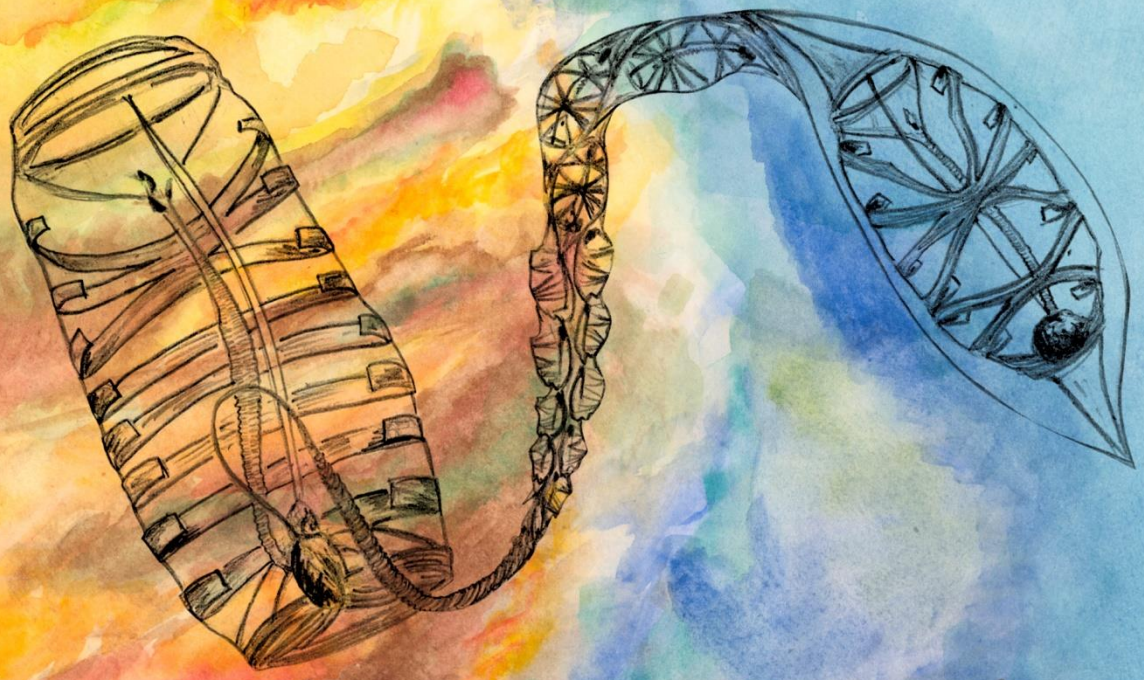
SPATIO-TEMPORAL PROCESSES EXPLAINING SALP AGGREGATIONS AND THEIR ROLE IN THE CATALAN SEA, NORTHWESTERN MEDITERRANEAN SEA



MARIA PASCUAL TORNER

BARCELONA. 2016

SPATIO-TEMPORAL PROCESSES EXPLAINING SALP AGGREGATIONS AND THEIR ROLE IN THE CATALAN SEA, NORTHWESTERN MEDITERRANEAN SEA

Processos espacio-temporals que expliquen les agregacions de salpes i el seu paper en el mar Català, Nord-oest del Mediterrani

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Tesi presentada per a l'obtenció del títol de Doctora per a la Universitat

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“Spatio-temporal processes explaining salp aggregations in the Catalan Sea, Northwestern Mediterranean”

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Graphic art: Link of the two generations of Salpa fusiformis (freehand drawing) and underwater landscape (waterpainting). Original work by Maria Pascual.

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Barcelona, July 2016

A tothom que m'ha guiat i

acompanyat en aquest camí

PREFACE

"Look deep into nature, and then you will understand everything better"

Albert Einstein

"L' única manera de fer una treball genial és estimar el que fas. Si encara no ho has trobat, segueix buscant!"

Alex Lorente

"I used to think the top environmental problems were global warming, environmental degradation and ecosystem collapse, and that we scientists could fix those problems with enough science. But I was wrong. The real problem is not those three items, but greed, selfishness and apathy. And for that we need a spiritual and cultural transformation. And we scientists don't know how to do that".

Gus Speth

ABSTRACT

Salps are marine pelagic tunicates that have evolved opportunistic skills to bloom under favorable conditions and persist during adverse periods. They experience population outbursts (blooms) which, combined with their efficient feeding mechanism, produce several ecological and societal consequences. Although salp blooms are common in the Catalan Sea during spring and autumn, their causes and effects on the ecosystem have never been studied in this area before. The general aim of the present thesis is to understand the spatial and temporal processes leading to salp blooms and estimate their trophic impact in the Catalan Sea, northwestern Mediterranean Sea. For this purpose, mechanistic (matrix models) and statistical models (GAMs) combined with *in situ* observations allowed us to propose the simplest mechanisms to account for bloom development. In contrast to previous hypotheses, we found that changes in female reproduction drive the population to latency under unfavorable conditions and trigger the bloom when conditions improve (Chapter 1). From a spatial scale, hydrodynamic factors mainly drove high local salp abundances, although biological variables (predator abundance) had secondary importance (Chapter 2). We observed the coexistence of contrasting diel vertical migration (DVM) patterns in a salp (nocturnal and diurnal migrations), which explains controversial conclusions in previous studies, but brings new questions about the drivers of DVM in salps (Chapter 3). The two species found produced contrasting trophic impacts: *Thalia democratica* was less abundant and its effect on the ecosystem seemed to be negligible while, *Salpa fusiformis* ingested a maximum of 69.92 mg C m^{-2} day^{-1} and defecated 35.76 mg C m^{-2} day^{-1}, contributing to the transport of organic matter to the deep ocean (Chapter 2). Our findings contribute to general knowledge in salp ecology. They lead us to consider evolutionary demographic studies to understand the potential benefits of their life cycle as an adaptation to environmental change and the mechanisms which maintain genetic variability after bloom-latency periods.

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GENERAL INTRODUCTION

Fitness: is the degree of reproductive success of a genotype relative to that of other genotypes within a population. In predictable environments, the best way to maximize fitness is to invest resources in improving individual competitive traits that increase survival until reproduction (i.e. defense structures, feeding strategies or parental care). Species that exhibit this strategy are K-strategists or equilibrium species (Macarthur and Wilson, 1967). In contrast, in unpredictable environments, it is better to allocate the resources to reproduction (i.e. high number of offspring, complex life cycle, high growth rates) for fast population growth and rapid colonization (r-strategist or opportunistic species; Macarthur and Wilson, 1967).. In nature, r- and K- should be endpoints of a continuum where species have a combination of r/K traits, therefore, this concept should be applied in a comparative sense only (Pianka, 1979; Adams, 1980; Reznick *et al*., 2002). Additionally, some species can change some of their traits in response to varying environmental conditions, for instance, shortening generation time (Troedsson *et al*., 2002) or varying offspring number (Lucas, 2001). Planktonic ecosystems are highly fluctuating environments exposed to small-scale changes in temperature, productivity or water column stability (Boero, 1994) and, consequently, there is a dominance of r-strategies.

Blooms: a consequence of the r-strategy in marine systems

The consequence of a planktonic species with dominance of r- traits is a rapid increase in abundance within a relatively short period of time (i.e. hours) which is called a "bloom". However, high densities are not only caused by an actively growing population (true bloom) but also a consequence of a passive or active accumulation of the individuals in one location (apparent bloom) (Graham *et al*., 2001). Therefore, factors driving salp aggregations will potentially affect biology, behavior and physical re-distribution of individuals (for instance, temperature, resource availability, presence of predators, fronts or currents). Since blooms are highly dynamic and occur in a three-dimensional environment, studies should focus both on the temporal and spatial scales, including the horizontal and vertical dimensions.

In such a complex scenario, ecological models combined with empirical work are required to study the processes involved in a bloom (Graham *et al*., 2001). There are two types of models: "empirical" (i.e. simple regression) and "mechanistic" (i.e. matrix models). First, empirical models describe trends from a data set using statistical tools and they inform whether or not there is a relationship between the variable and the parameters. Second, mechanistic models are built from a conceptual description of a process and, therefore, they give us information about the mechanisms underlying this relationship. Both types are realistic although empirical models are more precise while mechanistic models allow for more general descriptors of a process (Guisan and Zimmermann, 2000).

Salps: an example of opportunistic species in the ocean

Salps (Tunicata) have evolved opportunistic traits allowing persistence in the typically unstable oceanic environments. They take advantage of favorable conditions to bloom but are also capable of enduring hostile periods. Most of these features depend on their complex life cycle, which alternates asexual and sexual phases (Figure 0.1). We can group these characteristics in three traits: High fecundity, low generation time and high survivorship of their younger stages. High fecundity is achieved by asexually producing between tens and hundreds of buds per stolon, a number which far exceeds reproduction rates of other zooplankton grazers (Alldredge and Madin, 1982). At the same time, sexual reproduction guarantees maintenance of genetic variability and simultaneous protogyny doubles the effective population size (Ghiselin, 1969; Alldredge and Madin, 1982).

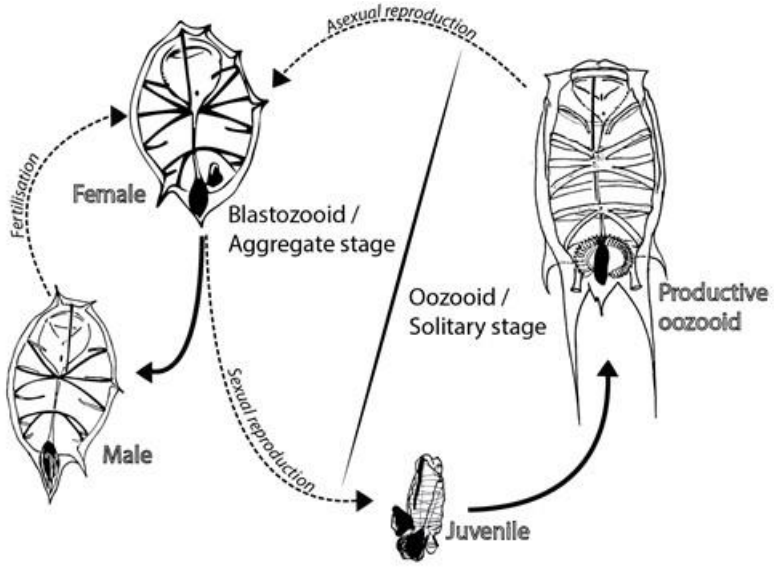

Figure 0.1. General salp life cycle (example for *Thalia democratica*): each blastozooid in a chain starts as a female and is impregnated almost immediately after its release. The female becomes male after giving birth to a single, free-swimming juvenile oozooid. Once it becomes sufficiently large, the oozooid becomes productive and sequentially releases up to 3 chains of blastozoids (females), closing the life cycle (Heron, 1987a).

In addition, salps have the lowest generation time among mesozooplankton species (46 hours, (Heron, 1972a)). This is due to their high individual growth rates (up to 28% increase in length per hour in *Thalia democratica* (Le Borgne and Moll, 1986)) and the absence of any larval stage (Alldredge and Madin, 1982). The combination of high fecundity and low generation time leads to an intrinsic rate of increase comparable to that of the phytoplankton species (Heron, 1972a). Third, the vivipary and maternal nutrition of the sexual generation reduces probability of predation on embryos which are born with a relative large size (Figure 0.2; Alldredge and Madin, 1982) and already equipped with early developed chains of females (Heron, 1972a; Braconnot *et al*., 1988).

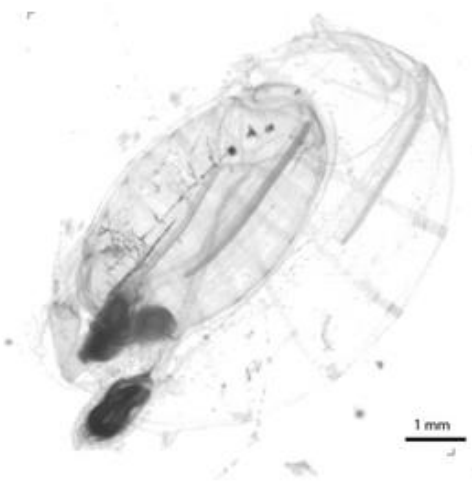

Figure 0.2. *T. democratica* blastozooid carrying an embryo. From a sample collected at Barcelona on 19/5/2014.

As opportunistic species, most resources are invested in reproductive traits, like the ones explained above, and less at individual level. However, these lasts are precisely optimized resulting the simplest but most effective bodies (Figure 0.3). Their composition is 95% water content which allows reaching large size rapidly and with low biomass cost (Madin *et al*., 1981). Large size may allow salps to feed under low food concentrations (Acuña, 2001) and -together with transparency and barrel shapes- conceal from visual predators and hinder manipulation, reducing mortality (Heron, 1972b; Verity and Smetacek, 1996). By rhythmic contractions of their circular muscle bands, they create a water flow through their bodies providing the means for respiration, feeding and swimming, all entailed in the same energetic cost (Heron, 1972b).

Efects of salp outbreaks

Salp blooms can exert notorious grazing impact (Dubischar and Bathmann, 1997), effectively outcompeting other filter feeders and altering the structure of the food web (Loeb and Santora, 2012). This is mainly because the high salp abundance is combined with its efficient feeding mechanism. The intermittent jet pulses and their flexible barrel shaped bodies let salps to continuously filter large volumes of water while swimming. They use a mucus peripharyngeal net (Figure 0.4) to retain particles comprising phytoplankton and heterotrophic microplankton (Vargas and Madin, 2004; Madin *et al*., 2006). Indeed, they are considered generalists feeders but the structure of their filtering nets retains particles of about 3-4 microns with high efficiency (Kremer and Madin, 1992; Madin and Kremer, 1995; Hereu *et al*., 2006). Comparatively, filtering rates of the largest salps (i.e. *Salpa cylindrica*; 5131 ml ind^{-1} h^{-1}(Madin *et al*., 1981)) can be much higher than rates of other mesozooplankton specs like copepods (i.e. *Acartia tonsa*; 76 ml ind^{-1} day^{-1} (Saiz and Kiorboe, 1995)). In addition, salp outbreaks signify an increase

in food availability for their predators including fish or medusa (Harbison, 1998), representing an energy shunt from ultraplankton to higher trophic levels (Deibel, 1985).

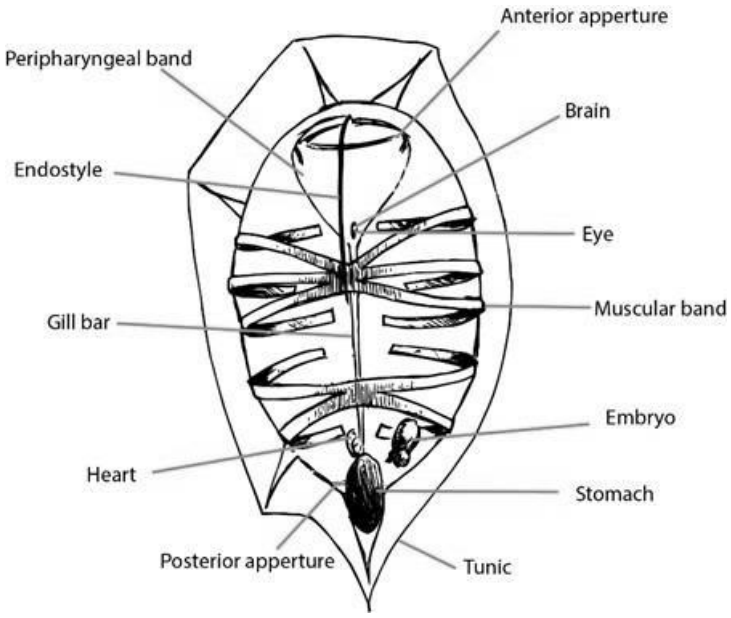

Figure 0.3. Schematic draw of *T. democratica* female (bastozooid) isolated from the chain. All body parts indicated are also present in the solitary form, except for the embryo.

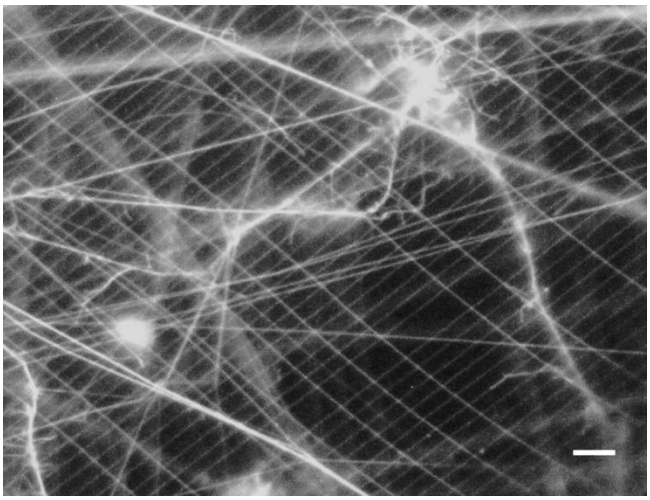

Figure 0.4. Peripharyngeal net of *Pegea confederata* from Sutherland *et al.* 2010. Scale bar corresponds to 1 µm.

Salp excretion may enrich the surrounding water with ammonium and enhance primary production (Alldredge and Madin, 1982). Moreover, through their high defecation rates and their sinking dead bodies, salps export particulate organic carbon (POC) to the deep ocean, thus contributing to the "biological pump" (Wiebe *et al*., 1979; Phillips *et al*., 2009; Gleiber *et al*., 2012; Lebrato *et al*., 2012). They continuously egest compact fecal pellets with high carbon content (Gleiber *et al*., 2012) and sinking velocities which are faster (43.5 - 1167.6 m day^{-1}) than these of copepods (26.5 - 159.5 m day^{-1}) or

euphausids (16.1 - 341.1 m day^{-1}) (Yoon *et al*., 2001). In some species, carbon transport is active, through diel vertical migration leading to defecation at greater depths (Wiebe *et al*., 1979). On the other hand, in a senescent bloom, high mortality events generate a massive drop of death bodies which take part of the so called "Jelly-fall" phenomenon (Lebrato *et al*., 2012). This organic matter input to deep waters may represent a significant food source for both pelagic and benthic species. In conclusion, salp blooms may play a relevant role in most oceans, especially in areas with seasonally high primary production like the northwestern Mediterranean Sea.

Salp aggregations in the Catalan Sea

Salps are generally less studied and often considered less relevant than other zooplankton groups like copepods, probably because crustaceans are more abundant and easy to collect and maintain in the laboratory (Alldredge and Madin, 1982). However, salps cause frustration among scientists when they clog the nets during scientific surveys. Salp blooms issues are also extended to other levels, for instance, collapsing fishing nets or blocking the seawater vacuum system filters in energy plants.

Existing studies of salps in the northwestern Mediterranean Sea are carried in the area of Villefranche-sur-mer and reveal that salps usually appear in spring and autumn after the seasonal phytoplankton blooms (Braconnot, 1963; Nival *et al*., 1990; Gorsky *et al*., 1991; Ménard *et al*., 1994; Licandro, 2006). The most frequent and abundant species are *T. democratica* and *Salpa fusiformis* (Figure 0.5), although other species can be found with less frequency and abundance such as *Pegea confederate* (Andersen *et al*., 1998), *Ilhea punctata*, *Salpa maxima* (Braconnot, 1973) or *Pegea bicaudata* (personal observation).

Salp blooms are also a common phenomenon in the Catalan Sea, being well known among fishermen who name it "gleix" (in Cap de Creus) or "llepó" (in Palamós). Indeed, fishermen assume that during some days in spring the fishing efficiency will be reduced due to jelly clogging of their nets. Salps can be sporadically found stranded on our beaches in spring and autumn and have also been reported blocking the seawater vacuum system of power plants in the Catalan coast. Despite the evidences and consequences of salp blooms, their causes and effects in the ecosystem have never been studied in this area before.

Thesis outline

The general aim of the present thesis is to understand the processes involved in salp blooms both in time (Chapter 1) and space (Chapter 2 and Chapter 3) and to estimate their trophic impact in the Catalan Sea, northwestern Mediterranean Sea. From a temporal perspective, we analyzed the environmental drivers of salp population dynamics and the key stages responsible for triggering their blooms and maintaining the population under unfavorable conditions (Chapter 1). Second, from a spatial perspective, we analyzed the correlation of salp aggregations with local physical and biological conditions and the

potential trophic impact of a bloom in the Catalan Sea (Chapter 2). Third, we studied the vertical migration behavior of salps in this area (Chapter 3).

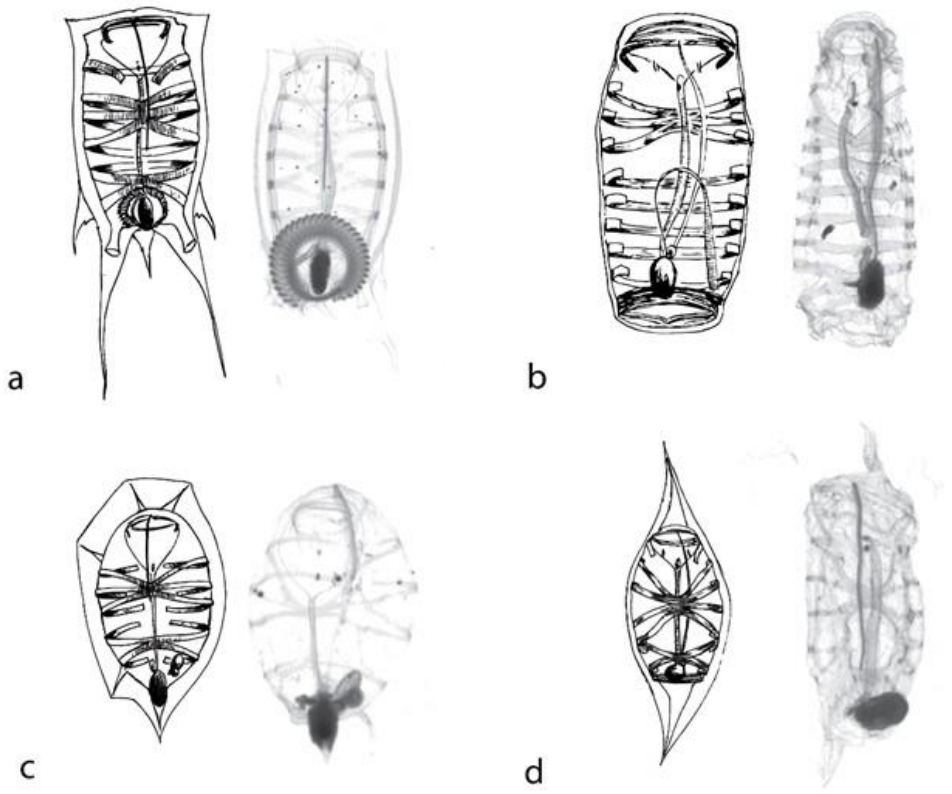

Figure 0.5. Pictures and schematic draws of the species studied in the present thesis. (a) *T. democratica* oozooid; (b) *S. fusiformis* oozooid; (c) *T. democratica* blastozooid; and (d) *S. fusiformis* blastozooid.

Chapter 1: "Environmental drivers of population dynamics in the salp *Thalia democratica* from *in situ*, short-term observations"

This chapter is focused on determining the environmental factor/s (temperature or/and chlorophyll concentration) that better explain changes in population dynamics of the salp *Thalia democratica*. We address this goal by combining a stage-specific matrix model with empirical modelling of the transition matrix elements. We obtained data to fit the model from eight surveys based on short-time series observations, each survey under different environmental conditions. Moreover, monthly samplings were also done during that time to have a temporal perspective. Both types of sample collection were conducted in Cadaqués and Barcelona during 2013 and 2014. This approach not only allowed us to describe population dynamics in each environmental situation but also to determine the role of the different stages during periods of active population growth or during population latency.

Chapter 2: "Spatial distribution of salps and their trophic impact in the Catalan Sea, northwestern Mediterranean"

This chapter is focused on analyzing the specific composition and the mesoscale distribution of salps in the Catalan Sea during the "FishJelly" cruise in June 2011. This is the first mesoscale study done on salps in the Northwestern Mediterranean Sea. We used a Geographical Information System (GIS) and empirical models (GAM) to answer how the spatial patterns are governed by local physical (temperature, salinity, depth, currents) and biological (chlorophyll-a and zooplankton concentrations) conditions. Last, we inferred ingestion and defecation rates to estimate the trophic impact of salp aggregations in the Catalan Sea.

Chapter 3: "Contrasting diel vertical migration patterns in *Salpa fusiformis* populations"

Previous literature about diel vertical migration (DVM) in *S. fusiformis* revealed a behavioral range from nocturnal migration, through no migration to diurnal migration. To determine which of those alternatives applies to this species in the Catalan Sea, we conducted vertically stratified samplings during the Fishjelly cruise in June 2011, where we considered both population structure and water column characteristics in the context of vertical migration.

CHAPTER 1

ENVIRONMENTAL DRIVERS OF THE POPULATION DYNAMICS OF THE SALP *THALIA DEMOCRATICA* FROM *IN SITU* OBSERVATIONS

Maria Pascual, Michael G. Neubert, José Luis Acuña, Andrew R. Solow, Carlos Dominguez-Carrió, Verónica Fuentes

ABSTRACT

Thalia democratica blooms are a recurrent phenomenon in many coastal areas of the Mediterranean Sea and have significant ecological effects. To better understand the environmental drivers of salp blooms, we conducted 8 surveys to sample *T. democratica* in contrasting seasonal, temperature and chlorophyll conditions. At each survey, short-term variations in the abundances of different salp stages were assessed by sampling the same population at 30-minute intervals. With these data we estimated the parameters in a set of stage-classified matrix population models representing different assumptions about the influence of temperature and chlorophyll on each stage. In the model that best explains our observations, only females are affected by changes in water temperature. Whether this is a direct influence of temperature or an indirect effect reflecting low food availability, female reproduction cessation slows population growth under unfavorable conditions. When conditions become favorable again, females liberate the embryo and change sex to male, allowing for mating under extremely low salp density and triggering the bloom. In contrast with previous findings, our results suggest that females, rather than oozooids, are responsible for latency periods in salp populations

INTRODUCTION

Salps are pelagic tunicates that feed on phytoplankton in many of the world's seas. Salp blooms are common in most oceans and have important ecological consequences. They generate episodic but intense downward fluxes of faecal pellets and dead bodies (Wiebe *et al,*. 1979; Duggins, 1981; Fortier *et al.*; 1994; Perissinotto and Pakhomov, 1998; Lebrato *et al*., 2012; Henschke *et al*., 2013; Smith *et al.*, 2014) and serve as prey and/or hosts for many pelagic and benthic organisms (Harbison, 1998; Henschke *et al*. 2013; O'Rorke *et al.*, 2015). Salp blooms can have important economic impacts as well. High salp densities can negatively impact fish farms (Giesecke *et al*., 2014), clog the cooling systems of power plants, and potentially reduce tourism due to their jellyfish-like appearance (Boero *et al*., 2013). These effects explain the growing interest in the mechanisms that drive salp blooms.

Salp populations exhibit "boom and bust" cycles due to the alternation between an asexual solitary stage (oozooid) and a sexual aggregated stage (blastozooid) over their life cycle (Figure 0.1). The particularities of this cycle, combined with high individual growth rates (up to 28% in length per hour (Le Borgne and Moll, 1986)), allows for very short generation times (approximately 2 days; Heron, 1987b)and large intrinsic rates of population increase (Alldredge and Madin, 1982).

The survival and growth rates that determine the rates of salp population growth have been estimated in several laboratory studies (*e.g.*, Heron 1972a; Deibel, 1982; Braconnot *et al*., 1988; Madin and Purcell, 1992). These estimates are highly variable and far from those obtained in the field (Heron and Benham, 1984; Madin and Deibel, 1998). Thus, direct observation remains the best approach to determine *in situ* growth and survival rates (Heron, 1972a, 1972b, Heron and Benham, 1984, 1985; Le Borgne and Moll, 1986; Tsuda and Nemoto, 1992; Loeb and Santora, 2012).

Field observations suggest that low temperature and high food availability lead to an increase in salp abundance (Heron and Benham, 1985; Andersen and Nival, 1986; Lavaniegos and Ohman, 2003; Licandro, 2006; Deibel and Paffenhöfer, 2009; Henschke *et al*., 2014). Much less evidence is available to explain how populations persist under unfavorable conditions, when temperature is relatively high and food availability is low. Based on field observations, Heron and Benham (1985) postulated that latent, low-density populations of *Thalia democratica* are mainly composed of a solitary stage in a state of arrested growth that slowly produces longer chains of blastozooids.

Recently, Henschke *et al.* (2015) built a population dynamic model for *T. democratica* in which the vital rates were constant and based on published laboratory or field estimates. Since vital rates may vary with oceanographic conditions, the stage-classified model should include environment-dependent transition rates. In this regard, several differential equation models supported that chlorophyll and/or temperature are sufficient drivers to describe salp population dynamics (Andersen and Nival, 1986; Henschke *et al.*, 2015).

The goal of the present study is to evaluate how *T. democratica* population dynamics change under different environmental conditions. For this purpose, we conducted short time series surveys around

different *T. democratica* blooms under contrasting environmental conditions and used these observations to fit temperature- and chlorophyll- dependent stage-classified matrix models. Our main findings contrast with a previous hypothesis (Heron and Benham, 1985) that pointed to the asexual stage as the responsible for latency periods: females limit their reproduction under unfavorable conditions, which in turn lowers the population growth rate. When favorable conditions appear again, females liberate the embryo and become male, allowing for mating under low salp density and triggering the bloom.

MATERIALS AND METHODS

Sampling area

All sampling stations were located in the Catalan Sea, in NW Mediterranean. The most relevant hydrographical structure in this area is the density front produced by differences in salinity between coastal and oceanic waters. Associated with this shelf-slope front, a current flowing southwards is formed (Font *et al*., 1988). Catalan coastal waters can be considered oligotrophic, although additional nutrient sources (such as river runoff) turn them into a more productive area than the open sea (Saiz *et al*., 2014). Primary production in the NW Mediterranean sea exhibits a strong seasonality, mainly forced by changes in surface temperature (Duarte *et al.*, 1999). Vertical mixing is produced as a result of winter cooling and, consequently, deep-sea nutrients enrich the photic zone. In early spring, phytoplankton blooms occur when surface waters begin warming and a thermocline is formed in the water column. A second and smaller rise in phytoplankton productivity takes place in autumn, when vertical mixing occurs again (Estrada, 1996).

Two locations were selected for the surveys. The first sampling site, Cadaqués (42 º 18.575 ’ N, 3 º 19.321 ’ E), is located in front of Cap de Creus, an area where the continental shelf is particularly narrow and oceanic waters exert a strong influence. In contrast, the second sampling site, Barcelona (41 º 20.844 ’ N, 2º 17.888 ’ E), is located in an area with a wider continental shelf, where the shelf-slope front is relatively far from shore (Figure 1.1).

Sample collection

Monthly time series- To determine the pattern of temporal variation of *T. democratica* populations, we conducted time-series surveys in both locations where monthly samples were collected during 2013 and 2014. Temperature and salinity profiles were obtained by deploying a CTD down to 20 m depth. Chlorophyll-a concentrations were measured in water samples obtained using a 5L Niskin bottle. Zooplankton samples were collected using a Bongo net (40 cm diameter, 300µm mesh size), obliquely towed for 10 minutes from 10 m depth to the surface. Sampling deeper layers or at certain times of the day was unnecessary since *T. democratica* is considered a non-migrant species and mainly occurs in

surface waters (Heron, 1972b; Tsuda and Nemoto, 1992). Samples were preserved in 5% formalin immediately after being collected.

Short time-series observations- When salps were easily recognizable in the first zooplankton sample of each monthly visit, we carried out the short-time series sampling methodology. From that point until the end of the bloom, we increased the sampling frequency provided that weather conditions allowed. Following Heron (1972b), each survey comprised 6 consecutive hauls, performed at 30 minute intervals, tracking a WOCE drifting buoy (Hansen and Poulain, 1996). Each haul started near the buoy that followed surface waters, thus tracking the salp population. If salp density was high enough to collapse the bongo net cod ends, towing time was reduced to 5 minutes. CTD and Niskin bottles were deployed near the drifting buoy after plankton samples were collected, as was also the case for the monthly surveys (i.e., 3−4 hours after sampling had begun).

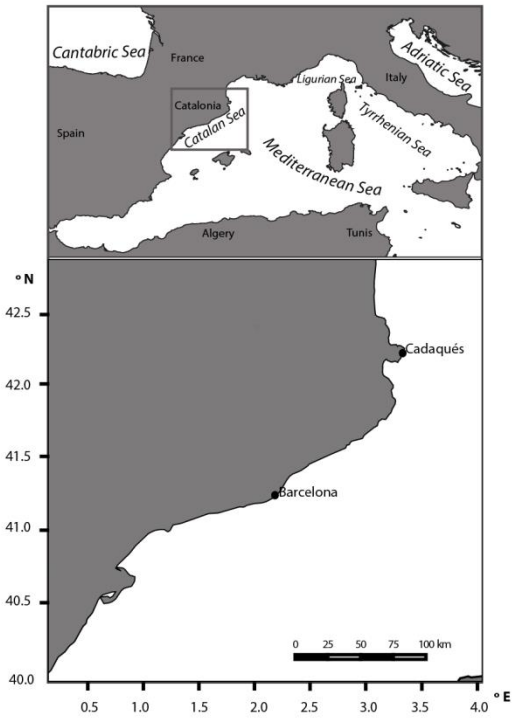

Figure 1.1. Map of the study locations: Cadaqués, located in the Cap de Creus (42 º 18.575 ' N, 3 º 19.321 ' E) and Barcelona, in the Central coast (41 º 20.844 ' N, 2 º 17.888 ' E).

Sample analyses

Salps efficiently retain particles above 2−3 µm in size (Kremer and Madin, 1992). To obtain an estimation of the concentration of phytoplankton available to salps, water samples were size-fractionated through 3 µm WHATMAN polycarbonate filters and glass fiber GF/F filters (0.45 µm). Chlorophyll-*a* was extracted from those filters during 24 h at 4 ºC using 90 % acetone (Venrick and Hayward, 1984). Absorbance of the acetone solution was measured using a fluorometer (Turner Designs, Sunnyvay, CA). We initially considered both the total aggregated and the > 3 µm chlorophyll concentrations. However,

total chlorophyll concentrations rendered a better model fit and both size fractions were highly correlated (Spearman's coefficients higher than 0.7). Thus, only total chl-a concentration results were used in our analyses.

T. democratica individuals were identified, separated from the original sample, and then scanned using a Zooscan (Grosjean *et al*. 2004; Figure 1.2). Individuals were measured from the posterior ridge of the gut until the opening (Foxton, 1966) using Image J software (Abramoff *et al*., 2004), measuring up to a maximum of 1000 individuals per blastozooid and oozooid. The number of buds per chain was also counted -up to a maximum of 50 oozooids per survey- only when the oldest chain was clearly distinguished from the stolon (Henschke *et al.,* 2014). These values were used to determine the maximum and minimum number of buds per chain in the models.

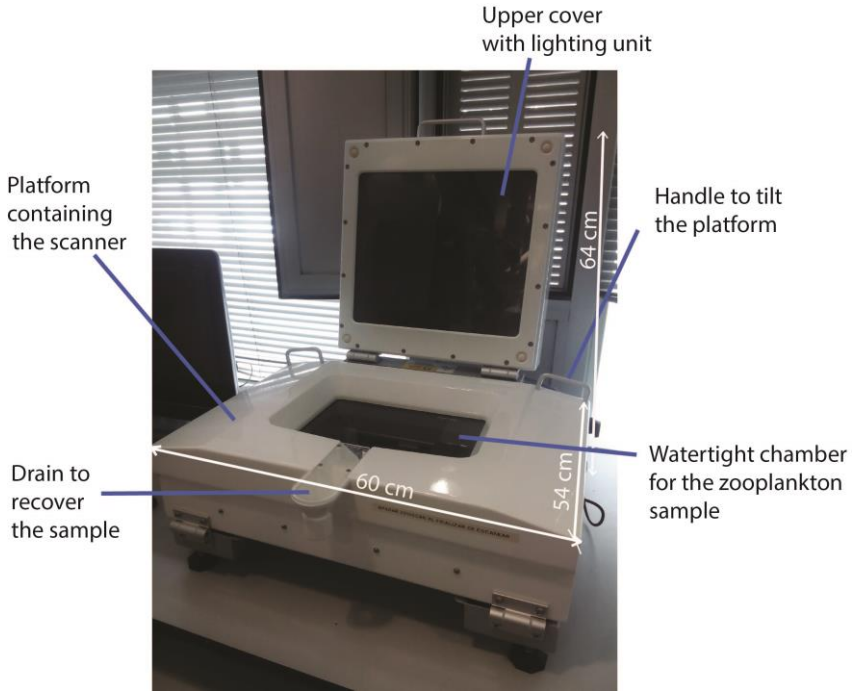

Figure 1.2. Picture of the Zooscan system which consists of a watertight chamber where the zooplankton sample can be placed and scanned without damaging the sample.

Individuals were classified in four stages depending on the blastozoid / oozooid form and size as described in Henschke *et al.* (2015), after applying a 20 % shrinkage correction due to the effects of formalin (Heron *et al.,* 1988). Size ranges were adjusted to our observations, adapting previous partitions to actual data from the population sampled. For example, the maximum length measured for a blastozooid carrying an embryo was 7 mm and oozooids containing a developed chain reached lengths of 8mm, measures similar to those found in other studies on *T. democratica* in the Mediterranean Sea (*e.g*. Braconnot and Jegu, 1981).Therefore, we classified individuals as: female (F, size range: 1 − 7 mm), male (M, size range: > 7 mm), juvenile oozooid (J, size range: 3 − 8 mm) and productive oozooid (PO, size range > 8 mm). The density of individuals (ind hm^{-3}) in each stage was calculated by dividing its abundance by the total volume of water filtered. When blastozooids or oozooids exceed 1000 individuals,

we multiplied their relative size frequencies by the total density of individuals to obtain the stage density. One individual count was added to all samples prior calculating the density values to avoid logarithms of zero in the parameter estimation procedure.

Model construction and parameter estimation

We modelled the population dynamics of *T. democratica* using a stage-classified matrix model based on the life cycle as represented in Figure 1.3). First, we classify all individuals in the population at time *t* as either female (F_t), male (M_t), juvenile oozooid (J_t) or reproductive oozooid (PO_t), and gather the counts of the classified individuals into a vector representing the population stage distribution at time *t*. The model projects the stage distribution from time *t* to time *t*+1 via matrix multiplication:

$$\begin{bmatrix} F_{t+1} \\ M_{t+1} \\ J_{t+1} \\ PO_{t+1} \end{bmatrix} = \begin{bmatrix} P_F & 0 & R_J & R_{PO} \\ G_F & P_M & 0 & 0 \\ R_F & 0 & P_J & 0 \\ 0 & 0 & G_J & P_{PO} \end{bmatrix} \begin{bmatrix} F_t \\ M_t \\ J_t \\ PO_t \end{bmatrix}. \qquad \text{(Eq.1)}$$

The entries in this matrix correspond to the rates of the transitions illustrated in Figure 1.3. P_M and P_{PO} are the survival rates for males and productive oozooids. Females at time *t* either survive and remain female (with probability P_F), or grow and become male (with probability G_F), or die. Since a female sheds a juvenile oozooid and becomes a male simultaneously, R_F=G_F. P_J and G_J are the probability that an oozooid remains a juvenile and the probability it grows to become a productive oozooid, respectively. R_J and R_{PO} give the rate of production of new females by juvenile and productive oozooids. (we assume reproduction is a birth-flow process *sensu* Caswell (2001)).

In general, each of these transitions, and so each of the positive elements of the transition matrix, may depend on temperature (T), or chlorophyll concentration (chl), or both. We incorporate these potential environmental effects through the parametric models listed in Table 1.1. For example, P_M represents the male survival probability to the following time step. Thus, it consists of two potential alternatives (to survive or not) and is accordingly modelled by a binomial logistic function. In contrast, P_F represents the probability of an event—remaining female—among a set of three different possibilities: to die, to remain in the same state, or to grow and become a male. Accordingly, a multinomial logistic function was used. Note that G_F represents the probability of a different event—to grow to male—among exactly the same set of possibilities as in P_F. Blastozooid production (R_{PO} and R_J) include a mean oozooid fecundity term ($\bar{f}$) and a mean newborn blastozooid survival term ($\bar{S}$) within the same time interval since oozooids produce chains continuously. To comport with our observations, the minimum (f_{min}) and maximum (f_{max}) number of blastozoids per oozooid were constrained between 14 (one chain with only 14 blastozooids) and 258 (3 chains with up to 68 blastozooids per chain).

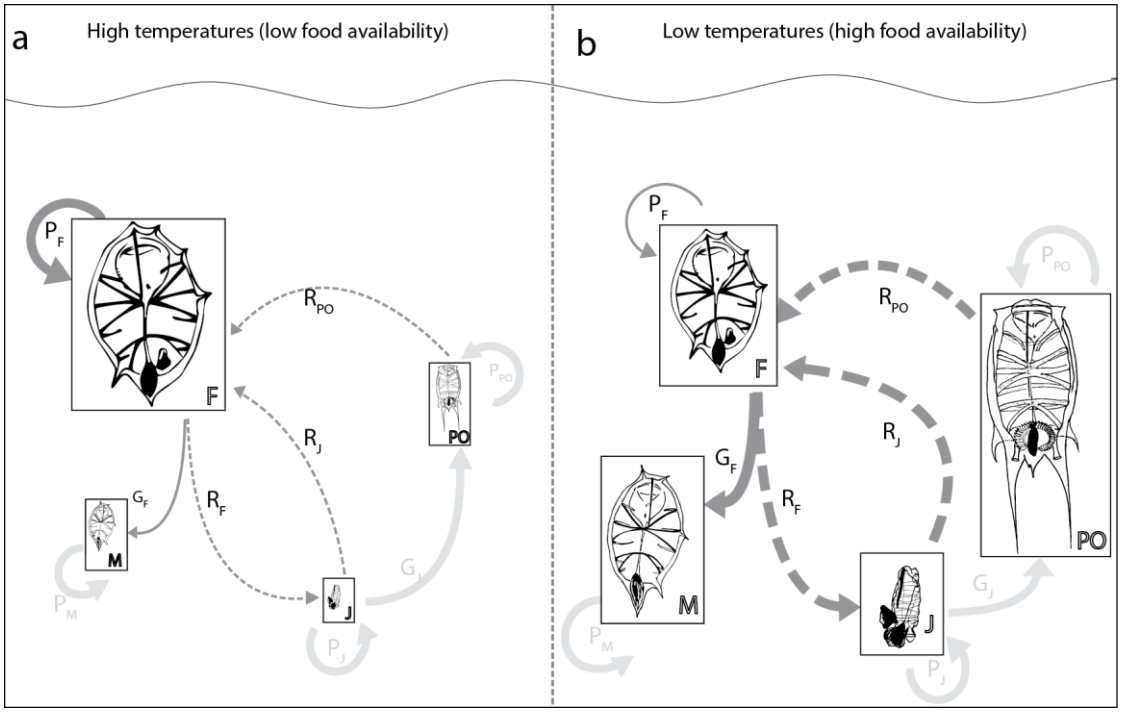

Figure 1.3. Life cycle flows under (a) high temperature and (b) low temperature following the selected model. Life stages are indicated by F (Females), M (males), J (juvenile oozooids) and PO (productive oozooids). P_F, P_M, P_J, P_{PO} are probabilities to remain in their corresponding stage and G_F and G_J are the probabilities to become male and productive oozooid, respectively. Dashed lines indicate reproductive flows (R_J, R_{PO} and R_F); dark and light grey arrows show temperature- dependent and constant fluxes, respectively; and dark grey wide lines indicate fluxes that increase in each scenario.

The general model (Eq. 1) involves a total of 25 parameters. Different restrictions on these parameters correspond to different hypotheses about the role of temperature and chlorophyll in the population dynamics of different life stages of *T. democratica* (see life cycle illustrated in Figure 1.3). To select among these hypotheses, we fit a total of 48 models. These models correspond to combinations of temperature-dependence only, chlorophyll-dependence only, and both temperature- and chlorophyll-dependence operating on all 16 possible combinations of life stages (see Annex Table A.1).

To estimate the parameters in this model, we must incorporate stochasticity that describes how variability in the data arose. Dennis *et al*. (1995) described the statistical advantages of adding noise on the log scale. Doing so transforms Eq. 1 to:

$$\begin{bmatrix} F_{t+1} \\ M_{t+1} \\ J_{t+1} \\ PO_{t+1} \end{bmatrix} = \begin{bmatrix} e^{E_F} & 0 & 0 & 0 \\ 0 & e^{E_M} & 0 & 0 \\ 0 & 0 & e^{E_J} & 0 \\ 0 & 0 & 0 & e^{E_{PO}} \end{bmatrix} \begin{bmatrix} P_F & 0 & R_J & R_{PO} \\ G_F & P_M & 0 & 0 \\ R_F & 0 & P_J & 0 \\ 0 & 0 & G_J & P_{PO} \end{bmatrix} \begin{bmatrix} F_t \\ M_t \\ J_t \\ PO_t \end{bmatrix} \quad \text{(Eq.2)}$$

where the vector $[E_F,E_M,E_J,E_{PO}]^T$ has a multivariate normal distribution with zero mean and variance-covariance matrix Σ. On the log scale we then have

$$\ln(F_{t+1}) = \ln(P_F F_t + R_J J_t + R_{PO} PO_t) + E_F \quad \text{(Eq. 3)}$$

$$\ln(M_{t+1}) = \ln(G_F F_t + P_M M_t) + E_M \quad \text{(Eq. 4)}$$

$$\ln(J_{t+1}) = \ln(R_F F_t + P_J J_t) + E_J \quad \text{(Eq. 5)}$$

$$\ln(PO_{t+1}) = \ln(G_J J_t + P_{PO} PO_t) + E_{PO} \quad \text{(Eq. 6)}$$

We fit the models described by Eq. (3)–Eq. (6) and Table A.1(see Annex) by nonlinear least squares. We compared models using the cross-validated one-step prediction errors of the log-transformed population counts. Cross-validation is commonly used in comparing models, like those in Table A.1 (see Annex), that differ in the number of fitted parameters (Claeskens and Hjort, 2008). Otherwise, using non-cross-validated sum of squared prediction errors would tend to favor models with more parameters. We then used the selected model to estimate the transition matrix, the population growth rate (λ) and the elasticity matrix for selected environmental conditions. We constructed approximate 0.95 confidence

Transition	Function	
P_F	$\frac{e^{\beta_{P_F} - \alpha_{P_F} * T - \delta_{P_F} * chl}}{1 + e^{\beta_{P_F} - \alpha_{P_F} * T - \delta_{P_F} * chl} + e^{\beta_{G_F} - \alpha_{G_F} * T - \delta_{G_F} * chl}}$	
G_F	$\frac{e^{\beta_{G_F} - \alpha_{G_F} * T - \delta_{G_F} * chl}}{1 + e^{\beta_{P_F} - \alpha_{P_F} * T - \delta_{P_F} * chl} + e^{\beta_{G_F} - \alpha_{G_F} * T - \delta_{G_F} * chl}}$	
R_F	$\frac{e^{\beta_{G_F} - \alpha_{G_F} * T - \delta_{G_F} * chl}}{1 + e^{\beta_{P_F} - \alpha_{P_F} * T - \delta_{P_F} * chl} + e^{\beta_{G_F} - \alpha_{G_F} * T - \delta_{G_F} * chl}}$	
P_M	$\frac{1}{1 + e^{\beta_{P_M} - \alpha_{P_M} * T - \delta_{P_M} * chl}}$	
P_J	$\frac{e^{\beta_{P_J} - \alpha_{P_J} * T - \delta_{P_J} * chl}}{1 + e^{\beta_{P_J} - \alpha_{P_J} * T - \delta_{P_J} * chl} + e^{\beta_{G_J} - \alpha_{G_J} * T - \delta_{G_J} * chl}}$	
P_{PO}	$\frac{1}{1 + e^{\beta_{P_{PO}} - \alpha_{P_{PO}} * T - \delta_{P_{PO}} * chl}}$	
G_J	$\frac{e^{\beta_{G_J} - \alpha_{G_J} * T - \delta_{G_J} * chl}}{1 + e^{\beta_{P_J} - \alpha_{P_J} * T - \delta_{P_J} * chl} + e^{\beta_{G_J} - \alpha_{G_J} * T - \delta_{G_J} * chl}}$	
R_J	$\bar{f} * \overline{S} = \frac{f * (G_J)}{2} * \sqrt{S_o}$	$f = f\min + \frac{f\max}{1 + e^{\gamma * T + \varepsilon * chl}}$
R_{PO}	$\bar{f} * \overline{S} = \frac{f + f * (P_{PO})}{2} * \sqrt{S_o}$	$S_0 = \frac{1}{1 + e^{\beta_{S_0} - \alpha_{S_0} * T - \delta_{S_0} * chl}}$

Table 1.1. Dependence of matrix elements (cf. Eq. 1) on temperature (*T*) and chlorophyll concentration (*chl*) by means of binomial or multinomial functions. *f* is the fecundity or number of blastozooids produced by an oozooid and S_0 is the survival of the new born blastozooids until the start of the next time interval. Note that α, β, δ, γ, ε, f_{min} and f_{max} are model parameters.

intervals for the fitted values of the stage counts conditional on the initial counts by the percentile bootstrap method based on 200 bootstrap samples of the residuals from the fitted model (Efron and Tibshirani, 1993). λ was calculated as the first eigenvalue of the transition matrix, and reflects the long-term behaviour of the population under constant conditions. The population decreases exponentially when $0<\lambda<1$ and increases when $\lambda>1$. The elasticity of λ with respect to one of the matrix elements indicates the

proportional contribution of this matrix element to λ, and was computed following standard methods (Caswell 2001).

RESULTS

The temperature range in Barcelona was wider than in Cadaqués (12.2−24.9 ºC vs. 11.6−23.7 ºC), while total chlorophyll-*a* concentrations were slightly lower in Barcelona (0.07−1.03 vs. 0.07−1.25 µg / l; Figure 1.4). *T. democratica* appeared from May to June-July, and between September and October in years 2013 and 2014 (Figure 1.4). Higher abundances were recorded in Cadaqués during spring time. *T. democratica* was the only salp forming blooms in all sampling events except for spring 2013 when *Salpa fusiformis* was also present. When salp abundance was low (1 ind 100 m^{-3} or less), populations were mostly composed by blastozooids (Figure 1.4).

Salp densities and meteorological conditions favored the development of 8 short time-series observations (marked with stars in Figure 1.4), each of them covering five time transitions. The total number of time transitions was 40, all of which were used to fit the models. The model that best explained the variability observed in our data included only females affected by temperature (see Annex Table A.1). This effect can be estimated using the model equation from Table 1.2. Accordingly, the probability of females growing to males (G_F) and the concomitant probability of releasing an embryo (R_F) decreased with temperature (Figure 1.5.a). In contrast, the probability of remaining a female (P_F) was higher in warmer waters. Within the temperature range of this study (14 to 22 ºC), G_F varied between 0.1 and 7.6 % for a 30-minute time step. The number of buds per oozooid per 30-minute time step was inversely correlated to temperature and ranged from 31 to 52. Population growth rate (λ) smoothly decreased with temperature from 0.946 to 0.784. Elasticities (proportional sensitivity of λ to variation in a particular matrix element) also varied with temperature. Values were more balanced at low temperatures, with slightly higher elasticities for P_{PO} (Figure 1.5.b). In contrast, elasticity values for P_F were clearly higher at high temperatures. For the sake of comparison with existing literature, it is possible to derive the stage-dependent survival rates from our model probabilities to remain in the same stage (P) and to grow until the next stage (G), following the methods given by Caswell (2001). An individual will remain in the same stage (P) if it survives (s) and does not grow (1-g), thus P = s * (1 - g). An individual will grow into the next stage (G) if it survives and grows, that is, G = s * g. By using P and G estimates from the best model, we could calculate survival rates (s) by solving a two-equation system. Survival values of each stage were similar to those reported by Henschke *et al*. (2015) as shown in Table 1.3.

DISCUSSION

We have explored the population dynamics of the salp *T. democratica* by combining a stage-specific matrix model with empirical modelling of the transition matrix elements. Our study highlights the key role of the female stage during periods of population latency, a conclusion that departs from previous

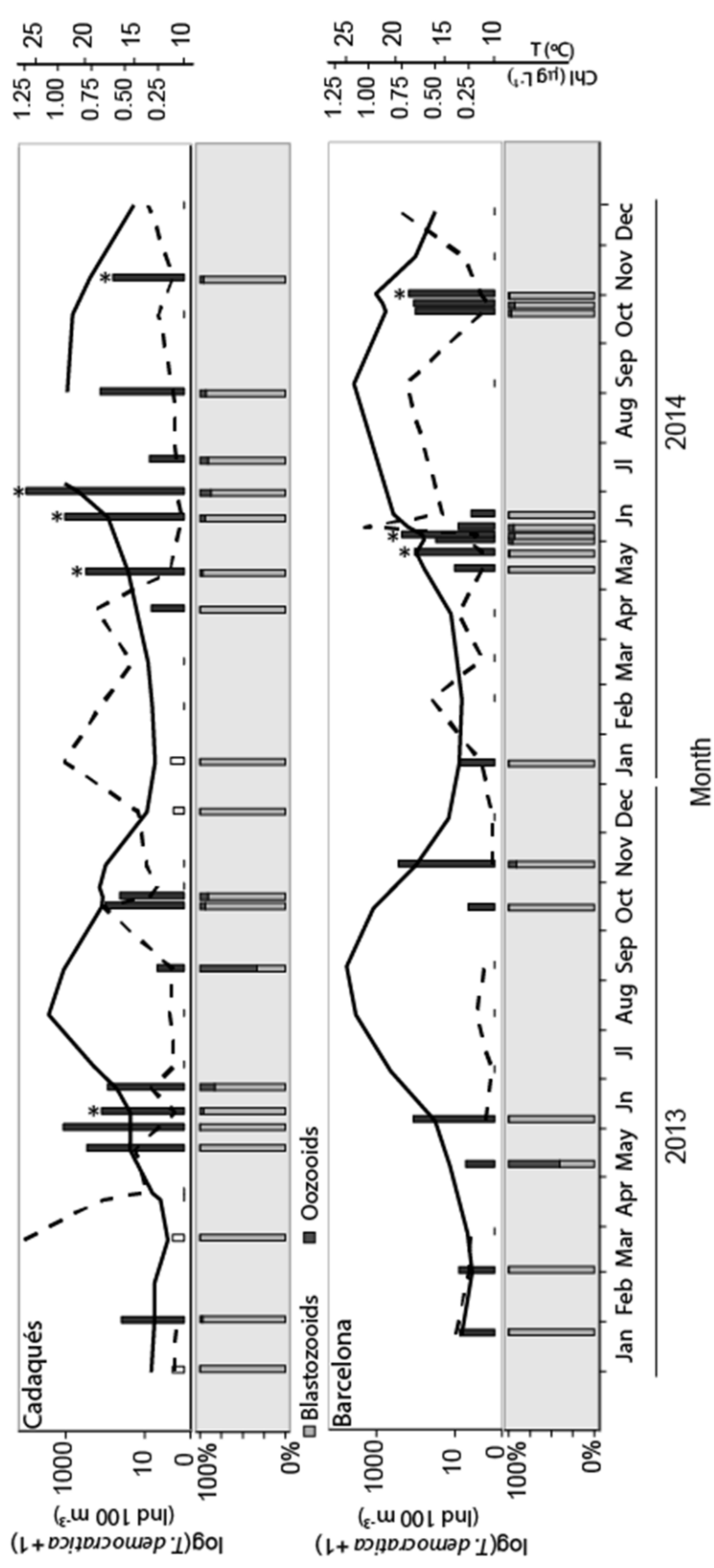

Figure 1.4. Temporal evolution during 2013 and 2014 of environmental parameters and salp populations in Cadaqués and Barcelona. Temperature are in solid line, total chlorophyll in dashed lines and *Thalia democratica* densities as vertical bars (empty bars indicates densities below 1 ind 100 m^{-3}). * highlights the short time-series studies, where only the first measurement is represented. The shaded parts, portray the percentage of blastozoids and oozooids in the population.

Matrix element	Function or fix value
P_F	$e^{-2.809 + 0.193 * T} / (1 + e^{-2.803 + 0.193 * T} + e^{3.945 - 0.415 * T})$
G_F/R_F	$e^{3.945 - 0.415 * T} / (1 + e^{-2.803 + 0.193 * T} + e^{3.945 - 0.415 * T})$
P_M	0.739
R_J	$0.011 * f$
G_J	0.204
P_J	0.615
R_{PO}	$0.009 * f$
P_{PO}	0.639
f	$14.001 + 222.26 / (1 + e^{0.112 * T})$
S_0	$1 / (1 + e^{4.518}) = 0.011$

Table 1.2. Matrix elements and its corresponding function or fix value resulting from the best model, that is, the one with the lowest cross-validation error (Cv) (model 1000) (see Annex Table 2).

studies (Heron and Benham, 1985). Our approach required samples of relatively dense salp populations to achieve meaningful parameter estimates. Consequently, phytoplankton assemblages may have beenovergrazed and chlorophyll measurements may not fully represent the actual food availability for the salp population. Moreover, population growth rates lower than 1 suggest that our observed, dense populations might be entering senescence. Bearing in mind these limitations, our one-time-step expected densities fitted reasonably well with our observations (see Annex Figure A.1) and the estimated stage-dependent survival rates were in consonance with those obtained from previous model-derived rates (*e.g.* Henschke *et al*. 2015; see Annex Table A.1).

The range of temperatures recorded was sufficient to evaluate its effects in salp dynamics. The model that best explained the variability observed in the population dynamics of *T. democratica* pointed to a direct, negative effect of temperature on females. Low temperatures were associated with favorable conditions for salps, while high temperatures corresponded to periods of salp population arrest (Figure 1.5). Although the effects of temperature seemed clear, these results could also be attributed to a direct influence on salp physiology or a seasonal indicator of primary production levels. In fact, temperature has traditionally been inversely related to primary production in the Mediterranean Sea (Saiz *et al*., 2014). There, the lowest water column temperatures occur in late winter/early spring, when stratification starts (Estrada, 1996), favoring phytoplankton and salp blooms (Ménard *et al*., 1994).

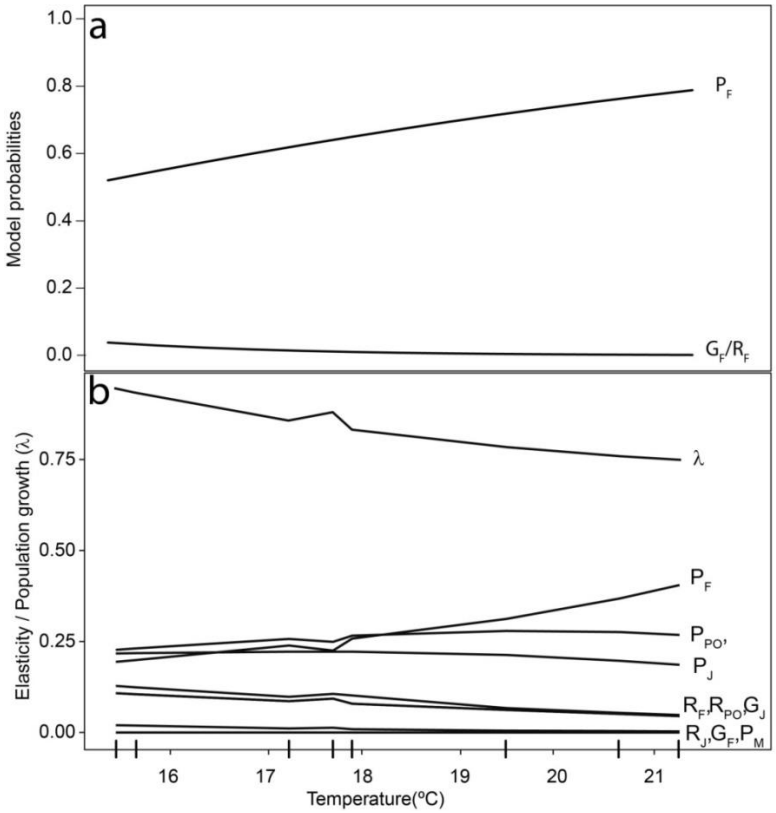

Figure 1.5.a. Female matrix parameters under different temperatures resulting from the best model selected. P_F, probability to remain in the female stage, G_F, probability to grow to male stage and R_F, give birth. Dashes on the x-axis indicate temperatures from the samples used to fit the model. **1.5..b.** Population growth (λ) and its elasticity respect each matrix parameters under different temperature levels. Matrix parameters (P, G, R) and its meaning are explained in methods.

Stage	Survival (This work)	Survival (Henschke *et al.* 2015)
Female (F)	0.51−0.81	0.84
Male (M)	0.739	0.55
Juvenile (J)	0.813	0.89
Productive (PO)	0.639	0.55

Table 1.3. Model stage-dependant survival calculated from our model P and G probabilities and compared with survival derived from the model of Henschke *et al*. (2015) assuming their daily survivals were constant.

These results are in contrast with those obtained in previous works, where chlorophyll-a, a measure of food availability, determined salp population dynamics (Heron and Benham, 1984; Andersen and Nival, 1986; Deibel and Paffenhöfer, 2009; Henschke *et al*., 2014). The chlorophyll-a range used in our study might be too narrow to observe any response, possibly due to overgrazing at the high salp densities we

observed. It is possible that primary production would describe food availability better than chlorophyll-a, but the methodology needed to obtain these values was logistically impossible in our study.

Elasticity analyses showed that the survival of solitary stages stimulated population growth during cold, favorable periods (Figure 1.5.b). These results are in agreement with other studies pointing to juvenile oozooid survival as the most sensitive vital parameter of the population dynamics (Henschke *et al*., 2015), as well as asexual reproduction, a key parameter for exponential growth (Alldredge and Madin, 1982; Andersen and Nival, 1986). The cessation of female reproduction during warm, unfavorable conditions caused low population growth rates (Figure 1.5.b). This finding contrasts with the hypotheses that the solitary stages would control the dynamics of latency periods in *T. democratica* populations (Heron and Benham, 1985). In our framework, under unfavorable conditions (high temperature and low food availability), females tended to invest the low energy input into slow growth while arresting reproduction, leading to slow population growth. In this sense, low-density populations (1 ind 100 m^{-3} or less) were exclusively dominated by the aggregate stage (Figure 1.4), indicating the potential role of females as a switch for population growth.

The probability of remaining in the same stage (P) exhibited higher elasticities than reproductive rates (R) in the model (Figure 1.5.b). In other words, shortening or enlarging the residence time in a given stage has more influence on population dynamics than producing more or less offspring (Heron, 1972b). *T. democratica* could control its population increase rates (r) through time, rather than clutch manipulation (*sensu* Aksnes and Giske, 1990*)*, as other pelagic tunicates like the appendicularian *Oikopleura dioica* would do (Subramaniam *et al*., 2014; but see Troedsson *et al*., 2002).

In contrast with hypothesis centred on the role of the oozooid stages (Heron and Benham, 1985), our results suggest that *T. democratica* females unfold a clockwork sequence of processes that initiates the bloom (Figure 1.3). Once the conditions improve from the latency, the female liberates an oozooid, which could carry a developing chain of daughter females (Heron, 1987a; Braconnot *et al*., 1988). When still physically close to its daughters, the female becomes a male. This situation would favor sex encounter in conditions of extreme population dilution. In an isolated group of closely related individuals, a sex ratio extremely skewed toward the females (i.e. one male, many daughters) should favor fitness maximization (Hamilton, 1967). Familiar groups of parasitoid wasps also showed such deviations from the stable 1:1 ratio under isolation inside their hosts when released from intense local mate competition (Werren, 1980). If true, this mechanism would imply inbreeding during the early stages of a bloom, a process that could be detected using genetic markers. It should also increase fertilization success among males and daughters. These testable predictions may set the base for future studies on salp dynamics.

CONCLUSIONS

We used an inverse method combining a stage-classified matrix population model, combined with empirical *in situ* observations, to understand how the vital rates of *T. democratica* vary with changing

environmental conditions. Our results point to females as the stage responsible for latency periods and not the asexual oozooid as previously hypothesized. Productive oozooid survival accounted for high population growth under favorable conditions, while female cessation lowered population growth under unfavorable conditions. In both scenarios, salps control population growth by time rather than clutch manipulation. After a latency period, females tend to release the oozooid–which is already generating chains of females– and turn to male. This circumstance triggers the bloom under extremely low population density by leaving the male close to its daughters, and thus favoring mating success. Therefore, we postulate that females may be the triggering mechanism to end the latency periods and initiate a salp bloom.

CHAPTER 2

SALPS SPATIAL DISTRIBUTION AND THEIR TROPHIC IMPACT IN THE CATALAN SEA, NORTHWESTERN MEDITERRANEAN

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ABSTRACT

Salps are pelagic tunicates that can rapidly increase in number and produce relevant effects in marine ecosystems. A regional approach is essential to understand their spatial distribution, but most research in the NW Mediterranean Sea is based on local scales. The present study aims to (1) analyze how mesoscale spatial patterns are structured by local physical and biological conditions; and (2) evaluate the trophic impact of a salp bloom in the Catalan Sea. We used geographic information system (GIS) and Generalized Additive Models (GAMs) to analyze salp spatial patterns and published allometric equations to estimate salp metabolic rates. Our results showed that hydrodynamic factors (shelf-slope front and onshore component of the current) mainly explained *Salpa fusiformis* spatial patterns, although this was influenced by biological variables (*e.g.*, low *Pelagia noctiluca* ephyrae abundance). *S. fusiformis* defecated a maximum of 39 mg C m^{-2} day^{-1}, increasing food supply for deep sea communities. The presence of *Thalia democratica* was associated with warm coastal waters and its low abundance produced a negligible trophic impact. This work shows the importance of considering both hydrodynamic and biological variables, including predators' abundance, in salp spatial analysis.

INTRODUCTION

Salps are pelagic tunicates widely distributed in all worlds' oceans. Their high local abundances can be due to an increase in population growth ("true bloom") or a passive accumulation of the individuals from a stable population ("apparent bloom") (Nival *et al*., 1990; Graham *et al*., 2001). Population growth can be extremely high in some salp species (i.e. a generation time of 2 days in *Thalia democratica* (Heron, 1972a)) coupling their abundance to the water column processes (i.e. water column stratification or increase in primary production) (Graham *et al*., 2001). At the same time, currents may disperse or aggregate salp populations depending on the limited horizontal swimming capacity (Höfer *et al*., 2015). Physical and biological factors influence salp spatial patterns by affecting salp biology (i.e., temperature, food availability, presence of predators or competitors) or individual re-dispersion (i.e., currents, eddies or fronts). High local salp abundance has been related to spatial variations in food availability and temperature affecting salp biology (Huskin *et al*., 2003; Hereu *et al*., 2006; Henschke *et al*., 2014). However, only a few studies have analyzed the direct influence of currents on salp dispersal (Everett *et al*., 2011; Höfer *et al*., 2015), and none considered the effect of predation, which may reduce local salp abundances. The question is whether locally high abundances can only be a consequence of accumulation, high population growth or both. Both hydrodynamic and biological terms should be included together to address that question.

When salps are abundant, they notably affect marine ecosystems due to their high feeding rates. They filter a wide size range of particles with high efficiency (Kremer and Madin, 1992; Madin and Kremer, 1995; Hereu *et al*., 2006), feeding mostly on phytoplankton but also on heterotrophic micro and mesoplankton (Vargas and Madin, 2004) or even on fecal pellets (Silver and Bruland, 1981; Huntley *et al*., 1989). Such grazing behavior (Alldredge and Madin, 1982) has a temporal impact on the entire pelagic community structure since it can outcompete other filter-feeders such as copepods (Bathmann, 1988). Salps are, in turn, preyed upon by numerous higher trophic species such as fish, crustaceans, medusae or ctenophores (Harbison, 1998; O'Rorke *et al*., 2015). They also defecate fast sinking fecal pellets that contribute to the marine snow and become food for benthic and deep sea communities when they reach the sea floor (Wiebe *et al*., 1979; Pomeroy and Deibel, 1980; Morris *et al*., 1988; Lebrato *et al*., 2012; Henschke *et al*., 2013; Smith *et al*., 2014).

These effects may be important in the Mediterranean ecosystems where high primary production is concentrated in spring and autumn, just when salps are conspicuous (Chapter 1, Andersen and Nival, 1986; Ménard *et al*., 1994b; Licandro, 2006). Despite the oligotrophic conditions in the Mediterranean Sea, several sources of enrichment (i.e., winter vertical mixing, occasional coastal upwelling, river runoff or frontal structures) can enhance primary production (Estrada, 1996). The Catalan coast, located in the northwestern Mediterranean, has a narrow continental shelf, excluding the vicinity of the Ebro river (in the South) and between submarine canyons (in the North) (Figure 2.1). A permanent shelf-slope density front along the shelf break separates the open sea high-salinity from lower-salinity shelf waters and is associated to a geostrophic current that flows from NE to SW (Font *et al*., 1988). This shelf-slope front usually contains high zooplankton biomass (Sabatés *et al*., 1989; Molinero *et al*., 2008) although its

location, strength and width can vary seasonally (Sabatés *et al*., 2004).

Salps have been less investigated than other zooplankton species in the northwestern Mediterranean Sea, probably because of their ephemeral appearance and patchy distribution. Several small-scale surveys have been conducted in the Ligurian Sea (Braconnot, 1963; Nival *et al*., 1990; Gorsky *et al*., 1991; Ménard *et al*., 1994; Licandro, 2006) but larger scale studies are necessary to understand how mesoscale structures affect salp distribution (Nival *et al*., 1990). The present study investigates (1) how the specific composition and the spatial patterns of salps in the Catalan Sea are structured by local physical (temperature, salinity, vorticity and current velocities) and biological (chlorophyll -a, non-salp zooplankton and *Pelagia noctiluca* ephyrae densities) conditions; and (2) the trophic impact of a salp bloom in the Catalan Sea.

MATERIALS AND METHODS

Sample collection

Sampling was done during the "FishJelly" cruise along the Catalan coast from June 15th to July 3th 2011 with 80 stations distributed in transects perpendicular to the shoreline (Figure 2.1). Stations were placed 7.5 nautical miles apart in each transect from near the coast to the slope. The mean distance between transects was 10 nautical miles. We used a CTD equipped with a fluorometer to obtain vertical profiles of temperature, salinity and fluorescence that were interpolated to 1m depth intervals. Water samples were collected with a rosette system at different depths, throughout the day and night, and filtered through glass fiber filters (GF/F) to obtain chlorophyll–*a* values for fluorometer calibration. Zooplankton was sampled by oblique tows, from a maximum depth of 200 m to the surface, with a Bongo net (40-cm diameter, 300-µm mesh) equipped with a flowmeter. After collection, samples were preserved in a 5 % buffered formaldehyde solution.

Sample analysis

Chlorophyll-*a* was extracted from the filters by adding 90% acetone and measuring their fluorescence with a fluorometer (Turner designs, Sunnyvay, CA) after storing them at 4ºC for 24 hours (Venrick and Hayward, 1984). Vertically mean chlorophyll-*a* concentrations (chl-a) (mean value between the depth of the chlorophyll maximum (DCM) and surface) were used for the analysis of spatial distribution of chlorophyll and trophic impact estimates. Total particulate organic carbon (POC) was estimated using the equation POC = 186.21 * chl-a * 0.35 according to Legendre and Michaud (1999) for oceanic waters with depths ≤ 300 m.

Salps were identified, counted and separated with a dissection stereoscope and then scanned using a Zooscan (Figure 1.2) (Grosjean *et al*., 2004). Salps life cycle alternates an aggregate generation, which

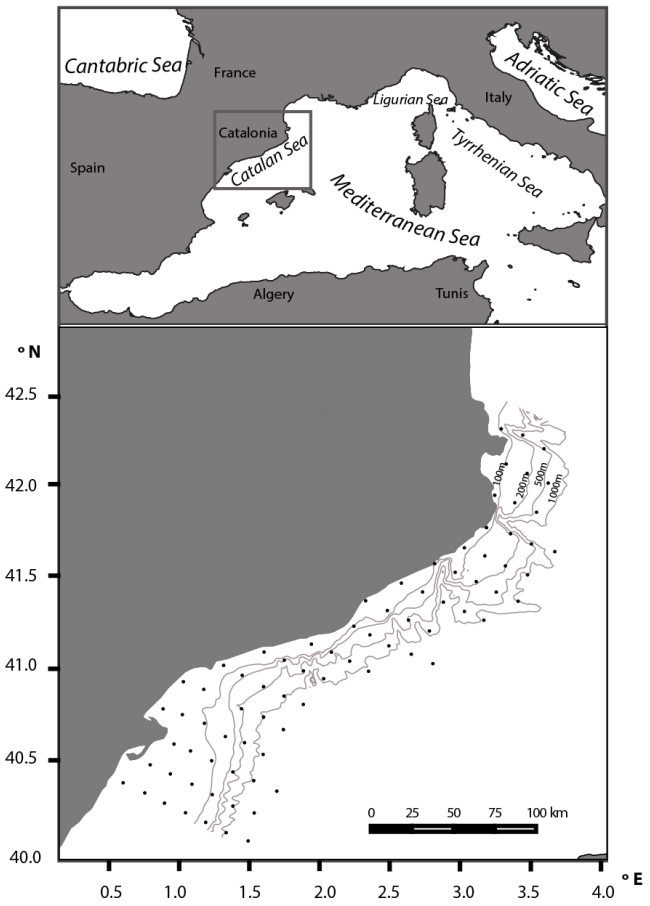

Figure 2.1. Sampling locations carried out on the FishJelly cruise in the Catalan Sea, NW Mediterranean Sea.

carries out the sexual reproduction, with a solitary generation that accomplishes the asexual reproduction. Both generations were treated separately for all estimations of metabolic rates (Heron and Benham, 1985). We measured the length of a maximum of 400 individuals of each species and stage from the posterior ridge of the gut to the oral opening (as in Foxton 1966) with Image J image analysis software (Abramoff *et al*., 2004). When salps were bent, this measure was done by tracing the endostyle. Before metabolic estimations, lenghts of the formalin-preserved individuals were converted to live length by applying a correction factor of 16 % (explained in Chapter 3). Metabolic rates were calculated from published allometric equations (Table 2.1). Abundance was determined by dividing counts by the water volume filtered (measured with the flowmeters) and expressed in individuals m^{-3}. For the sake of comparison with data in the literature, metabolic rates were expressed in units per m^{-2} by multiplying their mean value by the corresponding volumetric abundance [ind m^{-3}] and haul depth [m].

Non-salp zooplankton was classified according to coarse taxonomic categories: Copepoda, crustacean larvae, appendicularia, cladocera, doliolida, chaetognata, echinodermata, ostracoda, decapoda, mollusca, amphipoda, miscidacea, isopoda and euphauseacea. When the category exceeded 100 individuals, an aliquote was extracted and counts were extrapolated to the whole sample volume afterwards. Then, we summed counts of all groups to calculate total number of non-salp zooplankton in

each station and used this value for the spatial analysis. Maps were done with the free software Quantum GIS (Team, 2013) using the UTM 31 WGS 84 projection.

Statistical analysis

The relationship between salp abundances and environmental factors was evaluated with generalized additive models (GAMs; Wood, 2006). This kind of statistical models fit the data by applying smooth functions along the gradient of predictor variables without forcing to any parametric shape (Kienast *et al*., 2012). We fixed each smooth function (*spline* functions) to a maximum of 5 degree polynomial (k=5) to avoid complex responses of little biological significance (Maynou *et al*., 2014). We used the Gamma error distribution and the logarithmic link function because salp abundances were continuous, positive and skewed to 0 data. One count was added prior density calculation since the Gamma distribution does not allow values of the response variable to be 0 (Zuur *et al*., 2009).

Function	Aggregate	Solitary	Reference
S. fusiformis			
Carbon weigth (W) [mgC]	$0.0005(L)^{2.78}$	$0.0014(L)^{2.05}$	(Cetta *et al*., 1986)
Clearance rate (CR) [ml ind.$^{-1}$ h^{-1}]	$0.0145(L)^{3.32}$	$0.162(L)^{2.27}$	(Andersen, 1985)
T. democratica			
Carbon weigth (W) [mgC]	$0.0014(L)^{2.04}$	$0.0029(L)^{1.59}$	(Heron *et al*., 1988)
Clearance rate (CR) [ml ind.$^{-1}$ h^{-1}]	$0.0624(L)^{2.75}$	$0.0624(L)^{2.75}$	(Mullin, 1983)
Ingestion rate (IR) [mgC ind^{-1} h^{-1}]	CR *POC		-
Ingestion on phytoplankton(IR phyto) [mgC ind^{-1} h^{-1}]	CR*Chl		-
Defecation rate (D) [µgC ind^{-1}h^{-1}]	IR*(1-e)		-
Grazing impact (%)	IR_{phyto}*270 $^{-1}$ *100		

Table 2.1. Equations to calculate carbon weight, clearance, ingestion, ingestion on phytoplankton, defecation rates and grazing impact. "L" stands for live length [mm] and "Chl" for mean chlorophyll -*a* concentration [mgC m^{-3}] that was previously converted to carbon biomass using a C/Chl ratio of 60 [mg C m^{-3}] (Nival *et al*., 1985). We assume that clearance rates are independent on the food concentration within our range of particulate organic concentrations (Andersen, 1985). "*e"* (48.8%) is the mean assimilation efficiency between percentage of assimilation in diets based on dinoflagelates (64%) and diatoms (32%) (Andersen, 1986), weighted by proportion of these groups in our study (52.6 and 47.3 %, respectively).We applied same efficiency rate for *T. democratica* since the lack of data in the bibliography. Defecation rate was defined as food ingested and not assimilated. Grazing impact was calculated using primary production [mg C m^{-2} day $^{-1}$] that Estrada (1996) determined in June 1993 in the same area.

A total of 10 candidates were evaluated as explanatory variables: depth (m), collection time of the day (h), salinity (at 100 m), temperature (at 5 m) (ºC), vorticity (10^{-6} s^{-1}), cross shore and along shore components of the geostrophic current velocity at 10 m (cm s^{-1}; V_{45} and U_{45}, respectively), chl-*a* (mg C m^{-3}), total non-salp zooplankton abundance (ind m^{-3}) and *Pelagia noctiluca* ephyrae abundance (ind m^{-3}). We used salinity at 100m depth because, in summer, the shelf-slope front may not be well defined at surface (Font *et al*., 1988). *Salpa fusiformis* might perform diel vertical migrations, which could induce a dependence of salp abundance on the time of the day that the sample was collected in stations deeper than 200 m. Collection time of the day was considered as explanatory variable in the model to assess this effect. The abundance of *P. noctiluca* ephyrae was also included as explanatory variable to consider predation effect because they were observed feeding on salps (Purcell *et al*., 2014). Biological variables (chl-*a*, non-salp zooplankton abundance and *P. noctiluca* ephyrae abundance) and depth were log-transformed to satisfy normality.

Correlation and co-linearity among pairs of explanatory variables were identified with linear regressions with p-value lower than 0.05 and a variance inflation factor (VIF) (using the package *usdm* in R) bigger than 3 (Zuur *et al*., 2009), respectively. When two variables were dependent, we retained the variable with the highest explained deviance in the model. We selected the best model by forward stepwise method: starting with the intercept-only model -without effect of any explanatory variable- and increasing complexity adding one variable each time. The selection criteria was based on comparing the Akaike Information Criterion (AIC; Wood, 2006) of each model, which measures the trade-off between model complexity and goodness of fit. The lower the AIC the better the model, until AIC decreased less than 5% compared with the one of the previous model. GAMs were fit and plotted using *mgcv* package in R (Wood, 2006) and all analysis were performed with the R platform (R Core Team, 2015).

RESULTS

Hydrographic conditions

The sea surface temperature differed between the northern (18.48 ºC) and southern (24.16 ºC) parts of the region with a marked thermal front perpendicular to the coastline around 41° 30’ N (Figure 2.2). At 100m depth, the horizontal variation of salinity (37.8 to 38.4) defined the shelf-slope front, separating the more saline open sea waters from the less saline shelf waters. Highest chl-*a* was detected in the coastal stations and near the shelf-slope front (0.267 µg L^{-1}) (Figure 2.2.c., 2.2.f). The DCM was between 60 and 80 m depth, located below the thermocline and shallower in the coastal stations. The southwestwards geostrophic current followed the continental side of the shelf-slope front and was associated to the density front. Three eddies were found on the continental shelf area: near Palamós, Barcelona and the Ebro river delta, although only the latter was well defined (Figure 2.2.g; 2.2.h).

Salp distribution

The two species found in this study showed different spatial distribution patterns (Figure 2.2). *T. democratica* was less abundant and spread all over the continental shelf, although it was also present at deeper stations; Its abundance was higher in areas with intermediate to high water temperature (Figure 2.2.a), being absent in the northern most colder part. Its distribution seemed to be related with eddy structures, although this pattern is less clear (Figure 2.2.g). On the contrary, *S. fusiformis* was more abundant and distributed all along the shelf break, in association with the shelf-slope front and associated current, being scarcely present in coastal waters (Figure 2.2.d). *S. fusiformis* was also linked to colder waters (Figure 2.2.b).

The selected GAMs for the abundances of *S. fusiformis* and *T. democratica* had 4 and 1 terms which explained the 41.7% and 27.7% of the total deviance respectively (Table 2.2). Temperature, salinity, V_{45}, chl-*a* and non-salp zooplankton abundance were correlated with depth. We chose depth for *S. fusiformis* model and temperature for *T. democratica* since they were the variables that most explained in each model. High *S. fusiformis* abundance was mainly explained by increasing depths (down to a maximum of 250m) (30.2%), the negative U_{45} (onshore component) (7.9%) and low *P.noctiluca* ephyrae abundance (3.6%) (Figure 2.3.a; 2.3.b; 2.3.c).The most parsimonious model for *T. democratica* abundance was only explained by the effect of water temperature with an optimal between 22-23 ºC (Figure 2.3.f; Table 2.2).

Trophic impact

The throphic impact of salps in the Catalan Sea is shown in Table 2.3. All rates were approximately 100 times lower in *T. democratica* than in *S. fusiformis* which was more abundant and had larger individual size in most of stations. *S. fusiformis* filtered up to 667.65 L m^{-2} day^{-1}, ingested 69.92 mg C m^{-2} day^{-1} of which approximately 50% was defecated; however, only 1/10 of the total ingestion was due to feeding on phytoplankton.

DISCUSSION

Hydrographic conditions and salp distribution

The gradient between the more saline oceanic waters and the less saline shelf waters defined the shelf-slope front at 100m depth. This frontal system was associated with the circulation patterns dominated by meandering behavior of the Northern current, both well-known feature of the region (Font *et al*., 1995; Flexas *et al*., 2002; Sabatés *et al*., 2004). The current-frontal system is particularly productive in terms of primary and secondary production (*e.g.* Estrada and Margalef, 1988; Alcaraz *et al*., 2007) and high zooplanktonic biomass and fish larvae concentrations have regularly been observed along the shelf-break in relation to the frontal convergence (Sabatés *et al*., 1989). However, the patterns observed are subject to considerable spatiotemporal variability due to frontal mesoscale activity (Sabatés *et al*., 2004). The high chl-*a* detected far from the coast, between 60 and 80 m depth, have been reported on different occasions in the area in relation to frontal dynamics (*e.g.* Estrada, 1985; Estrada and Salat, 1989). Over the shelf, mainly in the southern part, chl-*a* patches were probably associated with low salinity and productive waters of the Ebro river runoff, characteristic of that area (Salat *et al.*, 2002; Sabatés *et al*.,

2009). Three eddies seem to be present in coastal waters as previously recorded in the area during summer (Sabatés *et al*., 2013), although the pattern was weak, except for the one in front of the Ebro river delta.

Analysis of the mesoscale distribution of dynamic populations requires longer survey times than smaller scale studies and this can cause negative consequences on the degree of synopticity of the distribution (Zhou, 1998). The minimum time logistically possible to conduct our survey was 10 days. During this period, spatial distribution should have not changed significantly since, in June-July, short-time scale changes in the water dynamics seem to be less important. Despite this possible limitation, our results agree with other studies on zooplankton distribution in the same area (Sabatés *et al*., 1989; Nival *et al*., 1990).

Salp distribution

We found that salp spatial patterns were mainly explained by physical factors (depth, across shore current component and temperature) but biological variables (*P. noctiluca* ephyrae abundance) played an additional role in the observed distributions. The two species found in the area showed different patterns: low *T. democratica* densities were distributed in coastal waters -in agreement with other studies (Nival *et al*., 1990; Hereu *et al*., 2006; Henschke *et al*., 2014)- while high *S. fusiformis* abundances were concentrated along the shelf break, in relation with the shelf-slope front and the geostrophic current (Figure 2.2). Nival *et al*. (1990) found similar patterns along one transect perpendicular to the shore in the Ligurian Sea, but they also observed *S. fusiformis* near the shore. In other regions, *S. fusiformis* was the least abundant when it was found with other species of *Thalia* (*Thalia orientalis*) (Hereu *et al*., 2006).

Water temperature explained 27.7% of the variability in *T. democratica* local abundances, showing an optimal effect on their abundances between 22 and 23 ºC. Despite this result, our maximum abundances were lower (< 1 ind m^{-3}) than those normally achieved during a *T. democratica* bloom (in the order of 100-1000 ind m^{-3} (Henschke *et al*., 2014; Chapter1)). In Chapter 1, warm temperatures negatively affected population growth of *T. democratica*. Therefore, the relation obtained between warm temperatures and high salp abundance may not mean that high temperatures accelerated their metabolism but that *T. democratica* was associated with warm coastal water mass. Passive accumulation would have influenced the distribution since high abundances are found associated with eddy structures (Figure 2.2.g), in good agreement with other studies (Deibel and Paffenhöfer, 2009; Everett *et al*., 2011). However, the pattern shown in Figure 2.2.g is weak and the contribution of vorticity in the model for this species was negligible. In contrast to our results, Henschke *et al* (2014) concluded that the largest *T. democratic*a abundances were mainly driven by an increase in phytoplankton fraction > 2µm which salps consume more efficiently.

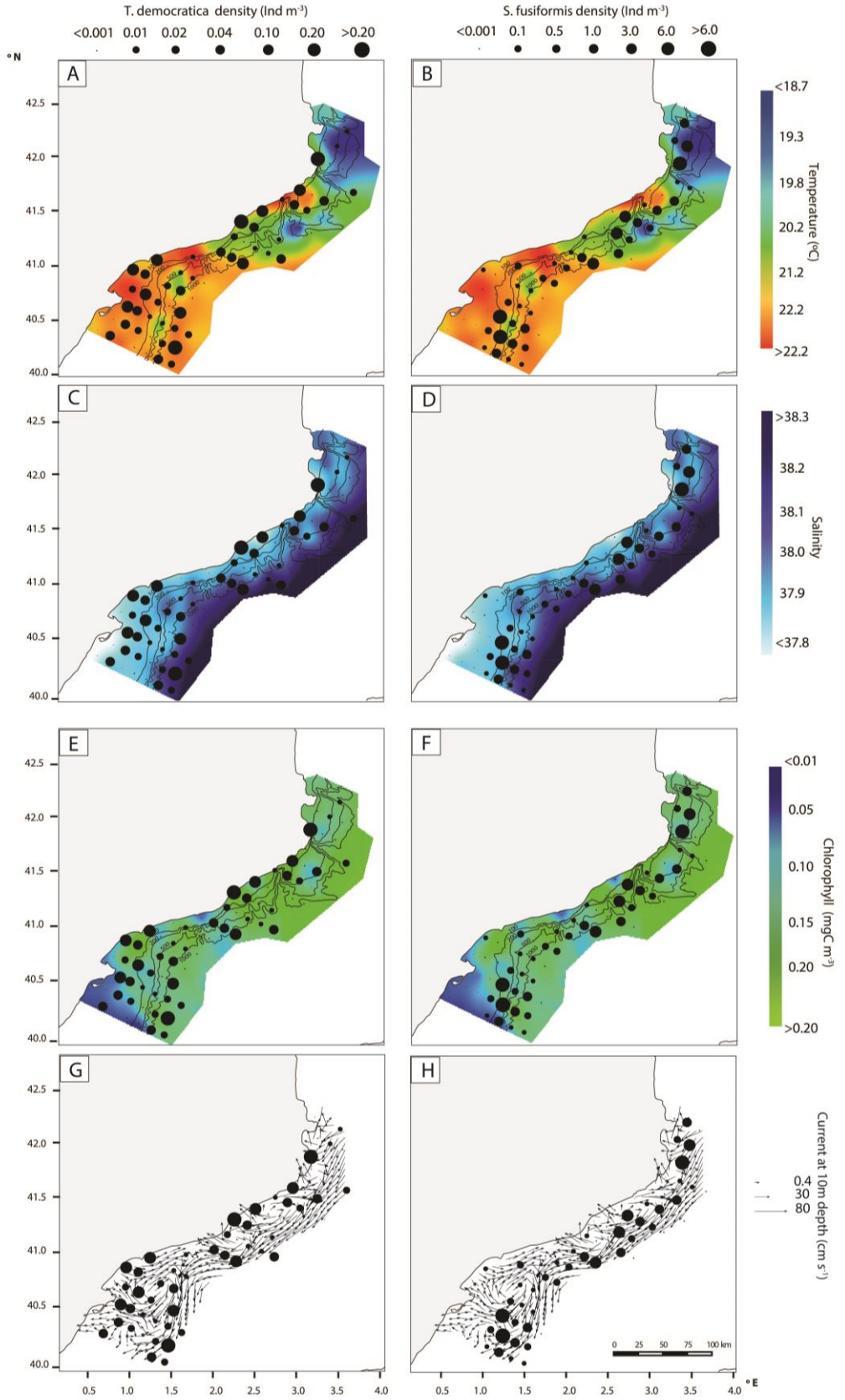

Figure 2.2. Salp abundance distributions laid over temperature at 5m (A and B), Salinity at 100m (c and d), integrated chl concentration e and f) and geostrophic current at 10 m (g and h). Salp abundance for *T. democratica* (a, c, e, g) and *S. fusiformis* (b, d, f, h) is represented by sized black circles. Isobaths denote from coast to open sea: 100, 200, 500 and 1000 m depth.

	Term	AIC	Dev	edf	p- value
S. fusiformis	NULL	64.370	0		
1	+s(log(Depth)+1)	31.469	30.2	3.416	<0.001
2	+s(U_{45})	21.260	38.1	1	<0.001
3	+s(log(*P.noctiluca* ephyra)+1)	17.344	41.7	1	<0.01
T. democratica	NULL	-323.482	0		
1	+s(Temperature)	-347.068	0.277	3.407	<0.001

Table 2.2. Forward stepwise selected GAMs. For *S. fusiformis* and *T. democratica* abundance, each row corresponds to a new explanatory variable added to the previous model. Last row in each case is the optimal model. AIC: Akaike Information Criterion; Dev: Deviance explained (%). The two last columns show the degrees of freedom (edf) and p-values of each term in the selected model.

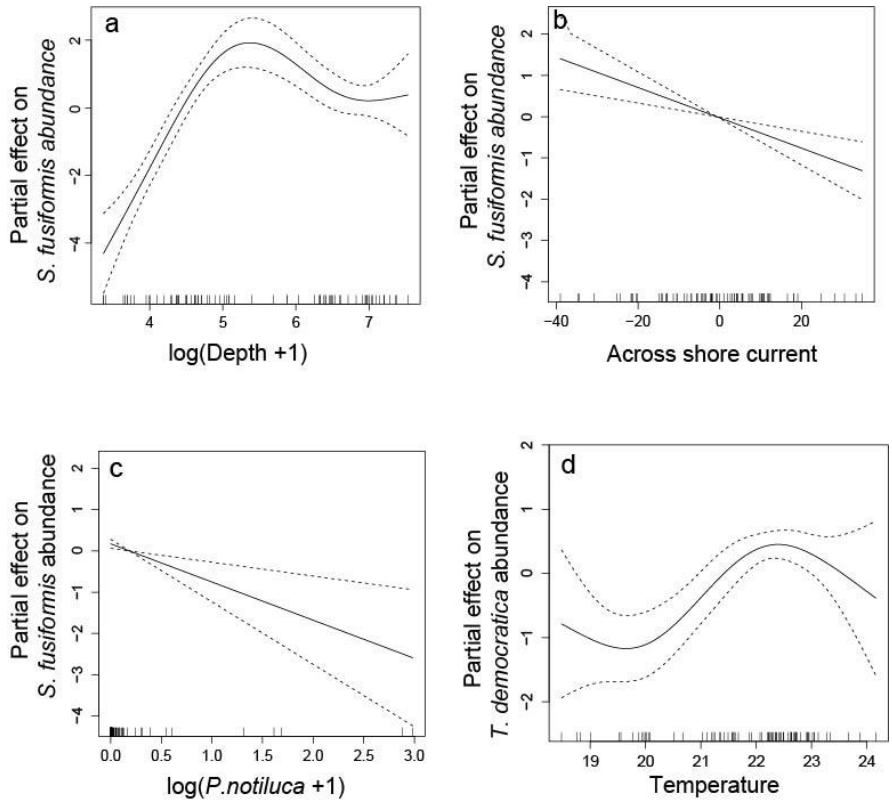

Figure 2.3. Partial effects of explanatory variables gradient that were significant in the generalized additive models for *S. fusiformis* (a, b, c), *T. democratica* (d). Dashed lines indicate 95% confidence intervals. a. Depth: bottom depth (m); b. Across shore current: U_{45} component of the current velocity (m s^{-1}); c. Temperature: water temperature at 5 m (ºC); d. *P. noctiluca*: *P. noctilica* ephyrae abundance (Ind m^{-3}); e. *S. fusiformis*: *S. fusiformis* abundance (Ind m^{-3}).

High abundances of *S. fusiformis* increased with depth (until a maximum in 250m approximately) and onshore current velocity, which together explained the 38.1% of its distribution (Table 2.2, Figure 2.2 and Figure 2.3). Stations with depths around 200m coincide with the hydrographic front and the onshore current indicates a transport of individuals from oceanic waters towards the coast. Hence, high *S. fusiformis* abundance resulted from the accumulation of individuals, incoming from oceanic waters, on the shelf-slope front. This result supports previous hypothesis about the transport of young *S. fusiformis* from the offshore region to the coast (Nival *et al* (1990)). Previous research has highlighted the importance of hydrographic structures in explaining high salps density (Huskin *et al*., 2003; Deibel and Paffenhöfer, 2009; Everett *et al*., 2011). Besides the direct effect of physical aggregation, salp accumulation itself -that favors mating during sexual reproduction- and high food availability typical in fronts (Sabatés *et al*., 2004) may stimulate population growth (Sabatés *et al*., 1989; Deibel and Paffenhöfer, 2009; Henschke *et al*., 2014). Following methods of Chapter 3, if we classify *S. fusiformis* individuals into different life stages, 42.5 % of the stations presented oozooids with chains, which suggested their populations were actively reproducing (Liu *et al*., 2012).

	S. fusiformis				***T. democratica***		
	min	**max**	**mean**	**Nival *et al* 1985**	**min**	**max**	**mean**
Abundance [Ind. m^{-3}]	$2.48*10^{-3}$	11.73	1.20	-	$2.66*10^{-3}$	$3.40*10^{-1}$	5.08
Biomass [mg C m^{-2}]	$1.68*10^{-3}$	1185.43	23.38	-	$1.51*10^{-3}$	1.53	0.13
Clearance rate [m^3 m^{-2} d^{-1}]	$5.63*10^{-6}$	0.67	64.25	0.562	$2.83*10^{-3}$	5.54	0.26
Ingestion rate [mg C m^{-2} d^{-1}]	$4.29*10^{-4}$	69.92	6.41	-	$1.63*10^{-4}$	$5.44*10^{-1}$	$5.58*10^{-2}$
Ingestion rate(only phytoplankton) [mg C m^{-2} d^{-1}]	$2.60*10^{-5}$	7.74	0.66	64.3	$6.0*10^{-6}$	$5.35*10^{-2}$	$5.64*10^{-3}$
Defecation rate [mg C m^{-2} d^{-1}]	$2.19*10^{-4}$	35.76	3.28	9	$8.30*10^{-5}$	$2.78*10^{-1}$	$2.85*10^{-2}$
Grazing impact [%]	$9.63*10^{-6}$	2.87	$2.44*10^{-3}$	35.5	$2.22*10^{-6}$	$2.00*10^{-2}$	$2.08*10^{-5}$

Table 2.3. Minimum, maximum and mean values of abundance, biomass, clearance rate, ingestion rates, defecation rate and grazing impact in the 80 stations along the Catalan coast. *S. fusiformis* values are compared with Nival *et al.* (1985).

The negative effect of *P. noctiluca* ephyrae on the abundance of *S. fusiformis* (Figure 2.3.c; Table 2.2) could be attributed to predation since salps represented the main contribution to the diet of *P. noctiluca* ephyrae during this survey (Tilves *et al*., *in prep*). This study first shows a possible contribution of predation on reducing local salp abundance.

Impact on the ecosystem

Due to their low abundances, *T. democratica* populations exerted a small trophic impact, while *S. fusiformis* populations had an impact comparable to that observed in the Ligurian Sea by the same species (Table 2.3; Nival *et al*., 1985). Their maximal clearance rates were similar but their ingestion and grazing impact were lower than those observed by Nival *et al*. (1985) (Table 2.3). If we include non-phytoplankton organic particles, defecation rates were ten times higher than only considering phytoplankton (3.96 mg C m^{-2} d^{-1}, Table 2.3) and comparable with the maximum POC flux in the northeast Pacific (38 mg C m^{-2} d^{-1}; Smith *et al*., 2014). With low influence of microbial activity (Caron *et al*., 1989) and a sinking velocity of 1000 – 2000 m day^{-1} (Morris *et al*., 1988), this material should take 1-2 days to reach the ocean floor, situated at ca. 1800m depth. Consequently, blooms of *S. fusiformis* blooms may rapidly transfer particulate organic matter from the ocean surface to the deep ocean; increasing the food available for benthic suspension feeders (Wiebe *et al*., 1979; Smith *et al*., 2014). This biomass represents 1.5 times the annual organic carbon mean supply near the shelf-slope (24 mg C m^{-2} day^{-1}; Puig and Palanques, 1998). Mediterranean benthic suspension feeders reproduce in spring-summer (Coma *et al*., 2000) and require some energy storage for reproduction (Gori *et al*., 2013). Seasonal reproduction in deep sea species may be regulated by variations in organic matter that sinks from the surface (Gage and Tyler., 1992).

The role of *T. democratica* in the transfer of organic matter to the sea floor may be negligible since their maximum defecation rate was low (Table 2.3) and the flocculent consistency of their fecal pellets cause a slow sinking rate (Pomeroy and Deibel, 1980). Coprophages and microbial populations can also eat and degrade those flocculent aggregates while suspended in the water column (Pomeroy *et al*., 1984; Alldredge *et al*., 1986).

CONCLUSIONS

In conclusion, the present study shows that it was mainly the hydrodynamic variables which explained the spatial patterns in the distribution of *S. fusiformis*, although biological variables played a secondary role. *T. democratica* was associated to warm coastal waters while *S. fusiformis* occurred in deep stations and affected by the onshore component of the current. The shelf-slope front acted like a barrier blocking the flow of *S. fusiformis* individuals towards the coast. Secondarily, a negative correlation with the density of *P. noctiluca* ephyrae influenced the effect of hydrographic factors in *S. fusiformis*. The trophic impact of *T. democratica* populations was almost negligible due to their low abundance. On the contrary, *S. fusiformis* exhibited high defecation rates, producing fecal pellets that would rapidly sink to the deep ocean. Increasing food supply might be essential for maintaining deep sea communities in ecosystems with seasonal variations in primary production. Regarding the importance of hydrodynamic factors and, secondarily, predator's abundance in explaining the spatial distribution of salps, further analysis should considered both types of variables.

CHAPTER 3

CONTRASTING DIEL VERTICAL MIGRATION PATTERNS IN *SALPA FUSIFORMIS* POPULATIONS

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ABSTRACT

Vertically stratified samplings at three locations in the Catalan Sea demonstrated the coexistence of two diel vertical migration (DVM) types in *Salpa fusiformis* populations. Salps performed diurnal migration in one station (K2) while nocturnal migration in the others (E3 and J3). K2 did not differ from the other stations in environmental conditions (temperature and chlorophyll-a concentration profiles). However, K2 had high abundance of productive oozooids and higher total abundance which suggests the population could be actively reproducing. Accordingly, we suggest that non-visual predators might exert a selective pressure towards diurnal migration of salps and that this process might occur faster if salp population is actively reproducing.

INTRODUCTION

Diel Vertical Migration (DVM) is a behavioral pattern where organisms swim vertically through the water column in a daily cycle. Differences in this migration pattern can be inter- or intra- specific (Osgood and Frost, 1994; Dale and Kaartvedt, 2000; Holliland *et al*., 2012) and individuals can change their behavior depending on the environmental conditions (Ohman, 1990; Fischer *et al*., 2015). Hypotheses explaining DVM in each situation are still under study. The most common DVM pattern is where individuals reach surface at night, and are in deeper waters during the day ('nocturnal migration'). This behavior is attributed to the trade-off between finding food at the surface and avoiding being eaten by their visual predators (Lampert, 1989).This hypothesis does not explain DVM behavior for migrants without visual predators or for diurnal migrations -where organisms are at the surface during the day and at deeper waters at night (Hammer *et al*., 1982; Ohman, 1990). Alternatively, other hypotheses have been suggested: migrators are following migrating prey (Hammer *et al*., 1982; Sims *et al*., 2005), escaping from migrating predators (Ohman *et al*., 1983), reducing metabolic expenditures (Enright, 1977), or aggregating for reproduction (Purcell and Madin, 1991).

Salps migration cannot be explained by avoidance of visual predation since their transparent barrel shape bodies are hardly visible -even during daytime- and some species migrate entirely within the photic layer (Purcell and Madin, 1991). Purcell and Madin (1991) hypothesized that *Cyclosalpa baekeri* migrates to surface at night to aggregate and increase mating success. Aggregations are essential for salp blooms since their sexual reproduction is based on internal fertilization (Boldrin *et al*., 2009) and is key for maintaining genetic variability (Alldredge and Madin, 1982). In addition to this possibility, additional hypotheses are required to explain why some salp species are non-migratory (i.e. *Thalia democratica* (Sardou *et al*., 1996; Gibbons, 1997)) and other species show unclear migration patterns. This is the case of *Salpa fusiformis* whose migration is subject to controversy: some studies reported nocturnal migration (Franqueville, 1971; Andersen *et al.,* 1998; Nogueira *et al.,* 2015) while others reported weak or no migration(Laval *et al*., 1992; Tsuda and Nemoto, 1992; Sardou *et al*., 1996). Liu *et al*. (2012) first reported diurnal DVM of *S.fusiformis* but only when the population was dominated by solitary and smaller aggregate forms, which suggested that the salps were actively reproducing. Their findings highlight the importance of considering population structure in DVM studies of salps. Although none of these works gave an alternative explanation for the migration pattern, their contrasting results might indicate *S. fusiformis* changes its migratory behavior.

The present work aims to clarify DVM in *S. fusiformis* in the Mediterranean Sea and evaluate the impact of population structure and water column characteristics on migratory patterns. Specifically, we assess whether *S. fusiformis* performed DVM and if so, if the migratory pattern was consistent in all of the surveyed locations.

MATERIALS AND METHODS

Sampling was conducted from June 26th to July 7th 2011in the Catalan Sea, North Western Mediterranean Sea,as part of the "Fishjelly Project" cruise. Three stations located at different depths were selected to perform stratified samplings: 'K2' (41º 23.27' N, 2º 32.18'E; depth=118m) on the continental shelf, 'E3' (40º 54.30'N, 1º 19.26'E; depth=190m) on the shelf break and 'J3' (41º 10.75'N, 2º 27.57'E; depth=600m) over the slope (Figure 3.1).Depth-stratified zooplankton samplingswereperformed during two consecutive day-night pairs, avoiding sunset and sunrise hours.MOCNESS net 1-m^2 opening mouth

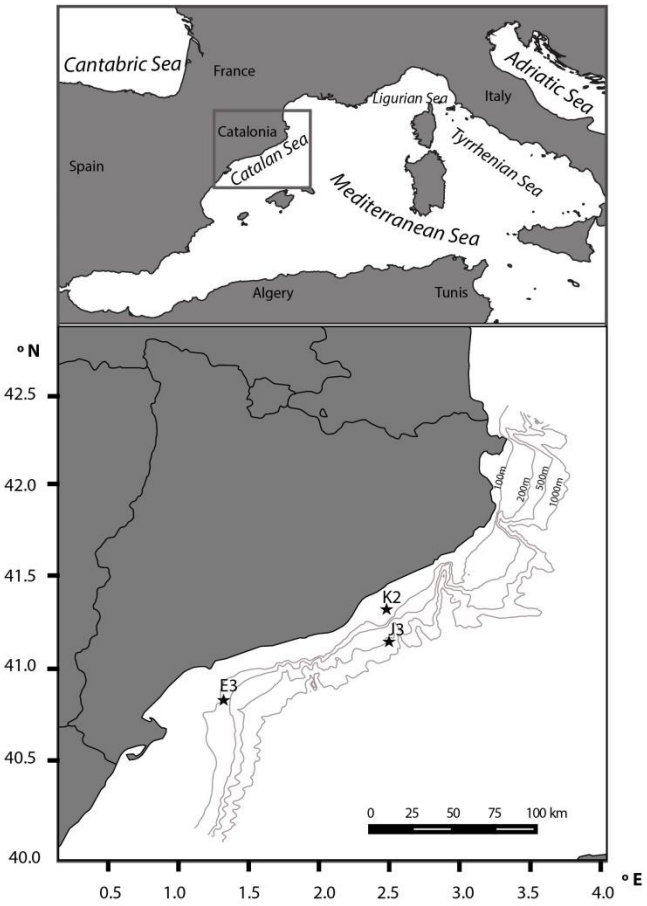

Figure 3.1. Samplings locations within the Catalan Sea, Northwestern Mediterranean Sea: K2 on the continental shelf, E3 on the shelf break and J3 on the shelf slope.

and 300µm mesh was deployed to collect the samples obliquely, moving from deep to shallow layers. The strata depth intervals were defined accordingly to the maximum depth in each station (E3: 25, 50, 100 and 150 m; J3: 25, 50, 100, 150, 250, 400 and 550 m; K2: 25, 50, 75 and 100 m). Ship speed was 2–2.5 knots. The volume of water filtered by each net was recorded by a flowmeter attached to the mouth of the net. Zooplankton samples were preserved in a 5% buffered formaldehyde solution immediately after collection. Vertical profiles of temperature, salinity and fluorescence were obtained by deploying a Neil Brown Mark III- CTD equipped with a Sea- Tech fluorometer. To calibrate the fluorometer, water samples for chlorophyll -a determination were collected with Niskin bottles mounted on a rosette system and closed at different depths, including the deep chlorophyll maximum (DCM), throughout the day and

night. Clorophyll-a extraction was done in 90% acetone and their fluorescence was measured with a Turner designs fluorometer (Sunnyvay, CA) after storage at 4ºC during 24h (Venrick and Hayward, 1984).

The number of individuals of each salp species and solitary/aggregate form were counted using a dissection stereoscope and separated from the zooplankton sample. Density estimates were calculated by dividing the counts by the volume of water filtered and then multiplying by the depth range of each stratum, to facilitate comparisons among strata. Densities were standardized to individuals per 100 m ^{2}. Individuals with signs of degradation were considered as sinking dead bodies and were not included in the analysis. We took pictures of individuals in each sample using a Zooscan (Grosjean *et al.*, 2004; Figure 1.2). A maximum of 400 individuals per each species and solitary/aggregate form were measured digitally with image J software (Abramoff *et al*., 2004) from the posterior ridge of the gut to the oral opening (Foxton, 1966). Live length was used to classify individuals by stage after shrinkage correction. We measured few individuals before adding formalin, and again two years later, to determine a percentage of shrinkage of 16%. Salps life cycle is based on an asexual and a sexual phase. In the asexual reproduction, solitary forms,also called oozooids, produce chains of females called blastozooids or aggregate forms. During the sexual reproduction, newborn females are impregnated and internally develop an embryo. Females will become males once they give birth to the young oozooid, closing the cycle. Accordingly, we classified *S. fusiformis* into five different life stages using size ranges extracted from Braconnot *et al*. (1988): B1(<4mm) blastozoids just released or still in the oozooid (in case that they have been accidentally released during manipulation), B2 (4-18mm) females that start developing the embryo, B3 (>18mm) females who have given birth (males), O1(<13mm) Oozooids that have not liberated the first chain yet, O2 (≥13mm) productive oozooids which are actively producing chains. We calculated the relative frequencies of each stage over the total number of individuals measured. We then estimated the densities of each stage in the sample by multiplying those frequencies by the total density of organisms.

Non-salp zooplankton were counted and identified according to coarse taxonomic categories (amphipoda, crustacean larvae, copepoda, appendicularia, cladocera, doliolida, chaetognatha, echinodermata, ostracoda and mollusca). When the number of individuals exceeded 100 we subsampled and extrapolated the count to the whole sample. Densities were determined using the same calculations as for salps and then standardized to 100 m^2.

To test for DVM in each variable from a total of 19 (stages of *S. fusiformis*, other salp species and non-salp zooplankton groups (Table 3.1)) the weighted mean depth (WMD) was calculated for each sampling station and time as follows

$$WMD(m) = \frac{\sum(n_i * d_i)}{\sum n_i}$$

where n_i is the density of individuals of a given taxon in depth stratum i and d_i is the midpoint of stratum i. One way - ANOVAs were conducted to test for DVM in each station and two-way ANOVAs were used for interaction between "day-night" and "station". Data were log-transformed when they did not satisfy normality.

RESULTS

The vertical structure of the water column was dominated by thermal stratification. Surface water temperature was around 22 ºC at stations K2 and J3 and slightly higher at E3 (23.10 ºC), remaining constant (~13.2ºC) below 100m depth. The vertical chlorophyll-a profiles showed a deep chlorophyll maximum (DCM) located beneath the thermocline. Both maximum chlorophyll -a concentration (0.53, 0.53 and 0.47 mg m^{-3} in stations E3, J3 and K2, respectively) and the depth of the DCM (60, 70 and 80 m in E3, J3 and K2, respectively) were similar in all stations (Figure 3.2).

	E3			**J3**			**K2**		
Species/ stage	Day	Night	pv	Day	Night	pv	Day	Night	pv
S. fusiformis									
Total	96.1 ±25.2	48.8 ±31.0	>0.1	366.8 ±91.1	33.8 ±28.1	<0.05	26.7± 6.4	53.1 ± 7.2	<0.1
Blastozooids (B1)	37.5±53.0	21.8 ±7.7	>0.1	276.9±113.8	18.5 ±7.1	<0.1	30.5 ± 7.0	59.0 ± 4.9	<0.05
Blastozooids (B2)	97.3 ±23.4	49.4 ±32.7	>0.1	376.3 ±84.2	34.5 ±29.1	<0.05	21.7 ± 6.4	39.4 ± 3.9	<0.1
Blastozooids (B3)	-	-	-	-	-	-	6.3 ± 8.8	18.8 ±265	>0.1
Oozooids (O1)	-	-	-	356.8±167.2	22.9 ±7.6	<0.1	42.2 ±17.7	48.7 ± 9.3	>0.1
Oozooids (O2)	-	-	-	-	25.0 ±17.7	>0.1	34.8 ± 5.3	72.3± 1.9	<0.05
T. democratica	20.1 ± 4.6	20.5±0.7	>0.1	15.4 ± 2.6	12.7 ± 0.3	>0.1	15.1 ± 3.7	29.2 ± 19.3	>0.1
Amphipods	90.9 ± 48.3	71.5±50.0	>0.1	87.0 ± 27.9	39.5 ±15.1	>0.1	32.5 ± 5.2	26.5 ± 5.8	>0.1
Crustacean larvae	80.6±27.2	47.9±1.2	>0.1	62.1±21.8	54.5±8.7	>0.1	55.2±0.1	44.2±8.2	>0.1
Copepoda	58.1±3.1	43.1±12.4	>0.1	65.4±13.5	55.2±2.9	>0.1	45.5±10.3	33.7±3.0	>0.1
Appendicularia	69.9±7.2	21.9±13.1	<0.05	59.2 ±17.1	67.9±9.8	>0.1	61.1±2.3	31.0±1.0	<0.01
Cladocera	19.1±8.1	27.0±19.2	>0.1	23.4±1.5	21.1±1.4	>0.1	13.4±0.2	13.2±0.4	>0.1
Doliolida	12.9±0.3	13.6±0.7	>0.1	24.5±7.5	37.8±31.0	>0.1	33.0±7.3	19.7±7.6	>0.1
Chaetognata	24.7±1.4	17.3±1.7	<0.05	31.4±0.1	31.7±22.4	>0.1	34.2±6.4	21.3±9.2	>0.1
Echinodermata	67.2±9.3	37.1±17.6	>0.1	29.4±10.9	16.8±3.8	>0.1	38.4±19.5	17.8±0.1	>0.1
Ostracoda	90.7±14.9	84.2±16.9	>0.1	119.5±6.6	90.9±30.6	>0.1	73.6±2.6	40.9±7.6	<0.05
Mollusca	24.5±6.2	17.9±2.3	>0.1	58.4±13.9	35.7±16.5	>0.1	32.6±13.7	25.3±15.6	>0.1

Table 3.1. Weighted mean depth (WMD) (Mean ± SD) of *S. fusiformis* (divided in the different life stages: B1, B2, B3, O1, O2), *T. democratica* and the non-salp zooplankton species in the three stations (E3,J3 and K2) during dayand night. 'pv' stands for the resulting p-value in the analysis of the variance

S. fusiformis was found at different depth strata depending on the time of day and its migration pattern differed significantly among stations ($F=10.17$; $p<0.05$) (Figure 3.2). In stations E3 and J3, *S. fusiformis* was found at depths below 50m during the day but at night it was generally found between the surface and 50 m (Figure 3.2). However, this trend was only significant in station J3 (Table 3.1). In contrast, individuals in station K2 were in the 0-50 m layer during the day and primarily in the 50-100 m stratum at night, although the pattern was marginally significant (Table 3.1; Figure 3.2). Maximal total abundances differed among stations: 31008 ind 100 m^{-2} (K2), 453 ind 100 m^{-2} (E3) and 2737 ind 100 m^{-2} (J3).

Stage composition of *S. fusiformis* also differed among stations. In station E3, the population was comprised of only females (B1 and B2) and both stages exhibited the same migration pattern (Figure 3.2; Table 3.1). However, none of the patterns in E3 were statistically significant (Table 3.1). In J3 there were females (B2) and oozooids that had not produced chains yet (O1), but very few productive oozooids (O2) and newborn blastozooids (B1). All stages were at surface during the night with statistical significance (Table 3.1). In contrast, in K2 all stages were present and productive oozooids (O2) and newborn blastozooids were dominant (Figure 3.2). Although all of them did a diurnal migration, this was only significant ($p<0.05$) in newborn blastozooids (B1) and productive oozooids (O2) and marginally significant ($p<0.1$) in females (B2) (Table 3.1). Males (B3) were only present in K2 the second night and day at 0-25 and 25-50m stratum, respectively and in much lower numbers than the blastozooids (B1 and B2) (72.43 and 6.29 males in $100m^{-2}$, for the second night and day, respectively).

The salp *T. democratica* was distributed mainly in the 0-30m layer and did not show signs of DVM. Differences in WMD between day and night were not statistically significant for most non-salp zooplankton groups, except for appendicularians at E3 and K2, chaetognaths at E3 and ostracods at K2 (Table 3.1).

DISCUSSION

This study is the first report of the coexistence of different migratory behaviors of a salp species within the same season and area: *S. fusiformis* performed nocturnal migration in stations E3 and J3 but diurnal migration in K2 (Figure 3.2; Table 3.1). Liu *et al.* (2012) found seasonal changes from inconsistent migratory behavior of *S. fusiformis* in December to a clear diurnal DVM in May and June. Both studies hint that *S. fusiformis* may adapt its migrant behavior to different situations, which would explain the contrasting patterns of DVM of *S. fusiformis* in previous research (Franqueville, 1971; Laval *et al*., 1992; Tsuda and Nemoto, 1992; Andersen *et al*., 1998). Variable DVM patterns have also been observed in other species: copepods ceased the migration in lakes with very low water transparency (Fischer *et al*., 2015) or in absence of predators (Bollens, 1991); two cladoceran species changed the migration seasonally (nocturnal DVM in June, no migration in July, and diurnal DVM in September) depending on the presence of predators (Lagergren *et al*., 2008); and basket sharks exhibited diurnal migration depending on the habitat type, possibly tracking the movement of their zooplankton prey (Sims *et al*., 2005).

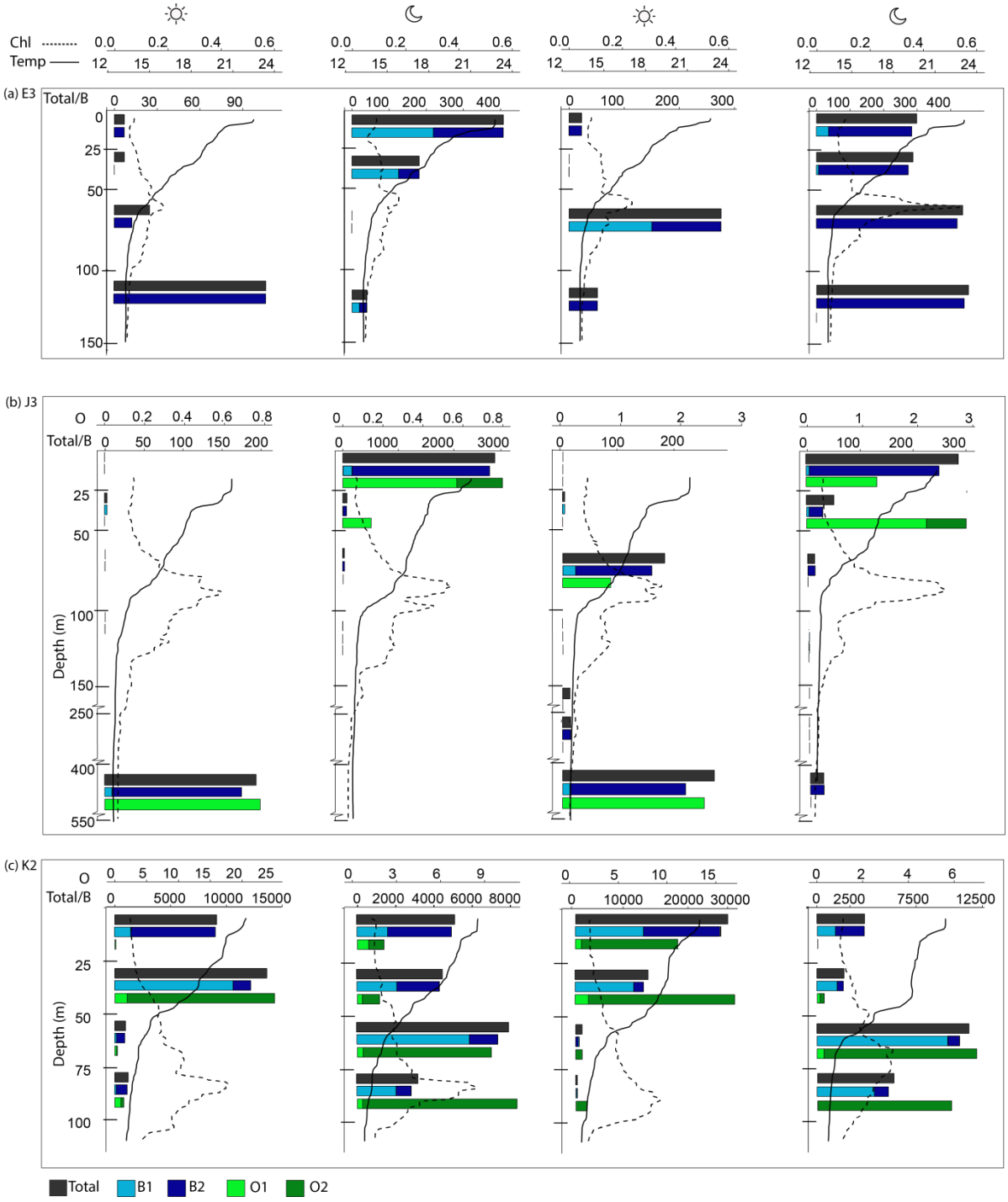

Figure 3.2. *S. fusiformis* abundance (Ind m^{-2}) at different depth strata during two consecutive pairs of night (☾) and day (☼) in stations (a) E3; (b) J3 and (c) K2. In each depth, upper bar portraits total salp abundance, middle bar are blastozooids (B) (B1and B2) and lower bar represent oozooids (O) (O1 and O2). Note there is aespecific scale for oozooidsand another for blastozooids and total salp number (Total) together. Dashed lines indicate vertical chlorophyll -a profiles (Chl (mg m^{-3})) and continuous lines show temperature profiles (Temp(ºC)).

The reasons for diurnal migration in salps are unknown. We did not find any significant environmental differences among K2 and the other two stations. K2 (110m) was much shallower than J3

(600m) but similar in depth to E3 (190m); all stations showed a marked thermocline, comparable temperature and chlorophyll-a ranges and a similar depth of the DCM. None of the other zooplankton species we observed performed diurnal migrations: *T. democratica* was distributed within the first 30 meters depth and did not exhibit DVM (Table 3.1), in agreement with previandous studies (Tsuda and Nemoto, 1992; Sardou *et al*., 1996; Gibbons, 1997); and most non-salp zooplankton groups did not perform clear migration (Table 3.1).Therefore, the only feature that made K2 differ from J3 and E3 was the *S. fusiformis* population itself. K2 had the maximal salp density and presented all life stages, especially productive oozooids (O2) and smaller blastozoids (B1) which significantly performed diurnal migration. In agreement with Liu *et al*. (2012), diurnal migration occurred when salps and, specifically productive oozooids, were abundant, which suggests salps were actively reproducing in K2.

The observation that the salps were most abundant and actively reproducing in K2 suggests possible hypotheses to explain why the migration pattern would change. High abundance could induce density-dependent processes; for instance, intraspecific competition or predation could increase at higher salp densities. Intraspecific competition can potentially be avoided if some stages exhibit diurnal migration while others do not. In K2 only diurnal migration of O2 and B1 was statistically significant but the other stages tend to perform the same pattern. Predation by non-selective species that feed on the most abundant prey- could increase in dense salp populations (Ohman and Hirche, 2001). If predators perform nocturnal DVM, the salp's diurnal migration would minimize spatial overlap with them, thereby decreasing mortality. A reduction of mortality would also occur in case of nocturnal predators that stay at surface. Indeed, in actively reproducing *S. fusiformis* populations, a decrease in mortality would favor population growth -especially if it affects oozooids: the most likely stage contributing to population growth under suitable conditions (Chapter 1; Henschke *et al*., 2015). Similarly, Ohman *et al*. (1983) calculated that a decrease in female mortality of only 16% in the copepod *Pseudocalanus* sp. was sufficient to compensate for the demographic costs of diurnal migration. Thus, diurnal migration of *S. fusiformis* might be a demographic advantage when there is presence of non-visual predators (referring to nocturnal predators or predators that perform nocturnal DVM).

Salps have a variety of non-visual predators (*e.g.*, cnidarians, ctenophores, amphipods; Harbison, 1998) two of which were present in the study area: amphipods (mostly *Phronima sedentaria*) and the jellyfish *Pelagia noctiluca*. In contrast to previous studies (Laval *et al*., 1992; Sardou *et al*., 1996), amphipods stayed at surface both day and night (Table 3.1), but *P. sedentaria* is likely to be a nocturnal predator (Diebel, 1988). On the other hand, *P. noctiluca* has been observed feeding on salps (Purcell *et al*., 2014). During the survey, *P. noctiluca* was mostly sighted at surface at night which suggests that it performed nocturnal migration (Tilves *et al.*, under review), consistent with observations in previous studies (Franqueville, 1971; Larson, 1986; Sardou *et al*., 1996; Ferraris *et al*., 2012).

How population changes the migration pattern under presence of predators could be explained by phenotypic plasticity -changing their behavior after detecting some stimuli- or by genotype selection after an environmental change (Ohman, 1990; Dam, 2013). If individuals changed their swimming direction as a scape response to non-visual predators, the three populations should have performed diurnal migration since *P. noctiluca* and amphipods were present in all stations. Concerning the second hypothesis, Ohman

(1990) suggested that in *Pseudocalanus*, the three migration patterns (nocturnal, diurnal and non-migration) could correspond to different genotypes, each dominating under a certain predation pressure: under visual predation, individuals with nocturnal migration genotype would survive and successfully reproduce, becoming dominant; consequently, under non-visual predation or low predation pressure, diurnal migration or non-migration genotypes would dominate, respectively (Ohman, 1990). Hypothetically, this change in dominance could occur within an event-time scale since salps have short generation times (approximately 14 days in *S. fusiformis* (Braconnot, 1963; Madin and Deibel, 1998)) and asexual reproduction that might amplify the genotype of the survivor oozooids (Barbuti *et al*., 2012). If this would be true, there would be a selection towards diurnal migration in all stations, but in the actively growing population (K2) the genotype dominance could have been achieved earlier. The potential event-scale adaptation of salps needs to be solved theoretically by building a population dynamics model to analyze how rapidly each genotype could become dominant under different predation pressures.

Conclusions

In conclusion, this study demonstrates for the first time that a salp can perform both nocturnal and diurnal migrations in the same season and study area. We suggest that in *S. fusiformis*, the type of migration pattern depends on the interaction between the population reproductive state and presence of predators: predation pressure by non-visual predators on salps might select diurnal migration genotype whose dominance in the population could be achieved earlier in actively reproducing populations. Further observations under variable abundance of *S. fusiformis* and the combining presence/absence of *P. noctiluca* or amphipods will allow us to test this hypothesis.

GENERAL DISCUSSION

Salps are eternal drifters. In contrast to other holoplankton species that can generate dormant stages or diapause eggs, they spend their whole life in the water column. Although salps have a certain swimming capacity to move vertically in the water column, they cannot avoid being accumulated or dispersed by water mass dynamics (Chapter 2; but see Höfer *et al*., 2015). Curiously, these organisms evolved from an ascidian, probably sessile ancestor (Govindarajan *et al*., 2011), to an r- life-cycle strategist living in the unstable water column. As a consequence, salp populations have to confront periods of extremely low food density and high predation, which could reduce to their local abundances (Chapter 2). Individuals may prevent starvation by means of high clearance rates due to their gelatinous barreled bodies (Acuña, 2001). Thus, they could survive during unproductive seasons but they might need a higher energy input to shift to a reproductive mode and trigger the bloom (Chapter 1). Accordingly, high abundances of salps are strongly linked to phytoplankton outbreaks (Deibel and Lowen, 2011; Henschke *et al*., 2014; Heron and Benham, 1984); On the other hand, under high predation pressure, occurring typical on bloom seasons, high fecundity allows salp populations to achieve large abundances enough to guaranty few survivors (Heron, 1972b).

Latency is essential for the occurrence of blooms since it maintains the population during adverse conditions, preventing from its complete disappearance. In general, planktonic species undergo the latency by shifting the life stage at individual level ("life cycle adjustments") or by reducing the total population abundance ("life history adjustments"; Figure 4.1; Boero *et al*., 2008). Clearly, salps use the latter strategy since they alternate periods of very low densities with periods of extremely high abundance (Figure 1.4). Most studies focused on determining the factors associated with the salp bloom period (Heron and Benham, 1985; Andersen and Nival, 1986; Lavaniegos and Ohman, 2003; Licandro, 2006; Deibel and Paffenhöfer, 2009; Henschke *et al*., 2014; Chapter 2) but less aimed to the latency mechanisms (Heron and Benham, 1985, Chapter 1). Heron and Benham (1985) conclude that the solitary stage carries out the latency after they observed a higher proportion of oozooids that were reproducing during a winter bloom. In contrast, we have provided evidence that females are responsible for latency periods, increasing the probability to trigger the bloom from a very dilute starting population (Chapter 1). What Heron and Benham (1985) observed could have been the late stage of a bloom rather than the population during a latency period. Indeed, the low reproduction rate of females that they describe is in accordance with our conclusion (Figure 1.5.a; Figure 1.5.a). Maybe, at the end of a bloom, there is an episode of liberation of chains, massively producing females that would be fecundated immediately to start the latency. Like a bloom of a dandelion flower, which produces lots of seeds which fly away, the end of a salp bloom would produce drifting seeds (females) that would be dispersed, increasing the chances that some of those females encounter a suitable environment to bloom (Figure 4.2). Once a female finds favorable conditions, it would tend to release the embryo and become a male (Figure 1.3.b). An hypothetical mating between a male and its daughters would facilitate the initiation of a bloom, although inbreeding, in addition to a founder effect, might reduce genetic variability of the resulting population. Whether such genetic impoverishment actually happens during a bloom, and how salps would

avoid its negative consequences, remains a mystery, although we suspect that this bottleneck effect might be reduced by mixing of different seed populations. Thankfully, these are aspects amenable to observation by means of genetic tracers.

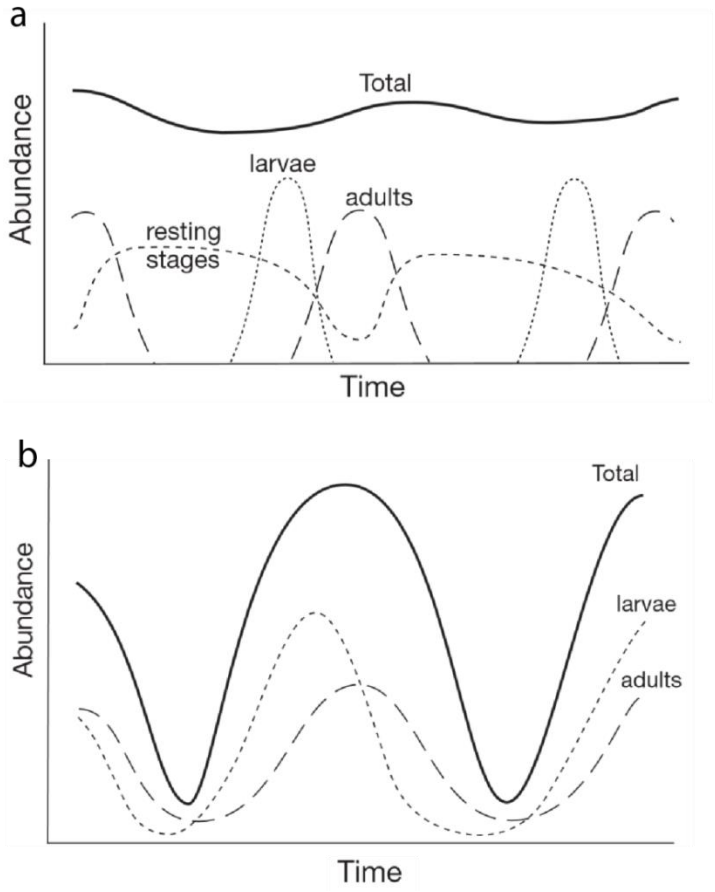

Figure 4.1 Abundance of species carrying out two different latency strategies: "life cycle adjustment" (a) and a "life history adjustment" (b). The time scale represented in x axis portray two consecutive periods of adverse conditions. From Boero *et al.,* 2008.

As far as we know, salps are one of few –or possibly the only– mesoplanktonic species that continuously alternate sexual and asexual reproduction (but see Chapter 1). While sexual reproduction is the key for maintaining genetic variability (Alldredge and Madin, 1982), asexual (clonal) reproduction might be a way to replicate many times the genotype of survivor oozooids, with a potential for rapid evolutionary selection of advantageous genotypes. Accordingly, fitness, which depends on the survival and mean fecundity of a certain genotype (Futuyma, 1988), might increase in individuals from populations that produce chains of blastozooids faster. A conceptual model for *Carassius gibelio* (Gibel carp), which alternates sexual and asexual populations, has shown that sexual reproduction creates possible candidates to be advantageous genotypes ("generation phase") while asexual reproduction amplifies the fittest ones ("amplification phase"; Barbuti *et al*., 2012). The time that a fittest genotype needs to dominate in a population was shorter when both percentage of asexual reproduction and strength

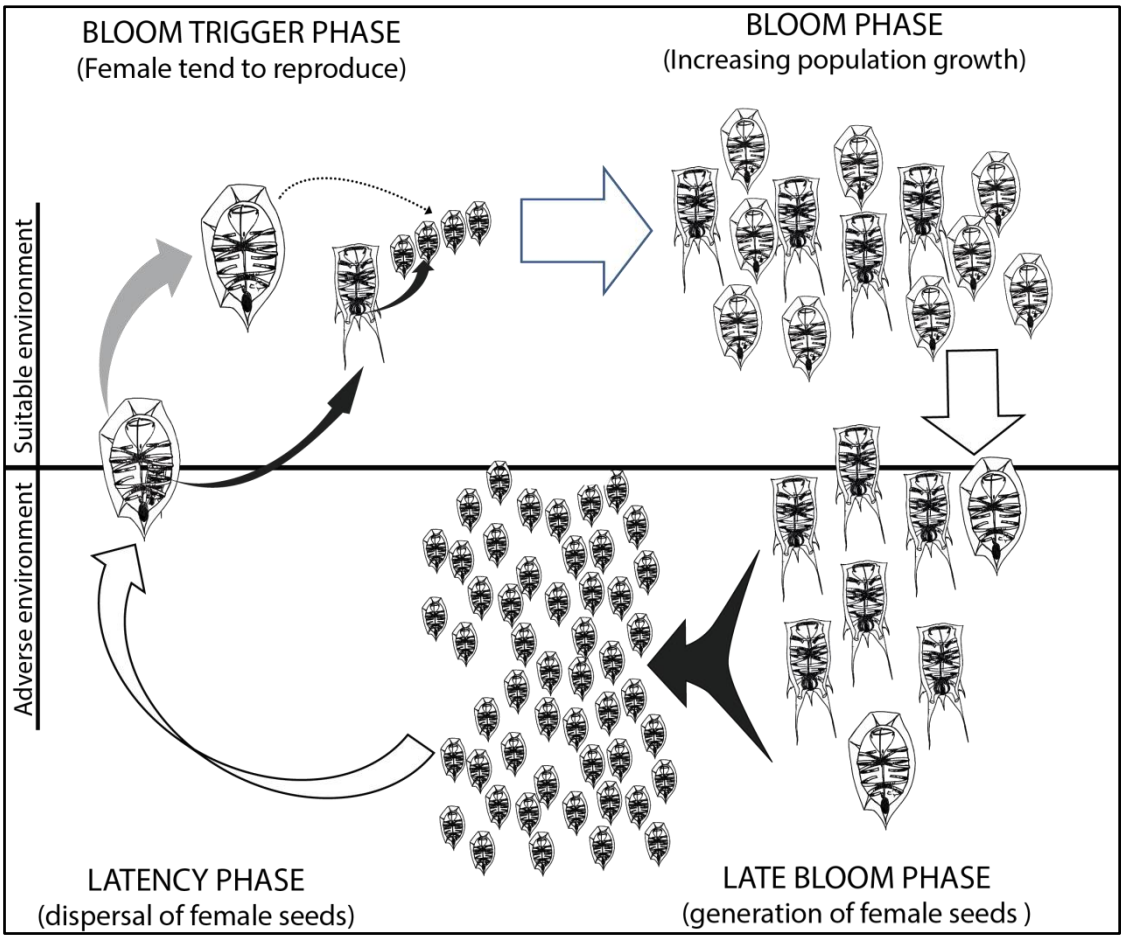

Figure 4.2. Conceptual scheme of the bloom-latency cycle hypothesis, representing the four phases: "bloom trigger phase" were the female liberates de embryo allowing the bloom to start; "bloom phase" when the population is actively reproducing and increasing in abundance; "Late bloom phase" characterized by higher proportion of oozooids reproducing and small females in arrested reproduction; and "latency phase" when females drift, growing slowly waiting for a suitable environment. White arrows: direction of the cycle, black arrows: liberation of individuals, and grey arrow: a female turning into a male; and dotted arrow: sperm liberation.

of the selection increased (Barbuti *et al*., 2012). If this is true for salps, suitable conditions for their population growth might in turn increase fitness of advantageous genotypes, accelerating the adaptation to short-time scale (i.e. days or weeks) selective forces (i.e. predation events) (Figure 4.3). This mechanism could be a possible explanation for the contrasting diel vertical migration patterns found in *S. fusiformis* (Chapter 3; Figure 3.2): predation by non-visual predators could exerted a selective force favoring diurnal migration, but the fittest genotype could have dominated earlier in the actively growing population. However, this hypothesis needs to be tested by modeling the dynamics of each genotype in the population after different selective pressures.

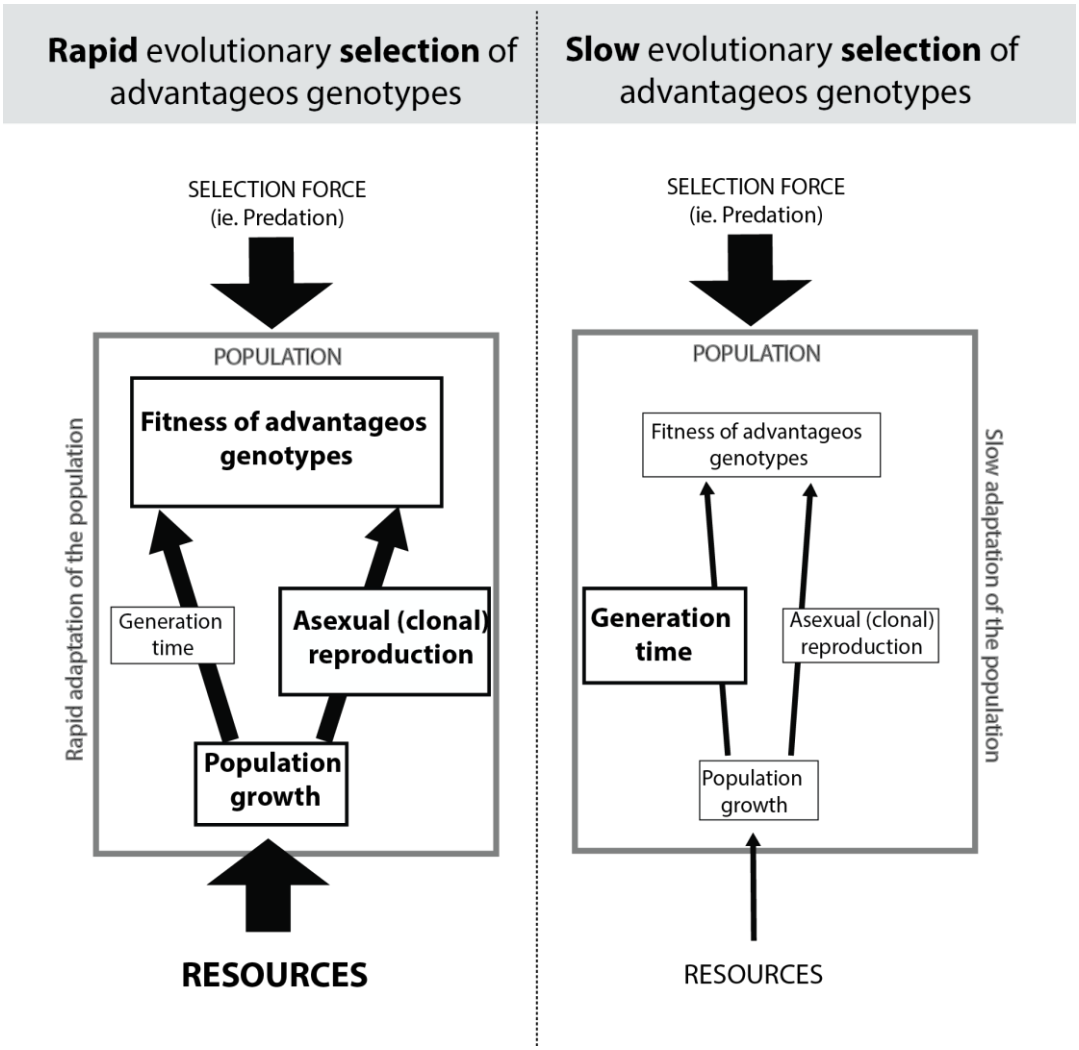

Figure 4.3. Conceptual scheme of the salps adaptation hypothesis: the same selection force is acting on two different salp populations: a population where abundant resources allow to higher population growth (left); and a population where less resources lead to reduced population growth (right). Wider arrows: higher contribution, thinner arrows: lower contribution. Bigger bold boxes mean greater values.

The results of this thesis lead us to consider evolutionary demographic studies to support the hypotheses suggested. Specifically, understanding how salp populations avoid bottle-neck effects after latency-bloom periods and the role of the salp life cycle in the potential adaptability to short-time scale environmental stressors. Genetics is a field still poorly explored in salps besides few phylogenetic and transcriptomic studies (Batta Lona, 2014; Govindarajan, Bucklin, and Madin, 2011), but it could be a necessary path to further understand the opportunistic skills of salps.

CONCLUSIONS

1. In contrast to previous hypotheses, our results point to the females as the stage responsible for entering to latency and triggering the bloom when conditions become suitable.

2. Under favorable conditions, productive oozooid survival accounted for high population growth while, under unfavorable conditions, cessation of female reproduction lowered population growth, leading the population to the latency.

3. After the latency, females tend to liberate the oozooid –that would be already generating chains of females– and turn to male. This situation increases the probability to trigger the bloom under extremely low population density since it favors mating success by leaving the male close to its daughters.

4. Salps control population growth by time rather than clutch manipulation since, in both situations (favorable and unfavorable conditions), probabilities to remain in the same stage had higher elasticities than reproductive rates.

5. Shelf-slope front and onshore component of the current mainly explained the spatial patterns in the distribution of *Salpa fusiformis*, although abundance of *Pelagia noctiluca* ephyrae played a secondary role.

6. The abundance of *T. democratica* was low in general and higher densities were associated to warm coastal waters.

7. The trophic impact of *T. democratica* populations was almost negligible due to their low abundances.

8. *S. fusiformis* ingested a maximum of 69.92 mg C m^{-2} day^{-1} and produced up to 35.76 mg C m^{-2} day^{-1} of fecal pellets, which represents 1.5 times the mean annual supply of organic matter near the slope in the Catalan Sea.

9. *S. fusiformis* performed nocturnal and diurnal diel vertical migrations (DVM). This result was the first evidence of coexistence of contrasting DVM in a salp species in the same season and study area.

10. We propose that, in *S. fusiformis*, the type of migration pattern might depend on the interaction between the population reproductive state and presence of predators.

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ANNEX

Model				Temperature			Chlorophyll -a			Temperature and chlorophyll -a		
F	M	J	PO	Cv	Opt	Θ	Cv	Opt	Θ	Cv	Opt	Θ
0	0	0	0	172.178	146.768	10	172.347	146.615	10	172.389	148.272	11
0	0	0	1	184.466	146.653	12	184.457	145.659	12	192.492	146.672	15
0	0	1	0	176.232	144.965	12	166.515	143.100	12	182.215	143.953	15
0	1	0	0	163.726	142.754	11	172.180	144.654	11	193.904	144.328	13
1	**0**	**0**	**0**	**160.141**	**137.4457**	**12**	173.456	144.608	12	185.730	137.940	15
0	1	0	1	165.647	145.760	13	184.825	143.700	13	206.212	143.475	17
0	1	1	0	168.627	140.9376	13	167.069	141.085	13	177.571	139.559	17
1	1	0	0	165.896	135.748	13	172.836	141.097	13	188.016	135.111	17
0	0	1	1	176.591	143.684	14	174.405	141.005	14	165.147	139.206	19
1	0	0	1	162.665	135.411	14	181.261	130.208	14	204.170	127.865	19
1	0	1	0	161.869	129.340	14	171.554	137.160	14	180.999	127.124	19
1	0	1	1	163.356	126.093	16	187.202	122.371	16	177.930	113.680	23
0	1	1	1	168.727	139.624	15	174.186	139.003	15	191.209	135.259	21
1	1	0	1	168.696	134.006	15	183.734	128.966	15	202.502	122.473	21
1	1	1	0	167.996	128.595	15	169.461	132.955	15	186.069	124.152	21
1	1	1	1	170.798	125.549	17	186.265	119.912	17	186.917	107.703	25

Table A.1. Summary of the model selection results. Digits in the first four columns indicate whether transitions out of the female (F), male (M), juvenile (J) and productive oozooids (PO) stages have (1) or have not (0) been modelled with chlorophyll and/or temperature effects. The following 9 columns report the residuals of the cross-validation method (Cv), of the non-linear least squares optimization (Opt) and the total number of parameters to optimize (Θ) for models including temperature, chlorophyll and both. Selected model is highlighted in bold.

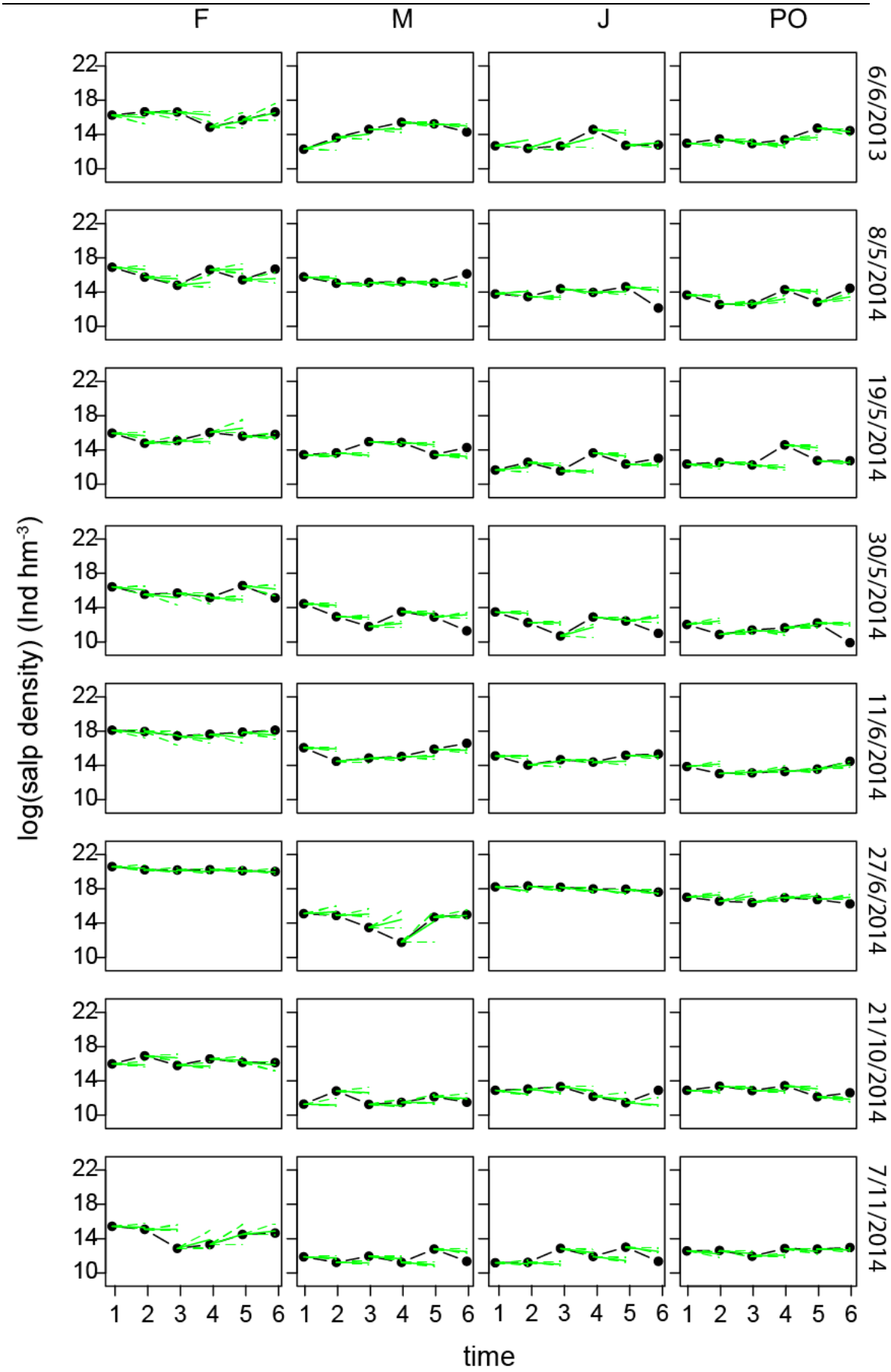

Figure A.1. Observed densities at time t+1 (black line) and its one-time-step expected densities given the observed densities at previous time t (green lines) corresponding to the selected model. Columns mean the different life stages (female (F), male (M), juvenile (J) and productive oozooid (PO)); and rows correspond to each sampling day. Confidence intervals are indicated by a grey dashed line.

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