



Universitat de Girona

ZOOPLANKTON STRUCTURE AND DYNAMICS IN  
MEDITERRANEAN MARSHES (EMPORDÀ  
WETLANDS): A SIZE-BASED APPROACH

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Universitat de Girona  
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Departament de Ciències Ambientals

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Mediterranean marshes (Empordà Wetlands):  
a size-based approach**

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per la Universitat de Girona

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## **ABSTRACT** (*In Catalan*)

L'estructura de la comunitat zooplanctònica dels Aiguamolls de l'Empordà, composició específica, dinàmica, diversitat i relacions tròfiques, s'ha estudiat a partir d'una aproximació basada en la mida.

L'aproximació s'ha basat en la model·lització de l'espectre de mida-biomassa de la comunitat zooplanctònica a partir de la distribució de Pareto, que al ser una distribució contínua evita que els resultats es vegin modificats per l'arbitrarietat que suposa la utilització de classes de mida. S'han observat tres tipus d'espectres de mida-biomassa que es classifiquen segons la seva forma. Els espectres de forma lineal s'ajusten millor al model de Pareto tipus I (model lineal) i es caracteritzen per una major abundància relativa dels organismes de mida petita respecte als de mida gran. Els espectres de forma corbada s'ajusten millor al model de Pareto tipus II (model no lineal) i es caracteritzen per una major abundància relativa dels organismes de mida gran. Per últim, les formes escalonades que tenen un ajust dolent als dos models i apareixen quan hi ha un valor alt d'abundància en una determinada classe de mida.

Aquests tres tipus d'espectres de mida-biomassa del zooplàncton canvien segons les condicions ambientals: en situacions d'entrada d'aigua són més freqüents els espectres lineals ja que les entrades de nutrients causen un creixement dels organismes de mida petita de manera que es compensa l'efecte de les interaccions competitives. Els espectres corbats són més freqüents en situacions de confinament quan els recursos són escassos i les interaccions ecològiques entre els organismes (intra i interespecífiques) prenen més rellevància de manera que es veuen més afavorides les espècies de mida gran que les de mida petita. Els espectres escalonats apareixen quan hi ha una dominància quasi absoluta d'una espècie i són el resultat de la seva dinàmica poblacional. Aquests escalons poden ser deguts a l'augment d'una espècie de rotífer (p.e. *Synchaeta* spp o *Brachionus* sp) després d'una pertorbació gràcies a la seva major capacitat de reacció, o bé quan, en una situació de dominància d'una espècie de calanoid, hi ha un augment del seu reclutament.

Les comunitats zooplanctòniques de les diferents llacunes de la maresma tenen una composició taxonòmica similar però una diversitat d'espècies, un patró estacional i una distribució de mides diferents. En el patró estacional de les llacunes temporànies es poden distingir sis situacions que estan condicionades per el cicle hidrològic i

dominades per les següents espècies: *Synchaeta* spp, *Diacyclops bicuspidatus*, *Eurytemora velox*. *Calanipeda aquae-dulcis*, *Cletocamptus confluens* and *Brachionus plicatilis*. La llacuna permanent, tot i presentar una diversitat més alta que les temporànies, té un patró estacional més simple, amb només dues situacions: la situació de *Synchaeta* spp. i la de *C. aquae-dulcis*. Aquest patró estacional més reduït i una distribució de mides dominada principalment per organismes de mida petita s'explicarien per la presència d'una comunitat de peixos en aquesta llacuna que és absent en les llacunes temporànies. La pressió de depredació de peixos sobre la mida corporal dona com a resultat espectres de mida-biomassa amb pendents més acusats i una disminució de la biomassa total en la llacuna permanent respecte a les temporànies. Així, l'efecte de la depredació dels peixos fa que la variació de l'espectre de mida-biomassa de les comunitats zooplànctòniques de la llacuna permanent no estigui únicament relacionat amb el cicle hidrològic, tal com passa en les llacunes temporànies, sinó amb la pressió de depredació dels peixos.

D'aquesta manera, l'espectre de mida-biomassa a escala ecològica es pot relacionar amb l'estabilitat de l'ecosistema, de manera que condicions estables com poden ser l'entrada constant de nutrients o la pressió de depredació constant dels peixos es caracteritzarien per espectres de forma corbada com a resultat de les interaccions ecològiques entre les diferents espècies. Per contra, condicions fluctuants com ara entrades de nutrients pulsàtils o la pressió de depredació variable, es caracteritzen per espectres de forma lineal, amb dominància de mides petites, com a conseqüència de la més ràpida reacció dels organismes petits després dels pulsos de nutrients o com a conseqüència de la major depredació sobre les mides més grans.

La distribució de Pareto es pot utilitzar per calcular un índex de diversitat de mides ( $\mu_s$ ) sempre que les dades segueixin la distribució de Pareto. Aquesta funció contínua té l'avantatge que evita l'arbitrarietat de les classes de mides. La diversitat de mides complementa la informació aportada per la diversitat d'espècies. En el cas de la comunitat de zooplàncton la diversitat de mides ha resultat ser un millor indicador del nivell d'estructuració que la diversitat d'espècies, els augments de la qual moltes vegades no són deguts a una elevada estructuració de la comunitat. La tendència a augmentar al llarg de la successió fa que la diversitat de mides pugui discriminar entre diferents estadis de la successió, en canvi això no es possible a partir de la diversitat d'espècies ja que pot assolir valors elevats tant en moments de pertorbacions elevades i freqüents com en moments de pertorbacions petites i escasses. En llacunes temporànies,

valors alts de diversitat de mides coincideixen en períodes de dominància d'una espècie de calanoid, períodes que representen les situacions més estables en aquestes llacunes. Els valors alts de diversitat de mides durant aquestes situacions d'exclusió competitiva indiquen que els diferents estadis d'una espècie de calanoid estan coexistent. Els calanoids dominen la comunitat en períodes de relativa oligotròfia i, per tant, l'única manera d'evitar la competència intraespecífica entre estadis és a partir de la repartició del nínxol tròfic dins de la mateixa espècie. En la llacuna permanent aquesta situació no es dona ja que l'exclusió competitiva entre espècies zooplanctòniques gairebé no té lloc degut a la pressió de depredació dels peixos.

L'anàlisi de la composició d'aminoàcids ens demostra que les espècies de copèpodes dominants als Aiguamolls de l'Empordà (*Eurytemora velox*, *Calanipeda aquae-dulcis*, *Diacyclops bicuspidatus odessanus* and *Acantocyclops robustus*) mostren un canvi gradual en la seva composició bioquímica al llarg de la seva ontogènesi. Aquestes diferències en la composició d'aminoàcids entre estadis no són degudes a diferències filogenètiques, ja que es tracta d'una sola espècie, ni a les condicions ambientals, ja que per cada espècie tots els estadis coexistien en una mateixa llacuna i per un mateix dia i, per tant, són degudes a les diferents dietes. Així, les diferents espècies de copèpodes mostren una repartició del nínxol tròfic entre els seus estadis de desenvolupament. Pel que fa a les espècies de dàfnids (*Daphnia pulicaria* and *Daphnia magna*), mostren una composició d'aminoàcids relativament constant durant el seu desenvolupament, fet que indicaria que tot els estadis s'alimenten del mateix recurs, és a dir, que juvenils i adults mostren un solapament del nínxol tròfic. La relació trobada entre la concentració de nutrients de les llacunes i el grau de solapament entre estadis de les espècies dominants mostra que la repartició del nínxol tròfic entre joves i adults és un possible mecanisme per tal d'evitar la competència intraespecífica. Els copèpodes, que tenen un baix solapament entre estadis, dominen en ambients on el recurs és limitat ja que la repartició del nínxol tròfic durant el desenvolupament els permet reduir la competència per l'aliment entre estadis. En les espècies de dàfnids, l'elevat solapament entre joves i adults els restringeix en llacunes o períodes amb elevada productivitat per tal d'evitar la competència intraespecífica. Així doncs, la competència intraespecífica juga un paper important a l'hora d'estructurar la comunitat de zooplàncton, juntament amb els dos altres factors que sovint són citats, la depredació i la competència interspecífica.

# 1. GENERAL INTRODUCTION

## 1.1. Approaches to the study of the community structure

Taxon-based, functional and size-based approaches have been used in studies of the structure of aquatic communities (e.g. Miracle, 1974; Sprules *et al.*, 1991; Gaedke, 1992; Gaedke and Straile, 1994; Rodríguez, 1994). Although it is the most commonly used, the taxon-based approach might fail by aggregating similar species with different ecological requirements or by aggregating different stages of the same species which feed on different resources. These problems might be solved by using a functional approach which classified organisms either by trophic levels (McQueen *et al.*, 1986), or by trophic guilds (e.g. Cohen *et al.*, 1993; Yodzis, 1993) and provide profound information about the food web structure (Gaedke, 1995). However, in order to cluster each organism into a specific functional group it is necessary to know its diet. This is not easy and, furthermore, diet may vary depending on food availability. Knowledge of the diet of the species may be derived from stomach content and faecal pellet analysis, by immunological and isotopic techniques and marker pigments. More recently, amino acid composition has been proved to be a good tool to quantify food niche in the field (Guisande *et al.*, 2002 and 2003). Nevertheless, many studies have only focused in the study of the adult stages of zooplankton organisms while the early stages, which dominate most communities (Hopcroft *et al.*, 2001), have been operationally ignored (see Hopcroft *et al.*, 1998, and references therein). Thus, diet composition of smaller plankton and early stages is, in general, poorly established as compared to large zooplankton and adult stages and this fact will determine the reliability of the functional approach. Furthermore, the separation between functional and taxonomic approaches is usually blurred since often functional approach is based in taxonomic aggregations of the organisms.

The size-based approach focuses on the aggregation of the organisms according to their individual body weight regardless of their taxonomy. It has significant advantages over the taxon-based and functional approaches, such as its relation with the metabolism and energy flux through community and its simplicity (e.g. Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1996), since it avoids defining distinct trophic levels or distinguishing between taxonomic groups. The main problems of a size-based approach

arise when organisms with equal sizes feed on different resources. However, trophic level has been positively related to body mass (Jennings *et al.*, 2002). Size-based approach is also suitable when a species is expected to change its trophic niche during development.

## 1.2. Biomass size distribution

Biomass size distribution has been used as a whole-community and ecosystem approach to study the structure and energy flow of pelagic food webs. It is based only on measurements of abundances and body sizes, and a few general assumptions on size relationships of metabolic activities and on size-dependent phenomena such as predator-prey size ratios. Abundance, metabolic activity, seasonal variability, reaction time to external perturbations, trophic position, prey size ranges and other attributes may be predicted from body mass (Quiñones, 1994; Rodríguez, 1994; Gaedke, 1995). According to these authors, in comparison to other approaches (food web analysis, network analysis and simulation models) it has many advantages since little effort is needed, it is relatively cost efficient, and it is reproducible for different pelagic ecosystems. Theoretical models regarding the distribution of biomass by size were developed in pelagic marine ecosystems (Sheldon *et al.*, 1972; Platt and Denman, 1977, 1978) and presented the hypothesis that planktonic biomass is regularly distributed in a continuous manner across logarithmic size classes. This regularity has been observed in many different environments such as oceanic ecosystems (Platt *et al.*, 1984; Rodríguez and Mullin, 1986), neritic ecosystems (e.g. Rodríguez *et al.*, 1987; Witek and Krajewska-Soltys, 1989; Ruiz *et al.*, 1996), coastal lagoons (Gilabert, 2001), inland lakes (e.g. Sprules and Munawar, 1986; Rodríguez *et al.*, 1990; Gaedke, 1992) and temporary lakes and ponds (García *et al.*, 1995; Boix, 2000; Quintana *et al.*, 2002).

Dickie *et al.* (1987) suggest examination of the spectrum at two levels. The *physiological* or *primary* scaling, which covers all sizes ranges and where physiological processes correlates with size, and the *ecological* or *secondary* scaling, which only operates at certain sizes ranges that coincide with functional groups having similar and size-independent growth efficiency (Dickie *et al.*, 1987; Boudreau *et al.*, 1991; Thiebaut and Dickie, 1992; Thiebaut and Dickie, 1993). While at physiological scaling organism abundance is inversely proportional to their size and the spectrum is linear, at ecological scaling it is ecological interactions that control the size structure of the

community and the regularity disappears (Rodríguez, 1994). This ecological scaling is more apparent in low structured and fluctuant ecosystems (Rodríguez *et al.*, 1990; García-Jiménez, 1991).

The biomass size spectrum most widely used is the normalised size spectrum, NB-SS (Platt and Denman, 1977). The established approach used to model normalised biomass size spectrum involves classifying organisms by logarithmic size classes according their weight, totalling biomass for each size class and dividing it by the width of the class to obtain the normalized biomass (see Blanco *et al.*, 1994). However NB-SS is dependent on choice of size scale and interval amplitude because it is a discrete model (Han and Straškraba, 1998). The use of continuous models was proposed in order to solve these problems. Vidondo *et al.* (1997) suggest using Pareto distribution, a continuous model widely used in other disciplines dealing with size-structured systems.

Pareto model gives better adjustment than NB-SS, especially in non-linear spectra which may be fitted to the non linear model of Pareto or Pareto type II, and is much less sensitive to gaps in the spectrum. Thus, Pareto type II model is appropriate when studying the ecological scaling of the spectrum where linearity tends to disappear, whereas Pareto type I has been used to study the physiological scaling (Vidondo, 1996).

### **1.3. Size diversity and trophic niche partitioning among sizes or stages**

To date, size-approach community studies have analysed biomass size spectrum shape so as to obtain information about the relative abundance of the organisms. This would be equivalent to the study of the specific composition using a taxonomic approach, or the relative abundance of the different functional groups with the functional approach. However, size-based studies usually go no further and other aspects of size-based community have been poorly studied, like diversity or the food web structure.

Ruiz (1994), following the work of Lurie and Wagensberg (1983, 1984), proposed a measure of size diversity based on the normalized size spectrum. Size diversity requires classifying organisms in different classes according to their size, a fact that implies different size diversity values depending on the size class intervals chosen. To overcome this problem an index appropriate for continuous variables ( $\mu_p$ ) using a probability density function was proposed by these authors. This index has been used for plankton community in Mediterranean coastal waters and has been found to be

sensitive to natural fluctuations. Since Pareto model is based in a probability density function it could be used to calculate an index of size diversity, whether at physiological scaling, as proposed by Ruiz (1994), or at ecological scaling, which has not been used yet.

Study of a size-based trophic food web and trophic niche requires knowledge of the species' diet, and of whether it changes during development. Among the studies dealing with zooplankton feeding, few investigate the feeding of different development stages of one species and, as far as we know, all are experimental (e.g. Poulet, 1977; Maly and Maly, 1974; Zánkai, 1991, Gophen, 1977; McQueen, 1969 and Jamieson 1980; Boersma, 1995). The study of trophic niche partitioning in different development stages based on the comparison of their amino acid composition gives information about intraspecific competition in the field. The fact that a species has trophic niche partitioning during development means the possibility to reduce intraspecific competition. However, the effect of intraspecific competition in structuring zooplankton communities has not yet been evaluated.

#### **1.4. Empordà Wetlands**

There are some studies about the zooplankton composition in fluctuant coastal Mediterranean environments (e.g. Bigot and Marazanof, 1965; Yúfera *et al.*, 1984; Menéndez and Comín, 1986; Toja *et al.*, 1991; López *et al.*, 1991; Comín *et al.*, 1994; Oltra and Miracle, 1992; Galindo *et al.*, 1994; Quintana *et al.*, 1998b) but size-based approaches are scarce (Lam-Hoai, 1991; Gilabert, 2001; Quintana *et al.*, 2002). These environments are characterised by a zooplankton community composed of a few species, which respond quickly to environmental changes. The Empordà Wetlands are an example of fluctuant Mediterranean environment and several reasons make them appropriate for the study of the variation of zooplankton community structure:

1. They show a great environmental variation over short scales of time and space (Quintana *et al.*, 1989a)
2. They are characterized by a tight physical-biological coupling, mostly explained by their shallowness, which means that variations in environmental variables are quickly propagated to the biological structure, as it has been found in other coastal lagoons (Silvert, 1983).

3. The specific composition of the zooplankton communities of these basins is simple, with few trophic interactions, and sometimes even monospecific, facts that make them especially suitable for investigations dealing with trophic niche determination.

4. Temporary and permanent basins are close together and have similar hydrological features. The main difference among them is that, whereas in the temporary basins the predation of zooplankton by fish is negligible, the permanent ones have fish populations which may cause significant changes in the biomass size spectrum.

### **1.5. Study approach**

Zooplankton community structure in Empordà Wetlands will be studied by means of a size-based approach. This approach will be lean by the taxonomic and functional approach to obtain a better resolution and complementary information.

First, community composition will be described by analysing the different types of biomass size spectra and relating them to the organisms present. As explained above, at this ecological scaling it is ecological principles that control the size structure of the community and it is usually distributed in domes (Rodríguez, 1994; Dickie *et al.*, 1987), so that it will probably be best described by the non lineal model of Pareto. Boix (2000) already described the ecological scaling of the planktonic and epibenthic organisms in a temporary pond and found it fitted the non lineal Pareto model best. Additionally, we will assess if it exists the *tertiary scaling* found by the same author and which was attributed to populational dynamics.

The temporal dynamics of the zooplankton community will be studied by analysing the changes in the shape of the biomass size spectrum, which are expected to be related to the environmental conditions and the organism dynamics. According to the model of Dickie *et al.* (1987) which proposed linear shape as a result of the allometric relationship between specific production and body mass but non-linear spectra as a result of high competitive interactions, different spectrum shapes would reflex ecological interactions between species or sizes. Thus the different types of spectra would be related with the availability of food resources. The spatial dynamics will be also studied by comparing basins with different water permanence. The main difference between temporary and permanent basins would be the presence of fish which have



already been found to cause significant changes in the size distribution of the zooplankton community (Zimmer *et al.*, 2001; Blumshine *et al.*, 2000; Mazumder *et al.*, 1988).

Diversity will also be studied by means of a size approach. Following the work of Lurie and Wagensberg (1983, 1984) and Ruiz (1994), and by using Pareto distribution, biomass size spectrum would provide us a way to calculate a size diversity index avoiding the previous classification in size classes. This size diversity is expected to be an alternative index to Shannon index (Pielou, 1969) in analysing the community structure. One advantage over species diversity would be that size diversity would avoid identifying organisms that are difficult or impossible to distinguish like early zooplankton stages.

Finally, the study of the zooplankton structure will focus on its internal trophic relations. Among trophic interactions, apart from predation by fish, probably the most important when determining the community structure of Empordà Wetlands zooplankton is intraspecific competition. These communities are usually composed of a few species and it is expected that the effect of intraspecific interactions will be more important than the effect of interspecific interactions. Furthermore, intraspecific competition has been less studied (e.g. Tessier *et al.*, 1983; Guisande and Gliwicz, 1992; Burns, 1995; Boersma, 1995) and nothing is known about their role in structuring zooplankton communities. According to Guisande *et al.* (2002 and 2003) trophic niche partitioning may be assessed by comparing amino acid composition among species. This methodology may also be used for comparing trophic niches among different development stages of the same species. It is expected that in the basins where resources are limited trophic niche partitioning would be an advantage since each development stages would be able to feed on different food resources, thus avoiding intraspecific competition.

## **1.6. Objectives**

The main objective of this study is to analyse composition, diversity, dynamics and trophic relationships of zooplankton community in Empordà Wetlands, by means of a size based approach.

This main objective split into different specific objectives:

1. To asses the usefulness of Pareto distribution to model biomass size spectrum at ecological scaling of the zooplankton community.
2. To establish the typology of the biomass size spectrum of the zooplankton community.
3. To assess the relationship between the different types of spectra and the available food supplies in the ecosystem.
4. To analyse the differences between zooplankton structure (species composition and size distribution) of permanent and temporary basins.
5. To analyse how the temporal variability of biomass size spectra is affected by nutrient inputs or by the presence of fish.
6. To test the use of Pareto distribution as a new method to compute size diversity, thus avoiding the previous classification in size classes.
7. To evaluate if size diversity, as an alternative to species diversity, is useful to describe the degree of structure of the zooplankton community of Empordà Wetlands.
8. To analyse the behaviour of size diversity in situations of competitive exclusion.
9. To assess if there is food niche partitioning as a function of the organism' size or stage at the intraspecific level.

10. If this food niche partitioning exists, to determine whether those species with different development stages dominate in habitats with low amount of food resources and, vice versa.

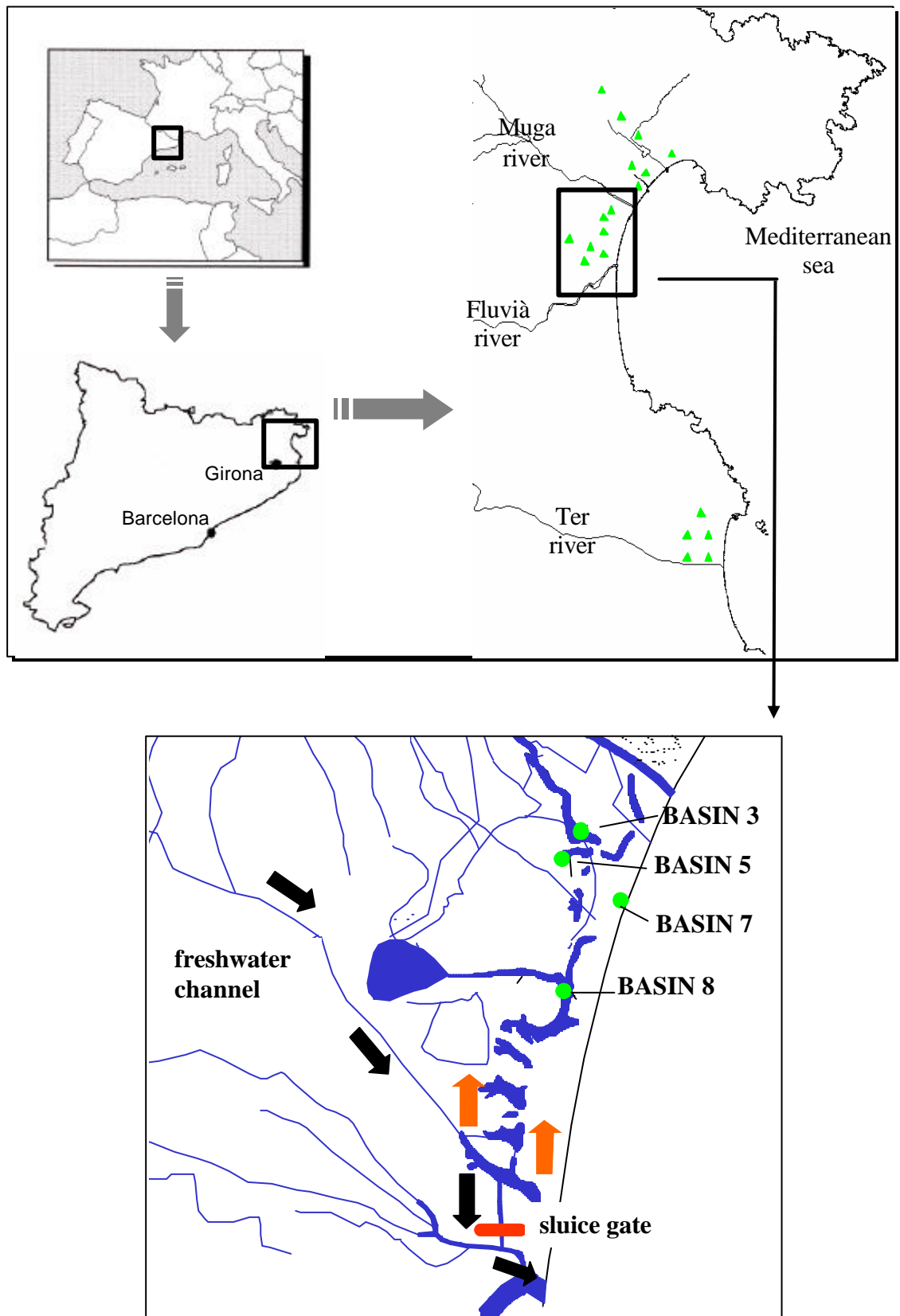
## 2. STUDY AREA

The study was located in the Empordà Wetlands (NE Iberian Peninsula), a set of Mediterranean shallow lentic waters free from tidal influence and with a wide range of environmental conditions (Figure 2.1). According to Trobajo *et al.* (2002) the waterbodies in these wetlands might be classified in 5 clusters: (1) confined coastal brackish or hyperhaline ponds, (2) semi-confined brackish coastal lagoons and ponds, (3) freshwater ponds with high nutrient input, (4) fluctuating freshwater systems and (5) freshwater springs. Furthermore, waterbodies of a different typology were sampled: (6) ricefields and constructed wetland systems. The hydrology of the waterbodies belonging to the first two clusters is affected by marine inputs, whereas the hydrology of the rest of lagoons is related to freshwater flux, following the pluvial or fluvial regime whereas marine influence is occasional or non-existent (Bach, 1990). Table 2.1 shows the range of conductivity, temperature and pH of these waterbodies (more details of these systems are found in Trobajo *et al.*, 2002). For the analysis of the intraspecific competition (chapter 7), study area was extended to the whole Empordà Wetlands (figure 2.1, table 2.2).

**Table 2.1.** Mean and range of variation of some physical and chemical parameters of the different kinds of waterbodies located in the Empordà (NE Spain). (1) confined coastal brackish or hyperhaline ponds, (2) semi-confined brackish coastal lagoons and ponds, (3) freshwater ponds with high nutrient input, (4) fluctuating freshwater systems and (5) freshwater springs. From Trobajo *et al.* (2002). Basins were sampled in 1997 and 1998.

Cluster	1	2	3	4	5
Number of waterbodies	4	10	5	11	3
Conductivity (mS cm <sup>-1</sup> )	49 (8.8-149)	18 (0.7-51)	1.2 (0.3-7.7)	3.8 (0.3-34)	1.1 (0.1-9.0)
Temperature (°C)	17 (2.9-29)	17 (4.7-34)	16 (7.9-24)	15 (3.8-29)	13 (8.8-20)
pH	8.06 (7.3-8.9)	8.17 (7.1-9.8)	7.54 (6.1-8.6)	7.68 (6.5-8.8)	7.10 (6.4-8.1)
NH <sub>4</sub> <sup>+</sup> (µM)	7.0 (0.0-117)	2.8 (0.0-50)	26 (0.1-118)	6.4 (0.0-231)	2.6 (0.1-60.8)
NO <sub>2</sub> <sup>-</sup> (µM)	0.8 (0.0-36)	0.7 (0.0-11.2)	4.9 (0.1-16.4)	2.4 (0.2-61.4)	5.5 (0.1-52)
NO <sub>3</sub> <sup>-</sup> (µM)	1.8 (0.0-33)	6.9 (0.0-87)	104 (17-277)	39 (0.0-327)	705 (357-1084)
SRP (µM)	4.8 (0.0-92)	1.2 (0.0-10)	2.7 (0.1-9.8)	3.1 (0.0-45)	0.9 (0.0-18)

**Figure 2.1.** Above: map of study area with the waterbodies, where organisms for the analysis of the intraspecific competition have been obtained, in green (chapter 7). Below: map shows the salt marshes with the four basins which were studied more intensively in chapters 4, 5 and 6.



**Table 2.2.** List of all waterbodies that were sampled in the study, including lagoons used only for the analysis of environmental conditions, where the species' dominance was estimated (see chapter 3.1.3 and 7). For details of waterbody typologies see text. Coordinate system: ED\_1950\_UTM\_Zone\_31N.

<b>NAMES OF WATERBODIES</b>	<b>X UTM</b> square 1 km <sup>2</sup>	<b>Y UTM</b> square 1 km <sup>2</sup>	<b>WATERBODY TYPOLOGIES</b>
Bassa del Fra Ramon	515	4653	1
Pletera, llacuna petita	515	4653	1
Bassa de l'Angula	512	4678	1
Clot de la Llúdriga	512	4678	1
Llacuna interior, Mas d'en Túries	509	4676	2
Passera Riereta Interior	508	4674	2
Llacuna mar, Mas d'en Túries (basin 3)	509	4675	2
Bassa Litoral (basin 5)	509	4675	2
Bassa Tamariu (basin 7)	509	4675	2
La Rogera (basin 8)	509	4674	2
Bassa Connectada	509	4675	2
Passera Riereta Mar	508	4674	2
Riereta	509	4674	2
Rec Muntanyeta	508	4674	2
Ter Vell, llacuna pont	515	4655	3
Rec del Molí, EDAR	507	4679	3
Salins Camping	510	4678	3
Tercer Pont	509	4681	4
Madral Pont mig	509	4681	4
Montmajor	507	4681	4
Rec del Molí de Castelló	506	4679	4
Caseta de l'Estany	510	4679	4
Comporta Interior	508	4673	4
Estany de Vilaüt	509	4682	4
Meandre del riu Fluvià, Llacuna	506	4670	4
Ter Vell, llacuna platja	516	4655	4
Ter Vell, llacuna bombeig	516	4655	4
Basses d'en Coll	516	4650	4
Ullals camí	513	4649	5
Ullals camp	513	4649	5
Ullals safareig	513	4649	5
SAC (constructed wetland system)	508	4677	6
Arrossars de Sant Pere	507	4673	6

In a more intensive way (chapter 4, 5 and 6), the salt marshes situated in the Empordà Wetlands Natural Park were studied (Figure 2.1). Four coastal basins, clustered by Trobajo *et al.* (2002) as semi-confined waterbodies, were selected. The

hydrology of these waterbodies is dominated by sudden marine intrusions during sea storms that occur very irregularly, although relatively frequently. When sea storms are intense basins may interconnect. After sea storms or intense rainfall the marshes remain confined for a long time and tend towards desiccation. Basin 8 is the only permanent one, whereas basin 3 is semi-permanent (not drying out every year). Basin 5 and 7 are temporary waters that dry out at least once a year for one or two months. The main environmental variables of the four coastal basins are described in table 2.3.

**Table 2.3.** Main morphometric characteristics and environmental variables (standard deviation in brackets) of the four salt marsh basins studied.

	<b>Basin 8</b>	<b>Basin 3</b>	<b>Basin 7</b>	<b>Basin 5</b>
Water permanence	permanent	semipermanent	temporary	temporary
Maximum flooded surface (m <sup>2</sup> )	87369	55837	1649	983
Water level (cm)	68 (23.7)	41 (27.8)	37 (30)	40 (25.9)
Conductivity EC <sub>25</sub> (mS·cm <sup>-1</sup> )	14.89 (7.9)	26.85 (9.6)	27.78 (9.7)	26.7 (13.0)
Dissolved inorganic nitrogen (DIN)(μM)	12.8 (36.3)	21.29 (63.7)	5.49 (25.0)	22.1 (78.6)
Soluble reactive phosphate (SRP) (μM)	1.85 (4.5)	4.30 (9.3)	0.86 (3.5)	7.39 ( 10.6)
Total nitrogen (TN) (μM)	139.9 (75.8)	189.09 ( 114.9)	154.8 (107.5)	203.8 (209.0)
Total phosphorus (TP) (μM)	4.26 (4.0)	10.10 (12.0)	4.64 (8.0)	17.33 (33.7)

Just one surface freshwater channel from the cultivated plain supplies the salt marshes, before acting as an escape to the sea for excess water. A sluice gate was installed in this drainage channel (figure 2.1). The resulting flux regulation has increased the duration and the frequency of flooding and has increased eutrophy in the salt marshes (Quintana *et al.*, 1998a).

In order to avoid spatial variability one single basin (basin 5) was selected for a more detailed study of the biomass-size spectrum (chapter 4). The temporary coastal basin chosen was one where fluctuation of environmental conditions is especially high. This basin is a little depression in the salt marsh with a high level of eutrophy, where nocturnal anoxias due to hypertrophic events are frequent. For further details of the hydrology of the basin, see basin 1 in Quintana *et al.* (1998a).

## 3. MATERIALS AND METHODS

### 3.1. Sampling design

Three sampling designs were performed according to the objectives of each chapter:

#### 3.1.1. Sampling for the analysis of biomass size spectra (chapters 4, 5, and 6)

In order to analyse the typology and temporal variability of biomass size spectra, four coastal basins in the salt marshes were sampled (figure 2.1). Water and zooplankton samples were taken weekly from a central point of these basins during four hydrological cycles, from September 1996 to August 2000, at a depth of 10-15cm. For chapter 4, only basin 5 was selected in order to avoid spatial variability.

Temperature, electrical conductivity ( $EC_{25}$ ), pH and water level were measured *in situ*. Alkalinity was measured after a few hours. Filtered and unfiltered samples were immediately frozen in the field for later analysis of inorganic and total nutrients, respectively:  $NH_4^+$ ,  $NO_2^-$ ,  $NO_3^-$ , soluble reactive phosphate (SRP), total nitrogen (TN) and total phosphorus (TP). Nutrient analysis followed Grasshoff *et al.* (1983) and total organic carbon was measured using a TOC analyser. The chlorophyll *a* was measured using Talling and Driver's expressions (1963) using 90% methanol as a solvent.

Each zooplankton sample was taken from 4 l of filtered 53  $\mu m$  water and was preserved *in situ* in 4% formalin. Some naupli larvae were cultivated in the laboratory to help identification. However, it was not possible to distinguish some larval stages at species level, such as naupli 1 and the early copepodite stages of some calanoids or cyclopoids. Biomass dry weight estimations were obtained, for most invertebrate species, from the allometric correlation between weight and body-length (Appendixes 1 and 2).

#### 3.1.2. Sampling for amino acid analysis (chapter 7)

For the amino acid analysis and further estimation of intraspecific competition (chapter 7), zooplankton was collected in a total of 19 waterbodies of the whole



Empordà Wetlands so as to cover the maximum environmental variation (figure 2.1). Zooplankton samples were taken during two periods of hydric stability: a winter period from February to April 2002, and a summer period in June 2002, because most of the lagoons become dry out during July or August. Species selected for this study are dominant in these waterbodies and represent different trophic strategies: two calanoids, *Eurytemora velox* and *Calanipeda aquae-dulcis*; two cyclopoids, *Diacyclops bicuspidatus odessanus* and *Acanthocyclops robustus*; and two daphnids, *Daphnia pulicaria* and *Daphnia magna*. Each species was collected from 2 to 4 different lagoons geographically separated in order to eliminate spatial variability.

### **3.1.3. Sampling for analysis of environmental conditions where species used for amino acid analysis dominate (chapter 7)**

For the analysis of environmental conditions where each species dominate (chapter 7), I used data from a previous study which was undertaken during the annual cycle of 1996-1997 and included a monthly sampling in a total of 33 lagoons of the whole Empordà Wetlands (see table 2.2). Each sampling includes aquatic invertebrates collected with a 250  $\mu\text{m}$  mesh (thus not including crustacean larval stages) and nutrient composition:  $\text{NH}_4^+$ ,  $\text{NO}_2^-$ ,  $\text{NO}_3^-$ , dissolved inorganic nitrogen ( $\text{DIN} = \text{NH}_4^+ + \text{NO}_2^- + \text{NO}_3^-$ ), TN, SRP and TP. Invertebrate sampling is described in Gifre *et al.* (2002).

To estimate the characteristics of the waterbodies that inhabit each zooplankton species analysed, nutrient concentration data of samples in which a certain species is the dominant was used, so that we ruled out those samples in which species are present but with low relatively abundance. Therefore, waterbodies were classified in relation to their dominant species.

## **3.2. Environmental situations**

In order to characterise different situations over time (chapter 4), I used the approach of Quintana *et al.* (1998b) to the Empordà salt marshes, with situations defined by their dominant species and flooding conditions and including the following 5 (the 6<sup>th</sup> described by these authors was not found here):

*Synchaeta* situation: sudden, massive flooding with nutrient entry following any intense disturbance (such as sea storms, rainfall or heavy freshwater flooding).

Cyclopoids situation: steady, low-level input of water and nutrients.

Calanoids situation: relatively oligotrophic situation, associated with hydric stability at the beginning of confinement.

*Gammarus* situation: periods of confinement close to dessication, with minimum water levels favouring the development of benthic species such as *Gammarus aequicauda* and some harpacticoids.

*Brachionus* situation: high organic matter concentrations caused by dessication in eutrophic basins and frequent hypertrophic events.

In some cases, especially following relatively intense flooding, abundant *Synchaeta* spp. mixed with the species dominating before the flood; this was named the ‘undefined *Synchaeta* situation’. Samples with a mixture of *Synchaeta* spp. and other zooplankters which appear later are also included. Other intermediate situations have been excluded.

### 3.3. Size distribution analysis

Size distributions were analysed using the underlying Pareto distribution parameters (Vidondo *et al.*, 1997). The Pareto distribution has a cumulative distribution of probability defined as:

$$\text{prob}(s \geq S) = K^c s^{-c}$$

$$\log[\text{prob}(s > S)] = c \log(K) - c \log(s)$$

where  $\text{prob}(s \geq S)$  is the probability that a size ( $s$ ) of an individual taken at random will be greater than a threshold size  $S$ , expressed as a function of  $s$ . In practice, the term  $\text{prob}(s \geq S)$  is calculated for each individual as the fraction of all individuals larger than or equal to itself ( $N_{s \geq S}/N_t$ ). The obtained results with the cumulative distribution of probability based on this probability estimation are equivalent to the normalized biomass size spectrum (Vidondo *et al.*, 1997). If the sizes are distributed according to a Pareto model (Pareto type I), the plot on a double-logarithmic scale will display a straight line. This lineal model may exhibit a lack of fit in certain datasets in which the abundance or biomass of small particles is lower than that predicted by a straight line (Ahrens and Peters, 1991; Wells and Goldberg, 1994). Vidondo *et al.* (1997) suggest

that such lack-of-fit problems may be overcome by using a Pareto type II distribution, with cumulative distribution of probability:

$$\log[\text{prob}(s>S)] = c \log(K + D) - c \log(s + D)$$

This equation differs from the original Pareto model only by the additive constant  $D$  that changes the function into a non-linear one. Estimators of  $c$ ,  $K$  and  $D$  can be obtained using this equation by means of an iterative nonlinear regression. The ordinary Pareto or Pareto type I model is a special case of the Pareto type II model when  $D=0$ .

From here on, in order to differentiate between the two types of Pareto the following abbreviations have been used:

$c_I$  and  $c_{II}$ : parameters of Pareto type I (lineal model) and Pareto type II (non-lineal model), respectively.

$r^2_I$  and  $r^2_{II}$ : goodness of fit to Pareto type I and to Pareto type II, respectively.

### 3.4. Diversity

Species diversity and evenness were measured using Shannon and Weaver index (Pielou, 1969). Species diversity was calculated in two ways: first by using species abundance (species diversity) and second by considering different larval stages as different species (species+stages diversity). In both cases diversity was calculated using numerical abundance. The reason for calculating diversity the second way is the assumption that nauplii and adult copepods may have different trophic functions due to their differences in size.

Size diversity was calculated following Lurie and Wagensberg (1983, 1984) who proposed an index ( $\mu$ ) appropriate for continuous variables, such as individual size, based on the function of probability density of individuals with respect to size:

$$\mathbf{m} = - \int_{s_i}^{s_{i+1}} p_i(s) \lg_2 p_i(s) ds$$

The use of the Pareto probability density function is proposed to calculate  $\mu$  (chapter 6.2). In order to obtain the maximal resolution in calculating size diversity only the spectra with high fit to Pareto type I or Pareto type II models ( $r^2$  higher than 0.9) were used.

Size diversity obtained from Pareto distribution ( $\mu_{s'}$ ) was compared with that calculated by using size classes (logarithm base 2) and applying Shannon index (size class diversity).

### **3.5. Analysis of amino acids and estimation of amino acid separation among stages**

For amino acid analysis (chapter 7) species were divided into four stages that were established as follows: For copepods, stage 1 comprises all naupli; stage 2 comprises copepodites C1 to C3; stage 3 comprises copepodites C4 and C5; and stage 4 correspond to adults. For daphnids, stage 1 comprises sizes equal or less than 1 mm; stage 2, sizes between 1mm to 1.5 mm; stage 3, sizes between 1.5 and 2.25 mm; stage 4, sizes bigger than 2.25 mm. The animals were immediately frozen in liquid nitrogen after collection and then isolated and prepared for analysis.

Amino acids analysis was performed on samples containing 1 to 30 individuals depending on the size of the stage, in order to establish a common amount of the total material. There were three to five replicates of each stage per lagoon. Amino acids were measured by high-performance liquid chromatography (HPLC) using Alliance system, a 474 scanning fluorescence detector, and a 15 x 3.9 Nova-Pack C<sub>18</sub> column (Van Wandelen and Cohen 1997). Amino acid standard H NCI0180 PIERCE was used for identification and quantification.

To show that amino acid composition discriminates between species and zooplankton stages, a discriminant analysis was performed on the amino acid composition of the different stages of each species. To avoid the problem associated with phylogeny the discriminant analysis was also performed individually to each species. The percentage of stages correctly classified for each species obtained in the discriminant analyses performed individually to each species was used as indicator of the overlap among the stages within each species. The overlap among stages is lower as the percentage of stages correctly classified is higher. We assume that intraspecific

competition should be higher in those species with a higher overlap in the amino acid composition (AAC) among stages.

## 4.1. INTRODUCTION

Dickie *et al.* (1987) proposed the examination of a secondary or ecological scaling of the biomass size spectrum identifiable at functional-group level (phytoplankton, zooplankton, fish) where abundance distribution as a function of body size is more influenced by ecological factors. According to these authors, size distribution within a functional group is more dependent on the ecological characteristics of the species in that group than on their physiological differences. It appears to be closely linked to food requirements in relation to biomass density distributions and predator-prey size ratios. This ecological scaling is more obvious in lightly-structured and fluctuating systems (Sprules, 1988; Rodríguez *et al.*, 1990; García-Jiménez, 1991). It becomes apparent when analysing distribution of the whole-spectrum residuals, which, in general, are distributed in domes each corresponding to an ecological group. As a consequence size distribution within a functional group is better described by polynomials than by a straight line (Boudreau and Dickie, 1989; Rodríguez *et al.*, 1990; Gasol *et al.*, 1991; Boix, 2000).

Recently, biomass size distribution has been analysed by adjustment to a linear model based on the Pareto type I distribution of probability (Vidondo *et al.*, 1997). This model is widely used in several disciplines (Winiwarter and Cempel, 1992) and in other fields within limnology (Pueyo, 1994) where size-structured systems are analysed, and has been used previously for analysis of the biomass size spectrum of plankton in Lake Konstanz (Vidondo, 1996), in coastal lagoons in the Empordà Wetlands (Quintana *et al.*, 2002) and in a temporary freshwater pond (Boix, 2000). Vidondo *et al.* (1997) suggest that a model based on the Pareto type II distribution, a non-linear function, provides a better fit to size distribution within a functional group than the linear model, which is more suited to the study of the community as a whole, in accordance with accepted biomass spectrum-theory (Dickie *et al.*, 1987; Sprules, 1988). However, in some situations the biomass size spectrum of a functional group shows a linear shape coinciding with an increase of resources and a lack of predation (Quintana *et al.*, 2002).

The objectives of this chapter are (1) to assess the usefulness of Pareto distribution to model biomass size spectrum at ecological scaling of the zooplankton community, (2) to establish which is the typology of the biomass size spectrum of the zooplankton community,

(3) to assess the relationship between the different types of spectra and the available food supplies in the ecosystem.

## 4.2. RESULTS

### 4.2.1 Physical and chemical characteristics of basin 5

Table 4.1 shows descriptive statistics of the main physical and chemical characteristics of the basin under study, where phosphorus and chlorophyll concentrations are high and inorganic nitrogen concentration is low. Oxygen saturation percentages (mid-day samples) fluctuated greatly, with frequent super-saturation giving nocturnal anoxia especially in summer, as verified by personal observation.

**Table 4.1.** Descriptive statistics of the main physical and chemical water parameters of basin 5.

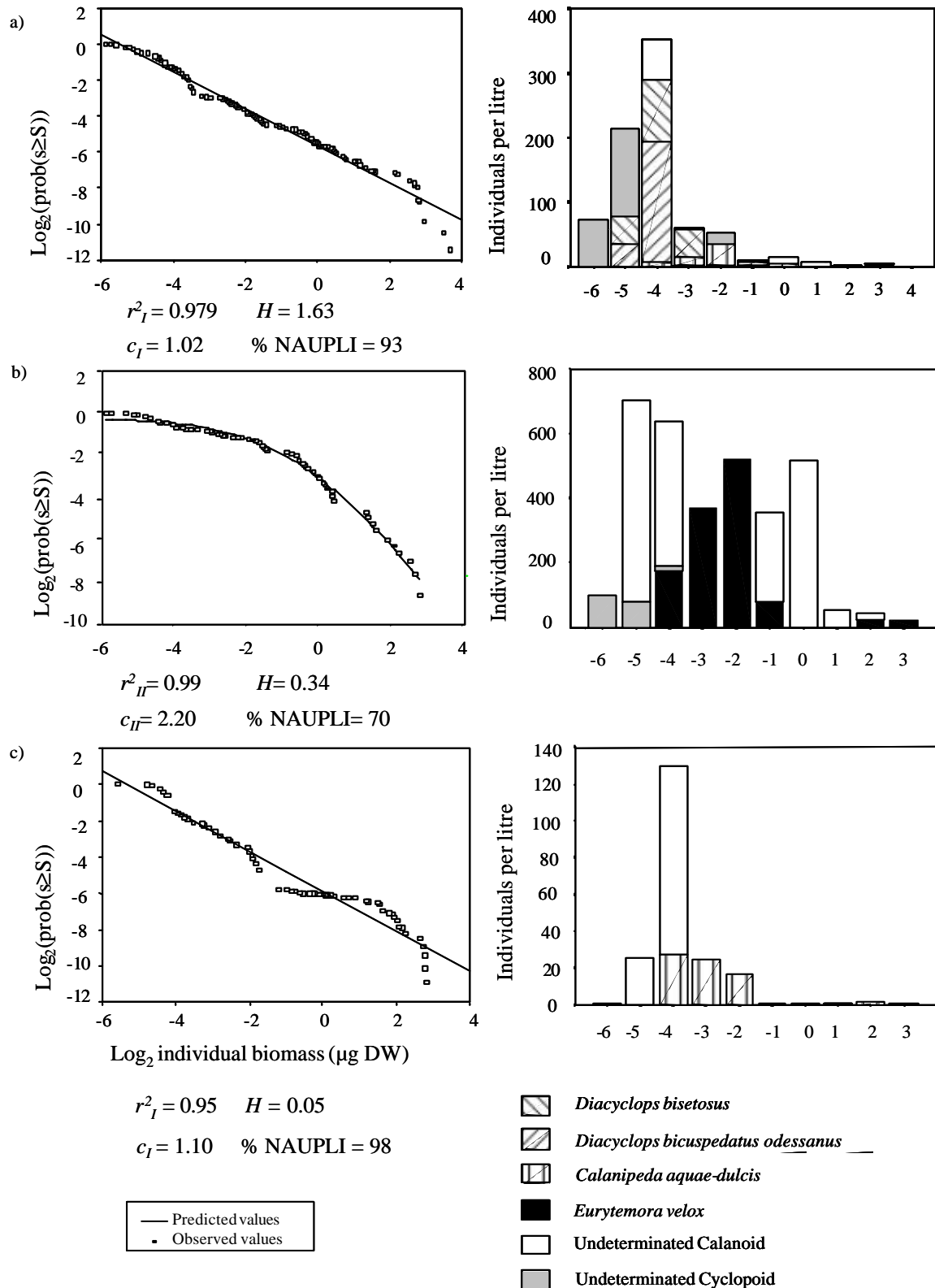
	Mean	Min.	Max.
<b>Conductivity EC<sub>25</sub></b> (mS·cm <sup>-1</sup> )	26.7	9.80	56.6
<b>Temperature</b> (°C)	16.4	4.70	34.7
<b>pH</b>	8.05	6.10	8.80
<b>% oxygen saturation</b>	84.9	1.0	239
<b>Alkalinity</b> (meq·l <sup>-1</sup> )	6.04	1.17	15.8
<b>NH<sub>4</sub><sup>+</sup></b> (μM)	11.3	0.00	261
<b>NO<sub>2</sub><sup>-</sup></b> (μM)	1.43	0.00	18.9
<b>NO<sub>3</sub><sup>-</sup></b> (μM)	10.3	0.00	246
<b>SRP</b> (μM)	7.39	0.00	52.8
<b>Total P</b> (μM)	17.3	0.88	182
<b>Total N</b> (μM)	203	44.0	924
<b>Chlorophyll</b> (μg·l <sup>-1</sup> )	20.7	0.83	164

### 4.2.2. Linear and curved shapes

The spectrum of every sample was fitted to both Pareto type I (PI) and Pareto type II (PII) models. 37 samples fitted better to a PII model and their corresponding spectra were classified as curved, while 31 fitted better to a PI model and they were classified as linear. The rest of the spectra had a low fit to either PI or PII model ( $r^2_I$  or  $r^2_{II}$  lower than 0.6). The linear shape indicates higher relative abundance of smaller sizes (figure 4.1a) while the curved shape indicates higher relative abundance of larger sizes (figure 4.1b).



**Figure 4.1.** Types of spectra and abundance of each size (a) linear spectrum, with better fit to linear model (Pareto type I), (b) curved spectrum, with better fit to non-linear model (Pareto type II), (c) example of step-like substructures. On the right hand, the corresponding graph of species abundance per litre of each size class.



Comparing samples, species diversity, species richness and evenness (see chapter 3.4) have significantly higher values in the samples with a linear spectrum than in the samples with a curved spectrum (ANOVA; species diversity  $F=6.5$ ,  $p<0.05$ , species richness  $F=5.1$ ,  $p<0.05$ , evenness  $F=4.2$ ,  $p<0.05$ ). Thus, the shape was more frequently linear in situations of high species diversity.

Taking into account only the fit to Pareto type I for all samples, the goodness of fit ( $r^2_I$ ) correlated positively with species diversity and species richness (table 4.2). The slope ( $c_I$ ) correlated negatively with species diversity and species+stages evenness, that is, size distribution tended to be flat ( $c_I$  was low) when species diversity was high. Correlations obtained for each taxonomic group showed that the goodness of fit to PI ( $r^2_I$ ) correlated positively to cyclopid abundance and the PI slope ( $c_I$ ) negatively to calanoid abundance (table 4.2).

Size distributions associated with all three flooding situations were steep (table 4.3); with confinement situations, Calanoids and *Gammarus* situations gave flatter slopes, although *Brachionus* situation was steep. Furthermore, the highest  $r^2_I$  values occurred in Cyclopid situations characteristic of flooding periods, and the lowest in *Gammarus* ones, which coincide with conditions previous to desiccation (see chapter 3.2 for the characterization of the community).

No correlations were found between the measured physical and chemical variables and the parameters of either PI or PII models.

**Table 4.2.** Pearson correlation coefficients between the goodness of fit ( $r^2_I$ ) and the slope ( $c_I$ ) of the Pareto I model, and community-related variables \* $p\leq 0.05$ , \*\* $p\leq 0.01$ .

Variable	$r^2_I$	$c_I$
Species diversity (Shannon index)	0.28*	
Species+stages diversity (Shannon index)	0,30*	-0,34**
Species+stages evenness		-0,41**

Species+stages richness	0,30*	
Log. Species richness	0,30*	0.29*
% of calanoids		-0,32*
% of cyclopoids	0,31*	

---

**Table 4.3:** Mean of the goodness of fit to Pareto type I ( $r^2_I$ ) and the slope of Pareto type I ( $c_I$ ) for each environmental situation. Standard deviation in brackets.

SITUATION	$r^2_I$ (SD)	$c_I$ (SD)
<i>Synchaeta</i>	0.82 (0.20)	1.17 (0.82)
Undefined <i>Synchaeta</i>	0.82 (0.15)	1.39 (0.84)
Cyclopoid	0.90 (0.00)	1.45 (0.54)
Calanoid	0.87 (0.12)	0.86 (0.40)
<i>Brachionus</i>	0.84 (0.11)	1.46 (0.52)
<i>Gammarus</i>	0.70 (0.11)	0.43 (0.00)

Likewise, during flooding periods (*Synchaeta*, undefined *Synchaeta* and Cyclopoids situations) a greater abundance of linear spectra was observed ( $\chi^2$  test,  $p < 0.05$ ) (Table 4.4). In contrast, during conditions of confinement (Calanoids, *Gammarus* and *Brachionus* situations), that is, of a lack of water supplies, curved spectra were more frequent ( $\chi^2$  test,  $p < 0.05$ ). In the *Synchaeta* situation only linear spectra were observed. Conversely, when the ecosystem tended to confinement (*Gammarus* situation) only curved spectra were found. In some *Brachionus* and *Gammarus* spectra, the curved shape was blurred by the presence of benthic species which are more abundant when water is confined.

**Table 4.4.** Number of spectra which fit better to a Pareto type I model and spectra which fit better to a Pareto type II model. Samples which did not belong to any situation have been excluded (12 samples). In brackets, the number of spectra exhibiting stepped substructures.

SITUATION		Type I	Type II
FLOODING	<i>Synchaeta</i>	3 (1)	0
	Undefined <i>Synchaeta</i>	4	1
	Cyclopoids	3 (1)	1
	<b>TOTAL</b>	<b>10 (2)</b>	<b>2</b>
CONFINEMENT	Calanoids	14 (6)	21
	<i>Brachionus</i>	1 (1)	6 (4)
	<i>Gammarus</i>	0	2
	<b>TOTAL</b>	<b>15 (7)</b>	<b>29 (4)</b>

#### 4.2.3. Stepped shapes

Both linear and curved shapes might exhibit step-like substructures (figure 4.1c), but they were rarer in the latter. The fit of these spectra to models is not satisfactory, because the presence of steps impedes convergence in the iterative process of adjustment to the PII model and gives a poor fit to the PI model even when there is a general linear trend.

In the smaller sizes, it was observed that a step coincided with an increase in the abundance of rotifers, in *Synchaeta* spp. after sudden flooding and *Brachionus* sp. after incidents of hypertrophy.

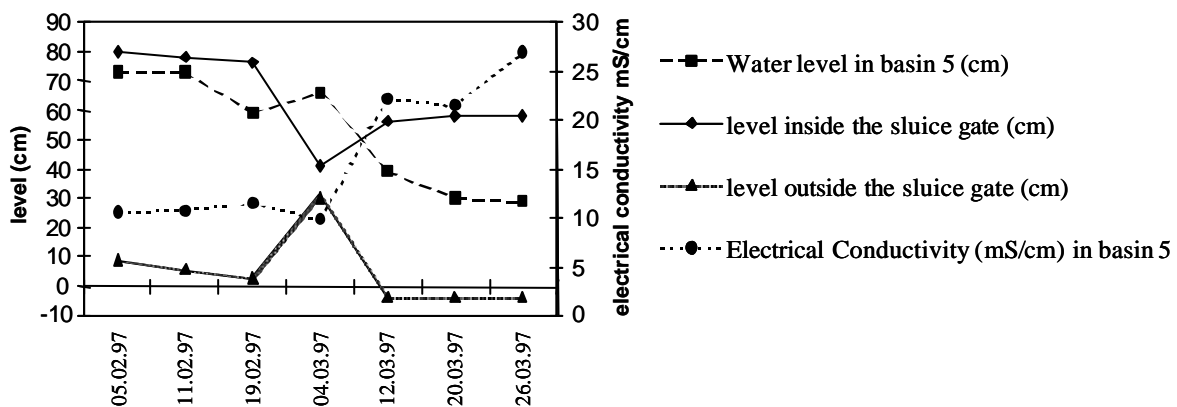
Double steps were also observed coinciding with moments when the community was almost exclusively made up of one species of copepod (usually calanoid). The first step was composed of nauplii, and the second of copepodites.

#### 4.2.4. Case example of temporal shift in spectrum shape

The following case study illustrates a spectrum shift from a linear to a curved shape, observed after flux change led to the use of the sluice gate situated in the marsh drainage channel, which avoids that water escapes to the sea (see chapter 2 and figure 2.1 for location). At the end of February, the sluice gate was opened in order to reduce the water level in the surrounding fields, thus stopping fresh water entering into the marshes for three days. The level of the basin, which had stayed high during flux regulation, now dropped quickly with the opening of the gate (figure 4.2). Although normal operation was soon resumed, the drop in flow in the drainage channel stopped the flow of fresh water into the marsh. From this moment on, basin levels decreased and conductivity progressively increased.

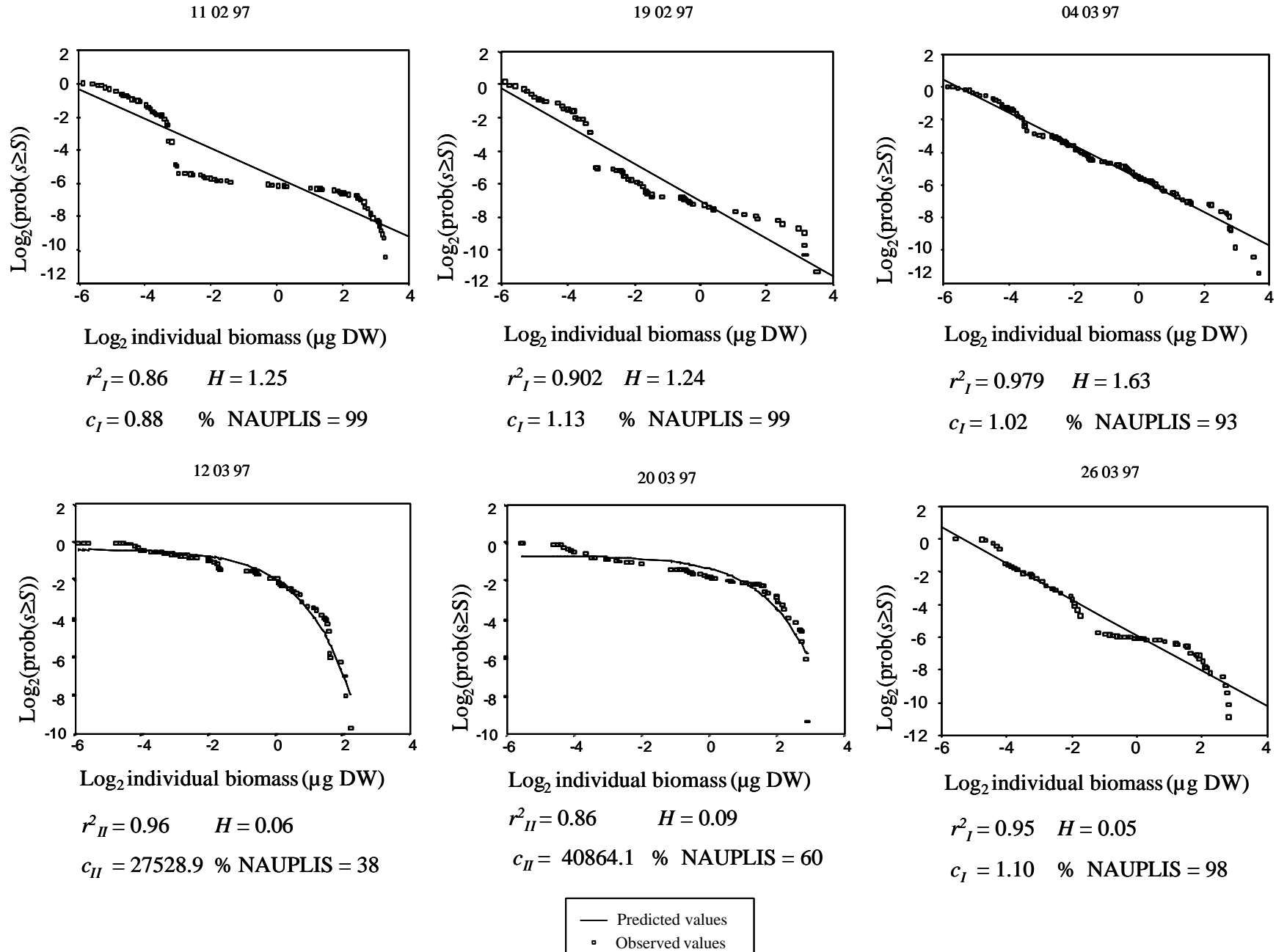
As a consequence of this unusual change from continuous water input to lack of input, some noteworthy changes in biomass size spectra and diversity values were observed before and after the opening of the gate (figure 4.3). Before opening the sluice gate, biomass size spectra showed a linear shape. Contrariwise, when confinement began after opening, biomass size spectra were curved. Double-step substructures were observed in periods both before and after the gate's opening.

**Figure 4.2.** Water level and electrical conductivity change in basin 5. Water level inside and outside the sluice gate regulating water flow in the drainage channel.



Changes in species composition were also clear. With fresh water input, the community had high species diversity and was composed of cyclopoids and calanoids (Cyclopoids situation). The community was composed mostly of *Diacyclops bicuspidatus odessanus*, *Diacyclops bisetosus*, and *Eurytemora velox*, with lesser abundances of *Halicyclops rotundipes*, and *Calanipeda aquae-dulcis*. Maximum species diversity was reached on 4 March when the community became dominated by calanoids. At this moment the most abundant species were *C. aquae-dulcis* and *E. velox*. When levels dropped the same community persisted despite very low diversity values, since most species disappeared and the community was composed almost exclusively of *C. aquae-dulcis*. The nauplii/copepodite ratio was very high in linear spectra, but not in curved spectra, where there were a high percentage of copepodites.

**Figure 43.** Next page, example that shows a spectrum shift from PI to PII. Above, days before opening the sluice gate. Below, days after opening the sluice gate.







## **4.3. DISCUSSION**

### **4.3.1. Stepped shapes and population dynamics**

The existence of steps within the biomass size spectrum of an ecological group has been attributed to population dynamics of the species in it (Dickie *et al.*, 1987). According to Boix (2000), in his analysis of a temporary pond aquatic community biomass size spectrum, these steps are more apparent during early flooding because inter- and intra-population interactions are not yet effective for population control and the variation in population size is explained basically by reproduction rates. This is the case in this study, with steps made up of rotifer species (e.g. *Synchaeta* spp. and *Brachionus* sp.), which appear immediately after a disturbance (water inputs or hypertrophic events, respectively) due to their greater reproductive capacity. As time passes this step disappears for two reasons: an increase in species blurs it, and competition and predation mechanisms come into play.

In general terms, these steps appear whenever an increase of biomass takes place in a particular size range and there is little overlapping between the size ranges of different species. In both observed cases (rotifer and calanoid steps), there was a near-absolute domination of the smaller-size range by one species, but while the rotifer step represents the complete population, the calanoid step is due to recruitment (nauplii). In both cases, size distribution effectively reflects the population dynamics of the dominant species involved.

### **4.3.2. Linear and curved shapes and their ecological implications**

Variation in fresh water and nutrient input in basin 5 is difficult to verify, since entry flows are not measurable and in many cases do not even increase level. For this reason it is difficult to correlate the shift in spectra from linear to curved shapes with changes in water flow unless there is a sudden change, as occurs in the example (figure 4.3). This, together with the delay between water input variation and organisms' reactions to it (Quintana *et al.*, 1998a) would explain the lack of correlation between Pareto parameters and the physical and chemical variables.

Nevertheless, these results show that the shape of the biomass-size distribution for the functional group of zooplankton changes according to environmental conditions. Under flooding conditions, with high energy input (*Synchaeta*, undefined *Synchaeta* and Cyclopoids situations), the community exhibits high species diversity and a linear spectrum. In confinement conditions (*Calanoids*, *Brachionus* and *Gammarus* situations) curved spectra are significantly more abundant.

The community change during confinement could be interpreted in the following way: in situations of confinement, due to the lack of nutrient input, the populations of the small-sized organisms decrease in number, and some of them disappear. In this situation of limited resource availability, intra- and interspecific interactions take on more relevance, favouring the displacement of biomass toward larger sizes. The result is a curved spectrum and a decrease of species diversity. Similarly, Boix (2000) found extremely high values of  $D$  in a temporary pond, coinciding with stress conditions close to desiccation, when larger individuals dominate and presumably interactions between species were especially high. Thus,  $D$  can be linked to the degree of ecological interaction between species within a functional group.

In contrast, under flooding conditions, nutrient input causes population growth of small-sized organisms, over compensating for the effect of competitive interactions. Thus, the spectrum becomes linear and the availability at each trophic level of a wider range of resources permits the development of a higher number of populations, thus increasing species richness and diversity.

According to Quintana *et al.* (1998b), flux regulation acts as a press type disturbance causing gradual changes to the community and, if the disturbance persists, the community acquires a new structure which persists while conditions are maintained (here this corresponds to the Cyclopoids situation). In this case, flux regulation prolongs the linear spectra characteristic of flooding periods, due to the continual fresh supplies of water and nutrients.

## 5.1. INTRODUCTION

The study of the dynamics of the biomass size distribution (at ecological scaling) in a single temporary basin of Empordà salt marshes (described in chapter 4) explains how the availability of resources conditions the shape of spectra. Linear shape spectra are found in situations of high nutrient inputs, which permit growth of small-sized organisms, over compensating for the effect of biotic interactions; while curved shape spectra are found in situations of lack of food, which lead to an increase in ecological interactions between individuals. External forcing as flooding or nutrient inputs have already been found to affect species composition of temporary basins of these salt marshes (Quintana *et al.*, 1998b) and their size structure at physiological scaling (Quintana *et al.*, 2002). However, nothing is known about the zooplankton size distribution of permanent basins in these salt marshes, where the predation pressure by fish is expected to be higher than in temporary ponds. Furthermore, few studies have dealt with the dynamics of the size structure of plankton in other shallow permanent fluctuating ecosystems, such as coastal lagoons (Gilabert, 2001) or saline inland lakes (García *et al.*, 1995).

The response of the size distribution to predation remains unclear since some authors indicated that fish affected the total biomass of organisms more than the shape of the biomass size distribution (Zimmer *et al.*, 2001) and others concluded that predation changes the shape more than the total biomass (Mazumder *et al.*, 1988). These different results might be due to the different diets of the fish species involved, that is, the rank of sizes consumed by the fish (Zimmer *et al.*, 2001). Seasonal differences in predation pressure from fish or ontogenic shifts in their diet might be a consequence of temporal variability of the biomass size spectrum as proposed by Zimmer *et al.* (2001).

Empordà salt marshes show the characteristics of a fluctuant Mediterranean system and rapid changes in nutrient supplies that take place in their basins produce temporal changes in the biomass size spectrum of aquatic organisms (see chapter 4). Since all the basins in Empordà salt marshes remain connected during intense sea storms and zooplankton species are able to disperse among basins, differences in specific composition and size structure among them will be a consequence of their local environmental conditions (i.e. the presence of fish) and not due to their background of

resting eggs. Fish can also disperse during floodings from permanent to temporary basins, but only in the permanent one form dense populations.

These ecological characteristics of Empordà salt marshes made them suitable to analyse, based either on the shape of the biomass size distribution in permanent basins depends mainly on nutrient inputs, as do temporary basins, or based on the presence of fish.

In this chapter the objectives were (1) to analyse the differences between zooplankton structure (species composition and size distribution) of permanent and temporary basins and (2) to analyse how the temporal variability of biomass size spectra is affected by nutrient inputs or by the presence of fish.

## 5.2. RESULTS

### 5.2.1. Differences between zooplankton community in permanent and temporary waterbodies

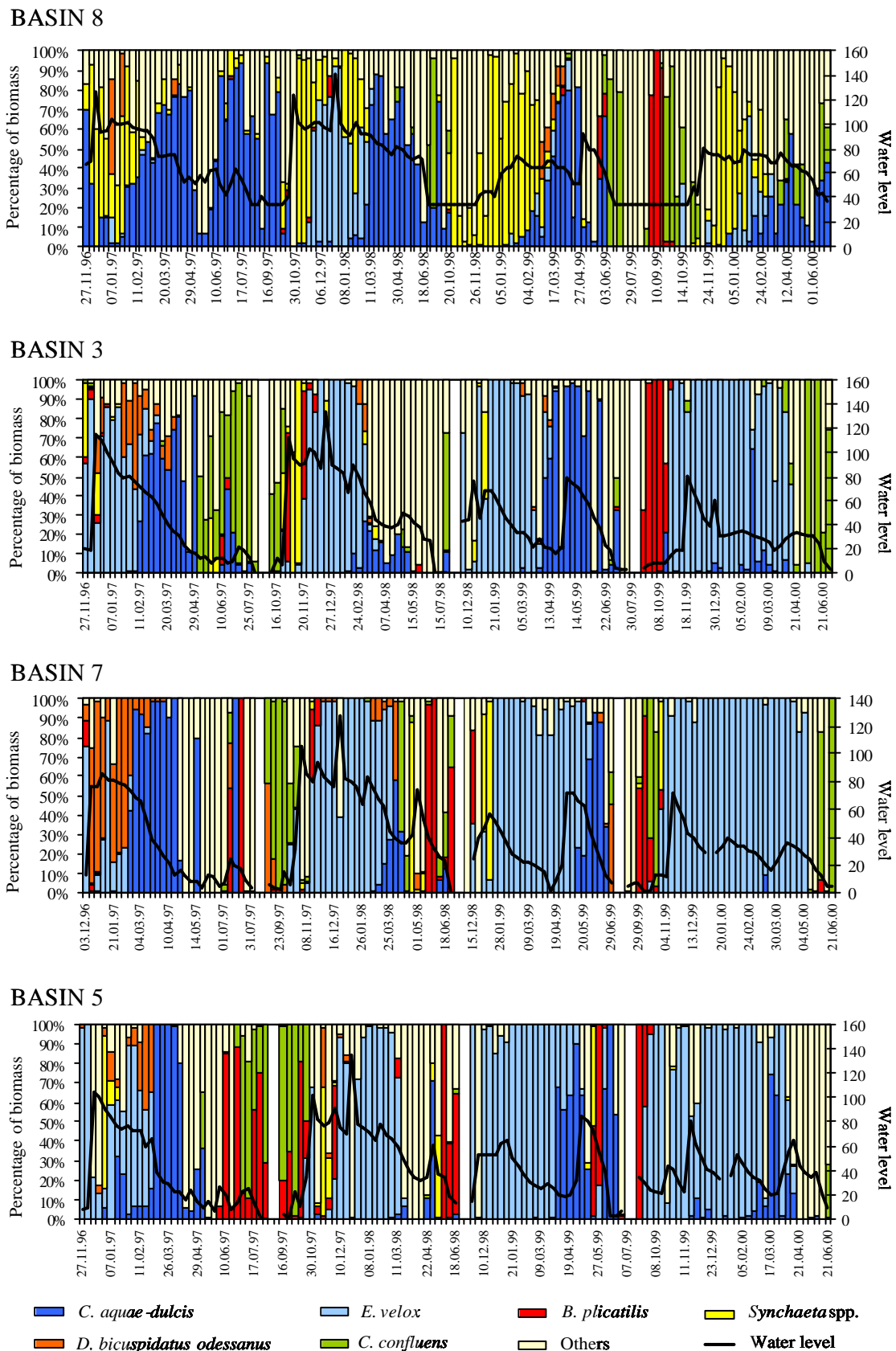
Zooplankton of the two temporary basins (basins 5 and 7) and the semi-permanent basin (basin 3) had similar seasonal patterns (figure 5.1) and the only difference between them were episodic events of the annual cycle (see figure 2.1 and table 2.3 for location and features of these basins). Six situations were identified which were conditioned to the hydrological cycle: (1) *Synchaeta* spp. dominated at the beginning of the cycle just after an intense input of water and it was replaced soon after with copepod populations, (2) populations were formed by the cyclopoid, *Diacyclops bicuspidatus*, and nauplii of the calanoid, *Eurytemora velox*, (3) later, when the water level began to decrease, late stages of *E. velox* developed reaching close to 100% of zooplankton total biomass, (4) in spring the population of *E. velox* was substituted by another calanoid, *Calanipeda aqua-dulcis*, (5) just before the basins dried out the harpacticoid, *Cletocamptus confluens*, developed, and (6) in the same conditions but only when there are incidents of hypertrophy the community was composed mainly by large populations of the rotifer, *Brachionus plicatilis*.

The permanent basin, despite having similar specific composition to the temporary basins, exhibited different relative species abundance and a more simplified seasonal pattern with only two situations: (1) *Synchaeta* spp. populations appeared after an intense flooding and maintained itself most of the winter, (2) *C. aquae-dulcis* dominated the rest of the year, but opposite to the temporary basins, it was also present during winter. Large populations of *E. velox* were not found and only dominated the community in one period during the 4 studied cycles and they only appeared as naupliar stages. Similarly, the appearance of *Brachionus plicatilis* and *Cletocamptus confluens* were also occasional.

When analysing the size structure (figure 5.2), the permanent basin differed greatly from the temporary basins for higher relative biomass of small sizes individuals. The permanent basin (basin 8) was dominated by naupli and rotifera whereas copepodites were scarce and only appearing during the spring. Alternately, in temporary basins, copepodites and adults dominated the community most of the year and naupli or

rotifera only predominated at the beginning of the hydrological cycle or during hypertrophies. Furthermore, total biomass ( $\mu\text{g l}^{-1}$  dry weight) was significantly lower in the permanent lagoon than in the rest of lagoons (table 5.1).

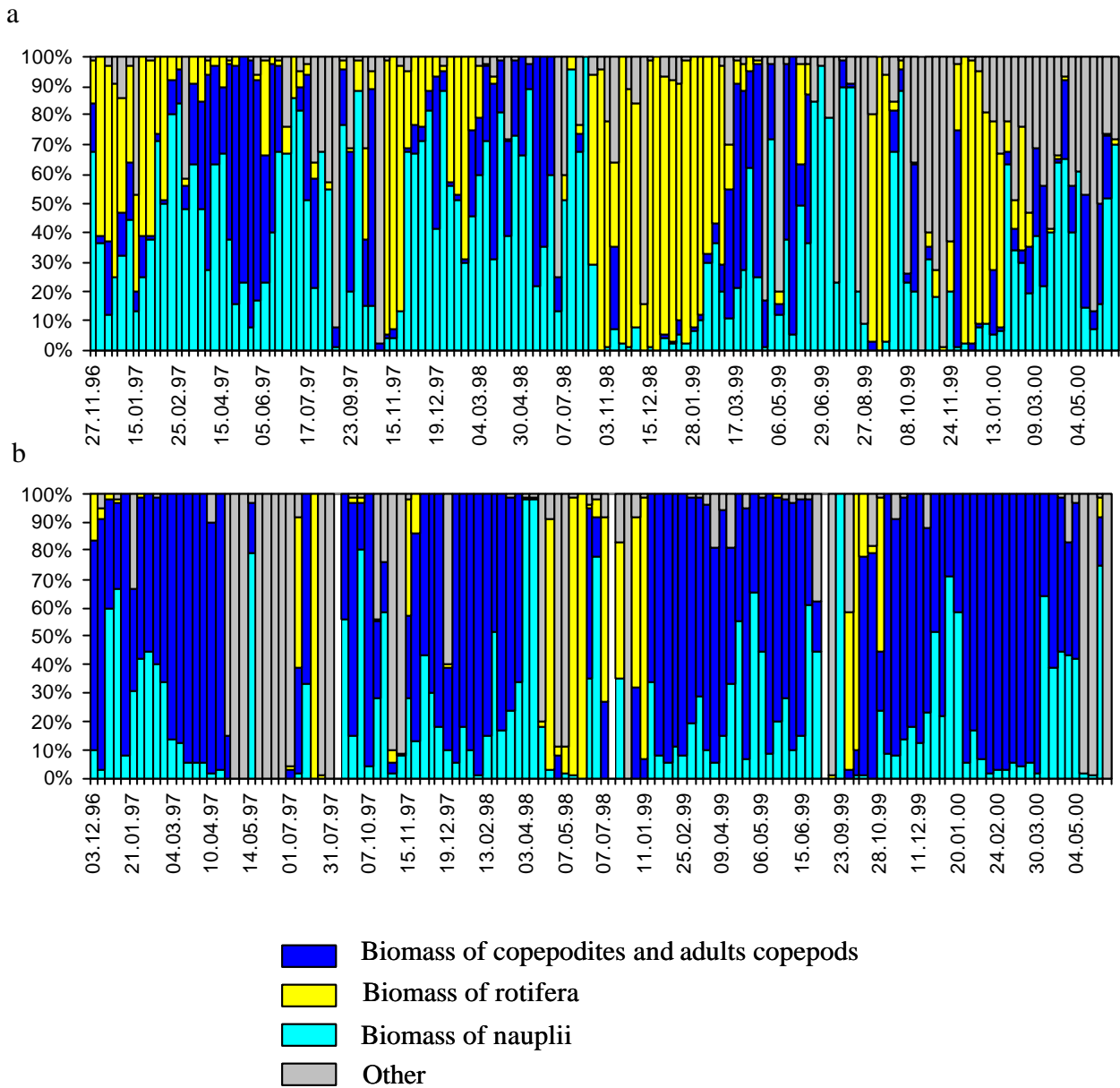
**Figure 5.1.** Biomass percentage evolution of the main zooplankton species of the four basins during the four annual cycles (1996-2000).







**Figure 5.2.** Biomass percentage of rotifera, nauplii and copepodites and adult copepods during the four cycles in (a) basin 8 (permanent) and (b) basin 7 (temporary), (1996-2000).



**Table 5.1.** Total zooplankton biomass ( $\mu\text{g}\cdot\text{l}^{-1}$ ) for each basin. ANOVA,  $p < 0.001$ ; Scheffé  $\mu_8 < (\mu_3 = \mu_5 = \mu_7)$ .

	mean	minimum	maximum	SD
<b>Basin 8 (permanent)</b>	42.5	0.29	2229	203
<b>Basin 3 (semi-permanent)</b>	255	0.18	6042	688
<b>Basin 5 (temporary)</b>	534	0.53	8371	1138
<b>Basin 7 (temporary)</b>	718	0.11	18967	2399

### 5.2.2. Variation over time of the biomass size spectrum for temporary and permanent waterbodies

When analysing spectra of the 4 basins during the 4 years, 168 fitted better to a PII model (curved shape spectra), while 192 fitted better to a PI model (linear shape spectra). The rest of the spectra (159) had a low fit to either PI or PII model ( $r^2_I$  or  $r^2_{II}$  lower than 0.6). The temporal evolution of biomass size spectrum of the zooplankton community (ecological scaling) for each basin of one chosen hydrological cycle (September 1996 to August 1997) is represented in figure 5.3.

Biomass size spectrum for temporary (basin 5 and 7) and semi-permanent (basin 3) basins followed the same pattern which was related to the hydrological cycle: (1) Biomass size spectrum had a linear shape after a winter sea storm that produced a massive input of water and also afterwards, while water levels remained high. (2) In contrast, it became curved during confinement when the water level decreased. Biomass size spectra with curved shapes coincided with periods where there was a dominance (more than 80% of individuals) of one single species, usually of calanoids (*C. aquaedulcis* or *E. velox*), which indeed were typical of the situations of the lack of water inputs (figure 5.3). In some cases (i.e. the last spectrum of basin 7), when the water level was very low (late spring or autumn) the shape became blurred coinciding with the presence of benthic species usually large in size which produced a second step in the spectrum.

Alternately, variations in biomass size spectrum for the permanent basin (basin 8) did not seem to be related to the hydrological cycle since both shapes were found either in flooding and confinement situations, and they were not related to dominance of certain species either.

After classifying the samples of the 4 years between those whose spectrum was linear shaped or curved shaped, an ANOVA was used to test if linear shapes and curved shapes were more frequent in different moments of the hydrological cycle. Results were consistent with that described before for temporal evolution, that is, water level was significantly higher in samples whose spectra were linear shaped ( $p < 0.05$ ), according with a higher linearity of the spectra during water inputs. However, as previously suggested, this functioning is not valid for the permanent basin (basin 8) in particular, since linear spectra were not significantly more abundant in flooding than in confinement situations. Furthermore, biomass size spectra of the permanent waterbody

showed significantly steeper slopes ( $c_I$ ) than biomass size spectra of temporary waterbodies (ANOVA,  $p < 0.001$ ) indicating a higher relative abundance of smaller sized organisms in the former.

### 5.2.3. Relationship between biomass size spectrum shape and species dominance

Biomass size spectra were also related to changes in relative abundance of species that compose it according to correlations on table 5.2. Since results were almost the same for temporary and permanent basins, I present the correlations calculated for all basins together.

When taking into account only the fit to Pareto type I for all the samples, an increase in copepodites and adult copepods was related to a flatter  $c_I$  as expected, because they are the larger-sized species in zooplankton biomass size spectrum. However, when analysed separately, cyclopoids and calanoids did not produce the same effect on the  $c_I$ : Cyclopoids were related to a steeper  $c_I$ , whereas calanoids, to a flatter  $c_I$ . Total rotifer biomass led to a low fit to both models (negative correlation to  $r^2_{I}$  and  $r^2_{II}$ ) and to a steeper  $c_I$ . When the most abundant rotifer species were separately analysed (*Synchaeta* spp. and *Brachionus plicatilis*), in both cases, an increase in their respectively biomass was related to a steeper  $c_I$  (positive correlation). *B. plicatilis* biomass was also related to a low fit to the linear model (negative correlation to  $r^2_{I}$ ).

Some differences were found between temporary and permanent basins. In the permanent basin the copepodites and adults' biomass of calanoids and cyclopoids did not have any effect on  $r^2_{I}$  and  $r^2_{II}$ , whereas in the temporary basins calanoids and cyclopoids had opposing effects, that is, calanoids were related to a high fit to Pareto type II (positive correlation to  $r^2_{II}$ ) and low fit to Pareto type I (negative correlation to  $r^2_{I}$ ) and cyclopoids were related to a high fit to Pareto type I.

As regards species diversity, differences between temporary and permanent basins were also found (table, 5.3). In temporary basins species diversity was slightly higher in those spectra which fit better to Pareto type I than those which fit Pareto type II. For the permanent basin there were no differences in species diversity between the two types of spectra.

**Table 5.2.** Spearman correlation coefficients between the fit to Pareto type I ( $r^2_I$ ), the slope of Pareto type I ( $c_I$ ), and the fit to Pareto type II ( $r^2_{II}$ ) and the biomass of zooplankters. Only correlations with  $p < 0.001$  are displayed. When temporary or permanent is indicated in brackets, the analysis is only for one typology of waterbody.

	$r^2_I$	$c_I$	$r^2_{II}$
Biomass of rotifera	-0.36	0.46	-0.27
Biomass of <i>Synchaeta</i> spp.		0.47	
Biomass of <i>Brachionus plicatilis</i>	-0.61	0.38	
Biomass of nauplii		0.41	
Biomass of Calanoids		-0.36	
Biomass of Cyclopoids		0.23	
Biomass of copepodites and adult calanoids (temporary)	-0.37	-0.58	0.34
Biomass of copepodites and adult cyclopoids (temporary)	0.30	0.22	
Biomass of copepodites and adult calanoids (permanent)		-0.57	

**Table 5.3.** Mean of Shannon species diversity (standard deviation in brackets) in samples whose spectrum fit better to PI model and samples whose spectrum fit better PII model in temporary and permanent basins.

	Linear model (Pareto type I)	Curved model (Pareto type II)	$p$
Temporary basins	0.94 (0.78)	0.76 (0.68)	<0.05
Permanent basins	1.50 (0.61)	1.46 (0.68)	n.s.

**Figure 5.3.** Temporal evolution of the shape of biomass size spectrum and the water level of the hydrological cycle, from September 1996 to August 1997. Spectrum with the highest fit (whether it was  $r^2_I$  or  $r^2_{II}$ ) was chosen for each month. Each colour represents the dominance (more than 80%) of a certain species. In light yellow samples with more than 20% of benthic species. All spectra have the same axis values as the first one.

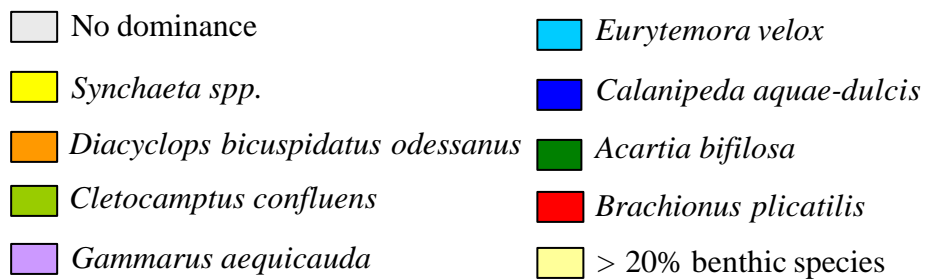
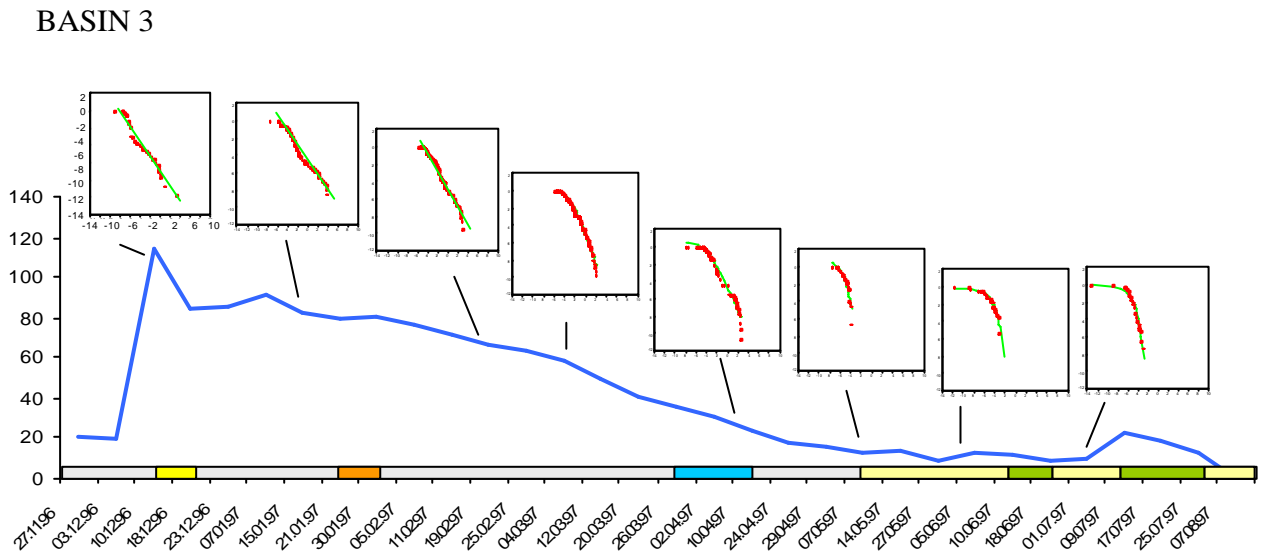
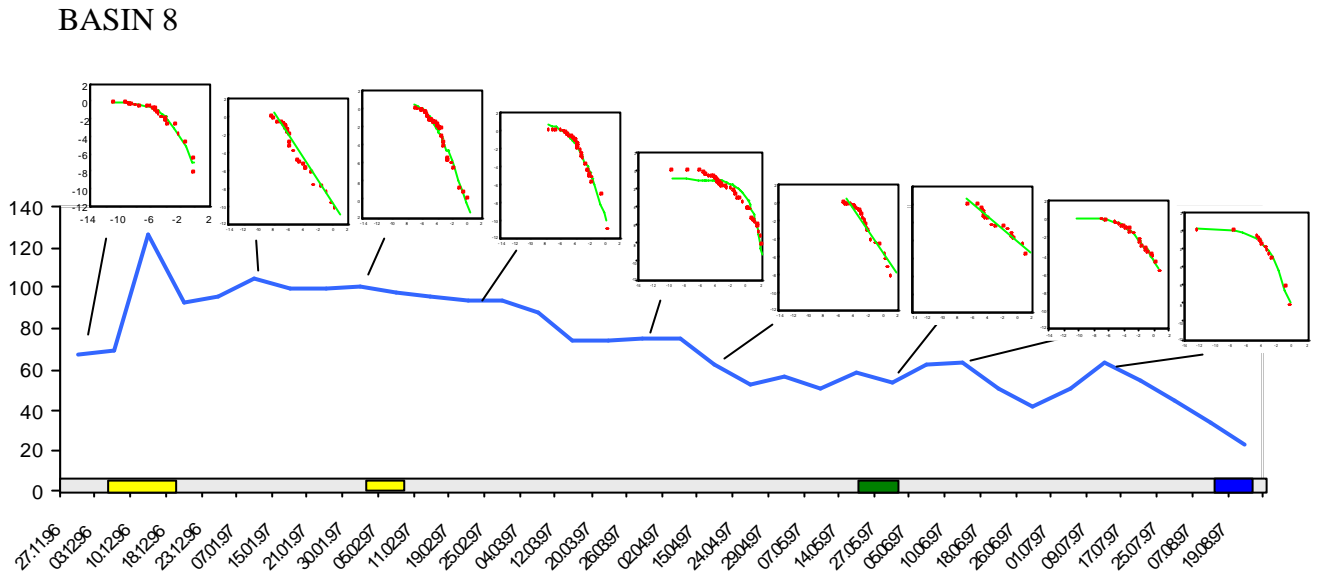
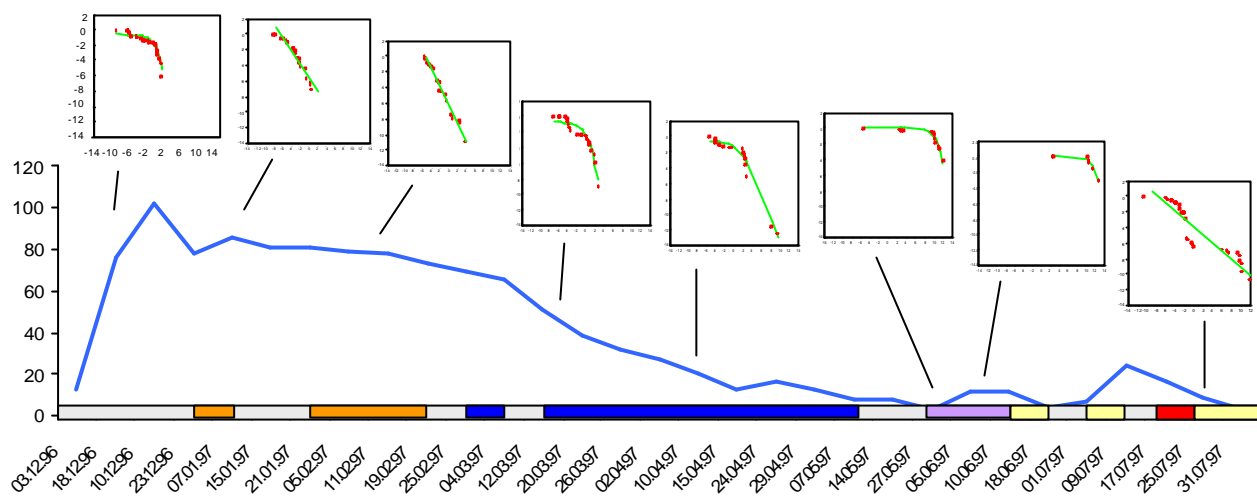
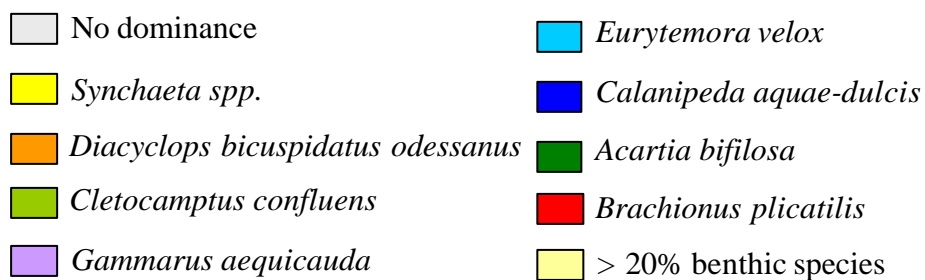
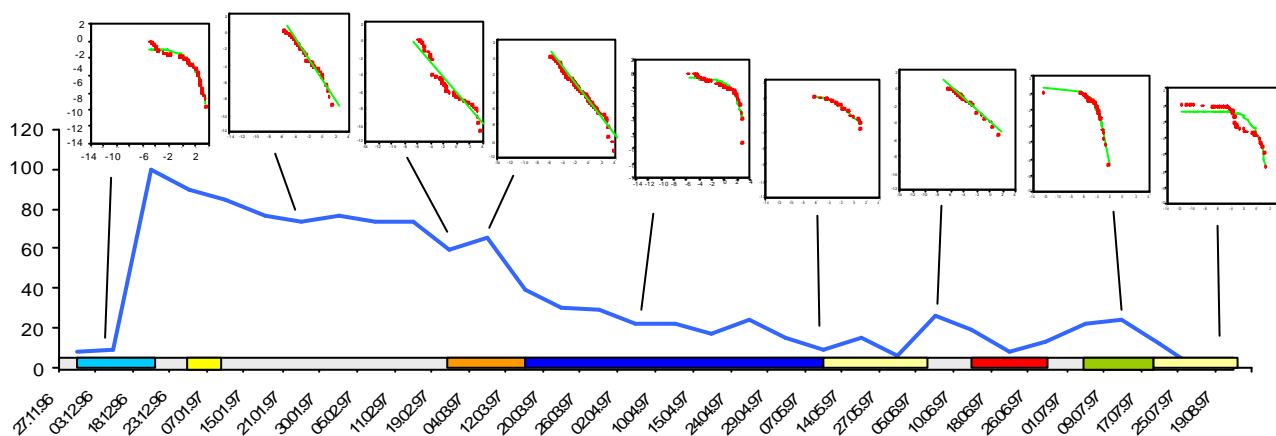


Figure 5.3. continued.

BASIN 7



BASIN 5

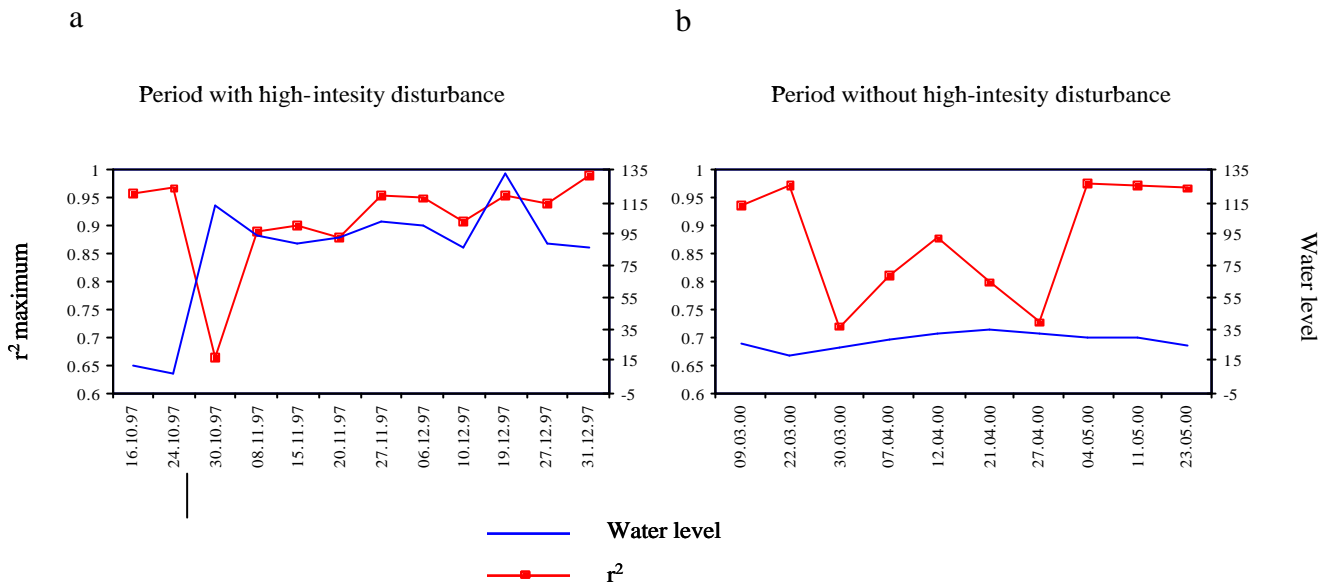


#### 5.2.4. Comparing the effect of disturbances on biomass size spectrum at physiological and at ecological scaling

Quintana *et al.* (2002) studied the biomass size spectrum at physiological scaling (including phytoplankton and zooplankton) of several basins in the same Empordà salt marshes and they found correlation between the fit to the Pareto type I ( $r^2$  of the regression) and several variables related to disturbances. Variables used were nutrient concentrations (SRP and DIN), species diversity and two measures,  $z_2$  and  $d_{gs}$ , which are related respectively with disturbance severity and intensity in zooplankton assemblages (see Quintana, 2002). Quintana *et al.* (2002) demonstrated that  $r^2$  of the whole plankton community diminishes after disturbances. In order to know if disturbances have the same effect on the biomass size spectrum at ecological scaling than that found for the whole community we used the same variables and correlated them with  $r^2_I$  and with the maximum  $r^2$  ( $r^2_{max}$ ), whether it was  $r^2_I$  or  $r^2_{II}$  (fit to the linear and to the curved model respectively). Alternately to the results obtained by Quintana *et al.* (2002) for the physiological scaling, when analysing the ecological scaling, I did not find any correlations between  $r^2_I$  or  $r^2_{max}$  and any of these variables related to disturbances (SRP, DIN and species diversity), not even  $z_2$  and  $d_{gs}$  which were calculated directly from relative abundance of different zooplankton species.

$r^2_{max}$  before and after the disturbances were compared by means of a paired data test and I found that, despite this lack of correlation between  $r^2$  and variables related to disturbances,  $r^2_{max}$  was high before the disturbance and dropped significantly with the disturbance (paired data,  $p < 0.01$ , figure 5.4a). However,  $r^2_{max}$  also showed changes of the same magnitude under stable conditions (while water level remained constant) with no apparent change in the environmental conditions (figure 5.4b). Therefore  $r^2$  of ecological scaling may diminish not only after an intense input of water (as the  $r^2$  of the physiological scaling), but also under stable conditions when water level and water physico-chemical composition remain constant.

**Figure 5.4.** Examples of variation over time of the fit to the Pareto model, which gives the highest  $r_2$  ( $r^2_{I}$  or  $r^2_{II}$ ) for basin 3. (a) Period with a high-intensity disturbance in the form of sea storm (date of sea storm indicated with an arrow), (b) period without high-intensity disturbances in which water level remained constant.





## 5.3. DISCUSSION

### 5.3.1. Zooplankton composition in permanent and temporary basins

A survey of the literature indicates differences between the biota of temporary and permanent waterbodies (Kenk, 1949; Williams, 1987; Wellborn *et al.*, 1996 and references therein; Galindo *et al.*, 1994; Hillman and Quinn, 2002; Collinson *et al.*, 1995), however the permanent and temporary basins of salt marshes of Empordà Wetlands have similar taxonomic composition as might be expected since during intense storms the whole system is flooded and basins are connected. Species composition and their temporal patterns described in this study coincide with those described by Quintana *et al.* (1998b), with a temporal pattern determined by the occurrence of irregular floods due to disturbances followed by a natural process of desiccation.

Despite the similar taxonomic composition, permanent and temporary basins differed in the relative abundance of species and in the temporal pattern. In permanent waters there was a higher abundance of rotifera (especially *Synchaeta* spp.) during a longer period and copepod populations were composed mainly by early stages (nauplii). As a consequence, size distribution differed greatly between temporary and permanent basins since the permanent basin was dominated mainly by smaller sizes. The presence of fish in the permanent waterbodies would explain the differences between size distributions of zooplankton in permanent and temporary waterbodies, which corresponded to the findings of several investigators, who reported a shift from larger to smaller organisms in the presence of planktivorous fish (e.g. Brooks and Dodson, 1965; Almond *et al.*, 1996; Dremmer and Smith, 1991; Lynch and Shapiro, 1981; Williams and Moss, 2003). The most common fish species found in basin 8 were *Liza microps*, *Cyprinus carpio*, *Pomatoschistus microps* and *Atherina boyeri* (Moreno-Amich *et al.*, 1999). Quantitative data of fish stock and their seasonal variability are not available. However, some observations (Pou, pers. comm.) have indicated that a high variability in species composition and density is dependent on hydrology (e.g. sea water or freshwater inputs, water level decrease) and often fish are found forming dense shoals. Although the impact of fish predation cannot be quantitatively evaluated, fish predation pressure might vary greatly over time. Complete flooding of the salt marsh favours fish

dispersion and their entry in temporary and semi-permanent basins. In fact, fish were occasionally found in these basins, but they never reached stable populations.

### **5.3.2. Variation of biomass size spectrum shape due to fluctuant conditions**

As has already been proposed in chapter 4, in temporary basins, where predation has little effect on zooplankton functional group, the shape of the biomass size spectrum is related to the hydrological cycle, which conditions the entry of nutrients to the ecosystem and thus the availability of food to the zooplankton. In fluctuating ecosystems, energy inputs during flooding would not limit zooplankton growth. Under these conditions competitive interactions among zooplankton species would be weak and the spectra would be linear due to the allometric relationship between growth (production) and body mass. In contrast, during confinement conditions the scarcity of food would decrease zooplankton growth and increase competitive and/or predatory interactions between zooplankton organisms which favour the greatest sizes thus leading to the appearance of curved spectra. Baca *et al.* (2000) demonstrated experimentally, that size distribution responded to nutrient addition by increasing smaller organisms more than larger organisms in both the benthic and pelagic habitats.

However, in permanent waterbodies zooplankton growth is not only conditioned by the variability of the resource availability but by the predation of planktivorous fish. Thus, the temporal variability of the spectra may also be a result of temporal differences in fish predation pressure. Several studies provide evidence that biomass size spectrum is affected by fish predation. Blumshine *et al.* (2000) found a positive relationship between the slopes of benthic invertebrate size spectra and consumption rates by percids and centrarchids. The same results were obtained by Mazumder *et al.* (1988) who reported a decrease of the mesoplankton associated with an increase of the nanoplankton with addition of fish, which resulted in steeper slopes of the size spectrum. Zimmer *et al.* (2001) suggested that consumption of fathead minnows (*Pimephales promelas*) impacted smaller invertebrates, which resulted in flatter slopes of the biomass size spectra. Therefore, biomass size spectra will be affected in different ways depending on the size selectivity feeding of the fish species present and the size range considered. In the permanent basin of Empordà, copepods (copepodites and adults), the largest sizes in the functional group of zooplankton, were scarce and most of the zooplankton biomass was composed of rotifera and nauplii. Alternately, in

temporary basins without fish predation, the greatest size classes were dominant in many occasions. Thus, consumption by fish in the permanent basin probably impacts more on the biggest invertebrates, which results in steeper slopes. The lower total biomass found in the permanent basin in comparison to the temporary basins might also be a consequence of fish predation, which confirms the findings of Zimmer *et al.* (2001). Mazumder *et al.* (1988) concluded that fish predation changes the shape of the size distribution more than the total biomass in the system.

According to Sprules and Goyke (1994), under stable conditions, each functional group (phytoplankton, zooplankton and fish) in the normalised size spectrum can be modelled by a series of parabolas. However, in our ecosystem fish predation was not constant, nor were the nutrient inputs. Hence, it seems likely that unstable situations might lead to a shift from curved shapes to linear shapes. Thus, periods of stable situations, like constant nutrient supplies, constant predation in the permanent waterbody or the lack of fish predation in temporary basins will be characterised by curved spectra that will shift to linear ones when one of this factor stops to be constant. In the case of a nutrient input it would cause an increase in the smaller sizes due to their greater ability to react, whereas when there is an increase in fish predation the relative abundance of larger sizes would decrease.

Species diversity values were lower in samples whose spectrum was curved than samples whose spectrum was linear in temporary basins, but not in the permanent one. Lower species diversity in PII samples in temporary basins would agree with a high competitive exclusion in these ecosystems under scarcity of nutrients (i.e. lack of inputs). On the other hand, PII samples appeared in permanent basins with the presence of fish (under constant fish predation pressure, according with the discussion above). In these conditions, fish may act as a “keystone predator” (Kerfoot and DeMott, 1984) favouring an increase in species diversity.

### **5.3.3. Responses of spectrum at ecological and physiological scaling**

When studying biomass size spectra at physiological scaling, Quintana *et al.* (2002) found that intense disturbances caused changes in the biomass size spectrum which result in a decrease of the fit to a linear shape (Pareto type I), so that  $r^2$  might be related to the stability of the community structure. The results showed that at ecological scaling,  $r^2$  of both linear shape spectra and curved shape spectra is not related to

stability, since low  $r^2$  were found after intense disturbances and during stable conditions. Therefore, disturbances have an effect on both the physiological and ecological scaling of the spectrum, although at ecological scaling other factors led to shifts in the shape of the spectrum such as the population dynamics of the dominant species and the interactions among species.

Like physiological scaling (Quintana *et al.*, 2002), at ecological scaling different species have different effects on the biomass size spectrum. Rotifera are the smallest organisms in the zooplankton of these basins that reach a considerable biomass. The most abundant rotifera, *Synchaeta* and *Brachionus*, developed after disturbances like water inputs and incidents of hypertrophy respectively, making the slope steeper. Their appearance was also associated with a decreasing of the fit to both models, because of the formation of domes in the smallest sizes of the biomass size spectra (see stepped shape spectra in chapter 4). The increase in the rotifera's abundance had the same effects on the physiological scaling of the spectra (Quintana *et al.*, 2002). It is worth noting that, despite having similar sizes, cyclopoids and calanoids produced opposing effects on the slope of the biomass size spectrum. Cyclopoids (among them the most abundant is *D. bicuspidatus odessanus*) grow only in situations of flooding periods and they were related to steeper slopes of the biomass size spectrum. Calanoids populations appeared sometime in their early stages during flooding periods, but populations with late stages were typical of situations of lack of inputs (Quintana *et al.*, 1998b) and related to flat spectra in ecological scaling as Quintana *et al.* (2002) had previously found for the physiological scaling.

## 6.1. INTRODUCTION

Ataxonomic diversity (according to Margalef, 1991) can be calculated by classifying organisms by their biomass or size (Platt and Denman, 1977, 1978; Platt *et al.*, 1984; Rodriguez and Mullin, 1986; Oindo *et al.*, 2001), their trophic level (Pianka, 1982; Aoki and Mizushima, 2001) or their ecological strategies (Weithoff *et al.*, 2001). Since ataxonomic diversity dispenses with species, it overcomes certain problems and it might complement the information given by species diversity. For example, species diversity requires highly time-consuming surveys when measuring over large areas (Oindo *et al.*, 2001) and an accurate determination of the species, which might be difficult in larval stages, both processes can be avoided by calculating ataxonomic diversity.

Several investigators calculated size diversity in different oceanic plankton communities (Parsons, 1969; Quiñones, 1992; Piontkovski and Van-de-Spoel, 1998). However, as Ruiz (1994) showed, a problem emerges when measuring size diversity, because we need to divide a continuum variable into an arbitrarily selected number of size classes. As a result, we have different size diversities for the same community depending on the number of size class intervals that we choose.

In order to overcome these problems, Lurie and Wagensberg (1983, 1984) proposed a measure of size diversity index appropriate for continuous variables ( $\mu$ ) based on the function of probability density of individuals with respect to size. However, Ruiz (1994) pointed out the difficulties of describing natural size distributions by means of a simple function. Therefore, he proposed a modification of this index to apply to normalized size spectrum. This index ( $\mu_p$ ) has been used for the plankton community in Mediterranean coastal waters and it was found to be sensitive to natural fluctuations. Nevertheless, Pareto distribution is based on a probability density function so it could be used to calculate size diversity in a simple way using the size diversity index of Lurie and Wagensberg (1983, 1984).

When studying species diversity, it has been proposed that it depends on the variation in the intensity of competition, predation and/or disturbance (Paine, 1966; Connell, 1978). The intermediate disturbance hypothesis has been suggested as an explanation of high diversity in environments with moderate rate of disturbances (Connell, 1978). If disturbances are rare, the community will progress towards

equilibrium with low diversity due to the elimination of the inferior competitors. Here, the diversity will depend on the patterns in resource partitioning that biotic interactions produce, which determine the coexistence and hence the observed species diversity (Richerson and Lum, 1980). However, it seems likely that in a situation of competitive exclusion resource partitioning between different sizes of a single species might exist so size diversity would also be indicative of resource partitioning. Accordingly, copepods have development stages with a wide range of sizes and it has been shown that selective feeding in nature might vary in those species among naupliar, copepodite and adult stages (Swadling and Marcus, 1994). Thus, niche differentiation among different sizes would determine the size diversity observed and it would be especially suitable to evaluate in situations of competitive exclusion.

The objectives of this study are (1) to test the use of Pareto distribution as a new method to compute size diversity, thus avoiding the previous classification in size classes, (2) to evaluate if size diversity, as an alternative to species diversity, is useful to describe the degree of structure of the zooplankton community of Empordà Wetlands and (3) to analyse the behaviour of size diversity in situations of competitive exclusion.

## 6.2. CALCULATION OF A SIZE DIVERSITY INDEX BY MEANS OF PARETO MODEL

The size diversity index ( $\mu$ ) proposed by Lurie and Wagensberg (1983, 1984) is based on a probability density function of individuals with respect to size ( $s$ ):

$$\mathbf{m} = - \int_{s_i}^{s_{i+1}} p_i(s) \lg_2 p_i(s) ds$$

Since Pareto distribution is based on a probability density function given by the following equation

$$pdf(s) = c(K + D)^c (s + D)^{-(c+1)}$$

we propose to use this function to calculate size diversity.

The size of each organism ( $s$ ) was standardised by dividing it by the minimum size of each sample ( $s_{min}$ ) (Winiwarter and Cempel, 1992):

$$s' = s/s_{min}$$

In this case comparisons between spectra are possible and  $\mu_s$  is independent from the units in which size is expressed.

To calculate this size diversity index, we assume that Pareto distribution adequately represents the size distribution of particles and we integrate the first equation after substituting  $pdf(s')$  (appendix 3). The resulting equation is:

$$\mathbf{m}_{s'} = - \left[ \log_2 e (K + D)^c (s' + D)^{-c} \left[ \ln [c(K + D)^c] - (c + 1) \left[ \ln (s' + D) + \frac{1}{c} \right] \right] \right]_{s'_{min}}^{s'_{max}}$$

since  $s'_{min} = 1$  then  $K = 1$  and

$$\mathbf{m}_{s'} = \left[ \log_2 e \left[ \ln [c(1 + D)^c] - (c + 1) \left[ \ln (1 + D) + \frac{1}{c} \right] \right] \right] - \left[ \log_2 e (1 + D)^c (s'_{max} + D)^{-c} \left[ \ln [c(1 + D)^c] - (c + 1) \left[ \ln (s'_{max} + D) + \frac{1}{c} \right] \right] \right]$$

Size diversity was only measured in these spectra with high fit to Pareto model ( $r^2_I$  or  $r^2_{II}$  higher than 0.9).

The advantages of this index is that it avoids choosing sizes classes and it is easy to calculate. In comparison with the index proposed by Ruiz (1994),  $\mu_s$  avoids the successive steps of transforming each size class of the biomass size spectrum into different functions of probability density.

For comparisons with size diversity ( $\mu_s$ ) two different diversities using Shannon Index (abundance measured as number of individuals) were calculated: the first one using species as units ( $H$ ) and the second one using size classes (logarithm base 2) as units (size class diversity).

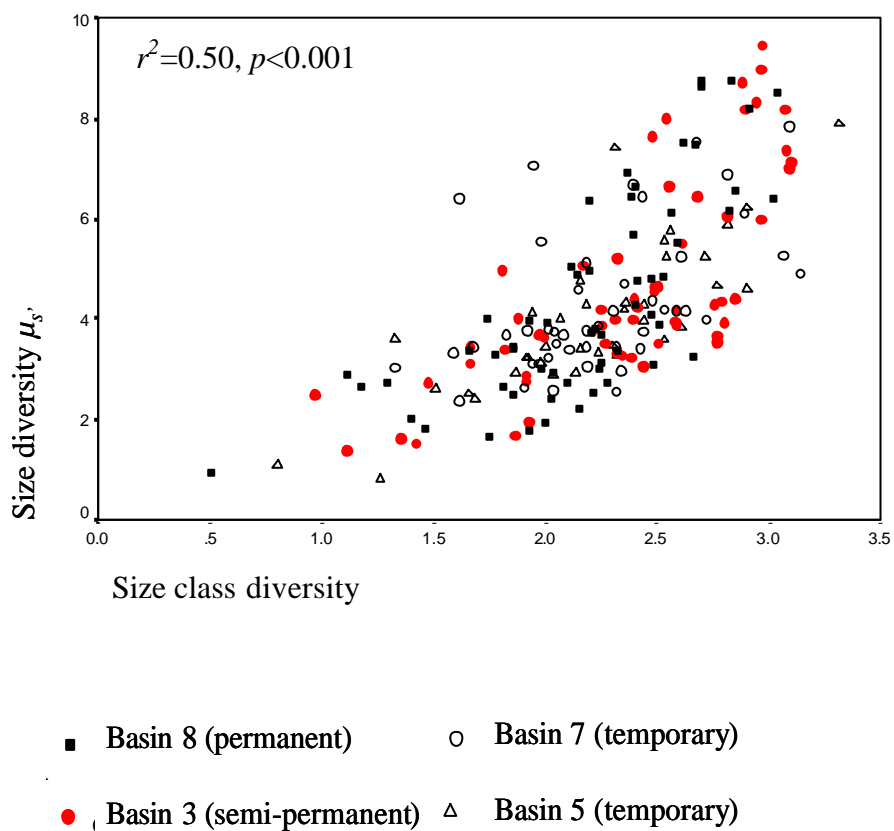


### 6.3. RESULTS

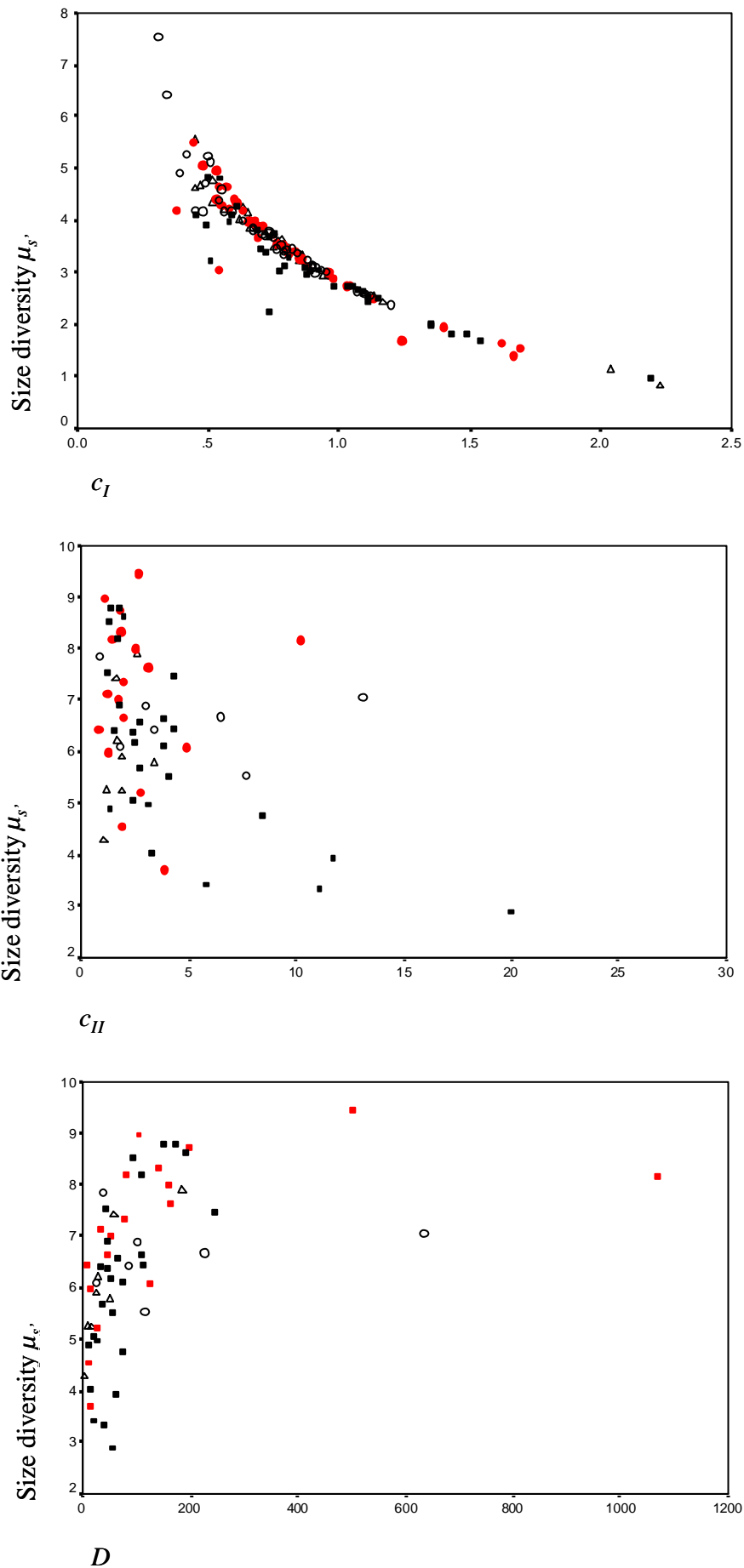
A significantly positive relationship was found between size class diversity and  $\mu_s$  ( $p < 0.001$ ,  $r^2 = 0.5$ ) indicating that the two methods used to calculate size diversity (see chapter 3.4) obtained similar results (figure 6.1).

Samples whose spectrum fit PII model better (curved shape spectrum) had higher  $\mu_s$  than samples whose spectrum fit PI model better (linear shape spectrum) (Kruskal-Wallis test,  $p < 0.001$ ). When the relationship between  $\mu_s$  and the spectrum parameters was analysed (figure 6.2 and table 6.1),  $c_I$  was found to be a good predictor of  $\mu_s$  in linear spectrum's samples ( $c_I$  is negatively correlated with  $\mu_s$ ) whereas  $c_{II}$  and  $D$  separately had a weak correlation with  $\mu_s$  in curved spectrum's samples. However,  $\mu_s$  could be correctly predicted with both  $c_{II}$  and  $D$  following equation in table 6.1.

**Figure 6.1.** Relationship between size class diversity and  $\mu_s$ .



**Figure 6.2.** Relationship between size diversity ( $\mu_s$ ) and parameters  $c_I$ ,  $c_{II}$  and  $D$  (see methods 3.3). Symbols as in figure 6.1.



**Table 6.1.** Regression between size diversity ( $\mu_{s'}$ ) and parameters  $c_I$ ,  $c_{II}$  and  $D$  (see methods 3.3).

		$\mu_{s'}$	$r^2$	$p$
<b>Pareto I</b>	$c_I$	2.81-2.63 $\ln c_I$	0.90	<0.001
<b>Pareto II</b>	$c_{II}$	7.35-0.94 $\ln c_{II}$	0.18	<0.001
	$D$	2.74+0.92 $\ln D$	0.43	<0.001
	$c_{II}$ & $D$	2.64+1.37 $\ln D$ -1.82 $\ln c_{II}$	0.99	<0.001

When comparing diversities among permanent and temporary basins,  $H$  was higher in the permanent (table 6.2). In contrast, there were no significant differences between  $\mu_{s'}$  of permanent and temporary basins.

**Table 6.2.** Mean of Shannon diversity ( $H$ ) and size diversity ( $\mu_{s'}$ ) with standard deviation in brackets in temporary and permanent basins.

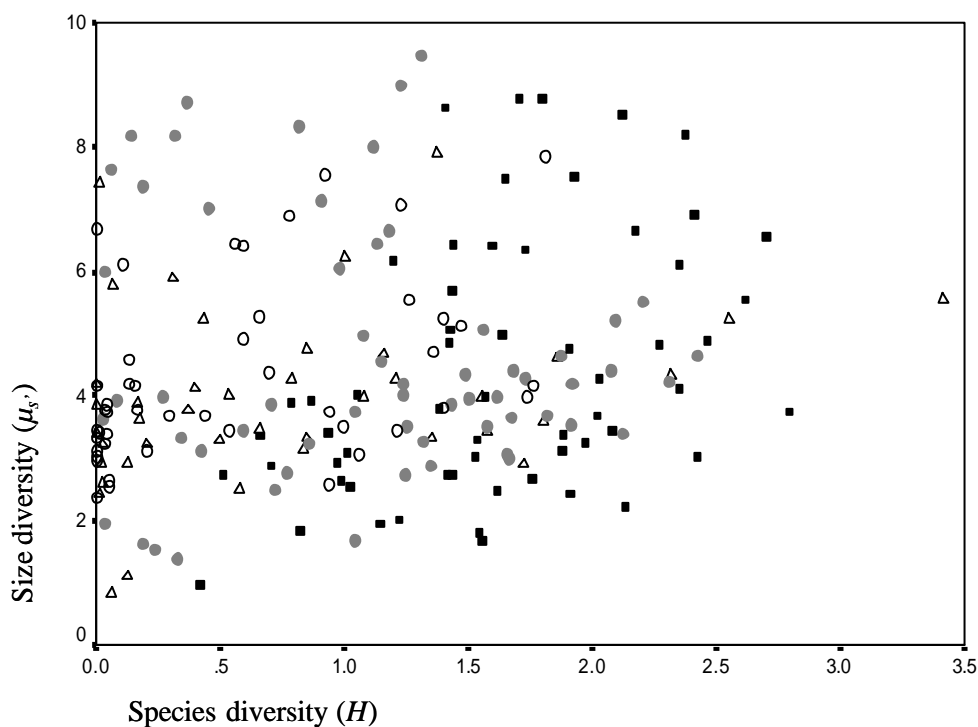
	<b>Permanent basins</b>	<b>Temporary basins</b>	$p$ Kruskal-Wallis test
<b>Species diversity (<math>H</math>)</b>	1.6 (0.6)	0.8 (0.7)	<0.001
<b>Size diversity (<math>\mu_{s'}</math>)</b>	4.3 (2.0)	4.3 (1.7)	n.s.

Figure 6.3 shows the relationship between  $\mu_{s'}$  and  $H$ . From here on I will refer to this representation as  $H$ - $\mu_{s'}$  plane. Although there was a significant correlation ( $p < 0.001$ ) between  $\mu_{s'}$  and  $H$ , the relationship was poor ( $r^2 = 0.06$ ). Furthermore, this relationship between both diversities was different in permanent and temporary basins (figure 6.4). While in the permanent basin a correlation between  $\mu_{s'}$  and  $H$  exists (Pearson correlation  $r^2 = 0.40$ ,  $p < 0.01$ ), it does not exist in temporary basins. In temporary basins situations with high  $H$  and  $\mu_{s'}$  were rare, but situations where  $\mu_{s'}$  was high and  $H$  was low were more frequent. In contrast, in the permanent basin the first situation did exist but the situation of high  $\mu_{s'}$  and low  $H$  lacked.

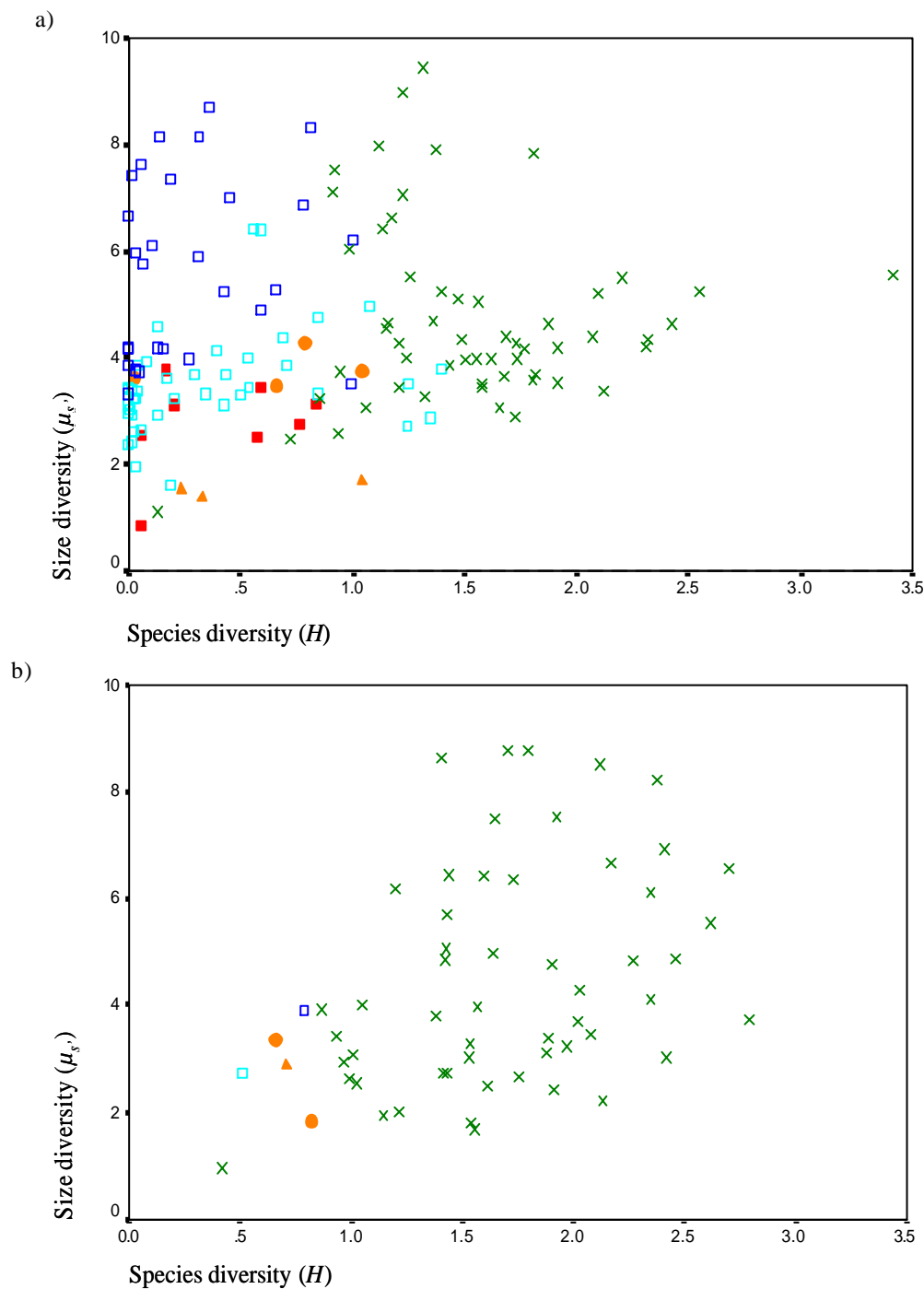
High  $\mu_s$ , coinciding with low  $H$  values in temporary basins (figure 6.4a) were mainly achieved in situations where calanoids dominated the community (more than 80%). Calanoid situation has been defined by Quintana *et al.*, 1998b as a situation of hydric stability without inputs of water and nutrients (see chapters 3.2 and 5.2.1). Oppositely, when any other species dominated the community in these temporary basins  $\mu_s$  was low. This dominance of other species corresponded to situations not persistent in time (Quintana *et al.*, 1998b), such as those dominated by rotifera or cyclopoids, or situations dominated by benthic species such as harpacticoids.  $\mu_s$  was also frequently low when nauplii of one species of calanoid reached more than 80% of the organisms of the community. However, these situations of nauplii dominance are transitional periods towards a situation where each calanoid stage is represented.

In contrast, in the permanent basin the highest  $\mu_s$  was found when there was also high  $H$  and there was not any situation with dominance of a single species which had high  $\mu_s$  (figure 6.4b). In fact, in very few cases the zooplankton community of the permanent basin was dominated by a single species and all of these situations were characterised by low  $\mu_s$  and low  $H$ .

**Figure 6.3.** Size diversity ( $\mu_s$ ) versus species diversity ( $H$ ),  $H$ - $\mu_s$  plane, in the different basins. Symbols as in figure 6.1.



**Figure 6.4.**  $H$ - $\mu_s$  plane in temporary basins (a) and the permanent basin (b). Symbols represent if there is dominance of a single species (more than 80% of organisms of total individuals).



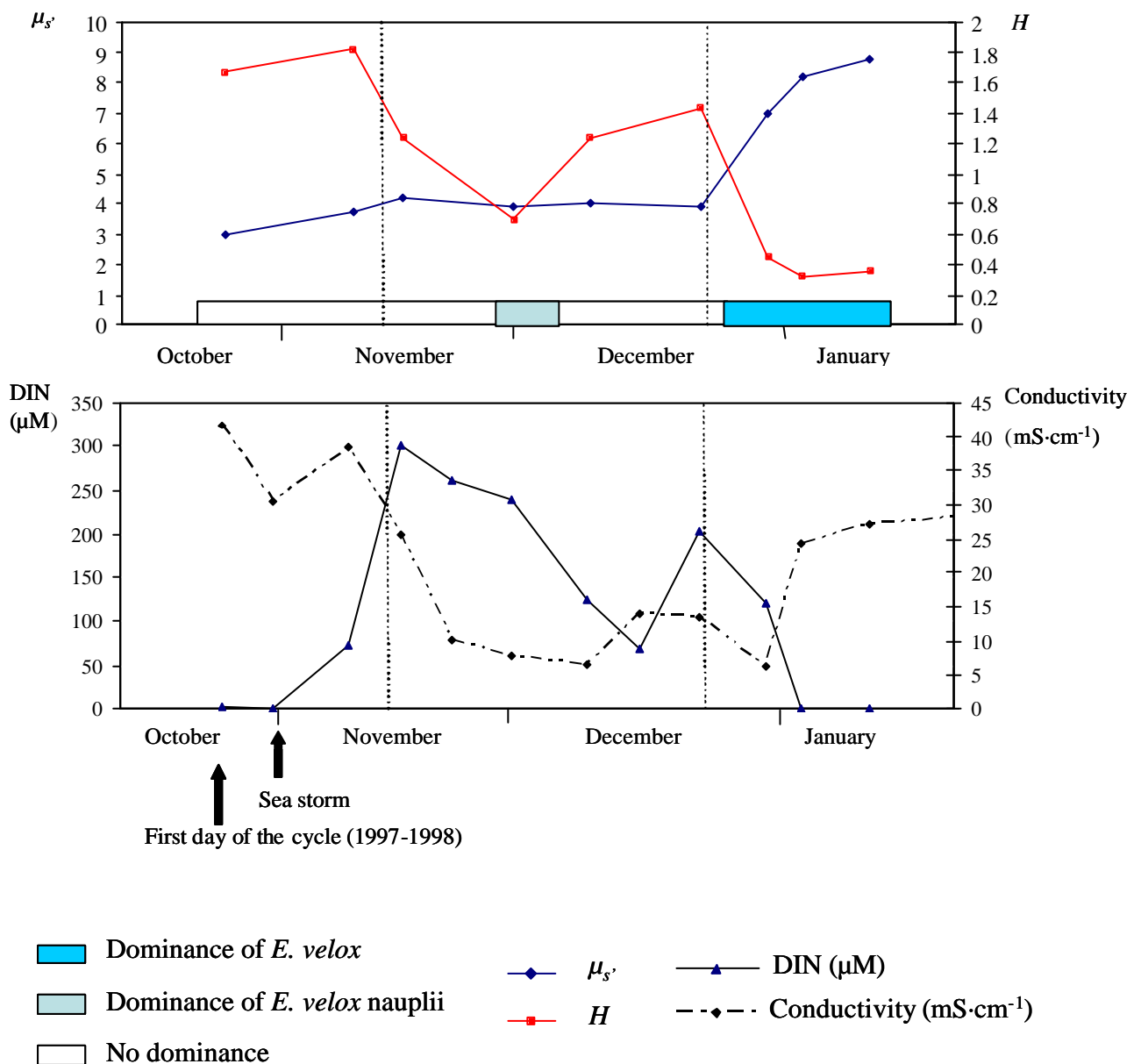
In temporary basins,  $\mu_s$  and  $H$  followed different temporal patterns throughout time as represented in the example of figure 6.5. In this example three environmental situations might be distinguished: a first flooding period of intense disturbances (more than 100% in water level increase), which comprised the filling of the basin and an intense sea storm when water levels reached its maximum and conductivity was high and DIN was low. The second situation corresponded to a low intensity flooding period with few, low and irregular fresh water supplies (less than 50% in water level increase). In these conditions DIN was high and conductivity was low. Finally, during the third period, the basin remained confined without water inputs. This lack of inputs caused an increase in conductivity and a decrease in DIN. When analysing diversities, during the first period of intense disturbances  $H$  was high and so was the species number  $\Theta$ , average species richness), during the second period  $H$  fluctuated and the species number decreased (7, average species richness) and during the third period, when calanoids dominated the community, both  $H$  and the species number (4, average richness) were minimum. In contrast,  $\mu_s$  was low during both flooding periods and increased when the community was dominated by calanoids.

Figure 6.6 shows the trajectories in  $H$ - $\mu_s$  plane observed immediately after several intense disturbances (sea storms or intense rainfalls). Zooplankton community of the different basins responded similarly:  $H$  was low before disturbance and increased after. The effect of the disturbance on  $\mu_s$  was not so clear and more variable among basins and disturbances.

In order to evaluate the behaviour of the diversity measures during stable periods the trajectories over time in the  $H$ - $\mu_s$  plane from the last input of water until it reached a situation of calanoid dominance was represented (figure 6.7). With the water input there was an appearance of new species which favoured an increase in  $H$ . From here on confinement began and the community reached a situation of competitive exclusion with dominance of calanoid species (low  $H$ ) but with high  $\mu_s$ . For different temporary basins similar trajectories were described, however, this trajectory was not found in the permanent basin, since predation did not reach the situation of competitive exclusion of calanoids. Intermediate situations between intense disturbances and stable periods, represented in figure 6.7, blurred these trajectories due to low but irregular inputs of water (i.e. the second period in figure 6.5). When the basin tended to desiccation the low water level sometimes might lead to an increase in species diversity due to the

appearance of some benthic species. Therefore this situation previous to desiccation was excluded of the representations.

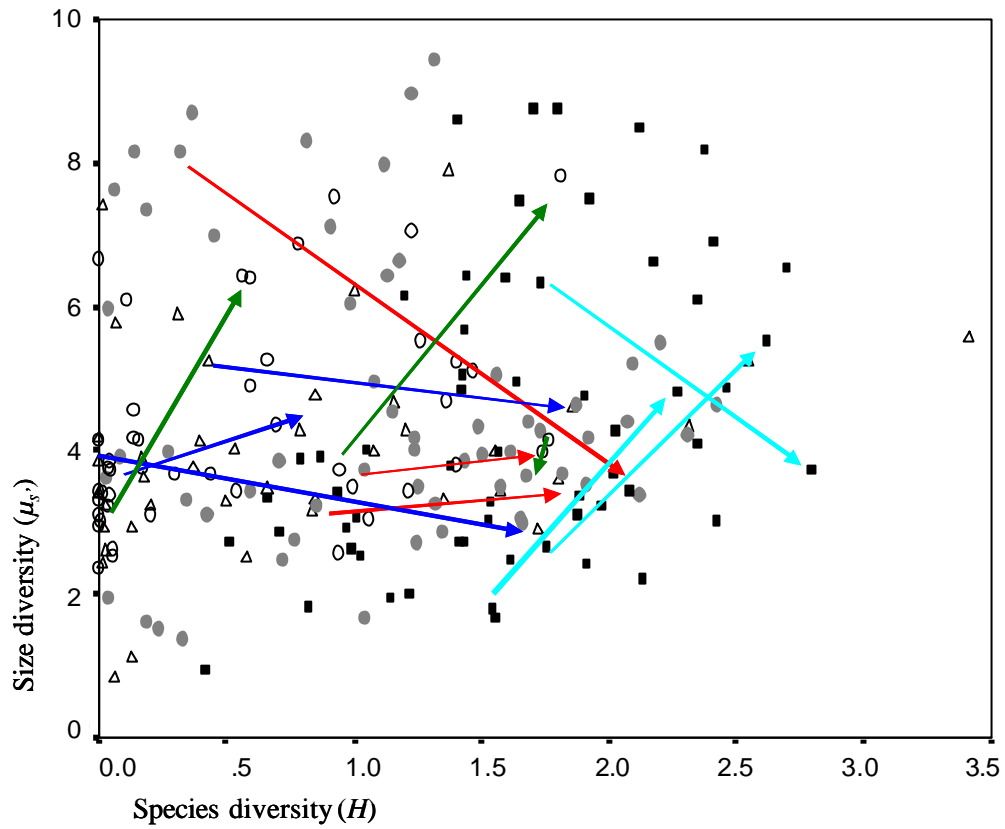
**Figure 6.5.** Above, example of the evolution of  $\mu_s$  and  $H$  throughout time of a temporary waterbody (basin 3). Blue colours represent periods of dominance of calanoids (more than 80 %). Below, evolution of DIN and conductivity for the same cycle. Discontinuous lines separate three periods: the first correspond to a period of intense disturbances (represented with an arrow), the second is a flooding period with low and irregular water inputs and the third is a confinement period without water inputs.





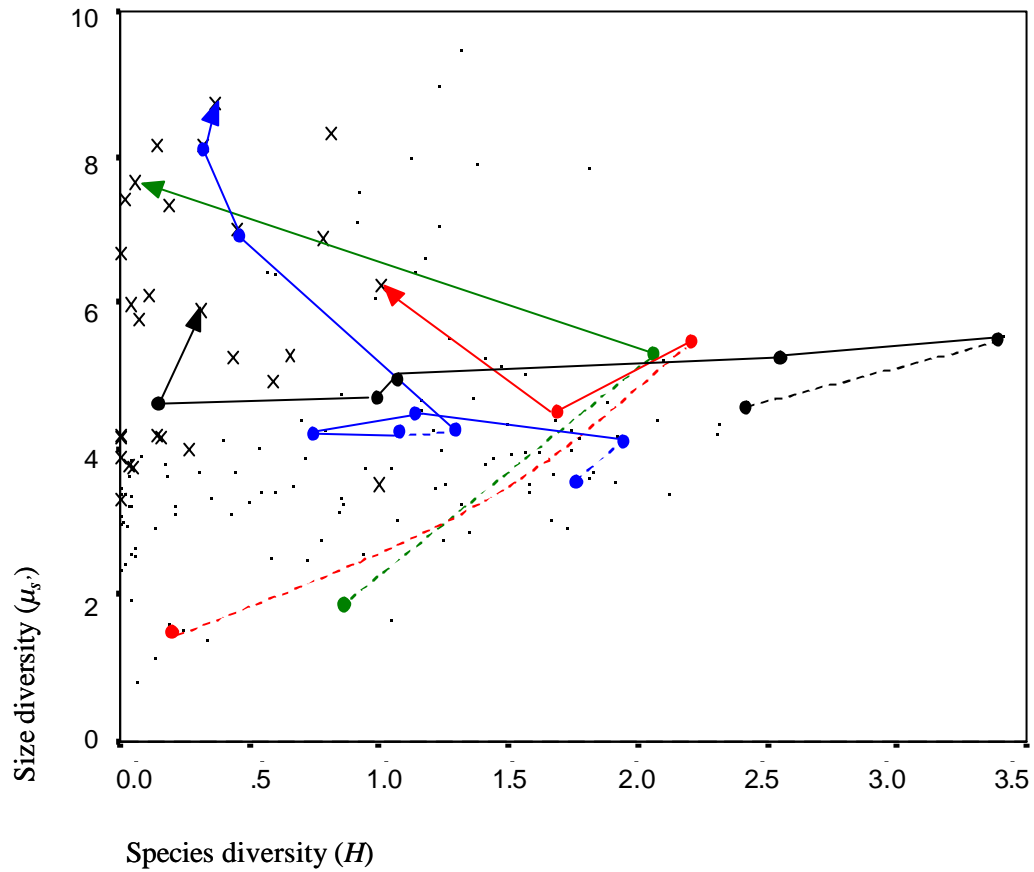


**Figure 6.6.** Effect of different high intensity disturbances (sea storms and intense rainfalls) in the  $H$ - $\mu_s$  plane. Each arrow represents the change of in both diversities before and after the disturbances for each basin. Symbols as in figure 6.1.



- Basin 8 (permanent)
- Basin 7 (temporary)
- Basin 3 (semi-permanent)
- Basin 5 (temporary)

**Figure 6.7.** Trajectories over time in the  $H-\mu_s$  plane from the last input of water until zooplankton community of temporary basins reaches a situation of calanoid dominance during confinement. The example on figure 6.5 corresponds to the blue trajectory. Discontinuous lines indicate the moment of the water input. Calanoid dominance is indicated with a cross and other situations with circles.



## 6.4. DISCUSSION

### 6.4.1. The measurement of size diversity by means of Pareto distribution

Pareto distribution has been found to be a useful tool to calculate size diversity ( $\mu_s$ ) by means of the index proposed by Lurie and Wagensberg (1983, 1984), provided that data follows Pareto distribution. The main advantage of this index is that it avoids the arbitrariness of dividing sizes in different class intervals that would imply different values of size diversity for the same sample or community. Thus, despite the existing relationship between  $\mu_s$  and size class diversity, the use of  $\mu_s$  is more suitable, because it is already known that size class diversity has a high coefficient of variation among different resolutions of the size scale within a particular size range (Ruiz, 1994). Oppositely,  $\mu_s$  is not influenced by changes in size scale resolution.

The weaknesses of  $\mu_s$  are inherent in the use of other size diversity index. The method of sampling determines which is the smallest organism ( $s_{min}$ ) and therefore it has an effect on the value of size diversity. As regards  $s_{max}$  has a little effect on the  $\mu_s$  since the value of the integral of the probability density function tends to 0 when increasing  $s_{max}$ .

The fact that linear spectra (which have higher relative abundance of small sizes, as commented in chapter 4) have in general less  $\mu_s$  than curved spectra coincides with the inverse relation between the slope of the biomass size spectrum and the size diversity index that other authors have reported (Platt and Denman, 1977, 1978; Rodríguez and Mullin, 1986), that is, ecosystems with a greater proportion of small particles have lower size diversity. Indeed,  $\mu_s$  of linear spectra can be directly estimated by the parameter  $c_I$  which is negatively correlated with  $\mu_s$ . In curved spectra,  $\mu_s$  is not directly estimated by  $c_{II}$  but by  $c_{II}$  and  $D$ .

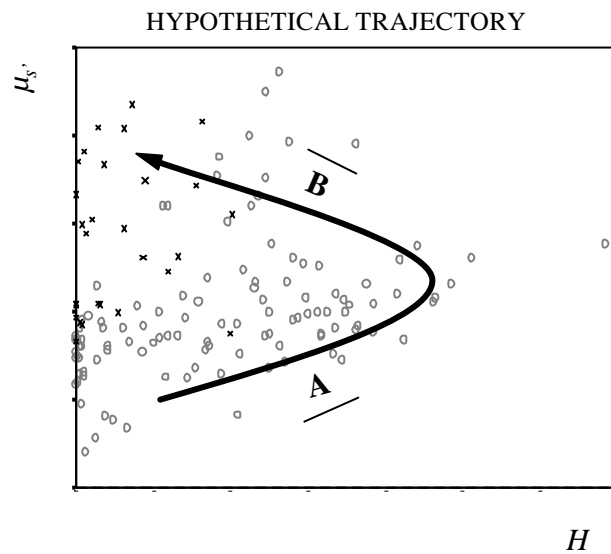
### 6.4.2. Relationship between species diversity and size diversity

There is little information about size diversity, which may be a consequence of the above mentioned problems when calculating it. Several studies deal with size diversity at the physiological level (e.g. Parsons, 1969; Quiñones, 1992). At the ecological level, there are studies dealing with phytoplankton (Ruiz, 1994), zooplankton (Piontkovski

and Van-der-Spoel, 1998) and studies dealing with large herbivores (Oindo *et al.*, 2001). Ruiz (1994) suggested that pulses in the smaller end of the size range yielded a decrease in size diversity, while pulses in the larger end yielded an increase of size diversity corresponding to a flatter spectrum. This fact might be generalised, since the present study also found minimum size diversities when rotifera (in the smaller end of the size range) dominated the community and maximum sizes diversities when calanoid species (in the larger end) dominated. Some of these studies have found positive correlations between size diversity and the conventional indexes of species diversity (Oindo *et al.*, 2001; Piontkovski and van-der-Spoel, 1998). Despite these findings the present results demonstrated that species and size diversity are more complementary than redundant. Differences between them are found in situations of competitive exclusion where low species diversities, but high size diversities are achieved. They also differ when comparing temporary and permanent waterbodies since species diversity is higher in the permanent one, whereas size diversity is similar in temporary and permanent basins. Competitive exclusion takes places in temporary basins when the community is dominated by calanoids and this situation is considered to be the most stable in these basins during periods of inundation (Quintana *et al.*, 1998b). In contrast, in the permanent basins selective predation prevents competitive exclusion in the stability period and probably that fact would explain why species diversity and size diversity were more coincidental. Hence, in a situation of competitive exclusion size diversity and species diversity might give different information, at least as far as the zooplankton community is concerned. Since high species diversities are achieved during fluctuating periods it seems likely that they are a consequence of the colonization by pioneering species during allochthonous water inputs, and not being related to the community structure processes. Water inputs represent an entry of energy and nutrients to the ecosystem which favour growth of different species with low competence between them producing an increase in species diversity. However, as soon as water inputs ceased and the system tends to oligotrophy, in few weeks the community is changed to a situation dominated by calanoids. Thus, high species diversity would be a transitional situation towards a situation of stability characterised by the dominance of one species of calanoid with low species diversity, but high size diversity (figure 6.8). The fact that size diversity is low during first flooding periods and reaches its maximum at the end of the cycle makes it useful to discriminate between different succession stages, whereas species diversity fluctuates during the succession. Indeed, as these

results show, size diversity might be better indicator of the degree of the community structure than species diversity, whose increases are sometimes not due to high community structure.

**Figure 6.8.** Hypothetical trajectory of the community in the  $H-\mu_s$  plane just after the water input until stability period begins and takes place the competitive exclusion. A, water input and appearance of new species and B, confinement and competitive exclusion. Calanoid dominance is indicated with a cross and other situations with circles.



#### 6.4.3. Relationship between size diversity and trophic structure

It has been empirically tested that organisms with higher body mass feed at higher trophic levels (Fry and Quiñones, 1994; France *et al.*, 1998). Indeed, Jennings *et al.* (2002) demonstrated that body mass is a good predictor of the trophic level. Margalef (1991) described size diversity as an ataxonomic diversity and he considered that size diversity helps to understand the past of the community, its organization and how it works. Furthermore, Aoki and Mizushima (2001) found a positive relationship between trophic diversity and food web stability.

As the present results have shown, in temporary basins of Empordà Wetlands the zooplankton community tends towards a situation of competitive exclusion dominated by calanoids and characterised by high size diversity. In these conditions, high size diversity means that all stages of a single species of calanoid are coexisting at the same

time with similar relative abundances and this is only persistent in time if intraspecific competition is weak. Weak intraspecific competition would be achieved if the resource production was abundant enough to maintain the rate of population growth (then population would only be limited by the effects of high population density), if differential predation over adults exists or if trophic niche partitioning among stages takes place. Predation is negligible in temporary basins (Wellborn *et al.*, 1996) and calanoids dominate the community during periods of relatively oligotrophy with hydric stability (see chapter 4, 5 and Quintana *et al.*, 1998b). In accordance to this, trophic niche partitioning has been reported in calanoids so as to reduce intraspecific feeding competition between juveniles and adults (Maly and Maly, 1974; Poulet, 1977; Zánkai, 1991; Bodgan and Gilbert, 1987; Hansen *et al.*, 1994). The possible existence of intraspecific trophic niche partitioning in calanoids is discussed in chapter 7. Hence, size diversity would give us additional information about trophic niche partitioning of the community, which is not detectable with species diversity and suggests that, in a situation of competitive exclusion, at least some zooplankton species have this trophic niche partitioning among different stages of the same species.

## 7.1. INTRODUCTION

Spatial and temporal changes in the abundance of zooplankton species are mainly controlled by abiotic factors. Water turnover rate, temperature, salinity and nutrient concentration were described as the principal factors affecting zooplankton distribution (Ambrogi *et al.*, 1989; Bamber *et al.*, 1992; Oltra and Miracle, 1992; Gulati *et al.*, 1992; Van Tongeren *et al.*, 1992; Quintana *et al.*, 1998b; Gifre *et al.*, 2002).

Among the biotic factors, predation has often been cited as the most relevant factor in determining the assemblages of zooplankton (Allan, 1973; Dodson, 1974; Arnott and Vanni, 1993). Exploitative competition may be also present in some habitats, because species often face food limitation (Threlkeld, 1976; Tessier and Goulden, 1982; Gliwicz, 1985; Duncan, 1989; Müller-Navarra and Lampert, 1996; Hansen and Hairston 1998; Guisande *et al.*, 2003). However, due to the obvious difficulties in performing field observations of food use, evidence of interspecific exploitative competition usually has relied on the co-occurrence (or lack of it) of species assigned to functional groups or guilds based solely on systematic.

Amino acid composition of zooplankton species has become an important tool to study food resource partitioning in zooplankton communities, because differences in the amino acid composition among zooplankton species indicate distinct food sources (Guisande *et al.*, 2002). In a study carried out in a food-limited environment in Pyrenean mountain lakes, it has been shown that there was a negative relationship between amino acid differentiation and co-occurrence among the cladocera and cyclopoid copepod. This negative relationship is indicative that interspecific exploitative competition, either at present or in the past by driving co-evolutionary histories, has been a significant factor in structuring the cladocera and cyclopoid communities in these oligotrophic lakes (Guisande *et al.*, 2003).

From the above, it is clear that depending on the habitat conditions, abiotic factors, predation and/or interspecific competition may play an important role in structuring zooplankton communities. However, as far we know, nothing has been shown about intraspecific competition.

In the zooplankton there are taxonomic groups with different developmental stages (copepods), but other species are without stage differentiation over their life cycles (cladocerans). It has been shown in copepods that selective feeding in nature

varied among naupliar, copepodite and adult stages (Swadling and Marcus, 1994). If this is so, in those species with different developmental stages there might be a trophic-niche differentiation and, hence, intraspecific competition pressure should be lower than in those species without different developmental stages. If intraspecific competition is important, those species without developmental stages should inhabit habitats with a higher amount of food resources to outweigh the loss of fitness caused by intraspecific competition.

Empordà Wetlands can be regarded as representative of Mediterranean coastal wetlands and they show a great environmental variation over short scales of time and space. This fact provides the suitable ecological conditions to develop the three most characteristic and abundant groups of zooplankton in continental waters and that have similar sizes: calanoids, cyclopoids and cladocera. Furthermore, zooplankton communities of these basins tend to be monospecific in numerous occasions, which makes them an especially suitable site for investigations dealing with intraspecific competition (see figure 2.1 and methods 3.5 for location and sampling, respectively).

The aims of this study were (1) to assess if there is food niche partitioning as a function of the organism's size or stage at intraspecific level and, (2) if this food niche partitioning exists, to determine whether those species with different development stages dominate in habitats with low amount of food resources and, vice versa.



## 7.2. RESULTS

### 7.2.1. Global differences in amino acid composition

Amino acid composition (AAC) for each species and stages are shown in table 7.1. A discriminant analyses performed to these amino acid data (see methods 3.5) showed that 45.9% of the cases were correctly classified (figure 7.1). There were differences in the AAC among species, but also among stages within each species.

The first and the second components of the global discriminant analysis explained 49.8% and 27.4% of the amino acid variance, respectively (table 7.2). Among calanoids, *Eurytemora velox* is located with daphnids and *Calanipeda aquae-dulcis* with cyclopoids. Daphnids and *E. velox* mainly differ from cyclopoids and *C. aquae-dulcis* in the proportion of serine (higher in the former) and glutamic acid (higher in the latter) (table 7.1). The different development stages of copepod species are situated in order from naupli to adults in the second component of the discriminant analysis. Tyrosine, valine and alanine have positive coordinate in this second axis, indicating that copepods tend to increase gradually the proportion of these amino acids during development. However, there were no important differences among the different stages of daphnids (figure 7.1).

### 7.2.2. Intraspecific variation of amino acid composition

Discriminant analysis has been performed for each species separately (figure 7.2). In this case, variability caused by phylogenetic differences is avoided, since all units in the analysis belong to the same species.

Results from the discriminant analysis for each species also differ between copepods and daphnids (figure 7.2). For the 4 species of copepods, the different development stages appear ordered in the first dimension, whilst adults and nauplii are closer in the second dimension arising a V-shaped distribution pattern. Calanoids have the highest percentage of stages correctly classified (75% *E. velox* and 72.7% *C. aquae-dulcis*) indicating a high amino acid differentiation between stages and hence, a low stage overlap. Cyclopoids have a lower amino acid differentiation (68.4 % and 42.5 of

**Table 7.1.** Amino acid composition (mean  $\pm$  SD weight percentage of total amino acids yield) of different species collected and their respective stages. ASP-aspartic acid; SER-serine; GLU-glutamic acid; GLY-glycine; HIS-histidine; ARG-arginine; THR-threonine; ALA-alanine; PRO-proline; TYR-tyrosine; VAL-valine; LYS-lysine; ILE-isoleucine; LEU-leucine; PHE-phenylalanine.

	<i>Eurytemora velox</i>				<i>Calanipeda aquae-dulcis</i>				<i>Acanthocyclops robustus</i>				<i>Diacyclops bicuspidatus odessanus</i>			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
ASP	10.5 $\pm$ 0.9	10.4 $\pm$ 0.5	11.1 $\pm$ 0.4	11.4 $\pm$ 0.4	10.3 $\pm$ 0.5	10.8 $\pm$ 0.5	11.2 $\pm$ 0.5	10.9 $\pm$ 0.8	10.8 $\pm$ 0.5	10.7 $\pm$ 1.2	11.2 $\pm$ 1.0	10.7 $\pm$ 0.4	10.7 $\pm$ 0.8	10.4 $\pm$ 0.3	10.6 $\pm$ 0.5	10.8 $\pm$ 0.7
SER	6.7 $\pm$ 1.5	6.0 $\pm$ 0.5	5.7 $\pm$ 0.2	5.6 $\pm$ 0.7	4.9 $\pm$ 0.7	4.7 $\pm$ 0.3	4.7 $\pm$ 0.3	4.7 $\pm$ 0.3	5.5 $\pm$ 1.5	4.9 $\pm$ 0.8	4.4 $\pm$ 0.6	4.3 $\pm$ 0.8	4.4 $\pm$ 0.9	4.5 $\pm$ 0.4	4.7 $\pm$ 0.5	4.4 $\pm$ 0.3
GLU	13.6 $\pm$ 1.2	12.9 $\pm$ 0.9	13.4 $\pm$ 0.4	14.4 $\pm$ 0.5	14.1 $\pm$ 0.7	15.0 $\pm$ 0.5	15.6 $\pm$ 0.6	15.4 $\pm$ 0.5	15.3 $\pm$ 0.8	15.7 $\pm$ 0.9	16.0 $\pm$ 1.0	16.1 $\pm$ 0.6	14.6 $\pm$ 0.5	14.9 $\pm$ 0.3	15.0 $\pm$ 0.9	15.7 $\pm$ 0.7
GLY	7.2 $\pm$ 2.4	6.7 $\pm$ 0.3	6.8 $\pm$ 0.4	6.9 $\pm$ 0.3	7.1 $\pm$ 0.9	6.9 $\pm$ 1.2	6.2 $\pm$ 0.6	6.4 $\pm$ 0.2	7.1 $\pm$ 1.9	6.3 $\pm$ 0.9	5.8 $\pm$ 0.3	6.6 $\pm$ 1.1	5.4 $\pm$ 1.7	6.2 $\pm$ 0.6	7.1 $\pm$ 0.5	6.8 $\pm$ 0.6
HIS	2.4 $\pm$ 0.3	2.5 $\pm$ 0.3	2.6 $\pm$ 0.1	2.6 $\pm$ 0.2	2.2 $\pm$ 0.2	1.8 $\pm$ 1.1	2.4 $\pm$ 0.3	2.5 $\pm$ 0.3	2.5 $\pm$ 0.4	2.1 $\pm$ 0.7	2.3 $\pm$ 0.2	2.5 $\pm$ 0.3	2.2 $\pm$ 0.3	2.5 $\pm$ 0.3	2.5 $\pm$ 0.3	2.4 $\pm$ 0.3
ARG	6.6 $\pm$ 1.1	5.8 $\pm$ 0.7	5.3 $\pm$ 0.6	5.5 $\pm$ 0.6	7.6 $\pm$ 1.1	7.5 $\pm$ 0.4	7.7 $\pm$ 1.0	7.4 $\pm$ 1.3	6.5 $\pm$ 2.2	6.9 $\pm$ 0.9	7.3 $\pm$ 0.7	7.4 $\pm$ 0.6	8.0 $\pm$ 1.3	7.3 $\pm$ 0.5	7.1 $\pm$ 1.2	7.7 $\pm$ 0.9
THR	6.2 $\pm$ 0.7	6.3 $\pm$ 0.5	5.8 $\pm$ 0.3	5.9 $\pm$ 0.4	5.3 $\pm$ 0.4	5.0 $\pm$ 0.4	4.9 $\pm$ 0.4	5.2 $\pm$ 0.4	5.6 $\pm$ 0.7	5.1 $\pm$ 0.5	5.1 $\pm$ 0.4	4.9 $\pm$ 0.4	5.8 $\pm$ 0.6	5.5 $\pm$ 0.4	5.2 $\pm$ 0.4	5.1 $\pm$ 0.3
ALA	8.1 $\pm$ 0.9	9.8 $\pm$ 0.8	9.8 $\pm$ 0.5	9.7 $\pm$ 0.8	8.9 $\pm$ 0.8	8.6 $\pm$ 1.6	8.3 $\pm$ 1.0	8.4 $\pm$ 0.9	8.3 $\pm$ 0.7	9.1 $\pm$ 1.0	9.3 $\pm$ 1.2	9.6 $\pm$ 1.1	9.8 $\pm$ 1.0	9.8 $\pm$ 0.7	9.8 $\pm$ 1.2	9.3 $\pm$ 0.9
PRO	6.1 $\pm$ 1.0	7.5 $\pm$ 0.6	7.2 $\pm$ 0.5	7.2 $\pm$ 0.6	4.4 $\pm$ 1.9	5.1 $\pm$ 0.4	5.2 $\pm$ 0.5	5.2 $\pm$ 0.3	4.9 $\pm$ 1.2	5.1 $\pm$ 1.3	5.5 $\pm$ 0.4	5.8 $\pm$ 0.6	6.6 $\pm$ 1.3	6.1 $\pm$ 0.3	6.4 $\pm$ 1.1	5.9 $\pm$ 0.5
TYR	2.0 $\pm$ 1.0	2.4 $\pm$ 1.0	2.3 $\pm$ 0.8	2.9 $\pm$ 1.0	0.5 $\pm$ 0.5	0.8 $\pm$ 0.7	1.7 $\pm$ 1.0	4.0 $\pm$ 1.3	0.4 $\pm$ 0.5	1.4 $\pm$ 0.9	1.9 $\pm$ 1.3	2.9 $\pm$ 1.4	1.2 $\pm$ 1.7	1.5 $\pm$ 1.0	2.1 $\pm$ 1.7	2.5 $\pm$ 1.4
VAL	5.3 $\pm$ 0.9	6.0 $\pm$ 0.7	6.2 $\pm$ 0.2	5.8 $\pm$ 0.5	5.7 $\pm$ 0.4	5.5 $\pm$ 0.3	5.5 $\pm$ 0.4	5.4 $\pm$ 0.2	5.2 $\pm$ 0.4	5.2 $\pm$ 0.7	5.5 $\pm$ 0.4	5.3 $\pm$ 0.5	5.1 $\pm$ 1.2	5.6 $\pm$ 0.3	5.3 $\pm$ 0.5	5.2 $\pm$ 0.3
LYS	8.1 $\pm$ 1.4	6.8 $\pm$ 0.5	7.1 $\pm$ 0.8	7.4 $\pm$ 0.5	11.7 $\pm$ 1.5	11.8 $\pm$ 1.0	9.9 $\pm$ 0.7	8.5 $\pm$ 1.0	10.8 $\pm$ 2.7	10.7 $\pm$ 1.7	9.6 $\pm$ 0.8	8.3 $\pm$ 1.0	9.1 $\pm$ 1.6	8.6 $\pm$ 0.7	8.2 $\pm$ 1.2	8.8 $\pm$ 0.8
ILE	5.0 $\pm$ 1.0	4.9 $\pm$ 0.8	5.2 $\pm$ 0.8	4.6 $\pm$ 0.6	5.1 $\pm$ 0.4	5.0 $\pm$ 0.2	5.2 $\pm$ 0.8	4.9 $\pm$ 0.3	5.1 $\pm$ 0.6	5.0 $\pm$ 0.8	5.0 $\pm$ 0.5	4.9 $\pm$ 0.7	4.9 $\pm$ 1.7	5.3 $\pm$ 0.4	5.2 $\pm$ 1.4	4.7 $\pm$ 0.4
LEU	7.4 $\pm$ 0.6	7.1 $\pm$ 0.3	6.8 $\pm$ 0.3	6.1 $\pm$ 1.3	7.7 $\pm$ 0.6	7.5 $\pm$ 0.2	7.4 $\pm$ 0.2	7.0 $\pm$ 0.5	7.5 $\pm$ 0.3	7.6 $\pm$ 0.6	7.1 $\pm$ 0.4	6.9 $\pm$ 0.3	7.6 $\pm$ 1.1	7.3 $\pm$ 0.4	6.8 $\pm$ 0.4	6.8 $\pm$ 0.4
PHE	4.8 $\pm$ 0.7	4.9 $\pm$ 0.5	4.6 $\pm$ 0.3	4.2 $\pm$ 0.3	4.4 $\pm$ 0.5	4.1 $\pm$ 0.3	4.1 $\pm$ 0.3	4.1 $\pm$ 0.4	4.6 $\pm$ 0.8	4.4 $\pm$ 0.5	4.0 $\pm$ 0.3	3.8 $\pm$ 0.2	4.5 $\pm$ 1.1	4.5 $\pm$ 0.2	4.1 $\pm$ 0.3	3.9 $\pm$ 0.2

Table 7.1. continued.

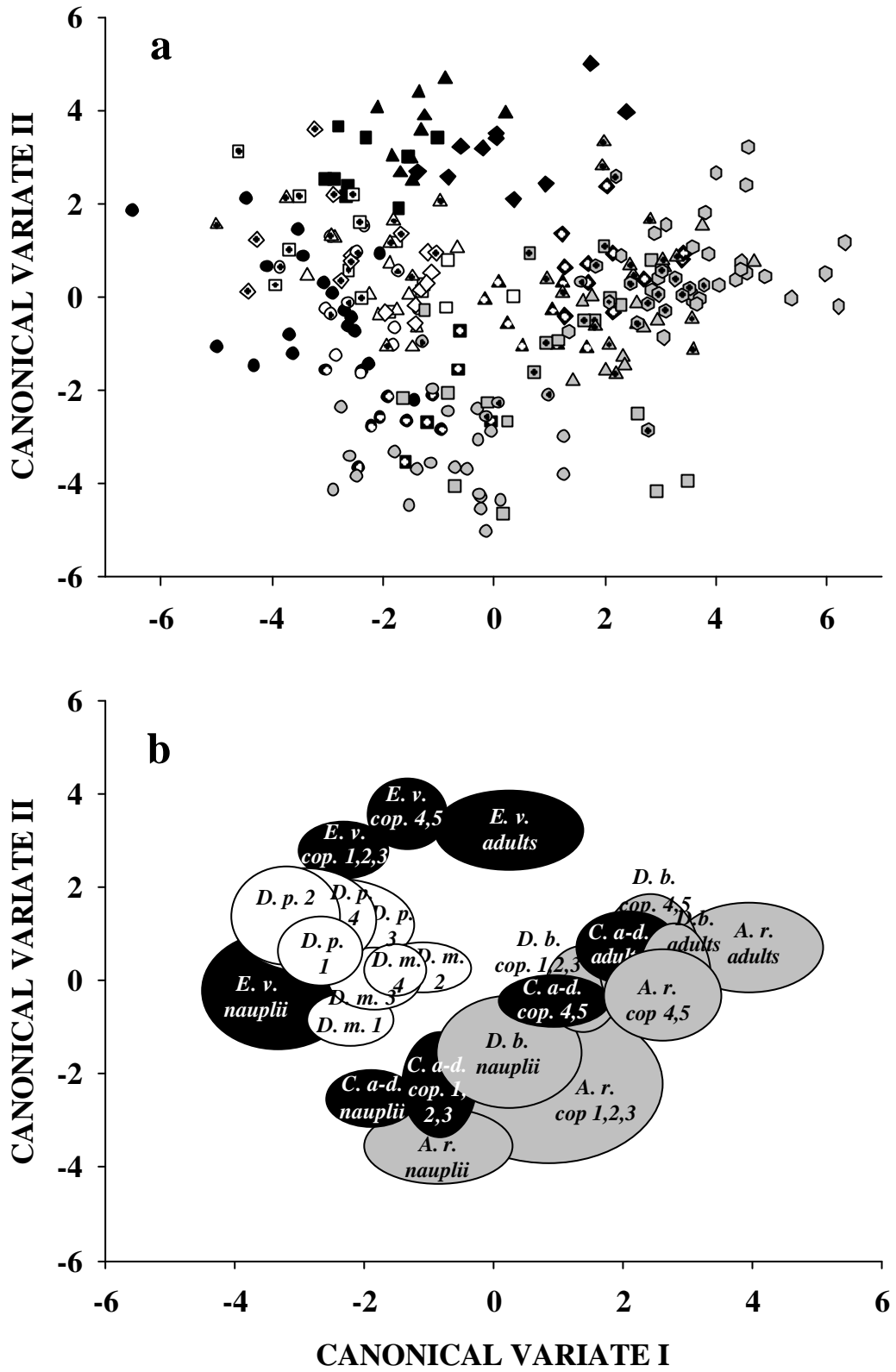
	<i>Daphnia magna</i>				<i>Daphnia pulex</i>			
	1	2	3	4	1	2	3	4
ASP	11.3±0.4	11.2±0.4	11.6±0.5	11.4±0.4	11.4±0.5	11.8±0.7	11.4±0.5	11.3±0.7
SER	5.6±0.8	5.2±0.2	5.6±0.5	5.3±0.4	5.7±0.4	5.9±0.4	6.0±0.6	6.2±0.8
GLU	14.6±0.3	14.8±0.4	14.6±0.4	14.1±0.7	14.0±0.6	14.1±0.5	14.0±0.5	13.8±0.8
GLY	6.4±0.7	6.3±0.4	6.2±0.5	6.0±0.1	6.3±0.5	6.3±0.9	6.6±0.8	6.6±0.9
HIS	2.0±0.2	2.1±0.3	2.1±0.3	2.1±0.1	2.2±0.2	1.9±0.5	2.3±0.4	2.1±0.4
ARG	7.0±0.4	7.6±0.3	7.1±0.4	7.8±0.5	6.7±0.5	6.4±0.8	6.3±0.9	6.5±1.1
THR	5.6±0.3	5.4±0.3	5.8±0.4	5.8±0.3	6.1±0.2	6.1±0.5	5.9±0.7	6.2±0.4
ALA	7.8±0.4	7.6±0.4	7.9±0.5	7.7±1.1	8.0±0.3	8.0±0.6	8.1±0.5	8.2±0.7
PRO	5.8±0.4	5.5±0.3	5.9±0.5	5.9±0.6	6.0±0.5	6.1±0.6	6.1±0.8	6.4±0.8
TYR	2.1±0.5	2.7±1.0	2.7±1.1	4.1±0.7	2.8±1.0	2.3±0.9	2.9±0.8	3.2±0.7
VAL	5.3±0.7	5.6±0.2	5.3±0.6	5.0±0.5	5.6±0.4	5.8±0.4	5.6±0.3	5.4±0.6
LYS	10.2±0.9	9.2±0.7	9.3±0.8	9.2±0.6	8.6±0.4	8.1±1.2	8.4±1.0	8.2±0.7
ILE	4.7±0.8	4.9±0.3	4.5±0.8	4.4±0.6	4.7±0.6	5.0±0.5	4.6±0.4	4.4±0.8
LEU	7.3±0.3	7.4±0.3	7.1±0.5	6.8±0.5	7.3±0.2	7.4±0.2	7.3±0.4	6.9±0.4
PHE	4.3±0.3	4.4±0.2	4.3±0.5	4.4±0.3	4.5±0.2	4.7±0.4	4.6±0.2	4.4±0.4

Table 7.2. Standardized canonical coefficients for the first two principal components of the discriminant analyses performed on the amino acid data. Acronyms as in table 7.1.

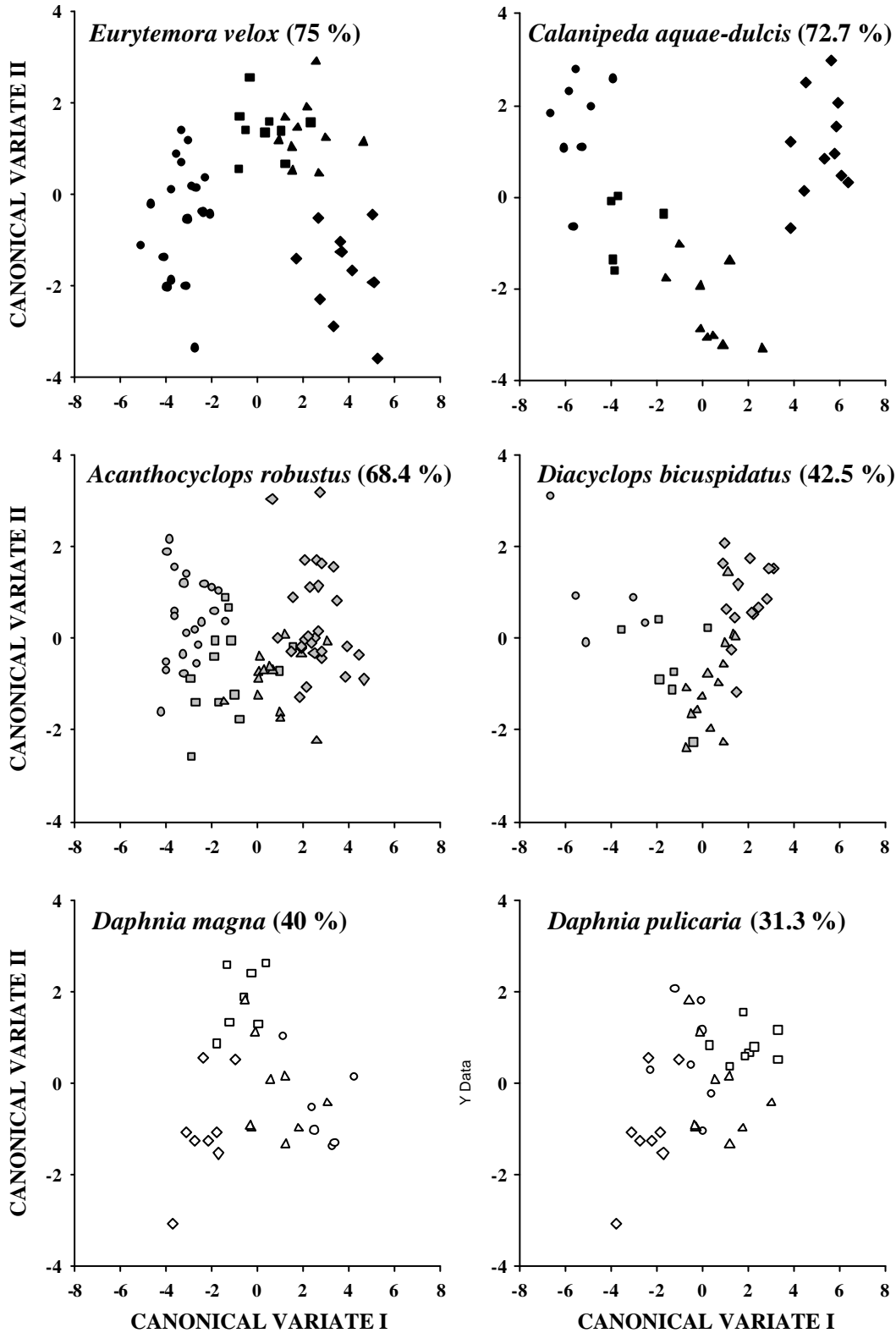
	FUNCTION	FUNCTION
	1	2
GLU	0.89	0.29
ALA	0.47	0.93
ILE	0.43	0.55
TYR	0.47	1.32
GLY	0.22	0.67
HIS	0.32	0.26
ARG	-0.06	0.90
PRO	0.08	0.87
VAL	-0.32	1.54
LEU	-0.18	0.11
LYS	-0.24	0.30
THR	-0.22	-0.11
ASP	-0.27	0.84
SER	-0.82	1.07

stages correctly classified for *Acanthocyclops robustus* and *Diacyclops bicuspidatus odessanus*, respectively), but the V-shaped distribution pattern is also apparent. However differentiation between stages is not so clear in daphnids and the different development stages do not appear ordered in the first dimension. The percentage of stages correctly classified is low (40% *D. magna* and 31.3% *D. pulicaria*), indicating a higher overlap between the different range sizes.

**Figure 7.1.** Next page, plots of (a) the two discriminant function scores for the amino acid composition of the zooplankton species and (b) the mean  $\pm$  SD of the scores. Calanoids (black symbols), cyclopoids (shaded symbols) and daphnids (open symbols). *Eurytemora velox* (*E. v.*, symbols without plus), *Calanipeda aquaedulcis* (*C. a-d.*, symbols with plus), *Diacyclops bicuspidatus odessanus* (*D. b.*, symbols with plus), *Acanthocyclops robustus* (*A. r.*, symbols without plus), *Daphnia pulicaria* (*D. p.*, symbols with plus) and *Daphnia magna* (*D. m.*, symbols without plus). Stages described in material and methods: stage 1 (circle), stage 2 (square), stage 3 (triangle) and stage 4 (diamond).



**Figure 7.2.** Plots of the first two discriminant function scores for amino acid composition obtained for each species. The percentage of stages correctly classified for each species obtained from the discriminant analysis is also shown. Symbols for the stages as mentioned in Figure 1.



### 7.2.3. Trophic state of the lagoons and stage overlap of the dominant species

In order to assess the possible relationship between the degree of stage overlap of a given species and the nutrient content where this species dominates, data of a more extensive sampling which includes 33 waterbodies was used (see chapter 3.1.3 and table 2.2). In this sampling species density and nutrient composition were simultaneously measured and samples clustered by their dominant species.

Nutrient composition and chlorophyll *a* of waters where each species is dominating was correlated to the percentage of cases correctly classified (overlap among stages) of each species. Correlations for all nutrients were significant and negative (table 7.3), that is, when increasing nutrient composition the percentage of stages correctly classified of the dominant species decrease, but it was not significant for chlorophyll *a*. Nutrients were used to perform a stepwise multiple regression with the percentage of stages correctly classified for each species and two variables were found significant, DIN/TN and SRP (table 7.4). Thus the lower percentage of stages correctly classified (high degree of stage overlap) the higher the ratio DIN/TN and SRP (high nutrient availability) (figure 7.3).

**Table 7.3.** Pearson correlation coefficients between nutrient concentrations in water and percentage of stages correctly classified ( $p < 0.01$ ) for the dominant species.

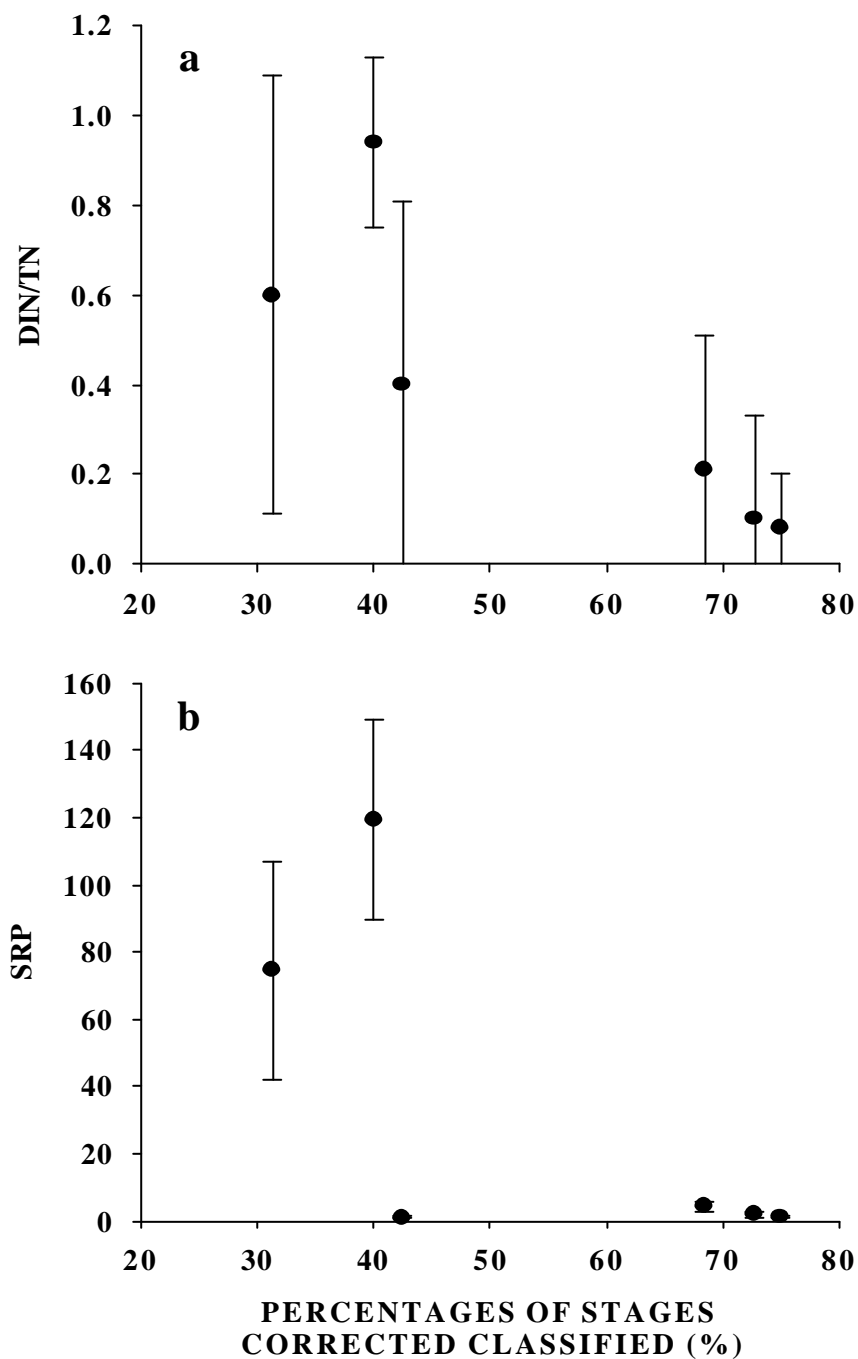
Nitrite	-0.33
Nitrate	-0.39
Ammonia	-0.33
Dissolved inorganic nitrogen (DIN)	-0.44
Total nitrogen (TN)	-0.27
DIN / TN	-0.66
Soluble reactive phosphate (SRP)	-0.57
Total phosphorus (TP)	-0.55
SRP / TP	-0.31
Dissolved organic nitrogen (DON)	0.37
Particulate phosphorus (PP)	-0.54
Chlorophyll <i>a</i>	n.s.
Soluble reactive phosphate/particulate phosphorus (SRP/PP)	0.29

**Table 7.4.** Regression coefficients and partial correlations in the multiple regression (stepwise) between the percentage of stages correctly classified and the variables listed in Table 5. Only DIN/TN and PO<sub>4</sub> have significant correlation.

<b>Variables</b>	<b>Partial correlation</b>	<b><i>b</i> (SD)</b>	<b>Sig.</b>	<b><i>r</i><sup>2</sup></b>	<b>Intercept(SD)</b>
<b>DIN/TN</b>	-0.39	-15.3 (3.13)	<0.001		
<b>SRP</b>	-0.34	-0.08 (0.02)	<0.001		
<b>Total regression</b>			<0.001	0.49	67.43 (1.22)



**Figure 7.3.** Shows the mean  $\pm$  2 SE of DIN/TN (a) and SRP (b) with the percentage of stages correctly classified for each species. Two groups are clearly distinguish: Calanoids have low overlap and low DIN/TN and SRP ( $\mu$ M) values and daphnids are in the opposite side with high stage overlap and high DIN/TN and SRP ( $\mu$ M) values. Cyclopoids are in the middle with intermediate stage overlap and intermediate values of DIN/TN but low SRP concentrations.



## 7.3. DISCUSSION

### 7.3.1. Feeding changes during development

AAC of different development stages of copepod species analysed demonstrate gradual changes in biochemical composition of these organisms during ontogeny. Other authors had found that biochemical composition of copepods varies with development. Carrillo *et al.* (1996) showed that the N:P ratio in *Mixodiaptomus laciniatus* declined with increased age. Schulz (1996) found that nauplii of copepod differed in elemental composition from adults, having lower C:P values. In contrast, *D. magna* and *D. pulicaria* have no significant changes in AAC during development. This agrees with the low intraspecific variability in cladocera elemental composition that other authors have found (Berberovic, 1990; Sarnelle, 1992; Sterner, 1993).

Guisande *et al.* (2002 and 2003) found differences in the AAC among adults of zooplankton species. These differences could be due to phylogeny, adaptation to habitats conditions and/or to trophic niche differentiation. In the present study, the intraspecific differences between AAC among different stages in copepods are not due to either phylogeny (in the discriminant analysis is compared the same species) or habitat conditions (for each species all the stages co-occur temporally and spatially) and, therefore, should be related to different diets.

Different studies provided evidences about diet changes during developmental stages of copepods species. For example, differences in the particle size consumed by calanoid copepodites and adults (Maly and Maly, 1974; Poulet, 1977; Zánkai, 1991) or different optimal prey size also in calanoids (Bodgan and Gilbert, 1987; Hansen *et al.*, 1994) as a consequence of morphological differences. Among cyclopoids, nauplii and early copepodites have been found to be more herbivorous, whereas late copepodite stages have a more predatory feeding (McQueen, 1969; Gophen, 1977; Jamieson, 1980). Differences in ingestion rates of rotifers with protection (lorica) between juveniles and adults have also been reported in *A. robustus* (Roche, 1990).

In contrast to copepods, no intraspecific variability in daphnids diet has been described, but a large overlap in the use of resources by adults and juveniles (Boersma, 1995). This could be explained by the fact that *Daphnia* species are non selective

feeders (Bern, 1994). These findings are in agreement with the present results, because the *Daphnia* species studied show a relatively constant AAC during ontogeny.

### **7.3.2. Niche overlap and intraspecific competition**

If intraspecific competition plays an important role in structuring of the zooplankton communities, food niche partitioning between different development stages will be one of the possible mechanisms to avoid. Thus, species whose stages feed on different food resources would be favoured under food limiting conditions, while those that do not have niche partitioning during ontogeny would be restricted to more productive or fluctuant environments, where the early stages would be able to avoid competition with adults. The relationship found between nutrient concentration and the degree of stage overlap of the dominant species seems to support this hypothesis. A high percentage of stages correctly classified, found in the four species of copepods, is indicative of trophic niche partitioning during development which might allow them to reduce feeding competition between adults and juveniles and, hence, to maintain stable populations in food-limited environments. On the other hand, as a consequence of the trophic niche overlap found in both daphnids, juveniles and adults would experience competition, which is expected to regulate their populations, restricting them to habitats or periods with high food availability.

Specifically, DIN/TN and SRP are the variables that better correlate with the stage overlap. It is to be expected that SRP is an indicator of the trophic state since it is usually one of the limiting nutrients and, as a consequence, would determine the productivity of a specific water body. However, nitrogen is often the limiting nutrient in marshes (Gambrell and Patrick, 1978), especially in salt marshes, which are highly affected by denitrification processes (Sullivan and Daiber, 1974; Valiela and Teal, 1974; Quintana *et al.*, 1998a). In Empordà wetlands, DIN concentration is clearly subject to the external entries since nitrogen inputs are mainly in inorganic form. However, with the lack of inputs, DIN disappears and nitrogen accumulates mainly in organic form (Quintana *et al.*, 1998a, Quintana *et al.* 1999, Trobajo *et al.*, 2002). Therefore, the ratio DIN/TN would be an indicator of the entries of nutrients to the basins in these ecosystems. However, temporal variation in food pulses will presumably cause a decrease in the correlations between nutrient concentrations and stage overlap due to the temporal delay in organisms' growth.

Several examples provide evidence that daphnids suffer from intraspecific competition and that they have mechanisms to avoid it (Frank, 1952; Seitz, 1984; Cox *et al.*, 1992; Guisande, 1993; Boersma, 1995; Hu and Tessier, 1995; Burns, 1995; Cáceres, 1998). Intraspecific competition can be a consequence of both low food levels (Tessier *et al.*, 1983; Guisande and Gliwicz, 1992; Burns 1995; Boersma, 1995; Hu and Tessier, 1995) or increasing animal density (Seitz, 1984; Cox *et al.*, 1992; Guisande, 1993; Burns, 1995). For example, it has been observed that when cladocera density increases the offspring clutch size is reduced (Seitz, 1984; Guisande, 1993; Matveev, 1993; Cleuvers *et al.*, 1997), females produce offspring earlier to reduce the risk of food limitation (Guisande, 1993), neonates are bigger in size and with higher dry weights (Guisande 1993; Cleuvers *et al.*, 1997), and they also increase survival capability by increasing lipid reserves (Tessier *et al.*, 1983; Cleuvers *et al.*, 1997). Habitat segregation between juveniles and adults on *Daphnia* species has also been observed (Hu and Tessier, 1995 and references therein).

Opposite to cladocerans, Poulet (1977) already described the existence of partially separated niches between young and adult calanoids, which benefits their populations, since it reduces intraspecific feeding competition and enhance juvenile survival and, hence, recruitment success.

### **7.3.3. Factors affecting the structure of the zooplankton communities**

There was debate about which is the most relevant factor in determining the assemblages of zooplankton. Vulnerability to invertebrate (Blaustein, 1998) and vertebrate predators (Drenner and McComas, 1980; Zaret, 1980; Lazzaro, 1987) were used to explain the relative competitive ability of daphnids and copepods in different habitats.

Interspecific competition has also been reported to play an important role in zooplankton communities structuring. However, there is some controversy about the way it operates. MacNaught (1975) suggested that diaptomid copepods are better adapted to low food concentrations as compared to *Daphnia* due to their higher ingestion rates at low cell concentrations and several field examples support this idea (see Schulze *et al.*, 1995 for references). Additionally, daphnids have higher ingestion rates than calanoids at high food concentrations, and have competitive advantage in nutrient rich environments (MacNaught, 1975; Richman and Dodson, 1983). However,

considering the threshold food concentrations of the species, some authors considered that large species suppress food concentrations to lower levels than small ones (Kreutzer and Lampert, 1999). This may explain why large cladocera depress the density of small zooplankton species (Vanni 1986, Soto and Hurlbert, 1991), and even of large copepods, because of the effect on their nauplii (Gliwicz and Rowan, 1984). Richman and Dodson (1983) proposed a general model that integrates not only food abundance, but also quality of food to explain temporal and zoogeographic dynamics of calanoid copepods and cladocerans, thus explaining the dominance of calanoids in some highly eutrophic conditions. Schulze *et al.* (1995) suggested that the relative abundance of daphnids and calanoids is unlikely to be a simple function of food quantity, because species like *Daphnia* spp. and *Diaptomus* spp. have similarly low food thresholds. They proposed that dominance also depends on temporal variation of resource abundance and they concluded that other factors, such as differences in life histories, foraging selectivity or predation vulnerability affect field distributions of these species.

In conclusion, it seems clear that it is not possible to establish which is the most important factor in structuring the zooplankton assemblages, because it varies among habitats. It has been demonstrated that intraspecific competition is higher in daphnids than in copepods and, the fact that daphnids dominate in habitats with higher nutrient supplies support the hypothesis that, in addition to abiotic factors, interspecific competition and predation, intraspecific competition might be also important in structuring zooplankton communities assemblages.

## 8. GENERAL DISCUSSION

### 8.1. Effect of the fluctuant conditions on the biomass size spectrum

Theoretical models dealing with biomass size distribution have been developed for planktonic systems under equilibrium conditions (Plat and Denman, 1977 and 1978), whereas studies regarding size distribution in fluctuating conditions are scarce.

Curved-shape biomass size spectra, at ecological scaling, have been reported during stable periods as a result of the ecological interactions among zooplankton species (Sprules and Goyke, 1994; Rodríguez, 1994). On the other hand, the present results suggest that under fluctuating environmental conditions, which in our basins are related to nutrient inputs, there are variations in the biomass size spectrum, which changes its shape from curved to linear. Similarly, variable fish predation pressure led to the appearance of linear shapes while several authors reported that constant predation/prey ratios result in curved shapes spectra (Sprules and Goyke, 1994). Hence, it is possible to relate the shape of the biomass size spectrum with the stability of the ecosystem. Therefore, spectra are curved under stable conditions when competitive interactions prevail, but are linear under fluctuant conditions, when spectra depend mainly on allometric relationship between growth (production) and body mass.

Differences between stable and fluctuant conditions may also be observed at physiological scaling. Rodríguez *et al.* (1987) reported changes in the slope of the spectrum in a marine ecosystem following a winter production pulse. Quintana *et al.* (2002) in the temporary basins of Empordà Wetlands describe changes in the shape of the biomass size spectrum (decrease in the fit to the lineal model and variation in the slope) after intense disturbances such as sea storms or freshwater inputs. In contrast, Marquet *et al.* (1990) found no significant changes in the slope between predator-disturbed and undisturbed sites in a benthic intertidal community where predation pressure was constant. Thus when working at both scales, the shape of the biomass size spectra and if it fits to the linear or non-linear models are related to the stability of the ecosystem.

Ecosystem stability also conditions the feeding behaviour of the organisms, at least in ecosystems as Empordà Wetlands where nutrient inputs are pulse-type. Species, such as *Daphnia* species, which might suffer from intraspecific competition due to

trophic overlap in their stages will be restricted to habitats with high food concentration or with frequent food pulses so as to reduce competition between juveniles and adults. In contrast, species with intraspecific trophic niche partitioning will be able to colonise habitats or periods with low resources. In our case, calanoids dominate salt marshes basins during periods of stability (confinement situations) which are characterised by the lack of nutrient inputs.

## **8.2. Differences between permanent and temporary environments**

Permanent and temporary waterbodies of Empordà salt marshes have similar taxonomic composition, but different relative abundance of organisms and temporal patterns. When analysing diversity, they differ in their species diversity, which is bigger in the permanent even though size diversity is similar. In fact, species diversity of the benthic community of these basins is also higher in the permanent basin (Gascón, 2003).

Since the main ecological difference between the permanent basins and the temporary basins studied is the presence of a fish community, we might conclude that fish predation causes a shift in the size distribution of the permanent basins and also influences the temporal pattern of their species present, however, it has no effect on their taxonomic composition. These results are in accordance with other studies dealing with manipulation of fish density which concluded that fish significantly reduced the density of some prey species, but only prey abundance were affected, not species composition (Wellborn *et al.*, 1996 and references therein).

There are few comparisons of the diversity of temporary and permanent waters in the literature and, furthermore, the results are unclear. When species richness is compared, higher species richness in permanent waterbodies is generally recorded (Williams, 1987; Collison *et al.*, 1995,). However, some authors reported higher (Balla and Davis, 1995) or similar (Bazzanti *et al.*, 2000; Boix *et al.*, 2001) species richness in temporary basins than in permanent ones. When species diversity is compared, Bazzanti *et al.* (2000) reported higher diversity of macroinvertebrates in permanent ponds, although differences were not significant. Boix (2000) did not find clear differences between diversity either. Alternately, Galindo *et al.* (1994) explained higher zooplankton diversities found in temporary waters in comparison to permanent waters

as a consequence of greater disturbances in temporary waters, which contributed to the elimination of dominant species and favoured resource partitioning.

Zooplankton of the temporary basins in Empordà salt marshes have a seasonal pattern, which was already described by Quintana *et al.* (1998b), with six situations, which are conditioned to the hydrological cycle and dominated by the following species: *Synchaeta* spp, *D. bicuspidatus*, *E. velox*, *C. aqua-dulcis*, *C. confluens* and *B. plicatilis*. However, fish might also have influenced this seasonal pattern in the permanent basin, because it is more simplified and it has only two situations: *Synchaeta* spp. populations appeared after an intense flooding and persisted nearly all winter and *C. aquae-dulcis* dominated the rest of the year.

The selective hypothesis described by Paine (1966, 1971) explains the maintenance of high local species diversity due to the selective predation on the dominant competitor, which prevents this dominant competitor from monopolizing the major resources (food or space). Presumably, this would be the reason why permanent basins have higher species diversity. Bonsdorff *et al.* (1995) demonstrated that predation and physical disturbances could have synergistic effects. Thus, the appearance of *Synchaeta* spp. is due to the effects of the sea storms but their persistence in the permanent basin could be interpreted as a result of the fish predation effect.

### **8.3. Species and size diversity**

The information about community structure given by size diversity is complementary from that given by species diversity. In temporary basins of Empordà salt marshes, species diversity reached its maximum during flooding periods when disturbances are frequent and when size diversity is generally low. Water inputs represent an entry of energy and nutrients to the ecosystem which favour the appearance of different species producing an increase in species diversity. However, this period of disturbances is usually short and, as soon as water inputs stop, the community tended towards a stability period during which competitive exclusion led to a decrease in species diversity. At the same time, high values of size diversity suggest a complex trophic structure, where different sizes of the same species have different roles. In this situation, the community is dominated by one species of calanoid. Low resource availability characterise these stability periods in Empordà Wetlands since confinement suppose a low entry of resources to the system. The existing trophic niche partitioning



between different development stages of calanoids reduces competition between them and permits their maintenance in habitats with low resource availability. The maximum values of size diversity in the situations of calanoid dominance are in accordance with the coexistence of all their stages. These situations do not appear in the permanent basin where competitive exclusion among zooplankters hardly takes place due to fish predation. According to Sommer *et al.* (1993) fish predation should be considered as a disturbance for zooplankton community since it stops the process towards competitive exclusion.

Size structure has been found to be a condition of intra- and interspecific competition, especially in crustacean zooplankton species which undergo developmental changes in habitat use and diet (Neill, 1975; Lynch, 1978). On the other hand, size structure is modified by size selective predation which, therefore, has the potential to alter the nature of these competitive interactions (Brooks and Dodson, 1965). Evidence regarding this fact have been described by Ebenman and Persson (1988), which suggested that intraspecific competition between age classes due to differences in size or morphology has important evolutionary and population dynamics consequences. Other investigators (Goulden and Hornig, 1980; Hu and Tessier, 1995) have reported that in *Daphnia* spp., stage structure is clearly important to population dynamics of a single species in simple, predator-free environments. On the other hand, several studies have emphasized that interspecific competition among zooplankton species are strongly influenced by stage structure (Neill, 1975; Hu and Tessier, 1995). Since size diversity provides us information about this size structure it would be use to investigate the community dynamics. The degree of community structure is the result of the ecological processes, such as intra- and interspecific competition and predation. Thus, size diversity might be better indicator of the degree of the community structure than species diversity, whose increases are sometimes not due to high degree of community structure. In particular, size diversity would be especially interesting to analyse in situations of competitive exclusion since it would be use to estimate the potential intraspecific competition. The tendency of size diversity to increase during succession would make it possible to discriminate between different succession stages, a fact that is not achieved by analysing only species diversity since it is low both under large and frequent or small and rare disturbances (Connell, 1978).

#### 8.4. Size as an aggregation method

Historically, zooplankton studies have focused mainly on adult stages as a consequence of whether the difficulty to correctly determinate juveniles to species level or to the use of inadequate collecting methods which underestimate juvenile stages. However, it has now become clear that early stages should not be undervalued since they play an essential role in the ecosystem, which might be different from the adults' role, and because they are critical intermediates between classical and microbial food webs (Hopcroft *et al.*, 2001 and reference therein). The use of a size based approach is an outstanding method of dealing with these problems and, furthermore, its use might also simplify the work in situations where similar species that can be mistaken coexist.

The existence of certain organisms, as calanoids and cyclopoids, which suffer from gradual changes in biochemical composition (Carrillo *et al.*, 1996; Schulz, 1996) and diet (e.g. Poulet, 1977; Jamieson, 1980; Zánkai, 1991; Maly and Maly, 1974) along ontogeny suggest the adequacy of the use of size approaches preferably to traditional taxonomic examination. Indeed, changes in trophic role that we have found in calanoids and cyclopods are only detectable by means of a size based approach. When describing trophic relationships in communities, the aggregation across individuals on the basis of size rather than species provides desirable simplifications. Jennings *et al.* (2002) demonstrated that body mass positively related to trophic level in benthic communities, hence the analysis of biomass size spectra could be used to describe changes in the trophic structure of communities. Zhou & Huntley (1997) also found that size approach could be used to estimate of population-dynamics parameters of individual growth rate and the intrinsic rate of increase.

In conclusion, size approach is especially suitable when dealing with communities composed of a lot of species (since it avoids the highly time-consuming determination of species) or very few species (since different ecological roles can be carry out for different stages of the same species), when larval determination is difficult and when species suffer from important changes along ontogeny, which are gradual and continuous and make it impossible to classify them into groups.

## 9.1. CONCLUSIONS *(in English)*

1. Three types of biomass size spectra for the functional group of zooplankton were found and they change according to environmental conditions: Linear shapes, which fit Pareto type I model better, curved shapes, which fit Pareto type II model better and stepped shape spectra, which usually fit either model poorly.
2. Linear shape spectra are more frequent in flooding situations, with high energy input (*Synchaeta*, undefined *Synchaeta* and Cyclopoids situations), when nutrient input causes population growth of small-sized organisms, more than compensating for the effect of competitive interactions.
3. In situations of confinement, when there is a lack of nutrient input, curved shape spectra are more frequent. In this situation of limited resource availability, intra- and inter-specific interactions take on more relevance, favouring the displacement of biomass toward larger sizes. Small-sized organisms decrease in number.
4. The existence of steps within the biomass size spectrum of an ecological group (stepped shape spectra) is attributed to population dynamics of the species in it. These steps appear whenever an increase of biomass takes place in a particular size range (e.g. *Synchaeta* spp and *Brachionus* sp) and there is little overlapping between the size ranges of different species.
5. Flux regulation acts as a press type disturbance causing gradual changes to the community and prolongs the linear spectra characteristic of flooding periods, due to the continual supplies of freshwater and nutrients.
6. Despite the similar taxonomic composition, permanent and temporary basins differ in the size distribution of organisms since the permanent basin is dominated mainly by smaller sizes, such as rotifera and calanoid nauplii. The presence of fish in the permanent waterbodies would explain the differences between sizes distributions of permanent and temporary waterbodies.

7. In temporary basins, where predation has little effect on zooplankton functional group, the shape of the biomass size spectrum is related to the hydrological cycle, which conditions the entry of nutrients to the ecosystem and thus the availability of food to the zooplankton. In permanent waterbodies zooplankton growth is not only conditioned by the availability of resources but by the predation of planktivorous fish, so that the temporal variability of the spectra may also be a result of temporal differences in fish predation pressure.
8. Size selective predation pressure of fish in the permanent basin impacts bigger invertebrates, giving steeper slopes in the biomass size spectra. The lower total biomass found in the permanent basin in comparison to the temporary basins might also be a consequence of fish predation.
9. As for the physiological scaling, biomass size spectrum at ecological scaling can be related to the stability of the ecosystem. Stable conditions, like constant nutrient supplies or constant fish predation, are characterized by curved shape spectra as a result of the ecological interactions among zooplankton species. Fluctuant conditions, like nutrient pulses and variable predation, are characterised by the appearance of linear shape spectra due to dominance of smaller sizes, whether as consequence of their greater ability to react after nutrient pulses or as a consequence of the size selective pressure on bigger sizes.
10. Pareto distribution can be used to calculate a size diversity index ( $\mu s'$ ) provided that data follow Pareto distribution. The advantage of this continuous function is that it avoids the arbitrariness introduced when using size classes.
11. In temporary basins, high values of size diversity coincide with periods of dominance of a single calanoid species (that is low species diversity) which represent the more stable situations in these basins. Since calanoids dominate the community during periods of relatively oligotrophy, trophic niche partitioning among different development stages would be the way to reduce intraspecific competition in these situations of competitive exclusion. In the permanent basin, this situation does not occur since competitive exclusion among zooplankters hardly takes place due to fish predation.

12. In zooplankton community of Empordà wetlands size diversity seems to be a better indicator of the degree of the community structure than species diversity, whose increases are sometimes not due to high degree of community structure. The tendency of size diversity to increase during succession **makes it useful** to discriminate between different succession stages, fact that is not achieved by analysing only species diversity since it is low both under large and frequent or small and rare disturbances.
13. The amino acid composition (AAC) of different development stages of copepod species analysed demonstrate gradual changes in biochemical composition of these organisms during ontogeny. These AAC differences found among stages and its ordenated change during development indicates a gradual change in diet during the life of these copepods, which means food niche partitioning during ontogeny.
14. *Daphnia* species analyzed show a relatively constant AAC and minor changes are not gradual during development which indicates that all stages feed on the same resources and therefore juveniles and adults suffer from trophic niche overlap.
15. There is a relationship between nutrient concentration (especially DIN/TN and SRP) of the basins and the degree of niche overlap between stages of the dominant species. Copepods, which have low stage overlap, are dominant in food-limited environments since trophic niche partitioning during development might allow them to reduce feeding competition between adults and juveniles. In *Daphnia* species, trophic niche overlap between juveniles and adults would restrict them to waters (or periods) with high productivity otherwise they would experience intraspecific competition.
16. Among the biotic factors, intraspecific competition plays an important role in structuring zooplankton assemblages together with the two factors often cited, predation and interspecific competition.
17. Size approach is an outstanding tool to study the structure of the zooplankton community since a low effort is needed and it is reproducible for different pelagic ecosystems. It is especially useful when the communities are composed of few

species, when larval stages determination is difficult and when species have gradual changes in their ecology during ontogeny.

## 9.2. CONCLUSIONS (in Catalan)

1. S'ha trobat tres tipus d'espectres de mida-biomassa dins del grup funcional del zooplàncton que canvien en funció de les condicions ambientals: formes lineals, que s'ajusten millor al model de Pareto tipus I, formes corbades, que s'ajusten millor al model de Pareto tipus II, i formes escalonades, que normalment tenen un pitjor ajustament a ambdós models.
2. Els espectres lineals són més freqüents en situacions d'inundació quan hi ha entrada d'energia (situacions de *Synchaeta*, indefinides amb *Synchaeta* i de Cíclopoides) i les entrades de nutrients causen el creixement dels organismes de mida petita de manera que es compensa l'efecte de les interaccions competitives.
3. En situacions de confinament, quan hi ha una manca d'entrades de nutrients, els espectres corbats són més freqüents. En aquesta situació de recursos limitats, les interaccions intra- i interespecífiques prenen més rellevància afavorint el desplaçament de la biomassa cap a les mides grans. Els organismes de mida petita disminueixen en nombre.
4. L'existència d'escalons a l'espectre de mida-biomassa a escala ecològica (espectres de forma escalonada) s'atribueix a les dinàmiques de poblacions d'algunes espècies. Aquests escalons apareixen quan té lloc un augment de la biomassa en una determinada classe de mida (p.e. *Synchaeta* spp. i *Brachionus* sp.) i hi ha poc solapament entre les classes de mides de les diferents espècies.
5. La regulació de fluxos actua com una pertorbació de tipus pressió causant canvis graduals en la comunitat i prolonga l'aparició dels espectres lineals característics dels períodes d'inundació degut a l'entrada continuada d'aigua i nutrients.
6. Malgrat tenir una composició taxonòmica similar, la llacuna permanent i les llacunes temporànies difereixen en la distribució de mides dels seus organismes ja que la llacuna permanent està dominada principalment per organismes de mida petita, tals com rotífers i nauplis de calanoides. La presència de peixos en la llacuna

permanent explicaria les diferències en les distribucions de mides respecte les temporànies.

7. En les llacunes temporànies, on la depredació té poc efecte en el grup funcional del zooplàncton, la forma de l'espectre de mida-biomassa està relacionada amb el cicle hidrològic el qual condiciona l'entrada de nutrients a l'ecosistema i, per tant, la disponibilitat d'aliment pel organismes. En les llacunes permanents el creixement del zooplàncton no només està condicionat per la quantitat de recurs disponible sinó també per la depredació dels peixos planctívors, de manera que la variació de l'espectre també pot ser conseqüència de diferències temporals en la pressió de depredació dels peixos.
8. La pressió de depredació selectiva dels peixos sobre la mida corporal en la llacuna permanent té efecte sobre els organismes de mida gran i dona com a resultat espectres de mida-biomassa amb pendents més acusades. La menor biomassa total en la llacuna permanent respecte les temporànies pot ser deguda també a la depredació dels peixos.
9. Com en el cas de l'escala fisiològica, la forma de l'espectre de mida-biomassa, a escala ecològica, es pot relacionar amb l'estabilitat de sistema. Condicions estables, com l'entrada constant de nutrients o la depredació constant per part dels peixos, es caracteritzen per espectres de forma corbada, com a resultat de les interaccions ecològiques entre les espècies de zooplàncton. Condicions fluctuants, com entrades pulsàtils de nutrients o la pressió de depredació variable, es caracteritzen per espectres de forma lineal gràcies a la dominància de les mides petites, com a conseqüència de la seva més ràpida reacció després de pulsos de nutrients, o bé com a conseqüència de la major pressió de depredació sobre les mides més grans.
10. La distribució de Pareto es pot utilitzar per calcular un índex de diversitat de mides ( $\mu_s$ ) sempre que les dades segueixin la distribució de Pareto. L'avantatge d'aquesta funció contínua és que evita l'arbitrarietat que suposa la utilització de classes de mides.



11. En llacunes temporànies, valors alts de diversitat de mides coincideixen amb períodes de dominància d'una sola espècie de calanoide (per tant, de baixa diversitat d'espècies) que representen les situacions més estables en aquestes llacunes. Com que calanoides dominen la comunitat en períodes de relativa oligotròfia, la repartició del nínxol tròfic entre els diferents estadis de desenvolupament seria la manera de disminuir la competència intraespecífica en aquestes situacions d'exclusió competitiva. En la llacuna permanent la depredació per part dels peixos no permet l'exclusió competitiva entre organismes del zooplàncton.
12. En la comunitat zooplanctònica dels Aiguamolls de l'Empordà la diversitat de mides sembla ser millor indicador del nivell d'estructuració de la comunitat que la diversitat d'espècies, els increments de la qual en alguns casos no són deguts a un alt grau d'estructuració de la comunitat. La tendència de la diversitat de mides a augmentar al llarg de la successió li permet discriminar entre diferents estadis de la successió, fet que no s'aconsegueix analitzant únicament la diversitat d'espècies ja que és baixa tant en moments de pertorbacions intenses i freqüents com petites i escasses.
13. La composició d'aminoàcids (AAC) dels diferents estadis de desenvolupament de les espècies de copèpodes analitzades demostren que hi ha un canvi gradual de la composició bioquímica d'aquests organismes al llarg de la seva ontogènesi. Aquestes diferències en la AAC entre estadis i el seu canvi ordenat durant el desenvolupament indiquen un canvi gradual en la dieta durant la vida d'aquests copèpodes, fet demostra que té lloc una repartició del nínxol tròfic al llarg de la ontogènesi.
14. Les espècies de *Daphnia* analitzades mostren una AAC relativament constant i els petits canvis detectats no són graduals durant el desenvolupament, fet que indica que tots els estadis s'alimenten del mateix recurs i, per tant, els juvenils i els adults mostren solapament del nínxol tròfic.
15. Hi ha una relació entra la concentració de nutrients (especialment DIN/TN i SRP) de les llacunes i el grau de solapament entre els estadis de les espècies dominants.

Els copèpodes, que tenen un baix solapament entre estadis, dominen en ambients on el recurs és limitat ja que la repartició del nínxol tròfic durant el desenvolupament els permetria reduir la competència per l'aliment entra joves i adults. En les espècies de *Daphnia*, el solapament del nínxol tròfic entre joves i adults els restringiria a llacunes o períodes amb elevada productivitat per tal d'evitar la competència intraespecífica.

16. Entre els factors biòtics, la competència intraespecífica juga un paper important a l'hora d'estructurar la comunitat de zooplàncton, juntament amb els dos altres factors que han estat sovint citats, la depredació i la competència interespecífica.
17. L'aproximació basada en la grandària corporal és una eina adequada a l'hora d'estudiar l'estructura de les comunitats de zooplàncton ja que l'esforç necessari és petit i és reproduïble en diferents ecosistemes pelàgics. És especialment útil quan la comunitat està composta per poques espècies, quan la determinació dels estadis larvaris és difícil i quan les espècies pateixen canvis graduals en la seva ecologia al llarg de la ontogènesi.

### 9.3. CONCLUSIONS *(in Spanish)*

1. Se encontraron tres tipos de espectros de tamaño-biomasa dentro del grupo funcional del zooplancton que cambian en función de las condiciones ambientales: formas lineales, que se ajustan mejor al modelo de Pareto tipo I, formas curvas, que se ajustan mejor al modelo de Pareto tipo II y formas escalonadas, que normalmente tienen un ajuste peor a los dos modelos.
2. Los espectros lineales son mas frecuentes en situaciones de inundación cuando hay entradas de energía (situaciones de *Synchaeta*, indefinidas con *Synchaeta* y de Ciclopoides) y las entradas de nutrientes causan el crecimiento de los organismos de tamaño pequeño de manera que se compensan los efectos de las interacciones competitivas.
3. En situaciones de confinamiento, cuando hay un déficit de entrada de nutrientes, los espectros curvados son más frecuentes. En esta situación de recursos limitados, las interacciones intra e interespecíficas adquieren más importancia favoreciendo el desplazamiento de la biomasa hacia tamaños más grandes. Los organismos de tamaño pequeño disminuyen su número.
4. La existencia de escalones en el espectro de tamaño-biomasa a escala ecológica (espectros de forma escalonada) se atribuye a las dinámicas poblacionales de algunas especies. Estos escalones aparecen cuando tiene lugar un aumento de la biomasa en una determinada clase de tamaño (p.e. *Synchaeta* spp. y *Brachionus* sp.) y hay poco solapamiento entre las clases de tamaño de las diferentes especies.
5. La regulación de flujos actúa como una perturbación de tipo presión causando cambios graduales en la comunidad y prolonga la aparición de los espectros lineales característicos de los periodos de inundación, debido a la entrada continuada de agua y nutrientes.
6. Aunque tienen una composición taxonómica similar, la laguna permanente y las lagunas temporales difieren en la distribución de tamaños de sus organismos ya que

la laguna permanente está dominada principalmente por organismos de tamaño pequeño, tales como rotíferos y nauplios de calanoides. La presencia de peces en la laguna permanente explicaría las diferencias en las distribuciones de tamaño respecto a las temporales.

7. En las lagunas temporales, donde la depredación tiene poco efecto en el grupo funcional del zooplancton, la forma del espectro de tamaño-biomasa está relacionada con el ciclo hidrológico, el cual condiciona la entrada de nutrientes al ecosistema y, por lo tanto, la disponibilidad de alimento para los organismos. En las lagunas permanentes el crecimiento del zooplancton no sólo está condicionado por la cantidad de recursos disponibles si no también por la depredación de los peces planctívoros.
8. La presión de depredación selectiva de los peces sobre el tamaño corporal en la laguna permanente tiene efecto sobre los organismos de tamaño grande y da como resultado espectros de tamaño-biomasa con pendientes más acusadas. La menor biomasa total en la laguna permanente respecto a las temporáneas puede ser debida también a la depredación de los peces.
9. Como en el caso de la escala fisiológica, la forma del espectro de tamaño-biomasa, a escala ecológica, se puede relacionar con la estabilidad del sistema. Condiciones estables, como la entrada constante de nutrientes o la depredación constante por parte de los peces se caracterizan por espectros de forma curva, como resultado de las interacciones ecológicas entre las especies de zooplancton. Condiciones fluctuantes, como entradas pulsátiles de nutrientes o la presión de depredación variable, se caracterizan por espectros de forma lineal gracias a la dominancia de los tamaños pequeños, como consecuencia de su más rápida reacción después de pulsos de nutriente, o bien como consecuencia de la mayor depredación sobre los tamaños grandes.
10. La distribución de Pareto se puede utilizar para calcular la diversidad de tamaños ( $\mu_s'$ ) siempre y cuando los datos sigan la distribución de Pareto. La ventaja de esta función continua es que evita la arbitrariedad que supone la utilización de clases de tamaños.

11. En lagunas temporales, valores altos de diversidad de tamaños coinciden con periodos de dominancia de una sola especie de calanoide (por tanto, de baja diversidad de especies) que representan las situaciones más estables en estas lagunas. Como los calanoides dominan la comunidad en periodos de relativa oligotrofia, la repartición del nicho trófico entre los diferentes estadios de desarrollo sería el modo disminuir la competencia intraespecífica en estas situaciones de exclusión competitiva. En la laguna permanente la depredación por parte de los peces no permite la exclusión competitiva entre los organismos zooplantónicos.
  
12. En la comunidad zooplantónica de los Aiguamolls de l'Empordà la diversidad de tamaños parece ser mejor indicador del nivel de estructuración de la comunidad que la diversidad de especies, los aumentos de la cual en algunos casos no son debidos a un elevado grado de estructuración de la comunidad. La tendencia de la diversidad de tamaños a aumentar a lo largo de la sucesión le permite discriminar entre los diferentes estadios de la sucesión. Esto no se consigue analizando únicamente la diversidad de especies, ya que es baja tanto en periodos de perturbaciones intensas y frecuentes como pequeñas y escasas
  
13. La composición de aminoácidos (AAC) de los diferentes estadios de desarrollo de las especies de copépodos analizadas demuestran que hay un cambio gradual de la composición bioquímica de estos organismos a lo largo de su ontogénesis. Estas diferencias en la AAC entre estadios y su cambio ordenado durante el desarrollo indican un cambio gradual en la dieta durante la vida de estos copépodos, hecho que demuestra que tiene lugar una repartición del nicho trófico a lo largo de la ontogénesis.
  
14. Las especies de *Daphnia* analizadas muestran una AAC relativamente constante i los pequeños cambios detectados no son graduales durante el desarrollo, hecho que indicaría que todos los estadios se alimentan del mismo recurso y, por lo tanto, los juveniles y los adultos muestran solapamiento del nicho trófico.
  
15. Hay una relación entre a concentración de nutrientes (especialmente DIN/NT y SRP) de las lagunas y el grado de solapamiento entre los estadios de las especies

dominantes. Los copépodos, que tienen un solapamiento bajo entre estadios, dominan en ambientes donde el recurso es limitado ya que la repartición del nicho trófico durante el desarrollo les permitiría reducir la competencia por el alimento entre jóvenes y adultos. En las especies de *Daphnia*, el solapamiento del nicho trófico entre jóvenes y adultos les limitaría en lagunas o periodos con elevada productividad para así evitar la competencia intraespecífica.

16. Entre los factores bióticos, la competencia intraespecífica juega un papel importante a la hora de estructurar la comunidad de zooplancton, conjuntamente con los dos factores habitualmente citados, la depredación y la competencia.
17. La aproximación basada en el tamaño corporal es una herramienta adecuada a la hora de estudiar la estructura de las comunidades del zooplancton ya que el esfuerzo necesario es pequeño y es reproducible en diferentes ecosistemas pelágicos. Es especialmente útil cuando la comunidad está compuesta por pocas especies, cuando la determinación de los estadios larvarios es dificultosa y cuando las especies sufren cambios graduales en su ecología a lo largo de la ontogénesis.

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**Appendix 1.** Geometric shapes and formulae used to estimate the volume of some of the zooplankton organisms. (Ru) from Ruttner-Kolisko (1977), (Ma) from Malley *et al.* (1989), (Qu,a) from Quintana (1995). *a*, *b* and *c*, length, width and height. Special features of the calculation of the volume are included in notes.

taxon	shape	volume	formula	notes	ref
<i>Brachionus</i> spp.	el·lipsoid	$4\pi r_1 r_2 r_3/3$	$0.52ab^2+0.052ab^2$	foot = 10% body	(Ru)
<i>Brachionus quadridentatus</i>	paral·lele·piped (triangular section)	$abc/2$	$0.25a^2b+0.025ab^2$	c=0.5a foot=10% body	(Qu,a)
<i>Notholca</i> spp.	segment of el·lipsoid	$\pi r_3(3 r_1 r_2/4+r_3^2)/6$	$0.078a2b+0.00416a^3$	c=0.2a	(Ru)
<i>Colurella adriatica</i>	el·lipsoid	$4\pi r_1 r_2 r_3/3$	$0.18a^2b+0.02a^3$	c= 0.34a	(Qu,a)
<i>Hexarthra</i> sp.	cone	$\pi r_1 r_2^2/3$	$0.346ab^2$	Appendices=33% body	(Ru)
<i>Synchaeta</i> spp.	el·lipsoid	$4\pi r_1 r_2 r_3/3$	$0.52ab^2$	b=c	(Ma)
<i>Keratella quadrata</i>	paral·lele·piped	$abc$	$ab^2$	b=c app.=5% V· caudal spines/a	(Ru)
<i>Lepadella</i> sp.	el·lipsoid	$4\pi r_1 r_2 r_3/3$	$0.52ab^2$	b=c	(Ma)
<i>Polyarthra</i> sp.	paral·lele·piped	$abc$	$0.4a^2b$	c=0.4a	(Ru)
<i>Cephalodella</i> sp.	el·lipsoid	$4\pi r_1 r_2 r_3/3$	$0.52ab^2$	b=c	(Ma)
<i>Testudinella</i> spp	cilindre	$\pi r_2^2 r_1$	$0.4ab^2$	b=c foot = 10% body	(Ru)

**Appendix 2.** Biomass estimations of the different species and their stages. F, formula used to estimate the biomass; V, volume; W, estimation of the biomass in  $\mu\text{g}$  of dry weight;  $a$ , length (mm);  $b$ , width (mm);  $c$ , height (mm); WW, wet weight; R, reference.

References: (Bo) Botrell *et al.* (1976); Dumont *et al.* (1975); (Fo) Foissner (1996); (Ga) García-Berthou (1990); (Jo) Johnston (1995); (Ma) Malley *et al.* (1989); (Me) Meier (1989); (Qu, a) Quintana (1995a); (Qu, b) Quintana (1995b); (Ru) Ruttner-Kolisko (1977); (Sc) Schönborn (1992); (Sm) Smock (1980).

Taxa	F	Shape	W	Taxa of reference	Note	R
<b>Ciliophora</b>						
<i>Eutintinnus</i> sp.	$W=0.11V$ (Sc)	el-lipsoid	$57.2 \cdot ab^2$		b=c	
<i>Strombidium</i> sp. 1	$W=0.11V$ (Sc)		0.0055			(Fo)
<i>Strombidium</i> sp. 2	$W=0.11V$ (Sc)		0.0055			(Fo)
<i>Strobilidium</i> sp.	$W=0.11V$ (Sc)		0.005			(Fo)
<i>Favela serrata</i>	$W=0.11V$ (Sc)		$26 \cdot ab^2$		b=c	(Sc)
<i>Didinium</i> sp.	$W=0.11V$ (Sc)		0.006			(Fo)
<i>Monodinium</i> sp.	$W=0.11V$ (Sc)		0.006			(Fo)
<i>Vortichella</i> sp.	$W=0.11V$ (Sc)	el-lipsoid	$57.2 \cdot ab^2$		b=c	
<i>Euplotes</i> sp.	$W=0.11V$ (Sc)		$41.6 \cdot ab^2$		b=c	(Sc)
<i>Lacrymaria sapropelica</i>	$W=0.11V$ (Sc)		0.0036			(Fo)
Undetermined Ciliate 1	$W=0.11V$ (Sc)	el-lipsoid	$57.2 \cdot ab^2$		b=c	
Undetermined Ciliate 2	$W=0.11V$ (Sc)	el-lipsoid	$57.2 \cdot ab^2$		b=c	
Undetermined Ciliate 3	$W=0.11V$ (Sc)	el-lipsoid	$22.88 \cdot a^2b$		c=0.4a	
Undetermined Ciliate 4	$W=0.11V$ (Sc)	el-lipsoid	$22.88 \cdot a^2b$		c=0.4a	
Undetermined Ciliate 5	$W=0.11V$ (Sc)	el-lipsoid	$57.2 \cdot ab^2$		b=c	
<b>Cnidaria</b>						
<i>Odessia maeotica</i>	$W=0.07V$ (Ma)		$18.2 \cdot a^3$			(Qu, a)
<b>Nematoda</b>						
Undetermined Nematode	$W=0.07V$ (Ma)		$54.95 \cdot ab^2$			(Qu, a)
<b>Rotifera</b>						
<i>Brachionus plicatilis</i>	$W=0.07V$ (Ma)		$36.4 \cdot ab^2 + 3.64 \cdot ab^2$			(Ru)
<i>Brachionus quadridentatus</i>	$W=0.07V$ (Ma)		$17.5 \cdot a^2b + 1.75 \cdot a^2b$			(Qu, a)
<i>Brachionus urceolaris</i>	$W=0.07V$ (Ma)		$36.4 \cdot ab^2 + 3.64 \cdot ab^2$			(Ru)
<i>Brachionus calyciflorus</i>	$W=0.07V$ (Ma)		$36.4 \cdot ab^2 + 3.64 \cdot ab^2$			(Ru)
<i>Brachionus</i> sp.	$W=0.07V$ (Ma)		$7.28 \cdot a^2b$			(Ru)
<i>Notholca liepettersoni</i>	$W=0.07V$ (Ma)		$5.46 \cdot a^2b + 0.29 \cdot a^3$			(Ru)
<i>Notholca squamula</i>	$W=0.07V$ (Ma)		$5.46 \cdot a^2b + 0.29 \cdot a^3$			(Ru)
<i>Notholca</i> sp.	$W=0.07V$ (Ma)		$5.46 \cdot a^2b + 0.29 \cdot a^3$			(Ru)
<i>Bdeloidella</i> sp.	$W=0.07V$ (Ma)		$36.4 \cdot ab^2$	<i>Tricocerca</i>		
<i>Colurella adriatica</i>	$W=0.07V$ (Ma)		$12.38 \cdot a^2b + 1.38 \cdot a^3$			(Qu, a)
<i>Lepadella</i> sp.	$W=0.07V$ (Ma)		$36.4 \cdot ab^2$			(Ma)
<i>Synchaeta</i> spp.	$W=0.07V$ (Ma)		$36.4 \cdot ab^2$			(Ma)
<i>Testudinella patina</i>	$W=0.07V$ (Ma)		$7.28 \cdot a^2b$			(Ru)
<i>Testudinella clypeata</i>	$W=0.07V$ (Ma)		$7.28 \cdot a^2b$			(Ru)
<i>Keratella quadrata</i>	$W=0.07V$ (Ma)		$23.1a^2b + 1.16a^2b$			(Ru)
<i>Hexarthra fennica</i>	$W=0.07V$ (Ma)		$24.22 \cdot ab^2$			(Ru)
<i>Polyarthra</i> sp.	$W=0.07V$ (Ma)		$28 \cdot a^2b$			(Ru)
<i>Cephalodella</i> sp.	$W=0.07V$ (Ma)		$36.4 \cdot ab^2$			(Ma)
Undetermined rotifera	$W=0.07V$ (Ma)		$36.4 \cdot ab^2$			(Ru)
<b>Anellida</b>						
<i>Nereis diversicolor</i>	$W=0.07V$ (Ma)		$54.95 \cdot ab^2$			(Qu, a)
Polychaeta (larva)	$W=0.07V$ (Ma)		$54.95 \cdot ab^2$			(Qu, a)
Oligochaeta	$W=0.07V$ (Ma)		$54.95 \cdot ab^2$			(Qu, a)

<b>Arthropoda: Arachnida</b>						
Undetermined water mite	W=0.07V (Ma)		18.2·a <sup>b</sup>			(Qu, a)
<b>Arthropoda: Crustacea</b>						
Undetermined Calanoid N1 & N2	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
Undetermined Calanoid N3 & N4	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
Undetermined Calanoid N5 & N6	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Eurytemora velox</i> N1 & N2	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Eurytemora velox</i> N3 & N4	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Eurytemora velox</i> N5 & N6	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Eurytemora velox</i> C1	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Eurytemora velox</i> C2	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Eurytemora velox</i> C3	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Eurytemora velox</i> C4	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Eurytemora velox</i> C5	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Eurytemora velox</i> C6	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Calanipeda aquae-dulcis</i> N1 & N2	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Calanipeda aquae-dulcis</i> N3 & N4	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Calanipeda aquae-dulcis</i> N5 & N6	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Calanipeda aquae-dulcis</i> C1	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Calanipeda aquae-dulcis</i> C2	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Calanipeda aquae-dulcis</i> C3	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Calanipeda aquae-dulcis</i> C4	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Calanipeda aquae-dulcis</i> C5	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Calanipeda aquae-dulcis</i> C6	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Acartia bifilosa</i> nauplii	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Acartia bifilosa</i> C1	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Acartia bifilosa</i> C2	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Acartia bifilosa</i> C3	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Acartia bifilosa</i> C4	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Acartia bifilosa</i> C5	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Acartia bifilosa</i> C6	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Acartia clausi</i>	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
<i>Acartia longiremis</i>	LnW=a+b·lnL		$e^{(1.0968+2.1951lnL)}$	<i>Diaptomus silicoides</i>		(Ma)
Undetermined Cyclopoid N1 & N2	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
Undetermined Cyclopoid N3 & N4	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
Undetermined Cyclopoid N5 & N6	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Diacyclops bisetosus</i> N1 & N2	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Diacyclops bisetosus</i> N3 & N4	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Diacyclops bisetosus</i> N5 & N6	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Diacyclops bisetosus</i> C1	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Diacyclops bisetosus</i> C2	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Diacyclops bisetosus</i> C3	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Diacyclops bisetosus</i> C4	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Diacyclops bisetosus</i> C5	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Diacyclops bisetosus</i> C6	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>D. bicuspidatus odessanus</i> N1 & N2	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>D. bicuspidatus odessanus</i> N3 & N4	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>D. bicuspidatus odessanus</i> N5 & N6	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>D. bicuspidatus odessanus</i> C1	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>D. bicuspidatus odessanus</i> C2	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>D. bicuspidatus odessanus</i> C3	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>D. bicuspidatus odessanus</i> C4	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>D. bicuspidatus odessanus</i> C5	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>D. bicuspidatus odessanus</i> C6	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Halicyclops rotundipes</i> nauplii	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Halicyclops rotundipes</i> C1	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Halicyclops rotundipes</i> C2	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Halicyclops rotundipes</i> C3	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Halicyclops rotundipes</i> C4	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Halicyclops rotundipes</i> C5	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
<i>Halicyclops rotundipes</i> C6	LnW=a+b·lnL		$e^{(0.6154+2.034lnL)}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)

<i>Cyclops</i> sp.	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(0.6154+2.034\text{lnL})}$	<i>Cyclops bicuspidatus thomasi</i>		(Ma)
Undetermined Harpacticoid nauplii	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(2.5265+4.4\text{lnL})}$	<i>Harpacticoida</i>		(Du)
<i>Cletocamptus confluens</i> C1	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(2.5265+4.4\text{lnL})}$	<i>Harpacticoida</i>		(Du)
<i>Cletocamptus confluens</i> C2	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(2.5265+4.4\text{lnL})}$	<i>Harpacticoida</i>		(Du)
<i>Cletocamptus confluens</i> C3	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(2.5265+4.4\text{lnL})}$	<i>Harpacticoida</i>		(Du)
<i>Cletocamptus confluens</i> C4	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(2.5265+4.4\text{lnL})}$	<i>Harpacticoida</i>		(Du)
<i>Cletocamptus confluens</i> C5	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(2.5265+4.4\text{lnL})}$	<i>Harpacticoida</i>		(Du)
<i>Cletocamptus confluens</i> C6	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(2.5265+4.4\text{lnL})}$	<i>Harpacticoida</i>		(Du)
<i>Nitocra spinipes</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(2.5265+4.4\text{lnL})}$	<i>Harpacticoida</i>		(Du)
<i>Nitocra lacustris</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(2.5265+4.4\text{lnL})}$	<i>Harpacticoida</i>		(Du)
<i>Canuella perplexa</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(2.5265+4.4\text{lnL})}$	<i>Harpacticoida</i>		(Du)
<i>Mesochra rapiens</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(2.5265+4.4\text{lnL})}$	<i>Harpacticoida</i>		(Du)
<i>Paronychocamptus nanus</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(2.5265+4.4\text{lnL})}$	<i>Harpacticoida</i>		(Du)
<i>Tisbe longicornis</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(2.5265+4.4\text{lnL})}$	<i>Harpacticoida</i>		(Du)
<i>Ergasilus</i> sp.	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(0.6154+2.034\text{lnL})}$	Cyclopoid		
Chydorinae	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(4.4935+3.93\text{lnL})}$	<i>Chidorus sphaericus</i>		(Du)
<i>Daphnia pulex</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(1.4660+3.1932\text{lnL})}$	<i>Daphnia pulex</i>		(Bo)
Undetermined crustacean larva	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(1.0968+2.1951\text{lnL})}$	<i>Diaptomus silicoïdes</i>		
Undetermined ostracod	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(3.33+2.8\text{lnL})}$	Ostracoda		(Jo)
<i>Cyprideis torosa</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(3.33+2.8\text{lnL})}$	Ostracoda		(Jo)
<i>Eucypris</i> sp.	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(3.33+2.8\text{lnL})}$	Ostracoda		(Jo)
<i>Protracheoniscus occidentalis</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-5.1605+2.721\text{lnL})}\cdot 1000$	<i>Gammarus</i>		(Qu, b)
<i>Lekanesphaera hookeri</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-5.1605+2.721\text{lnL})}\cdot 1000$	<i>Gammarus</i>		(Qu, b)
Undetermined isopod	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-5.1605+2.721\text{lnL})}\cdot 1000$	<i>Gammarus</i>		(Qu, b)
<i>Gammarus</i> sp.	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-5.1605+2.721\text{lnL})}\cdot 1000$			(Qu, b)
<i>Gammarus aequicauda</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-5.1605+2.721\text{lnL})}\cdot 1000$			(Qu, b)
<i>Mesopodopsis slabberi</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-5.1605+2.721\text{lnL})}\cdot 1000$	<i>Gammarus</i>		(Qu, b)
<b>Arthropoda: Diptera</b>						
<i>Aedes detritus</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-6.86+3.003\text{lnL})}\cdot 1000$			(Qu, b)
<i>Aedes</i> sp.	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-6.86+3.003\text{lnL})}\cdot 1000$			(Qu, b)
<i>Chironomus salinarius</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-5.2785+2.32\text{lnL})}\cdot 1000$	Orthocladinae/Chironomidae		(Sm)
<i>Chironomus</i> sp.	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-5.2785+2.32\text{lnL})}\cdot 1000$	Orthocladinae/Chironomidae		(Sm)
Orthocladidae	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-5.2785+2.32\text{lnL})}\cdot 1000$	Orthocladinae/Chironomidae		(Sm)
<i>Cricotopus</i> sp.	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-5.2785+2.32\text{lnL})}\cdot 1000$	Orthocladinae/Chironomidae		(Sm)
Undetermined chironomid (midge)	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-5.2785+2.32\text{lnL})}\cdot 1000$	Orthocladinae/Chironomidae		(Sm)
Ceraptogonidae	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-9.3774+3.795\text{lnL})}\cdot 1000$			(Me)
Ceraptogonidae (pupa)	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-9.3774+3.795\text{lnL})}\cdot 1000$			(Me)
<i>Setacera micans</i>	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$		$e^{(-5.9914+2.572\text{lnL})}\cdot 1000$			(Me)
<b>Mollusca: Gastropoda</b>						
Undetermined gastropod	$W=0.07V$ (Ma)		$13.1\cdot a^3$			(Qu, a)
<b>Chordata</b>						
Fish larva	$\text{LnW}=\text{a}+\text{b}\cdot\text{lnL}$ ,		$e^{(-4.213+3.216\text{lnL})}\cdot 200$	<i>Aphanius iberus</i>	$W=0.2WW$	(Ga)



### Appendix 3. Integration of $\mu_s$

$$\begin{aligned} \mathbf{m}_s &= p(s) \log_2 p(s) = p(s) \ln p(s) \log_2 e = \log_2 e p(s) \ln [c(K+D)^c (s+D)^{-(c+1)}] = \\ & \log_2 e p(s) [\ln [c(K+D)^c] - (c+1) \ln (s+D)] = \log_2 e c(K+D)^c (s+D)^{-(c+1)} [\ln [c(K+D)^c] - (c+1) \ln (s+D)] \end{aligned}$$

If this equation is integrated

$$\int p(s) \log_2 p(s) ds = \log_2 e [c(K+D)^c] \ln [c(K+D)^c] \int (s+D)^{-(c+1)} ds - \log_2 e [c(K+D)^c] (c+1) \int (s+D)^{-(c+1)} \ln (s+D) ds \quad (1) \quad (2)$$

$$(1) \int (s+D)^{-(c+1)} ds = \frac{(s+D)^{-c}}{-c}$$

$$\begin{aligned} (2) \int (s+D)^{-(c+1)} \ln (s+D) ds &= -\frac{(s+D)^{-c}}{c} \ln (s+D) + \frac{1}{c} \int \frac{(s+D)^{-c}}{s+D} ds = \\ & -\frac{(s+D)^{-c}}{c} \ln (s+D) + \frac{1}{c} \int (s+D)^{-(c+1)} ds = -\frac{(s+D)^{-c}}{c} \ln (s+D) - \frac{1}{c^2} (s+D)^{-c} = -\frac{1}{c} (s+D)^{-c} \left[ \ln (s+D) + \frac{1}{c} \right] \end{aligned}$$

Therefore  $\mu_s$  is:

$$\begin{aligned} \mathbf{m}_s &= \log_2 e [c(K+D)^c] \ln [c(K+D)^c] \frac{(s+D)^{-c}}{-c} - \log_2 e [c(K+D)^c] (c+1) \left( -\frac{1}{c} \right) (s+D)^{-c} \\ & \left[ \ln (s+D) + \frac{1}{c} \right] = \log_2 e (K+D)^c (s+D)^{-c} \left[ -\ln [c(K+D)^c] + (c+1) \left[ \ln (s+D) + \frac{1}{c} \right] \right] \\ \mathbf{m}_s &= \int p(s) \log_2 p(s) ds = \log_2 e (K+D)^c (s+D)^{-c} \left[ \ln [c(K+D)^c] - (c+1) \left[ \ln (s+D) + \frac{1}{c} \right] \right] \end{aligned}$$