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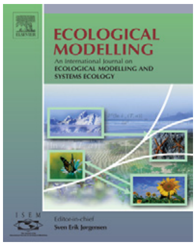

Structuring pelagic trophic networks from the biomass size spectra

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ABSTRACT

The selection and establishment of the structure (number and compartments, aggregation criteria, and trophic links) of the food webs is a critical task in trophic modelling. The present work proposes a systematic method to structure trophic networks in pelagic food webs. The biomass-size spectrum (BSS) is a well-established approach to analyze the structure of pelagic communities, and the body size is especially related to the ecological role of the organisms in the pelagic environment. To structure food webs, this work uses detailed arrangements of the community in size classes with increasing widths (like Sheldon-type BSS) as first aggregation criteria, and BSS theory as a framework to integrate the available knowledge about feeding selectivity in order to obtain a method to identify the trophic links between compartments. Diet composition matrices were estimated through the combination of a probability of encounter for each food type and a specific probability of ingestion related to the food size selectivity and other food quality characteristics (*e.g.*, morphology and nutritional quality). The feasibility of this approach has been illustrated through data of size-structured communities extracted from the literature including different planktonic predator guilds (nanoflagellates, cladoceran-dominated zooplankton and copepod-dominated zooplankton) in a high mountain lake (La Caldera, Spain), two subtropical wetland lakes (meso-oligotrophic Laguna Galarza and eutrophic Laguna Iberá, Argentina) and a marine microcosm (Alborán Sea, Mediterranean). The identification of "who eats whom" and "by how much" also allows for more accurate analyses of the trophic control in the BSS. Extensive analyses of the balance between top-down and bottom-up controls were developed for the feeding interactions of the study cases.

1. Introduction

Since the first developments of the biomass-size spectrum (BSS) theory during 1970s (Kerr, 1974; Sheldon et al., 1972, 1977), this tool has been widely used in the analysis of the pelagic food web structure. The existence of regular patterns in the pelagic BSS has also allowed examining general energetic characteristics of food webs (*e.g.*, Sprules and Munawar, 1986; Kerr and Dickie, 2001; San Martín et al., 2006). Linear BSS (plotted on a log–log scale) are related to ecosystems close to steady state and are characterized by a continuum of functional guilds or "trophic size positions" along the size gradient (Rodríguez and Mullin, 1986; Gaedke, 1992). The perturbations in the ecosystem are reflected in the shape of the BSS, appearing domes and troughs. This undulation mainly appears as a consequence of the unbalanced feeding interactions between

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well-defined trophic size positions (Thiebaux and Dickie, 1992; Kerr and Dickie, 2001; Cózar et al., 2003). The position of organisms in the size spectrum determines to a wide extent the ecological guild and the trophic niche of the organisms, especially in pelagic ecosystems (Pearre, 1986; Sharf et al., 2000). Predator:prey size ratio is often showed as the primary cause of food selectivity (*e.g.*, Peters, 1983; Hansen et al., 1994; Neubert et al., 2000). These characteristics give a particular significance to the use of the body size and the BSS as framework to structure pelagic food webs, a critical task in the trophic modelling.

The underlying theory supporting the relationship between the shape of the BSS and energetic characteristics of the food webs is based on several classical models mainly developed between mid-1970s and early 1990s (Kerr, 1974; Platt and Denman, 1978; Borgmann, 1982; Thiebaux and Dickie, 1992; Silvert, 1993). These theoretical models explore the general flow of biomass from the smallest to the largest organisms through size-dependent processes. Predation processes govern the mass flow and the shape of the spectrum in these models. However, the use of a fixed predator:prey ratio to relate each predator size class with a prey size class limits the application of these general models in specific food webs in nature. Recently, Benoit and Rochet (2004) introduced the concept of a distributed predator:prey size ratio to the theoretical modelling of the spectrum. Predators could feed not only on prey of a unique size class, but also on a range of prey size classes. Nevertheless, the existing approach still needs to be refined to model real trophic networks. Firstly, a general optimum linear-size ratio of 10 is traditionally assumed in the modelling of pelagic ecosystems (*e.g.*, Kerr, 1974; Sheldon et al., 1977; Silvert, 1993). Hansen et al. (1994) showed, however, that the optimum predator:prey ratio may be highly variable (between 1 and 100), but also showed how the ratios are consistent within functional groups. They suggested an additional classification of predators which depends on the feeding modes (*e.g.*, filter feeders and raptorial feeders) in order to use more specific predator:prey ratios in the trophic modelling purposes. Secondly, food selection can be also conditioned by other characteristics independent of the body size, which should be considered for a more realistic modelling. There is evidence suggesting that some prey of singular morphology can be less ingestible compared with other prey of similar size (*e.g.*, Margalef, 1978; Gliwicz, 1990). Filamentous cyanobacteria, for instance, are common organisms characterized by a low ingestibility that hampers the feeding process of cladocerans (Gragnani et al., 1999; DeMott et al., 2001; Ghadouani et al., 2003). Nutritional-quality selectivity is also commonly reported among microphages able to consume living and non-living particles (Bern, 1990).

During the last decades, numerous studies have increased the knowledge of the role of the factors controlling the food selectivity in the pelagic environment (*e.g.*, Pearre, 1986; Sharf et al., 2000; Hansen et al., 1994). The consideration in trophic models of any set of factors contributing to food selection can be made possible from probability methods (Chesson, 1983). To apply this approach, BSS offers a suitable framework to arrange the pelagic community components as well as the varied existing information about the pelagic food selectivity. The general goal of this work is the establishment of the bases of a systematic method for integrating the information about feeding selectivity into diet matrices. The goal undertakes a basic task in ecology, who eats whom, and allows for varied applications on ecological modelling related to the analysis of food web structure, species' interaction strength, population dynamics or community stability. In this work, the method was applied to assess the balance between top-down and bottom-up trophic controls between the functional guilds or trophic positions of the BSS.

2. Study sites

Data of the planktonic biomass-size structures in four aquatic ecosystems (La Caldera Lake, Laguna Galarza, Laguna Iberá and a microcosm experiment on Alborán Sea waters) were extracted from the literature (Table 1). Predator guilds of nanoflagellates, cladoceran-dominated zooplankton and copepod-dominated zooplankton were analyzed. Diet composition matrices were estimated from the BSS corresponding to the phase of complete development of the predator guild, that is, when they had reached the maximum biomass after the growth period. We will refer to this phase as high-biomass phase of the predator guild (HBP). BSS during the low-biomass phase of the predators (LBP), before the growth period, were also used for comparative purposes (Table 1).

La Caldera is an oligotrophic, high-mountain small lake located in Sierra Nevada (Spain). The lake is characterized by a persistent and large biomass gap in the central range of the plankton BSS (Echevarría et al., 1990). Biomass is accumulated in the small phytoplankton size range (under 10 μm of equivalent spherical diameter, ESD) and in the zooplankton size range (above 100 μm ESD). The oligotrophic nature of this lake is suggested as a possible cause of this biomass gap during most of the year (Echevarría et al., 1990), but the gap strikingly remains even during particular events of higher productivity. In this work, the hypothesis of top-down forcing of this gap during one of these events of higher productivity was examined. We analyzed a phytoplankton bloom linked to a period of abnormally high rainfall and nutrient availability in September 1987 (Echevarría et al., 1990). The increase of zooplankton biomass in this study scenario was mainly related with the development of a population of considerably large cladocerans (*Daphnia pulex*).

Laguna Galarza and Laguna Iberá are subtropical shallow lakes located in *Esteros del Iberá* wetland (northeast Argentina). Laguna Galarza shows a meso-oligotrophic status, whereas Laguna Iberá shows signs of eutrophication (Cózar et al., 2003). The phytoplankton community of Laguna Galarza shows a relatively high species diversity. In Laguna Iberá, however, long filamentous cyanobacteria (mainly *Lyngbya limnetica*) represent the major fraction of the phytoplankton biomass, holding stable biomass accumulations in the BSS throughout the year. The zooplankton community of Laguna Galarza was dominated by large-sized copepods whereas small-sized cladocerans dominate in Laguna Iberá. We compared the diet compositions and the influence of filamentous cyanobacteria on these two zooplankton communities.

Using a natural community from the NW sector of Alborán Sea (Western Mediterranean), Cózar and Echevarría (2005) generated an artificial phytoplankton bloom by adding nutri-

Table 1 – Data sources and characteristics of the feeding interactions analyzed (see Table 2 for notations)

Predator guild	Prey	Ecosystem	Characteristics of the study period	Time lag between LBP and HBP	Source
Metazooplankton dominated by large-sized cladocerans	Plankton community	La Caldera Lake	Rainfall-induced bloom (September 1987)	20 days	Echevarría (1991)
Metazooplankton dominated by large-sized copepods	Plankton community	Laguna Galarza	Seasonal spring bloom (December 1999)	3 months	Cózar et al. (2003)
Metazooplankton dominated by small-sized cladocerans	Plankton community dominated by filamentous cyanobacteria	Laguna Iberá	Seasonal spring bloom (December 1999)	3 months	Cózar et al. (2003)
Protozooplankton dominated by nanoflagellates	Bacterial community	Alboran microcosm	Artificially induced bloom by adding nutrients	5 days	Cózar and Echevarría (2005)

Table 2 – Notations

LBP	Low-biomass phase of the predator guild
HBP	High-biomass phase of the predator guild
BSS	Biomass-size spectrum
S_N	Nominal size of a particular size class of the BSS
i	Prey size class, $i \in [1,\ldots,n]$
j	Predator size class
t	Prey morphotype, $t \in [1,\ldots,r]$
k	Nutritional food type, $k \in [1,\ldots,m]$
S_i	Prey nominal size
S_j	Predator nominal size
C_{ij}	Clearance percentages of the sized predator j on the sized prey i
$I_{S_{ij}}$	Size selectivity index of the sized predator j for the food size i
SSS	Food size selectivity spectra of a sized predator or a predator guild (calculated from $I_{S_{ij}}$)
$I^t_{M_{ij}}$	Morphological-quality selectivity index of the predator j for food morphotype t of the size class i
$I^k_{N_{ij}}$	Nutritional-quality selectivity index of the predator j for the nutritional food type k of the size class i
α^{kt}_{ij}	Overall probability of ingestion given encounter of food type ikt for the sized predator j
N^{kt}_i	Abundance of the food type ikt
P^{kt}_{ij}	Fraction of the food type ikt relative to the other food types foraged in the diet of the sized predator j
DSS	Diet-size spectra of a sized predator or a predator guild (calculated from P^{kt}_{ij})

ents in a microcosm experiment maintaining high turbulence. In the experiment, the heterotrophic community was represented by bacteria and nanoflagellates. Large-sized metazoan predators were scarce. After the phytoplankton bloom, the bacterial abundance increased simultaneously to the biomass of nanoflagellates, suggesting bottom-up control. However, a significant positive correlation between the average size of bacteria colonies and the biomass of predators was also found, suggesting some top-down control of bacteria size structure. We analyzed the trophic control in this microbial feeding interaction.

3. Methods

The first criterion to be applied in the aggregation process of the pelagic communities was the size of the organisms. BSS were built by arranging the organisms in size-classes with increasing widths, following a geometric 2^n series (*sensu* Sheldon et al., 1972). Narrower size classes were used to describe the size structure of the smaller organisms. A nominal size within each size class was identified in order to perform a more suitable use of the size-related information (*e.g.*, predator:prey size ratios and allometric metabolic models). The algorithm proposed by Blanco et al. (1998) was applied to calculate the optimum nominal size (S_N) of a particular size class:

$$S_N = S_L\left(\frac{c^{b+1}-1}{(c-1)(b+1)}\right)^{1/b}$$

where S_L is the lower limit of size class, c is the ratio of the geometrical increasing of classes (2 in this study), and b is the linear slope of the size spectra of normalized biomass (divided by the amplitude of the size class; Platt and Denman, 1978) on a double log plot.

Predators within each size class were subsequently aggregated into large functional groups with similar feeding modes and consistent predator:prey size ratios (S_j:S_i). Following the criterion of Hansen et al. (1994), predators were grouped in meroplankton, cladocerans, copepod nauplii, copepods, rotifers, ciliates and flagellates.

Preys within each size class were classified according to their morphology (spheroid and filaments) and nutritional quality (living and inert particles).

To establish and weight the trophic links between predators and preys, we use a food size selectivity index ($I_{S_{ij}}$) and other selectivity indices related to characteristics independent of body size such as morphology and nutritional quality ($I^t_{M_{ij}}, I^k_{N_{ij}}$). Methods to evaluate these selectivity indices are described in the following sections.

3.1. *Food size selectivity*

In the literature, the food size selectivity of a particular functional group of predators is usually quantified as clearance percentages (C_{ij}) at several S_j:S_i ratios in relation to a maximum clearance rate at the optimal S_j:S_i. The valuable review of Hansen et al. (1994) provided S_j:S_i corresponding to the maximum C_{ij}, and to the 50% and 10% of the maximum C_{ij} below (50%-min and 10%-min) and above (50%-max and 10%-max) the optimal S_j:S_i for a wide set of functional groups of planktonic predators. These C_{ij} data at different S_j:S_i were linearly interpolated to obtain continuous distributions of prey size selectivity for the predator groups. Subsequently, a food size selectivity index ($I_{S_{ij}}$) was estimated as clearance percentages in relation to the total clearance in the *n* size classes of the BSS foraged by *j*. Therefore, the preference of the sized predator *j* for the prey size *i* was estimated as

$$IS_{ij} = \frac{C_{ij}}{\sum_{i=1}^{n} C_{ij}}$$

$I_{S_{ij}}$ ranges between 0 and 1 ($I_{S_{ij}} \in [0,1]$) and the sum of all size selectivity indices of the *n* sized resources ingestible by *j* must be equal to 1 ($\sum_{i=1}^{n} I_{S_{ij}} = 1$). We will refer to the histograms representing the variability of $I_{S_{ij}}$ along the size spectra as prey size selectivity spectra (SSS). SSS establishes the trophic links of each sized predator with the size classes of the BSS and perform a first weighting of these links.

Hansen et al. (1994) did not provide a quantitative description of the 10%-min S_j:S_i of cladocerans and the 10%-min and -max S_j:S_i of flagellates. In this work, the lower limit of cladoceran SSS was established at 1000:1 ESD ratio. Researchers have rarely reported a S_j:S_i up to 1000 in cladocerans (DeMott, 1982; Vaqué and Pace, 1992). The lower and upper limits of flagellate SSS were established with the usual prey size range reported for most flagellate groups (chrysophytes, bicoecids, pedinellids prymnesiophytes, and kinetoplasts), that is, from 2:1 to 8:1 ESD ratio (*e.g.*, Fenchel, 1982; Chrzanowski and Šimek, 1990; Moestrup and Andersen, 1991).

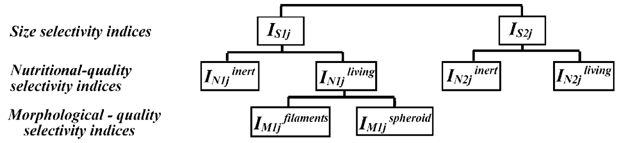

Fig. 1 – Example of multiplication successions of selectivity indices to estimate different probabilities of ingestion (α_{ij}^{kt}). Suppose a predator *j* foraging in two food size classes (*i* = 1, 2). Consequently, two size selectivity indices need to be estimated, I_{S1j} and I_{S2j} (see first level: size selectivity). Inert and living particles are available in each size class (*k* = *inert* and *living*). Thus, four nutritional-quality selectivity indices are needed (see second level). Two different morphotypes of living particles are available in *i* = 1, filamentous cyanobacteria and spheroid prey (*t* = *filaments* and *spheroid*). Two morphological-quality selectivity indices are needed (see third level). The predator has a choice of five food types characterized by five different α_{ij}^{kt}. For instance, the ingestion probability of class 1 spheroid prey would be $\alpha_{1j}^{\text{living spheroid}} = I_{S1_j} I_{N1_j}^{\text{living}} I_{M1_j}^{\text{spheroid}}$; and the ingestion probability of class 2 inert particles would be $\alpha_{2j}^{\text{inert}} = I_{S2_j} I_{N1_j}^{\text{inert}}$.

3.2. *Food selectivity in relation to characteristics independent of the size*

Food selection is, to a wide extent, determined by the size but it may depend on other food characteristics (Bern, 1990; DeMott et al., 2001). Selectivity related to characteristics independent of body size was considered through specific selectivity indices. In this work, we used a selectivity index related to the prey morphology ($I^t_{M_{ij}}$) and a selectivity index related to the food nutritional quality ($I^k_{N_{ij}}$) (Fig. 1).

Suppose a sized predator *j* has a choice of *m* prey morphotypes distributed in *n* size classes. The morphological selectivity index for a morphotype *t* in the size class *j* would be given by

$$I^t_{M_{ij}} = \frac{C^t_{ij}}{\sum_{i=1}^{n}\sum_{t=1}^{m} C^t_{ij}},$$

where C^t_{ij} is the clearance rate of *j* for the morphotype *t* in the size class *i*. $I^t_{M_{ij}}$ shows identical properties to $I_{S_{ij}}$ ($I^t_{M_{ij}} \in [0, 1]$; $\sum_{i=1}^{n}\sum_{t=1}^{m} I^t_{M_{ij}} = 1$).

Numerous studies deal with the negative effect of cyanobacteria filaments blooms on the feeding process (*e.g.*, Gliwicz, 1990, Gragnani et al., 1999, Ghadouani et al., 2003), although quantitative size-based studies are scarce. DeMott et al. (2001) compared C_{ij} for a wide size range of cladocerans in a medium composed by *Scenedesmus* sp. and another one mainly composed by filamentous cyanobacteria. They showed how the effect of the cyanobacteria filaments on C_{ij} depends on predator size. The allometric function for C^t_{ij} showed little o no change with increasing predator size (S_j)

for cladocerans feeding in the medium composed by spheroid preys (t = spheroid), and C^{spheroid}_{ij} was around 1.10 for the whole size range of predators. By contrast, the C^{t}_{ij} declined sharply with increasing S_j in the medium with cyanobacteria filaments (t = filaments): $C^{\text{filaments}}_{ij} = 619S_j^{-0.775}$, $R = 0.8246$, $P < 0.001$. Since filamentous cyanobacteria were quantitatively important in Laguna Iberá, we need to estimate and use an $I^{t}_{M_{ij}}$ to consider this morphological influence on the trophic flow. Using C^{t}_{ij} functions of DeMott et al. (2001) to estimate $I^{t}_{M_{ij}}$, note that the morphological selectivity is not independent of the body size and considers the dependence on the predator size (S_j). $I^{t}_{M_{ij}}$ for the same prey morphotype in the same size class is different for different sized predators.

The ability to discriminate among particles with different nutritional quality is also relevant in crustaceans (Bern, 1990). A nutritional-quality selectivity index ($I^{k}_{N_{ij}}$) was used to model this selection ability. Suppose that a predator j has a choice of r nutritional food types in n size classes. The selectivity for a nutritional food type k in the size class i would be

$$I^{k}_{N_{ij}} = \frac{C^{k}_{ij}}{\sum_{i=1}^{n}\sum_{k=1}^{r} C^{k}_{ij}}, \tag{1}$$

where C^{k}_{ij} is the clearance rate of j for the nutritional food type k of the size class i. $I^{k}_{N_{ij}} \in [0, 1]$ and $\sum_{i=1}^{n}\sum_{k=1}^{r} I^{k}_{N_{ij}} = 1$). Bern (1990) estimated the selectivity by nutritive living particles for several crustacean species and for four size classes of food particles. He estimated a selectivity index as the ratio of C^{k}_{ij} for k = living particles to C^{k}_{ij} for k = inert particles ($C^{\text{living}}_{ij}/C^{\text{inert}}_{ij}$). Copepods showed selection ability throughout the whole size range foraged, however cladocerans showed some selectivity only for relatively large prey size. Using Bern's data, the relevance of detritus particles on crustacean diets was compared in Laguna Galarza and Laguna Iberá. Crustacean species were selected in order to match the zooplankton composition of the study lakes (Cózar, 2003). Data from *Eudiaptomus gracilis* were used for the copepod community and data from *Bosmina coregoni*, *Chydorus sphaericus* and *Diaphanosoma brachyurum* were used for cladocerans. Body length was converted to body volume, and subsequently ESD, using general geometric formulae with the best fit to body shape. The extrapolation of $C^{\text{living}}_{ij}/C^{\text{inert}}_{ij}$ indices along the whole consumption size range was performed by power fitting of the selectivity data as function of S_j:S_i as ESD ratio. We obtained for copepods: $C^{\text{living}}_{ij}/C^{\text{inert}}_{ij} = 2325(S_j : S_i)^{-1.398}$, $R = 0.7007$, $P = 0.0795$, $n = 7$ and for cladocerans: $C^{\text{living}}_{ij}/C^{\text{inert}}_{ij} = 13.273(S_j : S_i)^{-0.603}$, $R = 0.6821$, $P = 0.0038$, $n = 16$). To estimate $I^{k}_{N_{ij}}$ from Eq. (1), the distributions of C^{living}_{ij} *vs.* S_j:S_i for copepods and cladocerans were obtained from Hansen et al. (1994), and C^{inert}_{ij} *vs.* S_j:S_i was derived from the equations extracted from Bern (1990). Note that, in this case, $I^{k}_{N_{ij}}$ depends on both predator size (S_j) and prey size (S_i).

3.3. *Integrating the selectivity indices into the diet-size spectrum*

The indices affecting the food selectivity ($I_{S_{ij}}, I^{k}_{N_{ij}}, I^{t}_{M_{ij}}$) were integrated into an overall probability of ingestion given encounter (α^{kt}_{ij}). This probability was obtained multiplying the particular selectivity indices of the food types available in the consumption size range of each sized predator (Fig. 1). In this way, $\alpha^{kt}_{ij} \in [0, 1]$ and $\sum_{i=1}^{n}\sum_{k=1}^{r}\sum_{t=1}^{m} \alpha^{kt}_{ij} = 1$. Predator diets depended on α^{kt}_{ij} as well as the probability of encounter with the different food types in the medium (DeMott, 1995). The abundance of each food type in the medium (N^{kt}_{i}) was used as an indicator of this probability of encounter (note that this approximation neglects differences in prey motility and specific detection distance of the predators). The fraction of a given food type (ikt) relative to the other food types present in the diet of j was estimated as

$$P^{kt}_{ij} = \frac{N^{kt}_{i}\alpha^{kt}_{ij}}{\sum_{i=1}^{n}\sum_{k=1}^{r}\sum_{t=1}^{m} N^{kt}_{i}\alpha^{kt}_{ij}}$$

The comparison of the relevance of detritus particles in the diets of the crustacean assemblages of Laguna Galarza and Iberá implies the knowledge of the abundance of detritus particles in each size class of the spectrum. Detrital size spectrum may be measured with particle counters, but these data were not available for the study cases. We used a theoretical approximation of the abundance of plankton-derived detritus (A_i), a major source of small detritus particles. Abundance-size spectra of plankton-derived detritus particles were estimated from a steady-state mass balance between production and losses rates of plankton-derived detritus particles in the water column. Production rates were estimated from allometric models for the lifetime of plankton and losses rates from the usual Stokes settling law. For a certain size class i:

$$B_i a {S_i}^{b} + A_i S_i V_i d = 0$$

where B_i is the plankton biomass in the size class i; S_i is the nominal size of i; a and b are the coefficients of the allometric models (McNiel and Lawton, 1970; Båmstedt and Skjoldal, 1980; Moloney and Field, 1989); A_i is the abundance of plankton-derived particles of i; V_i is the settling velocity for S_i; d is the mean depth of the lake.

Diet matrices of a predator size class or a predator guild were shown on histograms of P^{kt}_{ij} along the size spectra. We will refer to these size-based illustrations of the diet matrices as diet-size spectra (DSS). DSS for functional guilds were estimated adding the individual DSS of each predator size class within the guild. Individual DSS were added weighting by the consumption rate and abundance of the predator size classes composing the guilds. Allometric models for the main functional groups (Ikeda, 1977; Moloney and Field, 1989) were used to estimate the consumption rates of the predator size classes.

4. Results

Trophic analyses were performed on whole predator guilds integrating individual diets of each predator size class within the guild. Between 40 and 450 feeding links between sizes classes of the BSS were considered to estimate each SSS or DSS of the predator guilds studied. SSS depend exclusively on intrinsic characteristics of the predator guild (size structure and functional composition). Therefore, SSS are useful to determine the foraging size window and the food size preference of a particular predator guild. DSS are also conditioned by the food abundance and diversity (size, morphology, and nutritional quality) in the ecosystem.

SSS were used to show the differences in food size preference of the predator guilds (Fig. 2). The optimal food size (with the highest clearance rate) for the protozooplankton community of Alborán microcosm was located around 0.7 μm ESD. The position of SSS along the BSS varied among the three-metazooplankton guilds studied. The optimal food size was located around 22 μm ESD in Laguna Galarza, 16 μm ESD in La Caldera and 2 μm ESD in Laguna Iberá. Zooplankton guilds of Laguna Galarza and La Caldera showed similar optimal food size but the foraging window was wider for the cladoceran-dominated guild of La Caldera. SSS in La Caldera did not show a log-normal distribution like in Laguna Galarza, reflecting the ability of large cladocerans to feed on the smallest microbial

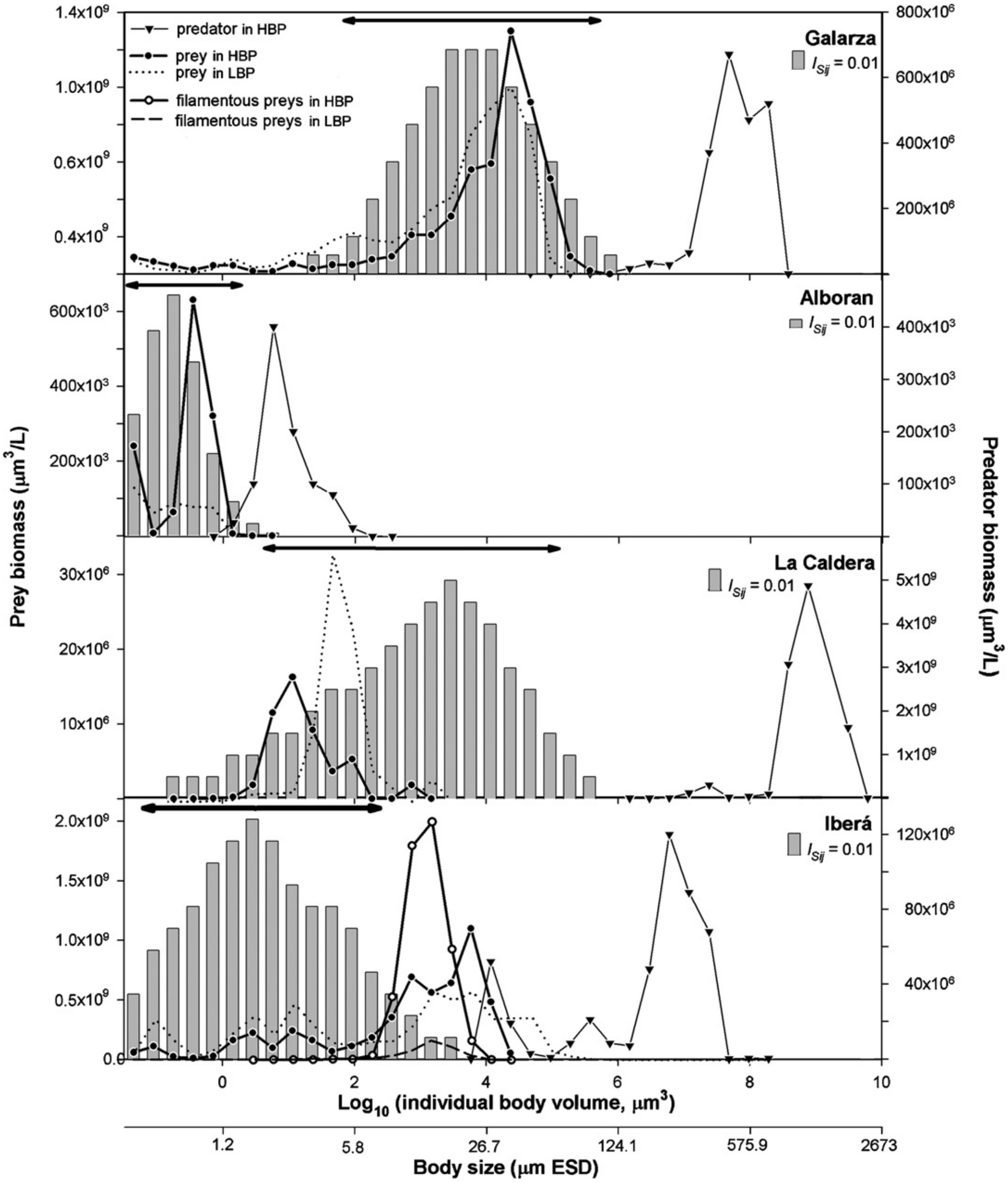

Fig. 2 – Size selectivity spectra (SSS) of predator guilds in Laguna Galarza, Alboran Sea microcosm, La Caldera Lake and Laguna Iberá. SSS are represented as histograms where the height of the bars indicates the size selectivity of the predator guild on each prey size class ($I_{S_{ij}}$). The bar height corresponding to $I_{S_{ij}} = 0.01$ is shown in legend. Optimal feeding windows are marked with arrows over the SSS. Optimal feeding windows include the size classes around the optimal food size which accumulate no less than 90% of the feeding capacity of the guild ($\Sigma I_{S_{ij}} \geq 0.90$). Prey and predator BSS are shown with continuous lines in HBP and broken lines in LBP. In Laguna Iberá, prey biomass is differentiated between filaments and other prey.

size classes (DeMott, 1982; Vaqué and Pace, 1992). The SSS of the cladoceran-dominated guild of Laguna Iberá showed also a wide foraging size interval on the microbial food web.

Fig. 2 also compares the prey BSS during the low-biomass phase (LBP) and high-biomass phases (HBP) of the predator guilds. In Laguna Galarza, prey BSS did not change considerably between LBP and HBP, being coupled with the predator SSS. In Alborán microcosm, the size range of the prey biomass accumulation was similar during both phases and matched with the size range covered by SSS, although prey BSS showed a certain reorganization when predator biomass increased. During the HBP, the prey biomass within the optimal food size decreased while increased below (small single bacteria) and above (long bacteria colonies) the optimal food size. Therefore, prey BSS showed a marked break coinciding with the optimal prey size. In La Caldera and Laguna Iberá, SSS were uncoupled with the prey BSS, especially during the HBP. Prey biomass was accumulated in the tails of SSS, towards relatively small-sized organisms in La Caldera and towards large-sized organisms in Laguna Iberá. The biomass percentage in the tails of SSS was higher during the HBP in both lakes. Besides the change in the prey size structure, an increase of the relative biomass of cyanobacteria filaments was observed in Laguna Iberá during the HBP (Fig. 2).

DSS modelled the real consumption of the predator guilds (Fig. 3). DSS showed the size classes of maximal consumption, around 22 μm ESD in Laguna Galarza, 7 μm ESD in Laguna Iberá, 3 μm ESD in La Caldera Lake and 0.9 μm ESD in Alborán microcosm. The size class of maximal consumption in Laguna Galarza coincided with the optimal food sizes of SSS. In Laguna Iberá and La Caldera, however, the highest consumption was located in the tails of SSS. The guild of heterotrophic nanoflagellates of Alborán microcosm illustrated an intermediate case. DSS showed the highest consumption in size classes (0.44 and 0.88 μm ESD) adjoining the optimal size classes (0.56 and 0.76 μm ESD, see SSS).

A more detailed description of diet composition was performed in Laguna Iberá and Laguna Galarza. Plankton-derived detritus was considered and two types of living resources were available, filamentous cyanobacteria and other prey. Large differences were found in the zooplankton diets of these wetland lakes. The average percentage of detritus in diet was 61% in the zooplankton community of Laguna Iberá and 29% in Laguna Galarza, and the average percentage of filamentous cyanobacteria was 9% in Laguna Iberá and <0.1% in Laguna Galarza.

5. Discussion

The analysis of the balance between top-down and bottom-up control usually consists in a qualitative assessment based on the knowledge of the different effects of these two trophic controls on the temporal co-variation of the biomass of prey and predators (Hairston et al., 1960; Cury et al., 2005) and on the prey size distributions (Brooks and Dodson, 1965; Jürgens et al., 1999). Regarding the biomass co-variation, top-down control occurs when an increase in predator biomass leads to a decrease in prey biomass while bottom-up control is considered when the increase in prey biomass is related with an increase in predator biomass. Although the availability of intensive time series is desirable, we use one reference scenario during the LBP to determine the biomass co-variability of prey and predators (Table 1). SSS were used in order to perform a more suitable identification of the prey size range corresponding to a particular predator guild. Zooplankton guilds can forage on specific size windows within the phytoplankton community, size windows within the microbial food web or size windows including portions of both communities (Fig. 2). Using SSS, we tried to quantify exclusively the prey biomass variability within the optimal feeding window and not the biomass accumulated in refuge size classes outside this window (Brooks and Dodson, 1965; Jürgens et al., 1999). Under top-down control, increases in the biomass of the refuge size classes can be linked to the increase in predator biomass, inducing errors in the estimates of the biomass variability if prey compartment is not accurately determined. We considered the optimal feeding window as the size classes concentrating no less than 90% of the feeding capacity of the predator guild ($\Sigma I_{S_{ij}} \geq 0.90$) (Fig. 2). In this way, refuge size classes are considered those classes not foraged or where the feeding efficiency is low. Therefore, increases in prey biomass

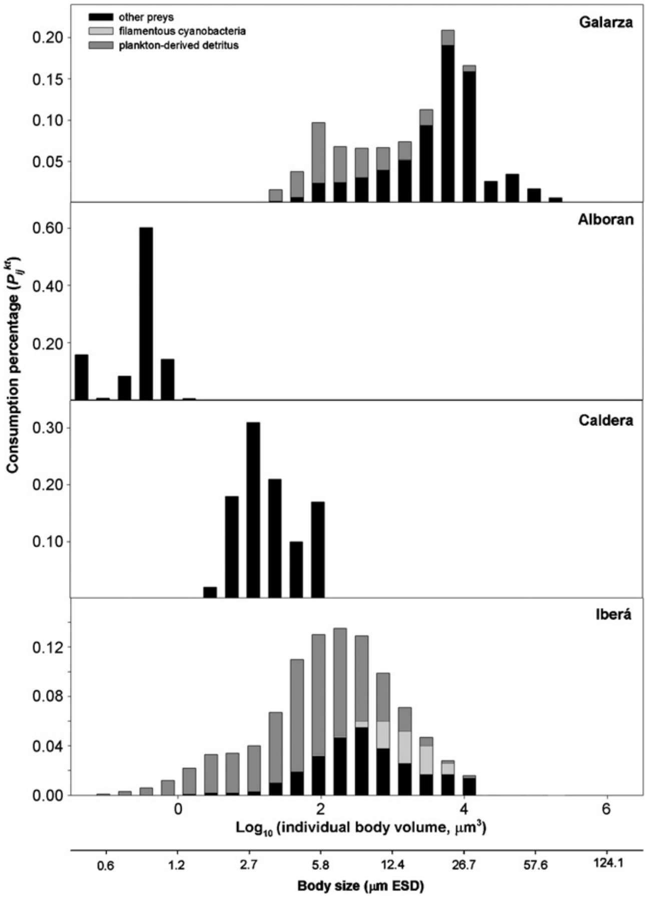

Fig. 3 – Diet-size spectra (DSS) of predator guilds in Laguna Galarza, Alboran Sea microcosm, La Caldera Lake and Laguna Iberá. DSS are represented as histograms where the height of the bars indicates the consumption fractions (P_{ij}^{kt}) for the predator guild. Plankton-derived detritus was considered in Laguna Galarza and Laguna Iberá.

Table 3 – Indicators examined for the balance between top-down and bottom-up forcing in single feeding interactions

	Galarza	Alboran	La Caldera	Iberá
Prey biomass variability (μm^3/L)	$+7.2 \times 10^7$	$+8.2 \times 10^5$	-3.0×10^7	-1.2×10^9
Predator biomass variability (μm^3/L)	$+2.0 \times 10^9$	$+7.4 \times 10^5$	$+8.3 \times 10^9$	$+4.1 \times 10^8$
Prey:predator biomass variability ratio	+0.04	+0.89	−0.004	−2.84
Prey:predator biomass ratio	+2.24	+1.37	+0.01	+3.28
Slope (Pearson correlation coefficient)	+1.13 (0.672**)	+0.33 (0.183)	−1.57 (0.407*)	−2.17 (0.705**)

Prey and predator biomass variability were estimated using the LBP reference scenarios shown in Fig. 2. Prey biomasses were quantified within the optimal feeding window ($\sum I_{S_{ij}} \geq 0.90$). Ratios of prey to predator biomass in HBP were calculated for the biomass of prey in the whole size range foraged ($I_{S_{ij}} > 0.01$). Slopes were obtained from the linear correlation of SSS against the BSS over the whole size range foraged in HBP (see text). Also shown are the Pearson coefficients of the linear correlations. Stars in correlation coefficients indicate significant relationships using confidence intervals of 90% (*) and 95% (**).

coupled to the increases in predator biomass were found in Laguna Galarza and Alborán microcosm (Table 3). This positive co-variation would be indicative of a bottom-up control. In La Caldera and Laguna Iberá, prey biomass decreased when that of predators increased, suggesting top-down control. The analysis of the co-variability of prey and predator biomasses is a suitable method to identify the nature of the dominant trophic forcing (*e.g.*, Cury et al., 2005), but only qualitative information is achieved. A quantitative approximation of the trophic forcing could be suggested from the ratio of prey biomass variability to the predator biomass variability. However, this ratio is hardly comparable between ecosystems or between feeding interactions linking different food web components (Table 3).

The quantitative assessing of the trophic forcing balance can be also focused on the trophic effects on prey size structure during the HBP. A top-down control is considered when large part of prey biomass is accumulated in refuge classes (Brooks and Dodson, 1965; Jürgens et al., 1999). Bottom-up control will occur, in turn, when the optimal feeding window is adjusted to prey BSS. Based on these definitions, we assessed the balance between top-down and bottom-up controls relating the predator SSS and the prey BSS. A linear fitting of SSS against the prey BSS was performed by the least-square method over the whole size range foraged ($I_{S_{ij}} > 0.01$). The sign and magnitude of the slope can be used as a quantitative indicator of the trophic control in the feeding interaction. Negative slopes would be related to top-down control (large biomass in the refuge size classes with low $I_{S_{ij}}$) whereas positive slopes would be related to bottom-down control (high coupling of SSS to BSS). Only well-coupled or well-uncoupled SSS and BSS will show significant correlation coefficients. Combined trophic controls or the lack of a clearly dominant trophic control will show slopes near to zero and, consequently, a low correlation. Anyway, slopes resulting from the least-squares fitting method offer an average quantification of the coupling between predator SSS and prey BSS (Fig. 4; Table 3). In order to be comparable the slopes extracted from different feeding interactions, prey biomass in BSS was used in the fitting as fraction in relation to the total biomass in the size range foraged.

The nature of the trophic control derived from the analyses of the prey size structure matched with those derived from the biomass co-variability (Table 3). Moreover, the magnitude of the slopes determined that the strongest bottom-up control occurred in Laguna Galarza. The size structure of the predator guild is adjusted in order to maximize its ability to consume the existing prey biomass distribution. In the Alborán microcosm, the statistically insignificant slope does not indicated any dominant trophic control. Strong top-down controls were found in La Caldera and Iberá. In these cases, there was a relevant downward forcing of zooplankton on phytoplankton. Structural adjustments within phytoplankton trophic positions occurred according to the susceptibility to be grazed. An increase of average body size of the phytoplankton has been often proposed as a rough indicator of a higher resistance to grazing (*e.g.*, Gaedke, 1992; Cottingham, 1999). Therefore, average body size increased from 14 to 32 μm ESD after the zooplankton bloom in Iberá. By contrast, decreasing the average body size of the prey guild was the result of the zooplankton predation in La Caldera. Average body size decreased from 5.2 to 3.2 μm ESD after zooplankton growth (Fig. 2).

The BSS of La Caldera Lake shows a large and persistent biomass gap between 10 and 100 μm ESD (Echevarría et al., 1990). The oligotrophic nature of this mountain lake could be the cause of this biomass gap in the phytoplankton size range,

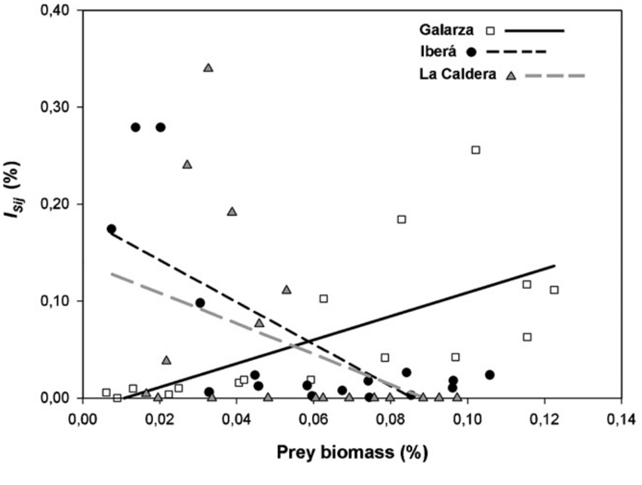

Fig. 4 – Linear least-square fitting of the predator SSS against the prey BSS in the statistically significant datasets: Laguna Galarza, Laguna Iberá and La Caldera Lake. Prey biomass is measured as fraction in relation to the total biomass in the size range foraged ($I_{S_{ij}} > 0.01$). Slopes and Pearson correlation coefficients are shown in Table 3.

suggesting a general bottom-up control of the phytoplankton during most of the year. However, similar large and persistent gaps have not been found in other freshwater (Sprules and Munawar, 1986; Gaedke, 1992) or oceanic (Sheldon et al., 1972; Rodríguez and Mullin, 1986) oligotrophic environments. In this work, the study scenario in La Caldera covered a period of high productivity linked to exceptionally strong rainfalls (September 1987), but even during this particular scenario, the large biomass gap persisted. The higher abundance and average body size of the zooplankton guild were relevant differences of this productive period in relation to the rest of the year. The prey:predator ratio of biomass and the biomass variability ratio were noticeably low (Table 3). Zooplankton community is generally dominated by copepods (*Mixodiaptomus laciniatus* and *Diaptomus cianeus*), but large cladocerans (*D. pulex*) dominated this particular period. The cause of the rapid and abundant presence of large cladocerans in the water column is probably related with the large population of *D. pulex* living between the rocks of the bottom of La Caldera (Echevarría et al., 1990). Pelagic food availability probably activates the vertical migration of *D. pulex* and prolongs the residence time of these organisms throughout the water column. Swarming in *D. pulex* is mainly influenced by food availability (Kleiven et al., 1996). In this way, the budget of efficient filterers existing in the bottom of La Caldera could prevent the eventual occurrence of organisms between 10 and 100 μm ESD during occasional high productive events through a strong top-down control. Note that the optimal feeding window of this predator guild just covers this spectrum gap (Fig. 2).

DSS showed better coupling to prey biomass accumulations than SSS in the top-down controlled feeding interactions of Laguna Iberá and La Caldera. Nevertheless, zooplankton feeding in these lakes cannot become as optimal as in Laguna Galarza, where bottom-up control dominated the feeding interaction. Feeding rates and energy transfer efficiencies along the BSS are maximized when the optimal food sizes (with the maximal clearance rate) coincide with the most abundant prey size classes. Therefore, growth rates of zooplankton in La Caldera and Iberá are probably diminished as a result of its sub-optimal feeding rates. Nutritive quality of zooplankton diet in Laguna Iberá must be also lower than in Laguna Galarza. Comparing the two subtropical wetland lakes, DSS showed quite higher percentages of detritus and cyanobacteria in Laguna Iberá (61% and 9%, respectively) than in Laguna Galarza (39% and <0.1%) (Fig. 3). The relevance of the plankton-derived detritus as food source for zooplankton is commonly reported by field studies in other eutrophic ecosystems dominated by filamentous cyanobacteria (Repka et al., 1998; Gulati et al., 2001). The lower feeding rates and poorer food quality of the zooplankton in Laguna Iberá agreed with the relative standing biomasses of prey and predator in the two lakes. Annual-averaged predator biomass was fivefold higher in Laguna Galarza despite prey biomass was threefold higher in Laguna Iberá (Cózar et al., 2003).

The present work shows how the estimation of SSS and DSS within BSS allows deepening in the analysis of real feeding interactions. SSS and related concepts such as optimal food size or feeding size window were essential for understanding the trophic control of the biomass accumulations and depletions in the size structure. DSS are able to consider large part of the complexity inherent in the real food webs by using simple probabilistic methods. Intra-specific diet shifts as result of the individual growth of the organisms or the size dependence of selectivity factors such as nutritional quality or morphology were considered in this study.

The contributions of this work attempt to progress in the refinement of an alternative (or complementary) size-based procedure to model trophic networks. The usefulness of the method has been illustrated in the analyses of single feeding interactions between functional groups. Perhaps, the major impediment to the further application of this method in ecological network analyses of entire communities is the need for an exhaustive size arrangement of the community. Nevertheless, a method based on the size spectrum may also add some assets to the existing approaches of network construction (see Fath et al., 2007). It offers an objective and well-established criterion to compartmentalize the community, especially suitable for pelagic communities covering several orders of magnitude in size (Sheldon et al., 1972; Kerr and Dickie, 2001). It offers a systematic way to obtain a first approach of both connectivity (“who eats whom”) and diet (“by how much”) matrices. In many cases, the lack of quantitative information about the diets forces the researchers to perform a first subjective filling of these matrices. This process is complex to realize (especially in small-sized organisms such as plankton) and often generates excessively simple or inaccurate networks, which may induce significant errors in the ecological analyses (Jørgensen and Fath, 2006; Fath, 2007). A detailed size-based compartmentalization of the food webs allows for a suitable use of the allometric theory, which offers empirical models across a wide range of metabolic processes and functional groups (*e.g.*, Peters, 1983; Brose et al., 2005). Moreover, the consideration of the effect of a key forcing variable such as the temperature on the metabolic processes and the ecological networks would be easily workable from the existing allometric theory (Duarte, 2007).

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