lentic herpetofauna in Yosemite National Park, USA. *Biological Conservation,* 121**,** 265-279.

KNOWLER, D. 2005. Reassessing the costs of biological invasion: Mnemiopsis leidyi in the Black sea. *Ecological Economics,* 52**,** 187-199.

KOENIGSTEIN, S., MARK, F. C., GÖßLING-REISEMANN, S., REUTER, H. & POERTNER, H. O. 2016. Modelling climate change impacts on marine fish populations: process-based integration of ocean warming, acidification and other environmental drivers. *Fish and Fisheries*.

KOLAR, C. S. & LODGE, D. M. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution,* 16**,** 199-204.

KOLAR, C. S. & LODGE, D. M. 2002. Ecological predictions and risk assessment for alien fishes in North America. *science*, 298**,** 1233-1236.

KRATINA, P., MAC NALLY, R., KIMMERER, W. J., THOMSON, J. R. & WINDER, M. 2014. Human-induced biotic invasions and changes in plankton interaction networks. *Journal of Applied Ecology,* 51**,** 1066-1074.

KUMAR, R., VARKEY, D. & PITCHER, T. 2016. Simulation of zebra mussels (Dreissena polymorpha) invasion and evaluation of impacts on Mille Lacs Lake, Minnesota: An ecosystem model. *Ecological Modelling*.

LANCELOT, C., STANEVA, J., VAN EECKHOUT, D., BECKERS, J. & STANEV, E. 2002. Modeling the impact of the human forcing on the ecological functioning of the northwestern Black Sea. *Estuarine, Coastal and Shelf Science,* 54**,** 473-500.

LANGSETH, B. J., ROGERS, M. & ZHANG, H. 2012. Modeling species invasions in Ecopath with Ecosim: an evaluation using Laurentian Great Lakes models. *Ecological Modelling,* 247**,** 251-261.

LARGE, S. I., FAY, G., FRIEDLAND, K. D. & LINK, J. S. 2013. Defining trends and thresholds in responses of ecological indicators to fishing and environmental pressures. *ICES Journal of Marine Science*, 70**,** 755-767.

LARSON, E. R., GALLAGHER, R. V., BEAUMONT, L. J. & OLDEN, J. D. 2014. Generalized “avatar” niche shifts improve distribution models for invasive species. *Diversity and Distributions,* 20**,** 1296-1306.

LARUELLE, G. G., REGNIER, P., RAGUENEAU, O., KEMPA, M., MORICEAU, B., LONGPHUIRT, S. N., LEYNAERT, A., THOUZEAU, G. & CHAUVAUD, L. 2009. Benthic-pelagic coupling and the seasonal silic cycle in the bay of brest (France): New insights from a coupled physical-biological model. *Marine Ecology Progress Series,* 385**,** 15-32.

LASSALLE, G., BOURDAUD, P., SAINT-BÉAT, B., ROCHETTE, S. & NIQUIL, N. 2014. A toolbox to evaluate data reliability for whole-ecosystem models: Application on the Bay of Biscay continental shelf food-web model. *Ecological Modelling,* 285**,** 13-21.

LASSEN, H., PEDERSEN, S. A., FROST, H. & HOFF, A. 2013. Fishery management advice with ecosystem considerations. *ICES Journal of Marine Science,* 70**,** 471-479.

LEHUTA, S., GIRARDIN, R., MAHÉVAS, S., TRAVERS-TROLET, M. & VERMARD, Y. 2016. Reconciling complex system models and fisheries advice: Practical examples and leads. *Aquatic Living Resources,* 29**,** 208.

LEJEUSNE, C., CHEVALDONNÉ, P., PERGENT-MARTINI, C., BOUDOURESQUE, C. F. & PÉREZ, T. 2010. Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends in Ecology & Evolution,* 25**,** 250-260.

LERCARI, D. & BERGAMINO, L. 2011. Impacts of two invasive mollusks, Rapana venosa (Gastropoda) and Corbicula fluminea (Bivalvia), on the food web structure of the Río de la Plata estuary and nearshore oceanic ecosystem. *Biological Invasions,* 13**,** 2053-2061.

LESLIE, H. M. & MCLEOD, K. L. 2007. Confronting the challenges of implementing marine ecosystem-based management. *Frontiers in Ecology and the Environment,* 5**,** 540-548.

LEVIN, L. & CROOKS, J. 2011. Functional consequences of invasive species in coastal and estuarine systems. *Treatise Estuar Coast Sci,* 7**,** 17-51.

LEVIN, P. S., FOGARTY, M. J., MURAWSKI, S. A. & FLUHARTY, D. 2009. Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. *PLoS Biol,* 7**,** e1000014.

LEVIN, P. S., KELBLE, C. R., SHUFORD, R. L., AINSWORTH, C., DEREYNIER, Y., DUNSMORE, R., FOGARTY, M. J., HOLSMAN, K., HOWELL, E. A. & MONACO, M. E. 2013. Guidance for implementation of integrated ecosystem assessments: a US perspective. *ICES Journal of Marine Science,* 71**,** 1198-1204.

LEVIN, S. A. & LUBCHENCO, J. 2008. Resilience, robustness, and marine ecosystem-based management. *BioScience,* 58**,** 27-32.

LEVINS, R. 1966. The strategy of model building in population biology. *American Scientist,* 54**,** 421-431.

LEWISON, R. L., CROWDER, L. B., READ, A. J. & FREEMAN, S. A. 2004. Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology & Evolution,* 19**,** 598-604.

LEWISON, R. L., CROWDER, L. B., WALLACE, B. P., MOORE, J. E., COX, T., ZYDELIS, R., MCDONALD, S., DIMATTEO, A., DUNN, D. C. & KOT, C. Y. 2014. Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. *Proceedings of the National Academy of Sciences,* 111**,** 5271-5276.

LIBRALATO, S., CACCIN, A. & PRANOVI, F. 2015. Modelling species invasions using thermal and trophic niche dynamics under climate change. *Frontiers in Marine Science,* 2**,** 29.

LIBRALATO, S., COLL, M., TUDELA, S., PALOMERA, I. & PRANOVI, F. 2008. Novel index for quantification of ecosystem effects of fishing as removal of secondary production. *Marine Ecology Progress Series,* 355**,** 107-129.

LIBRALATO, S., CHRISTENSEN, V. & PAULY, D. 2006. A method for identifying keystone species in food web models. *Ecological Modelling,* 195**,** 153-171.

LIGHT, T. & MARCHETTI, M. P. 2007. Distinguishing between invasions and habitat changes as drivers of diversity loss among California's freshwater fishes. *Conservation Biology,* 21**,** 434-446.

LINDEMAN, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology,* 23**,** 399-417.

LINK, J. 2010a. *Ecosystem-based fisheries management: confronting tradeoffs,* Cambridge University Press.

LINK, J. S. 2004. A general model of selectivity for fish feeding: a rank proportion algorithm. *Transactions of the American Fisheries Society,* 133**,** 655-673.

LINK, J. S. 2010b. Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: a plea for PREBAL. *Ecological Modelling,* 221**,** 1580-1591.

LINK, J. S., IHDE, T., HARVEY, C., GAICHAS, S. K., FIELD, J., BRODZIAK, J., TOWNSEND, H. & PETERMAN, R. 2012. Dealing with uncertainty in ecosystem models: the paradox of use for living marine resource management. *Progress in Oceanography,* 102**,** 102-114.

LINK, J. S., YEMANE, D., SHANNON, L. J., COLL, M., SHIN, Y.-J., HILL, L. & BORGES, M. D. F. 2010. Relating marine ecosystem indicators to fishing and environmental drivers: an elucidation of contrasting responses. *ICES Journal of Marine Science,* 67**,** 787-795.

LIQUETE, C., PIRODDI, C., DRAKOU, E. G., GURNEY, L., KATSANEVAKIS, S., CHAREF, A. & EGOH, B. 2013. Current status and future prospects for the assessment of marine and coastal ecosystem services: a systematic review. *PloS one,* 8**,** e67737.

LIU, Y., OLAUSSEN, J. O. & SKONHOFT, A. 2014. Fishy fish? The economic impacts of escaped farmed fish. *Aquaculture Economics and Management,* 18**,** 273-302.

LONG, R. D., CHARLES, A. & STEPHENSON, R. L. 2015. Key principles of marine ecosystem-based management. *Marine Policy,* 57**,** 53-60.

LOTZE, H. K., COLL, M. & DUNNE, J. 2011a. Historical changes in marine resources, food-web structure and ecosystem functioning in the Adriatic Sea. *Ecosystems,* 14**,** 198-222.

LOTZE, H. K., COLL, M., MAGERA, A. M., WARD-PAIGE, C. & AIROLDI, L. 2011b. Recovery of marine animal populations and ecosystems. *Trends in Ecology & Evolution,* 26**,** 595-605.

LOTZE, H. K., LENIHAN, H. S., BOURQUE, B. J., BRADBURY, R. H., COOKE, R. G., KAY, M. C., KIDWELL, S. M., KIRBY, M. X., PETERSON, C. H. & JACKSON, J. B. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *science,* 312**,** 1806-1809.

LOWRY, E., ROLLINSON, E. J., LAYBOURN, A. J., SCOTT, T. E., AIELLO-LAMMENS, M. E., GRAY, S. M., MICKLEY, J. & GUREVITCH, J. 2013. Biological invasions: a field synopsis, systematic review, and database of the literature. *Ecology and evolution,* 3**,** 182-196.

LLEONART, J. 2015. Mediterranean Fisheries. Stocks, Assessments and Exploitation Status *IEMed Mediterranean Yearbook 2015, Strategics Sectors, Economy & Territory***,** 276-281.

MACDONALD, J. I., TONKIN, Z. D., RAMSEY, D. S., KAUS, A. K., KING, A. K. & CROOK, D. A. 2012. Do invasive eastern gambusia (Gambusia holbrooki) shape wetland fish assemblage structure in south-eastern Australia? *Marine and Freshwater Research,* 63**,** 659-671.

MACIAS, D., GARCIA-GORRIZ, E., PIRODDI, C. & STIPS, A. 2014. Biogeochemical control of marine productivity in the Mediterranean Sea during the last 50 years. *Global Biogeochemical Cycles,* 28**,** 897-907.

MACISAAC, H. J., JOHANNSSON, O. E., YE, J., SPRULES, W. G., LEACH, J. H., MCCORQUODALE, J. A. & GRIGOROVICH, I. A. 1999. Filtering impacts of an introduced bivalve (Dreissena polymorpha) in a shallow lake: Application of a hydrodynamic model. *Ecosystems,* 2**,** 338-350.

MACKINSON, S. 2013. Combined analyses reveal environmentally driven changes in the North Sea ecosystem and raise questions regarding what makes an ecosystem model's performance credible? *Canadian Journal of Fisheries and Aquatic Sciences,* 71**,** 31-46.

MACKINSON, S., DASKALOV, G., HEYMANS, J. J., NEIRA, S., ARANCIBIA, H., ZETINA-REJÓN, M., JIANG, H., CHENG, H., COLL, M. & ARREGUIN-SANCHEZ, F. 2009a. Which forcing factors fit? Using ecosystem models to investigate the relative influence of fishing and changes in primary productivity on the dynamics of marine ecosystems. *Ecological Modelling,* 220**,** 2972-2987.

MACKINSON, S., DEAS, B., BEVERIDGE, D. & CASEY, J. 2009b. Mixed-fishery or ecosystem conundrum? Multispecies considerations inform thinking on long-term management of North Sea demersal stocks. *Canadian Journal of Fisheries and Aquatic Sciences,* 66**,** 1107-1129.

MACHIAS, A., VASSILOPOULOU, V., VATSOS, D., BEKAS, P., KALLIANIOTIS, A., PAPACONSTANTINOU, C. & TSIMENIDES, N. 2001. Bottom trawl discards in the northeastern Mediterranean Sea. *Fisheries Research,* 53**,** 181-195.

MADEIRA, D., NARCISO, L., CABRAL, H. N. & VINAGRE, C. 2012. Thermal tolerance and potential impacts of climate change on coastal and estuarine organisms. *Journal of Sea Research,* 70**,** 32-41.

MAGNEA, U., SCIASCIA, R., PAPARELLA, F., TIBERTI, R. & PROVENZALE, A. 2013. A model for high-altitude alpine lake ecosystems and the effect of introduced fish. *Ecological Modelling,* 251**,** 211-220.

MAINALI, K. P., WARREN, D. L., DHILEEPAN, K., MCCONNACHIE, A., STRATHIE, L., HASSAN, G., KARKI, D., SHRESTHA, B. B. & PARMESAN, C. 2015. Projecting future expansion of invasive species: comparing and improving methodologies for species distribution modeling. *Global Change Biology,* 21**,** 4464-4480.

MARBÀ, N., JORDÀ, G., AGUSTI, S., GIRARD, C. & DUARTE, C. M. 2015. Footprints of climate change on Mediterranean Sea biota. *Frontiers in Marine Science,* 2**,** 56.

MARGALEF, R. 1985. Introduction to the Mediterranean. *In:* MARGALEF, R. (ed.) *Key Environments: Western Mediterranean.* New York: Pergamon Press.

MARIS, V., HUNEMAN, P., COREAU, A., KÉFI, S., PRADEL, R. & DEVICTOR, V. 2017. Prediction in ecology: promises, obstacles and clarifications. *Oikos,* 0**,** 1-12.

MARSHALL, K. N., LEVIN, P. S., ESSINGTON, T. E., KOEHN, L. E., ANDERSON, L. G., BUNDY, A., CAROTHERS, C., COLEMAN, F., GERBER, L. R. & GRABOWSKI, J. H. 2018. Ecosystem-Based Fisheries Management for Social–Ecological Systems: Renewing the Focus in the United States with Next Generation Fishery Ecosystem Plans. *Conservation Letters,* 11**,** e12367.

MAVRUK, S. & AVSAR, D. 2008. Non-native fishes in the Mediterranean from the Red Sea, by way of the Suez Canal. *Reviews in fish biology and fisheries,* 18**,** 251-262.

MAVRUK, S., BENGIL, F., YELDAN, H., MANASIRLI, M. & AVSAR, D. 2017. The trend of lessepsian fish populations with an emphasis on temperature variations in Iskenderun Bay, the Northeastern Mediterranean. *Fisheries Oceanography*.

MAYNOU, F., SBRANA, M., SARTOR, P., MARAVELIAS, C., KAVADAS, S., DAMALAS, D., CARTES, J. E. & OSIO, G. 2011. Estimating trends of population decline in long-lived marine species in the Mediterranean Sea based on fishers' perceptions. *PloS one,* 6**,** e21818.

MCCAULEY, D. J., PINSKY, M. L., PALUMBI, S. R., ESTES, J. A., JOYCE, F. H. & WARNER, R. R. 2015. Marine defaunation: Animal loss in the global ocean. *science,* 347**,** 1255641.

MCGEOCH, M. A., SPEAR, D., KLEYNHANS, E. J. & MARAIS, E. 2012. Uncertainty in invasive alien species listing. *Ecological applications,* 22**,** 959-971.

MCLEOD, K. L., LUBCHENCO, J., PALUMBI, S. R. & ROSENBERG, A. A. 2005. Scientific consensus statement on marine ecosystem-based management. *Signed by,* 221**,** 1-21.

MERRIE, A., KEYS, P., METIAN, M. & ÖSTERBLOM, H. 2017. Radical ocean futures-scenario development using science fiction prototyping. *Futures*.

METCALF, S. J. 2010. Qualitative models to complement quantitative ecosystem models for the analysis of data-limited marine ecosystems and fisheries. *Reviews in Fisheries Science,* 18**,** 248-265.

MICHELI, F., HALPERN, B. S., WALBRIDGE, S., CIRIACO, S., FERRETTI, F., FRASCHETTI, S., LEWISON, R., NYKJAER, L. & ROSENBERG, A. A. 2013. Cumulative Human Impacts on Mediterranean and Black Sea Marine Ecosystems: Assessing Current Pressures and Opportunities. *PloS one,* 8**,** e79889.

MIEHLS, A. L. J., MASON, D. M., FRANK, K. A., KRAUSE, A. E., PEACOR, S. D. & TAYLOR, W. W. 2009. Invasive species impacts on ecosystem structure and function: A comparison of the Bay of Quinte, Canada, and Oneida Lake, USA, before and after zebra mussel invasion. *Ecological Modelling,* 220**,** 3182-3193.

MILLER, D. H., KREIS JR, R. G., HUANG, W. C. & XIA, X. 2010. Application of a lower food web ecosystem productivity model for investigating dynamics of the invasive species Bythotrephes longimanus in Lake Michigan. *Biological Invasions,* 12**,** 3513-3524.

MILLER, R. R., WILLIAMS, J. D. & WILLIAMS, J. E. 1989. Extinctions of North American fishes during the past century. *Fisheries,* 14**,** 22-38.

MOHER, D., LIBERATI, A., TETZLAFF, J. & ALTMAN, D. G. 2010. Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *International Journal of Surgery,* 8**,** 336-341.

MOLNAR, J. L., GAMBOA, R. L., REVENGA, C. & SPALDING, M. D. 2008. Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment,* 6**,** 485-492.

MORA, C., TITTENSOR, D. P., ADL, S., SIMPSON, A. G. & WORM, B. 2011. How many species are there on Earth and in the ocean? *PLoS biology,* 9**,** e1001127.

MORISSETTE, L. 2007. *Complexity, cost and quality of ecosystem models and their impact on resilience: a comparative analysis, with emphasis on marine mammals and the Gulf of St. Lawrence.* PhD thesis, University of British Columbia.

MOULLEC, F., BEN RAIS LASRAM, F., COLL, M., GUILHAUMON, F., HALOUANI, G., HATTAB, T., LE LOC'H, F. & SHIN, Y.-J. 2016. Climate change impacts on marine resources - from individual to ecosystem responses. In Chapter 1. Climate change impacts on marine ecosystems and resources. *In:* EDITIONS, A. I. (ed.) *The Mediterranean Region under Climate Change - A Scientific Update.* Montpellier, France.

MOUTOPOULOS, D. K. & KOUTSIKOPOULOS, C. 2014. Fishing strange data in national fisheries statistics of Greece. *Marine Policy,* 48**,** 114-122.

MUNDAY, P. L., WARNER, R. R., MONRO, K., PANDOLFI, J. M. & MARSHALL, D. J. 2013. Predicting evolutionary responses to climate change in the sea. *Ecology letters,* 16**,** 1488-1500.

MURRAY, A. G. & PARSLOW, J. S. 1999. Modelling of nutrient impacts in Port Phillip Bay - A semi-enclosed marine Australian ecosystem. *Marine and Freshwater Research,* 50**,** 597-611.

MYERS, R. A. & WORM, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature,* 423**,** 280-283.

N'GUYEN, A., HIRSCH, P. E., ADRIAN-KALCHHAUSER, I. & BURKHARDT-HOLM, P. 2016. Improving invasive species management by integrating priorities and contributions of scientists and decision makers. *Ambio,* 45**,** 280-289.

NADER, M., INDARY, S. & BOUSTANY, L. 2012. The puffer fish Lagocephalus sceleratus (Gmelin, 1789) in the Eastern Mediterranean. *EastMed Technical Documents (FAO).*

NILSSON, E., SOLOMON, C. T., WILSON, K. A., WILLIS, T. V., LARGET, B. & VANDER ZANDEN, M. J. 2012. Effects of an invasive crayfish on trophic relationships in north-temperate lake food webs. *Freshwater Biology,* 57**,** 10-23.

NIXON, S. 2004. The Artificial Nile *American Scientist,* 92**,** 158-165.

NIXON, S. W. 2003. Replacing the Nile: are anthropogenic nutrients providing the fertility once brought to the Mediterranean by a great river? *AMBIO: A journal of the human environment,* 32**,** 30-39.

NORKKO, J., REED, D. C., TIMMERMANN, K., NORKKO, A., GUSTAFSSON, B. G., BONSDORFF, E., SLOMP, C. P., CARSTENSEN, J. & CONLEY, D. J. 2012. A welcome can of worms? Hypoxia mitigation by an invasive species. *Global Change Biology,* 18**,** 422-434.

NOVOA, A., SHACKLETON, R., CANAVAN, S., CYBELE, C., DAVIES, S. J., DEHNEN-SCHMUTZ, K., FRIED, J., GAERTNER, M., GEERTS, S. & GRIFFITHS, C. L. 2018. A framework for engaging stakeholders on the management of alien species. *Journal of Environmental Management,* 205**,** 286-297.

NUNES, A. L., TRICARICO, E., PANOV, V. E., CARDOSO, A. C. & KATSANEVAKIS, S. 2015. Pathways and gateways of freshwater invasions in Europe. *Aquatic Invasions,* 10**,** 359-370.

NYAMWEYA, C., STURLUDOTTIR, E., TOMASSON, T., FULTON, E. A., TAABU-MUNYAHO, A., NJIRU, M. & STEFANSSON, G. 2016. Exploring Lake Victoria ecosystem functioning using the Atlantis modeling framework. *Environmental Modelling and Software,* 86**,** 158-167.

NYKJAER, L. 2009. Mediterranean Sea surface warming 1985–2006. *Climate Research,* 39**,** 11-17.

OCCHIPINTI-AMBROGI, A. 2007. Global change and marine communities: alien species and climate change. *Marine pollution bulletin,* 55**,** 342-352.

OCCHIPINTI-AMBROGI, A. & SAVINI, D. 2003. Biological invasions as a component of global change in stressed marine ecosystems. *Marine pollution bulletin,* 46**,** 542-551.

OCZKOWSKI, A. J., NIXON, S. W., GRANGER, S. L., EL-SAYED, A.-F. M. & MCKINNEY, R. A. 2009. Anthropogenic enhancement of Egypt's Mediterranean fishery. *Proceedings of the National Academy of Sciences,* 106**,** 1364-1367.

ODUM, E. P. 1969. The strategy of ecosystem development. *Science,* 164**,** 262-270.

ODUM, E. P. 1971. *Fundamentals of ecology,* Philadelphia, Saunders

ODUM, E. P. 1985. Trends expected in stressed ecosystems. *BioScience,* 35**,** 419-422.

OGUZ, T., DUCKLOW, H. W., PURCELL, J. E. & MALANOTTE-RIZZOLI, P. 2001. Modeling the response of top-down control exerted by gelatinous carnivores on the Black Sea pelagic food web. *Journal of Geophysical Research: Oceans (1978–2012),* 106**,** 4543-4564.

OGUZ, T., FACH, B. & SALIHOGLU, B. 2008a. Invasion dynamics of the alien ctenophore Mnemiopsis leidyi and its impact on anchovy collapse in the Black Sea. *Journal of Plankton Research,* 30**,** 1385-1397.

OGUZ, T., SALIHOGLU, B. & FACH, B. 2008b. A coupled plankton–anchovy population dynamics model assessing nonlinear controls of anchovy and gelatinous biomass in the Black Sea. *Marine Ecology Progress Series,* 369**,** 229-256.

OJAVEER, H., GALIL, B. S., CAMPBELL, M. L., CARLTON, J. T., CANNING-CLODE, J., COOK, E. J., DAVIDSON, A. D., HEWITT, C. L., JELMERT, A. & MARCHINI, A. 2015. Classification of non-indigenous species based on their impacts: considerations for application in marine management. *PLoS biology,* 13**,** e1002130.

OLDEN, J. D. & TAMAYO, M. 2014a. Incentivizing the public to support invasive species management: Eurasian milfoil reduces lakefront property values. *PloS one,* 9**,** e110458.

OLDEN, J. D. & TAMAYO, M. 2014b. Incentivizing the public to support invasive species management: Eurasian milfoil reduces lakefront property values. *PLoS ONE,* 9.

OLDEN, J. D., VANDER ZANDEN, M. J. & JOHNSON, P. T. J. 2011. Assessing ecosystem vulnerability to invasive rusty crayfish (Orconectes rusticus). *Ecological Applications,* 21**,** 2587-2599.

OLSON, D. M., DINERSTEIN, E., WIKRAMANAYAKE, E. D., BURGESS, N. D., POWELL, G. V., UNDERWOOD, E. C., D'AMICO, J. A., ITOUA, I., STRAND, H. E. & MORRISON, J. C. 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience,* 51**,** 933-938.

ONIKURA, N., MIYAKE, T., NAKAJIMA, J., FUKUDA, S., KAWAMATO, T. & KAWAMURA, K. 2013. Predicting potential hybridization between native and non-native Rhodeus ocellatus subspecies: The implications for conservation of a pure native population in northern Kyushu, Japan. *Aquatic Invasions,* 8**,** 219-229.

OPITZ, S. 1996. *Trophic interactions in Caribbean coral reefs*, WorldFish.

ORESKES, N. 2003. The Role of Quantitative Models in Science Naomi Oreskes. *Models in ecosystem science,* 13.

ORR, J. C., FABRY, V. J., AUMONT, O., BOPP, L., DONEY, S. C., FEELY, R. A., GNANADESIKAN, A., GRUBER, N., ISHIDA, A. & JOOS, F. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature,* 437**,** 681-686.

ORTIZ, M. & STOTZ, W. 2007. Ecological and eco-social models for the introduction of the abalone Haliotis discus hannai into benthic systems of north-central Chile: Sustainability assessment. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 17**,** 89-105.

PACE, M. L., FINDLAY, S. E. & FISCHER, D. 1998. Effects of an invasive bivalve on the zooplankton community of the Hudson River. *Freshwater Biology,* 39**,** 103-116.

PADILLA, D. K., ADOLPH, S. C., COTTINGHAM, K. L. & SCHNEIDER, D. W. 1996. Predicting the consequences of dreissenid mussels on a pelagic food web. *Ecological Modelling,* 85**,** 129-144.

PAGNUCCO, K. S. & RICCIARDI, A. 2015. Disentangling the influence of abiotic variables and a non-native predator on freshwater community structure. *Ecosphere,* 6**,** 1-17.

PAINE, R. T. 1966. Food web complexity and species diversity. *American Naturalist***,** 65-75.

PAINE, R. T. 1969. A note on trophic complexity and community stability. *The American Naturalist,* 103**,** 91-93.

PALOMARES, M. & PAULY, D. 2017. SeaLifeBase. World Wide Web electronic publication. www.sealifebase.org, version (08/2017).

PALOMERA, I., OLIVAR, M. P., SALAT, J., SABATÉS, A., COLL, M., GARCÍA, A. & MORALES-NIN, B. 2007. Small pelagic fish in the NW Mediterranean Sea: an ecological review. *Progress in Oceanography,* 74**,** 377-396.

PARRAVICINI, V., AZZURRO, E., KULBICKI, M. & BELMAKER, J. 2015. Niche shift can impair the ability to predict invasion risk in the marine realm: an illustration using Mediterranean fish invaders. *Ecology letters,* 18**,** 246-253.

PARSONS, E., FAVARO, B., AGUIRRE, A. A., BAUER, A. L., BLIGHT, L. K., CIGLIANO, J. A., COLEMAN, M. A., COTE, I. M., DRAHEIM, M. & FLETCHER, S. 2014. Seventy-One Important Questions for the Conservation of Marine Biodiversity. *Conservation Biology,* 28**,** 1206-1214.

PAULY, D. & CHRISTENSEN, V. 1995. Primary production required to sustain global fisheries. *Nature,* 374**,** 255-257.

PAULY, D., CHRISTENSEN, V., DALSGAARD, J., FROESE, R. & TORRES, F. 1998. Fishing down marine food webs. *science,* 279**,** 860-863.

PAULY, D., CHRISTENSEN, V., GUÉNETTE, S., PITCHER, T. J., SUMAILA, U. R., WALTERS, C. J., WATSON, R. & ZELLER, D. 2002. Towards sustainability in world fisheries. *Nature,* 418**,** 689-695.

PAULY, D., ULMAN, A., PIRODDI, C., BULTEL, E. & COLL, M. 2014. 'Reported'versus' likely'fisheries catches of four Mediterranean countries. *Scientia Marina,* 78**,** 11-17.

PAULY, D. & ZELLER, D. 2016. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nature communications,* 7**,** ncomms10244.

PAYNE, M. R., BARANGE, M., CHEUNG, W. W., MACKENZIE, B. R., BATCHELDER, H. P., CORMON, X., EDDY, T. D., FERNANDES, J. A., HOLLOWED, A. B. & JONES, M. C. 2015. Uncertainties in projecting climate-change impacts in marine ecosystems. *ICES Journal of Marine Science,* 73**,** 1272-1282.

PECK, L. S. 2011. Organisms and responses to environmental change. *Marine Genomics,* 4**,** 237-243.

PECK, M. A., ARVANITIDIS, C., BUTENSCHÖN, M., CANU, D. M., CHATZINIKOLAOU, E., CUCCO, A., DOMENICI, P., FERNANDES, J. A., GASCHE, L. & HUEBERT, K. B. 2016. Projecting changes in the distribution and productivity of living marine resources: a critical review of the suite of modelling approaches used in the large European project VECTORS. *Estuarine, Coastal and Shelf Science*.

PEJCHAR, L. & MOONEY, H. A. 2009. Invasive species, ecosystem services and human well-being. *Trends in Ecology & Evolution,* 24**,** 497-504.

PEREIRA, H. M., LEADLEY, P. W., PROENÇA, V., ALKEMADE, R., SCHARLEMANN, J. P., FERNANDEZ-MANJARRÉS, J. F., ARAÚJO, M. B., BALVANERA, P., BIGGS, R. & CHEUNG, W. W. 2010. Scenarios for global biodiversity in the 21st century. *science,* 330**,** 1496-1501.

PERRY, A. L., LOW, P. J., ELLIS, J. R. & REYNOLDS, J. D. 2005. Climate change and distribution shifts in marine fishes. *science,* 308**,** 1912-1915.

PIGNEUR, L. M., FALISSE, E., ROLAND, K., EVERBECQ, E., DELIÈGE, J. F., SMITZ, J. S., VAN DONINCK, K. & DESCY, J. P. 2014. Impact of invasive

Asian clams, Corbicula spp., on a large river ecosystem. *Freshwater Biology,* 59**,** 573-583.

PINE, W. E., KWAK, T. J. & RICE, J. A. 2007. Modeling management scenarios and the effects of an introduced apex predator on a coastal riverine fish community. *Transactions of the American Fisheries Society,* 136**,** 105-120.

PINNEGAR, J. K., TOMCZAK, M. T. & LINK, J. S. 2014. How to determine the likely indirect food-web consequences of a newly introduced non-native species: A worked example. *Ecological Modelling,* 272**,** 379-387.

PINSKY, M. L. & PALUMBI, S. R. 2014. Meta-analysis reveals lower genetic diversity in overfished populations. *Molecular Ecology,* 23**,** 29-39.

PIRIA, M., COPP, G. H., DICK, J. T., DUPLIĆ, A., GROOM, Q., JELIĆ, D., LUCY, F. E., ROY, H. E., SARAT, E. & SIMONOVIĆ, P. 2017. Tackling invasive alien species in Europe II: threats and opportunities until 2020. *Management of Biological Invasions,* 8**,** 273-286.

PIRODDI, C., COLL, M., LIQUETE, C., MACIAS, D., GREER, K., BUSZOWSKI, J., STEENBEEK, J., DANOVARO, R. & CHRISTENSEN, V. 2017. Historical changes of the Mediterranean Sea ecosystem: modelling the role and impact of primary productivity and fisheries changes over time. *Scientific Reports*.

PIRODDI, C., COLL, M., STEENBEEK, J., MOY, D. M. & CHRISTENSEN, V. 2015a. Modelling the Mediterranean marine ecosystem as a whole: addressing the challenge of complexity. *Marine Ecology Progress Series,* 533**,** 47-65.

PIRODDI, C., GIOVANNI, B. & VILLY, C. 2010. Effects of local fisheries and ocean productivity on the northeastern Ionian Sea ecosystem. *Ecological Modelling,* 221**,** 1526-1544.

PIRODDI, C., TEIXEIRA, H., LYNAM, C. P., SMITH, C., ALVAREZ, M. C., MAZIK, K., ANDONEGI, E., CHURILOVA, T., TEDESCO, L. & CHIFFLET, M. 2015b. Using ecological models to assess ecosystem status in support of the European Marine Strategy Framework Directive. *Ecological Indicators,* 58**,** 175-191.

PITCHER, T. J. & CHEUNG, W. W. 2013. Fisheries: Hope or despair? *Marine pollution bulletin,* 74**,** 506-516.

PLAGÁNYI, É. E. 2007. *Models for an ecosystem approach to fisheries*, Food & Agriculture Org.

PLAGÁNYI, É. E., PUNT, A. E., HILLARY, R., MORELLO, E. B., THÉBAUD, O., HUTTON, T., PILLANS, R. D., THORSON, J. T., FULTON, E. A. & SMITH, A. D. 2014. Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. *Fish and Fisheries,* 15**,** 1-22.

POLOCZANSKA, E. S., BURROWS, M. T., BROWN, C. J., GARCÍA MOLINOS, J., HALPERN, B. S., HOEGH-GULDBERG, O., KAPPEL, C. V., MOORE, P. J., RICHARDSON, A. J. & SCHOEMAN, D. S. 2016. Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science,* 3**,** 62.

POLOVINA, J. J. 1984. Model of a coral reef ecosystem. The Ecopath moel and its application to french Frigate Shoals. *Coral reefs,* 3**,** 1-11.

POR, F. 2009. Tethys returns to the Mediterranean: Success and limits of tropical re-colonization. *BioRisk,* 3**,** 5-19.

POR, F. D. 1978a. *Lessepsian migration: the influx of Red Sea biota into the Mediterranean by way of the Suez Canal*, Springer-Verlag Berlin.

POR, F. D. 1978b. *Lessepsian migration: the influx of Red Sea biota into the Mediterranean by way of the Suez Canal*, Springer Science & Business Media.

POR, F. D. 2012. *Lessepsian migration: the influx of Red Sea biota into the Mediterranean by way of the Suez Canal*, Springer Science & Business Media.

PÖRTNER, H.-O. & PECK, M. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology,* 77**,** 1745-1779.

PUCCIA, C. J. & LEVINS, R. 1985. *Qualitative modeling of complex systems,* Harvard University Press Cambridge, MA.

PUNT, A. & BUTTERWORTH, D. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals Arctocephalus pusillus pusillus and the Cape hakes Merluccius capensis and M. paradoxus. *South African Journal of Marine Science,* 16**,** 255-285.

PYŠEK, P. & RICHARDSON, D. M. 2010. Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources,* 35**,** 25-55.

PYŠEK, P., RICHARDSON, D. M., PERGL, J., JAROŠÍK, V., SIXTOVÁ, Z. & WEBER, E. 2008. Geographical and taxonomic biases in invasion ecology. *Trends in Ecology & Evolution,* 23**,** 237-244.

RAHEL, F. J. 2002. Homogenization of freshwater faunas. *Annual review of ecology and systematics,* 33**,** 291-315.

RAITSOS, D. E., BEAUGRAND, G., GEORGOPOULOS, D., ZENETOS, A., PANCUCCI-PAPADOPOULOU, A. M., THEOCHARIS, A. & PAPATHANASSIOU, E. 2010. Global climate change amplifies the entry of tropical species into the Eastern Mediterranean Sea. *Limnology and Oceanography,* 55**,** 1478.

RAMÍREZ, F., COLL, M., NAVARRO, J., BUSTAMANTE, J. & GREEN, A. J. 2018. Spatial congruence between multiple stressors in the Mediterranean Sea may reduce its resilience to climate impacts. *Scientific reports,* 8**,** 14871.

RAMSEY, D. & VELTMAN, C. 2005. Predicting the effects of perturbations on ecological communities: what can qualitative models offer? *Journal of Animal Ecology,* 74**,** 905-916.

RAVIER, C. & FROMENTIN, J. M. 2004. Are the long-term fluctuations in Atlantic bluefin tuna (Thunnus thynnus) population related to environmental changes? *Fisheries Oceanography,* 13**,** 145-160.

REED-ANDERSEN, T., CARPENTER, S. R., PADILLA, D. K. & LATHROP, R. C. 2000. Predicted impact of zebra mussel (Dreissena polymorpha) invasion on water clarity in Lake Mendota. *Canadian Journal of Fisheries and Aquatic Sciences,* 57**,** 1617-1626.

RICCIARDI, A. 2003. Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. *Freshwater Biology,* 48**,** 972-981.

RICCIARDI, A. 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. *Diversity and Distributions,* 12**,** 425-433.

RICCIARDI, A., HOOPES, M. F., MARCHETTI, M. P. & LOCKWOOD, J. L. 2013. Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs,* 83**,** 263-282.

RICCIARDI, A., RASMUSSEN, J. & WHORISKEY, F. 1995. Predicting the intensity and impact of Dreissena infestation on native unionid bivalves from Dreissena field density. *Canadian Journal of Fisheries and Aquatic Sciences,* 52**,** 1449-1461.

RICE, J. 2003. Environmental health indicators. *Ocean & Coastal Management,* 46**,** 235-259.

RILOV, G. 2016. Multi-species collapses at the warm edge of a warming sea. *Scientific reports,* 6**,** 36897.

RILOV, G. & CROOKS, J. 2009. *Biological invasions in marine ecosystems: ecological, management and geographic perspectives.,* Berlin, Sprinter-Verlag.

RILOV, G. & GALIL, B. 2009. Marine bioinvasions in the Mediterranean Sea–history, distribution and ecology. *Biological invasions in marine ecosystems.* Springer.

RILOV, G., PELEG, O., YERUHAM, E., GARVAL, T., VICHIK, A. & RAVEH, O. 2018. Alien turf: Overfishing, overgrazing and invader domination in south-eastern Levant reef ecosystems. *Aquatic Conservation: marine and freshwater ecosystems,* 28**,** 351-369.

RIVETTI, I., FRASCHETTI, S., LIONELLO, P., ZAMBIANCHI, E. & BOERO, F. 2014. Global warming and mass mortalities of benthic invertebrates in the Mediterranean Sea. *PloS one,* 9**,** e115655.

ROBERTS, C. M., O'LEARY, B. C., MCCAULEY, D. J., CURY, P. M., DUARTE, C. M., LUBCHENCO, J., PAULY, D., SÁENZ-ARROYO, A., SUMAILA, U. R. & WILSON, R. W. 2017. Marine reserves can mitigate and promote adaptation to climate change. *Proceedings of the National Academy of Sciences,* 114**,** 6167-6175.

ROBINSON, J. P., WILLIAMS, I. D., EDWARDS, A. M., MCPHERSON, J., YEAGER, L., VIGLIOLA, L., BRAINARD, R. E. & BAUM, J. K. 2017. Fishing degrades size structure of coral reef fish communities. *Global Change Biology,* 23**,** 1009-1022.

ROBSON, B. J. 2014a. State of the art in modelling of phosphorus in aquatic systems: review, criticisms and commentary. *Environmental Modelling & Software,* 61**,** 339-359.

ROBSON, B. J. 2014b. When do aquatic systems models provide useful predictions, what is changing, and what is next? *Environmental Modelling & Software,* 61**,** 287-296.

ROCKSTRÖM, J., STEFFEN, W., NOONE, K., PERSSON, Å., CHAPIN, F. S., LAMBIN, E. F., LENTON, T. M., SCHEFFER, M., FOLKE, C. & SCHELLNHUBER, H. J. 2009. A safe operating space for humanity. *Nature,* 461**,** 472-475.

ROCHET, M.-J. & TRENKEL, V. M. 2003. Which community indicators can measure the impact of fishing? A review and proposals. *Canadian Journal of Fisheries and Aquatic Sciences,* 60**,** 86-99.

ROGERS, M. W., BUNNELL, D. B., MADENJIAN, C. P., WARNER, D. M. & ROSE, K. 2014. Lake Michigan offshore ecosystem structure and food web changes from 1987 to 2008. *Canadian Journal of Fisheries and Aquatic Sciences,* 71**,** 1-15.

ROMANUK, T. N., ZHOU, Y., BROSE, U., BERLOW, E. L., WILLIAMS, R. J. & MARTINEZ, N. D. 2009. Predicting invasion success in complex ecological networks. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 364**,** 1743-1754.

ROMBOUTS, I., BEAUGRAND, G., FIZZALA, X., GAILL, F., GREENSTREET, S., LAMARE, S., LE LOC'H, F., MCQUATTERS-GOLLOP, A., MIALET, B. & NIQUIL, N. 2013. Food web indicators under the Marine Strategy Framework Directive: from complexity to simplicity? *Ecological Indicators,* 29**,** 246-254.

ROSE, K. A., ALLEN, J. I., ARTIOLI, Y., BARANGE, M., BLACKFORD, J., CARLOTTI, F., CROPP, R., DAEWEL, U., EDWARDS, K. & FLYNN, K. 2010. End-to-end models for the analysis of marine ecosystems: challenges, issues, and next steps. *Marine and Coastal Fisheries,* 2**,** 115-130.

ROSENBERG, A. A. & MCLEOD, K. L. 2005. Implementing ecosystem-based approaches to management for the conservation of ecosystem services. *Marine ecology. Progress series,* 300**,** 270-274.

ROUSOU, M., GANIAS, K., KLETOU, D., LOUCAIDES, A. & TSINGANIS, M. 2014. Maturity of the pufferfish Lagocephalus sceleratus in the southeastern Mediterranean Sea. *Sexuality and Early Development in Aquatic Organisms,* 1**,** 35-44.

ROWE, D. K. 2007. Exotic fish introductions and the decline of water clarity in small North Island, New Zealand lakes: A multi-species problem. *Hydrobiologia,* 583**,** 345-358.

ROWE, M. D., ANDERSON, E. J., WANG, J. & VANDERPLOEG, H. A. 2015a. Modeling the effect of invasive quagga mussels on the spring phytoplankton bloom in Lake Michigan. *Journal of Great Lakes Research,* 41**,** 49-65.

ROWE, M. D., OBENOUR, D. R., NALEPA, T. F., VANDERPLOEG, H. A., YOUSEF, F. & KERFOOT, W. C. 2015b. Mapping the spatial distribution of the biomass and filter-feeding effect of invasive dreissenid mussels on the winter-spring phytoplankton bloom in Lake Michigan. *Freshwater Biology,* 60**,** 2270-2285.

ROY, E. D., MARTIN, J. F., IRWIN, E. G., CONROY, J. D. & CULVER, D. A. 2011. Living within dynamic social-ecological freshwater systems: System parameters and the role of ecological engineering. *Ecological Engineering,* 37**,** 1661-1672.

RUESINK, J. L. & COLLADO-VIDES, L. 2006. Modeling the increase and control of Caulerpa taxifolia, an invasive marine macroalga. *Biological Invasions,* 8**,** 309-325.

RUIZ, G. M., FOFONOFF, P. W., CARLTON, J. T., WONHAM, M. J. & HINES, A. H. 2000. Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. *Annual review of ecology and systematics,* 31**,** 481-531.

SABATES, A., MARTIN, P., LLORET, J. & RAYA, V. 2006. Sea warming and fish distribution: the case of the small pelagic fish, Sardinella aurita, in the western Mediterranean. *Global Change Biology,* 12**,** 2209-2219.

SABINE, C. L., FEELY, R. A., GRUBER, N., KEY, R. M., LEE, K., BULLISTER, J. L., WANNINKHOF, R., WONG, C., WALLACE, D. W. & TILBROOK, B. 2004. The oceanic sink for anthropogenic CO2. *science,* 305**,** 367-371.

SALA, E., KIZILKAYA, Z., YILDIRIM, D. & BALLESTEROS, E. 2011. Alien marine fishes deplete algal biomass in the eastern Mediterranean. *PloS one,* 6**,** e17356.

SALA, E. & KNOWLTON, N. 2006. Global marine biodiversity trends. *Annu. Rev. Environ. Resour.,* 31**,** 93-122.

SARA, M. 1985. Ecological factors and their biogeographic consequences in the Mediterranean ecosystems. *Mediterranean marine ecosystems.* Springer.

SCOTT, E., SERPETTI, N., STEENBEEK, J. & HEYMANS, J. J. 2016. A Stepwise Fitting Procedure for automated fitting of Ecopath with Ecosim models. *SoftwareX*.

SCHEFFER, M., BARRETT, S., CARPENTER, S., FOLKE, C., GREEN, A., HOLMGREN, M., HUGHES, T., KOSTEN, S., VAN DE LEEMPUT, I. &

NEPSTAD, D. 2015. Creating a safe operating space for iconic ecosystems. *science,* 347**,** 1317-1319.

SCHEFFER, M., CARPENTER, S., FOLEY, J. A., FOLKE, C. & WALKER, B. 2001. Catastrophic shifts in ecosystems. *Nature,* 413**,** 591-596.

SCHLAEPFER, M. A., SAX, D. F. & OLDEN, J. D. 2011. The potential conservation value of non-native species. *Conservation Biology,* 25**,** 428-437.

SCHWALB, A. N., BOUFFARD, D., BOEGMAN, L., LEON, L., WINTER, J. G., MOLOT, L. A. & SMITH, R. E. H. 2014. 3D modelling of dreissenid mussel impacts on phytoplankton in a large lake supports the nearshore shunt hypothesis and the importance of wind-driven hydrodynamics. *Aquatic Sciences,* 77**,** 95-114.

SEEBENS, H., BLACKBURN, T. M., DYER, E. E., GENOVESI, P., HULME, P. E., JESCHKE, J. M., PAGAD, S., PYŠEK, P., WINTER, M. & ARIANOUTSOU, M. 2017. No saturation in the accumulation of alien species worldwide. *Nature communications,* 8**,** 14435.

SEEBENS, H., SCHWARTZ, N., SCHUPP, P. J. & BLASIUS, B. 2016. Predicting the spread of marine species introduced by global shipping. *Proceedings of the National Academy of Sciences,* 113**,** 5646-5651.

SERPETTI, N., BAUDRON, A., BURROWS, M., PAYNE, B., HELAOUËT, P., FERNANDES, P. & HEYMANS, J. 2017. Impact of ocean warming on sustainable fisheries management informs the Ecosystem Approach to Fisheries. *Scientific reports,* 7**,** 13438.

SETTLE, C. & SHOGREN, J. F. 2002. Modeling native-exotic species within Yellowstone Lake. *American Journal of Agricultural Economics,* 84**,** 1323-1328.

SHABTAY, A., PORTMAN, M. E., OFIR, E., CARMEL, Y. & GAL, G. 2018. Using ecological modelling in marine spatial planning to enhance ecosystem-based management. *Marine Policy,* 95**,** 14-23.

SHALTOUT, M. & OMSTEDT, A. 2014. Recent sea surface temperature trends and future scenarios for the Mediterranean Sea. *Oceanologia,* 56**,** 411-443.

SHANNON, L., COLL, M., BUNDY, A., GASCUEL, D., HEYMANS, J. J., KLEISNER, K., LYNAM, C. P., PIRODDI, C., TAM, J. & TRAVERS-TROLET, M. 2014. Trophic level-based indicators to track fishing impacts across marine ecosystems. *Marine Ecology Progress Series,* 512**,** 115-140.

SHANNON, L., CHRISTENSEN, V. & WALTERS, C. 2004. Modelling stock dynamics in the southern Benguela ecosystem for the period 1978–2002. *African Journal of Marine Science,* 26**,** 179-196.

SHARMA, S., VANDER ZANDEN, M. J., MAGNUSON, J. J. & LYONS, J. 2011. Comparing climate change and species invasions as drivers of coldwater fish population extirpations. *PloS one,* 6**,** e22906.

SHERMAN, K. & DUDA, A. M. 1999. Large marine ecosystems: an emerging paradigm for fishery sustainability. *Fisheries,* 24**,** 15-26.

SHIGANOVA, T. 1998. Invasion of the Black Sea by the ctenophore Mnemiopsis leidyi and recent changes in pelagic community structure. *Fisheries Oceanography,* 7**,** 305-310.

SHIN, Y.-J. & CURY, P. 2004. Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. *Canadian Journal of Fisheries and Aquatic Sciences,* 61**,** 414-431.

SHIN, Y.-J., HOULE, J. E., AKOGLU, E., BLANCHARD, J. L., BUNDY, A., COLL, M., DEMARCQ, H., FU, C., FULTON, E. A. & HEYMANS, J. J. 2018. The specificity of marine ecological indicators to fishing in the face of environmental change: A multi-model evaluation. *Ecological Indicators,* 89**,** 317-326.

SHIN, Y.-J. & SHANNON, L. J. 2010. Using indicators for evaluating, comparing, and communicating the ecological status of exploited marine ecosystems. 1. The IndiSeas project. *ICES Journal of Marine Science: Journal du Conseil,* 67**,** 686-691.

SHIN, Y.-J., SHANNON, L. J., BUNDY, A., COLL, M., AYDIN, K., BEZ, N., BLANCHARD, J. L., DE FATIMA BORGES, M., DIALLO, I. & DIAZ, E. 2010. Using indicators for evaluating, comparing, and communicating the ecological status of exploited marine ecosystems. 2. Setting the scene. *ICES Journal of Marine Science: Journal du Conseil,* 67**,** 692-716.

SIMBERLOFF, D. 2000. No reserve is an island: marine reserves and nonindigenous species. *Bulletin of Marine Science,* 66**,** 567-580.

SIMBERLOFF, D., MARTIN, J.-L., GENOVESI, P., MARIS, V., WARDLE, D. A., ARONSON, J., COURCHAMP, F., GALIL, B., GARCÍA-BERTHOU, E. & PASCAL, M. 2013. Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution,* 28**,** 58-66.

SIMBERLOFF, D. & VON HOLLE, B. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions,* 1**,** 21-32.

SIOKOU-FRANGOU, I., CHRISTAKI, U., MAZZOCCHI, M., MONTRESOR, M., RIBERA D'ALCALÁ, M., VAQUÉ, D. & ZINGONE, A. 2010. Plankton in the open Mediterranean Sea: a review. *Biogeosciences,* 7**,** 1543-1586.

SMITH, A., FULTON, E., HOBDAY, A., SMITH, D. & SHOULDER, P. 2007. Scientific tools to support the practical implementation of ecosystem-based fisheries management. *ICES Journal of Marine Science,* 64**,** 633-639.

SMITH, D. C., FULTON, E. A., APFEL, P., CRESSWELL, I. D., GILLANDERS, B. M., HAWARD, M., SAINSBURY, K. J., SMITH, A. D., VINCE, J. & WARD, T. M. 2017. Implementing marine ecosystem-based management: lessons from Australia. *ICES Journal of Marine Science,* 74**,** 1990-2003.

SOMOT, S., SEVAULT, F. & DÉQUÉ, M. 2006. Transient climate change scenario simulation of the Mediterranean Sea for the twenty-first century using a high-resolution ocean circulation model. *Climate Dynamics,* 27**,** 851-879.

SONIN, O., SPANIER, E., LEVI, D., PATTI, B., RIZZO, P. & ANDREOLI, M. G. 2007. Nanism (dwarfism) in fish: a comparison between red mullet Mullus barbatus from the southeastern and the central Mediterranean. *Marine Ecology Progress Series,* 343**,** 221-228.

SORTE, C. J., WILLIAMS, S. L. & ZEREBECKI, R. A. 2010. Ocean warming increases threat of invasive species in a marine fouling community. *Ecology,* 91**,** 2198-2204.

SOURNIA, A. 1973. *La production primaire planctonique en Méditerranée; essai de mise à jour,* Cooperative Investigations in the Mediterranean, International Coordinator and Operational Unit; Étude en commun de la Méditerranée, Coordonnateur international et Unité opérationnelle.

SPALDING, M. D., FOX, H. E., ALLEN, G. R., DAVIDSON, N., FERDAÑA, Z. A., FINLAYSON, M., HALPERN, B. S., JORGE, M. A., LOMBANA, A. & LOURIE, S. A. 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience,* 57**,** 573-583.

STAPANIAN, M. A., KOCOVSKY, P. M. & ADAMS, J. V. 2009. Change in diel catchability of young-of-year yellow perch associated with establishment of dreissenid mussels. *Freshwater Biology,* 54**,** 1593-1604.

STAPP, P. & HAYWARD, G. D. 2002. Effects of an introduced piscivore on native trout: Insights from a demographic model. *Biological Invasions,* 4**,** 299-316.

STATGRAPHICS-CENTURION 2009. Statpoint technologies. INC. version 16.1.11 (32-bits).

STEENBEEK, J., COLL, M., GURNEY, L., MÉLIN, F., HOEPFFNER, N., BUSZOWSKI, J. & CHRISTENSEN, V. 2013. Bridging the gap between ecosystem modeling tools and geographic information systems: Driving a food web model with external spatial–temporal data. *Ecological Modelling,* 263**,** 139-151.

STEENBEEK, J., CORRALES, X., PLATTS, M. & COLL, M. 2018. Ecosampler: A new approach to assessing parameter uncertainty in Ecopath with Ecosim. *SoftwareX,* 7**,** 198-204.

STEFFEN, W., RICHARDSON, K., ROCKSTRÖM, J., CORNELL, S. E., FETZER, I., BENNETT, E. M., BIGGS, R., CARPENTER, S. R., DE VRIES, W. & DE WIT, C. A. 2015. Planetary boundaries: Guiding human development on a changing planet. *science,* 347**,** 1259855.

STELZENMÜLLER, V., COLL, M., MAZARIS, A. D., GIAKOUMI, S., KATSANEVAKIS, S., PORTMAN, M. E., DEGEN, R., MACKELWORTH, P., GIMPEL, A. & ALBANO, P. G. 2018. A risk-based approach to cumulative effect assessments for marine management. *Science of The Total Environment,* 612**,** 1132-1140.

STERGIOU, K. I. & KARPOUZI, V. S. 2001. Feeding habits and trophic levels of Mediterranean fish. *Reviews in fish biology and fisheries,* 11**,** 217-254.

STERGIOU, K. I., SOMARAKIS, S., TRIANTAFYLLOU, G., TSIARAS, K. P., GIANNOULAKI, M., PETIHAKIS, G., MACHIAS, A. & TSIKLIRAS, A. C. 2016. Trends in productivity and biomass yields in the Mediterranean Sea Large Marine Ecosystem during climate change. *Environmental Development,* 17**,** 57-74.

STERN, N., LEVITT, Y., GALIL, B., DIAMANT, A., YOKEŞ, M. & GOREN, M. 2014. Distribution and population structure of the alien Indo-Pacific Randall's threadfin bream Nemipterus randalli in the eastern Mediterranean Sea. *Journal of Fish Biology,* 85**,** 394-406.

STERNBERG, M., GABAY, O., ANGEL, D., BARNEAH, O., GAFNY, S., GASITH, A., GRÜNZWEIG, J. M., HERSHKOVITZ, Y., ISRAEL, A., MILSTEIN, D., RILOV, G., STEINBERGER, Y. & ZOHARY, T. 2015. Impacts of climate change on biodiversity in Israel: an expert assessment approach. *Regional Environmental Change,* 15**,** 895-906.

STEWART, T. J., O'GORMAN, R., GARY SPRULES, W. & LANTRY, B. F. 2010. The bioenergetic consequences of invasive-induced food web disruption to lake Ontario alewives. *North American Journal of Fisheries Management,* 30**,** 1485-1504.

STOBBERUP, K., MORATO, T., AMORIM, P. & ERZINI, K. 2009. Predicting weight composition of fish diets: converting frequency of occurrence of prey to relative weight composition. *The Open Fish Science Journal,* 2**,** 42-49.

STRAYER, D. L. 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology,* 55**,** 152-174.

STUART-SMITH, R. D., EDGAR, G. J., BARRETT, N. S., KININMONTH, S. J. & BATES, A. E. 2015. Thermal biases and vulnerability to warming in the world's marine fauna. *Nature,* 528**,** 88-92.

SUARI, Y. & BRENNER, S. 2015. Decadal biogeochemical history of the south east Levantine basin: Simulations of the river Nile regimes. *Journal of Marine Systems,* 148**,** 112-121.

SUKHDEV, P. 2008. *The economics of ecosystems and biodiversity. An interim report,* na.

SWARTZ, W., SALA, E., TRACEY, S., WATSON, R. & PAULY, D. 2010. The spatial expansion and ecological footprint of fisheries (1950 to present). *PloS one,* 5**,** e15143.

TAM, J. C., LINK, J. S., ROSSBERG, A. G., ROGERS, S. I., LEVIN, P. S., ROCHET, M.-J., BUNDY, A., BELGRANO, A., LIBRALATO, S. & TOMCZAK, M. 2017. Towards ecosystem-based management: identifying operational food-web indicators for marine ecosystems. *ICES Journal of Marine Science,* 74**,** 2040-2052.

TAŞKAVAK, E., MATER, S. & BILECENOĞLU, M. 1998. Kızıldeniz göçmeni balıkların Doğu Akdeniz kıyılarımızdaki (Mersin-Samandağ) dağılımı ve bölge balıkçılığına etkileri. III. *Su Ürünleri Sempozyumu. Erzurum***,** 151-162 (In Turkish).

THOMPSON, L. C., GIUSTI, G. A., WEBER, K. L. & KEIFFER, R. F. 2013. The native and introduced fishes of Clear Lake: A review of the past to assist with decisions of the future. *California Fish and Game,* 99**,** 7-41.

THOMS, M. C. 2006. Variability in riverine ecosystems. *River Research and Applications,* 22**,** 115-121.

THOMSEN, M. S., BYERS, J. E., SCHIEL, D. R., BRUNO, J. F., OLDEN, J. D., WERNBERG, T. & SILLIMAN, B. R. 2014. Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. *Marine Ecology Progress Series,* 495**,** 39-47.

THRESHER, R. E. & KURIS, A. M. 2004. Options for managing invasive marine species. *Biological Invasions,* 6**,** 295-300.

TITTENSOR, D., COLL, M. & WALKER, N. D. 2018. A protocol for the intercomparison of marine fishery and ecosystem models: Fish-MIP v1. 0.

TORRES, M. Á., COLL, M., HEYMANS, J. J., CHRISTENSEN, V. & SOBRINO, I. 2013. Food-web structure of and fishing impacts on the Gulf of Cadiz ecosystem (South-western Spain). *Ecological Modelling,* 265**,** 26-44.

TOWNHILL, B., PINNEGAR, J., TINKER, J., JONES, M., SIMPSON, S., STEBBING, P. & DYE, S. 2017. Non-native marine species in north-west Europe: Developing an approach to assess future spread using regional downscaled climate projections. *Aquatic Conservation: marine and freshwater ecosystems,* 27**,** 1035-1050.

TRAVERS, M., SHIN, Y.-J., JENNINGS, S. & CURY, P. 2007. Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. *Progress in Oceanography,* 75**,** 751-770.

TSAGARAKIS, K., COLL, M., GIANNOULAKI, M., SOMARAKIS, S., PAPACONSTANTINOU, C. & MACHIAS, A. 2010. Food-web traits of the North Aegean Sea ecosystem (Eastern Mediterranean) and comparison with other Mediterranean ecosystems. *Estuarine, Coastal and Shelf Science,* 88**,** 233-248.

TSAGARAKIS, K., PALIALEXIS, A. & VASSILOPOULOU, V. 2013. Mediterranean fishery discards: review of the existing knowledge. *ICES Journal of Marine Science: Journal du Conseil***,** fst074.

TSIKLIRAS, A. C., DINOULI, A., TSIROS, V.-Z. & TSALKOU, E. 2015. The Mediterranean and Black Sea fisheries at risk from overexploitation. *PloS one,* 10**,** e0121188.

TURNER, S. J., THRUSH, S., HEWITT, J., CUMMINGS, V. & FUNNELL, G. 1999. Fishing impacts and the degradation or loss of habitat structure. *Fisheries Management and Ecology,* 6**,** 401-420.

TYBERGHEIN, L., VERBRUGGEN, H., PAULY, K., TROUPIN, C., MINEUR, F. & DE CLERCK, O. 2012. Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography,* 21**,** 272-281.

ULANOWICZ, R. & PUCCIA, C. 1990. Mixed trophic impacts in ecosystems. *Coenoses,* 5**,** 7-16.

ULANOWICZ, R. E. 1986. *Growth and Development: Ecosystems Phenomenology*, Springer Verlag, New York, 203 pp.

ULMAN, A., ÇIÇEK, B. A., SALIHOGLU, I., PETROU, A., PATSALIDOU, M., PAULY, D. & ZELLER, D. 2015a. Unifying the catch data of a divided island: Cyprus’s marine fisheries catches, 1950–2010. *Environment, Development and Sustainability,* 17**,** 801-821.

ULMAN, A., SAAD, A., ZYLICH, K., PAULY, D. & ZELLER, D. 2015b. Reconstruction of Syria's fisheries catches from 1950-2010: signs of overexploitation *Acta Ichthyologica et Piscatoria,* 15.

VÁCLAVÍK, T. & MEENTEMEYER, R. K. 2009. Invasive species distribution modeling (iSDM): Are absence data and dispersal constraints needed to predict actual distributions? *Ecological Modelling,* 220**,** 3248-3258.

VALLS, A., COLL, M. & CHRISTENSEN, V. 2015. Keystone species: toward an operational concept for marine biodiversity conservation. *Ecological Monographs,* 85**,** 29-47.

VAN GUILDER, M. A. & SEEFELT, N. E. 2013. Double-crested Cormorant (Phalacrocorax auritus) chick bioenergetics following round goby (Neogobius melanostomus) invasion and implementation of cormorant population control. *Journal of Great Lakes Research,* 39**,** 153-161.

VAN ZUIDEN, T. M., SHARMA, S. & MACISAAC, H. 2016. Examining the effects of climate change and species invasions on Ontario walleye populations: can walleye beat the heat? *Diversity and Distributions,* 22**,** 1069-1079.

VANCOUVER, P. M. 2015. Roberts Bank Terminal 2-Environmental Impact Statement. Canadian Environmental Agency Reference No. 80054. 124 pp. .

VASILAKOPOULOS, P., MARAVELIAS, C. D. & TSERPES, G. 2014. The Alarming Decline of Mediterranean Fish Stocks. *Current Biology,* 24**,** 1643-1648.

VERGÉS, A., TOMAS, F., CEBRIAN, E., BALLESTEROS, E., KIZILKAYA, Z., DENDRINOS, P., KARAMANLIDIS, A. A., SPIEGEL, D. & SALA, E. 2014. Tropical rabbitfish and the deforestation of a warming temperate sea. *Journal of Ecology,* 102**,** 1518-1527.

VIERROS, M., CRESSWELL, I. D., BRIDGEWATER, P. & SMITH, A. D. 2015. *Ecosystem approach and ocean management*.

VILÀ, M., BASNOU, C., PYŠEK, P., JOSEFSSON, M., GENOVESI, P., GOLLASCH, S., NENTWIG, W., OLENIN, S., ROQUES, A. & ROY, D. 2009. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment,* 8**,** 135-144.

VOLOVIK, Y. S., VOLOVIK, S. P. & MYRZOYAN, Z. A. 1995. Modelling of the Mnemiopsis sp. population in the Azov Sea. *ICES Journal of Marine Science: Journal du Conseil,* 52**,** 735-746.

WALRATH, J. D., QUIST, M. C. & FIREHAMMER, J. A. 2015. Trophic Ecology of Nonnative Northern Pike and their Effect on Conservation of Native Westslope Cutthroat Trout. *North American Journal of Fisheries Management,* 35**,** 158-177.

WALTERS, C., CHRISTENSEN, V. & PAULY, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in fish biology and fisheries,* 7**,** 139-172.

WALTERS, C., PAULY, D. & CHRISTENSEN, V. 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems,* 2**,** 539-554.

WALTERS, C. J., CHRISTENSEN, V., MARTELL, S. J. & KITCHELL, J. F. 2005. Possible ecosystem impacts of applying MSY policies from single-species assessment. *ICES Journal of Marine Science: Journal du Conseil,* 62**,** 558-568.

WALTERS, C. J. & MARTELL, S. J. 2004. *Fisheries ecology and management,* Princeton University Press.

WALTHER, G.-R., POST, E., CONVEY, P., MENZEL, A., PARMESAN, C., BEEBEE, T. J., FROMENTIN, J.-M., HOEGH-GULDBERG, O. & BAIRLEIN, F. 2002. Ecological responses to recent climate change. *Nature,* 416**,** 389.

WALTHER, G.-R., ROQUES, A., HULME, P. E., SYKES, M. T., PYŠEK, P., KÜHN, I., ZOBEL, M., BACHER, S., BOTTA-DUKÁT, Z. & BUGMANN, H. 2009. Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution,* 24**,** 686-693.

WATSON, R. A., CHEUNG, W. W., ANTICAMARA, J. A., SUMAILA, R. U., ZELLER, D. & PAULY, D. 2013. Global marine yield halved as fishing intensity redoubles. *Fish and Fisheries,* 14**,** 493-503.

WATSON, R. A. & MORATO, T. 2013. Fishing down the deep: Accounting for within-species changes in depth of fishing. *Fisheries Research,* 140**,** 63-65.

WENGER, S. J., ISAAK, D. J., LUCE, C. H., NEVILLE, H. M., FAUSCH, K. D., DUNHAM, J. B., DAUWALTER, D. C., YOUNG, M. K., ELSNER, M. M., RIEMAN, B. E., HAMLET, A. F. & WILLIAMS, J. E. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences of the United States of America,* 108**,** 14175-14180.

WHIPPLE, S. J., LINK, J. S., GARRISON, L. P. & FOGARTY, M. J. 2000. Models of predation and fishing mortality in aquatic ecosystems. *Fish and Fisheries,* 1**,** 22-40.

WISZ, M. S., POTTIER, J., KISSLING, W. D., PELLISSIER, L., LENOIR, J., DAMGAARD, C. F., DORMANN, C. F., FORCHHAMMER, M. C., GRYTNES, J. A. & GUISAN, A. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological reviews,* 88**,** 15-30.

WONHAM, M. J. & LEWIS, M. A. 2009. Modeling marine invasions: current and future approaches. *Biological invasions in marine ecosystems.* Springer.

WOODFORD, D. J., COCHRANE, T. A., MCHUGH, P. A. & MCINTOSH, A. R. 2011. Modelling spatial exclusion of a vulnerable native fish by introduced trout in rivers using landscape features: A new tool for conservation management. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 21**,** 484-493.

WORM, B., BARBIER, E. B., BEAUMONT, N., DUFFY, J. E., FOLKE, C., HALPERN, B. S., JACKSON, J. B., LOTZE, H. K., MICHELI, F. & PALUMBI, S. R. 2006. Impacts of biodiversity loss on ocean ecosystem services. *science,* 314**,** 787-790.

WORM, B. & BRANCH, T. A. 2012. The future of fish. *Trends in Ecology & Evolution,* 27**,** 594-599.

WORM, B., HILBORN, R., BAUM, J. K., BRANCH, T. A., COLLIE, J. S., COSTELLO, C., FOGARTY, M. J., FULTON, E. A., HUTCHINGS, J. A. & JENNINGS, S. 2009. Rebuilding global fisheries. *science,* 325**,** 578-585.

YURISTA, P. M. & SCHULZ, K. L. 1995. Bioenergetic analysis of prey consumption by Bythotrephes cederstroemi in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences,* 52**,** 141-150.

ZAR, J. 1984. *Biostatistical analysis,* Londo, UK, Prentice-Hall.

ZELLER, D., CASHION, T., PALOMARES, M. & PAULY, D. 2018. Global marine fisheries discards: a synthesis of reconstructed data. *Fish and Fisheries,* 19**,** 30-39.

ZENETOS, A., ÇINAR, M. E., CROCETTA, F., GOLANI, D., ROSSO, A., SERVELLO, G., SHENKAR, N., TURON, X. & VERLAQUE, M. 2017. Uncertainties and validation of alien species catalogues: The Mediterranean as an example. *Estuarine, Coastal and Shelf Science.*

ZENETOS, A., GOFAS, S., VERLAQUE, M., ÇINAR, M. E., GARCIA RASO, J., BIANCHI, C., MORRI, C., AZZURRO, E., BILECENOGLU, M. & FROGLIA, C. 2010. Alien species in the Mediterranean Sea by 2010. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part I. Spatial distribution.

ZENETOS, A., GOFAS, S., MORRI, C., ROSSO, A., VIOLANTI, D., RASO, J. G., ÇINAR, M. E., ALMOGI-LABIN, A., ATES, A. & AZZURRO, E. 2012. Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union’s Marine Strategy Framework Directive (MSFD). Part 2. Introduction trends and pathways. *Mediterranean Marine Science,* 13**,** 328-352.

ZHANG, H., CULVER, D. A. & BOEGMAN, L. 2008. A two-dimensional ecological model of Lake Erie: application to estimate dreissenid impacts on large lake plankton populations. *Ecological Modelling,* 214**,** 219-241.

ZHANG, H., CULVER, D. A. & BOEGMAN, L. 2011. Dreissenids in Lake Erie: An algal filter or a fertilizer? *Aquatic Invasions,* 6**,** 175-194.

ZHANG, H., RUTHERFORD, E. S., MASON, D. M., BRECK, J. T., WITTMANN, M. E., COOKE, R. M., LODGE, D. M., ROTHLISBERGER, J. D., ZHU, X. & JOHNSON, T. B. 2016. Forecasting the Impacts of Silver and Bighead Carp on the Lake Erie Food Web. *Transactions of the American Fisheries Society,* 145**,** 136-162.

ANNEXES

ANNEX 1

Online supplementary information chapter 2.1

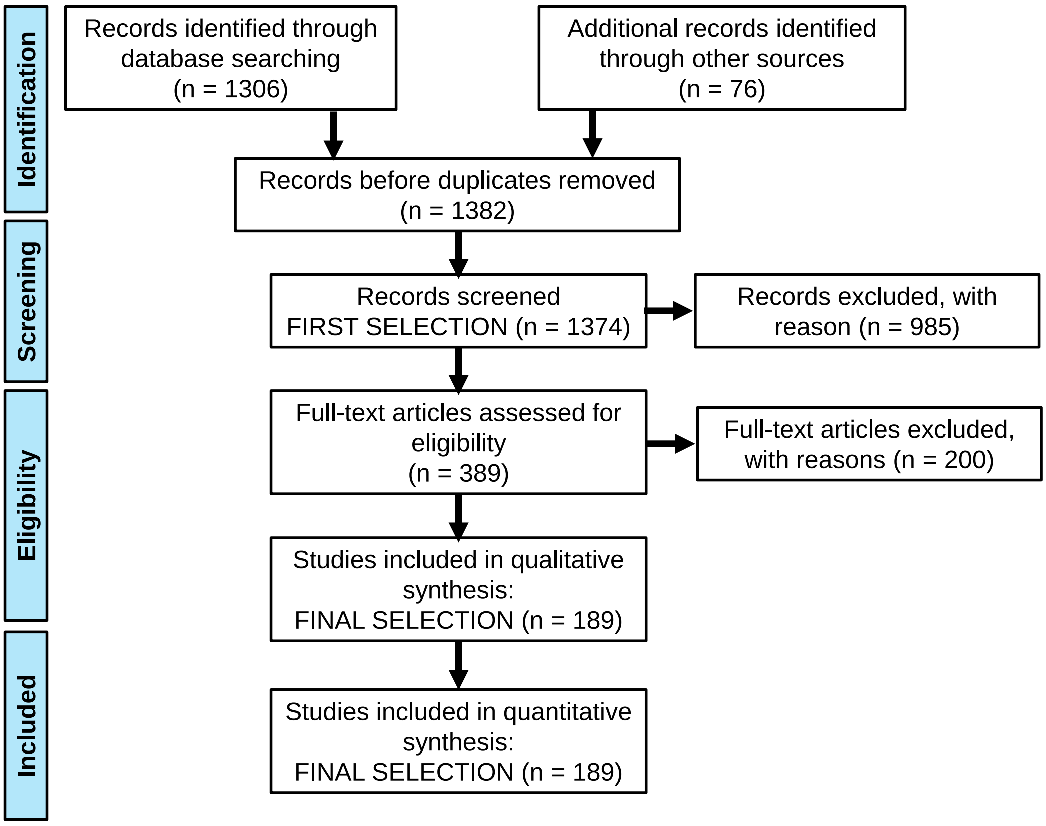


Fig. S1. Flow diagram of the methodological approach (PRISMA) used in the systematic review.

Final list of articles included in the review

Akoglu, E., Salihoglu, B., Libralato, S., Oguz, T., Solidoro, C., 2014. An indicator-based evaluation of Black Sea food web dynamics during 1960-2000. Journal of Marine Systems 134, 113-125.

Amundsen, P.A., Lafferty, K.D., Knudsen, R., Primicerio, R., Kristoffersen, R., Klemetsen, A., Kuris, A.M., 2013. New parasites and predators follow the introduction of two fish species to a subarctic lake: Implications for food-web structure and functioning. Oecologia 171, 993-1002.

Anderson, K.R., Chapman, D.C., Wynne, T.T., Masagounder, K., Paukert, C.P., 2015. Suitability of Lake Erie for bigheaded carps based on bioenergetic models and remote sensing. Journal of Great Lakes Research 41, 358-366.

Aravena, G., Villate, F., Uriarte, I., Iriarte, A., Ibáñez, B., 2009. Response of Acartia populations to environmental variability and effects of invasive congenerics in the estuary of Bilbao, Bay of Biscay. Estuarine, Coastal and Shelf Science 83, 621-628.

Arbach Leloup, F., Desroy, N., Le Mao, P., Pauly, D., Le Pape, O., 2008. Interactions between a natural food web, shellfish farming and exotic species: The case of the Bay of Mont Saint Michel (France). Estuarine, Coastal and Shelf Science 76, 111-120.

Arias-González, J.E., González-Gándara, C., Luis Cabrera, J., Christensen, V., 2011. Predicted impact of the invasive lionfish Pterois volitans on the food web of a Caribbean coral reef. Environmental Research 111, 917-925.

Auer, M.T., Tomlinson, L.M., Higgins, S.N., Malkin, S.Y., Howell, E.T., Bootsma, H.A., 2010. Great Lakes Cladophora in the 21st century: Same algae-different ecosystem. Journal of Great Lakes Research 36, 248-255.

Baird, D., Asmus, H., Asmus, R., 2012. Effect of invasive species on the structure and function of the Sylt-Rømø Bight ecosystem, northern Wadden Sea, over three time periods. Marine Ecology Progress Series 462, 143-162.

Bajer, P.G., Beck, M.W., Cross, T.K., Koch, J.D., Bartodziej, W.M., Sorensen, P.W., 2016. Biological invasion by a benthivorous fish reduced the cover and species richness of aquatic plants in most lakes of a large North American ecoregion. Global Change Biology 22, 3937-3947.

Beisner, B.E., Ives, A.R., Carpenter, S.R., 2003. The effects of an exotic fish invasion on the prey communities of two lakes. Journal of Animal Ecology 72, 331-342.

Benjamin, J.R., Fausch, K.D., Baxter, C.V., 2011. Species replacement by a nonnative salmonid alters ecosystem function by reducing prey subsidies that support riparian spiders. Oecologia 167, 503-512.

Berdnikov, S.V., Selyutin, V.V., Vasilchenko, V.V., Caddy, J.F., 1999. Trophodynamic model of the Black and Azov Sea pelagic ecosystem: Consequences of the comb jelly, Mnemiopsis leydei, invasion. Fisheries Research 42, 261-289.

Beville, S.T., Kerr, G.N., Hughey, K.F.D., 2012. Valuing impacts of the invasive alga Didymosphenia geminata on recreational angling. Ecological Economics 82, 1-10.

Bierman, V.J., Kaur, J., DePinto, J.V., Feist, T.J., Dilks, D.W., 2005. Modeling the role of zebra mussels in the proliferation of blue-green algae in Saginaw Bay, Lake Huron. Journal of Great Lakes Research 31, 32-55.

Blamey, L.K., Plagányi, É.E., Branch, G.M., 2013. Modeling a regime shift in a kelp forest ecosystem caused by a lobster range expansion. Bulletin of Marine Science 89, 347-375.

Blamey, L.K., Plagányi, T.E., Branch, G.M., 2014. Was overfishing of predatory fish responsible for a lobster-induced regime shift in the Benguela? Ecological Modelling 273, 140-150.

Blanchet, S., Loot, G., Dodson, J.J., 2008. Competition, predation and flow rate as mediators of direct and indirect effects in a stream food chain. Oecologia 157, 93-104.

Blukacz-Richards, E.A., Koops, M.A., 2012. An integrated approach to identifying ecosystem recovery targets: Application to the Bay of Quinte. Aquatic Ecosystem Health and Management 15, 464-472.

Bocaniov, S.A., Smith, R.E.H., Spillman, C.M., Hipsey, M.R., Leon, L.F., 2014. The nearshore shunt and the decline of the phytoplankton spring bloom in the Laurentian Great Lakes: Insights from a three-dimensional lake model. Hydrobiologia 731, 151-172.

Boegman, L., Loewen, M.R., Culver, D.A., Hamblin, P.F., Charlton, M.N., 2008a. Spatial-dynamic modeling of algal biomass in lake erie: Relative impacts of dreissenid mussels and nutrient loads. Journal of Environmental Engineering 134, 456-468.

Boegman, L., Loewen, M.R., Hamblin, P.F., Culver, D.A., 2008b. Vertical mixing and weak stratification over zebra mussel colonies in western Lake Erie. Limnology and Oceanography 53, 1093-1110.

Boulêtreau, S., Cucherousset, J., Villéger, S., Masson, R., Santoul, F., 2011. Colossal aggregations of giant alien freshwater fish as a potential biogeochemical hotspot. PLoS ONE 6.

Bourdeau, P.E., Pangle, K.L., Peacor, S.D., 2015. Factors affecting the vertical distribution of the zooplankton assemblage in Lake Michigan: The role of the invasive predator Bythotrephes longimanus. Journal of Great Lakes Research 41, 115-124.

Bunnell, D.B., Johnson, T.B., Knight, C.T., 2005. The impact of introduced round gobies (Neogobius melanostomus) on phosphorus cycling in central Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 62, 15-29.

Byers, J.E., Goldwasser, L., 2001. Exposing the mechanism and timing of impact of nonindigenous species on native species. Ecology 82, 1330-1343.

Caldow, R.W.G., Stillman, R.A., Dit Durell, S.E.A.L.V., West, A.D., McGrorty, S., Goss-Custard, J.D., Wood, P.J., Humphreys, J., 2007. Benefits to shorebirds from invasion of a non-native shellfish. Proceedings of the Royal Society B: Biological Sciences 274, 1449-1455.

Caraco, N.F., Cole, J.J., Raymond, P.A., Strayer, D.L., Pace, M.L., Findlay, S.E.G., Fischer, D.T., 1997. Zebra mussel invasion in a large, turbid river: Phytoplankton response to increased grazing. Ecology 78, 588-602.

Cerino, D., Overton, A.S., Rice, J.A., Morris Jr, J.A., 2013. Bioenergetics and Trophic Impacts of the Invasive Indo-Pacific Lionfish. Transactions of the American Fisheries Society 142, 1522-1534.

Ciancio, J., Beauchamp, D.A., Pascual, M., 2010. Marine effect of introduced salmonids: Prey consumption by exotic steelhead and anadromous brown trout in the Patagonian Continental Shelf. Limnology and Oceanography 55, 2181-2192.

Clavero, M., Hermoso, V., Aparicio, E., Godinho, F.N., 2013. Biodiversity in heavily modified waterbodies: Native and introduced fish in Iberian reservoirs. Freshwater Biology 58, 1190-1201.

Colvin, M.E., Pierce, C.L., Stewart, T.W., 2015. A food web modeling analysis of a Midwestern, USA eutrophic lake dominated by non-native Common Carp and Zebra Mussels. Ecological Modelling 312, 26-40.

Cook, G.S., Fletcher, P.J., Kelble, C.R., 2014. Towards marine ecosystem based management in South Florida: Investigating the connections among ecosystem pressures, states, and services in a complex coastal system. Ecological Indicators 44, 26-39.

Cooke, S.L., Hill, W.R., 2010. Can filter-feeding Asian carp invade the Laurentian Great Lakes? A bioenergetic modelling exercise. Freshwater Biology 55, 2138-2152.

Corrales, X., Ofir, E., Coll, M., Goren, M., Edelist, D., Heymans, J., Gal, G., 2017. Modeling the role and impact of alien species and fisheries on the Israeli marine continental shelf ecosystem. Journal of Marine Systems 170, 88-102.

Correa, C., Hendry, A.P., 2012. Invasive salmonids and lake order interact in the decline of puye grande Galaxias platei in western Patagonia lakes. Ecological Applications 22, 828-842.

Cox, S.P., Kitchell, J.F., 2004. Lake superior ecosystem, 1929-1998: Simulating alternative hypotheses for recruitment failure of lake herring (Coregonus artedi). Bulletin of Marine Science 74, 671-683.

Crane, D.P., Einhouse, D.W., 2015. Changes in growth and diet of smallmouth bass following invasion of Lake Erie by the round goby. Journal of Great Lakes Research.

Crane, D.P., Farrell, J.M., Einhouse, D.W., Lantry, J.R., Markham, J.L., 2015. Trends in body condition of native piscivores following invasion of Lakes Erie and Ontario by the round goby. Freshwater Biology 60, 111-124.

Cha, Y., Stow, C.A., Bernhardt, E.S., 2013. Impacts of dreissenid mussel invasions on chlorophyll and total phosphorus in 25 lakes in the USA. Freshwater Biology 58, 192-206.

Cha, Y., Stow, C.A., Nalepa, T.F., Reckhow, K.H., 2011. Do invasive mussels restrict offshore phosphorus transport in lake huron? Environmental Science and Technology 45, 7226-7231.

Daskalov, G.M., 2002. Overfishing drives a trophic cascade in the Black sea. Marine Ecology Progress Series 225, 53-63.

De Amorim, S.R., Umetsu, C.A., Toledo, D., Camargo, A.F.M., 2015. Effects of a non native species of Poaceae on aquatic macrophyte community composition: A comparison with a native species. Journal of Aquatic Plant Management 53, 191-196.

Dembkowski, D.J., Willis, D.W., Blackwell, B.G., Chipps, S.R., Bacula, T.D., Wuellner, M.R., 2015. Influence of Smallmouth Bass Predation on Recruitment of Age-0 Yellow Perch in South Dakota Glacial Lakes. North American Journal of Fisheries Management 35, 736-747.

Descy, J.P., Everbecq, E., Gosselain, V., Viroux, L., Smitz, J., 2003. Modelling the impact of benthic filter-feeders on the composition and biomass of river plankton. Freshwater Biology 48, 404-417.

Descy, J.P., Leitao, M., Everbecq, E., Smitz, J.S., Delige, J.F., 2012. Phytoplankton of the river loire, France: A biodiversity and modelling study. Journal of Plankton Research 34, 120-135.

Downing, A.S., Van Nes, E.H., Janse, J.H., Witte, F., Cornelissen, I.J.M., Scheffer, M., Mooij, W.M., 2012. Collapse and reorganization of a food web of Mwanza Gulf, Lake Victoria. Ecological Applications 22, 229-239.

Ferguson, J.M., Taper, M.L., Guy, C.S., Syslo, J.M., 2012. Mechanisms of coexistence between native bull trout (Salvelinus confluentus) and non-native lake trout (Salvelinus namaycush): Inferences from pattern-oriented modeling. Canadian Journal of Fisheries and Aquatic Sciences 69, 1-15.

Feroz Khan, M., Panikkar, P., 2009. Assessment of impacts of invasive fishes on the food web structure and ecosystem properties of a tropical reservoir in India. Ecological Modelling 220, 2281-2290.

Fetahi, T., Schagerl, M., Mengistou, S., Libralato, S., 2011. Food web structure and trophic interactions of the tropical highland lake Hayq, Ethiopia. Ecological Modelling 222, 804-813.

Fishman, D.B., Adlerstein, S.A., Vanderploeg, H.A., Fahnenstiel, G.L., Scavia, D., 2009. Causes of phytoplankton changes in Saginaw Bay, Lake Huron, during the zebra mussel invasion. Journal of Great Lakes Research 35, 482-495.

Foley, C.J., Andree, S.R., Pothoven, S.A., Nalepa, T.F., Höök, T.O., 2017. Quantifying the predatory effect of round goby on Saginaw Bay dreissenids. Journal of Great Lakes Research 43, 121-131.

Fontaine, T.D., Stewart, D.J., 1992. Exploring the effects of multiple management objectives and exotic species on great lakes food webs and contaminant dynamics. Environmental Management 16, 225-229.

Francis, T.B., Wolkovich, E.M., Scheuerell, M.D., Katz, S.L., Holmes, E.E., Hampton, S.E., 2014. Shifting regimes and changing interactions in the Lake Washington, U.S.A., plankton community from 1962-1994. PLoS ONE 9.

Fresard, M., Boncoeur, J., 2006. Controlling the biological invasion of a commercial fishery by a space competitor: a bioeconomic model with reference to the bay of St-Brieuc scallop fishery. Agricultural and Resource Economics Review 35, 78.

Frésard, M., Boncoeur, J., 2006. Costs and benefits of stock enhancement and biological invasion control: The case of the Bay of Brest scallop fishery. Aquatic Living Resources 19, 299-305.

Glaser, D., Rhea, J.R., Opdyke, D.R., Russell, K.T., Ziegler, C.K., Ku, W., Zheng, L., Mastriano, J., 2009. Model of zebra mussel growth and water quality impacts in the Seneca River, New York. Lake and Reservoir Management 25, 49-72.

Gobin, J., Lester, N.P., Cottrill, A., Fox, M.G., Dunlop, E.S., 2015. Trends in growth and recruitment of Lake Huron lake whitefish during a period of ecosystem change, 1985 to 2012. Journal of Great Lakes Research 41, 405-414.

Green, S.J., Akins, J.L., Maljković, A., Côté, I.M., 2012. Invasive lionfish drive Atlantic coral reef fish declines. PLoS ONE 7, e32596.

Green, S.J., Dulvy, N.K., Brooks, A.M.L., Akins, J.L., Cooper, A.B., Miller, S., ɤoté, I.M., 2014. Linking removal targets to the ecological effects of invaders: A predictive model and field test. Ecological Applications 24, 1311-1322.

Gribben, P.E., Wright, J.T., 2006. Sublethal effects on reproduction in native fauna: Are females more vulnerable to biological invasion? Oecologia 149, 352-361.

Grosholz, E., Lovell, S., Besedin, E., Katz, M., 2011. Modeling the impacts of the European green crab on commercial shellfisheries. Ecological Applications 21, 915-924.

Gucu, A., 2002. Can overfishing be responsible for the successful establishment of Mnemiopsis leidyi in the Black Sea? Estuarine, Coastal and Shelf Science 54, 439-451.

Gudimov, A., Kim, D.K., Young, J.D., Palmer, M.E., Dittrich, M., Winter, J.G., Stainsby, E., Arhonditsis, G.B., 2015. Examination of the role of dreissenids and macrophytes in the phosphorus dynamics of Lake Simcoe, Ontario, Canada. Ecological Informatics 26, 36-53.

Halstead, J.M., Michaud, J., Hallas-Burt, S., Gibbs, J.P., 2003. Hedonic Analysis of Effects of a Nonnative Invader (Myriophyllum heterophyllum) on New Hampshire (USA) Lakefront Properties. Environmental Management 32, 391-398.

Harvey, C.J., Kareiva, P.M., 2005. Community context and the influence of non-indigenous species on juvenile salmon survival in a Columbia River reservoir. Biological Invasions 7, 651-663.

Hattab, T., Lasram, F.B.R., Albouy, C., Romdhane, M.S., Jarboui, O., Halouani, G., Cury, P., Le Loc'h, F., 2013. An ecosystem model of an exploited southern Mediterranean shelf region (Gulf of Gabes, Tunisia) and a comparison with other Mediterranean ecosystem model properties. Journal of Marine Systems 128, 159-174.

Haught, S., von Hippel, F.A., 2011. Invasive pike establishment in Cook Inlet Basin lakes, Alaska: Diet, native fish abundance and lake environment. Biological Invasions 13, 2103-2114.

He, J.X., Bence, J.R., Madenjian, C.P., Pothoven, S.A., Dobiesz, N.E., Fielder, D.G., Johnson, J.E., Ebener, M.P., Cottrill, R.A., Mohr, L.C., 2014. Coupling age-structured stock assessment and fish bioenergetics models: a system of time-varying models for quantifying piscivory patterns during the rapid trophic shift in the main basin of Lake Huron. Canadian Journal of Fisheries and Aquatic Sciences 72, 7-23.

Hermoso, V., Clavero, M., Blanco-Garrido, F., Prenda, J., 2011. Invasive species and habitat degradation in Iberian streams: An analysis of their role in freshwater fish diversity loss. Ecological Applications 21, 175-188.

Hermoso, V., Clavero, M., Kennard, M.J., 2012. Determinants of fine-scale homogenization and differentiation of native freshwater fish faunas in a Mediterranean Basin: Implications for conservation. Diversity and Distributions 18, 236-247.

Higgins, S.N., Althouse, B., Devlin, S.P., Vadeboncoeur, Y., Vander Zanden, M.J., 2014. Potential for large-bodied zooplankton and dreissenids to alter the productivity and autotrophic structure of lakes. Ecology 95, 2257-2267.

Higgins, S.N., Vander Zanden, M.J., Joppa, L.N., Vadeboncoeur, Y., 2011. The effect of dreissenid invasions on chlorophyll and the chlorophyll: Total phosphorus ratio in north-temperate lakes. Canadian Journal of Fisheries and Aquatic Sciences 68, 319-329.

Hoffman, J.C., Smith, M.E., Lehman, J.T., 2001. Perch or plankton: Top-down control of Daphnia by yellow perch (Perca flavescens) or Bythotrephes cederstroemi in an inland lake? Freshwater Biology 46, 759-775.

Horsch, E.J., Lewis, D.J., 2009. The effects of aquatic invasive species on property values: Evidence from a quasi-experiment. Land Economics 85, 391-409.

Hossain, M., Arhonditsis, G.B., Koops, M.A., Minns, C.K., 2012. Towards the development of an ecosystem model for the Hamilton Harbour, Ontario, Canada. Journal of Great Lakes Research 38, 628-642.

Hossain, M.M., Perhar, G., Arhonditsis, G.B., Matsuishi, T., Goto, A., Azuma, M., 2013. Examination of the effects of largemouth bass (Micropterus salmoides) and bluegill (Lepomis macrochirus) on the ecosystem attributes of lake Kawahara-oike, Nagasaki, Japan. Ecological Informatics 18, 149-161.

Isaev, A.V., Eremina, T.R., Ryabchenko, V.A., Savchuk, O.P., 2016. Model estimates of the impact of bioirrigation activity of Marenzelleria spp. on the Gulf of Finland ecosystem in a changing climate. Journal of Marine Systems.

Jaarsma, N.G., Bergman, M., Schulze, F.H., Vaate, A.B.D., 2007. Macro-invertebrates in a dynamic river environment: Analysis of time series from artificial substrates, using a 'white box' neural network modelling method. Aquatic Ecology 41, 413-425.

Jellyman, P.G., Harding, J.S., 2016. Disentangling the stream community impacts of Didymosphenia geminata: How are higher trophic levels affected? Biological Invasions 18, 3419-3435.

Jiang, L., Xia, M., Ludsin, S.A., Rutherford, E.S., Mason, D.M., Marin Jarrin, J., Pangle, K.L., 2015. Biophysical modeling assessment of the drivers for plankton dynamics in dreissenid-colonized western Lake Erie. Ecological Modelling 308, 18-33.

Johnson, T.B., Bunnell, D.B., Knight, C.T., 2005. A potential new energy pathway in central Lake Erie: the round goby connection. Journal of Great Lakes Research 31, 238-251.

Kao, Y.-C., Adlerstein, S.A., Rutherford, E.S., 2016. Assessment of Top-Down and Bottom-Up Controls on the Collapse of Alewives (Alosa pseudoharengus) in Lake Huron. Ecosystems, 1-29.

Kao, Y.C., Adlerstein, S., Rutherford, E., 2014. The relative impacts of nutrient loads and invasive species on a Great Lakes food web: An Ecopath with Ecosim analysis. Journal of Great Lakes Research 40, 35-52.

Kateregga, E., Sterner, T., 2009. Lake victoria fish stocks and the effects of water hyacinth. Journal of Environment and Development 18, 62-78.

Katsanevakis, S., Tempera, F., Teixeira, H., 2016. Mapping the impact of alien species on marine ecosystems: the Mediterranean Sea case study. Diversity and Distributions, n/a-n/a.

Kinter, B.T., Ludsin, S.A., 2013. Nutrient inputs versus piscivore biomass as the primary driver of reservoir food webs. Canadian Journal of Fisheries and Aquatic Sciences 70, 367-380.

Kitchell, J.F., Cox, S.P., Harvey, C.J., Johnson, T.B., Mason, D.M., Schoen, K.K., Aydin, K., Bronte, C., Ebener, M., Hansen, M., Hoff, M., Schram, S., Schreiner, D., Walters, C.J., 2000. Sustainability of the Lake Superior fish community: Interactions in a food web context. Ecosystems 3, 545-560.

Kitchell, J.F., Schindler, D.E., Ogutu-Ohwayo, R., Reinthal, P.N., 1997. The Nile perch in Lake Victoria: interactions between predation and fisheries. Ecological Applications 7, 653-664.

Knapp, R.A., 2005. Effects of nonnative fish and habitat characteristics on lentic herpetofauna in Yosemite National Park, USA. Biological Conservation 121, 265-279.

Knowler, D., 2005. Reassessing the costs of biological invasion: Mnemiopsis leidyi in the Black sea. Ecological Economics 52, 187-199.

Knowler, D., Barbier, E.B., 2005. Managing the black sea anchovy fishery with nutrient enrichment and a biological invader. Marine Resource Economics 20, 263-285.

Kratina, P., Mac Nally, R., Kimmerer, W.J., Thomson, J.R., Winder, M., 2014. Human-induced biotic invasions and changes in plankton interaction networks. Journal of Applied Ecology 51, 1066-1074.

Kumar, R., Varkey, D., Pitcher, T., 2016. Simulation of zebra mussels (Dreissena polymorpha) invasion and evaluation of impacts on Mille Lacs Lake, Minnesota: An ecosystem model. Ecological Modelling.

Lancelot, C., Staneva, J., Van Eeckhout, D., Beckers, J., Stanev, E., 2002. Modeling the impact of the human forcing on the ecological functioning of the northwestern Black Sea. Estuarine, Coastal and Shelf Science 54, 473-500.

Langseth, B.J., Rogers, M., Zhang, H., 2012. Modeling species invasions in Ecopath with Ecosim: an evaluation using Laurentian Great Lakes models. Ecological Modelling 247, 251-261.

Laruelle, G.G., Regnier, P., Ragueneau, O., Kempa, M., Moriceau, B., Longphuirt, S.N., Leynaert, A., Thouzeau, G., Chauvaud, L., 2009. Benthic-pelagic coupling and the seasonal silic cycle in the bay of brest (France): New insights from a coupled physical-biological model. Marine Ecology Progress Series 385, 15-32.

Laxson, C.L., McPhedran, K.N., Makarewicz, J.C., Telesh, I.V., Macisaac, H.J., 2003. Effects of the non-indigenous cladoceran Cercopagis pengoi on the lower food web of Lake Ontario. Freshwater Biology 48, 2094-2106.

Le Pape, O., Guérault, D., Désaunay, Y., 2004. Effect of an invasive mollusc, American slipper limpet Crepidula fornicata, on habitat suitability for juvenile common sole Solea solea in the Bay of Biscay. Marine Ecology Progress Series 277, 107-115.

Lee, V.A., Johnson, T.B., 2005. Development of a bioenergetics model for the round goby (Neogobius melanostomus). Journal of Great Lakes Research 31, 125-134.

Lercari, D., Bergamino, L., 2011. Impacts of two invasive mollusks, Rapana venosa (Gastropoda) and Corbicula fluminea (Bivalvia), on the food web structure of the Río de la Plata estuary and nearshore oceanic ecosystem. Biological Invasions 13, 2053-2061.

Li, L., Pitcher, T.J., Devlin, R.H., 2015. Potential risks of trophic impacts by escaped transgenic salmon in marine environments. Environmental Conservation 42, 152-161.

Liao, F.H., Wilhelm, F.M., Solomon, M., 2016. The effects of ambient water quality and eurasian watermilfoil on lakefront property values in the Coeur d'Alene area of northern Idaho, USA. Sustainability (Switzerland) 8, 1-12.

Libralato, S., Caccin, A., Pranovi, F., 2015. Modelling species invasions using thermal and trophic niche dynamics under climate change. Frontiers in Marine Science 2, 29.

Light, T., Marchetti, M.P., 2007. Distinguishing between invasions and habitat changes as drivers of diversity loss among California's freshwater fishes. Conservation Biology 21, 434-446.

Liu, Y., Olaussen, J.O., Skonhoft, A., 2014. Fishy fish? The economic impacts of escaped farmed fish. Aquaculture Economics and Management 18, 273-302.

MacDonald, J.I., Tonkin, Z.D., Ramsey, D.S.L., Kaus, A.K., King, A.K., Crook, D.A., 2012. Do invasive eastern gambusia (Gambusia holbrooki) shape wetland fish assemblage structure in south-eastern Australia? Marine and Freshwater Research 63, 659-671.

Macisaac, H.J., Johannsson, O.E., Ye, J., Sprules, W.G., Leach, J.H., McCorquodale, J.A., Grigorovich, I.A., 1999. Filtering impacts of an introduced bivalve (Dreissena polymorpha) in a shallow lake: Application of a hydrodynamic model. Ecosystems 2, 338-350.

Madenjian, C.P., 1995. Removal of algae by the zebra mussel (Dreissena polymorpha) population in western Lake Erie: a bioenergetics approach. Canadian Journal of Fisheries and Aquatic Sciences 52, 381-390.

Madenjian, C.P., Hondorp, D.W., Desorcie, T.J., Holuszko, J.D., 2005. Sculpin community dynamics in Lake Michigan. Journal of Great Lakes Research 31, 267-276.

Magnea, U., Sciascia, R., Paparella, F., Tiberti, R., Provenzale, A., 2013. A model for high-altitude alpine lake ecosystems and the effect of introduced fish. Ecological Modelling 251, 211-220.

Marrack, L., Beavers, S., O’Grady, P., 2015. The relative importance of introduced fishes, habitat characteristics, and land use for endemic shrimp occurrence in brackish anchialine pool ecosystems. Hydrobiologia 758, 107-122.

Matsuishi, T., Muhoozi, L., Mkumbo, O., Budeba, Y., Njiru, M., Asila, A., Othina, A., Cowx, I., 2006. Are the exploitation pressures on the Nile perch fisheries resources of Lake Victoria a cause for concern? Fisheries Management and Ecology 13, 53-71.

Mavuti, K., Moreau, J., Munyandorero, J., Plisnier, P.D., 1996. Analysis of trophic relationships in two shallow equatorial lakes Lake Naivasha (Kenya) and Lake Ihema (Rwanda) using a multispecifies trophic model. Hydrobiologia 321, 89-100.

Miehls, A.L.J., Mason, D.M., Frank, K.A., Krause, A.E., Peacor, S.D., Taylor, W.W., 2009a. Invasive species impacts on ecosystem structure and function: A comparison of Oneida Lake, New York, USA, before and after zebra mussel invasion. Ecological Modelling 220, 3194-3209.

Miehls, A.L.J., Mason, D.M., Frank, K.A., Krause, A.E., Peacor, S.D., Taylor, W.W., 2009b. Invasive species impacts on ecosystem structure and function: A comparison of the Bay of Quinte, Canada, and Oneida Lake, USA, before and after zebra mussel invasion. Ecological Modelling 220, 3182-3193.

Miller, D.H., Kreis Jr, R.G., Huang, W.C., Xia, X., 2010. Application of a lower food web ecosystem productivity model for investigating dynamics of the invasive species Bythotrephes longimanus in Lake Michigan. Biological Invasions 12, 3513-3524.

Morales, Y., Weber, L., Mynett, A., Newton, T., 2006. Mussel dynamics model: a hydroinformatics tool for analyzing the effects of different stressors on the dynamics of freshwater mussel communities. Ecological Modelling 197, 448-460.

Morales, Y., Weber, L.J., Mynett, A.E., Newton, T.J., 2007. Simulating the effect of invasive species on native freshwater mussel communities. International Journal of River Basin Management 5, 267-277.

Moreau, J., Ligtvoet, W., Palomares, M., 1993. Trophic relationship in the fish community of Lake Victoria, Kenya, with emphasis on the impact of Nile perch (Lates niloticus), Trophic models of aquatic ecosystems. ICLARM conference proceedings, pp. 144-152.

Morozov, A.Y., Nezlin, N.P., Petrovskii, S.V., 2005. Invasion of a top predator into an epipelagic ecosystem can bring a paradoxical top-down trophic control. Biological Invasions 7, 845-861.

Murray, A.G., Parslow, J.S., 1999. Modelling of nutrient impacts in Port Phillip Bay - A semi-enclosed marine Australian ecosystem. Marine and Freshwater Research 50, 597-611.

Myers, J.T., Jones, M.L., Stockwell, J.D., Yule, D.L., 2009. Reassessment of the predatory effects of rainbow smelt on ciscoes in lake superior. Transactions of the American Fisheries Society 138, 1352-1368.

Natugonza, V., Ogutu-Ohwayo, R., Musinguzi, L., Kashindye, B., Jónsson, S., Valtysson, H.T., 2016. Exploring the structural and functional properties of the Lake Victoria food web, and the role of fisheries, using a mass balance model. Ecological Modelling 342, 161-174.

Negus, M.T., 1995. Bioenergetics modeling as a salmonine management tool applied to minnesota waters of lake superior. North American Journal of Fisheries Management 15, 60-78.

Negus, M.T., Schreiner, D.R., Halpern, T.N., Schram, S.T., Seider, M.J., Pratt, D.M., 2008. Bioenergetics evaluation of the fish community in the western arm of lake superior in 2004. North American Journal of Fisheries Management 28, 1649-1667.

Nilsson, E., Solomon, C.T., Wilson, K.A., Willis, T.V., Larget, B., Vander Zanden, M.J., 2012. Effects of an invasive crayfish on trophic relationships in north-temperate lake food webs. Freshwater Biology 57, 10-23.

Norkko, J., Reed, D.C., Timmermann, K., Norkko, A., Gustafsson, B.G., Bonsdorff, E., Slomp, C.P., Carstensen, J., Conley, D.J., 2012. A welcome can of worms? Hypoxia mitigation by an invasive species. Global Change Biology 18, 422-434.

Nyamweya, C., Sturludottir, E., Tomasson, T., Fulton, E.A., Taabu-Munyaho, A., Njiru, M., Stefansson, G., 2016. Exploring Lake Victoria ecosystem functioning using the Atlantis modeling framework. Environmental Modelling and Software 86, 158-167.

Oguz, T., Ducklow, H.W., Purcell, J.E., Malanotte-Rizzoli, P., 2001. Modeling the response of top-down control exerted by gelatinous carnivores on the Black Sea pelagic food web. Journal of Geophysical Research: Oceans 106, 4543-4564.

Oguz, T., Fach, B., Salihoglu, B., 2008a. Invasion dynamics of the alien ctenophore Mnemiopsis leidyi and its impact on anchovy collapse in the Black Sea. Journal of Plankton Research 30, 1385-1397.

Oguz, T., Salihoglu, B., Fach, B., 2008b. A coupled plankton–anchovy population dynamics model assessing nonlinear controls of anchovy and gelatinous biomass in the Black Sea. Marine Ecology Progress Series 369, 229-256.

Olden, J.D., Tamayo, M., 2014. Incentivizing the public to support invasive species management: Eurasian milfoil reduces lakefront property values. PLoS ONE 9.

Olden, J.D., Vander Zanden, M.J., Johnson, P.T.J., 2011. Assessing ecosystem vulnerability to invasive rusty crayfish (Orconectes rusticus). Ecological Applications 21, 2587-2599.

Onikura, N., Miyake, T., Nakajima, J., Fukuda, S., Kawamato, T., Kawamura, K., 2013. Predicting potential hybridization between native and non-native Rhodeus ocellatus subspecies: The implications for conservation of a pure native population in northern Kyushu, Japan. Aquatic Invasions 8, 219-229.

Ortiz, M., Stotz, W., 2007. Ecological and eco-social models for the introduction of the abalone Haliotis discus hannai into benthic systems of north-central Chile: Sustainability assessment. Aquatic Conservation: Marine and Freshwater Ecosystems 17, 89-105.

Pace, M.L., Findlay, S.E., Fischer, D., 1998. Effects of an invasive bivalve on the zooplankton community of the Hudson River. Freshwater Biology 39, 103-116.

Padilla, D.K., Adolph, S.C., Cottingham, K.L., Schneider, D.W., 1996. Predicting the consequences of dreissenid mussels on a pelagic food web. Ecological Modelling 85, 129-144.

Pagnucco, K.S., Ricciardi, A., 2015. Disentangling the influence of abiotic variables and a non-native predator on freshwater community structure. Ecosphere 6, 1-17.

Pigneur, L.M., Falisse, E., Roland, K., Everbecq, E., Deliège, J.F., Smitz, J.S., Van Doninck, K., Descy, J.P., 2014. Impact of invasive Asian clams, Corbicula spp., on a large river ecosystem. Freshwater Biology 59, 573-583.

Pine, W.E., Kwak, T.J., Rice, J.A., 2007. Modeling management scenarios and the effects of an introduced apex predator on a coastal riverine fish community. Transactions of the American Fisheries Society 136, 105-120.

Pinnegar, J.K., Tomczak, M.T., Link, J.S., 2014. How to determine the likely indirect food-web consequences of a newly introduced non-native species: A worked example. Ecological Modelling 272, 379-387.

Porath, M.T., Peters, E.J., Eichner, D.L., 2003. Impact of alewife introduction on walleye and white bass condition in Lake McConaughy, Nebraska, 1980-1995. North American Journal of Fisheries Management 23, 1050-1055.

Pothoven, S.A., Madenjian, C.P., 2008. Changes in consumption by alewives and lake whitefish after dreissenid mussel invasions in Lakes Michigan and Huron. North American Journal of Fisheries Management 28, 308-320.

Pranovi, F., Libralato, S., Raicevich, S., Granzotto, A., Pastres, R., Giovanardi, O., 2003. Mechanical clam dredging in Venice lagoon: Ecosystem effects evaluated with a trophic mass-balance model. Marine Biology 143, 393-403.

Qualls, T.M., Dolan, D.M., Reed, T., Zorn, M.E., Kennedy, J., 2007. Analysis of the impacts of the zebra mussel, Dreissena polymorpha, on nutrients, water clarity, and the chlorophyll-phosphorus relationship in lower Green Bay. Journal of Great Lakes Research 33, 617-626.

Raborn, S.W., Miranda, L.E., Driscoll, M.T., 2002. Effects of simulated removal of striped bass from a southeastern reservoir. North American Journal of Fisheries Management 22, 406-417.

Reed-Andersen, T., Carpenter, S.R., Padilla, D.K., Lathrop, R.C., 2000. Predicted impact of zebra mussel (Dreissena polymorpha) invasion on water clarity in Lake Mendota. Canadian Journal of Fisheries and Aquatic Sciences 57, 1617-1626.

Ricciardi, A., 2003. Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. Freshwater Biology 48, 972-981.

Ricciardi, A., Rasmussen, J., Whoriskey, F., 1995. Predicting the intensity and impact of Dreissena infestation on native unionid bivalves from Dreissena field density. Canadian Journal of Fisheries and Aquatic Sciences 52, 1449-1461.

Rogers, M.W., Bunnell, D.B., Madenjian, C.P., Warner, D.M., 2014. Lake Michigan offshore ecosystem structure and food web changes from 1987 to 2008. Canadian Journal of Fisheries and Aquatic Sciences 71, 1072-1086.

Rosa, R., Carvalho, A.R., Angelini, R., 2014. Integrating fishermen knowledge and scientific analysis to assess changes in fish diversity and food web structure. Ocean and Coastal Management 102, 258-268.

Rowe, D.K., 2007. Exotic fish introductions and the decline of water clarity in small North Island, New Zealand lakes: A multi-species problem. Hydrobiologia 583, 345-358.

Rowe, M.D., Anderson, E.J., Wang, J., Vanderploeg, H.A., 2015a. Modeling the effect of invasive quagga mussels on the spring phytoplankton bloom in Lake Michigan. Journal of Great Lakes Research 41, 49-65.

Rowe, M.D., Obenour, D.R., Nalepa, T.F., Vanderploeg, H.A., Yousef, F., Kerfoot, W.C., 2015b. Mapping the spatial distribution of the biomass and filter-feeding effect of invasive dreissenid mussels on the winter-spring phytoplankton bloom in Lake Michigan. Freshwater Biology 60, 2270-2285.

Roy, E.D., Martin, J.F., Irwin, E.G., Conroy, J.D., Culver, D.A., 2010. Transient social-ecological stability: The effects of invasive species and ecosystem restoration on nutrient management compromise in lake erie. Ecology and Society 15.

Roy, E.D., Martin, J.F., Irwin, E.G., Conroy, J.D., Culver, D.A., 2011. Living within dynamic social-ecological freshwater systems: System parameters and the role of ecological engineering. Ecological Engineering 37, 1661-1672.

Rutherford, E.S., Rose, K.A., Mills, E.L., Forney, J.L., Mayer, C.M., Rudstam, L.G., 1999. Individual-based model simulations of a zebra mussel (Dreissena polymorpha) induced energy shunt on walleye (Stizostedion vitreum) and yellow perch (Perca flavescens) populations in Oneida Lake, New York. Canadian Journal of Fisheries and Aquatic Sciences 56, 2148-2160.

Ruzycki, J.R., Beauchamp, D.A., Yule, D.L., 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications 13, 23-37.

Schindler, D.E., Carter, J.L., Francis, T.B., Lisi, P.J., Askey, P.J., Sebastian, D.C., 2012. Mysis in the Okanagan Lake food web: A time-series analysis of interaction strengths in an invaded plankton community. Aquatic Ecology 46, 215-227.

Schneider, D.W., 1992. A bioenergetics model of zebra mussel, Dreissena polymorpha, growth in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 49, 1406-1416.

Schoen, E.R., Beauchamp, D.A., Overman, N.C., 2012. Quantifying latent impacts of an introduced piscivore: Pulsed predatory inertia of lake trout and decline of kokanee. Transactions of the American Fisheries Society 141, 1191-1206.

Schwalb, A.N., Bouffard, D., Boegman, L., Leon, L., Winter, J.G., Molot, L.A., Smith, R.E.H., 2014. 3D modelling of dreissenid mussel impacts on phytoplankton in a large lake supports the nearshore shunt hypothesis and the importance of wind-driven hydrodynamics. Aquatic Sciences 77, 95-114.

Settle, C., Shogren, J.F., 2002. Modeling native-exotic species within Yellowstone Lake. American Journal of Agricultural Economics 84, 1323-1328.

Shan, K., Li, L., Wang, X., Wu, Y., Hu, L., Yu, G., Song, L., 2014. Modelling ecosystem structure and trophic interactions in a typical cyanobacterial bloom-dominated shallow Lake Dianchi, China. Ecological Modelling 291, 82-95.

Sharma, S., Vander Zanden, M.J., Magnuson, J.J., Lyons, J., 2011. Comparing climate change and species invasions as drivers of coldwater fish population extirpations. PLoS ONE 6.

Stapanian, M.A., Kocovsky, P.M., Adams, J.V., 2009. Change in diel catchability of young-of-year yellow perch associated with establishment of dreissenid mussels. Freshwater Biology 54, 1593-1604.

Stapp, P., Hayward, G.D., 2002. Effects of an introduced piscivore on native trout: Insights from a demographic model. Biological Invasions 4, 299-316.

Stewart, T.J., O'Gorman, R., Gary Sprules, W., Lantry, B.F., 2010. The bioenergetic consequences of invasive-induced food web disruption to lake Ontario alewives. North American Journal of Fisheries Management 30, 1485-1504.

Stewart, T.J., Sprules, W.G., 2011. Carbon-based balanced trophic structure and flows in the offshore Lake Ontario food web before (1987-1991) and after (2001-2005) invasion-induced ecosystem change. Ecological Modelling 222, 692-708.

Taraborelli, A.C., Fox, M.G., Johnson, T.B., Schaner, T., 2010. Round goby (Neogobius melanostomus) population structure, biomass, prey consumption and mortality from predation in the Bay of Quinte, Lake Ontario. Journal of Great Lakes Research 36, 625-632.

Tsagarakis, K., Coll, M., Giannoulaki, M., Somarakis, S., Papaconstantinou, C., Machias, A., 2010. Food-web traits of the North Aegean Sea ecosystem (Eastern Mediterranean) and comparison with other Mediterranean ecosystems. Estuarine, Coastal and Shelf Science 88, 233-248.

van der Lee, A.S., Johnson, T.B., Koops, M.A., 2017. Bioenergetics modelling of grass carp: Estimated individual consumption and population impacts in Great Lakes wetlands. Journal of Great Lakes Research.

Van Guilder, M.A., Seefelt, N.E., 2013. Double-crested Cormorant (Phalacrocorax auritus) chick bioenergetics following round goby (Neogobius melanostomus) invasion and implementation of cormorant population control. Journal of Great Lakes Research 39, 153-161.

Van Zuiden, T.M., Sharma, S., MacIsaac, H., 2016. Examining the effects of climate change and species invasions on Ontario walleye populations: can walleye beat the heat? Diversity and Distributions 22, 1069-1079.

Vigliano, P.H., Beauchamp, D.A., Milano, D., Denegri, M.A., Macchi, P.J., Alonso, M.F., Asorey, M.I.G., Ciancio, J.E., Lippolt, G., Rechencq, M., Barriga, J.P., 2009. Quantifying predation on galaxiids and other native organisms by introduced rainbow trout in an ultraoligotrophic lake in northern Patagonia, Argentina: A bioenergetics modeling approach. Transactions of the American Fisheries Society 138, 1405-1419.

Villanueva, M., Moreau, J., Cowx, I., 2002. Recent trends in the Lake Victoria fisheries assessed by ECOPATH. Fishing News books, Blackwell Science.

Villanueva, M.C.S., Isumbisho, M., Kaningini, B., Moreau, J., Micha, J.C., 2008. Modeling trophic interactions in Lake Kivu: What roles do exotics play? Ecological Modelling 212, 422-438.

Vinson, M.R., Baker, M.A., 2008. Poor growth of rainbow trout fed New Zealand mud snails Potamopyrgus antipodarum. North American Journal of Fisheries Management 28, 701-709.

Volovik, Y.S., Volovik, S.P., Myrzoyan, Z.A., 1995. Modelling of the Mnemiopsis sp. population in the Azov Sea. ICES Journal of Marine Science: Journal du Conseil 52, 735-746.

Walrath, J.D., Quist, M.C., Firehammer, J.A., 2015. Trophic Ecology of Nonnative Northern Pike and their Effect on Conservation of Native Westslope Cutthroat Trout. North American Journal of Fisheries Management 35, 158-177.

Walsh, J.R., Carpenter, S.R., Van Der Zanden, M.J., 2016. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. Proceedings of the National Academy of Sciences of the United States of America 113, 4081-4085.

Wenger, S.J., Isaak, D.J., Luce, C.H., Neville, H.M., Fausch, K.D., Dunham, J.B., Dauwalter, D.C., Young, M.K., Elsner, M.M., Rieman, B.E., Hamlet, A.F., Williams, J.E., 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proceedings of the National Academy of Sciences of the United States of America 108, 14175-14180.

Wong, M.C., Dowd, M., 2014. Role of Invasive Green Crabs in the Food Web of an Intertidal Sand Flat Determined from Field Observations and a Dynamic Simulation Model. Estuaries and Coasts 37, 1004-1016.

Woodford, D.J., Cochrane, T.A., McHugh, P.A., McIntosh, A.R., 2011. Modelling spatial exclusion of a vulnerable native fish by introduced trout in rivers using landscape features: A new tool for conservation management. Aquatic Conservation: Marine and Freshwater Ecosystems 21, 484-493.

Young, B.L., Padilla, D.K., Schneider, D.W., Hewett, S.W., 1996. The importance of size-frequency relationships for predicting ecological impact of zebra mussel populations. Hydrobiologia 332, 151-158.

Yurista, P.M., Schulz, K.L., 1995. Bioenergetic analysis of prey consumption by Bythotrephes cederstroemi in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 52, 141-150.

Zhang, H., Culver, D.A., Boegman, L., 2008. A two-dimensional ecological model of Lake Erie: application to estimate dreissenid impacts on large lake plankton populations. Ecological Modelling 214, 219-241.

Zhang, H., Culver, D.A., Boegman, L., 2011. Dreissenids in Lake Erie: An algal filter or a fertilizer? Aquatic Invasions 6, 175-194.

Zhang, H., Rutherford, E.S., Mason, D.M., Breck, J.T., Wittmann, M.E., Cooke, R.M., Lodge, D.M., Rothlisberger, J.D., Zhu, X., Johnson, T.B., 2016. Forecasting the Impacts of Silver and Bighead Carp on the Lake Erie Food Web. Transactions of the American Fisheries Society 145, 136-162.

Table S1. Information extracted from each selected article (ordered by year).

Paper ID (surname and year)	Type of environment (terrestrial/freshwater/ marine/transitional)	Year of publication	Marine Biogeographic region	Terrestrial Biogeographic region	Location (country)	Specific location (if relevant)	Ecosystem type	Number of alien species included in the model	Alien species (type of organism)	Alien Species (habitat)	Alien species (trophic level)
van der Lee et al., 2017	Freshwater	2017		Nearctic	Canada	Lake Erie and Lake Ontario (Great Lakes)	Lake	1	Fish	Demersal	Low TL
Foley et al., 2017	Freshwater	2017		Nearctic	US	Saginaw Bay (Lake huron, Great Lakes)	Lake	1	Fish	Demersal	Medium TL
Corrales et al., 2017	Marine	2017	Temperate Northern Atlantic		Israel	Mediterranean Sea	Sea	41	Fish and Crustaceans	Both	Multiple TL
Zhang et al., 2016	Freshwater	2016		Nearctic	Canada and US	Lake Erie	Lake	2	Fish	Pelagic	Low TL
Walsh et al., 2016	Freshwater	2016		Nearctic	US	Lake Mendota	Lake	1	Zooplankton	Pelagic	Low TL
Van Zuiden et al., 2016	Freshwater	2016		Nearctic	Canada	722 lakes in Ontario	Lake	1	Fish	Pelagic	High TL
Nyamweya et al., 2016	Freshwater	2016		Afrotropical	Uganda, Kenya and Tanzania	Lake Victoria	Lake	2	Fish	Demersal	Multiple TL
Natugonza et al., 2016	Freshwater	2016		Afrotropical	Uganda, Kenya and Tanzania	Winam Gulf (Lake Victoria)	Lake	2	Fish	Demersal	Multiple TL
Liao et al., 2016	Freshwater	2016		Nearctic	US	Lake Coeur d’Alene	Lake	1	Plant	Demersal	Low TL
Kumar et al., 2016	Freshwater	2016		Nearctic	US	Mille Lacs Lake	Lake	2	Fish and bivalvia	Demersal	Low TL

Katsanevakis et al., 2016	Marine	2016	Temperate Northern Atlantic		Mediterranean Sea	Mediterranean Sea	Sea	60	Phytoplankton, Macroalgae, Cnidaria, Bryozoa, Polychaeta, Mollusca, Ascidacea and Fish	Both	Multiple TL
Kao et al., 2016	Freshwater	2016		Nearctic	US	Lake Huron	Lake	6	Bivalvia and Fish	Both	Multiple TL
Jellyman and Harding, 2016	Freshwater	2016		Australasian	New Zeland	South Island	Streams and rivers	1	Freshwater diatom	Pelagic	Low TL
Isaev et al., 2016	Marine	2016	Temperate Northern Atlantic		Findland-Russia-Estonia	Gulf of Findland	Sea	1	Polychaete	Demersal	Low TL
Bajer et al., 2016	Freshwater	2016		Nearctic	US	Minnesota	Lakes	1	Fish	Demersal	Low TL
Walrath et al., 2015	Freshwater	2015		Nearctic	US	Lake Coeur d'Alene	Lake	1	Fish	Demersal	High TL
Rowe et al., 2015	Freshwater	2015		Nearctic	US	Lake Michigan	Lakes	2	Bivalvia	Demersal	Low TL
Rowe et al., 2015	Freshwater	2015		Nearctic	US	Lake Michigan	Lakes	1	Bivalvia	Demersal	Low TL
Pagnucco and Ricciardi, 2015	Freshwater	2015		Nearctic	Canada	St. Lawrence River	River	1	Fish	Demersal	Multiple TL
Marrack et al., 2015	Estuarine	2015	Eastern Indo-Pacific		US	Island of Hawai	Anchialine habitats	2	Fish and prawn	Both	Multiple TL
Libralato et al., 2015	Marine	2015	Temperate Northern Atlantic		Italy and Croatia	Gulf of Venice	Sea	26	Fish, mollusca (bivalvia and gastropoda), crustacea (shrimps and crabs), jellyfish, zooplankton (micro and macro), polychaeta	Both	Multiple TL
Li et al., 2015	Marine	2015	Temperate Northern Pacific		Canada	Strait of Georgia (British Columbia)	Sea	1	Fish	Demersal	High TL
Jiang et al., 2015	Freshwater	2015		Nearctic	Canada and US	Lake Erie	Lake	2	Bivalvia	Demersal	Low TL
Gudimov et al., 2015	Freshwater	2015		Nearctic	Canada	Lake Simcoe	Lake	2	Bivalvia	Demersal	Low TL

Gobin et al., 2015	Freshwater	2015		Nearctic	Canada	Lake Huron	Lake	2	Bivalvia	Demersal	Low TL
Dembkowski et al., 2015	Freshwater	2015		Nearctic	US	Clear Lake and Pickerel lake (south Dakota)	Lakes	1	Fish	Demersal	High TL
De Amorim et al., 2015	Freshwater	2015		Neotropical	Brazil	Itanhaém River (Sao Paulo state)	River	1	Plant	Demersal	Low TL
Crane et al., 2015	Freshwater	2015		Nearctic	US	Lake Erie and Lake Ontario (Great Lakes)	Lake	1	Fish	Demersal	Medium TL
Crane and Einhouse, 2015	Freshwater	2015		Nearctic	US	Lake Erie	Lake	1	Fish	Demersal	Medium TL
Colvin et al., 2015	Freshwater	2015		Nearctic	US	Clear Lake (Iowa)	Lake	2	Bivalvia and Fish	Demersal	Low TL
Bourdeau et al., 2015	Freshwater	2015		Nearctic	US	Lake Michigan	Lake	1	Zooplankton	Pelagic	Low TL
Anderson et al., 2015	Freshwater	2015		Nearctic	US	Lake Erie and Lake St. Clair	Lake	2	Fish	Pelagic	Low TL
Wong and Dowd, 2014	Marine	2014	Temperate Northern Atlantic		Canada	Little Port Joli Lagoon (Nova Scotia, Canada)	Lagoon	1	Crab	Demersal	Medium TL
Shan et al., 2014	Freshwater	2014		Indomalaya	China	Lake Dianchi (China)	Lake	4	Fish	Both	Multiple TL
Schwalb et al., 2014	Freshwater	2014		Nearctic	Canada	Lake Simcoe	Lake	2	Bivalvia	Demersal	Low TL
Rosa et al., 2014	Freshwater	2014		Neotropical	Brazil	Extremoz Lagoon (Brazil)	Lagoon	1	Fish	Demersal	High TL
Rogers et al., 2014	Freshwater	2014		Nearctic	US	Lake Michigan	Lake	6	Bivalvia, zooplankton, fish	Both	Multiple TL
Pinnegar et al., 2014	Marine	2014	Temperate Northern Atlantic		France	Bay of Carvi (Corsica)	Sea	1	Fish	Pelagic	High TL

Pigneur et al., 2014	Freshwater	2014		Palearctic	France, Belgium and the Netherlands	River Meuse	River	1	Bivalvia	Demersal	Low TL
Olden and Tamayo, 2014	Freshwater	2014		Nearctic	US	King County (Washington state)	Lake	1	Plant	Demersal	Low TL
Liu et al., 2014	Freshwater	2014		Nearctic	Norway	Norway	River	1	Fish	Demersal	High TL
Kratina et al., 2014	Estuarine	2014	Temperate Northern Pacific		US	San Francisco Estuary	Estuary	7	Bivalve and zooplankton	Both	Low TL
Kao et al., 2014	Freshwater	2014		Nearctic	US	Saginaw Bay	Lake	7	Fish, Bivalvia and zooplankton	Both	Multiple TL
Higgins et al., 2014	Freshwater	2014		Nearctic and Paleartic	North America and Europe	North America and Europe	Lake	2	Bivalvia	Demersal	Low TL
He et al., 2014	Freshwater	2014		Nearctic	US and Canada	Lake Huron	Lake	1	Fish	Demersal	High TL
Green et al., 2014	Marine	2014	Tropical Atlantic		Bahamas	Eleuthera island (Bahamas)	Sea	2	Fish	Demersal	High TL
Francis et al., 2014	Freshwater	2014		Nearctic	US	Lake Washington (USA)	Lake	1	Zooplankton	Pelagic	Low TL
Cook et al., 2014	Estuarine	2014	Tropical Atlantic		US	Florida	Sea and Estuarine	not specified			
Bocaniov et al., 2014	Freshwater	2014		Nearctic	US	Lake Erie	Lake	2	Bivalvia	Demersal	Low TL
Blamey et al., 2014	Marine	2014	Temperate Southern Africa		South Africa	East of Cape Hangklip (South Africa)	Sea	1	Lobster	Demersal	Medium TL
Akoglu et al., 2014	Marine	2014	Temperate Northern Atlantic		Turkey	Black Sea	Sea	1	Ctenophora	Pelagic	Medium TL
Van Guilder and Seefelt, 2013	Freshwater	2013		Nearctic	US	Beaver Archipelago of Northern Lake Michigan	Lake	1	Fish	Demersal	Medium TL

Onikura et al., 2013	Freshwater	2013		Palearctic	Japan	Kyushu Island (Japan)	Lake	1	Fish	Demersal	Medium TL
Magnea et al., 2013	Freshwater	2013		Palearctic	Italy	Gran Paradiso National Park (Alps)	Lakes	1	Fish	Pelagic	Medium TL
Kinter and Ludsin, 2013	Freshwater	2013		Nearctic	US	3 Ohio lakes	Lake	1	Fish	Demersal	High TL
Hossain et al., 2013	Freshwater	2013		Palearctic	Japan	lake Kawahara-oike, Nagasaki	Lake	2	Fish	Pelagic	Multiple TL
Hattab et al., 2013	Marine	2013	Temperate Northern Atlantic		Tunisia	Gulf of Gabes	Gulf	2	Crustaceans	Pelagic	Low TL
Clavero et al., 2013	Freshwater	2013		Palearctic	Spain and Portugal	Iberian peninsula	Reservoirs	26	Fish	Both	Multiple TL
Cha et al., 2013	Freshwater	2013		Nearctic	US	25 Lakes	Lakes	2	Bivalvia	Demersal	Low TL
Cerino et al., 2013	Marine	2013	Tropical Atlantic		Bahamas	Bahamas	Sea	2	Fish	Demersal	High TL
Blamey et al., 2013	Marine	2013	Temperate Southern Africa		South Africa	East of Cape Hangklip (South Africa)	Sea	1	Lobster	Demersal	Medium TL
Amundsen et al., 2013	Freshwater	2013		Palearctic	Norway	Takvatn lake	Lake	7	Fish, parasites and birds	Pelagic	Multiple TL
Schoen et al., 2012	Freshwater	2012		Nearctic	US	Lake Chelan	Lake	2	Fish	Pelagic	Multiple TL
Schindler et al., 2012	Freshwater	2012		Nearctic	Canada	Okanagan Lake	Lake	1	Shrimp	Pelagic	Medium TL
Norkko et al., 2012	Marine	2012	Temperate Northern Atlantic		Findland, Estonia, Rusia	Stockholm archipelago	Sea	3	Polychatete	Demersal	Low TL
Nilsson et al., 2012	Freshwater	2012		Nearctic	US	Northern Highlands Lake District (Wisconsin)	Lake	1	Crab	Demersal	Medium TL
MacDonald et al., 2012	Freshwater	2012		Australasian	Australia	Ovens River (Australia)	River	1	Fish	Pelagic	Medium TL

Langseth et al., 2012	Freshwater	2012		Nearctic	US	Lake Huron and Lake Michigan	Lake	4	Fish, zooplankton and bivalvia	Both	Multiple TL
Hossain et al., 2012	Freshwater	2012		Nearctic	Canada	Hamilton Harbour (Lake Ontario)	Lake	3	Fish and bivalvia	Demersal	Multiple TL
Hermoso et al., 2012	Freshwater	2012		Palearctic	Spain-Portugal	Guadiana River	River	not specified	Fish		
Ferguson et al., 2012	Freshwater	2012		Nearctic	US	Flathead River	Lakes	1	Fish	Pelagic	High TL
Green et al., 2012	Marine	2012	Tropical Atlantic		Bahamas	New Providence	Sea	2	Fish	Demersal	High TL
Downing et al., 2012	Freshwater	2012		Afrotropical	Tanzania	Mwanza (Lake Victoria)	Lake	2	Fish	Both	Multiple TL
Descy et al., 2012	Freshwater	2012		Palearctic	France	River Loire (France)	River	1	Bivalvia	Demersal	Low TL
Correa and Henry, 2012	Freshwater	2012		Neotropical	Chile	Ayse´n region (Patagonia)	Lake	2	Fish	Pelagic	High TL
Blukacz-Richards and Koops, 2012	Freshwater	2012		Nearctic	Canada	Bay of Quinte	Lake	1	Bivalvia	Demersal	Low TL
Beville et al., 2012	Freshwater	2012		Australasian	New Zealand	North Canterbury (New Zealand)	Lake, river and streams	1	Alga	Pelagic	Low TL
Baird et al., 2012	Marine	2012	Temperate Northern Atlantic		German-Denmark	Sylt-Rømø Bight ecosystem (isle of Sylt) (German-Denmark)	semi-enclosed basin	2	Bivalvia	Demersal	Low TL
Zhang et al., 2011	Freshwater	2011		Nearctic	US and Canada	Lake Erie	Lake	2	Bivalvia	Demersal	Low TL
Woodford et al., 2011	Freshwater	2011		Australasian	New Zealand	Waimakariri and Waitaki Rivers (New Zealand)	River	2	Fish	Pelagic	High TL

Wenger et al., 2011	Freshwater	2011		Nearctic	US	Western United States	Streams	3	Fish	Pelagic	High TL
Stewart and Sprules, 2011	Freshwater	2011		Nearctic	US	Lake Ontario	Lake	4	Bivalvia and cladoceran	Both	Low TL
Sharma et al., 2011	Freshwater	2011		Nearctic	US	Wisconsin (US)	Lakes	1	Fish	Pelagic	Medium TL
Roy et al., 2011	Freshwater	2011		Nearctic	US and Canada	Sandusky Bay (Lake Erie)	Lake	2	Bivalvia	Demersal	Low TL
Olden et al., 2011	Freshwater	2011		Nearctic	US	Wisconsin (US)	Lakes and rivers	1	Crab	Demersal	Medium TL
Lercari and Bergamino, 2011	Estuarine	2011	Temperate South America		Uruguay and Argentina	Río de la Plata estuary	Estuary	2	Gastropoda and Bivalvia	Demersal	Multiple TL
Higgins et al., 2011	Freshwater	2011		Nearctic	US and Canada	North America	Lakes	2	Bivalvia	Demersal	Low TL
Hermoso et al., 2011	Freshwater	2011		Palearctic	Spain-Portugal	Guadiana River	River	10	Fish	Both	Multiple TL
Haught and von Hippel, 2011	Freshwater	2011		Nearctic	US	Cook Inlet Basin (alaska)	Lakes	1	Fish	Demersal	High TL
Grosholz et al., 2011	Marine	2011	Temperate Northern Pacific		US	West coast of the United States	Estuary	1	Crab	Demersal	Medium TL
Fetahi et al., 2011	Freshwater	2011		Afrotropical	Ethiopia	lake Hayq	Lake	3	Fish	Pelagic	Low TL
Cha et al., 2011	Freshwater	2011		Nearctic	US	Saginaw Bay	Lake	2	Bivalvia	Demersal	Low TL
Boulêtreau et al., 2011	Freshwater	2011		Palearctic	France	Rhone River (France)	River	1	Fish	Demersal	High TL
Benjamin et al., 2011	Freshwater	2011		Palearctic	US	Rocky Mountains	Streams	1	Fish	Pelagic	Medium TL
Arias-Gonzalez et al., 2011	Marine	2011	Tropical Atlantic		Mexico	Alacranes Reef (Mexico)	Reef	1	Fish	Demersal	High TL
Tsagarakis et al., 2010	Marine	2010	Temperate Northern Atlantic		Greece	North Aegean Sea (Strymonikos Gulf and Thracian Sea)	Sea and Gulf	1	Ctenophora	Pelagic	Medium TL

Annex 1

Taraborelli et al., 2010	Freshwater	2010		Nearctic	US	Bay of Quinte	Lake	1	Fish	Demersal	Medium TL
Stewart et al., 2010	Freshwater	2010		Nearctic	US	Lake Ontario	Lake	1	Bivalvia and cladoceran	Both	Low TL
Roy et al., 2010	Freshwater	2010		Nearctic	US	Sandusky Bay (Lake Erie)	Lake	2	Bivalvia	Demersal	Low TL
Miller et al., 2010	Freshwater	2010		Nearctic	US	Lake Michigan	Lake	1	Zooplankton	Pelagic	Low TL
Cooke and Hill, 2010	Freshwater	2010		Nearctic	US and Canada	Laurentian Great Lakes	Lake	2	Fish	Pelagic	Low TL
Ciancio et al., 2010	Marine	2010	Temperate South America		Argentina	Patagonian Continental Shelf (Argentina)	Sea	2	Fish	Pelagic	High TL
Auer et al., 2010	Freshwater	2010		Nearctic	US and Canada	Laurentian Great Lakes	Lake	2	Bivalvia	Demersal	Low TL
Vigliano et al., 2009	Freshwater	2009		Neotropical	Argentina	Lake Moreno (Patagonia)	Lake	1	Fish	Pelagic	High TL
Stapanian et al., 2009	Freshwater	2009		Nearctic	US	East Harbor State Park (Lake Erie)	Lake	2	Bivalvia	Demersal	Low TL
Myers et al., 2009	Freshwater	2009		Nearctic	Canada	Thunder and Black bays (lake superior)	Lake	1	Fish	Pelagic	Medium TL
Miehls et al., 2009	Freshwater	2009		Nearctic	US	Oneida Lake	Lake	2	Bivalvia	Demersal	Low TL
Miehls et al., 2009	Freshwater	2009		Nearctic	Canada	Bay of Quinte	Lake	2	Bivalvia	Demersal	Low TL
Laruelle et al., 2009	Marine	2009	Temperate Northern Atlantic		France	Bay of Brest	Bay	1	Bivalvia	Demersal	Low TL
Kateregga and Sterner, 2009	Freshwater	2009		Afrotropical	Uganda, Kenya and Tanzania	Lake Victoria	Lake	1	Plant	Demersal	Low TL
Horsch and Lewis, 2009	Freshwater	2009		Nearctic	US	Wisconsin (US)	Lake	1	Plant	Demersal	Low TL
Glaser et al., 2009	Freshwater	2009		Nearctic	US	Seneca River (US)	River	1	Bivalvia	Demersal	Low TL
Fishman et al., 2009	Freshwater	2009		Nearctic	US	Saginaw Bay	Lake	1	Bivalvia	Demersal	Low TL

Feroz Khan and Pinnikar, 2009	Freshwater	2009		Indomalayan	India	Kelavarapalli reservoir (India)	Reservoir	3	Fish	Both	Multiple TL
Aravena et al., 2009	Estuarine	2009	Temperate Northern Atlantic		Spain	Bilbao estuary	Estuary	1	copepoda	Pelagic	Low TL
Zhang et al., 2008	Freshwater	2008		Nearctic	US and Canada	Lake Erie	Lake	2	Bivalvia	Demersal	Low TL
Vinson and Baker, 2008	Freshwater	2008		Nearctic	US	Green River, Utah, downstream from Flaming Gorge Dam	River	1	Snail, Gastropoda	Demersal	Low TL
Villanueva et al., 2008	Freshwater	2008		Afrotropical	Congo and Ruanda	Lake Kivu	Lake	3	Fish	Both	Multiple TL
Pothoven and Madenjian, 2008	Freshwater	2008		Nearctic		Lakes Michigan and Huron	Lake	2	Bivalvia	Demersal	Low TL
Oguz et al., 2008	Marine	2008	Temperate Northern Atlantic		Turkey, Bulgaria, Romania, Ukraine, Russia and Georgia	Black Sea	Sea	1	Ctenophore	Pelagic	Medium TL
Oguz et al., 2008	Marine	2008	Temperate Northern Atlantic		Turkey, Bulgaria, Romania, Ukraine, Russia and Georgia	Black Sea	Sea	1	Ctenophore	Pelagic	Medium TL
Negus et al., 2008	Freshwater	2008		Nearctic	US	Lake Superior	Sea	2	Fish	Both	High TL
Boegman et al., 2008	Freshwater	2008		Nearctic	US and Canada	Lake Erie	Lake	2	Bivalvia	Demersal	Low TL
Boegman et al., 2008	Freshwater	2008		Nearctic	US and Canada	Lake Erie	Lake	2	Bivalvia	Demersal	Low TL
Blanchet et al., 2008	Freshwater	2008		Nearctic	Canada	Malbaie river	River	1	Fish	Pelagic	High TL
Arbach Leloup et al., 2008	Marine	2008	Temperate Northern Atlantic		France	Bay of Mont Saint Michel	Bay	1	Gastropoda	Demersal	Low TL

Rowe, 2007	Freshwater	2007		Australasian	New Zealand	New Zealand (north)	Lake	6	Fish	Both	Multiple TL
Qualls et al., 2007	Freshwater	2007		Nearctic	US	Lower Green Bay (Lake Michigan)	Lake	1	Bivalvia	Demersal	Low TL
Pine et al., 2007	Freshwater	2007		Nearctic	US	Neuse River (Contentnea Creek)	River	1	Fish	Demersal	High TL
Ortiz and Stotz, 2007	Marine	2007	Temperate South America		Chile	North-central coast of Chile	Sea	1	Gastropoda	Demersal	Low TL
Morales et al., 2007	Freshwater	2007		Nearctic	US	Upper Mississippi River	River	1	Bivalvia	Demersal	Low TL
Light and Marchetti, 2007	Freshwater	2007		Nearctic	US	California’s major watersheds	watersheds	not specified	Fishes		
Jaarsma et al., 2007	Freshwater	2007		Palearctic	Netherlands	Rhine and Meuse rivers	River	2	Amphipoda	Demersal	Low TL
Caldow et al., 2007	Marine	2007	Temperate Northern Atlantic		UK	Poole Harbour	Sea	1	Bivalvia	Demersal	Low TL
Morales et al., 2006	Freshwater	2006		Nearctic	US	Upper Mississippi River	River	1	Bivalvia	Demersal	Low TL
Matsuishi et al., 2006	Freshwater	2006		Afrotropical	Uganda, Kenya and Tanzania	Lake Victoria	Lake	1	Fish	Demersal	High TL
Gribben and Wright, 2006	Estuarine	2006	Temperate Australasia		Australia	Lake Conjola	Estuary	1	Alga	Demersal	Low TL
Frésard and Boncoeur, 2006	Marine	2006	Temperate Northern Atlantic		France	Bay of Brest	Bay	1	Gastropoda	Demersal	Low TL
Frésard and Boncoeur, 2006	Marine	2006	Temperate Northern Atlantic		France	Bay of St-Brieuc	Bay	1	Gastropoda	Demersal	Low TL

Morozov et al., 2005	Marine	2005	Temperate Northern Atlantic		Turkey, Bulgaria, Romania, Ukraine, Russia and Georgia	Black Sea	Sea	1	Ctenophore	Pelagic	Medium TL
Madenjian et al., 2005	Freshwater	2005		Nearctic	US	Lake Michigan	Lake	1	Fish	Pelagic	Medium TL
Lee and Johnson, 2005	Freshwater	2005		Nearctic	US	Lake Erie and Lake St. Clair	Lake	1	Fish	Demersal	Medium TL
Knowler and Barbier, 2005	Marine	2005	Temperate Northern Atlantic		Turkey, Bulgaria, Romania, Ukraine, Russia and Georgia	Black Sea	Sea	1	Ctenophore	Pelagic	Medium TL
Knowler, 2005	Marine	2005	Temperate Northern Atlantic		Turkey, Bulgaria, Romania, Ukraine, Russia and Georgia	Black Sea	Sea	1	Ctenophore	Pelagic	Medium TL
Knapp, 2005	Freshwater	2005		Nearctic	US	Yosemite National Park (California)	lentic water bodies	2	Fish	Pelagic	High TL
Johnson et al., 2005	Freshwater	2005		Nearctic	US and Canada	Lake Erie	lake	1	Fish	Demersal	Medium TL
Harvey and Kareiva, 2005	Freshwater	2005		Nearctic	US	John Day Reservoir	Reservoir	4	Fish	Both	Multiple TL
Bunnell et al., 2005	Freshwater	2005		Nearctic	US and Canada	Lake Erie	lake	1	Fish	Demersal	Medium TL
Bierman et al., 2005	Freshwater	2005		Nearctic	US	Saginaw Bay	lake	1	Bivalvia	Demersal	Low TL
Le Pape et al., 2004	Marine	2004	Temperate Northern Atlantic		France	Bay of Biscay	Sea	1	Bivalvia	Demersal	Low TL
Cox and Kitchell, 2004	Freshwater	2004		Nearctic	US and Canada	Lake Superior	Lake	2	Fish	Both	Multiple TL
Ruzycki et al., 2003	Freshwater	2003		Nearctic	US	Yellowstone Lake	Lake	1	Fish	Pelagic	High TL

Ricciardi, 2003	Freshwater	2003		Nearctic	US and Canada	North America	Lakes and rivers	1	Bivalvia	Demersal	Low TL
Pranovi et al., 2003	Marine	2003	Temperate Northern Atlantic		Italy	Venice lagoon	Lagoon	1	Bivalvia	Demersal	Low TL
Porath et al., 2003	Freshwater	2003		Nearctic	US	Lake McConaughy	Lake	1	Fish	Pelagic	Medium TL
Laxson et al., 2003	Freshwater	2003		Nearctic	US	Lake Ontario	lake	1	Crustacea-zooplankton	Pelagic	Low TL
Halstead et al., 2003	Freshwater	2003		Nearctic	US	New Hampshire	lake	1	Plant	Demersal	Low TL
Descy et al., 2003	Freshwater	2003		Palearctic	France, Luxemburg and Germany	Moselle river	River	1	Bivalvia	Demersal	Low TL
Beisner et al., 2003	Freshwater	2003		Nearctic	US	Crystal and Sparkling Lakes	Lake	1	Fish	Pelagic	Medium TL
Villanueva and Moreau, 2002	Freshwater	2002		Afrotropical	Uganda, Kenya and Tanzania	Lake Victoria	Lake	2	Fish	Demersal	Multiple TL
Stapp and Hayward, 2002	Freshwater	2002		Nearctic	US	Yellowstone Lake	Lake	1	Fish	Pelagic	High TL
Settle and Shogren, 2002	Freshwater	2002		Nearctic	US	Yellowstone Lake	Lake	1	Fish	Pelagic	High TL
Raborn et al. 2002	Freshwater	2002		Nearctic	US	Norris Reservoir (Tennessee)	Reservoir	1	Fish	Demersal	High TL
Lancelot et al., 2002	Marine	2002	Temperate Northern Atlantic		Turkey, Bulgaria, Romania, Ukraine, Russia and Georgia	Black Sea	Sea	1	Ctenophore	Pelagic	Medium TL
Gucu, 2002	Marine	2002	Temperate Northern Atlantic		Turkey, Bulgaria, Romania, Ukraine, Russia and Georgia	Black Sea	Sea	1	Ctenophore	Pelagic	Medium TL

Daskalov, 2002	Marine	2002	Temperate Northern Atlantic		Turkey, Bulgaria, Romania, Ukraine, Russia and Georgia	Black Sea	Sea	1	Ctenophore	Pelagic	Medium TL
Oguz et al., 2001	Marine	2001	Temperate Northern Atlantic		Turkey, Bulgaria, Romania, Ukraine, Russia and Georgia	Black Sea	Sea	1	Ctenophore	Pelagic	Medium TL
Hoffman et al., 2001	Freshwater	2001		Nearctic	US	Long Lake Grand Traverse County	Lake	1	Zooplankton	Pelagic	Low TL
Byers and Goldwasser, 2001	Marine	2001	Temperate Northern Pacific		US	Bolinas Lagoon	Sea	1	Gastropoda	Demersal	Low TL
Reed-Andersen et al., 2000	Freshwater	2000		Nearctic	US	Lake Mendota	Lake	1	Bivalvia	Demersal	Low TL
Kitchell et al., 2000	Freshwater	2000		Nearctic	US	Lake Superior	Lake	5	Fish	Both	Multiple TL
Rutherford et al., 1999	Freshwater	1999		Nearctic	US	Oneida Lake	Lake	1	Bivalvia	Demersal	Low TL
Murray and Parslow, 1999	Marine	1999	Temperate Australasia		Australia	Port Phillip Bay	Lake	1	Annelid	Demersal	Low TL
MacIsaac et al., 1999	Freshwater	1999		Nearctic	US	Lake Erie	lake	1	Bivalvia	Demersal	Low TL
Berdnikov et al., 1999	Marine	1999	Temperate Northern Atlantic		Turkey, Bulgaria, Romania, Ukraine, Russia and Georgia	Black Sea	Sea	1	Ctenophore	Pelagic	Medium TL
Pace et al., 1998	Freshwater	1998		Nearctic	US	Hudson river estuary	River	1	Bivalvia	Demersal	Low TL
Kitchell et al., 1997	Freshwater	1997		Afrotropical	Uganda, Kenya and Tanzania	Lake Victoria	Lake	1	Fish	Demersal	High TL

Caraco et al., 1997	Freshwater	1997		Nearctic	US	Hudson river estuary	River	1	Bivalvia	Demersal	Low TL
Young et al., 1996	Freshwater	1996		Nearctic	US	Lake Erie	Lake	1	Bivalvia	Demersal	Low TL
Padilla et al., 1996	Freshwater	1996		Nearctic	US	Lake Michigan	Lake	1	Bivalvia	Demersal	Low TL
Mavuti et al., 1996	Freshwater	1996		Afrotropical	Kenya and Rwanda	Lake Naivasha	lake	4	Fish	Both	Multiple TL
Yurista and Schulz, 1995	Freshwater	1995		Nearctic	US	Lake Michigan	Lake	1	Zooplankton	Demersal	Low TL
Volovik et al., 1995	Marine	1995	Temperate Northern Atlantic		Ucraine and Russia	Azov Sea	Sea	1	Ctenophore	Pelagic	Medium TL
Ricciardi et al., 1995	Freshwater	1995		Nearctic	US and Canada	St. Lawrence River	River	2	Bivalvia	Demersal	Low TL
Negus, 1995	Freshwater	1995		Nearctic	US	Lake Superior	Lake	3	Fish	Pelagic	High TL
Madenjian, 1995	Freshwater	1995		Nearctic	US	Lake Erie	Lake	1	Bivalvia	Demersal	Low TL
Moreau et al., 1993	Freshwater	1993		Afrotropical	Kenya	Lake Victoria	Lake	2	Fish	Demersal	Multiple TL
Schneider, 1992	Freshwater	1992		Nearctic	US and Canada	Lakes Erie, Michigan, Huron, Ontario, and Superior	Lake	1	Bivalvia	Demersal	Low TL
Fontaine and Stewart, 1992	Freshwater	1992		Nearctic	US	Lake Michigan	Lake	1	Zooplankton and fish	Both	Multiple TL

Paper ID (surname and year)	Model Category	Was the model based on data or theoretical?	Data type: Temporal (static-comparison between periods-dynamic)	Data type: Spatial (non-spatial-comparison between sites-fully spatial)	Were other external drivers taken into account (e.g., climate changes, pollution, fisheries …)? (yes/no)	Describe which external drivers of change were taken into account	Was the model validated? (yes/no)
van der Lee et al., 2017	Bioenergetic and simple population model	Based on data	dynamic	comparison between sites	yes	Temperature conditions	yes
Foley et al., 2017	Bioenergetic model	Based on data	dynamic	non-spatial	no		no
Corrales et al., 2017	EwE	Based on data	comparison between periods	non-spatial	yes	Fishing	yes
Zhang et al., 2016	EwE	Theoretical	dynamic	non-spatial	yes	Nutrient loading and fisheries	yes
Walsh et al., 2016	MARSS model	Based on data	dynamic	non-spatial	yes	P loading and temperature	yes
Van Zuiden et al., 2016	Multiple regression models	Based on data	dynamic	non-spatial	yes	Climate change	yes
Nyamweya et al., 2016	Atlantis	Based on data	dynamic	fully spatial	yes	Fisheries, nutrient loading and temperature	yes
Natugonza et al., 2016	EwE	Based on data	comparison between periods	non-spatial	yes	Fisheries	yes
Liao et al., 2016	Hedonic pricing model	Based on data	static	non-spatial	no		yes
Kumar et al., 2016	EwE	Based on data	dynamic	non-spatial	yes	Fisheries	yes
Katsanevakis et al., 2016	CIMPAL	Based on data	static	fully spatial	no		no
Kao et al., 2016	EwE	Based on data	dynamic	non-spatial	yes	Fishing and nutrient loading	yes
Jellyman and Harding, 2016	Partial Least Square path model	Based on data	static	non-spatial	no		no
Isaev et al., 2016	Three-dimensional SPBEM model	Based on data	dynamic	fully spatial	yes	Nutrient load and climate change	no
Bajer et al., 2016	Linear model (simple and multivariate)	Based on data	static	comparison between sites	no		no
Walrath et al., 2015	Bioenergetic model	Based on data	dynamic	non-spatial	no		no
Rowe et al., 2015	Geostatistical model to predict dreissenids biomass (spatial)	Based on data	dynamic	fully spatial	no		yes
Rowe et al., 2015	Biophysical model	Based on data	dynamic	fully spatial	no		yes
Pagnucco and Ricciardi, 2015	Multiple regression models and structural equation modeling	Based on data	static	comparison between sites	no		no

Marrack et al., 2015	Generalized additive model (GAM)	Based on data	static	non-spatial	no		no
Libralato et al., 2015	EwE	Theoretical	dynamic	non-spatial	yes	Fishing and climate change (temperature rise and changes in primary production)	no
Li et al., 2015	EwE	Theoretical	dynamic	non-spatial	yes	Fishing and climate change (temperature rise and changes in primary production)	no
Jiang et al., 2015	Biogeochemical model	Based on data	dynamic	fully spatial	yes	Nutrient loading	yes
Gudimov et al., 2015	Total phosphorous mass model	Based on data	dynamic	fully spatial	yes	Nutrient loading	yes
Gobin et al., 2015	Growth model and recruitment model	Based on data	dynamic	non-spatial	yes	Temperature	no
Dembkowski et al., 2015	Bioenergetic model	Based on data	comparison between periods	comparison between sites	no		no
De Amorim et al., 2015	Generalized linear model (GLM)	Based on data	static	comparison between sites	no		no
Crane et al., 2015	Quantile regression models	Based on data	comparison between periods	non-spatial	yes	Temperature	no
Crane and Einhouse, 2015	Von Bertalanffy growth model	Based on data	comparison between periods	non-spatial	no		no
Colvin et al., 2015	EwE	Based on data	comparison between periods	non-spatial	yes	Fisheries	no
Bourdeau et al., 2015	Multiple linear regression models and ordinary least squares regression	Based on data	comparison between periods	non-spatial	yes	Environment (temp, light, chl-A) and limnological parameters (epilimnion depth, epilimnion temperature, hypolimnion depth, hypolimnion temperature, Chl a concentration and the depth of its maximum, Secchi depth and attenuation coefficient	no
Anderson et al., 2015	Bioenergetic model	Based on data	dynamic	non-spatial	yes	Temperature	no
Wong and Dowd, 2014	EwE	Based on data	dynamic	non-spatial	yes	Fisheries	no
Shan et al., 2014	EwE	Based on data	static	non-spatial	yes	Fisheries	no
Schwalb et al., 2014	ELCOM-CAEDYM model with a mussel sub-model to include mussel energetics and dynamics	Based on data	dynamic	fully spatial	yes	Nutrients (dissolved 02, P, N, N, silica) and temperature	yes
Rosa et al., 2014	EwE	Based on data	dynamic	non-spatial	yes	Fisheries	no

Rogers et al., 2014	EwE	Based on data	dynamic	non-spatial	yes	Fisheries	yes
Pinnegar et al., 2014	EwE	Theoretical	dynamic	non-spatial	yes	Fisheries	no
Pigneur et al., 2014	PEGASE with POTAMON model	Based on data	dynamic	fully spatial	yes	Hydrodynamic (gauging stations), temperature (thermal release from power plants), and nutrient loading	yes
Olden and Tamayo, 2014	Hedonic model	Based on data	static	non-spatial	no		yes
Liu et al., 2014	Bioeconomic model	Based on data	dynamic	non-spatial	yes	Fisheries	no
Kratina et al., 2014	Multivariate autoregressive (MAR) models	Based on data	comparison between periods	comparison between sites	yes	Temperature	no
Kao et al., 2014	EwE	Based on data	dynamic	non-spatial	yes	Fisheries and nutrient loads	yes
Higgins et al., 2014	Lake autotrophic structure model (LAS)	Based on data	dynamic	non-spatial	yes	Nutrient loading	no
He et al., 2014	Age-structured model with bioenergetic model	Based on data	dynamic	non-spatial	no		yes
Green et al., 2014	Size-structured model of predation	Based on data	dynamic	non-spatial	yes	Fishing	no
Francis et al., 2014	Multivariate autoregressive (MAR) models	Based on data	dynamic	non-spatial	yes	Nutrients (P) and temperature	yes
Cook et al., 2014	DPSER (EBM-Driver-Pressure-State-Ecosystem service-Response) model	Theoretical	static	non-spatial	yes	Fisheries, climate change	no
Bocaniov et al., 2014	ELCOM-CAEDYM model with a mussel sub-model to include mussel energetics and dynamics	Based on data	dynamic	fully spatial	yes	Nutrient load and temperature	yes
Blamey et al., 2014	MICE	Based on data	dynamic	non-spatial	yes	Fisheries	yes
Akoglu et al., 2014	EwE	Based on data	comparison between periods	non-spatial	yes	Fishery	no
Van Guilder and Seefelt, 2013	Bioenergetic model	Based on data	comparison between periods	non-spatial	no		no
Onikura et al., 2013	Generalized linear model (GLM)	Based on data	static	fully spatial	no		no
Magnea et al., 2013	Simplified lake ecosystem mathematical model (food web model)	Based on data	dynamic	non-spatial	yes	Nutrient loading	yes
Kinter and Ludsin, 2013	EwE	Based on data	dynamic	non-spatial	yes	Fisheries and nutrient loading	no
Hossain et al., 2013	EwE	Based on data	static	non-spatial	no		no

Hattab et al., 2013	EwE	Based on data	static	non-spatial	yes	Fisheries	no
Clavero et al., 2013	Multiple regression models and Structural equation modeling	Based on data	static	non-spatial	yes	Footprint	yes
Cha et al., 2013	Bayesian hierarchical regressions	Based on data	comparison between periods	comparison between sites	no		no
Cerino et al., 2013	Bioenergetic model	Based on data	dynamic	non-spatial	no		yes
Blamey et al., 2013	MICE	Based on data	dynamic	comparison between sites	yes	Fisheries	yes
Amundsen et al., 2013	Pelagic food web	Based on data	comparison between periods	non-spatial	no		no
Schoen et al., 2012	Bioenergetic model	Based on data	static	non-spatial	no		yes
Schindler et al., 2012	Multivariate autoregressive models (MARs)	Based on data	dynamic	comparison between sites	yes	Temperature	yes
Norkko et al., 2012	Reactive-transport model	Based on data	dynamic	non-spatial	no		yes
Nilsson et al., 2012	Hierarchical Bayesian model	Based on data	static	comparison between sites	no		no
MacDonald et al., 2012	Species occupancy models, boosted regression trees and linear and logistic regression models	Based on data	static	comparison between sites	no		no
Langseth et al., 2012	EwE	Based on data	dynamic	non-spatial	yes	Fisheries	yes
Hossain et al., 2012	EwE	Based on data	static	non-spatial	yes	Fisheries	no
Hermoso et al., 2012	MARS and regression models (Structural equation models)	Based on data	dynamic	non-spatial	yes	Land uses and water quality	no
Ferguson et al., 2012	Competition model, predation model and null model	Based on data	static	non-spatial	no		no
Green et al., 2012	Linear mixed-effect model	Based on data	comparison between periods	non-spatial	no		no
Downing et al., 2012	EwE	Based on data	comparison between periods	non-spatial	yes	Fisheries	no
Descy et al., 2012	PEGASE with POTAMON model	Based on data	dynamic	comparison between sites	yes	Hydrodynamic (gauging stations), temperature (thermal release from power plants), and nutrient loading	yes
Correa and Henry, 2012	Linear models and structural equation modelling	Based on data	static	comparison between sites	no		yes

Blukacz-Richards and Koops, 2012	EwE	Based on data	static	non-spatial	yes	Fisheries	no
Beville et al., 2012	Behavioural choice model	Based on data	static	non-spatial	yes	Fisheries	no
Baird et al., 2012	Quantified network models	Based on data	comparison between periods	non-spatial	no		no
Zhang et al., 2011	Two-dimensional hydrodynamic and water quality model (CE-QUAL-W2)	Based on data	dynamic	fully spatial	yes	Nutrient loading	no
Woodford et al., 2011	GIS-based spatial model	Based on data	static	fully spatial	no		yes
Wenger et al., 2011	SDMs	Based on data	dynamic	fully spatial	yes	Temperature	yes
Stewart and Sprules, 2011	EwE	Based on data	comparison between periods	non-spatial	yes	Fishing	no
Sharma et al., 2011	SDMs	Based on data	dynamic	fully spatial	yes	Climate change	yes
Roy et al., 2011	Social-ecological model	Based on data	dynamic	fully spatial	yes	Nutrient loading and water temperature	yes
Olden et al., 2011	SDMs	Based on data	dynamic	fully spatial	yes	Recreational users of lakes	yes
Lercari and Bergamino, 2011	EwE	Based on data	static	non-spatial	yes	Fishing	no
Higgins et al., 2011	Least square regressions and ANCOVA	Based on data	comparison between periods	comparison between sites	no		no
Hermoso et al., 2011	Multiple regression model and structural equation modeling (SEM)	Based on data	static	non-spatial	yes	Habitat degradation	yes
Haught and von Hippel, 2011	Curvilinear regression, multiple linear regression and multiple logistic regression	Based on data	static	comparison between sites	no		yes
Grosholz et al., 2011	Bioeconomic model	Based on data	dynamic	comparison between sites	yes	Fishing	yes
Fetahi et al., 2011	EwE	Based on data	comparison between periods	non-spatial	yes	Fishing	no
Cha et al., 2011	Mass balance model of phosphorus	Based on data	dynamic	non-spatial	yes	Nutrient loading	no
Boulêtreau et al., 2011	Mass balance model of phosphorus	Based on data	static	non-spatial	no		no
Benjamin et al., 2011	Linear mixed model	Based on data	static	comparison between sites	no		yes

Arias-Gonzalez et al., 2011	EwE	Based on data	dynamic	non-spatial	yes	Fishing	yes
Tsagarakis et al., 2010	EwE	Based on data	static	non-spatial	yes	Fishing	no
Taraborelli et al., 2010	Bioenergetic model	Based on data	dynamic	comparison between sites	no		no
Stewart et al., 2010	Stochastic population-based bioenergetic models	Based on data	dynamic	non-spatial	yes	Climate change	no
Roy et al., 2010	Social–ecological systems (SESs)	Based on data	dynamic	non-spatial	yes	Temperature and nutrient loading	yes
Miller et al., 2010	Lake Michigan Ecosystem Model (LM-Eco)	Based on data	dynamic	fully spatial	no		yes
Cooke and Hill, 2010	Bioenergetic model	Based on data	dynamic	comparison between sites	no		no
Ciancio et al., 2010	Bioenergetic model	Based on data	dynamic	comparison between sites	no		no
Auer et al., 2010	Mass-balance modeling approach	Based on data	static	comparison between sites	no		no
Vigliano et al., 2009	Bioenergetic model	Based on data	dynamic	non-spatial	no		no
Stapanian et al., 2009	Two-tiered modelling approach	Based on data	dynamic	non-spatial	no		yes
Myers et al., 2009	Bioenergetic model	Based on data	static	comparison between sites	no		no
Miehls et al., 2009	ENA	Based on data	comparison between periods	non-spatial	no		no
Miehls et al., 2009	ENA	Based on data	comparison between periods	comparison between sites	no		no
Laruelle et al., 2009	2-dimensional physical and biological/reactive-transport model	Based on data	dynamic	fully spatial	no		yes
Kateregga and Sterner, 2009	Schaefer model	Based on data	dynamic	non-spatial	yes	Fishing	no
Horsch and Lewis, 2009	Hedonic model	Based on data	dynamic	comparison between sites	yes	Water clarity and fishing (recreational)	yes
Glaser et al., 2009	Dynamic water quality model	Based on data	dynamic	fully spatial	yes	Nutrients	yes
Fishman et al., 2009	Dynamic ecosystem model of the lower trophic levels	Based on data	dynamic	fully spatial	yes	Nutrients and temperature	yes
Feroz Khan and Pinnikar, 2009	EwE	Based on data	static	non-spatial	yes	Fishing	no
Aravena et al., 2009	Transfer function (TF) models	Based on data	dynamic	comparison between sites	yes	River discharge and temperature	yes

Zhang et al., 2008	Two-dimensional hydrodynamic and water quality model (CE-QUAL-W2)	Based on data	dynamic	fully spatial	yes	Nutrient loading	yes
Vinson and Baker, 2008	Bioenergetic model	Based on data	dynamic	non-spatial	no		no
Villanueva et al., 2008	EwE	Based on data	static	non-spatial	yes	Fishing	no
Pothoven and Madenjian, 2008	Bioenergetic model	Based on data	comparison between periods	comparison between sites	no		no
Oguz et al., 2008	Coupled model of bioenergetic-based anchovy population dynamics and lower trophic food web structure	Based on data	dynamic	non-spatial	yes	Fishing and nutrient loading	yes
Oguz et al., 2008	Coupled model of bioenergetic-based anchovy population dynamics and lower trophic food web structure	Based on data	dynamic	non-spatial	yes	Fishing and nutrient loading	yes
Negus et al., 2008	Bioenergetic	Based on data	dynamic	comparison between sites	no		no
Boegman et al., 2008	Two-dimensional hydrodynamic and water-quality reservoir model, CE-QUAL-W2	Based on data	dynamic	fully spatial	yes	Nutrients	yes
Boegman et al., 2008	Two-dimensional hydrodynamic and water-quality reservoir model, CE-QUAL-W2	Based on data	dynamic	fully spatial	yes	Nutrients	yes
Blanchet et al., 2008	Mixed linear models (competition and predation) and GLMs with fish growth rate, invertebrate biomass and Chl-A	Based on data	comparison between periods	comparison between sites	no		yes
Arbach Leloup et al., 2008	EwE	Based on data	static	non-spatial	yes	Fishing	no
Rowe, 2007	ANCOVA and regression analysis	Based on data	static	comparison between sites	no		no
Qualls et al., 2007	Regression models	Based on data	comparison between periods	comparison between sites	no		no
Pine et al., 2007	EwE	Based on data	dynamic	non-spatial	yes	Fisheries	no
Ortiz and Stotz, 2007	Loop models of ecological and socio-economic systems	Based on data	dynamic	non-spatial	yes	Fisheries	no

Morales et al., 2007	Mussel dynamics model (Ecohydraulic modeling)	Based on data	dynamic	fully spatial	yes	Temperature and flow patterns (dam near study area) and nutrients (water quality)	yes
Light and Marchetti, 2007	Linear regression models and multiple regression models	Based on data	comparison between periods	comparison between sites	yes	Habitat degradation (hydrological modification and land use)	yes
Jaarsma et al., 2007	Multiple linear regression modelling and neural network modelling	Based on data	dynamic	comparison between sites	no		no
Caldow et al., 2007	Individuals-based models	Based on data	dynamic	non-spatial	no		no
Morales et al., 2006	Mussel dynamics model (Ecohydraulic modeling)	Based on data	dynamic	fully spatial	yes	Temperature and flow patterns (dam near study area) and nutrients (water quality)	yes
Matsuishi et al., 2006	EwE	Based on data	dynamic	comparison between sites	yes	Fisheries	no
Gribben and Wright, 2006	ANCOVA	Based on data	dynamic	comparison between sites	no		no
Frésard and Boncoeur, 2006	Economic model	Based on data	dynamic	non-spatial	yes	Fisheries	no
Frésard and Boncoeur, 2006	Economic model	Based on data	dynamic	non-spatial	yes	Fisheries	no
Morozov et al., 2005	Generic nutrient-phytoplankton-zooplankton (N-P-Z) model	Theoretical	dynamic	non-spatial	no		no
Madenjian et al., 2005	Regression models	Based on data	dynamic	non-spatial	no		yes
Lee and Johnson, 2005	Bioenergetic model	Based on data	dynamic	comparison between sites	yes	Temperature	yes
Knowler and Barbier, 2005	Bioeconomic model	Based on data	dynamic	non-spatial	yes	Fishing and nutrient and temperature	yes
Knowler, 2005	Bioeconomic model	Based on data	dynamic	non-spatial	yes	Fishing and nutrients	no
Knapp, 2005	GAM	Based on data	comparison between periods	comparison between sites	no		no
Johnson et al., 2005	Bioenergetic model	Based on data	dynamic	non-spatial	no		no
Harvey and Kareiva, 2005	EwE	Based on data	dynamic	non-spatial	yes	Fisheries	no
Bunnell et al., 2005	Individual-based bioneregetic model	Based on data	dynamic	non-spatial	no		no
Bierman et al., 2005	Bioenergetic model coupled with eutrophication model	Based on data	dynamic	fully spatial	yes	Nutrients and temperature	yes
Le Pape et al., 2004	GLM	Based on data	comparison between periods	comparison between sites	no		no
Cox and Kitchell, 2004	EwE	Based on data	dynamic	non-spatial	yes	Fisheries	yes

Ruzycki et al., 2003	Age-structured bioenergetics modeling approach	Based on data	dynamic	non-spatial	no		no
Ricciardi, 2003	Least-squares regression	Based on data	comparison between periods	comparison between sites	no		no
Pranovi et al., 2003	EwE	Based on data	comparison between periods	non-spatial	yes	Fisheries	no
Porath et al., 2003	GLM	Based on data	comparison between periods	non-spatial	no		no
Laxson et al., 2003	Bioenergetic model and the physiological method of Winberg	Based on data	dynamic	comparison between sites	no		no
Halstead et al., 2003	Hedonic method	Based on data	static	non-spatial	no		no
Descy et al., 2003	POTAMON	Based on data	dynamic	fully spatial	no		yes
Beisner et al., 2003	First-order multivariate (or vector) autoregressive models, MAR	Based on data	dynamic	non-spatial	no		yes
Villanueva and Moreau, 2002	EwE	Based on data	dynamic	non-spatial	yes	Fisheries	no
Stapp and Hayward, 2002	Stage-structured models	Based on data	dynamic	non-spatial	yes	Fisheries	no
Settle and Shogren, 2002	Integrated economic-biological model	Based on data	dynamic	non-spatial	yes	Fisheries	no
Raborn et al. 2002	Bioenergetic model	Based on data	dynamic	non-spatial	no		no
Lancelot et al., 2002	Ecological model BIOGEN	Based on data	dynamic	fully spatial	yes	Nutrient loading and fisheries	yes
Gucu, 2002	EwE	Based on data	comparison between periods	non-spatial	yes	Fisheries	no
Daskalov, 2002	EwE	Based on data	dynamic	non-spatial	yes	Fisheries and eutrophication	yes
Oguz et al., 2001	One-dimensional physical-biological ecosystem model	Based on data	dynamic	non-spatial	no		yes
Hoffman et al., 2001	Bioenergetic model	Based on data	dynamic	non-spatial	no		no
Byers and Goldwasser, 2001	Individual-based model	Based on data	dynamic	non-spatial	no		yes
Reed-Andersen et al., 2000	Bioenergetic model of zebra mussel coupled with phytoplankton growth model	Based on data	dynamic	non-spatial	no		yes
Kitchell et al., 2000	EwE	Based on data	dynamic	non-spatial	yes	Fisheries	no
Rutherford et al., 1999	Individual-based model	Based on data	dynamic	non-spatial			yes

Murray and Parslow, 1999	Biogeochemical model	Based on data	dynamic	fully spatial	yes	Nutrients loading	yes
MacIsaac et al., 1999	Hydrodynamic model	Based on data	dynamic	fully spatial	no		yes
Berdnikov et al., 1999	Trophodynamic model	Based on data	dynamic	fully spatial	yes	Salinity and temperature and fisheries	yes
Pace et al., 1998	Intervention time series model	Based on data	dynamic	comparison between sites	no		yes
Kitchell et al., 1997	Bioenergetic model	Based on data	dynamic	non-spatial	yes	Fisheries	no
Caraco et al., 1997	Mass-balance approach	Based on data	dynamic	fully spatial			yes
Young et al., 1996	Bioenergetic model	Based on data	dynamic	non-spatial	no		no
Padilla et al., 1996	Mathematical model of trophic interactions	Based on data	dynamic	comparison between sites	no		yes
Mavuti et al., 1996	EwE	Based on data	static	non-spatial	yes	Fisheries	no
Yurista and Schulz, 1995	Bioenergetic model	Based on data	dynamic	non-spatial	no		no
Volovik et al., 1995	Ecological-mathematical model	Based on data	dynamic	fully spatial	yes	Temperature	yes
Ricciardi et al., 1995	Linear regression models and Poisson model	Based on data	dynamic	comparison between sites	no		yes
Negus, 1995	Bioenergetic model	Based on data	dynamic	non-spatial	no		no
Madenjian, 1995	Bioenergetic model	Based on data	dynamic	non-spatial	no		yes
Moreau et al., 1993	EwE	Based on data	comparison between periods	non-spatial	yes	Fisheries	no
Schneider, 1992	Bioenergetic model	Based on data	dynamic	comparison between sites	no		yes
Fontaine and Stewart, 1992	Mathematical model of the food web	Based on data	dynamic	non-spatial	yes	Nutrient load and pollution	yes

Paper ID (surname and year)	Could the model assess uncertainty? (yes/no)	Was the uncertainty evaluated? (yes/not)	Was the model used to provide management recommendations? (yes/no)	In case the model has been used to provide management recommendations, which?	Have the recommendations been used by decision makers? (yes/no)	How many impacts on ecosystem services were modelled?	How many impacts on biodiversity were modelled?	Total number of impacts modelled	Negative/ positive impacts?	Number of indicators
van der Lee et al., 2017	yes	yes	no		no		1	1	negative	3
Foley et al., 2017	yes	yes	no		no		1	1	negative	1
Corrales et al., 2017	yes	yes	no		no	1	4	5	both	9
Zhang et al., 2016	yes	yes	no		no		3	3	negative	2
Walsh et al., 2016	don't know	no	no		no	1	2	3	negative	5
Van Zuiden et al., 2016	don't know	no	no		no		1	1	negative	1
Nyamweya et al., 2016	yes	no	no		no		2	2	negative	2
Natugonza et al., 2016	yes	no	no		no	1	3	4	negative	14
Liao et al., 2016	don't know	no	no		no	1		1	negative	1
Kumar et al., 2016	yes	no	no		no		2	2	both	1
Katsanevakis et al., 2016	yes	yes	no		no		1	1	negative	1
Kao et al., 2016	yes	no	no		no		4	4	negative	8
Jellyman and Harding, 2016	don't know	no	no		no		2	2	both	3
Isaev et al., 2016	don't know	no	no		no		1	1	negative	13
Bajer et al., 2016	don't know	no	no		no		2	2	negative	2
Walrath et al., 2015	don't know	no	no		no		1	1	negative	1
Rowe et al., 2015	yes	yes	no		no		1	1	negative	1
Rowe et al., 2015	don't know	no	no		no		1	1	negative	2

Pagnucco and Ricciardi, 2015	don't know	no	no	no		2	2	both	3
Marrack et al., 2015	no	no	no	no		1	1	negative	1
Libralato et al., 2015	yes	yes	no	no		3	3	both	3
Li et al., 2015	yes	yes	no	no		2	2	both	1
Jiang et al., 2015	yes	yes	no	no	1	2	3	both	10
Gudimov et al., 2015	yes	yes	no	no	1	1	2	positive	2
Gobin et al., 2015	don't know	no	no	no		2	2	negative	2
Dembkowski et al., 2015	no	no	no	no		1	1	negative	1
De Amorim et al., 2015	no	no	no	no		1	1	negative	2
Crane et al., 2015	no	no	no	no		1	1	both	1
Crane and Einhouse, 2015	no	no	no	no		1	1	both	2
Colvin et al., 2015	no	yes	no	no	1	3	4	both	3
Bourdeau et al., 2015	no	no	no	no		1	1	negative	1
Anderson et al., 2015	no	no	no	no		1	1	negative	8
Wong and Dowd, 2014	no	no	no	no		2	2	both	16
Shan et al., 2014	yes	no	no	no		2	2	both	3
Schwalb et al., 2014	yes	yes	no	no		2	2	negative	5
Rosa et al., 2014	yes	no	no	no		3	3	both	1
Rogers et al., 2014	yes	no	no	no		3	3	both	4
Pinnegar et al., 2014	yes	yes	no	no		2	2	both	3
Pigneur et al., 2014	don't know	no	no	no	1	2	3	both	5
Olden and Tamayo, 2014	don't know	no	no	no	1		1	negative	1

Liu et al., 2014	don't know	yes	no		no	2	1	3	both	3
Kratina et al., 2014	no	no	no		no		1	1	negative	1
Kao et al., 2014	yes	no	no		no		2	2	both	1
Higgins et al., 2014	don't know	no	no		no	1	3	4	both	5
He et al., 2014	don't know	no	no		no		1	1	negative	2
Green et al., 2014	yes	yes	yes	Suppressing invaders below densities which cause ecological harm	no		1	1	negative	1
Francis et al., 2014	yes	yes	no		no		4	4	both	3
Cook et al., 2014	no	no	no		no	7	4	11	negative	2
Bocaniov et al., 2014	yes	no	no		no		1	1	negative	1
Blamey et al., 2014	yes	yes	no		no		2	2	negative	1
Akoglu et al., 2014	yes	no	no		no	1	5	6	both	9
Van Guilder and Seefelt, 2013	yes	yes	no		no		1	1	negative	1
Onikura et al., 2013	don't know	no	no		no		1	1	negative	1
Magnea et al., 2013	yes	yes	no		no		1	1	both	1
Kinter and Ludsin, 2013	yes	no	yes	Reduce nutrient loading to half. While not an exhaustive list, other non-point source nutrient management options that can lead to reduced nutrient runoff	no	2	1	3	both	1
Hossain et al., 2013	yes	yes	no		no		3	3	both	3
Hattab et al., 2013	yes	no	no		no		1	1	negative	2
Clavero et al., 2013	don't know	no	no		no		1	1	negative	1
Cha et al., 2013	yes	yes	no		no		2	2	negative	2
Cerino et al., 2013	yes	no	no		no		1	1	negative	2

Blamey et al., 2013	yes	yes	no		no		1	1	negative	2
Amundsen et al., 2013	no	no	no		no		3	3	both	8
Schoen et al., 2012	don't know	no	no		no		1	1	negative	1
Schindler et al., 2012	don't know	no	no		no		2	2	negative	2
Norkko et al., 2012	no	no	no		no		1	1	positive	3
Nilsson et al., 2012	yes	yes	no		no		2	2	both	2
MacDonald et al., 2012	don't know	no	no		no		2	2	both	5
Langseth et al., 2012	yes	no	no		no		2	2	both	1
Hossain et al., 2012	yes	no	no		no		2	2	both	2
Hermoso et al., 2012	no	no	no		no		1	1	negative	1
Ferguson et al., 2012	no	no	no		no		2	2	negative	1
Green et al., 2012	yes	yes	no		no		1	1	negative	1
Downing et al., 2012	yes	no	no		no	1	3	4	both	8
Descy et al., 2012	don't know	no	no		no		1	1	negative	2
Correa and Henry, 2012	don't know	no	no		no		1	1	negative	1
Blukacz-Richards and Koops, 2012	yes	yes	no		no		2	2	negative	1
Beville et al., 2012	no	no	yes	Closure of all mainstream-rivers and closure of the Waimakariri River	no	1		1	negative	1
Baird et al., 2012	don't know	no	no		no		3	3	both	11
Zhang et al., 2011	don't know	no	no		no		3	3	both	4
Woodford et al., 2011	don't know	no	no		no		1	1	negative	1
Wenger et al., 2011	no	no	yes	conserving cutthroat trout or rainbow trout habitat	no		1	1	negative	1
Stewart and Sprules, 2011	yes	yes	no		no		3	3	both	5

Sharma et al., 2011	don't know	no	yes	Reduce greenhouse emissions (slowing rate of warming), regulations and public education can help to reduce dispersal of alien, and enhance water quality in lakes by decreasing nutrient loads and increasing hypolimnetic oxygen concentrations	no		1	1	negative	1
Roy et al., 2011	yes	yes	yes	increased on-site phosphorus load reductions, coupled with ecosystem restoration and investment in low-cost nutrient efficiency technology	no	2	2	4	negative	5
Olden et al., 2011	don't know	no	yes	First, public education and outreach could be targeted at high-risk locations Second, those lakes identified at greatest risk of invasion could be used as sentinel locations for ongoing monitoring, increasing the chances of early detection by state and public surveys. Third, voluntary or enforced catch-and-release programs for bass and sunfish could be implemented on those lakes most vulnerable to O. rusticus invasion,	no		1	1	negative	2
Lercari and Bergamino, 2011	yes	no	no		no		2	2	both	7
Higgins et al., 2011	don't know	no	no		no		1	1	negative	1
Hermoso et al., 2011	don't know	no	yes	1) Prevent active and accidental introductions; 2) active management to reduce harmful effects and prevent further spread (eradication or long-term control of invasive species at key times of year, extend flows in regulated rivers and reduce dispersal rates from reservoirs	no		2	2	negative	2

Haught and von Hippel, 2011	don't know	no	no		no		1	1	negative	1
Grosholz et al., 2011	yes	yes	no		no	1	1	2	negative	3
Fetahi et al., 2011	yes	no	no		no		3	3	both	5
Cha et al., 2011	yes	yes	no		no		1	1	both	8
Boulêtreau et al., 2011	no	no	no		no		1	1	negative	2
Benjamin et al., 2011	yes	yes	no		no		1	1	negative	1
Arias-Gonzalez et al., 2011	yes	yes	yes	Eradication programs would only be successful if all ages of the spawners can be targeted and if the program is long-term, through a build-up of potential predators, such as, e.g., large groupers. Different policy options could be applied to maintain the lionfish population to levels of low density in the Atlantic: restore and protect the stock of piscivorous fishes such as grouper, sharks, barracudas, etc., releasing pressure on native coral reef species	no		3	3	both	3
Tsagarakis et al., 2010	yes	yes	no		no		2	2	both	2
Taraborelli et al., 2010	yes	yes	no		no		1	1	negative	2
Stewart et al., 2010	yes	yes	no		no		1	1	negative	12
Roy et al., 2010	yes	yes	yes	Increased management of external phosphorus loading potentially	no	2	2	4	negative	5
Miller et al., 2010	don't know	no	no		no		1	1	negative	1
Cooke and Hill, 2010	yes	yes	no		no		1	1	negative	4
Ciancio et al., 2010	don't know	no	no		no		1	1	negative	1

Auer et al., 2010	don't know	no	no	no		1	1	negative	1
Vigliano et al., 2009	don't know	no	no	no		1	1	negative	3
Stapanian et al., 2009	don't know	no	no	no		1	1	negative	1
Myers et al., 2009	don't know	no	no	no		1	1	negative	3
Miehls et al., 2009	don't know	no	no	no		3	3	both	8
Miehls et al., 2009	don't know	no	no	no		3	3	both	8
Laruelle et al., 2009	don't know	no	no	no		2	2	negative	4
Kateregga and Sterner, 2009	don't know	no	no	no	1		1	negative	1
Horsch and Lewis, 2009	don't know	no	no	no	1		1	negative	1
Glaser et al., 2009	don't know	no	no	no	1	2	3	both	6
Fishman et al., 2009	don't know	no	no	no	1	3	4	both	3
Feroz Khan and Pinnikar, 2009	yes	no	no	no		2	2	both	1
Aravena et al., 2009	no	no	no	no		1	1	negative	1
Zhang et al., 2008	yes	yes	no	no	1	3	4	both	5
Vinson and Baker, 2008	don't know	no	no	no		1	1	negative	2
Villanueva et al., 2008	yes	no	no	no		3	3	both	1
Pothoven and Madenjian, 2008	don't know	no	no	no		1	1	negative	3
Oguz et al., 2008	yes	no	no	no		2	2	negative	2
Oguz et al., 2008	yes	yes	no	no		2	2	negative	3
Negus et al., 2008	no	no	no	no		1	1	negative	2
Boegman et al., 2008	don't know	no	no	no	1	2	3	both	2

Boegman et al., 2008	don't know	no	no		no	1	3	4	both	5
Blanchet et al., 2008	don't know	no	no		no		2	2	both	4
Arbach Leloup et al., 2008	yes	no	no		no		3	3	both	9
Rowe, 2007	don't know	no	no		no	1		1	negative	1
Qualls et al., 2007	don't know	no	no		no	1	1	2	both	5
Pine et al., 2007	yes	yes	yes	Maintain populations at low densities, moderate sustained levels of flathead catfish exploitation may release native fish groups from predation by and competition with flathead catfish. Management agencies could promote harvest of flathead catfish populations by offering a bounty or subsidy system to commercial fishers and simultaneously developing a market for the fish product. Increasing the size and intensity of the recreational fishery is an equally important aspect of any effort to reduce flathead catfish biomass and provide sustained fishing pressure	no		2	2	both	1
Ortiz and Stotz, 2007	don't know	no	no		no		2	2	negative	2
Morales et al., 2007	yes	no	no		no		1	1	negative	3
Light and Marchetti, 2007	don't know	no	no		no		1	1	negative	2
Jaarsma et al., 2007	don't know	no	no		no		2	2	negative	1
Caldow et al., 2007	don't know	no	no		no		1	1	positive	1
Morales et al., 2006	yes	yes	no		no		1	1	negative	3

Matsuishi et al., 2006	yes	no	yes	1) establish co-management, 2) key areas with restricting access to the fishery, 3) the ban on beach seining and use of small mesh sized nets should be imposed, 4) active fishing methods, such as lampooning and drift net fishing should be made illegal, 5) reducing post-harvest losses and increasing the value of the product for the export market	no	1	2	3	both	2
Gribben and Wright, 2006	don't know	no	no		no		1	1	negative	3
Frésard and Boncoeur, 2006	yes	yes	yes	Test a restoration program for native bivalve and invasion control. Each year, a zone of 300 ha is cleaned up, and 10million aquaculture juvenile scallops are sown intensively in this. The area is closed to fishing for three years, after which scallops are harvested.	no	1	1	2	negative	1
Frésard and Boncoeur, 2006	yes	yes	yes	Test a program. The strategy of this program relies on a distinction between two stages, which might be called “rollback” and “containment”: the first one is characterized by a high level of invasive species harvesting, in order to decrease significantly the level of invasion; the second step is intended to consolidate the outcome of the “rollback” phase, by harvesting each year the natural surplus produced by the existing biomass	no	1	1	2	negative	6
Morozov et al., 2005	don't know	no	no		no		1	1	negative	1

Madenjian et al., 2005	don't know	no	yes	Control of alewife abundance is a prerequisite for restoration of the deep-water sculpin population	no		2	2	negative	1
Lee and Johnson, 2005	yes	yes	no		no		1	1	negative	1
Knowler and Barbier, 2005	don't know	no	no		no	1	2	3	negative	1
Knowler, 2005	don't know	no	no		no	1	2	3	negative	2
Knapp, 2005	don't know	no	no		no		1	1	negative	1
Johnson et al., 2005	yes	yes	no		no		1	1	negative	1
Harvey and Kareiva, 2005	yes	yes	no		no		2	2	both	2
Bunnell et al., 2005	don't know	no	no		no		1	1	negative	7
Bierman et al., 2005	yes	yes	no		no	1	2	3	both	10
Le Pape et al., 2004	don't know	no	no		no		1	1	negative	1
Cox and Kitchell, 2004	yes	no	no		no		2	2	negative	1
Ruzycki et al., 2003	no	no	no		no		1	1	negative	3
Ricciardi, 2003	no	no	no		no		2	2	both	3
Pranovi et al., 2003	yes	no	no		no	1	3	4	both	16
Porath et al., 2003	no	no	no		no		1	1	both	1
Laxson et al., 2003	don't know	no	no		no		1	1	negative	2
Halstead et al., 2003	don't know	no	no		no	2		2	negative	1
Descy et al., 2003	don't know	no	no		no	1	2	3	both	12
Beisner et al., 2003	don't know	no	no		no		2	2	both	1
Villanueva and Moreau, 2002	yes	no	no		no	1	2	3	both	2

Stapp and Hayward, 2002	yes	yes	yes	Development of control programs that reduce survival of all age classes of lake trout in addition to focusing on adult trout capable of consuming catchable cutthroat trout. Changes in fishing regulations that might counteract the effects of lake trout as current regulations concentrate human mortality on age 4 trout. To reduce mortality on juvenile and young adult age classes would be to restrict angling at the lake to catch and release activities only.	no		2	2	negative	2
Settle and Shogren, 2002	don't know	no	no		no	2	2	4	negative	2
Raborn et al. 2002	yes	yes	no		no		1	1	negative	1
Lancelot et al., 2002	don't know	no	no		no		2	2	both	1
Gucu, 2002	yes	no	no		no	1	3	4	both	3
Daskalov, 2002	yes	no	no		no	1	2	3	both	1
Oguz et al., 2001	don't know	no	no		no		2	2	both	2
Hoffman et al., 2001	don't know	no	no		no		1	1	negative	3
Byers and Goldwasser, 2001	don't know	no	no		no		1	1	negative	8
Reed-Andersen et al., 2000	yes	yes	no		no	1	1	2	both	3
Kitchell et al., 2000	yes	no	yes	To increase the abundance of lean lake trout, both their stocks and that of their primary prey (herring) must be protected from exploitation.	no		2	2	both	1
Rutherford et al., 1999	yes	yes	no		no		2	2	both	23

Murray and Parslow, 1999	don't know	no	no		no		3	3	both	4
MacIsaac et al., 1999	yes	yes	no		no	1	1	2	both	2
Berdnikov et al., 1999	yes	yes	no		no		3	3	both	27
Pace et al., 1998	yes	yes	no		no		1	1	negative	7
Kitchell et al., 1997	no	no	no		no	1	1	2	negative	7
Caraco et al., 1997	yes	yes	no		no		1	1	negative	2
Young et al., 1996	no	no	no		no		1	1	negative	2
Padilla et al., 1996	yes	yes	no		no		2	2	negative	3
Mavuti et al., 1996	yes	no	no		no		2	2	both	2
Yurista and Schulz, 1995	yes	yes	no		no		1	1	negative	2
Volovik et al., 1995	don't know	no	no		no		1	1	negative	1
Ricciardi et al., 1995	no	no	no		no		1	1	negative	4
Negus, 1995	don't know	no	no		no		1	1	negative	2
Madenjian, 1995	yes	yes	no		no		1	1	negative	1
Moreau et al., 1993	yes	no	no		no		3	3	negative	4
Schneider, 1992	don't know	no	no		no		1	1	negative	1
Fontaine and Stewart, 1992	don't know	no	yes	The model indicates that the effects of phosphorus and lamprey management on salmonine contaminants will be small in comparison to the simulated effects of Bythotrephes.	no	1	2	3	both	1

ANNEX 2

X.Corrales, E. Ofir, M. Coll, M. Goren, D. Edelist, J.J. Heymans, G. Gal
Modeling the role and impact of alien species and fisheries on the Israeli marine continental shelf ecosystem Journal of Marine Systems 170 (2017), 88-102

Pages 278 to 328 of the thesis, containing these article and supplementary material are available at the editor's web

https://www.sciencedirect.com/science/article/pii/S0924796316302329

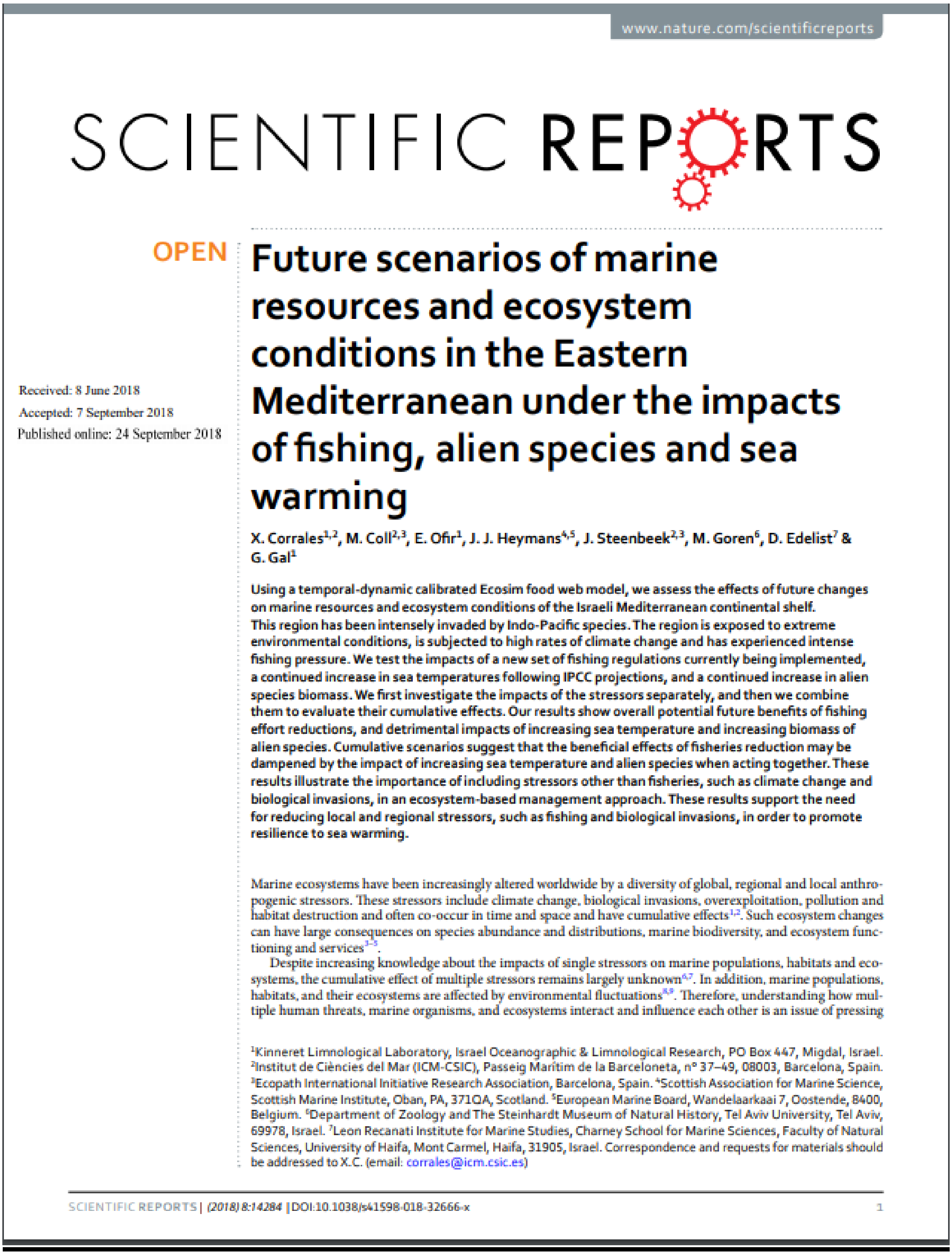
ANNEX 3

X. Corrales, M. Coll, E. Ofir, C. Piroddi, M. Goren, D. Edelist, J. J. Heymans, J. Steenbeek, V. Christensen, G. Gal
Hindcasting the dynamics of an Eastern Mediterranean marine ecosystem under the impacts of multiple stressors. Mararine Ecology Progress Series 580:17-36.

Pages 330 to 354 of the thesis, containing these article are available at the editor's web

https://www.int-res.com/abstracts/meps/v580/p17-36/

ANNEX 4



www.nature.com/scientificreports

SCIENTIFIC REPORTS

OPEN

Received: 8 June 2018
Accepted: 7 September 2018

Future scenarios of marine resources and ecosystem conditions in the Eastern Mediterranean under the impacts of fishing, alien species and sea warming

X. Corrales[1,2], M. Coll[2,3], E. Ofir[1], J. J. Heymans[4,5], J. Steenbeek[2,3], M. Goren[6], D. Edelist[7] & G. Gal[1]

Using a temporal-dynamic calibrated Ecosim food web model, we assess the effects of future changes on marine resources and ecosystem conditions of the Israeli Mediterranean continental shelf. This region has been intensely invaded by Indo-Pacific species. The region is exposed to extreme environmental conditions, is subjected to high rates of climate change and has experienced intense fishing pressure. We test the impacts of a new set of fishing regulations currently being implemented, a continued increase in sea temperatures following IPCC projections, and a continued increase in alien species biomass. We first investigate the impacts of the stressors separately, and then we combine them to evaluate their cumulative effects. Our results show overall potential future benefits of fishing effort reductions, and detrimental impacts of increasing sea temperature and increasing biomass of alien species. Cumulative scenarios suggest that the beneficial effects of fisheries reduction may be dampened by the impact of increasing sea temperature and alien species when acting together. These results illustrate the importance of including stressors other than fisheries, such as climate change and biological invasions, in an ecosystem-based management approach. These results support the need for reducing local and regional stressors, such as fishing and biological invasions, in order to promote resilience to sea warming.

Marine ecosystems have been increasingly altered worldwide by a diversity of global, regional and local anthropogenic stressors. These stressors include climate change, biological invasions, overexploitation, pollution and habitat destruction and often co-occur in time and space and have cumulative effects[1,2]. Such ecosystem changes can have large consequences on species abundance and distributions, marine biodiversity, and ecosystem functioning and services[3–5].

Despite increasing knowledge about the impacts of single stressors on marine populations, habitats and ecosystems, the cumulative effect of multiple stressors remains largely unknown[6,7]. In addition, marine populations, habitats, and their ecosystems are affected by environmental fluctuations[8,9]. Therefore, understanding how multiple human threats, marine organisms, and ecosystems interact and influence each other is an issue of pressing

[1]Kinneret Limnological Laboratory, Israel Oceanographic & Limnological Research, PO Box 447, Migdal, Israel. [2]Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta, n° 37–49, 08003, Barcelona, Spain. [3]Ecopath International Initiative Research Association, Barcelona, Spain. [4]Scottish Association for Marine Science, Scottish Marine Institute, Oban, PA, 371QA, Scotland. [5]European Marine Board, Wandelaarkaai 7, Oostende, 8400, Belgium. [6]Department of Zoology and The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, 69978, Israel. [7]Leon Recanati Institute for Marine Studies, Charney School for Marine Sciences, Faculty of Natural Sciences, University of Haifa, Mont Carmel, Haifa, 31905, Israel. Correspondence and requests for materials should be addressed to X.C. (email: corrales@icm.csic.es)

importance. To address this challenge, a shift towards a more comprehensive analysis and management of human activities is required, as emphasised by the ecosystem-based management (EBM) approach[10,11].

The EBM approach has sparked great interest among the scientific community and new tools have been developed in recent decades. Within this context, ecosystem modelling approaches have increasingly been adopted as useful tools to study marine ecosystems as a whole and to forecast ecosystem dynamics and develop and test future scenarios for marine ecosystems[12–14].

Ecosystem models and ecological forecasts face several obstacles linked to ecosystem characteristics and include high uncertainty[15,16]. Nevertheless, they have the potential to contribute significantly to achieving goals in marine conservation and management by offering guidance to decision-makers[17]. Their use in assessments, policy support, and decision-making can provide insights into how the ecosystem could respond to plausible future stressors, enabling the development of adaptive management strategies, and allowing for exploration of the implications of alternative management options[13,18,19].

One of the most commonly used ecosystem modelling software is Ecopath with Ecosim (EwE), which has been widely applied to model aquatic food webs[20,21]. This approach has been used to hindcast and forecast future human impacts on aquatic food webs, such as fishing[22], and increasingly other stressors like climate change[23] and biological invasions[24]. EwE has been applied within the scope of evaluating cumulative impacts of human activities[25]. For example, Serpetti, *et al.*[26] assessed the cumulative impact of sea warming and sustainable levels of fishing pressure in the West Coast of Scotland. In addition, Libralato, *et al.*[27] developed temporal simulations to explore the effects of the arrival of invasive species, changes in primary production and sea warming in the Adriatic Sea.

The Mediterranean Sea is a semi-enclosed sea that is highly impacted by anthropogenic activities[1,2]. The Mediterranean is a global hotspot of alien species[2,28,29], especially its eastern basin due to the opening and continuous enlargement of the Suez Canal[30,31]. Currently, 821 species are described as established alien species in the Mediterranean Sea[32]. In addition, the high impact of fishing in the area has been shown by several analyses, indicating that most of the stocks are fully exploited or overexploited[33,34]. Climate change is also strongly affecting Mediterranean marine biota and ecosystems[35,36], mainly due to substantial temperature increases[37,38]. In fact, the Mediterranean is under a process of "meridionalization" and "tropicalization" of the northern and southern sectors, respectively, mainly due to the northward expansion of native thermophilic species and the introduction of (mainly tropical) alien species through the Suez Canal and the Strait of Gibraltar[39,40]. In addition, the Mediterranean is being altered by other anthropogenic activities such as habitat loss and degradation, pollution, and eutrophication, making the Mediterranean Sea a hotspot of global change[41,42].

Within this context, the marine ecosystem of the Israeli Mediterranean coast, located in the eastern part of the basin, has been altered in recent decades mainly due to species invasions, unsustainable fishing activities, and increasing water temperature[29,43,44]. As a result, great changes in its biodiversity and functioning have occurred[29,30,45,46]. The importance of each stressor has rarely been investigated, and available studies suggest a general strong impact of increasing sea water temperature and more specific impacts of fishing activities and alien species[36,46].

Recently, new fishing regulations took effect in the Israeli Mediterranean continental shelf (hereafter referred to as ICS), which includes a reduction in fishing effort for several fleets with the aim of recovering fish stocks. However, it is expected that the rate of invasion and the impact of alien species and climate change will increase in the future due to the recent enlargement of the Suez Canal and sea warming[47,48].

In this study, we used a temporally dynamic food web model of the ICS ecosystem[49], previously constructed and fitted to available time series of observational data from 1994 to 2010[46], to assess potential future ecological effects of different global change scenarios. These scenarios included different fisheries management alternatives, sea warming following IPCC (Intergovernmental Panel on Climate Change) projections and projected increases in the biomass of alien species over the next 50 years (2010–2060).

Results

Baseline scenario. Under the baseline simulation (Scn1), the model predicted a decreasing biomass trend over time for the biomass of several groups (Figs 1 and 2). Alien invertebrates significantly decreased (Fig. 2), due to the depletion of alien crabs and shrimps (Fig. 1). Other medium trophic level organisms, such as goatfishes and small native demersal fishes, suffered significant large declines (Fig. 1). These decreases were due to the increase of various predators and competitors (for trophic interactions, see Figure S2b (hereafter referenced only as Figure S2b) and current negative impacts of sea warming. For example, small native demersal fishes decreased due to the increase of competitors such as earlier and new alien demersal fishes (Figs S2b and 1), the increasing predation of alien lizardfish (Fig. 3f) and the negative impact of current SST. The model also showed a significant large decline of large demersal native fishes due to their overexploitation (Fig. 3d). In addition, vulnerable species such as turtles and seabirds were projected to significantly decrease (Figs 1 and 2), due to the notable impact of fishing activities on their populations (Figure S2b).

In contrast, the model predicted significant large increases in alien fishes (both demersal and pelagic) (Fig. 2), such as earlier and new alien demersal fishes, alien lizardfish and alien medium pelagic fishes (Figs 1 and 3e). This may be due to their earlier overexploitation prior to the reduction in fishing effort between 2007 and 2010, which is mainly due to a recent decreasing activity of trawl fleet (the most important fleet in the area). This follows current biomass increases due to possible empty niches and the depletion of native competitors (Figure S2b). Mullets (Fig. 3a), sharks and rays (Fig. 1) significantly increased over time. This may be due to the decline in the fishing effort between 2007 and 2010.

Within this scenario, forage fish and invertebrate biomass decreased significantly with time while predatory biomass and total catch significantly increased over time (Fig. 4). Community indicators, such as mTLco and

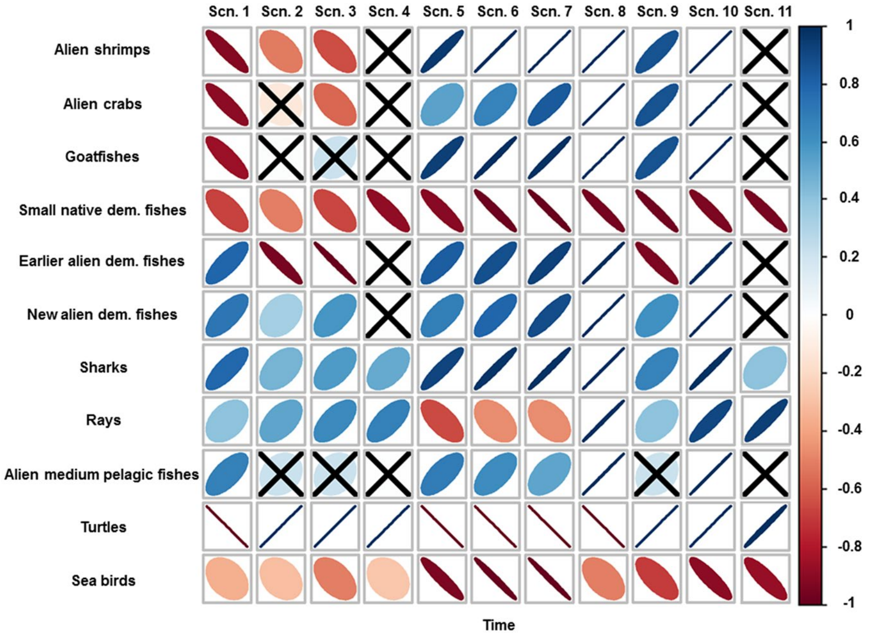


Figure 1. Spearman's rank correlation between selected biomasses of functional groups and time for the ten future scenarios (Table 1). Positive correlations are in blue and negative correlations in red. Legend colour shows the correlation coefficient and its correspondent colour gradient. Colour intensity and the size of the ellipses are proportional to the correlation coefficients, with more diffused and wider ellipses representing lower correlation strengths. When the indicator is non-significant (>0.05), it is represented with an "X" symbol.

mTLc, and indicators related to ecosystem development theory such as TST and FCI significantly decreased with time, while PL significantly increased (Fig. 4).

Fishing scenarios. Under scenarios that only included changes (decreases) in fishing effort (Scn2 and Scn3), the model predicted mixed trends with both significant large decreases and increases in medium trophic level groups and significant large increases in high trophic level groups (Fig. 1). For example, alien invertebrates significantly decreased while vulnerable species significantly increased (Fig. 2). Alien shrimps, small native demersal fishes, earlier alien demersal fishes and alien herbivores significantly decreased over time (Figs 1 and 3e). This is due to the increasing predation mortality as a consequence of the recovery of top predators (Figure S2b) and also, in some cases, a result of negative impacts of sea warming. In addition, the model predicted a significant decrease of sea birds due to the fewer discards caused by the reduction of the trawl fleet (Fig. 1). In contrast, the model predicted significant large increases of top predators, such as hake, large native demersal fishes, alien lizardfish, demersal sharks and rays and skates (Figs 1 and 3b,d,f). The model also showed increasing trends for mullets, new alien demersal fishes and turtles (Figs 1 and 3a), due to the reduction in fishing effort. Most of these trends were exacerbated in Scn3, with the closure of the trawl fleet. For example, the model predicted major and faster recoveries for mullets, hake, large native demersal fishes and alien lizardfish (Fig. 3a,b,d,f), while alien shrimps, small native demersal fishes, earlier alien demersal fishes and sea birds had stronger negative impacts (Fig. 1).

Under Scn4, which assessed the impacts of the new fishing regulations while keeping the biomass of alien species constant, the model showed important effects of alien species. For example, hake and large native demersal fish presented better recoveries than in Scn2 (Fig. 3b,d). For hake, this may be due to competition for resources with alien lizardfish, while for large native demersal fishes it may be due to a higher abundance of their key prey, such as rocky fishes, small native demersal fishes and earlier alien demersal fishes.

Within these three scenarios (Scn2, Scn3 and Scn4), most of the ecological indicators presented significant increasing trends (Fig. 4). For example, total biomass, invertebrate biomass, predatory biomass and total catch showed significant increasing trends (Fig. 4). In addition, mTLco and mTLc significantly increased (Fig. 4). FCI significantly increased in all scenarios while PL had non-significant trends in Scn2 and Scn3 and decreased in Scn4 (Fig. 4).

Sea warming scenarios. Under scenarios of sea warming (Scn5, Scn6 and Scn7), the model predicted different responses of species to rising SST (Fig. 1). The model showed significant increases of alien invertebrates and alien fishes (both demersal and pelagic), while native fishes (both demersal and pelagic) and vulnerable species decreased (Fig. 2). These trends were exacerbated as temperature increased (Figs 1 and 2).

For specific groups, the model predicted significant increasing trends for alien shrimps, alien crabs, goatfishes, earlier and new alien demersal fishes and sharks (Fig. 1). These increases may be due to the depletion of competitors and predators (Figure S2b). In contrast, small native demersal fishes declined due to unfavourable thermal conditions, and rays and skates were projected to strongly decline (Fig. 1). A total collapse of mullets was

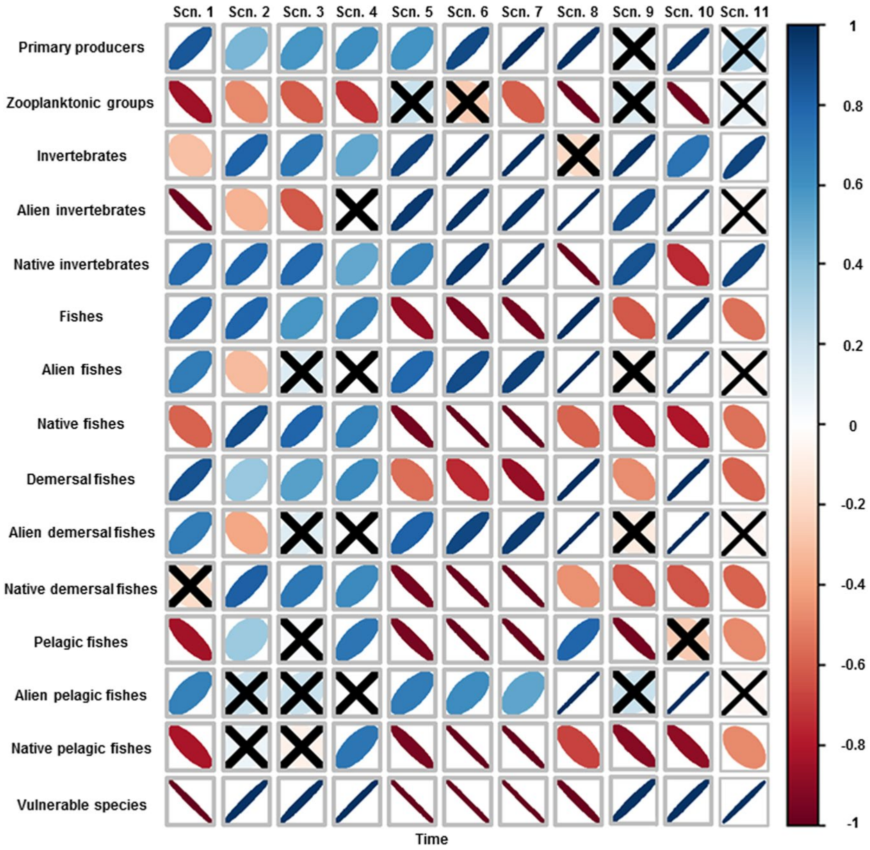


Figure 2. Spearman's rank correlation between the biomass of aggregated groups and time for the ten future scenarios (Table 1). Positive correlations are in blue and negative correlations in red. Legend colour shows the correlation coefficient and its correspondent colour gradient. Colour intensity and the size of the ellipses are proportional to the correlation coefficients, with more diffused and wider ellipses representing lower correlation strengths. When the indicator is non-significant (>0.05), it is represented with an "X" symbol.

predicted under the intermediate and worst IPCC projections (Fig. 5a), while hake and rocky fishes were predicted to be almost depleted in the worst case of sea warming (Fig. 5b,c). Large native demersal fishes were projected to be positively impacted as temperature increases (Fig. 5d), although they showed negative trends due to their overexploitation. Alien herbivores and alien lizardfish biomass significantly increased in all climate scenarios, with major increases as temperature rose except for the alien lizardfish in the worst-case scenario (Fig. 5e,f)

Within these scenarios, we observed significant decreasing trends for most of the ecological indicators, with stronger correlations as temperature increased (Fig. 4). However, invertebrate biomass, mTLc and PL showed increasing trends (Fig. 4).

Alien species scenario. Under the scenario that assessed the impact of alien species forced to follow current biomass trends (Scn8), the model predicted strong impacts on the food web (Figs 1 and 2). Within this scenario, native invertebrates, native fishes (both demersal and pelagic) and vulnerable species declined significantly (Fig. 2).

For specific groups, the model predicted significant decreases of small native demersal fishes due to current thermal conditions and increasing predation mortality and competition (Figure S2b). Similarly, turtles and sea birds declined due to a decline of their main prey (Figs S2b and 4). Mullets were predicted to be slightly negatively impacted, due to their initial recovery as a result of the decreasing fishing effort in 2007–2010 and the negative impacts of alien species (Figs S2b and 6a). Rocky fishes declined significantly, due to a higher abundance of competitors and predators (Figs S2b and 6c). In contrast, hake and large native demersal fishes (Fig. 6b,d) as well as demersal sharks and rays and skates (Fig. 1) significantly increased. This may be due to reduced fishing activities and a higher abundance of alien prey (Figure S2b), although native prey exhibited opposite trends (Fig. 2).

Under this scenario, total biomass, predatory biomass and total catch significantly increased (Fig. 4). In contrast, forage fish, invertebrate biomass and Kempton's index significantly decreased (Fig. 4). FCI and PL were projected to decline significantly, while TST increased (Fig. 4).

Cumulative scenarios. When assessing the cumulative effects of new Israeli fishing regulations and an intermediate scenario of an increase in SST, while alien species biomass was not forced (Scn9), the model projected biomass increases for native invertebrates, alien groups (both invertebrates and fishes) and vulnerable species, while the biomass of native fishes (both demersal and pelagic) significantly decreased (Fig. 2). For specific

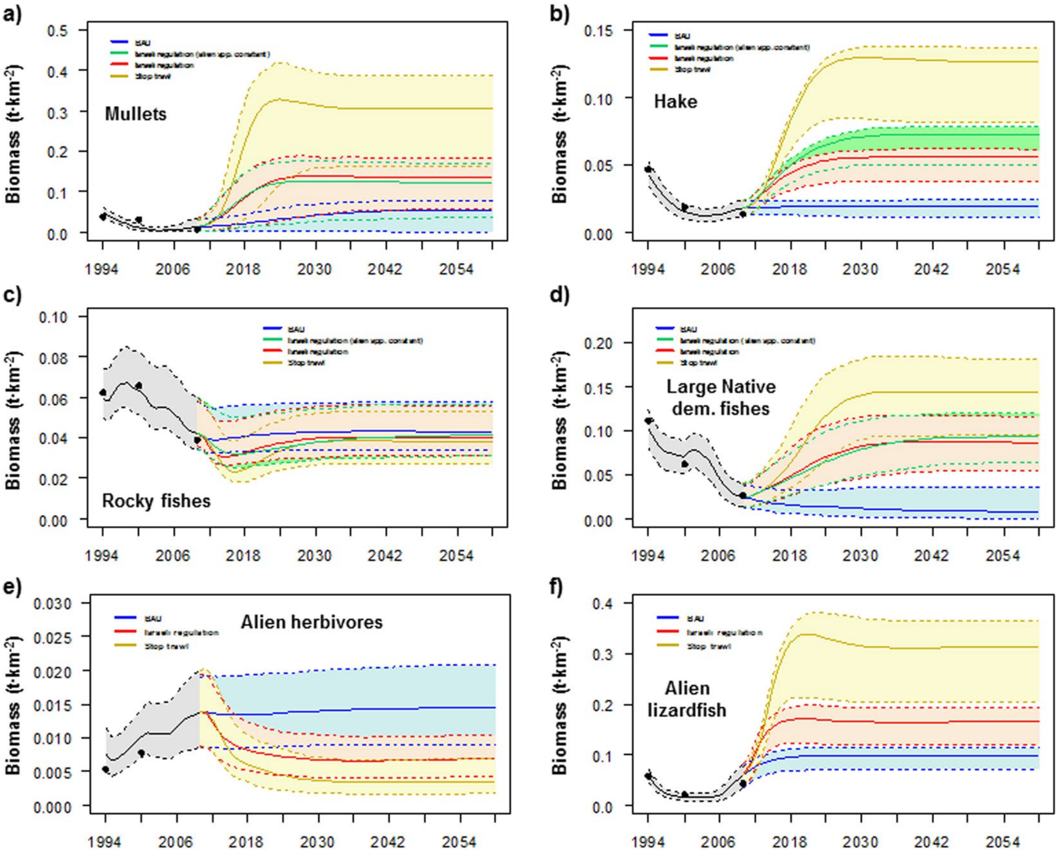


Figure 3. Comparison between the predicted (solid lines) and observed (dots) time series of biomass (t·km^2), and scenarios results for (**a**) mullets, (**b**) hake, (**c**) rocky fishes, (**d**) large native demersal fishes, (**e**) alien herbivores and (**f**) alien lizardfish under different future scenarios of fishing for the Israeli Mediterranean continental shelf (ICS) ecosystem model for the period 1994–2060. Black line represents historical model predictions and coloured lines represent different scenarios. Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

Scenario	Name	Fishing	Temperature	Alien species
1	BAU (business as usual)	Kept at 2010 levels	Kept at 2010 level	Model predicts
2	Israeli regulation	New Israeli regulations	Kept at 2010 level	Model predicts
3	Stop trawl	New Israeli regulations + stop trawl in 3 years	Kept at 2010 level	Model predicts
4	Israeli regulation (alien spp. constant)	New Israeli regulations	Kept at 2010 level	Force (kept at 2010 levels)
5	RCP2.6	Kept at 2010 levels	Best-case	Model predicts
6	RCP4.5	Kept at 2010 levels	Intermediate	Model predicts
7	RCP8.5	Kept at 2010 levels	Worst-case	Model predicts
8	Increase alien species	Kept at 2010 levels	Kept at 2010 level	Force (increase)
9	Combination (no forcing of alien spp.)	New Israeli regulations	Intermediate	Model predicts
10	Combination (forcing of alien spp.)	New Israeli regulations	Intermediate	Force (increase)
11	Combination (forcing alien spp. constant)	New Israeli regulations	Intermediate	Force (kept at 2010 levels)

Table 1. List of scenarios and stressor conditions.

groups, the biomass of some significantly increased such as alien shrimps and crabs, goatfishes, new alien demersal fishes, demersal sharks, rays and skates, and turtles (Fig. 1). In addition, significant increases were observed for hake, large demersal fishes and alien lizardfish, but their recoveries were of a lower magnitude than Scn10 due to the limitation of alien prey (Fig. 7b,d,f). In fact, hake declined at the end of the simulation due to sea warming (Fig. 7b). In contrast, the biomass of small native demersal fishes, earlier alien demersal fishes and sea birds significantly decreased (Fig. 1). In addition, the model predicted significant declines in mullets and rocky fishes (Fig. 7a,c), although they showed better trajectories than Scn10, due to lower impacts of alien species. Alien herbivores also declined (Fig. 7e), due to recoveries of predators (both native and alien) (Figure S2b).

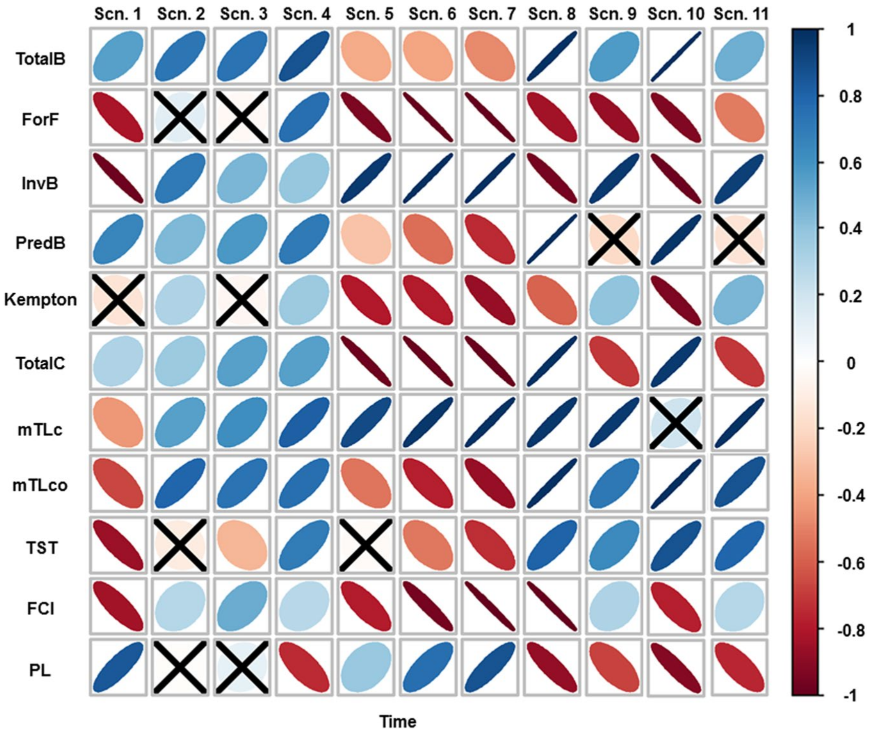


Figure 4. Spearman's rank correlation between the ecological indicators analysed and time for the ten scenarios (Table 1). Positive correlations are in blue and negative correlations in red. Legend colour shows the correlation coefficient and its correspondent colour gradient. Colour intensity and the size of the ellipses are proportional to the correlation coefficients, with more diffused and wider ellipses representing lower correlation strengths. When the indicator is non-significant (>0.05), it is represented with an "X" symbol. TotalB = Total biomass (t·km^{-2}); ForF = Forage fish (t·km^{-2}); InvB = Invertebrate biomass (t·km^{-2}); PredB = Predatory biomass (t·km^{-2}); Kempton = Kempton's index; TotalC = Total catch (t·km^{-2}·year^{-1}); mTLco = mean Trophic Level of the community; mTLc = mean Trophic Level of the catches; TST = Total System Throughput (t·km^{-2}·year^{-1}); FCI = Finn's Cycling Index (%); PL = Path length.

Under this scenario, total biomass, invertebrate biomass, mTLc and mTLco significantly increased, while forage fish and total catch significantly declined (Fig. 4). TST and FCI were projected to increase, while PL declined (Fig. 4).

When assessing the cumulative effects of the new Israeli fishing regulations, the intermediate scenario of sea warming and an increase in alien biomass following current trends (Scn10), the model predicted a significant decreasing pattern of native invertebrates and native fishes (both demersal and pelagic), while vulnerable species significantly increased (Fig. 2). Several groups that were negatively affected included small native demersal fishes and sea birds (Fig. 1). In addition, the model predicted a near collapse of mullets (Fig. 7a), despite the reduction of fishing effort, and a significant decline of rocky fishes (Fig. 7c). In contrast, demersal sharks, rays and skates and turtles significantly increased (Fig. 1). In addition, hake and large native demersal fishes were predicted to increase (Fig. 7b,d), mainly due to reduced fishing effort and a higher abundance of alien prey (Figure S2b), although native prey significantly declined and there was negative impact of SST on hake.

Within this scenario, forage fish, invertebrate biomass and Kempton's index significantly decreased, while predatory biomass, total catch and mTLco significantly increased (Fig. 4). FCI and PL were projected to decline significantly, while TST increased (Fig. 4).

Finally, under the assessment of the cumulative impact of the new Israeli fishing regulations and the intermediate scenario of sea warming, while keeping the biomass of alien species constant (Scn11), the model highlighted the important effects of alien species. For example, native invertebrates increased more than in Scn9 and native fishes decreased less than Scn9 and Scn10 (Fig. 2). For specific groups, small native demersal fishes decreased less than Scn9 and Scn10 (Fig. 1). Hake presented a better trajectory than Scn9 (Fig. 7b). This could be due to a less competition for resources with alien lizardfish, which biomass was kept at constant population levels. However, it presented a worst trajectory than Scn10 (Fig. 7), which could be due less prey availability. On the other hand, large native demersal fishes presented a worse trajectory than Scn9 and Scn10 (Fig. 7d), which could be also due to less prey availability. Mullets and rocky fishes presented similar trajectories than Scn9 (Fig. 7a,c), which may be related to similar predation rates and competition for resources in both scenarios.

Within this scenario, ecological indicators presented similar trends to Scn9 (Fig. 4). In several cases slightly better trends than Scn9 were observed, such as in forage fish, Kempton's index, mTLc and mTLco, while total catch and PL presented slightly worse trends than Scn9 (Fig. 4).

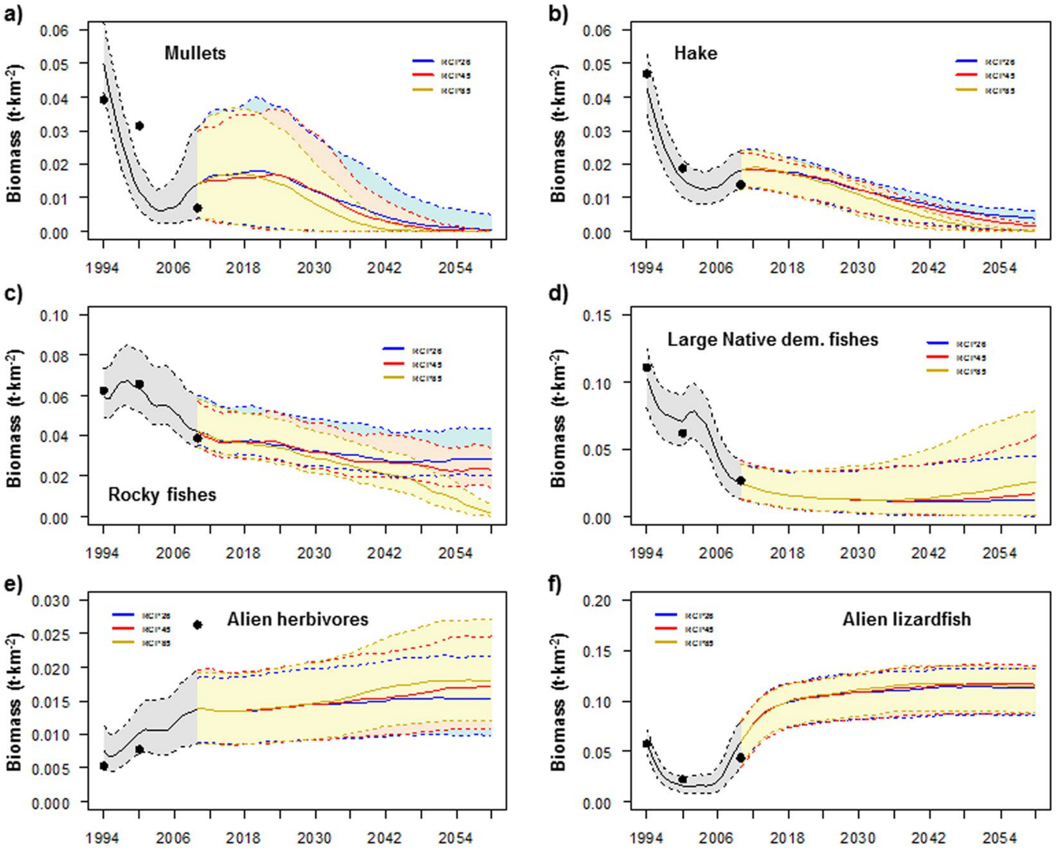


Figure 5. Comparison between the predicted (solid lines) and observed (dots) time series of biomass (t·km^2), and scenarios results for (**a**) mullets, (**b**) hake, (**c**) rocky fishes, (**d**) large native demersal fishes, (**e**) alien herbivores and (**f**) alien lizardfish under different future scenarios of climate change for the Israeli Mediterranean continental shelf (ICS) ecosystem model for the period 1994–2060. Black line represents historical model predictions and coloured lines represent different scenarios. Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

Common patterns of future scenarios. In general, primary producers increased in most of the scenarios (Fig. 2). This can be attributed to the decrease of zooplanktonic groups in most of the scenarios (Fig. 2), which is due to increased predation on these groups. Alien invertebrates decreased in scenarios that only fishing reductions were applied while increasing in the other scenarios (Fig. 2). This can be attributed to increasing predation and decreasing predation and competition, respectively. Alien fishes increased in all scenarios due to reductions of competition and predators except in Scn2 (Fig. 2), where there is a large decrease in earlier alien demersal fishes attributed to higher predation rates (Fig. 1). New alien demersal fishes increased in all the scenarios, which may due to fishing reductions and/or the decrease of competition (both native and alien groups). Native fishes decreased in all scenarios except those scenarios where only fishing reductions were applied (Fig. 1). Specifically, small native demersal fishes decreased in all scenarios. This general pattern is due to unfavorable thermal conditions, while for specific scenarios we can add increasing predation (fishing reductions) and competition for resources (alien species scenarios) or both (cumulative scenarios) as the main drivers of the ecological patterns. Vulnerable species increased in all scenarios that implied reductions in fishing activities (Fig. 2), although sea birds decreased in all scenarios (Fig. 1).

Discussion

In the current context of global change and ecological crisis, there is an increasing demand for approaches that can forecast potential impacts of human stressors, in addition to environmental pressures[16]. In this study, we used a temporal dynamic food web model for the Israeli Mediterranean continental shelf that accounted for different environmental and human impacts, such as sea warming, fisheries and alien species, to assess potential futures of marine resources and ecosystem conditions of the Eastern Mediterranean Sea. Despite several limitations, this study represents to our knowledge the first attempt to evaluate potential impacts of future conditions in the Eastern Mediterranean Sea in an ecosystem context combining different global change stressors.

Our results highlight that under current conditions (the baseline scenario) several species will remain depleted or even greatly decline, due to unfavourable thermal conditions, increasing impacts of alien species, and unsustainable fishing activities. Meanwhile, alien groups will continue to increase in abundance, as many of these species have higher thermal tolerances. This general degradation of the system is also captured by the decline of

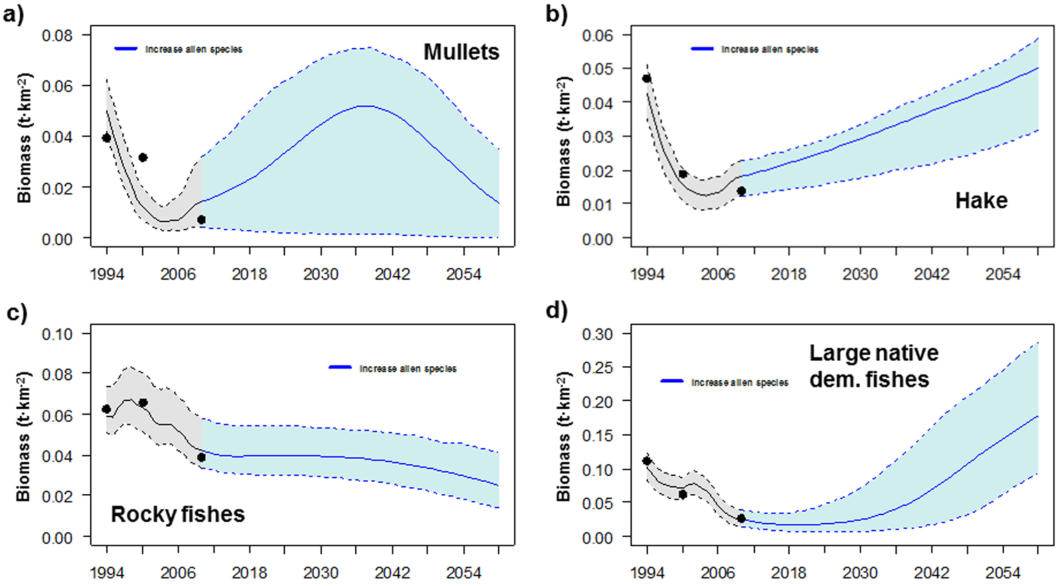


Figure 6. Comparison between the predicted (solid lines) and observed (dots) time series of biomass (t·km^2), and scenarios results for (**a**) mullets, (**b**) hake, (**c**) rocky fishes (or small native demersal fishes) and (**d**) large native demersal fishes under the future scenario of increasing the biomass of alien species for the Israeli Mediterranean continental shelf (ICS) ecosystem model for the period 1994–2060. Black line represents historical model predictions and coloured lines represent different scenarios. Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

ecological indicators linked with ecosystem condition, such as mTLc, mTLco and FCI. These results are in line with Corrales, *et al.*[46], where results indicated a historical degradation pattern of the food web over the last two decades (1990–2010) due to the impacts of alien species, climate change and fishing. However, other ecological indicators increased, such as total biomass, predatory biomass and PL. This could be due to the fact that reductions of native species in terms of biomass and path lengths are compensated by the increase of alien species.

In contrast, when fishing effort for several fleets was reduced, our results highlighted a potential restoration of several exploited groups including commercially important species such as hake, mullets and large native demersal fishes, and some vulnerable species such as sharks and rays and skates. Alien groups (fish and crustaceans) were negatively impacted, mainly due to the recovery of predators, while native groups were positively affected. This overall improvement of some marine resources was captured by several ecological indicators that showed a trend of increasing values, such as the predatory biomass, Kempton's Index, mTLc, mTLco and FCI.

Fishing has been identified as one of the main stressors on marine ecosystems[50,51], and studies have shown the potential benefits of fishing reduction[52,53]. Our results highlighted the benefits of reducing fishing activities on the exploited marine organisms and ecosystem in the Eastern Mediterranean Sea, and support the call for a reduction in fishing capacity and exploitation levels worldwide if marine resources are to recover[53,54].

The scenarios of sea warming showed potential detrimental impacts on the food web, with the impacts becoming greater as temperature increased. Within these scenarios, native species were negatively impacted, and we observed some collapses, while alien species were favoured. In line with this, several ecological indicators, including Kempton's Index, mTLco and FCI suggested a potential degradation of the ecosystem. Predicted collapses of some native species in this study may not indicate a total collapse of the species in the Eastern Mediterranean Sea, but may indicate that if these species are to persist in the ecosystem, they may have to migrate to northern areas or to deeper and cooler waters outside of the modelled area, or they will have to adapt. Shifts in species distributions (latitudinal and bathymetric) in relation to climate change have been observed and predicted in many areas of the world[55–57]. Bathymetric shifts and species collapses have been observed recently in the study area associated with sea warming and the proliferation of alien species[29,58]. In addition, several studies have predicted important changes in species distributions due to sea warming in the Mediterranean Sea[48,59]. In fact, the increasing importance of alien species (thermophilic biota) concurrent with sea warming has led to the tropicalization of the Mediterranean biota[40].

Our projections of the impact of sea warming present some limitations. For example, the temperature response/preferences used in our study are subject to uncertainty, as they came from a global database (AquaMaps)[60], although we did incorporate local knowledge to adapt the global responses to local conditions (see Corrales, *et al.*[46] for more details). In addition, due to the lack of information on the responses to the explanatory variable change, our model did not incorporate salinity, which has been suggested as an important environmental factor in the study area[61]. Also, other impacts of climate change were not considered. For example, ocean acidification, which mainly acts on invertebrates and basal species, can have strong impacts on the food web[62,63]. Furthermore, our model does not account for the possible acclimatization, selection, and adaptation of species to climate change. Correctly predicting the impacts of climate change on marine organisms and ecosystems remains

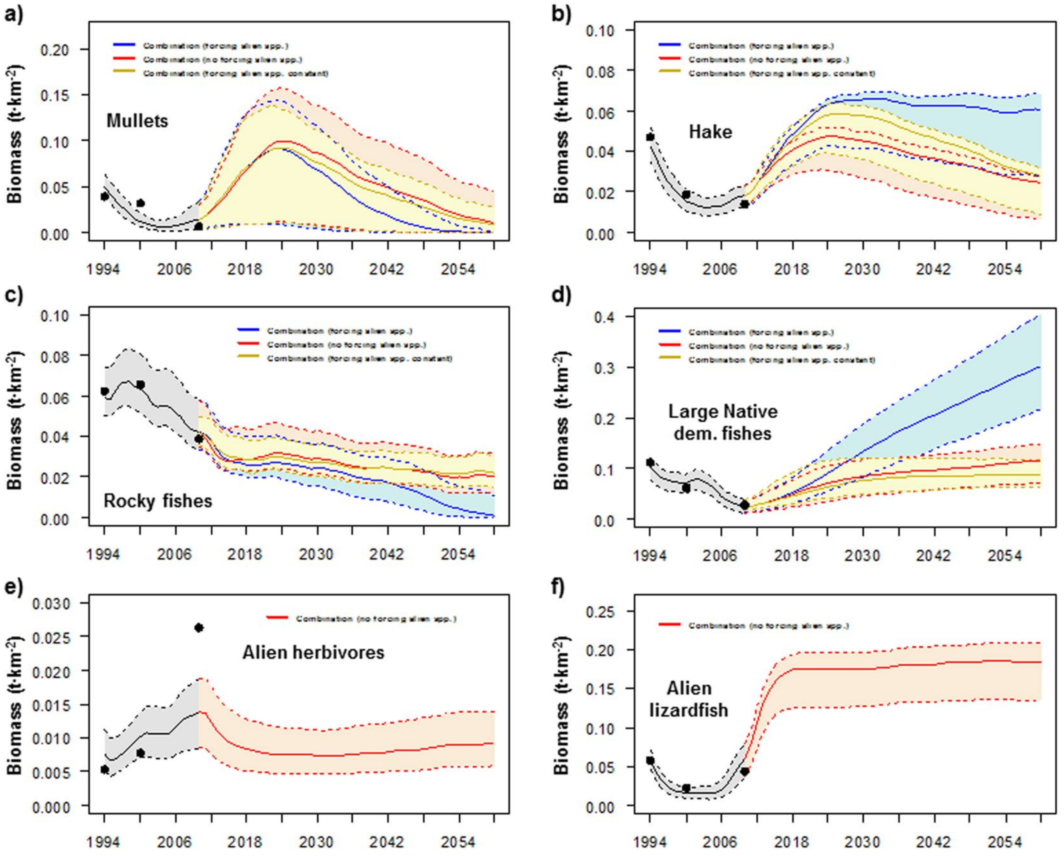


Figure 7. Comparison between the predicted (solid lines) and observed (dots) time series of biomass (t·km^2), and scenarios results for (**a**) mullets, (**b**) hake, (**c**) rocky fishes, (**d**) large native demersal fishes, (**e**) alien herbivores and (**f**) alien lizardfish under different future scenarios of a combination of stressors for the Israeli Mediterranean continental shelf (ICS) ecosystem model for the period 1994–2060. Black line represents historical model predictions and coloured lines represent different scenarios. Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine. Scenarios that include forcing of the biomass are not shown.

challenging due to a general lack of knowledge about the capacity of organisms to adapt to rapid climate change[64]. In addition, our model is a temporal-dynamic representation of the ecosystem and does not explicitly incorporate spatial dynamics (such as movement of species) and therefore the potential movement of species to deeper waters or latitudinal (northward) shifts are not captured. Within this context, the new habitat foraging capacity model of the spatial-temporal module of EwE, Ecospace[65,66], has provided a step forward for temporal-spatial modelling by combining species distribution and food web models. As new information becomes available, our modelling exercise should be updated and improved, so model predictions would become increasingly valuable for understanding cumulative impacts within a spatial-temporal dynamic framework.

Our results highlighted the potential negative impacts of alien species on marine species and food webs, either when extrapolating current trends to the future, or when allowing EwE to predict their future abundance. Alien species proliferation causes the collapse of small native demersal fishes and a degradation pattern in the food web, as shown by different ecological indicators (i.e., predatory biomass, Kempton's index, mTLco, FCI and PL). Biological invasions are considered a major threat to local biodiversity[28,67]. Although no complete extinctions have yet been reported in the Mediterranean Sea as a direct result of alien species, there are many examples of sudden declines and local extirpations of native species concurrent with the proliferation of alien species[29,68].

It is important to note that our model has a limited capacity to assess the impacts of alien species. Our study only considers alien fish and crustacean (shrimps and crabs) species, since for other groups no information was available to be considered within our temporal modelling approach[69]. However, the invasion of other organisms seems to be of the same magnitude or even greater[69,70]. In addition, the information about pelagic fishes were limited and the definition of small and medium pelagic fishes groups within the model includes both native and alien species[46]. Finally, several new alien species have invaded the Eastern Mediterranean Sea in recent years and were not included in the model[31,32]. One of these species, the lionfish (*Pterois miles*), has alarmed the scientific community, arriving in the Mediterranean Sea in 1991[71] but not recorded again until 2012[72]. This species has had detrimental effects on invaded ecosystems, such as the Caribbean Sea[73]. It is expected that the current and future enlargement of the Suez Canal and future sea warming will allow the invasion of more species[74], and that the Eastern Mediterranean Sea can become an extension of the Red Sea in terms of species composition, even including reef building corals[75,76].

Under cumulative stressor scenarios, our study showed that the beneficial effects of fisheries reduction could be dampened by the combined impacts of sea warming and alien species. For example, mullets, hake and predators in general may not recover if sea warming and alien species impacts are also at play. These results highlight the need to include stressors other than fisheries, such as climate change and biological invasions, in the assessment of risk and the implementation of an ecosystem-based management approach to correctly assess the future of marine ecosystems. Serpetti, *et al.*[26], using an EwE model on the west coast of Scotland, highlighted that ocean warming could jeopardize sustainable fisheries practices in the future. Our results are complementary to this study and suggest that regional and global scale impacts such as biological invasions and sea warming can impair, or at least limit, the outputs of local fisheries management measures.

There is an increasing need to identify and quantify the biophysical thresholds that must not be exceeded, so as to prevent catastrophic shifts in ecosystems. Catastrophic shifts can be defined as persistent and substantial reorganizations of the structure and functioning of ecosystems and from which their recovery is difficult or impossible[77,78]. The boundaries of several processes (e.g., climate change and biodiversity loss) define the "safe operating space" for humanity[78]. However, crossing certain boundaries may take the ecosystem beyond its "safe operating space", where the risk of unpredictable and damaging change is very high. Our results highlighted the fact that a reduction in fishing activities promotes the resilience of some species to climate change and the impacts of alien species in the Eastern Mediterranean Sea, with resilience defined as the capacity of species and ecosystems to resist and absorb disturbance and their ability to recover[79,80]. In addition, some native species reacted better to reduced fishing activities when alien species were maintained at constant levels in the absence and presence of sea warming. However, once a boundary is crossed, a species can collapse. In our study, this is the case for mullets and hake. These species have been severely impacted in recent decades by fishing activities, alien species (goatfishes and alien lizardfish, respectively), and sea warming[46,68,81–83]. In the cumulative impact scenarios, these functional groups initially benefited from reduced fishing effort. However, once the boundary of thermal tolerance was crossed, mullets and hake decreased notably. When we forced an increase in alien species biomass, in addition to sea warming, mullets collapsed due to the additional effects of predation and competition, while hake biomass remained almost constant due to the higher abundance of prey. Our study illustrates that complex dynamics between environmental and ecological processes may interact in the future and it is essential to take them into account.

In recent decades, human activities have exponentially increased[1]. These include local stressors such as overfishing, habitat destruction and pollution, and regional and global stressors, such as biological invasions and climate change. Such anthropogenic effects impose large impacts on marine organisms and ecosystems, affecting ecosystem structure and services[4,67,84]. Organisms and ecosystems already stressed by fishing are more vulnerable to further impacts such as climate change and biological invasions[55,85]. As temperature will increase in the future and options for the management of ocean warming are limited at the local and regional scale, reducing local and regional threats such as overexploitation and biological invasions, may be one of the solutions to promoting resilience to climate change, ensuring the capacity to exploit marine resources safely and preserving ecosystem functions and services[57,86].

Different management actions have been used for reducing the impacts of fisheries, including, among others, the establishment of catch limits, fishing effort reductions, increasing gear selectivity and the implementation of Marine Protected Areas (MPAs)[87]. MPAs have been suggested as an effective tool to mitigate impacts of climate change and alien species[88,89], although biological invasions have been largely disregarded in marine conservation plans[90] and the effectiveness of MPAs in preventing invasions has been questioned[91]. The prevention of new introductions should be a priority in the development of effective policies, followed by early detection, rapid response and possible eradication of alien species[92]. In the context of our study area, some authors have suggested installing an environmental barrier in the Suez Canal, such as an hypersaline lock, since it may "reduce the likelihood of species migration through canals"[93]. In fact, "the Suez Canal had, for nearly a century, a natural salinity barrier in the form of the high salinity Bitter Lakes"[93]. In addition, although eradication is challenging, some countries have initiated eradication programs to minimize the impacts of alien species in the marine environment. For example, in Cyprus, governmental authorities encouraged fishermen to catch alien poisonous pufferfish (*Lagocephalus sceleratus*)[94], which have detrimental effects on native biota and fisheries[95].

Ecological indicators are quantitative measurements that provide information about key ecosystem characteristics. They are increasingly used to document ecosystem status and to track the effects of anthropogenic and environmental stressors on marine ecosystems, as well as the effectiveness of management measures; making them a valuable tool within the EBM framework[96–98]. We showed that trophic level-based indicators (mTLc and mTLco) were informative about the effects of fishing pressure, as they decreased in the baseline scenario (high fishing pressure) while increasing in all scenarios where fishing reductions were implemented. However, they exhibited opposite trends in sea warming scenarios. The predatory biomass indicator also indicated potential benefits of fishing restrictions, as well as detrimental impacts of sea warming. In addition, Kempton's index successfully tracked fishing pressure, sea warming and impacts of alien species. Therefore, our study illustrates how several ecological indicators obtained from EwE models can be useful to assess ecosystem status[99,100], but they may show complex trends to interpret as additional pressures to marine ecosystems are investigated.

Material and Methods

Study area.

The Israeli Mediterranean continental shelf (ICS) ecosystem (Figure S1) is located in the Eastern Mediterranean Sea, also known as the Levantine Sea. The Levantine Sea has the hottest, most saline and most oligotrophic waters in the Mediterranean Sea[101,102] as a result of high evaporation rates, very low riverine inputs and limited vertical mixing.

Currently, the Levantine Sea is the world's most invaded marine ecoregion, with important effects on the food web[29,103]. In addition, it has been suggested that intense fishing pressure has jeopardized the sustainability of fishing activities[104]. Finally, the waters of the Levantine Sea are warming at higher rates than the global average[37,105], with important effects on marine biota[36,58].

Overview of the modelling approach. The ecological modelling approach Ecopath with Ecosim (EwE)[106] was used to model the study area. The EwE approach consists of three main modules: the mass-balance routine Ecopath, the time dynamic routine Ecosim and the spatial-temporal dynamic module Ecospace. For an extensive review of EwE principles, basic concepts, capabilities and limitations, see Christensen and Walters[106] and Heymans, *et al.*[107].

The Ecopath mass-balance model was developed using EwE version 6.5 (www.ecopath.org) to characterise the structure and functioning of the ICS and to assess the past and current impact of alien species and fishing[49]. The model covered an area of 3,725 km^2, with coastal waters up to 200 m in depth. It represented two time periods (1990–1994 and 2008–2010), including 39 and 41 functional groups, respectively, from primary producers to top predators and considers specific groups for alien species (Figure S2a; Table S1)[49]. This model took into account the main fleets operating in the area, including bottom trawl, purse seine and artisanal fisheries, and recreational fishers. Direct and indirect trophic impacts between functional groups and fleets are shown in Figure S2b.

Based on the Ecopath model, the time dynamic module Ecosim[108] was constructed and fitted to time series of data from 1994 to 2010. The model was used to consider the combined effect of alien species, fishing activities and changes in sea surface temperature and primary productivity[46]. Ecosim uses a set of differential equations to describe biomass dynamics, expressed as:

$$\frac{dB_i}{dt} = \left(\frac{P}{Q}\right)_i \cdot \sum Q_{ji} - \sum Q_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i \tag{1}$$

where dB_i/dt is the growth rate of group (i) during time t in terms of its biomass B_i; $(P/Q)_i$ is the net growth efficiency of group (i); M_i is the non-predation mortality rate; F_i is the fishing mortality rate; e_i is the emigration; and I_i is the immigration rate[106]. Consumption rates (Q_{ij}) are calculated based on the "foraging arena" theory[109], which divides the biomass of a prey into a vulnerable and a non-vulnerable fraction and the transfer rate or vulnerability between the two fractions determines the trophic flow between the predator and the prey. The vulnerability concept incorporates density-dependency and expresses how far a group is from its carrying capacity[106,110]. For each predator-prey interaction, consumption rates are calculated as:

$$Qij = \frac{a_{ij} * v_{ij} * B_i * P_j * T_i * T_j * M_{ij}/D_j}{v_{ij} + v_{ij} * T_i * M_{ij} + a_{ij} * M_{ij} * P_i * T_j/D_j} * f(Env_{function}, t) \tag{2}$$

where a_{ij} is the rate of effective search for prey (i) by predator (j), v_{ij} is the vulnerability parameter, Ti represents prey relative feeding time, T_j is the predator relative feeding time, B_i is prey biomass, P_j is predator abundance, M_{ij} is the mediation forcing effects, and D_j represents effects of handing time as a limit to consumption rate[109,110]. Environmental response functions ($Env_{function}$, t), which represents the tolerance relationship of a species to an environmental parameter (here defined with a minimum and maximum levels and the 10th and 90th preferable quantiles), can be used to account for environmental drivers that change overtime, such as temperature. The intercept between the environmental response function and the environmental driver is used to calculate a multiplier factor (f) (eq. 2), which then modifies the consumption rates of a species, or functional group, with a maximum value of 1 and declining values (and thus limiting the foraging capacity of a group) when the environmental driver deviates from the optimum values[26,66].

A time series of nominal fishing effort from the Fisheries Department of the Ministry of Agriculture and Rural Development of Israel was used to drive the model by modifying fishing mortality on targeted groups. A time series of annual sea surface temperature (SST, upper 30 meters) from 1994 to 2010 and temperature response functions were used to drive the temporal dynamics of sensitive functional groups with available information (mostly crustaceans and fish groups)[46]. Time series of SST were obtained from the Mediterranean Forecasting System Copernicus (http://marine.copernicus.eu/). Environmental response functions, which here determine optimum temperatures and thermal tolerance, were obtained initially from AquaMaps[60] and were modified incorporating expert local knowledge (see Corrales, *et al.*[46] and Table S2 for further details).

Simulation of future scenarios. We used the temporal dynamic module Ecosim to evaluate the effect of plausible future scenarios for major stressors in the area (Table 1). With the exception of the two new alien groups (new alien demersal fishes and alien medium pelagic fishes), we used the original Ecosim configuration that was fitted to the time series of data[46]. For these two new alien groups, low vulnerability values had been estimated by the model in the fitting procedure, impeding a further increase in biomass of these groups in the future. As a continuous increase in biomass of these groups is expected, we applied a high vulnerability value ($v = 10$) to them to allow a larger change in the baseline predation mortality. All future scenarios were run for 50 years, from 2010 to 2060, and included variations of different stressors (Table 1). Primary production, in the absence of information about projected potential changes, was kept constant in all the scenarios from 2010 to 2060.

The original configuration of the dynamic model was used as a baseline simulation (Business as usual (BAU)) (Scn1). We then assessed the impact of various fisheries management strategies while keeping constant temperature levels from 2010 to 2060. Scn2 included the new fishing regulations approved by the Fisheries Department of the Ministry of Agriculture and Rural Development of Israel in 2016. These regulations, among other components, consist of a reduction in fishing efforts for the trawling and artisanal sectors and impose restrictions on the recreational fishers. For the trawl fleet, a complete cessation of its activity between April and June was implemented. In addition, the trawl fleet in the northern part of the country is to be mostly eliminated. These two

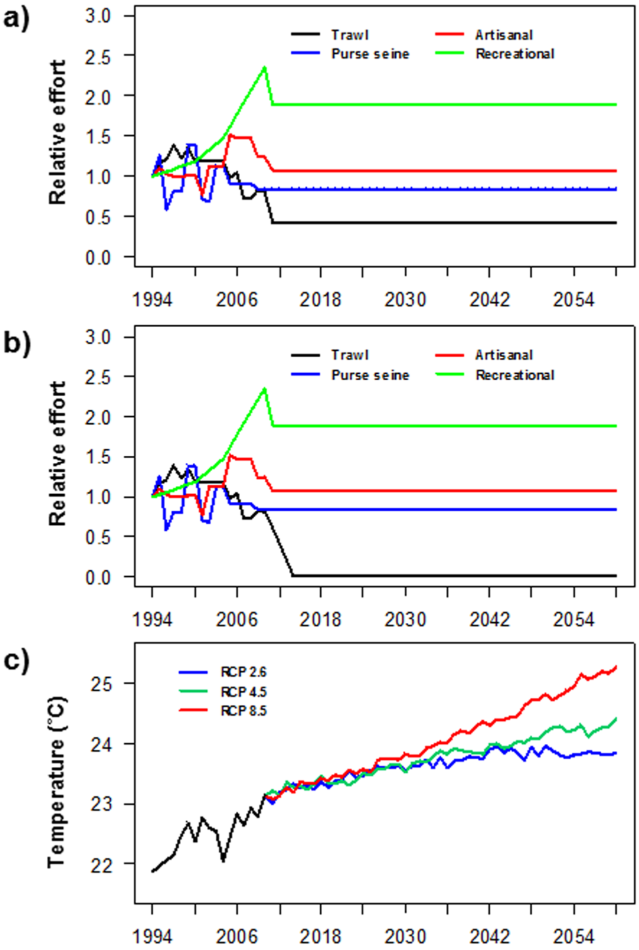


Figure 8. Stressors in the Israeli Mediterranean continental shelf (ICS) ecosystem for the period 1994–2060 considered in this study: (**a**) relative fishing effort by fleet as a result of the application of the new Israeli law starting in 2010 in the simulations; (**b**) relative fishing effort by fleet as a result of the application of the new Israeli law with the closure of the trawl fleet after three years of reduction from 2010; and (**c**) historical annual sea surface temperature (black line) and its projection under the three scenarios of IPCC projections.

regulations were implemented in our scenario and represented a reduction in trawl effort of nearly 50% (Fig. 8a). For the artisanal fleet, a ban between April and May was implemented and implied a reduction in fishing effort of nearly 15% (Fig. 8a). For recreational fishers, the new regulation restricted their capacity to a maximum catch of 5 kg per day. In the absence of detailed data about recreational effort and being conservative, a reduction of 20% of the effort was applied (Fig. 8a). In addition, some sectors of the Israeli society have called for a ban of trawling altogether. Therefore, we ran a scenario that applies the new fishing regulations with trawling eliminated within the first 3 years of the simulation (Fig. 8b) (Scn3). In addition, to quantify only the effects of these new fishing regulations, we ran a scenario keeping the biomass of alien species and temperature constant from their 2010 levels to 2060 (Scn4).

To predict the impact of sea warming on the ICS ecosystem, future SST projections of the study area were obtained from the Royal Netherlands Meteorological Institute Climate explorer (http://climexp.knmi.nl). We calculated SST projections under the four scenarios of greenhouse emissions (RCP2.6, RCP4.5, RCP6 and RCP8.5). As SST from this explorer did not match the SST from COPERNICUS, we calculated SST anomalies for the 2010–2060 period and these SST anomalies were applied to the COPERNICUS time series (Fig. 8c). Due to similar trends of the intermediate scenarios (RCP4.5 and RCP6), we applied only the RCP4.5 scenario. Therefore, the scenarios conducted to simulate potential impacts of sea warming were RCP2.6 (Scn5), RCP4.5 (Scn6) and RCP8.5 (Scn7). In these scenarios, fishing effort was kept constant from its 2010 levels to 2060.

To forecast future impacts of alien species, we forced the biomass of alien groups to follow current trends (Figure S3), while keeping fishing effort and SST constant from their 2010 levels to 2060 (Scn8).

In addition, we evaluated the combined impacts of the stressors simultaneously through three scenarios. In Scn9 (combination without forcing alien species), we merged scenarios 2 and 6, thus combining the new fishing regulations with an intermediate increase in SST, and we left alien species to change through the time (we did not force their biomass). In Scn10 (combination with forcing alien species), we merged scenarios 2, 6 and 8, thus combining the new fishing regulations, the intermediate increase in SST and an increase in the biomass of alien species following current trends. In Scn11 (combination with forcing alien species constant), we merged scenarios 2 and 6, thus combining the new fishing regulations, the intermediate increase in SST, and we force alien species to keep them at 2010 levels.

Analysis. We analysed changes in the biomass of selected functional groups. These groups were chosen taking into account their inclusion in the time series fitting (see Corrales, *et al.*[46]) and considering their importance (economic and ecological importance, such as commercial species and vulnerable species). In addition, functional groups were aggregated taking into account their ecological role, taxonomy, habitat and between alien and native functional groups. Therefore, we defined separate groups as primary producers, zooplanktonic species, invertebrates, fishes and vulnerable species (which included sea turtles, sea birds and dolphins). Invertebrates and fishes were split into native and alien groups, and fishes were also divided between demersal and pelagic.

In addition, a selection of ecological indicators was used to evaluate the impacts of ecological changes on the ecosystem over time:

(1) Total biomass (excluding detritus) ($t \cdot km^{-2}$), which included biomass of all the functional groups excluding detritus (detritus and discards). This indicator was used to quantify changes at the whole ecosystem level[20].
(2) Forage fish biomass ($t \cdot km^{-2}$), which included the biomass of benthopelagic fishes, small pelagic fishes, mackerel and horse mackerel. This indicator was analysed to quantify changes in the pelagic compartment[111].
(3) Invertebrate biomass ($t \cdot km^{-2}$), which included biomass of benthic invertebrate groups. This indicator was used to assess the dynamics of benthic invertebrates in the ecosystem, which tends to benefit from reductions in fish and predator biomass[112].
(4) Predatory biomass ($t \cdot km^{-2}$), which included biomass of all the groups with TL ≥ 4 and tends to decrease with increasing fishing impact in marine ecosystems[113].
(5) Kempton's index, which expresses biomass diversity by considering those organisms with trophic levels ≥ 3 and tends to decrease with ecosystem degradation[114].
(6) Total catch ($t \cdot km^{-2} \cdot year^{-1}$), which includes the annual catches of the different fleets and provides an idea of total fisheries removals[111].
(7) Mean Trophic Level of the catch (mTLc), which expresses the TL of the catch, reflects the fishing strategy of the fleet and is used to quantify the impact of fishing[112].
(8) Mean Trophic Level of the community (mTLco), which expresses the Trophic Level (TL) of the whole ecosystem, reflects the structure of the ecosystem and is used to quantify the impact of fishing[113].
(9) Total System Throughput ($t \cdot km^{-2} \cdot year^{-1}$) (TST), which estimates the total flows in the ecosystem and is a measure of ecosystem size[115].
(10) Finn's Cycling Index (FCI, %), which represents the proportion of the TST that is recycled in the system and is an indicator of stress and structural differences[116].
(11) Path length (PL), defined as the average number of compartments through which a unit of inflow passes, which is an indicator of stress[117].

Assessing uncertainty. Monte Carlo simulations and the Ecosampler plug-in were used to evaluate the impact of uncertainty in Ecopath input parameters (biomass, production and consumption rates) on Ecosim outputs (biomass and catch trends, and ecological indicators)[107,118,119]. We ran 500 Monte Carlo simulations for each scenario based on input parameter pedigree, which documents the quality of the input data (see Table S3 for confidence intervals of all input parameter), to determine the 5% and 95% confidence intervals for Ecosim outputs. Finally, a Spearman's rank correlation test implemented in R software v 3.4.2 was used to assess the correlation between model outputs (predicted results without uncertainty analysis) with time.

References

1. Halpern, B. S. *et al.* Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature communications* **6** (2015).
2. Costello, M. J. *et al.* A census of marine biodiversity knowledge, resources, and future challenges. *PloS one* **5**, e12110 (2010).
3. Pereira, H. M. *et al.* Scenarios for global biodiversity in the 21st century. *science* **330**, 1496–1501 (2010).
4. Worm, B. *et al.* Impacts of biodiversity loss on ocean ecosystem services. *science* **314**, 787–790 (2006).
5. McCauley, D. J. *et al. Marine defaunation: Animal loss in the global ocean.* **347**, 1255641 (2015).
6. Crain, C. M., Kroeker, K. & Halpern, B. S. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology letters* **11**, 1304–1315 (2008).
7. Côté, I. M., Darling, E. S. & Brown, C. J. Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society of London B: Biological Sciences* **283**, https://doi.org/10.1098/rspb.2015.2592 (2016).
8. Cury, P. M. *et al.* Ecosystem oceanography for global change in fisheries. *Trends in Ecology & Evolution* **23**, 338–346 (2008).
9. Link, J. S. *et al.* Relating marine ecosystem indicators to fishing and environmental drivers: an elucidation of contrasting responses. *ICES Journal of Marine Science* **67**, 787–795 (2010).
10. Leslie, H. M. & McLeod, K. L. Confronting the challenges of implementing marine ecosystem-based management. *Frontiers in Ecology and the Environment* **5**, 540–548 (2007).
11. Rosenberg, A. A. & McLeod, K. L. Implementing ecosystem-based approaches to management for the conservation of ecosystem services. *Marine ecology. Progress series* **300**, 270–274 (2005).
12. Fulton, E. A. *et al.* Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish and Fisheries* **12**, 171–188 (2011).
13. Acosta, L. A. *et al.* In *Methodological assessment of scenarios and models of biodiversity and ecosystem services* [Ferrier, S. *et al.* (eds)] (ed IPBES)43–100 (2016).
14. Christensen, V. Ecological Networks in Fisheries: Predicting the Future? *Fisheries* **38**, 76–81 (2013).

15. Link, J. S. *et al*. Dealing with uncertainty in ecosystem models: the paradox of use for living marine resource management. *Progress in Oceanography* **102**, 102–114 (2012).
16. Maris, V. *et al*. Prediction in ecology: promises, obstacles and clarifications. *Oikos* **0**, 1–12 (2017).
17. Hyder, K. *et al*. Making modelling count-increasing the contribution of shelf-seas community and ecosystem models to policy development and management. *Marine Policy* **61**, 291–302 (2015).
18. Ferrier, S. *et al*. In IPBES, 2016: Methodological assessment of scenarios and models of biodiversity and ecosystem services [S. Ferrier *et al*. (eds.)] (2016).
19. Merrie, A., Keys, P., Metian, M. & Österblom, H. Radical ocean futures-scenario development using science fiction prototyping. *Futures* (2017).
20. Heymans, J. J., Coll, M., Libralato, S., Morissette, L. & Christensen, V. Global Patterns in Ecological Indicators of Marine Food Webs: A Modelling Approach. *PloS one* **9**, e95845 (2014).
21. Colléter, M. *et al*. Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. *Ecological Modelling* **302**, 42–53 (2015).
22. Christensen, V. & Walters, C. In *Ecosystem approaches to fisheries: a global perspective. Cambridge University Press, Cambridge* 189–205 (Cambridge University Press, 2011).
23. Ainsworth, C. *et al*. Potential impacts of climate change on Northeast Pacific marine foodwebs and fisheries. *ICES Journal of Marine Science: Journal du Conseil*, *fsr043* (2011).
24. Pinnegar, J. K., Tomczak, M. T. & Link, J. S. How to determine the likely indirect food-web consequences of a newly introduced non-native species: A worked example. *Ecological Modelling* **272**, 379–387 (2014).
25. Coll, M. *et al*. Modelling dynamic ecosystems: venturing beyond boundaries with the Ecopath approach. *Reviews in fish biology and fisheries* **25**, 413–424 (2015).
26. Serpetti, N. *et al*. Impact of ocean warming on sustainable fisheries management informs the Ecosystem Approach to Fisheries. *Scientific reports* **7**, 13438 (2017).
27. Libralato, S., Caccin, A. & Pranovi, F. Modelling species invasions using thermal and trophic niche dynamics underclimate change. *Frontiers in Marine Science* **2**, 29 (2015).
28. Molnar, J. L., Gamboa, R. L., Revenga, C. & Spalding, M. D. Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment* **6**, 485–492 (2008).
29. Edelist, D., Rilov, G., Golani, D., Carlton, J. T. & Spanier, E. Restructuring the Sea: profound shifts in the world's most invaded marine ecosystem. *Diversity and Distributions* **19**, 69–77 (2013).
30. Katsanevakis, S. *et al*. Invading the Mediterranean Sea: biodiversity patterns shaped by human activities. *Marine Ecosystem Ecology* **1**, 32 (2014).
31. Galil, B. S., Marchini, A. & Occhipinti-Ambrogi, A. East is east and West is west? Management of marine bioinvasions in the Mediterranean Sea. *Estuarine, Coastal and Shelf Science* (2016).
32. Zenetos, A. *et al*. Uncertainties and validation of alien species catalogues: The Mediterranean as an example. *Estuarine, Coastal and Shelf Science* (2017).
33. Vasilakopoulos, P., Maravelias, C. D. & Tserpes, G. The Alarming Decline of Mediterranean Fish Stocks. *Current Biology* **24**, 1643–1648 (2014).
34. Tsikliras, A. C., Dinouli, A., Tsiros, V.-Z. & Tsalkou, E. The Mediterranean and Black Sea fisheries at risk from overexploitation. *PloS one* **10**, e0121188 (2015).
35. Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C. F. & Pérez, T. Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends in Ecology & Evolution* **25**, 250–260 (2010).
36. Givan, O., Edelist, D., Sonin, O. & Belmaker, J. Thermal affinity as the dominant factor changing Mediterranean fish abundances. *Global Change Biology* (2017).
37. Nykjaer, L. Mediterranean Sea surface warming 1985–2006. *Climate Research* **39**, 11–17 (2009).
38. Shaltout, M. & Omstedt, A. Recent sea surface temperature trends and future scenarios for the Mediterranean Sea. *Oceanologia* **56**, 411–443 (2014).
39. Bianchi, C. N. *et al*. The changing biogeography of the Mediterranean Sea: from the old frontiers to the new gradients. *Boll. Mus. Ist. Biol. Univ. Genova* **75**, 81–84 (2013).
40. Bianchi, C. N. In *Biodiversity in Enclosed Seas and Artificial Marine Habitats* 7–21 (Springer, 2007).
41. Coll, M. *et al*. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PloS one* **5**, e11842 (2010).
42. Coll, M. *et al*. The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves. *Global Ecology and Biogeography* **21**, 465–480 (2012).
43. Goren, M., Shults, D. & Gafni, A. The Current State of Fish and Israel's Fisheries in the Mediterranean Sea. A special report to the Society for the Protection of Nature in Israel (SPNI). *English version. 1-80pp. Tel Aviv* (2013).
44. Sternberg, M. *et al*. Impacts of climate change on biodiversity in Israel: an expert assessment approach. *Regional Environmental Change* **15**, 895–906 (2015).
45. Galil, B. & Goren, M. In *The Mediterranean Sea* 463–478 (Springer, 2014).
46. Corrales, X. *et al*. Hindcasting the dynamics of an Eastern Mediterranean marine ecosystem under the impacts of multiple stressors. *Marine Ecology Progress Series* **580**, 17–36 (2017).
47. Galil, B., Marchini, A., Occhipinti-Ambrogi, A. & Ojaveer, H. The enlargement of the Suez Canal—Erythraean introductions and management challenges. *Management of Biological Invasions* **8**, 141–152 (2017).
48. Albouy, C. *et al*. Projected climate change and the changing biogeography of coastal Mediterranean fishes. *Journal of Biogeography* **40**, 534–547 (2013).
49. Corrales, X. *et al*. Modeling the role and impact of alien species and fisheries on the Israeli marine continental shelf ecosystem. *Journal of Marine Systems* **170**, 88–102 (2017).
50. Jackson, J. B. *et al*. Historical overfishing and the recent collapse of coastal ecosystems. *science* **293**, 629–637 (2001).
51. Lotze, H. K. *et al*. Depletion, degradation, and recovery potential of estuaries and coastal seas. *science* **312**, 1806–1809 (2006).
52. Lotze, H. K., Coll, M., Magera, A. M., Ward-Paige, C. & Airoldi, L. Recovery of marine animal populations and ecosystems. *Trends in Ecology & Evolution* **26**, 595–605 (2011).
53. Worm, B. *et al*. Rebuilding global fisheries. *science* **325**, 578–585 (2009).
54. Pauly, D. *et al*. Towards sustainability in world fisheries. *Nature* **418**, 689–695 (2002).
55. Poloczanska, E. S. *et al*. Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science* **3**, 62 (2016).
56. Pörtner, H.-O. & Peck, M. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology* **77**, 1745–1779 (2010).
57. Stuart-Smith, R. D., Edgar, G. J., Barrett, N. S., Kininmonth, S. J. & Bates, A. E. Thermal biases and vulnerability to warming in the world's marine fauna. *Nature* **528**, 88–92 (2015).
58. Rilov, G. Multi-species collapses at the warm edge of a warming sea. *Scientific reports* **6**, 36897 (2016).
59. Lasram, B. R. *et al*. The Mediterranean Sea as a 'cul-de-sac'for endemic fishes facing climate change. *Global Change Biology* **16**, 3233–3245 (2010).
60. Kaschner, K., Watson, R., Trites, A. & Pauly, D. Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. *Marine Ecology Progress Series* **316**, 285–310 (2006).

61. Mavruk, S. & Avsar, D. Non-native fishes in the Mediterranean from the Red Sea, by way of the Suez Canal. *Reviews in fish biology and fisheries* **18**, 251–262 (2008).
62. Orr, J. C. *et al.* Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* **437**, 681–686 (2005).
63. Fabry, V. J., Seibel, B. A., Feely, R. A. & Orr, J. C. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science* **65**, 414–432 (2008).
64. Munday, P. L., Warner, R. R., Monro, K., Pandolfi, J. M. & Marshall, D. J. Predicting evolutionary responses to climate change in the sea. *Ecology letters* **16**, 1488–1500 (2013).
65. Steenbeek, J. *et al.* Bridging the gap between ecosystem modeling tools and geographic information systems: Driving a food web model with external spatial–temporal data. *Ecological Modelling* **263**, 139–151 (2013).
66. Christensen, V. *et al.* Representing variable habitat quality in a spatial food web model. *Ecosystems* **17**, 1397–1412 (2014).
67. Katsanevakis, S. *et al.* Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. (2014).
68. Galil, B. Loss or gain? Invasive aliens and biodiversity in the Mediterranean Sea. *Marine pollution bulletin* **55**, 314–322 (2007).
69. Rilov, G. & Galil, B. In *Biological invasions in marine ecosystems* 549–575 (Springer, 2009).
70. Galil, B. *et al.* International arrivals: widespread bioinvasions in European Seas. *Ethology Ecology & Evolution* **26**, 152–171 (2014).
71. Golani, D. & Sonin, O. New records of the Red Sea fishes, Pterois miles (Scorpaenidae) andPteragogus pelycus (Labridae) from the eastern Mediterranean Sea. *Japanese Journal of Ichthyology* **39**, 167–169 (1992).
72. Bariche, M., Torres, M. & Azzurro, E. The presence of the invasive Lionfish Pterois miles in the Mediterranean Sea. *Mediterranean Marine Science* **14**, 292–294 (2013).
73. Green, S. J., Akins, J. L., Maljković, A. & Côté, I. M. Invasive lionfish drive Atlantic coral reef fish declines. *PloS one* **7**, e32596 (2012).
74. Galil, B. S. *et al.* 'Double trouble': the expansion of the Suez Canal and marine bioinvasions in the Mediterranean Sea. *Biological Invasions*, 1–4 (2014).
75. Givan, O., Parravicini, V., Kulbicki, M. & Belmaker, J. Trait structure reveals the processes underlying fish establishment in the Mediterranean. *Global Ecology and Biogeography* **26**, 142–153 (2017).
76. Por, F. Tethys returns to the Mediterranean: Success and limits of tropical re-colonization. *Bio Risk* **3**, 5–19 (2009).
77. Scheffer, M., Carpenter, S., Foley, J. A., Folke, C. & Walker, B. Catastrophic shifts in ecosystems. *Nature* **413**, 591–596 (2001).
78. Rockström, J. *et al.* A safe operating space for humanity. *Nature* **461**, 472–475 (2009).
79. Côté, I. M. & Darling, E. S. Rethinking ecosystem resilience in the face of climate change. *PLoS biology* **8**, e1000438 (2010).
80. Levin, S. A. & Lubchenco, J. Resilience, robustness, and marine ecosystem-based management. *BioScience* **58**, 27–32 (2008).
81. Gucu, A. & Bingel, F. Hake, Merluccius merluccius L., in the northeastern Mediterranean Sea: a case of disappearance. *Journal of Applied Ichthyology* **27**, 1001–1012 (2011).
82. Halim, Y. & Rizkalla, S. Aliens in Egyptian Mediterranean waters. A check-list of Erythrean fish with new records. *Mediterranean Marine Science* **12**, 479–490 (2011).
83. Edelist, D. *Fishery management and marine invasion in Israel* PhD thesis thesis, University of Haifa, Faculty of Humanities, Department of Maritime Civilizations (2012).
84. Doney, S. C. *et al.* Climate change impacts on marine ecosystems. *Marine Science* **4** (2012).
85. Occhipinti-Ambrogi, A. & Savini, D. Biological invasions as a component of global change in stressed marine ecosystems. *Marine pollution bulletin* **46**, 542–551 (2003).
86. Scheffer, M. *et al.* Creating a safe operating space for iconic ecosystems. *science* **347**, 1317–1319 (2015).
87. FAO. Marine Protected Areas as a Tool for Fisheries Management. MPAs, fisheries management and the ecosystem approach. FI Project Websites. 26 April 2007. [12 January 2018]. (2007).
88. Roberts, C. M. *et al.* Marine reserves can mitigate and promote adaptation to climate change. *Proceedings of the National Academy of Sciences* **114**, 6167–6175 (2017).
89. Francour, P., Mangialajo, L. & Pastor, J. Mediterranean marine protected areas and non-indigenous fish spreading. Fish Invasions of the Mediterranean Sea: Change and renewal. D. Golani & B. Appelbaum-Golani eds, Pensoft Publisher, Sofia-Moscow, 127–144 (2010).
90. Giakoumi, S. *et al.* Space invaders; biological invasions in marine conservation planning. *Diversity and Distributions* **22**, 1220–1231 (2016).
91. Simberloff, D. No reserve is an island: marine reserves and nonindigenous species. *Bulletin of Marine Science* **66**, 567–580 (2000).
92. CBD. Sixth Conference of the Parties, the Hague, the Netherlands. 7–19 April 2002: Decision VI/23: Alien Species that Threaten Ecosystems, Habitats or Species to Which is Annexed Guiding Principles for the Prevention, Introduction and Mitigation of Impacts of Alien Species that Threaten Ecosystems, Habitats or Species. http://www.biodiv.org (2002).
93. Hewitt, C., Minchin, D., Olenin, S. & Gollasch, S. In *Bridging Divides* 301–306 (Springer, 2006).
94. Rousou, M., Ganias, K., Kletou, D., Loucaides, A. & Tsinganis, M. Maturity of the pufferfish Lagocephalus sceleratus in the southeastern Mediterranean Sea. *Sexuality and Early Development in Aquatic Organisms* **1**, 35–44 (2014).
95. Nader, M., Indary, S. & Boustany, L. The puffer fish Lagocephalus sceleratus (Gmelin, 1789) in the Eastern Mediterranean. *East Med Technical Documents (FAO)* (2012).
96. Shin, Y.-J. & Shannon, L. J. Using indicators for evaluating, comparing, and communicating the ecological status of exploited marine ecosystems. 1. The IndiSeas project. *ICES Journal of Marine Science: Journal du Conseil* **67**, 686–691 (2010).
97. Shin, Y.-J. *et al.* Using indicators for evaluating, comparing, and communicating the ecological status of exploited marine ecosystems. 2. Setting the scene. *ICES Journal of Marine Science: Journal du Conseil* **67**, 692–716 (2010).
98. Fulton, E. A., Smith, A. D. & Punt, A. E. Which ecological indicators can robustly detect effects of fishing? *ICES Journal of Marine Science* **62**, 540–551 (2005).
99. Lassen, H., Pedersen, S. A., Frost, H. & Hoff, A. Fishery management advice with ecosystem considerations. *ICES Journal of Marine Science* **70**, 471–479 (2013).
100. Piroddi, C. *et al.* Using ecological models to assess ecosystem status in support of the European Marine Strategy Framework Directive. *Ecological Indicators* **58**, 175–191 (2015).
101. Azov, Y. Eastern Mediterranean—a marine desert? *Marine pollution bulletin* **23**, 225–232 (1991).
102. Brasseur, P., Beckers, J.-M., Brankart, J. & Schoenauen, R. Seasonal temperature and salinity fields in the Mediterranean Sea: Climatological analyses of a historical data set. *Deep Sea Research Part I: Oceanographic Research Papers* **43**, 159–192 (1996).
103. Goren, M., Galil, B. S., Diamant, A. & Stern, N. Invading up the food web? Invasive fish in the southeastern Mediterranean Sea. *Marine Biology* **163**, 180 (2016).
104. Edelist, D., Sonin, O., Golani, D., Rilov, G. & Spanier, E. Spatiotemporal patterns of catch and discards of the Israeli Mediterranean trawl fishery in the early 1990s: ecological and conservation perspectives. *Scientia Marina* **75**, 641–652 (2011).
105. Belkin, I. M. Rapid warming of large marine ecosystems. *Progress in Oceanography* **81**, 207–213 (2009).
106. Christensen, V. & Walters, C. J. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* **172**, 109–139 (2004).
107. Heymans, J. J. *et al.* Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecological Modelling* (2016).

108. Walters, C., Christensen, V. & Pauly, D. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in fish biology and fisheries* **7**, 139–172 (1997).
109. Ahrens, R. N., Walters, C. J. & Christensen, V. Foraging arena theory. *Fish and Fisheries* **13**, 41–59 (2012).
110. Christensen, V., Walters, C., Pauly, D. & Forrest, R. Ecopath with Ecosim version 6 user guide. *Lenfest Ocean Futures Project, University of British Columbia, Vancouver* (2008).
111. Hilborn, R. & Walters, C. J. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. *Reviews in fish biology and fisheries* **2**, 177–178 (1992).
112. Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. Fishing down marine food webs. *science* **279**, 860–863 (1998).
113. Rochet, M.-J. & Trenkel, V. M. Which community indicators can measure the impact of fishing? A review and proposals. *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 86–99 (2003).
114. Kempton, R. & Taylor, L. Models and statistics for species diversity (1976).
115. Ulanowicz, R. E. *Growth and Development: Ecosystems Phenomenology*. (Springer Verlag, New York, 203 pp, 1986).
116. Finn, J. T. Measures of ecosystem structure and function derived from analysis of flows. *Journal of theoretical Biology* **56**, 363–380 (1976).
117. Christensen, V. Ecosystem maturity—towards quantification. *Ecological Modelling* **77**, 3–32 (1995).
118. Coll, M. & Steenbeek, J. Standardized ecological indicators to assess aquatic food webs: The ECOIND software plug-in for Ecopath with Ecosim models. *Environmental Modelling & Software* **89**, 120–130 (2017).
119. Steenbeek, J., Corrales, X., Platts, M. & Coll, M. Ecosampler: A new approach to assessing parameter uncertainty in Ecopath with Ecosim. *SoftwareX* **7**, 198–204 (2018).

Acknowledgements

XC was supported by an IOLR scholarship under the DESSIM project ("A Decision Support System for the management of Israel's Mediterranean Exclusive Economic Zone"). MC was partially funded by the European Commission through the Marie Curie Career Integration Grant Fellowships – PCIG10-GA-2011-303534 - to the BIOWEB project. MC and JS were partially funded by the European Union's Horizon research program grant agreement No. 689518 for the MERCES project.

Author Contributions

X.C., M.C., E.O., J.H., J.S., M.G., D.E. and G.G. designed the study and analyses. X.C., M.C., J.H. and G.G. analysed data. J.S. and M.C. contributed with new methods. X.C. wrote the manuscript with assistance from M.C. and G.G. and input from J.H., E.O., J.S., M.G. and D.E.

Additional Information

Supplementary information accompanies this paper at https://doi.org/10.1038/s41598-018-32666-x.

Competing Interests: The authors declare no competing interests.

ANNEX 5

SoftwareX 7 (2018) 198–204

Contents lists available at ScienceDirect

SoftwareX

journal homepage: www.elsevier.com/locate/softx

Original software publication

Ecosampler: A new approach to assessing parameter uncertainty in Ecopath with Ecosim

Jeroen Steenbeek [a,*], Xavier Corrales [b,c], Mark Platts [d], Marta Coll [a,b]

[a] *Ecopath International Initiative Research Association, Barcelona, Spain*
[b] *Institut de Ciències del Mar (ICM-CSIC), Barcelona, Spain*
[c] *Israel Oceanographic and Limnological Research Institute, Migdal, Israel*
[d] *Ardent Data Analytics, LLC. Delray Beach, Fl, USA*

A R T I C L E I N F O

Article history:
Received 21 October 2017
Received in revised form 26 June 2018
Accepted 26 June 2018

Keywords:
Ecopath with Ecosim
Ecological modelling
Input parameter sensitivity
Ecosampler

A B S T R A C T

The widely used Ecopath with Ecosim (EwE) food web modelling approach has been extended with a new module to measure the impact of input parameter sensitivity on its results. Ecosampler records samples – alternate mass-balanced parameter sets for a food web model – from the built-in Monte Carlo routine, and replays these samples through all of EwE modules and any loaded plug-in. Via Ecosampler, output variation due to base input parameter sensitivity can be captured, of any computational component including the temporal module Ecosim, the spatial-temporal module Ecospace, and plug-ins such as Ecological Network Analysis, Value Chain, and Ecological Indicators.

Software metadata

(executable) Software metadata description	*Please fill in this column*
Current software version	*Ecopath with Ecosim 6.6-Beta*
Permanent link to executables of this version	http://ecopath.org/download/ecopath-6-6-beta/ *(installer)*
Legal Software License	*GNU Lesser General Public License v2*
Computing platform / Operating System	*Microsoft Windows XP Service Pack 3 or newer*
Installation requirements & dependencies	*This executable requires Microsoft.NET Framework 4.5 or newer; Microsoft Office 2010 or newer OR Microsoft Access 2010 or newer database drivers.*
If available link to user manual– if formally published include a reference to the publication in the reference list	*The user manual is included in the installer of Ecosampler*
Support email for questions	development@ecopath.org

Code metadata

Code metadata description	*Please fill in this column*
Current code version	*V1*
Permanent link to code/repository used of this code version	https://github.com/ElsevierSoftwareX/SOFTX_2018_57
Legal Code License	*GNU Lesser General Public Licence v2*
Code versioning system used	*Apache Subversion (SVN)*
Software code languages, tools, and services used	*Microsoft Visual Studio Community Edition 2017, Visual Basic.Net, C#*
Compilation requirements, operating environments & dependencies	*Minimum requirements: Microsoft Windows XP Service Pack 3, .NET Framework 4.5, Visual Studio 2010. Although not needed for compilation, Microsoft Office 2010 or Microsoft Access 2010 database drivers are required to load standard EwE models into the compiled product*
If available Link to developer documentation/manual	http://sources.ecopath.org/trac/Ecopath/
Support email for questions	development@ecopath.org

---

* Correspondence to: Ecopath International Initiative, Barcelona, 08193, Spain.
E-mail addresses: jeroen.steenbeek@gmail.com (J. Steenbeek), corrales@icm.csic.es (X. Corrales), mark@ardentdataanalytics.com (M. Platts), mcoll@icm.csic.es (M. Coll).

https://doi.org/10.1016/j.softx.2018.06.004

1. Introduction

"Ecopath with Ecosim" or EwE is a freely available and open-source food web modelling approach widely applied to assess the impact of human exploitation and environmental change on predominantly aquatic food webs. The EwE approach consists of a three computational modules: Ecopath, a mass-balance energy accounting model to capture relevant components, their interactions, and their exploitation in a food web; Ecosim, which applies the Ecopath assumptions across time; and Ecospace, which adds a spatial dimension to the temporal dynamics [1,2]. In addition, the EwE approach contains a range of analytical modules, and features a powerful plug-in system that allows third-part analytical tools to seamlessly integrate into the flow of EwE and its computational models [3].

A limitation of EwE has been the lack of facilities to measure the impact of parameter uncertainty on its predictions [4]. The ability of ecosystem models to reproduce observed trends and patterns in nature depends on a thorough understanding of ecosystem behaviour, and because this understanding is always incomplete, and models are necessary simplifications of reality, the parameterization of ecosystem models *de facto* suffers from uncertainty. By considering input parameter uncertainty, ranges of possible outcomes give a better understanding of the reliability of model predictions [1,5–7].

During its development history, the EwE feature set gained – and at times lost – tools that partially addressed this issue. A Monte Carlo engine was added to assess the impact of sensitivity in key Ecopath parameters on Ecosim predictions [1,6,8]. EcoRanger, which provided a Monte Carlo-like approach to find the best fitting Ecopath parameter set to a series of user-defined criteria [9], received criticism for making it too easy to 'fix' faulty models and was discontinued with the release of EwE version 6.0 [10]. Two distinct management strategy evaluation tools include Ecopath input parameter uncertainty when evaluating the impact of alternative fishing policies [3,11]. The stepwise fitting routine automates the process of testing ranges of hypotheses to find the best statistical fit to time series [12]. Last, the recently added Ecological Indicators (ECOIND) plug-in includes input parameter uncertainty on a range of ecological indicators [8]. However, to date the EwE approach is left wanting the means to explore the impact of parameter uncertainty on all of its predictions.

EwE models are being increasingly used for policy and management advice, such as the Roberts Bank terminal EIA [13] and the Louisiana Delta Management plan [14], and integration of the EwE approach into international assessment frameworks (e.g., [15]). Lacking an out-of-the box feature to perform system-wide input parameter sensitivity testing has led to the development of third party toolboxes such as DataReli [16] and ecopath_matlab—a MATLAB implementation of a partial feature set of EwE to assess the impact of input parameter uncertainty on ecological network indicators [5]. Consequently, it has become imperative that the EwE approach gains the native ability to provide insights into how parameter sensitivity can affect the predictions of any module of EwE [4,6,17,18].

We have built a new module to address these needs, Ecosampler, which we present in this paper. To illustrate its capabilities, we apply Ecosampler to a food web model of the Israeli Mediterranean continental shelf [19,20], and explore the impact of parameter uncertainty on key ecological indicators delivered by two external analytical plug-ins: Ecological Network Analysis and ECOIND.

2. Problems and background

The main challenge to developing a EwE-wide parameter uncertainty module is that the EwE approach is open-ended in scope. The EwE source code is free and open source, which means that anyone can use and extend the code within code license terms [10]. The code is modular, which allows programmers to replace or omit EwE building blocks, or to integrate EwE food web modelling logic into their own code, for addressing specific research questions [3]. The source code is highly extensible through the plug-in system, which allows programmers to connect any logic into the EwE execution flow without having to alter the EwE source code [3,10]. This flexibility, as shown in Fig. 1, has given the EwE desktop software significant new functionality through third-party plug-ins, while the EwE computational engines have been embedded in custom analytical code scripts [3,7,8,13,21]. The challenge was to define a model uncertainty framework that can address parameter uncertainty in existing and future module of EwE, in any existing and future plug-in, while supporting the modular structure of EwE.

A EwE-wide uncertainty assessment module needs to vary the Ecopath input parameter set. The built-in Monte Carlo routine varies Ecopath input parameters intervals in search of alternate mass-balanced models. The coefficient of variation can be entered, or can be obtained from data pedigree—a measure of confidence in the data source of each parameter [1]. Monte Carlo then assesses if alternate mass-balanced models, where all energy in the system is accounted for without requiring outside sinks or sources (ecotrophic efficiency values <= 1), yield a better statistical fit to observations in the temporal module Ecosim. The built-in Monte Carlo routine had two major limitations for our purposes: (1) it could not vary all Ecopath input parameters, and (2) finding alternate mass-balanced parameter sets for complex or tightly constrained models could be very time consuming task. Separating the Monte Carlo logic from Ecosim for building an uncertainty engine was not a feasible task. However, EwE already offered a series of plug-in points that expose the flow of the Monte Carlo routines to external code.

A EwE-wide uncertainty assessment module requires capturing outputs of all model routines, including those produced by existing and future plug-ins. To keep EwE open-ended in scope, the plug-in system does not pose restrictions to the workings of plug-ins, nor does it prescribe data formats for computed results. Centralized collection and analysis of an open-ended number of output formats is therefore an unrealistic option. However, EwE users typically consume the various outputs of EwE through custom written scripts in R, Matlab, Excel macros, etc., for further analysis. To facilitate this type of use, EwE already contains an auto-save system to control which core models, and which subscribed plug-ins, automatically write their results to file. The auto-save system thus offers a useful venue for capturing model outputs as it already ties in to common EwE workflows.

3. Software framework

Ecosampler was implemented as an extension to the EwE core using Microsoft Visual Basic .NET. Ecosampler operates in three separate modes: record, review, and run.

In record mode, Ecosampler listens to the execution of the built-in Monte Carlo routine. When Monte Carlo finds an alternate mass-balanced parameter set for the loaded model, Ecosampler intercepts the parameters variations made by Monte Carlo, and stores this parameter set in the EwE model database as a sample (Fig. 2).

In review mode, EwE software users can load samples, one at the time, into the Ecopath desktop software. Sample values and their impact on the various model components can be checked, and samples producing ecologically unrealistic results can be deleted.

In run mode, Ecosampler loads a number of samples, one at the time. For each sample, the default EwE output folder is rerouted to a unique folder, and its Ecopath parameter values are written

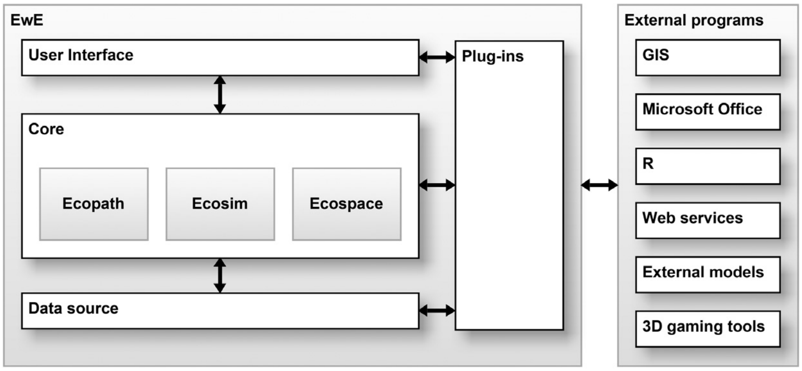


Fig. 1. The modular structure of the Ecopath with Ecosim source code, separating data access, computations, and user interface into exchangeable components. A plug-in system provides the means to extend the EwE model, and to connect to other software external to the EwE software.
Source: Adapted from Steenbeek et al., 2016.

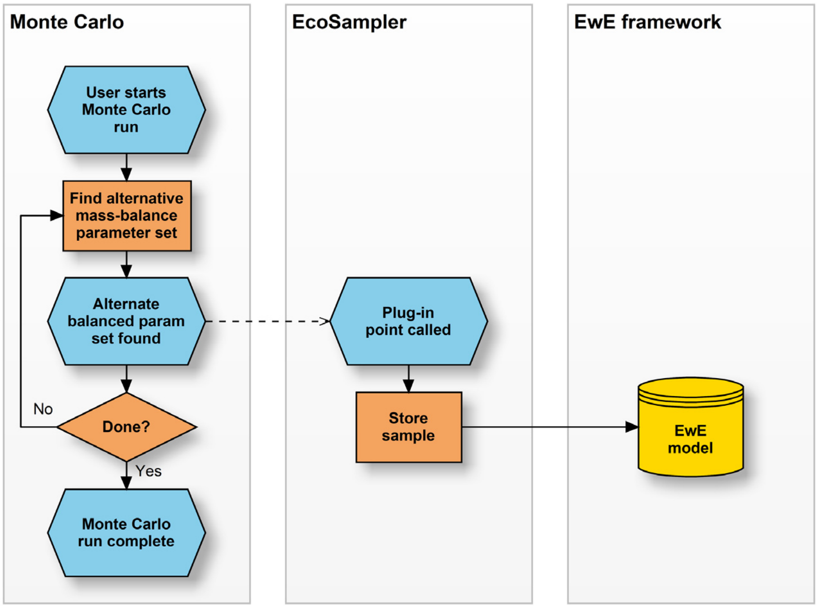


Fig. 2. Flow chart of Ecosampler record mode. Through the plug-in system, Ecosampler listens to the execution of the Monte Carlo routines and intercepts and stores alternate mass-balanced Ecopath parameter sets.

to that folder. Then, Ecosampler runs the mass-balanced model Ecopath, the time-dynamic model Ecosim (if loaded), and the temporal–spatial model Ecospace (if loaded), restores the initial Ecopath parameter sets, and restores the default EwE output location. Any EwE core module and any plug-in that is connected to these core modules will run, and, if configured to automatically write outputs, will write their predictions to the rerouted output folder values to drive (Fig. 3). At this point, the uncertainty analysis can then be performed using statistical software of choice.

In addition, Ecosampler needs to consider the possibility that stored samples can become invalid when the master Ecopath model is modified. Samples are alternate representations of the master Ecopath model, and when the EwE user modifies the Ecopath parameters of the master model, samples are assumed to be no longer valid alternatives of the Ecopath master parameter set as any parameter modification may alter the balanced state of the model. To safeguard sample validity, Ecosampler integrates itself into the EwE save system, and offers EwE users the choice to delete all stored samples when modified Ecopath parameters are about to be saved.

4. Implementation

We extended the functionality of the built-in Monte Carlo routine to allow perturbation of Ecopath basic input parameters fisheries landings and discards, biomass accumulation rates, and diets, in addition to the parameters biomass, production, consumption, ecotrophic efficiency, and biomass accumulation that Monte Carlo was already capable of varying. The coefficients of variation for landings and discards can be obtained from the pedigree values for catch data. Two different methods to vary the diet matrices were added: using Dirichlet distributions [7], or using normal distributions where coefficients of variation can be obtained from diet pedigree. Instructions how to use the Dirichlet distributions to vary diets are included in the supplementary material (Appendix A, Supplementary File 1).

We also provided Ecosampler with the ability to import samples from other model databases. The process of finding alternative mass-balanced parameter sets through Monte Carlo can take a long time for tightly constrained Ecopath models, or models with complex diet matrices. To speed up the process of finding and

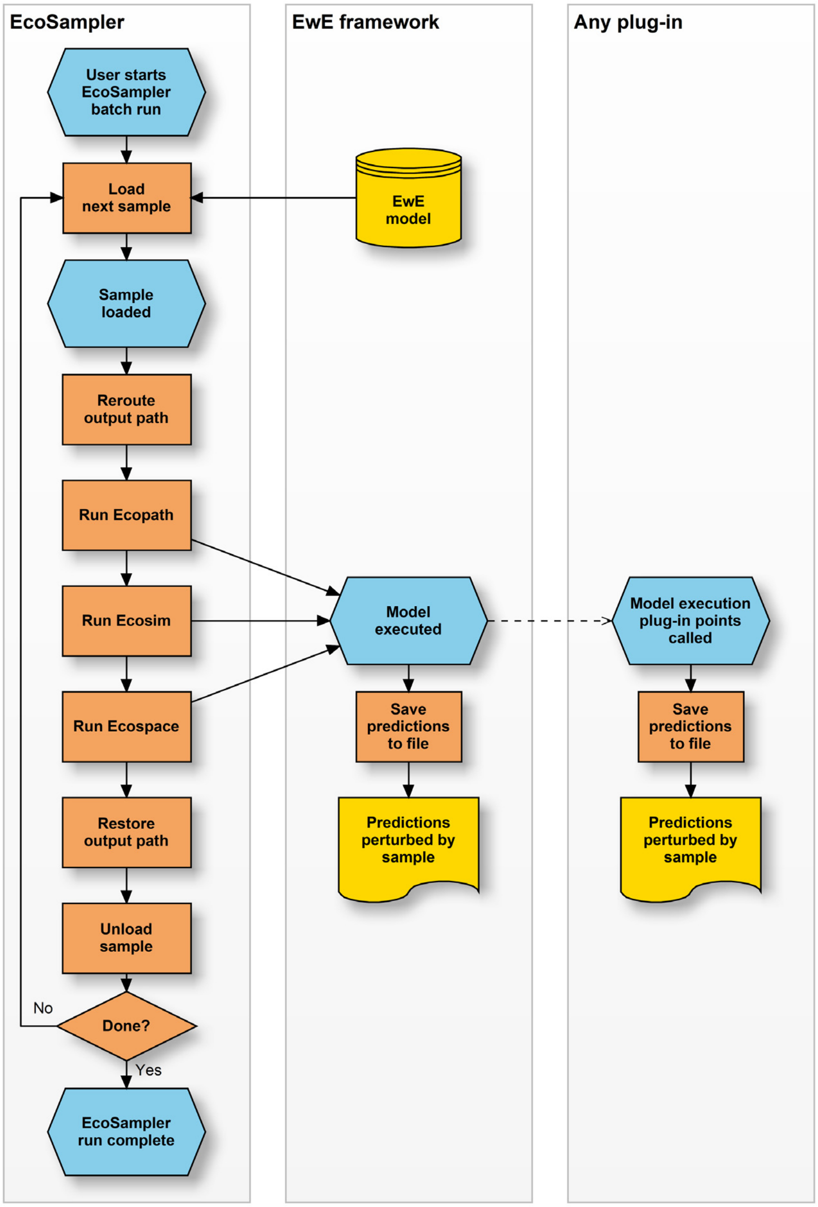


Fig. 3. Flow chart of Ecosampler batch run mode. Samples are loaded, one at the time, into Ecopath. Ecosampler first alters the base output path, after which it executes the Ecopath, Ecosim, and Ecospace models. Connected plug-ins automatically execute as well. Any component configured to save its output to drive will do so. Ecosampler will then clean up after itself by restoring the output path and restoring the Ecopath parameter set to its initial state.

recording samples for such models, EwE users can record samples on different computers, each using a copy of the same EwE model database. Via the import functionality, samples recorded into copies of an EwE model database can be brought into the master model database for performing Ecosampler batch runs.

The user guide to Ecosampler is included in the supplementary material of this manuscript (Appendix A, Supplementary File 2).

5. Case study

We used Ecosampler to assess parameter uncertainty on a range of indicators computed by the Ecological Network Analysis (ENA) and ECOIND plug-ins. As an example, we used a previously built food web model that represents the Israeli Mediterranean continental shelf ecosystem. The model was fitted to time series of data from 1994 to 2010 considering the combined impacts of alien species, fishing activities, and changes in sea surface temperature and primary productivity on the local food web [20].

We ran 1000 Monte Carlo simulations where Ecopath parameters biomass (B), production (P/B) and consumption (Q/B) rates, and ecotrophic efficiency (EE) were varied. The coefficients of variation were obtained from the pedigree routine, as defined in Corrales et al. [19]. Ecosampler recorded more than five-hundred alternate mass-balanced Ecopath models. We then ran these samples through the temporal module Ecosim, the ‘Ecological Network Analysis’ plug-in, and the Ecological Indicators’ plug-in, to assess the impact of input parameter uncertainty onto the output of these modules.

For a description of the steps taken to record and validate the samples, and for an in-depth description of the content of the samples, please refer to the supplementary material (Appendix A, Supplementary File 3).

Perturbed ENA and ECOIND indicators were analysed through a custom written R script. Biomass results from the Monte Carlo routine, and indicators delivered by ENA and ECOIND plug-ins, were used to plot the range of outputs (the 5th and 95th

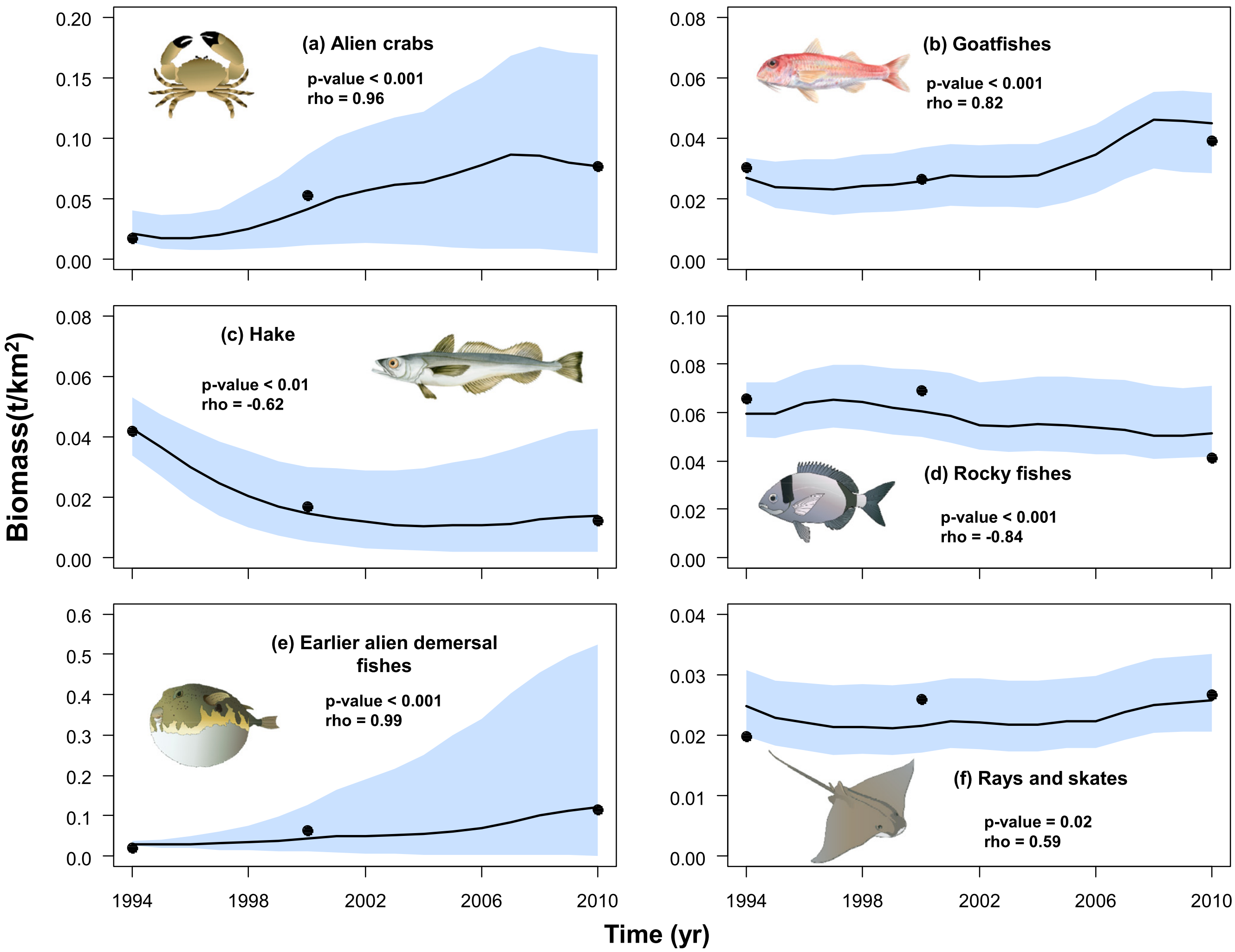


Fig. 4. Predicted (solid lines) versus observed (dots) biomass for various functional groups of the model for the Israeli Mediterranean continental shelf ecosystem model for the period 1994–2010 (modified from Corrales et al., 2017a). Blue shadows represent the 5th and 95th percentiles obtained from Ecosampler-perturbed model outputs. Rho and p-values were obtained from Spearman's rank correlation test. Image credits http://ian.umces.edu/symbols/.

percentiles) to assess uncertainty. Finally, we used Spearman's rank correlation statistical test to assess the correlation between model outputs (biomass and ecological indicators) and time. We selected the following indicators:

(1) Predatory biomass, that includes biomass of all the groups with Trophic Level (TL) $\geq$ 4 and tends to decrease with increasing fishing impact [22];
(2) Kempton's Q index, which expresses biomass diversity of organism with TL $\geq$ 3 and tends to decrease with ecosystem degradation [23];
(3) Mean TL of the community (mTLco), which expresses the TL of the whole food web (living groups) and is used to quantify the impact of fishing [22];
(4) Total System Throughput (TST), which estimates the total flows in the food web and is a measure of ecosystem size and indicates if the ecosystem is in equilibrium [24];
(5) Finn's Cycling Index (FCI), which expresses the proportion of the TST that is recycled in the system and is an indicator of stress [24];
(6) Path Length (PL), defined as the average number of groups that flows passes through and is an indicator of stress [25].

Historical model predictions satisfactorily match observed data (for further information, see Corrales et al. [20]). The model shows a decreasing historical pattern for the biomass of several groups (Fig. 4). For example, hake (Fig. 4c) and rocky fishes (Fig. 4d) showed significant declines. On the contrary, biomass of alien crabs (Fig. 4a), goatfishes (Fig. 4b) and earlier alien demersal fishes (Fig. 4e) significantly increase over time, while rays and skates (Fig. 4f) show a non-significant increasing trend. Historical biomass trends produced by the model show great variation in uncertainty between functional groups, which is due to large variations in the confidences of model inputs for these functional groups. For example, alien crabs (Fig. 4a) and earlier alien demersal fishes (Fig. 4e) present the widest confidence intervals while goatfishes (Fig. 4b), rocky fishes (Fig. 4d) and rays and skates (Fig. 4f) show the narrowest confidence intervals. Although parameter uncertainty in some cases is large, main patterns are generally captured.

The results also show that the ecosystem has substantially changed from 1994 to 2010 (Fig. 5; for further information, see Corrales et al. [20]). For example, predatory biomass first decreased and then increased, with an overall non-significant increasing trend (Fig. 5a). This is due to the decline of predators in the mid-nineties and the recovery and explosive increase of alien predators from 2007 and onward [20]. The mTLco shows a non-significant decreasing pattern (Fig. 5b), which is attributed to overfishing and the explosive increase of alien species [20]. The Kempton's index fluctuates over time with a non-significant decreasing trend

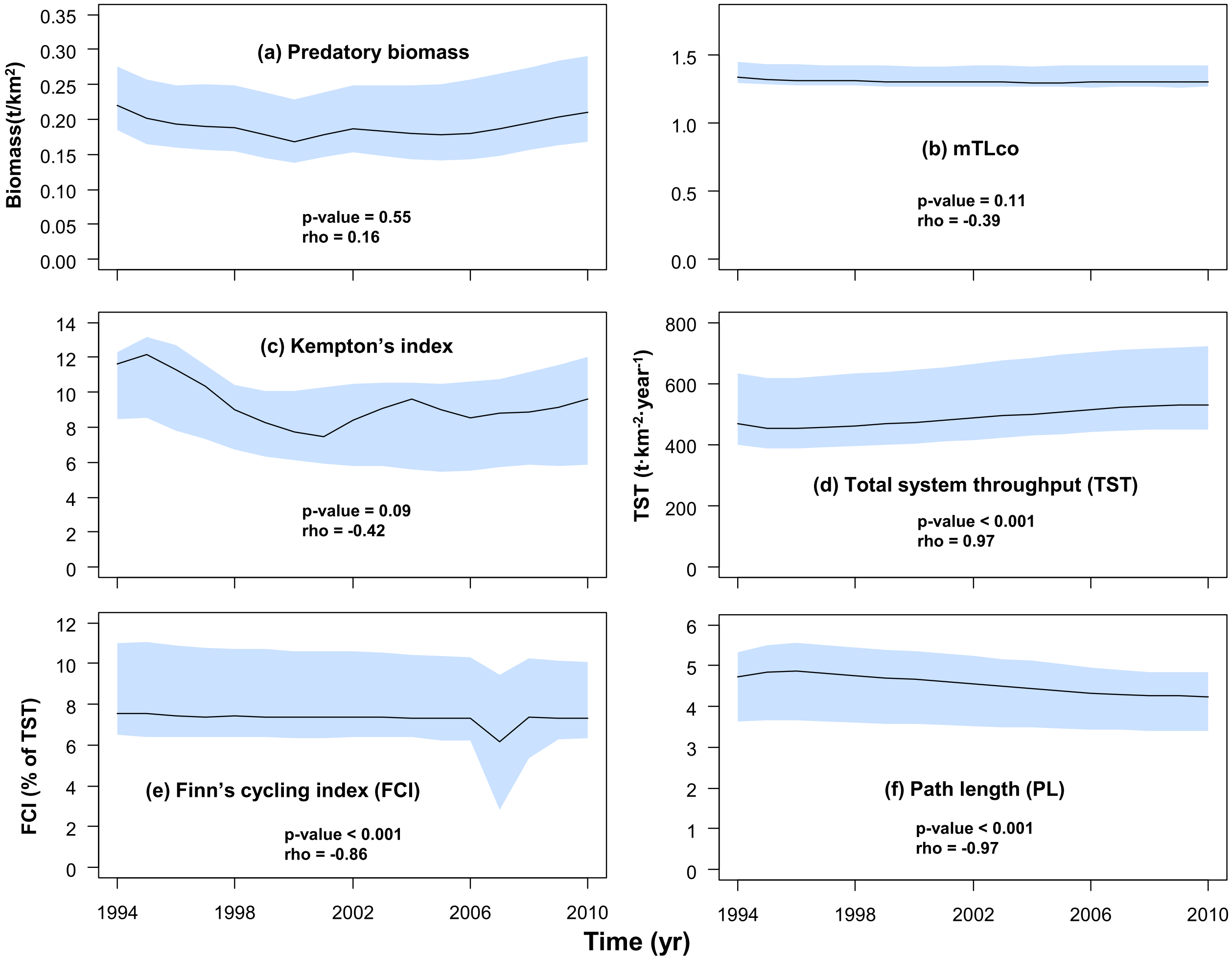


Fig. 5. Ecological indicators resulting from the Israeli Mediterranean continental shelf ecosystem. Black lines represent model predictions using the initial Ecopath model (without any Ecosampler perturbation); blue shadows represent the 5% and 95% percentiles obtained from Ecosampler-perturbed model outputs. Rho and p-values were obtained from Spearman's rank correlation test.

(Fig. 5c), in line with results of predatory biomass. The TST parameter presents a significant increasing trend (Fig. 5d), indicating an ecosystem that is not in equilibrium. This trend is attributed to a higher primary productivity, and the increasing importance of alien species in the ecosystem [20]. The FCI and PL parameters show a decreasing trend, indicating a pattern of degradation of the ecosystem during the period [20]. Results also show the different sensitivity of indicators to Ecopath input parameters (Fig. 5). For example, predatory biomass, mTLco and PL seem to be less sensitive than Kempton's index, TST and FCI. As in biomass outputs, the main patterns of ecological indicators are generally captured (Fig. 5).

Besides exploring the impact of uncertainty on model output, the sampled space of alternative balanced models offers a wealth of information. In the supplementary material (Appendix A, Supplementary File 3) we demonstrate how this data can be accessed and the type of information it contains. To illustrate, looking at the statistics gathered from the Ecosampler perturbations, it is interesting that alternate balanced models allowed for an average of 3% increase of biomasses, 6% increase in production rates, while allowing for 3% reduction in consumption rates and ecotrophic efficiencies (Fig. 1, Appendix A, Supplementary File 3). Further analysis can be developed to provide a better understanding of the model structure itself.

6. Impact

Ecological models in general, and Ecopath with Ecosim models in specific, are increasingly applied in a wide range of scientific disciplines and management settings. Knowing model output confidence is essential to assess and interpret EwE model predictions with more certainty [26] for such applications. To this end, Ecosampler provides a powerful engine to assess the impact of Ecopath input parameter uncertainty on any computational module in the EwE approach.

The utility of Ecosampler ranges far beyond the calculation of indicators as presented here in the case study. Knowing and propagating parameter uncertainty onto any module of the EwE approach, and any existing and future plug-in, can aid efforts such as spatial and temporal model comparisons, exploring model behaviour, exploring behaviours and responses of indicators over time, etc. In particular, Ecosampler holds potential for fisheries management and policy exploration, where it offers support by providing estimates of risk around reference points, as well as providing insights into the uncertainty around ecological impacts of harvest control rules (e.g, [7,27]). In addition, the resampled input parameter space provides a wealth of information that can be used to attain deeper understanding of the ecosystem model and the represented ecosystem. By providing information on the input parameters to which the ecosystem functioning is most sensitive, Ecosampler can play an important role in providing evidence on where further research efforts should be focused.

It is important to note that the Ecosampler framework can currently only be used to assess the impact of parameter uncertainty in most commonly entered Ecopath parameters. A future version of Ecosampler should be able to vary the remaining Ecopath parameters, and key parameters to Ecosim such as vulnerabilities, Ecospace parameters like dispersal rates, and perhaps even functional responses used by the Habitat Foraging Capacity Model [28].

We wish to stress that randomly sampling baseline parameters in complex food webs, where variables are often correlated and/or have compounding effects, may trigger changes in the functioning of food web. For instance, resampling diets may trigger predator functional responses in Ecosim. These kind of cascading effects will have impacts throughout food web, and must be taken into account when interpreting results produced via Ecosampler.

7. Conclusions

In this paper a new module for the Ecopath with Ecosim food web modelling approach, Ecosampler, was presented. Ecosampler can be used to assess the impact of basic Ecopath input parameter uncertainty on any computation module of EwE, and any plug-in. This open-ended applicability of Ecosampler offers a foundation for new applications of EwE, far beyond the current capabilities offered by existing parameter uncertainty testing tools for EwE models.

Acknowledgements

Ecosampler was realized through funding from the European Commission through the Marie Curie Career Integration Grant Fellowships PCIG10-GA-2011-303534 to the BIOWEB project. This study is a contribution to the projects SafeNET (EU-DGMARE MARE/2014/41) and MERCES (European Union's Horizon research and innovation programme grant agreement No 689518). XC was supported by an IOLR scholarship under the DESSIM project (''A Decision Support System for the management of Israel's Mediterranean Exclusive Economic Zone'').

Appendix A. Supplementary data

Supplementary material related to this article consists of three files:

File 1—Using Dirichlet distributions to vary diets.pdf
File 2—Ecosampler user manual.pdf
File 3—Using Ecosampler.pdf

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.softx.2018.06.004.

References

[1] Christensen V, Walters CJ. Ecopath with Ecosim: methods, capabilities and limitations. Ecol Model 2004;172:109–39. http://dx.doi.org/10.1016/j.ecolmodel.2003.09.003.

[2] Walters C. Impacts of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected areas: how large should protected areas be?. Bull Mar Sci 2000;66:745–57.

[3] Steenbeek J, Buszowski J, Christensen V, Akoglu E, Aydin K, Ellis N, et al. Ecopath with Ecosim as a model-building toolbox: Source code capabilities, extensions, and variations. Ecol Model 2016;319:178–89. http://dx.doi.org/10.1016/j.ecolmodel.2015.06.031.

[4] Guesnet V, Lassalle G, Chaalali A, Kearney K, Saint-Béat B, Karimi B, et al. Incorporating food-web parameter uncertainty into Ecopath-derived ecological network indicators. Ecol Model 2015;313:29–40.

[5] Kearney K. ecopath_matlab: A Matlab-based implementation of the Ecopath food web algorithm. J Open Source Softw 2017 http://joss.theoj.org/papers/55cdc396174664e690bec9b2fa7c50bf [Accessed 12 June 2017].

[6] Plaganyí EP, Butterworth DS. A critical look at the potential of ecopath with ecosim to assist in practical fisheries management. Afr J Mar Sci 2004;26:261–87.

[7] Platts M, Mackinson S. A routine for evaluating the performance of management strategies with Ecopath with Ecosim: MSE plugin methods and users guide, Cefas and Ecopath International Initiative, Lowestoft; 2017. http://dx.doi.org/10.14466/CefasDataHub.44.

[8] Coll M, Steenbeek J. Standardized ecological indicators to assess aquatic food webs: The ECOIND software plug-in for Ecopath with Ecosim models. Environ Model Softw 2017;89:120–30. http://dx.doi.org/10.1016/j.envsoft.2016.12.004.

[9] Christensen V, Pauly D. Ecological modeling for all. Naga ICLARM Q 1996;19:25–26.

[10] Christensen V, Lai S. Ecopath with Ecosim 6: the sequel. Sea Us Proj Newsl 2007;43.

[11] Mackinson S, Platts M, Garcia C, Lynam C. Evaluating the fishery and ecological consequences of the proposed North Sea multi-annual plan. PLoS One 2018;13:e0190015. http://dx.doi.org/10.1371/journal.pone.0190015.

[12] Scott E, Serpetti N, Steenbeek J, Heymans JJ. A Stepwise Fitting Procedure for automated fitting of Ecopath with Ecosim models. SoftwareX 2016;5:25–30. http://dx.doi.org/10.1016/j.softx.2016.02.002.

[13] Canadian Environmental Assessment Agency, Roberts Bank Terminal 2 Project - Environmental Impact Statement, Canadian Environmental Assessment Agency, Roberts Band, Delta, B.C; 2015. Available from: https://www.ceaa-acee.gc.ca/050/document-eng.cfm?document=101482. [Accessed 6 May 2015].

[14] de Mutsert K, Lewis KA, Steenbeek J, Buszowski J, Milroy S, Cowan Jr JH. Louisiana Coastal Area Delta Management Ecosystem Modeling: Delta Management Fish and Shellfish Ecosystem Model, Louisiana Coastal Protection and Restoration Authority, Baton Rouge, Louisiana; 2015.

[15] Stips A, Dowell M, Somma F, Coughlan C, Piroddi C, Bouraoui F, et al. Towards an integrated water modelling toolbox. Ispra, Italy: Joint Research Centre - Institute for Environment and Sustainability; 2015. http://mcc.jrc.ec.europa.eu/documents/201603214045.pdf.

[16] Lassalle G, Bourdaud P, Saint-Béat B, Rochette S, Niquil N. A toolbox to evaluate data reliability for whole-ecosystem models: Application on the Bay of Biscay continental shelf food-web model. Ecol Model 2014;285:13–21. http://dx.doi.org/10.1016/j.ecolmodel.2014.04.002.

[17] Essington TE. Evaluating the sensitivity of a trophic mass-balance model (Ecopath) to imprecise data inputs. Can J Fish Aquat Sci 2007;64:628–37.

[18] Pauly D, Christensen V, Walters C. Ecopath, ecosim, and ecospace as tools for evaluating ecosystem impact of fisheries. ICES J Mar Sci J Cons 2000;57:697–706.

[19] Corrales X, Ofir E, Coll M, Goren M, Edelist D, Heymans JJ, et al. Modeling the role and impact of alien species and fisheries on the Israeli marine continental shelf ecosystem. J Mar Syst 2017;170:88–102.

[20] Corrales X, Coll M, Ofir E, Piroddi C, Goren M, Edelist D, et al. Hindcasting the dynamics of an eastern mediterranean marine ecosystem under the impacts of multiple stressors. Mar Ecol Prog Ser 2017;580:17–36. http://dx.doi.org/10.3354/meps12271.

[21] Christensen V, Coll M, Buszowski J, Cheung WWL, Frölicher T, Steenbeek J, et al. The global ocean is an ecosystem: simulating marine life and fisheries. Glob Ecol Biogeogr 2015;24:507–17. http://dx.doi.org/10.1111/geb.12281.

[22] Rochet M-J, Trenkel VM. Which community indicators can measure the impact of fishing? A review and proposals. Can J Fish Aquat Sci 2003;60:86–99.

[23] Ainsworth CH, Pitcher TJ. Modifying Kempton's species diversity index for use with ecosystem simulation models. Ecol Indic 2006;6:623–30.

[24] Finn JT. Measures of ecosystem structure and function derived from analysis of flows. J Theoret Biol 1976;56:363–80.

[25] Christensen V. Ecosystem maturity—towards quantification. Ecol Model 1995;77:3–32.

[26] Heymans JJ, Coll M, Link JS, Mackinson S, Steenbeek J, Christensen V. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. Ecol Model 2016;331:173–84. http://dx.doi.org/10.1016/j.ecolmodel.2015.12.007.

[27] Gaichas SK, Seagraves RJ, Coakley JM, DePiper GS, Guida VG, Hare JA, et al. A framework for incorporating species, fleet, habitat, and climate interactions into fishery management. Front Mar Sci 2016;3. http://dx.doi.org/10.3389/fmars.2016.00105.

[28] Christensen V, Coll M, Steenbeek J, Buszowski J, Chagaris D, Walters CJ. Representing variable habitat quality in a spatial food web model. Ecosystems 2014;1–16. http://dx.doi.org/10.1007/s10021-014-9803-3.