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CHANGES IN THE SHAPE OF ZOOPLANKTON BIOMASS-SIZE SPECTRA AT ECOLOGICAL SCALING IN A FLUCTUATING ECOSYSTEM (EMPORDÀ WETLANDS, NE SPAIN)

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SIZE DISTRIBUTION
PARETO MODEL
MEDITERRANEAN COASTAL LAGOONS
SALT MARSHES

ABSTRACT. – The biomass-size spectrum, at ecological scaling of zooplankton community in a fluctuating basin of Empordà Wetlands was analysed by adjustment to a model based on the Pareto distribution. Different shapes of spectra have been related to the availability of resources. Under flooding conditions biomass-size spectra fit better a linear model (Pareto Type I), whereas in confinement conditions curved shape biomass-size spectra (Pareto Type II) were more frequent. Results suggest that under flooding conditions competitive and predatory interactions are low and size distributions reflect mainly population growth, especially of small-size organisms. The result is a linear spectrum. On the other hand, during confinement conditions interactions between species would acquire more relevance due to the lack of resources, favouring the displacement of biomass toward larger sizes. The result is a curved spectrum and a decrease of diversity. Thereby, the shape of the biomass-size spectrum is an indicator of the degree of ecological interactions within the zooplankton functional group.

DISTRIBUTION DE TAILLE
MODÈLE DE PARETO
LAGUNES MÉDITERRANÉENNES
MARAIS

RÉSUMÉ. – Le spectre de taille-biomasse, à l'échelle écologique de la communauté du zooplancton dans une cuvette fluctuante du marais de l'Empourdà a été analysé par ajustement à un modèle basé sur la distribution de Pareto. Les formes différentes de spectres de taille-biomasse sont reliées à la disponibilité des ressources. Dans des conditions d'inondation, les spectres de taille-biomasse s'ajustent mieux à un modèle linéaire (Pareto Type I), alors que dans des conditions de confinement, les spectres s'ajustant à des courbes (Pareto type II) sont plus fréquents. Les résultats suggèrent que dans les conditions d'inondation les interactions compétitives sont faibles et les prédateurs sont rares, et la distribution de la taille reflète principalement l'augmentation de la population, surtout pour les organismes de petite taille. Le résultat est un spectre linéaire. En revanche, pendant des conditions de confinement les interactions entre espèces seraient plus importantes en raison du manque de ressources, favorisant ainsi le déplacement de la biomasse vers de plus grandes tailles. Le résultat est un spectre courbe et une baisse de la diversité. Ainsi, la forme du spectre de taille-biomasse est indicatrice du degré d'interactions écologiques dans le groupe fonctionnel du zooplancton.

INTRODUCTION

Observation of regularities in the distribution of size in some aquatic ecosystems has led to use body size as a community-organising unit, based on the relationships between body size and variables describing the main ecological processes taking place in the environment. Variables such as respiration, production, growth rate and ingestion rate are correlated allometrically to body size (Peters 1983, Calder 1984). Some authors (Platt & Denman 1977, 1978, Rodríguez & Mullin 1986) have proposed an allometric relationship between organism abundance and size, whereas others (Sheldon *et al.* 1972, Sprules & Munawar 1986, Duarte *et al.*

1986, Blanco *et al.* 1994) have proposed that abundance is inversely proportional to body size. Quiñones *et al.* (2003) have shown that differences can be due to the units (carbon or volume) in which organism size is expressed. In any case, this regular structure is a typical feature of the biomass-size spectrum when it covers the size range of the whole community, and is what Dickie *et al.* (1987) called the physiological or primary scaling.

The same authors remark on the existence of a secondary or ecological scaling 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 distribu-

tion within a functional group is more dependent on the ecological interactions of the species in it, which mainly favours big sized organisms, 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 (Dickie *et al.* 1987). This ecological scaling is more obvious in slightly-structured and fluctuating systems (Sprules 1988, Rodríguez *et al.* 1990, García-Jiménez 1991) and 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 & Dickie 1989, Rodríguez *et al.* 1990, Gasol *et al.* 1991, Boix *et al.* 2004).

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 & Cempel 1992) and in other fields within limnology (Pueyo 1994) where size-structured systems are analysed, and was used previously for analysis of the biomass 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 fact that linear shape spectra (which indicate higher relative numerical abundance of smaller sizes, provided that the slope is negative) are a consequence of the allometric relationship between growth (production) and body mass and curved spectra (which indicate lower relative abundance of smaller sizes; Vidondo *et al.* 1997) are the result of ecological interactions between different species or sizes (Kerr & Dickie 2001 and references therein, Rodríguez 1994, Brucet 2003) suggests that the analysis of the shape of the spectrum might be a way to evaluate the degree of ecological interactions in the zooplankton functional group. This could be successfully analysed in fluctuating ecosystems, where rapid changes in nutrient supplies produce temporal changes in the biomass size spectrum of aquatic organisms as has been observed in Empordà salt marshes (Quintana *et al.* 2002).

The objectives of this study are: (1) to assess the usefulness of the 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 ecological interactions within the zooplankton functional group.

METHODS

Study area: The Empordà Wetlands comprise a group of coastal lagoons and Mediterranean salt marshes free from tidal influence. The hydrology of the area is dominated by sudden marine intrusions during sea storms that occur very irregularly, although relatively frequently. After sea storms or intense rainfall the marshes remain confined for a long time and tend towards desiccation. Just one surface fresh-water channel from the cultivated plain supplies the whole lagoon system and it also acts as an escape to the sea for excess water. A sluice gate was installed in this drainage channel. 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).

One single basin of the lagoon system was selected in order to avoid spatial variability. The temporary basin studied 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 location and further details of the hydrology (Table I, top), the physical and chemical characteristics and the species composition of the basin, see basin 1 in Quintana *et al.* (1998a) and (1998b).

Sampling design and analysis: Water samples (116 samples) were taken weekly from a central point of the basin from September 1996 to June 2000 at a depth of 10-15 cm. Temperature, electrical conductivity (EC₂₅), 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 (NH₄⁺, NO₂⁻, NO₃⁻, soluble reactive phosphate, total nitrogen and total phosphorus). Nutrient analysis followed Grasshoff *et al.* (1983) and total organic carbon (TOC) was measured using a TOC analyser. The chlorophyll *a* was measured using Talling & Driver's expressions (1963) using 90% methanol as a solvent.

Each zooplankton sample was taken from 4 l of filtered 53 µm water and was preserved in 4% formalin. The term zooplankton is used to define the free-living invertebrate community, given that it is mainly composed of copepods and rotifers, although this community is not strictly planktonic as occasionally benthic species are present. Some copepod nauplii were cultivated in the laboratory to help identification. However, it was not possible to distinguish some larval stages, such as nauplius 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 (see Quintana *et al.*, 1998b and Brucet 2003 for more details of biomass estimations and of invertebrate community composition). Diversity and evenness were measured using Shannon & Wiener index (Krebs 2001). Diversity was calculated in two ways: first by using species abundance (diversity of species) and second by considering different larval stages as different species (diversity of species+stages). 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 (Poulet 1977, Hansen *et al.* 1994, Brucet 2003).

Due to their low numbers, samples with low organism counts taken immediately after a high disturbance have not been included in the analysis.

Size distribution analysis: Size distributions were analysed using underlying Pareto distribution parameters (Vidondo *et al.* 1997). The Pareto distribution has a cumulative distribution of probability defined as: $\text{prob}(s \geq S) = k \cdot s^{-c}$ 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 ($N_{s \geq S}/N_i$). The cumulative distribution of probability based on this probability estimation is equivalent to the normalized biomass-size spectrum (Vidondo *et al.* 1997). If the sizes are distributed according to a Pareto model, the plot on a double-logarithmic scale will display a straight line. This linear 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 & Peters 1991, Wells & 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 as: $\text{Log}[\text{prob}(s > S)] = c \log(K + D) - c \log(S + D)$.

This equation differs from the original Pareto model only by the additive constant D that changes the function into a non-linear one. The ordinary Pareto or Pareto type-I is a special case of the second type when $D=0$.

In order to differentiate between the two types of Pareto the following abbreviations have been used: r^2_I and r^2_{II} : goodness of fit (coefficient of determination) to Pareto type I and to Pareto type II, respectively. c_I and c_{II} : parameters of Pareto type I (linear model) and Pareto type II (non-linear model), respectively.

Correlations between biomass spectrum parameters and environmental variables or those related to the structure of the community were calculated by means of Pearson's coefficient of correlation. Samples were excluded which were taken immediately after a disturbance and which held low numbers of individuals (less than 10 individuals·L⁻¹).

Environmental situations: The community was characterised over time using Quintana *et al.* (1998b)'s approach to the zooplankton community of Empordà salt marshes as a whole, with situations defined by the flooding conditions and their most numerically dominant species. It includes the following five (the 6th described by these authors was not found here):

“*Synchaeta*”: situations dominated by *Synchaeta* spp. correspond to sudden massive flooding with nutrient en-

try following any intense disturbance (such as sea storms, rainfall or heavy freshwater flooding).

“Cyclopoids”: situations dominated by cyclopoids correspond to periods of steady, low-level input of water and nutrients.

“Calanoids”: situations dominated by calanoids correspond to relatively oligotrophic situation, associated with hydric stability.

“*Gammarus*”: situations dominated by benthic species such as *Gammarus aequicauda* and some harpacticoids correspond to periods of confinement which are frequent during the spring and at the beginning of summer.

“*Brachionus*”: situations dominated by *Brachionus plicatilis* correspond to periods of confinement with high concentrations caused by dessication in eutrophic basins and with 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 in this group. Other intermediate situations have been excluded.

RESULTS

Physical and chemical characteristics of the basin

Table I (middle) 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.

Linear and curved shapes of zooplankton biomass-size spectra

The spectrum of every sample was fitted to both Pareto type I (PI) and Pareto type II (PII) models. 37 samples fit PII better than PI and their corresponding spectra were classified as curved, while 31 samples fit PI better than PII and they were classified as linear. The rest of the spectra (48 samples) 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 high relative abundance of smaller sizes (Fig. 1a) while the curved shape indicates high abundance of larger sizes (Fig. 1b).

Comparing samples, species diversity, species richness and evenness 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 $F=4.2$, $p<0.05$).

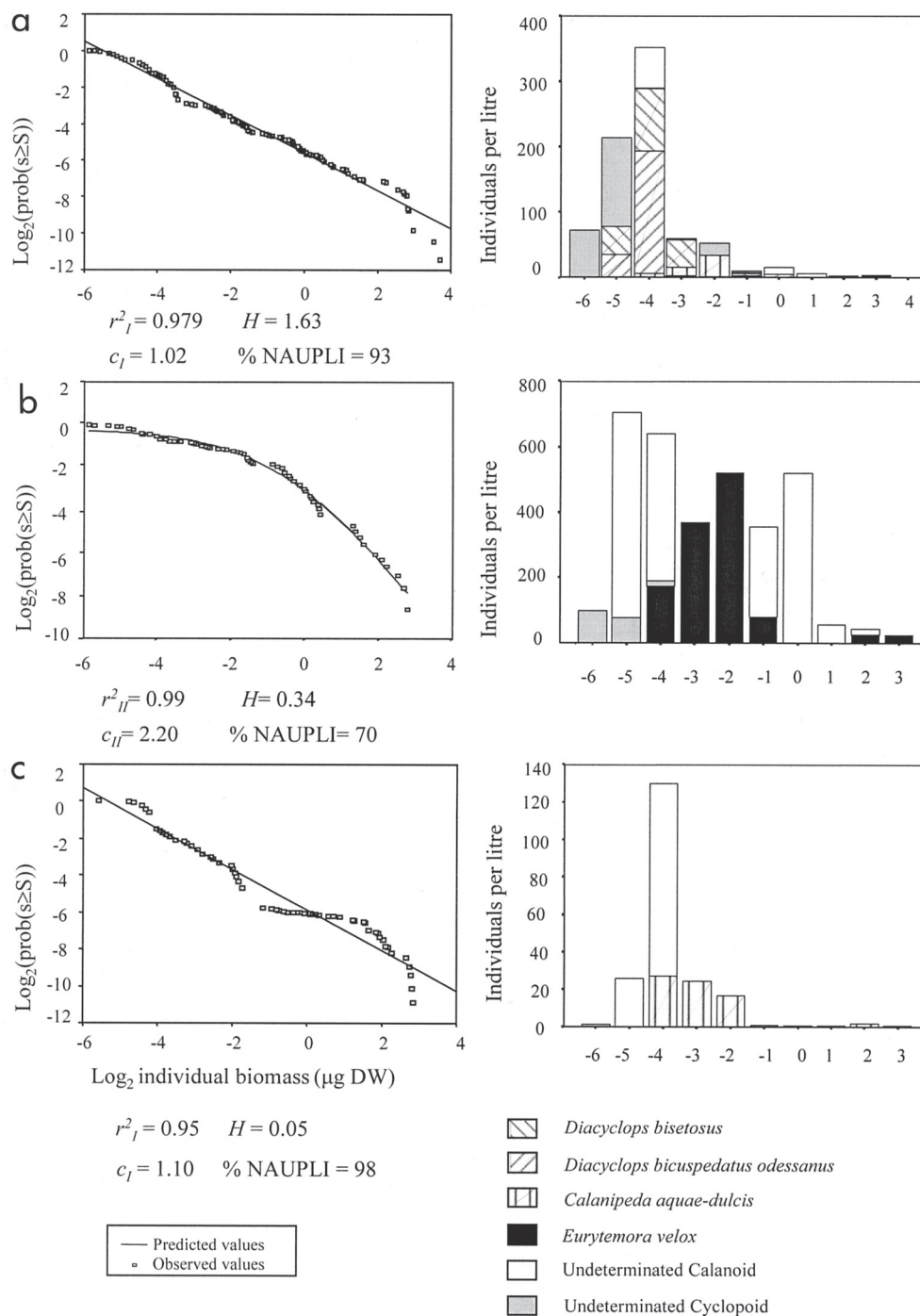


Fig. 1. – Types of spectra and abundance of each size (a) linear spectrum, with better fit to linear model (Pareto type I), (b) curved spectrum, with better fit to non-linear model (Pareto type II), (c) example of step-like substructures. On the right hand, the corresponding graph of species abundance per litre of each size class.

Taking into account only the fit to Pareto type I for all samples (68 samples), the goodness of fit (r^2_I) correlated positively with species diversity and species richness (Table I bottom). The slope (c_I) correlated negatively with species diversity and species+stages evenness, that is, size distribu-

tion 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 cyclopoid abundance and the PI slope (c_I) negatively to calanoid abundance (Table I bottom).

Table I. – Top: main morphometric characteristics of the studied basin, measured when being full. From Quintana (1995). Middle: descriptive statistics of the main physical and chemical water parameters. Bottom: 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 (* $p \leq 0.05$, ** $p \leq 0.01$). The number of samples is 68.

Height of water surface above mean sea level (m)		0.8		
Height above sea level of deepest point (m)		0.0		
Mean depth (m)		0.3		
Length (m)		84		
Mean width (m)		11		
Surface area, S (m ²)		983		
Volume, V (m ³)		252		
Development of volume		0.9		
Approximate area of the reception basin, Ac (m ²)		18750		
Ac / S		19		
Ac / V		74		

	n	Mean	Min.	Max.
Conductivity EC ₂₅ (mS·cm ⁻¹)	116	26.7	9.80	56.6
Temperature (°C)	116	16.4	4.70	34.7
pH	116	8.05	6.10	8.80
% oxygen saturation	116	84.9	1.0	239
Alkalinity (meq·l ⁻¹)	116	6.04	1.17	15.8
NH ₄ ⁺ (μM)	116	11.3	0.00	261
NO ₂ ⁻ (μM)	116	1.43	0.00	18.9
NO ₃ ⁻ (μM)	116	10.3	<0.05	246
SRP (μM)	116	7.39	<0.03	52.8
Total P (μM)	31	17.3	0.88	182
Total N (μM)	31	203	44.0	924
Chlorophyll (μg·l ⁻¹)	116	20.7	0.83	164

Variable	r^2_I	c_I
Diversity of species (Shannon index)	0,28*	
Diversity of species+stages (Shannon index)	0,30*	-0,34**
Evenness of species+stages		-0,41**
Number of species+stages	0,31*	
Log. number of species	0,30*	0.29*
% of calanoids		-0,32*
% of cyclopoids	0,31*	

Table II. – Top: 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. The number of samples is 56. Samples which do not belong to any situation have been excluded (12 samples). Bottom: number of spectra which better fit to a Pareto type I distribution and spectra which better fit to a Pareto type II distribution in flooding and confinement situations. The number of samples is 56. Samples which do not belong to any situation have been excluded (12 samples). In brackets, the number of spectra exhibiting stepped substructures.

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

SITUATION	Type I	Type II
FLOODING	"Synchaeta"	3 (1)
	"Undefined Synchaeta"	4
	"Cyclopoids"	3 (1)
	TOTAL	10 (2)
CONFINEMENT	"Calanoids"	14 (6)
	"Brachionus"	1 (1)
	"Gammarus"	0
	TOTAL	15 (7)

Size distributions associated with all three flooding situations were steep (Table II top); with confinement situations, “Calanoids” and “*Gammarus*” situations gave flatter slopes, although “*Brachionus*” situation was steep. Furthermore, the highest r^2_1 values occurred in “Cyclopoid” situations characteristic of flooding periods, and the lowest in “*Gammarus*” ones, which coincide with conditions previous to desiccation.

Likewise, during flooding periods (“*Synchaeta*”, “undefined *Synchaeta*” and “Cyclopoid” situations) a greater abundance of linear spectra was observed (χ^2 test, $p < 0.05$) (Table II bottom). In contrast, during conditions of confinement (“Calanoids”, “*Gammarus*” and “*Brachionus*” situations), that is, of a lack of water supplies, curved spectra were more frequent (χ^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.

After classifying the samples of the 4 years between those whose spectrum was linear shaped or curved shaped, we tested if linear shapes and curved shapes were more frequent in different moments of the hydrological cycle. Results were consistent with that described before for environmental situations, that is, water level was significantly higher in samples whose spectra were linear shaped (ANOVA, $F=19.1$, $p < 0.01$), according with a higher linearity of the spectra during water inputs.

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

Stepped shapes

In some cases, both linear and curved shapes exhibited step-like substructures (Fig. 1c), but they were rarer in the curved shapes. The steps’ appearance reduces its fit to the model, 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 hypertrophy.

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

Case example of temporal shift in spectrum shape

The following case shows 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. 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 entry into the marshes for three days. The level of the basin which had stayed high during flux regulation now dropped quickly with the gate’s opening (Fig. 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 spectra and diversity values were observed before and after the gate’s opening (Fig. 3). Before opening the sluice gate, biomass spectra showed a linear shape. Contrariwise, when confinement began after opening, biomass spectra showed a curved shape. Double-step substructures were observed in periods both before and after the gate’s opening.

Changes in species composition were also clear. With fresh-water input, the community had high diversity and was composed of cyclopoids and calanoids “Cyclopoid” situation. The community was composed mostly of *Diacyclops bicuspidatus*

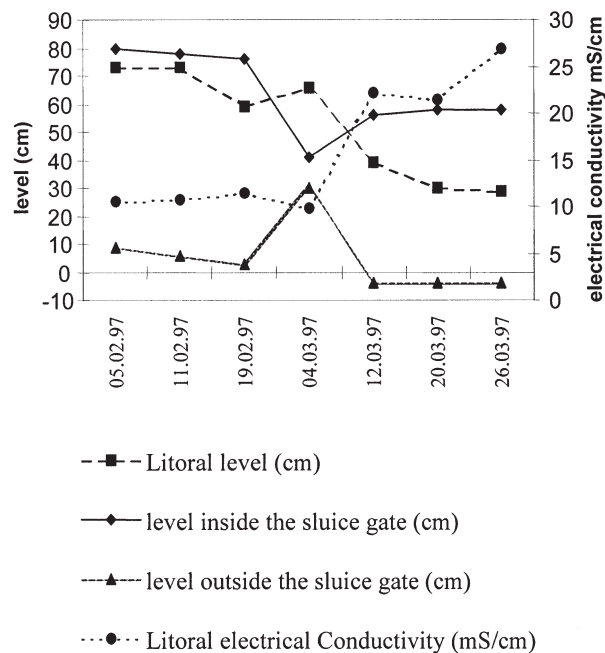


Fig. 2. – Water level change and electrical conductivity in the basin. Water level inside and outside the sluice gate regulating water flow in the drainage channel.

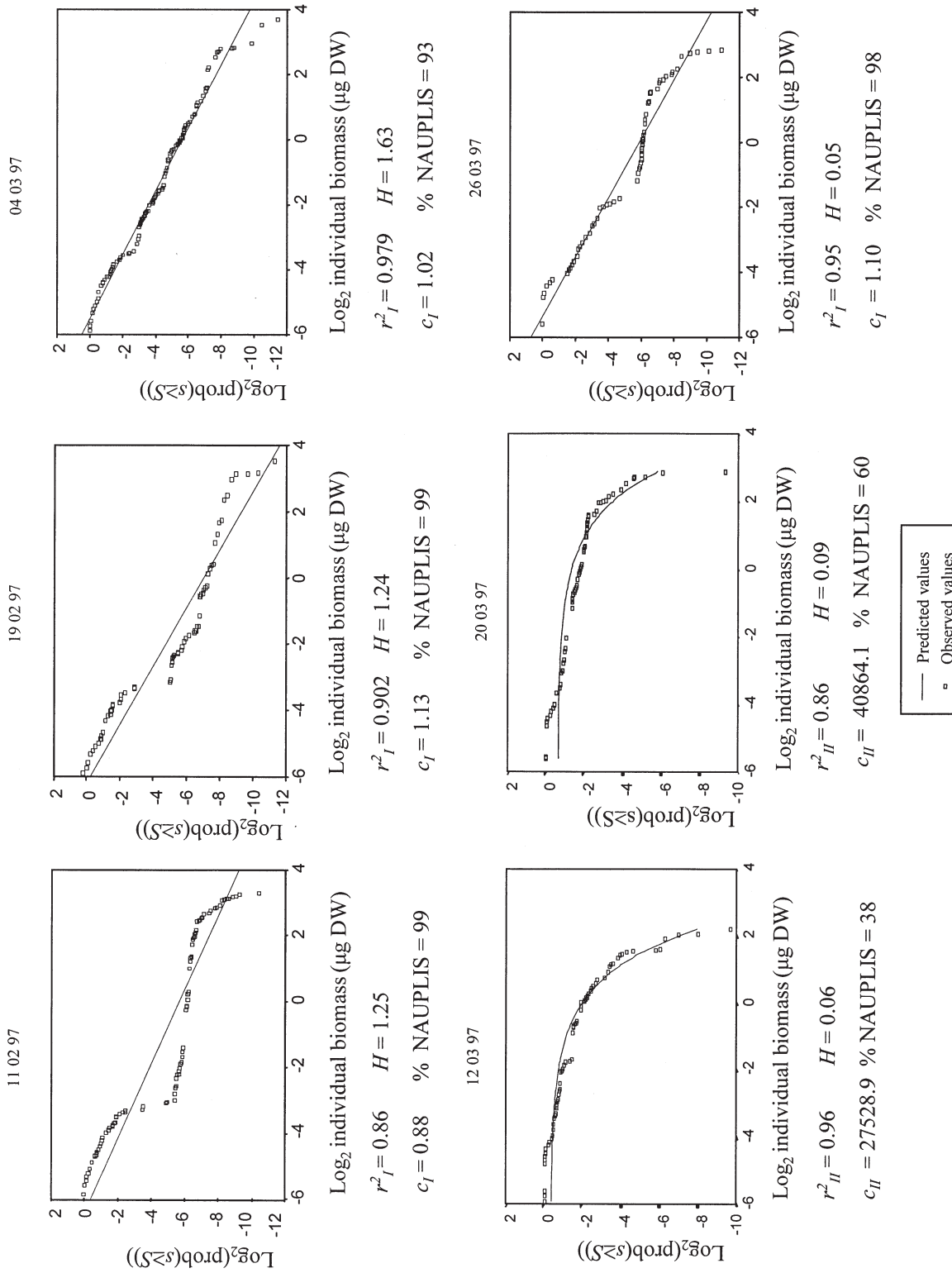


Fig. 3. – Example that shows a spectrum shift from PI to PII. Above, days before opening the sluice gate. Below, days after opening the sluice gate.

odessanus, *Diacyclops bisetosus*, and *Eurytemora velox*, with lesser abundances of *Halicyclops rotundipes* and *Calanipeda aquae-dulcis*. Maximal 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 naupli/copepodite ratio was very high in linear spectra, but not in curved spectra, with their high percentage of copepodites.

DISCUSSION

Stepped shapes and population dynamics

Dickie *et al.* 1987 attributed the existence of steps within the biomass size spectrum of an ecological group to population dynamics of the species in it. 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. On the other hand, Sprules & Goyke (1994) suggested that steps are as a consequence of an apparently stable, inner pattern of predation relations within an ecological group. In our study, steps do not seem to be caused by a pattern of predation relations but by population dynamics. For example, 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, steps in size distribution are unstable and reflect the population dynamics of the dominant species involved.

Linear and curved shapes and their ecological implications

Variation in fresh water and nutrient input in this basin is difficult to quantify, since entry flows

are not measurable. 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 (Fig. 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.

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 a linear spectrum and the availability at each trophic level of a wide range of resources permits the development of a higher number of populations, thus increasing species richness and diversity. In confinement conditions ("Calanoid", "*Brachionus*" and "*Gammarus*" situations) curved spectra are significantly more frequent and there is a decrease of species diversity probably due to the scarcity of resources and the effect of the competitive exclusion.

According to Dickie *et al.* (1987) different spectrum shapes would reflect ecological interactions between species or sizes. Thus, in situations of confinement, due to the lack of nutrient inputs, 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 would take on more relevance, favouring the displacement of biomass toward larger sizes. The result is a curved spectrum. Similarly, Boix (2000) found extremely curved shape spectra (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.

In contrast, under flooding conditions, nutrient input would cause population growth of small-sized organisms, over compensating for the effect of competitive interactions, which are relatively weak. Thus, the spectrum becomes linear indicating that size distribution is close to that expected by differences in allometric growth. 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. 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. In this case, flux regulation prolongs the linear spectra characteristic of flooding periods, due to the continual fresh supplies of water and nutrients.

We might conclude that the shape of the biomass size spectrum at ecological scaling show us the relative importance of the physical versus the biological control of the zooplankton community structure. As has been also reported by other authors (Sprules & Goyke 1994, Rodríguez 1994), under stable conditions, curved-shape biomass size spectra mainly appear as a result of the biological control of the zooplankton community structure. On the other hand, under fluctuating environmental conditions, which in our basins are related to nutrient inputs, physical control prevails and biomass-size distribution is a function of the population growth rate of different species, which results in a linear spectrum.

CONCLUSIONS

1 - Three types of biomass size spectra for the functional group of zooplankton were found and they changed according to environmental conditions: Linear shapes, which fit Pareto type I model better, curved shapes, which fit better Pareto type II model and stepped shape spectra, which usually fit poorly either model. 2 - Linear shape spectra are more frequent in flooding situations, with high energy input, when nutrient input causes population growth of small-sized organisms, more than compensating for the effect of competitive interactions. 3 - Curved shape spectra are found in situations of lack of food, which lead to an increase in ecological interactions between individuals that favour larger sizes. 4 - The analysis of the shape of the spectrum is a way to evaluate the degree of ecological interactions in the zooplankton functional group. 5 - The existence of steps within the biomass size spectrum of an ecological group 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 and there is little overlapping between the size ranges of different species.

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