Food-web structure in two shallow salt lakes in Los Monegros (NE Spain): energetic vs dynamic constraints

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Abstract

Energetic and dynamic constraints have been proposed as rival factors in determining food-web structure. Food-web length might be controlled either by the amount of energy entering the web (energetic constraints) or by time span between consecutive disturbances relative to time needed to build up a population (dynamic constraints). Dynamic constraints are identified with processes functioning at a regional scale such as climate, lithology and hydrogeology. Energetic constraints are related with processes operating both at a regional and a local scale. We studied the contribution of energetic constraints to food-web organization in two temporary saline lakes with similar dynamic constraints. Lakes were sampled fortnightly during two hydroperiods (1994/1995 and 1995/1996). Differences in energetic constraints between lakes result in divergent assemblages of primary producers. Consumer assemblages in both lakes, however, are similar in species composition although differ in total biomass and species abundances. Food-webs are short with a high proportion of omnivores. To simulate an increase in the energy input entering to these systems, an addition of nutrients (to a final concentration of 100 μg·l^{-1} P-PO$_4{}^{3-}$) was done in mesocosms placed within the lakes in order to obtain an increase in the phytoplankton biomass. No significant response to nutrient enrichment was found in food-web structure (composition, density or biomass).

Introduction

Relative importance of processes responsible for the structure of food webs are subject to considerable debate. An explanation based on energetic constraints suggests that food web complexity is limited by the availability of energy entering the food web, i.e. longer food chains are expected in more productive ecosystems (Hutchinson, 1959; Fretwell, 1977, 1987; Oksanen, 1983, 1991; Oksanen, et al., 1981; Yodzis, 1981, 1984). An alternative explanation hypothesizes that short food chains are more stable than long ones because of their faster return times after environmental disturbances because food chain length is driven by population dynamics, i.e, dynamic constraints (Pimm & Lawton, 1977; Pimm, 1982; Pimm et al., 1991; but see Sterner et al., 1997 for a critique). As long food chains take time to develop, frequent unpredictable disturbances should promote short food chains. Thus, food chain length may reflect environmental predictability (Pimm & Lawton, 1977; Pimm, 1982; Pimm & Kitching, 1987; Pimm et al., 1991; Havens, 1994).

Some studies which have considered the influence of both kinds of constraints on food webs of ephemeral aquatic ecosystems have shown that an increase in productivity cannot increase food chain length beyond the capacity of the community to provide new predators (Pimm & Kitching, 1987; Jenkins et al., 1992).

Ephemeral salt lakes are systems that experience a wide range of dynamic and energetic constraints. Disturbance appears as episodes of either high salinity or desiccation with a variable degree of predictability (Comín et al., 1991; Florín & Montes, 1998). Primary production is also highly variable among lakes (Hammer, 1986; Javor, 1989). Quite frequently, although not necessarily, each kind of constraint is associated with factors operating at regional or local scales. Climate, geology and lithology are controlled at a regional scale and bound the main factors determining salt lake dynamic constraints. Energetic constraints are more tightly related with features operating at a local scale like landscape microtopography, sediment granulometry, nutrient dynamics or water–sediment interactions.

Here, we explore the contribution of energetic constraints to food web structure when dynamic constraints are similar. We studied a pair of small shallow salt lakes in Los Monegros District (northeastern Spain); these neighboring lakes share many features which are determined at a regional scale and which determine their dynamic constraints (duration of the aquatic phase, ionic composition and fluctuations in salinity). However, because they have different kinds of primary producers, the lakes differ in their energetic constraints by nearly two orders of magnitude (Díaz–Palma, 1998), a characteristic that seems to be set at the local scale. Accordingly, longer and more complex food-webs are expected to occur in the more productive lake.

Materials and methods

Study site

Piñol (41° 26′ 36″ N/0° 15′ 42″ W) and La Muerte (41° 26′ 05″ N/0° 16′ 04″ W) are two small (11.9 ha and 11.5 ha, respectively), shallow (maximum depth: 40 cm), ephemeral inland salt lakes located in Los Monegros district, northeastern Spain. Together with many other small pools, these lakes lie on a plateau at 340 m a.s.l. within a Tertiary basin rich in marl and gypsum with limestones in the upper part (Quirantes, 1971). The area has a semiarid Mediterranean climate with low mean annual rainfall (300 mm) and high potential evapotranspiration (778 mm) (Pueyo & Inglés, 1987). Although air temperature and rainfall are highly variable, there is a fairly regular behavior with long-term periodicities at 12 and 6 months, respectively. Spectral analyses of mean monthly temperature and average rainfall data for the period 1961–1990 were performed to assess this behavior (Fig. 1).

All lakes in the area are filled with rainfall but groundwater has a strong influence. The aquatic phase is short (3–4 months) and during dry years most of the lakes in the area remain dry. Wind, with a main north-western component, is strong and persistent (Pueyo, 1980).

The lakes of the study differ in the granulometry of sediment. La Muerte has coarser particles (including medium and coarse sand) than Piñol (mainly fine sand, clay and silt), which allows the development of complex and compact microbial mats (Guerrero & De Wit, 1992). Composition of the biological communi-

Table 1. Composition of primary producers in lakes La Muerte and Piñol in the two periods of study. Samples of the first period are from open water, those of the second period are from open water and mesocosms

| Lake	Algae	1994/95 Lake water	1995/96 Lake water	1995/96 Mesocosms
MUERTE	***Bacillariophyceae* (Diatoms)**			
	Cyclotella bodanica	+	+	+
	Entomoneis alata	+	+	–
	Hantzschia amphyoxis	+	+	+
	Navicula sp.	+	+	+
	Nitzschia closterium	+	+	–
	Nitzschia acicularis	–	–	+
	Surirella sp.	–	–	+
	Fragilaria crotonensis	–	–	+
	Asterionella formosa	–	–	+
	Pinnularia sp.	–	–	+
	Amphora sp.	–	–	+
	Cymbella sp.	–	–	+
	Gyrosigma sp.	–	–	+
	Dytilum sp.	–	–	+
	***Chlorophyceae* (Green algae)**			
	Chlamydomonas sp.	+	+	+
	Dunaliella sp.	+	+	+
	Tetrastium sp.	–	–	+
	Scenedesmus sp.	–	–	+
	Ankistrodesmus sp.	–	–	+
	Dictyosphaerium sp.	–	–	+
	Monoraphidium sp.	–	–	+
	Oocystis sp.	+	+	+
	Franceia sp.	+	+	–
	***Cyanophyceae* (Blue-green algae)**			
	Anabaena constricta	+	+	+
	Anabena sphaerica	–	–	+
	Chroococcus sp.	+	+	+
	Oscillatoria limnetica	+	+	+
	Nostoc sp.	–	–	+
	Pseudoanabaena sp.	+	+	+
	Phormidium sp.	+	+	+
	Gloeocapsa sp.	+	+	–
PIÑOL	***Bacillariophyceae* (Diatoms)**			
	Cyclotella bodanica	+	+	+
	Hantzschia amphyoxis	+	+	+
	Navicula sp.	+	+	+
	Nitzschia acicularis	–	–	+
	Fragilaria crotonensis	–	–	+
	Asterionella formosa	–	–	+
	Pinnularia sp.	–	–	+
	Amphora sp.	–	–	+
	Cymbella sp.	-	-	+
	***Chlorophyceae* (Algas verdes)**			
	Dunaliella sp.	+	+	+
	Scenedesmus sp.	-	-	+
	Monoraphidium sp.	+	+	+
	Oocystis sp.	+	+	+
	Binuclearia tetrana	+	+	-
	***Cyanophyceae* (Blue-green algae)**			
	Anabaena constricta	+	+	+
	Anabena sphaerica	-	-	+
	Oscillatoria limnetica	+	+	+
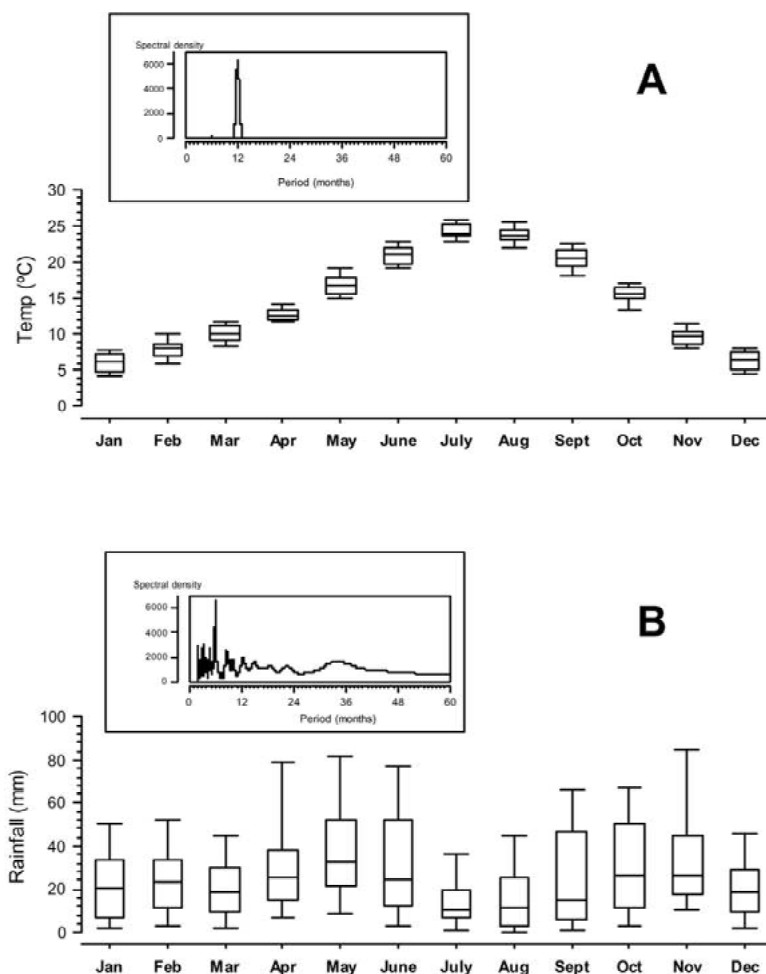
Figure 1. Mean monthly temperature (A) and average rainfall (B) for the period 1961–1990. Plots include median, 25th and 75th percentiles (boxes) and 5th and 95th percentiles (whiskers). Above each plot are the spectral analyses for each variable.

ties from both lakes are different at primary producers level but not at consumer levels (Tables 1 and 2).

Sampling

In order to describe community composition and food web structure, both lakes were sampled in two consecutive hydroperiods: November 1994–February 1995 and January 1996–March 1996 . The aim of the former sampling was to determine the composition of the biological communities and their relative abundances; monthly samples were taken using a plastic corer (inner diameter 5.4 cm; 10 replicates). During the second sampling period, an experimental approach was used. Thirty artificial enclosures (mesocosms), plastic cylinders (inner diameter 19 cm), were placed randomly in each lake. Energy enters in the lakes in the form

of primary producers (algae and microbial mats) and animals which are produced and stocked every consecutive hydroperiod. To examine the effect of an increase in energy input, half of the mesocosms were enriched in phosphorous with a solution of H_2KPO_4 to a final concentration of 100 μg P-PO$_4^{3-}$·l^{-1} (initial concentrations in both lakes were between 20 and 30 μg P-PO$_4^{3-}$·l^{-1}). Manipulation of the concentrations of phosphorus was chosen because the analysis of N:P weight ratio measured (32–381 in Piñol and 65–503 in La Muerte) during the first period indicates phosphorus limitation in both lakes (Alcorlo, 1999). Six mesocosms (three treated, three control) were sampled fortnightly.

In both periods, phytoplankton samples were taken directly in unfiltered water and preserved in a Lugol

Table 2. Composition and mean relative abundances as percentages of the metazoan communities of Lake Piñol and Lake La Muerte. C: Control mesocosms, T: Treatment mesocosms

Taxonomic group	Taxonomic species	Piñol			La Muerte		
		1994/95, n=40	1995/96 C, n=15	1995/96 T, n=15	1994/95, n=40	1995/96 C, n=15	1995/96 T, n=15
Cilliata	*Fabrea salina*	11.85	-	-	2.65	-	-
Rotatoria	*Hexarthra fennica*	21.77	11.04	3.18	15.33	33.81	15.70
Nematoda	sp.	38.28	78.94	87.59	52.30	62.72	77.10
Turbelaria	sp.	25.79	-	-	1.36	-	-
Copepoda	*Arctodiaptomus salinus* *Cletocamptus retrogressus*	0.43	-	-	0.41	-	-
Anostraca	*Branchinectella media*	0.82	3.64	2.86	3.80	0.17	0.30
Ostracoda	*Candelacypris aragonica*	0.82	6.36	6.35	11.05	3.12	6.58
Diptera	sp.	0.14	-	-	12.35	-	-
Coleoptera	*Bledius furcatus* *Agabus nebulosus*	- -	- -	- -	0.53	-	-

solution. Metazoans were sampled by passing the water column in the corers through a sieve (60 μm mesh size) and collecting the top 2 cm of sediment. Samples were fixed *in situ* with a neutralised isotonic 4% formaldehyde solution. Once in the lab, samples were washed and preserved in ethanol (70%) (Downing & Rigler, 1984). Qualitative samples of metazoans were also collected during the second period in order to evaluate the cage effect of the mesocosms.

Physico-chemical variables measured *in situ* in open water during the former period and inside mesocosms during the second included depth, water temperature, electrical conductivity at 25 °C (conductivity-meter WTW LF96), pH (pH-meter Crison 506), dissolved oxygen (oximeter WTW), total alkalinity and phenolphthalein alkalinity (Aminot & Chaussepied, 1993). Chlorophyll *a*, total phosphorus (total P), total nitrogen (total N), dissolved organic matter (DOM), particulate organic matter (POM) and total dissolved solids (TDS) were measured according to standard techniques (APHA, 1991). Also during the second period studied, organic content in sediment (APHA, 1991) and total phosphorus concentration

(Andersen, 1976) were measured from the sediments retained in the mesocosms.

Principal Component Analysis (PCA) was performed in order to explore the temporal changes in the main features of the lakes.

Description of the food webs

Trophic relationships were determined from direct observations in aquaria at the laboratory, analysis of gut contents under a dissecting microscope (for anostracans and ostracods), and from records in the literature. Accordingly, three trophic categories are used: primary producers, intermediate consumer species and top consumer species. Taxonomic species were assigned to those categories trying to keep the identification of each taxonomic unit with a trophic species whenever possible in order to obtain a good resolution of the assemblage of the food web (Hairston & Hairston, 1993) (see Table 3). Following Briand (1983), Sprules & Bowerman (1988) and Hairston & Hairston (1993), primary producers were lumped together in a single trophic species. Ontogenetic stages with different feeding behaviours were not separated.

Table 3. Classification of taxonomic units occurring in the lakes into trophic species. Asterisk (*) indicates omnivore species, (**) cannibalistic species

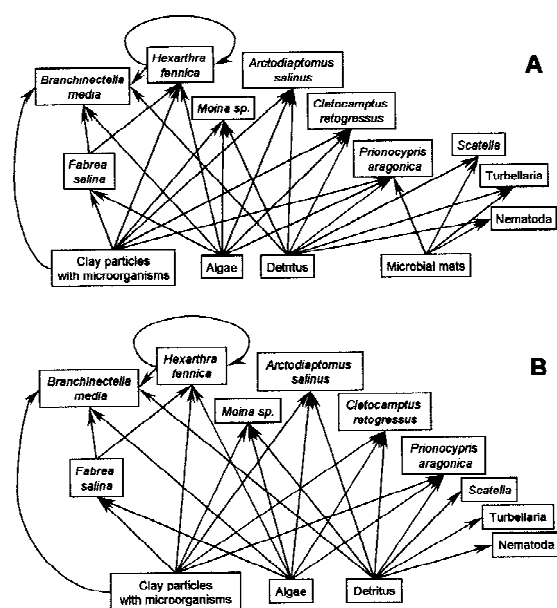| Basal species	Intermediate species	Top species
Algae	*Fabrea salina*	Turbellaria
Microbial mats	*Hexarthra fennica***	Nematoda
Detritus		Diptera
Clay particles with microorganisms		*Moina**
		*Cletocamptus retrogressus**
		*Arctodiaptomus salinus**
		*Prionocypris aragonica**
		*Branchinectella media**

Figure 2. Standard food web diagrams for the lakes studied.(1994/1995). (A) La Muerte Lake, (B) Piñol Lake.

Food webs were constructed by drawing feeding relations from predation matrix (see Figs 2 and 3) and trophic interactions (see Table 3) for all taxa present in each lake at each sampling period (Sprules & Bowerman, 1988). The following food web descriptors were calculated (see Table 4):

– S: total number of (trophic) species.

– Number of cannibalistic species.

– Number of top species: species on which nothing else in the web feeds.

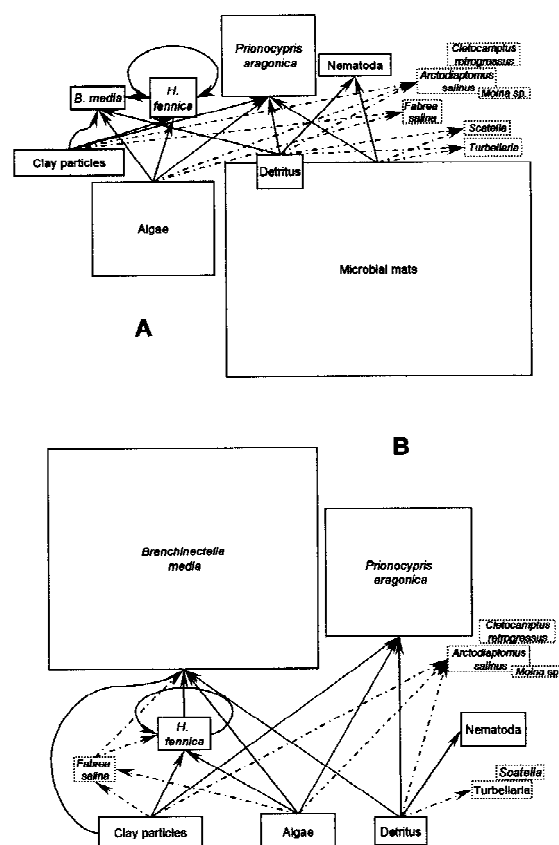– Number of intermediate species: species that have both predators and prey within the web.

Figure 3. Food web diagrams weighted for biomass in the different trophic taxa (1995/1996). Species absent in the mesocosms but known to be in the lake are drawn with dashed lines. (A) La Muerte Lake, (B) Piñol Lake.

– Number of basal species: species that have predators but do not prey another species within the web; they feed on detritus and/or algae.

- Number of omnivore species: species that feed on more than one trophic level.
- L: number of trophic connections or linkages between species including cannibalistic interactions.
- Connectance (C): proportion of potential feeding links realised in a community. It is calculated as $L/(S^2)$, the number of realised trophic interactions divided by the number of possible interactions, and is termed 'directed connectance' (Martínez, 1991). It is an estimate of the mean proportion of niche space exploited by each species (Warren, 1995).

Biomass estimation in mesoscosms

Individual biovolumes were estimated for each organism in the samples (or for a representative number when abundances were high) from length and width measurements (see Table 5 for formulas) obtained with an image analysis system. Meiofaunal and algae biovolumes were translated into dry weight by assuming a specific gravity of 1.13 and 1.0 g·cm^{-3}, respectively (Wieser, 1960). For the anostracans, dry weight was estimated as 10% of wet weight, itself estimated using the length-weight relationship provided by Thièry (1987) for a similar species. Biomass values were expressed as carbon content which is assumed to be about 40% of dry weight (Feller & Warwick, 1988). Standing stock of the microbial mats was inferred from primary production estimates (Díaz-Palma, 1998).

A two way ANOVA was performed to test for changes in density and biomass due to experimental phosphorus enrichment.

Results and discussion

Environmental factors affecting Piñol and La Muerte lakes follow the same pattern of fluctuation. Temperature behaves in a regular manner annually. Average temperature is similar from year to year. Rainfall is erratic; it mainly occurs in periods which are six months apart, spring and autumn (Fig. 1). As in other saline lakes, biological communities vary according to physico-chemical changes of the water and to climatological fluctuations. The first and second axes of a Principal Component Analysis (PCA) account for the 51% of the variance of the data (Alcorlo et al., 1997). The first Principal Component (26%) is related to changes in water level thus reflecting temporal evolution of the system through the flooding period. The second Principal Component (24%) summarizes changes in biological activity, mainly the dominance of either phytoplankton (Piñol) or phytobenthos (La Muerte).

Primary producers differ in diversity and abundances in the lakes (Table 1). Metazoan richness, however, is similar in both lakes, poor in species and composed of organisms adapted to stressed, fluctuating and relatively unpredictable environments. There was also a strong variation in metazoan abundances in the periods of the study (Table 2). Although, methods used to sample these organisms changed between sampling periods, analysis from qualitative samples reflect that abundances of cilliates, copepods, cladocerans and turbellarians during the 1995/96 period were smaller than in the 1994/1995 period. To overcome the dry period, animals living in temporary habitats produce resistant stages which are not evenly distributed. Thus, presence of low-abundant taxa within mesocosms is dependent on whether enclosures have been placed over such clumps (Alcorlo, 1999).

Food chains are short, with most of the routes in the web defining two level chains (Figs 2 and 3). Short food-webs are characteristic of resilient and benthic systems (Pimm & Lawton, 1977; Briand, 1983; May, 1986; Pimm, 1988; Pimm et al., 1991; Hairston & Hairston, 1993).

There are, two intermediate species (*Fabrea salina* and *Hexarthra fennica*) which determine three level routes; those species are not dominant in numbers or in biomass (Tables 2 and 7). Food chain length in these systems is mainly controlled by the duration of the aquatic phase and the ecophysiological requirements of saline environments. The latter factor limits the number of species capable of successfully invading these systems whereas duration of aquatic phase constitute a dynamic constraint (Schneider, 1997).

Because detritus is produced at different trophic levels, detritivores are considered to be omnivores. Thus, food-webs at both lakes have a large number of omnivores. The importance of omnivory in food-web structure have been recently stressed (Hairston & Hairston, 1993; Warren, 1994, 1995; Polis & Strong, 1996).

Differences in food-web statistics exist between sampling periods. Connectance values estimated in the first sampling period (1994/95) were similar to those found in other types of ecosystems (Martinez, 1992; Warren, 1995); they were high in the experimental set (Table 4). As most species in these lakes lack active

Table 4. Food web statistics. Relative abundance (%) of species between brackets. Asterisk (**) indicates cannibalistic species and considered an intermediate species. (*) indicates omnivore species and considered top

	La Muerte				Piñol			
	1994/1995		1995/1996		1994/1995		1995/1996	
S (num. of species)	14		8		13		7	
Cannibalistic species	1	(7)**	1	(12.5)**	1	(7.5)**	1	(14)**
Top species	8	(57)	3	(37.5)	8	(62)	3	(43)
Intermediate species	2	(14)	1	(12.5)	2	(15)	1	(14)
Basal species	4	(29)	4	(50)	3	(23)	3	(43)
Omnivore species	8	(57)*	4	(50)*	8	(62)*	4	(51)*
L (links)	25		14		21		12	
d=L/S	1.78		1.75		1.62		1.71	
Connectance	0.12		0.22		0.15		0.24	

Table 5. Relationships used to estimate biovolume (V, in μm^3) or body weight (W, in mg) for different taxa (1995/1996)

Taxa	Variables measured	Formula	Reference
Algae	L: body length (μm)	Biovolume (several	Smayda (1978)
	A: body width (μm)	relationships)	
			Wetzel &Likens (1991)
Hexarthra fennica	L: body length (μm)	$V= 0.26 \cdot L \cdot A^2$	Ruttner-Kolisko (1977) in:
	A: body width (μm)		Downing & Rigler (1984)
Nematoda	L: body length (μm)	$V=L \cdot A^2 \cdot 16 \cdot 10^{-5}$	Feller & Warwick (1988)
	A: body width (μm)		
Prionocypris aragonica	L: body length (mm)	$V=450 \, L \cdot A^2$	Feller & Warwick (1988)
	A: body width (mm)		
Branchinectella media	L: body length (mm)	$W=0.0078 \cdot L^{2.1706}$	Thièry (1987)

dispersal, the composition of the communities which develop inside the enclosures was constrained to those species with resistant stages stored in the sediment before the enclosures were put in place. Therefore, rare species were less likely to be included in the mesocosms. Indeed, experimental communities have almost 50% less species than those communities observed in open waters in 1994/95. In spite of this reduction in species number, density of links (L/S) inside the mesocosms remained rather constant whereas connectance (L/S^2) increased with decreasing species richness (Table 4). This result fits the link-species scaling law (Cohen & Newman, 1985) which states that the number of links per species is constant and

scale invariant at roughly two (1.62–1.78 in our study). Hence, each species was linked to a constant number of species, independent of how many species were in the community. The alternative hypothesis, the constant connectance hypothesis (Martinez, 1991), suggests that each species is linked to a fixed fraction of the species in the web; i.e. the more species in the web the more species a predator would prey upon. Although Martinez (1992) rejected the link-species scaling law following the analysis of 175 food webs, it seems plausible that short (two levels) detritus-based food-webs might conform the expectations of such law. This is likely to be the case when decline of species richness is mainly due to disturbances in col-

onisation events which mostly affect consumers but seldom concern producers. Without any significant change of food supply average number of links of the remaining species will remain the same.

Traditional food-web diagrams do not properly reflect differences in functioning between lakes as the importance of rare species is overestimated (Fig. 2). When interaction strength is not incorporated into food-web analysis, food-web statistics seem to miss biologically important processes (Paine, 1980, 1988, 1992). A better approach would be to include estimates of the actual biomass allocated to each taxon in such diagrams (Fig. 3). Doing that, functional differences between both lakes become evident. Piñol lake is a system driven by consumers (top-down control) where detritus feeders, anostracans and ostracods, represent most of the amount of biomass (20 times more than in La Muerte, Table 6). Water turbidity is high due to sediment resuspension by wind action, thus precluding macrophyte development. Animals feed actively on particles and algae suspended in the water column. Nevertheless, a large fraction of phytoplankton, mainly diatoms, cannot be effectively used by filter feeders because of their large size. On the contrary, primary producers, especially microbial mats, are the species which manage most of the energy flowing through the system in La Muerte lake (bottom-up control). In terms of biomass, they represent a major component and dominate the metabolism of the lake (Alcorlo et al., unpublished data). Microbial mats cover the whole lake bed acting as a natural barrier to sediment resuspension.

No significant effects on food-web structure, in metazoan species density or in biomass, were observed in either lake as a consequence of nutrient enrichment (Table 7). Enriched mesoscosms in La Muerte experienced a significant increase in biomass of primary producers compared to control enclosures (Table 7). However, this effect was limited to only one sampling date (one month after the start of the experiment) and cannot be causally related to nutrient enrichment. Considering the whole community there is no significant response in biomass to the treatment applied (Table 7). Indeed, the system seems to be buffered against nutrient enrichment. Phosphorous added disappears immediately from the water column (Alcorlo et al., unpublished data), most likely because it reacts with dissolved ionic compounds which are abundant in these lakes; precipitating to the sediment. Average ionic formula in La Muerte is: Na-(Mg)-Cl-SO_4, and Na-Mg-Cl-(SO_4) in Piñol. However, no sig-

nificant differences were detected in total amounts of total phosphorus of the sediments between treated and control mesoscosms because the differences between the basal concentrations of total phosphorus in the sediments and the amount of phosphorus added to the water differed by two orders of magnitude (P added= $100\ \mu g\ l^{-1}$ or 0.1 ppm, Mean Total P sediments Piñol: 0.06 mgP/g sed$\pm$0.01 or 60 ppm; Mean Total P in La Muerte= 0.04 mgP/g sed$\pm$0.01 or 40 ppm).

Analysis of variance also shows significant differences in metazoan density (Piñol, $F=7.96$, $p<0.05$) and phytoplankton density (La Muerte, $F=27.10$, $p<0.0001$) between sampling dates. This was interpreted as changes due to population growth.

In summary, the salt lakes studied do differ in the kind and quantity of primary producers and, hence, in primary production but share the same food-web structure which is not modified even when nutrients are added. Factors working at the regional scale, which are related to dynamic constraints, seem to exert a control on food-web structure overriding possible influences of energetic constraints. Main dynamic constraints are aquatic phase duration and water chemistry, both controlled by processes at the regional scale.

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Table 6. Total biomass (mg C · m^{-2}) allocated to each taxa

Lake	Date	Anostracans	Nematods	Ostracods	Rotifers	Algae
Piñol	1/17/96	157.34	0.48	26.52	0.01	0.98
	2/2/96	282.18	1.25	139.77	0.13	2.69
	2/17/96	130.73	2.19	45.66	0.87	3.86
	3/1/96	103.35	2.67	41.24	1.01	2.40
	3/13/96	71.55	4.24	100.55	0.64	1.62
Muerte	1/17/96	0.87	1.58	0.90	0.027	2.63
	2/2/96	0.01	0.09	0.99	0.04	18.26
	2/17/96	0.008	0.23	33.19	0.24	41.89
	3/1/96	–	0.14	8.11	0.14	6.69
	3/13/96	–	0.18	5.76	0.02	3.71

Table 7. Results of analysis of variance of biomass in relation to phosphorus enrichment

	Consumers			Phytoplankton			All		
	Treatment	Date	Treatment × Date	Treatment	Date	Treatment × Date	Treatment	Date	Treatment × Date
La Muerte									
df	1	4	4	1	4	4	1	4	4
F-ratio	0.4691	2.4836	0.8209	8.6637	21.9529	1.219	3.1521	2.3764	1.0968
p	0.5012	0.0766	0.5271	0.008	<0.0001	0.3341	0.091	0.0864	0.3852
Piñol									
df	1	4	4	1	4	4	1	4	4
F-ratio	2.3538	0.7338	0.1627	0.0114	5.9936	1.4479	2.3793	0.7095	0.1592
p	0.1406	0.5797	0.9548	0.9163	0.003	0.2591	0.1386	0.5949	0.9565

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