Biomass, size structure and trophic compartments of the metazooplankton in the Sontecomapan Lagoon (Veracruz, Mexico)

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ABSTRACT: In this chapter, based on re-analysis of previous published data, we study the biomass, trophic component and size structure of the zooplankton in the Sontecomapan Lagoon, in order to better evaluate its trophic status and assess its possible incidence on food transfers, eutrophication and terminal productivity in this lagoon. Our results show very low values of zooplankton biomass and zooplankton/phytoplankton ratio, compared to literature data, revealing an overall low food-transfer at the basis of the food chain. The size-structure is in average dominated by small organisms which suggests a predation impact from fish on larger organisms (calanoid copepods). This impact was particularly important during the north wind season perhaps in relation with the breeding cycles of important fish species such as *Cathorops aguadulce*. However, tidal inputs of large-sized coastal marine organisms (e.g. *Paracalanus aculeatus*, *Temora turbinata* and *Centropages velificatus*)

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seems to compensate this "erosion" of large zooplankton in the region close to the communication channel. Our data analyses confirm the top-down effect on zooplankton, but also show that bottom-up forces affect phytoplankton (NH_4 limitation) and zooplankton (phytoplankton limitation), meanwhile the top-down control by herbivorous zooplankton on phytoplankton is very low (<10% of the phytoplankton stock day^{-1}).

Introduction

Tropical coastal lagoons like Sontecomapan, are often considered as hot spots for biodiversity and are among the most productive ecosystems in the world (Mitsch & Gosselink, 1993; Day *et al.*, 2012), but they are also very sensitive to human activities and climate variability (Cloern *et al.*, 2016). Their high productivity combined with favorable hydrodynamic conditions, as well as the presence of sheltered areas (as mangroves) make these ecosystems good nursery areas for many fish species (Esteves *et al.*, 2008). Fisheries of these lagoon environments are often key sectors for the economy of local population. However, the fishery potential is highly dependent on planktonic productivity that is, in itself, essential to support the diversity of higher trophic levels. The phytoplankton, first pelagic primary producer, forms the basis of the trophic network. Zooplankton is then a major link between lower and higher trophic levels hence supporting their biodiversity (Rose *et al.*, 2010).

Zooplankton organisms often represent essential prey for larvae, crustaceans and fish juveniles, and become a key for their recruitment (Munk, 1997; Østergaard *et al.*, 2005). Furthermore, in lagoon and coastal marine ecosystems the zooplankton includes large proportions of early larval stages of many benthic and nektonic organisms, some having high commercial value, and are thus key for their recruitment (Archambault & Bourget, 1999). When composed mainly of herbivorous organisms, zooplankton exert a top-down control on primary production and then is a key for controlling accumulation of phytoplankton and eutrophication (Sommer & Sommer, 2006; York *et al.*, 2014). Then, to evaluate the fishery potential of lagoon ecosystems, it is essential to evaluate the biomass and size structure of the different trophic compartments of the planktonic ecosystem (Jeppesen *et al.*, 2000).

Fishing represents a major consumptive heritage use of the coastal lagoons along the Gulf coast of Mexico which produce around 90,000 tons annually (Smardon, 2006). In the Sontecomapan Lagoon, fishing activity takes place both at sea and the lagoon with

a 289 boat fleet. It targets mainly three species of fish (*Mugil cephalus*, *Arius melanopus*, *Cathorops aguadulce*, *Eugerres* sp.), crabs (*Callinectes* sp., *Mennipe mercenari*), and prawn (*Litopenaeus setiferus*). The ichthyofauna of the lagoon is very rich, with 52 fish species that belong to 24 families and 41 genera reported by Rodríguez-Varela *et al.* (2010), however, Castillo-Rivera & Lara-Domínguez (this issue) more recently reported 115 species corresponding to 26 orders, 41 families and 84 genera.

In a previous work (Benítez-Díaz Mirón *et al.*, 2014) we showed that transparency, salinity, and food availability were important drivers for zooplankton abundance, composition and diversity. We also discussed that the low zooplankton density found in the lagoon, compared to other eutrophic coastal lagoons, could be attributed to the combined effects of high water exchanges, low depth and high transparency, favoring instability and vulnerability to UV-effects and/or to visual predation.

In this chapter, focused on the biomass and size structure of zooplankton, we completed this analysis, in order to better evaluate the trophic status of the planktonic ecosystems and assess the possible incidence on food transfers, eutrophication and terminal productivity.

Materials and Methods

Three sampling surveys, covering a 10-station network with different characteristics (Figure 1) were performed in March (26 to 29), June (11 to 14) and November (19 to 22), 2010 corresponding to dry, rainy and north wind seasons respectively. During each survey the ten stations were sampled once for environmental variables, bacterial abundance, chlorophyll concentration and zooplankton. All sampling and measurements were performed during daylight hours (between 9:00 and 16:00 h). The sampling strategy, and the measurements techniques for the abiotic (transparency, pH, salinity, temperature, nutrients) and biotic (bacteria biomass and chlorophyll pigments), variables are detailed in Benítez-Díaz Mirón *et al.* (2014).

The zooplankton was collected using a cylinder-conical net (64 μm in mesh opening size, 30 cm in mouth diameter and 1 m in length) and the samples were preserved with 4% formalin.

Zooplankton taxa identification and enumeration were performed as in Benítez-Díaz Mirón *et al.* (2014).
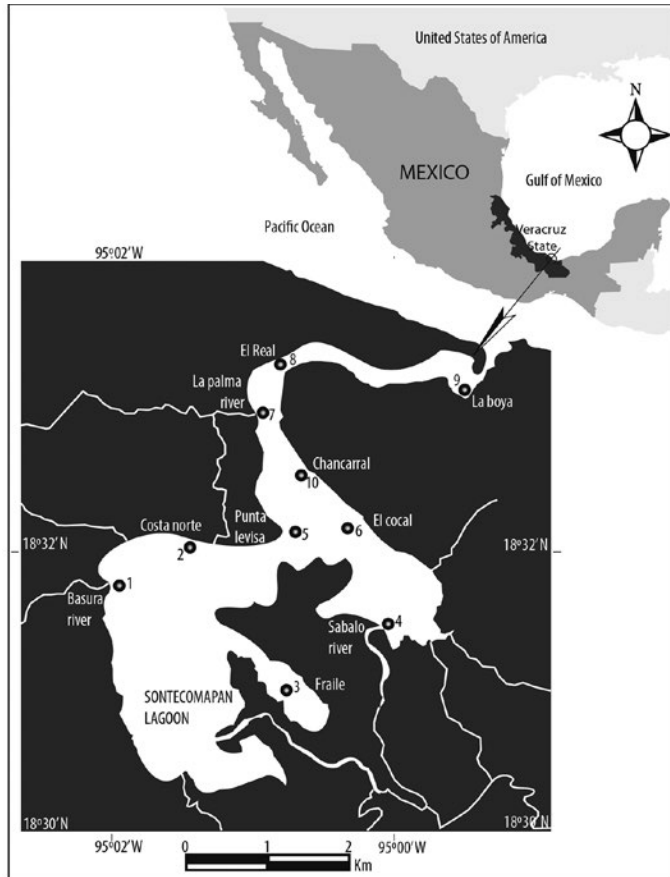
Figure 1. Sontecomapan Lagoon with the location and number of each sampling station.

Individual size and weight of zooplankton organisms and estimation of zooplankton biomass

The biovolume (μm³) of rotifers was determined by measuring 20 individuals of each species, using the formulae described by Ruttner-Kolisko (1977). The biomass was then estimated assuming a relative density of 1.0. For species that appeared less frequently, such that the total of necessary individuals for measurements were not attained, the corresponding values of biomass were obtained from Dumont *et al.* (1975), Sarma *et al.* (2008) and Basinska *et al.* (2010).

The individual sizes of the other zooplankton taxa were computed from literature: summarized data for copepod species in Razouls *et al.* (2005-2017), mean size values of the other taxa, from Pagano & Saint-Jean (1994; lagoon Ebrié, Ivory Coast). Then the

individual weight (as carbon, dry weight and wet weight units) were computed using length-weight relationships from the literature: Mauchline (1998) for calanoid copepods, Chisholm & Roff (1990) for other copepods, and Davis & Wiebe (1985) for other zooplankton taxa.

The individual size, biovolume and weight for each taxon are summarized in Table 1.

To assess the spectrum size, we expressed the size of all organisms with an equivalent spherical diameter computed from the wet weight values and assuming a relative density of 1.

The biomass of each taxon (expressed as mg C m^{-3}) was obtained multiplying the abundance values from Benítez-Díaz Mirón et $al.$ (2014) by the individual carbon weights.

Zooplankton taxa diets and constitution of trophic categories

Using common data from literature the zooplankton taxa were grouped into three categories according to their feeding modes (Table 1):

- Detritus - feeders included Poecilostomatoid copepods (genera $Oncaea$ and $Corycaeus$), harpacticoid copepods (genera $Canuella, Tisbe,$ and undetermined), polychaete larvae and chironomid larvae.
- Predators / carnivorous included cyclopoid copepods from freshwater origin belonging to the genera $Mesocyclops$ and $Thermocyclops$, chaetognaths, hydrachnids, and other water mites.
- Herbivorous-omnivorous (suspension feeders) included all other zooplankton taxa.

Estimation of zooplankton carbon demand and grazing impact

Zooplankton carbon demand (ZCD) of suspension feeding zooplankton was computed based on estimates of biomass and ration:

$$ZCD \ (mgC \ m^{-3} \ d^{-1}) = Ration \ B_{zoo}$$

where B_{zoo} is the biomass of zooplankton in mgC m^{-3}, and Ration is the amount of food consumed per unit of biomass, calculated as:

$$Ration \ (d^{-1}) = (gz + r) \ / \ A$$

where gz is the growth rate, r is the weight specific respiration and A is assimilation efficiency; gz was calculated following Zhou et $al.$ (2010)

Table 1. Mean values of individual size (as equivalent spherical diameter, ESD, and total length), volume and weight (as wet weight, dry weight and carbon weight) of the zooplankton taxa recorded. The second column indicates the trophic group (based on literature knowledge): H=herbivorous / omnivorous, D=detritivorous, C=carnivorous

Taxa	Trophic group	ESD μm	Length μm	Volume μm^3	Wet weight μg ind^{-1}	Dry weight μg ind^{-1}	Carbon weight μg ind^{-1}
ROTIFERA							
Brachionus plicatilis Müller, 1786	H	103		0.57	0.571	0.057	0.026
Brachionus angularis Gosse, 1851	H	62		0.13	0.127	0.013	0.006
Brachionus dimidiatus Bryce, 1931	H	145		1.59	1.591	0.159	0.072
Keratella americana Carlin, 1943	H	74		0.22	0.216	0.022	0.010
Keratella quadrata (Müller, 1786)	H	101		0.53	0.533	0.053	0.024
Platyias quadricornis (Ehrenberg, 1832)	H	182		3.16	3.165	0.316	0.142
Plationus patulus (Müller, 1786)	H	87		0.35	0.347	0.035	0.016
Euchlanis incisa Carlin, 1939	H	104		0.60	0.597	0.060	0.027
Euchlanis dilatata Ehrenberg, 1832	H	109		0.68	0.677	0.068	0.030
Lecane bulla (Gosse, 1851)	H	70		0.18	0.176	0.018	0.008
Lecane quadridentata (Ehrenberg, 1830)	H	86		0.33	0.327	0.033	0.015
Lecane lunaris (Ehrenberg, 1830)	H	62		0.13	0.127	0.013	0.006
Lecane nana (Murray, 1913)	H	57		0.09	0.095	0.009	0.004
Lepadella (Lepadella) donneri Koste, 1972	H	74		0.21	0.212	0.021	0.010
Lepadella (Lepadella) patella (Müller, 1773)	H	64		0.14	0.139	0.014	0.006
Mytilina ventralis (Ehrenberg, 1830)	H	184		3.26	3.262	0.326	0.147
Mytilina bisulcata Luks, 1912	H	107		0.65	0.647	0.065	0.029
Synchaeta oblonga Ehrenberg, 1832	H	222		5.76	5.761	0.576	0.259
Synchaeta bicornis Smith, 1904	H	217		5.37	5.365	0.537	0.241
Trichotria tetractis Ehrenberg, 1830	H	106		0.63	0.630	0.063	0.028
Testudinella patina Hermann, 1783	H	90		0.39	0.388	0.039	0.017
CLADOCERA							
Chydorus sp.	H	416	446	37.59	37.592	3.759	1.692
Ceriodaphnia sp.	H	201	360	4.28	4.283	0.428	0.193
Penilia avirostris Dana, 1849	H	295	613	13.50	13.500	1.350	0.608
COPEPODA							
Non identified nauplii	H	133	156	1.24	1.244	0.124	0.056
Acartia tonsa Dana, 1852	H	436	800	43.29	43.295	4.329	1.948
Centropages velificatus Oliveira, 1947	H	1203	1700	912.18	912.179	91.218	41.048
Paracalanus aculeatus Giesbrecht, 1888	H	754	1100	224.20	224.202	22.420	10.089
Phaenna sp.	D	792	2000	259.91	259.915	25.991	11.696
Temora turbinata Dana, 1852	H	896	1500	376.46	376.459	37.646	16.941
Pseudodiaptomus sp.	H	558	784	90.74	90.739	9.074	4.083
Mesocyclops spp.	C	390	846	30.98	30.976	3.098	1.394
Oithona nana Giesbrecht, 1892	H	264	600	9.67	9.672	0.967	0.435
Oithona sp.	H	264	600	9.67	9.672	0.967	0.435
Corycaeus sp.	D	433	800	42.37	42.369	4.237	1.907
Oncaea venusta Philippi, 1843	D	536	1100	80.53	80.527	8.053	3.624
Euterpina acutifrons Dana, 1852	D	361	600	24.55	24.546	2.455	1.105
Canuella sp.	D	503	1000	66.81	66.806	6.681	3.006
Tisbe sp.	D	503	1000	66.81	66.806	6.681	3.006
unidentified Harpacticoid sp1	D	320	500	17.17	17.171	1.717	0.773
unidentified Harpacticoid sp2	D	503	1000	66.81	66.806	6.681	3.006
OTHER HOLOPLANKTON							
Ostracods	H	594	500	109.62	109.620	32.886	5.919
Nematoda	H	502	2000	66.10	66.097	6.610	2.313
Appendicularia	H	283	1122	11.90	11.900	1.190	0.536
Chaetognatha	C	334	2847	19.43	19.428	1.748	0.680
Hidroarachnida	C	131	500	1.17	1.169	0.222	0.093
Watermite	C	104	400	0.59	0.586	0.111	0.047
MEROPLANKTON							
Polychaeta larvae	D	256	1000	8.80	8.800	0.880	0.308
Polychaeta juveniles	D	96	362	0.46	0.458	0.046	0.016
Cirripeda larvae	H	289	337	12.60	12.600	1.260	0.567
Chironomid larvae	D	502	2000	66.10	66.097	6.610	2.313
Gasteropod larvae	H	240	156	7.20	7.200	0.720	0.324

Table 1. (Continuation)

Taxa	Trophic group	ESD μm	Length μm	Volume μm³	Wet weight μg ind⁻¹	Dry weight μg ind⁻¹	Carbon weight μg ind⁻¹
Bivalve larvae	H	132	120	1.20	1.200	0.120	0.054
MICRONEKTON							
Decapod larvae	C	547	2000	85.56	85.564	16.26	6.85
Fish larvae	C	1229	2500	971.19	971.189	174.81	76.72

$$g\,(w, T, C_a) = 0.033 \left(\frac{C_a}{C_a + 205e^{-0.125T}} \right) e^{0.09T} W^{-0.06}$$

as a function of sea water temperature (T, °C), food availability (C_a, mgC m⁻³, estimated from Chl-*a*), and individuals weight (w, mgC).

Following Nival *et al.* (1975) we considered a constant value of A = 0.7 d⁻¹

Respiration, r, was estimated from gz using an empirical relationship established for tropical lagoon zooplankton by Pagano & Saint-Jean (1994):

$$\text{Ln } r = 0.134 \ln gz - 0.340$$

We compared ZCD to the phytoplankton stock, converted to carbon assuming a classical C:Chl-*a* ratio of 50:1 to estimate the potential clearance of phytoplankton by copepods.

Data analysis

In the results, all mean values are presented with indication of standard deviation (mean ± SD).

Two-way ANOVAs were performed to test the effects of sampling survey (dry season, rainy season and north wind season), stations on the biotic and abiotic parameters and on zooplankton. We used linear model after checking for normal distribution of each variable using Saphiro-Wilk test. Tukey's post-hoc test of honest significant difference (HSD) was also performed to compare the mean group values.

Stepwise multiple regression analyses were conducted to explain the variability in zooplankton and phytoplankton biomasses. Relationships were tested between these biomasses and variables describing main environmental conditions (temperature, salinity, oxygen), food resources (nutrients for phytoplankton and phytoplankton for zooplankton) and potential consumers (herbivorous zooplankton for phytoplankton, and fish and decapod larvae for zooplankton).

The spatial and seasonal variability of biomass percentages of zooplankton groups or biomass percentages of zooplankton size classes were tested using principal component analyses (PCA). In each analysis zooplankton and phytoplankton biomass, temperature

and salinity were considered as additional variables. To increase homoscedasticity, all the data were transformed (log + 1) before analysis.

ANOVA and regression analyses were performed with Statistica v6 software. PCAs were performed with PRIMER 6 software.

Results

Taxonomic and trophic composition of the zooplankton biomass

Zooplankton biomass varied between 0.1 and 230 mgC m^{-3} with a very high outlier value (230 mg m^{-3}) at station 4 during the dry season linked to a zooplankton patch (mostly due to the cyclopoid copepod *Oithona nana*) (Fig. 2), thus this value was discarded from the statistical data analysis. The mean biomass was significantly higher during the dry season than during the rainy and north wind seasons (ANOVA, p=0.018; Fig. 2) whereas no significant difference was found between stations despite a very high mean value at station 6 (Cocal) (Fig. 2) due to the maximal value (35 mg C m^{-3}) recorded during the dry season. The zooplankton biomass was strongly dominated by copepods except in some occasions where other holoplankton (station 1, dry season, stations 7 and 9, rainy season) or meroplankton (stations 2 and 3, dry season, stations 2 and 5, north wind season) became very abundant and even dominant. Cladocerans and rotifers represented a very low fraction of the biomass, and almost disappeared during the north wind season together with other holoplankton, therefore, during the north wind season the zooplankton biomass was quite exclusively composed of copepods and meroplankton organisms.

The comparison of phytoplankton biomass with the biomass of the main zooplankton trophic groups revealed a very unbalanced trophic chain, with a very strong biomass decrease between the first two trophic levels (phytoplankton and herbivorous); in most cases, except at station 4 during the dry season, due to the patch of *Oithona nana* (Fig. 3). The mean herbivorous/phytoplankton ratio was 1.5% ± 0.28% with most values <1%. Detritivores represented up to 45% of the zooplankton biomass, with a mean percentage of 7.9 ± 2.2%. Predaceous zooplankton was always <1% of the biomass and were absent in many cases.

Biomass size-structure

The zooplankton biomass was dominated by small organisms of the size-class <200 μm, representing up to 97% of the total biomass (mean = 33 ± 5%; Fig. 4). The largest size-class (>600 μm) was the second in terms of importance (0 to 95% of the biomass; mean = 19.9 ± 5.2%), whereas the intermediate class (300-400 μm) was the less representative (0-13%; mean = 1.9 ± 0.6%). This resulted roughly in a bimodal size-structure with

two peaks, for small and large organisms. This bimodal size-distribution disappeared during the north wind season, with a significant increase of the smallest class (<200μm) and a significant decrease of the largest one (>600 μm), as compared to the two other seasons (ANOVA, p=0.008 and 0.016 respectively). In stations close to the communication with the ocean (stations 7, 8 and 9) the size-distribution was shifted towards large organisms with a significant reduction of the smallest class (<200 μm) and a significant increase of the largest one (>600 μm) as compared with the other stations (ANOVA, p=0.003 and 0.045 respectively).
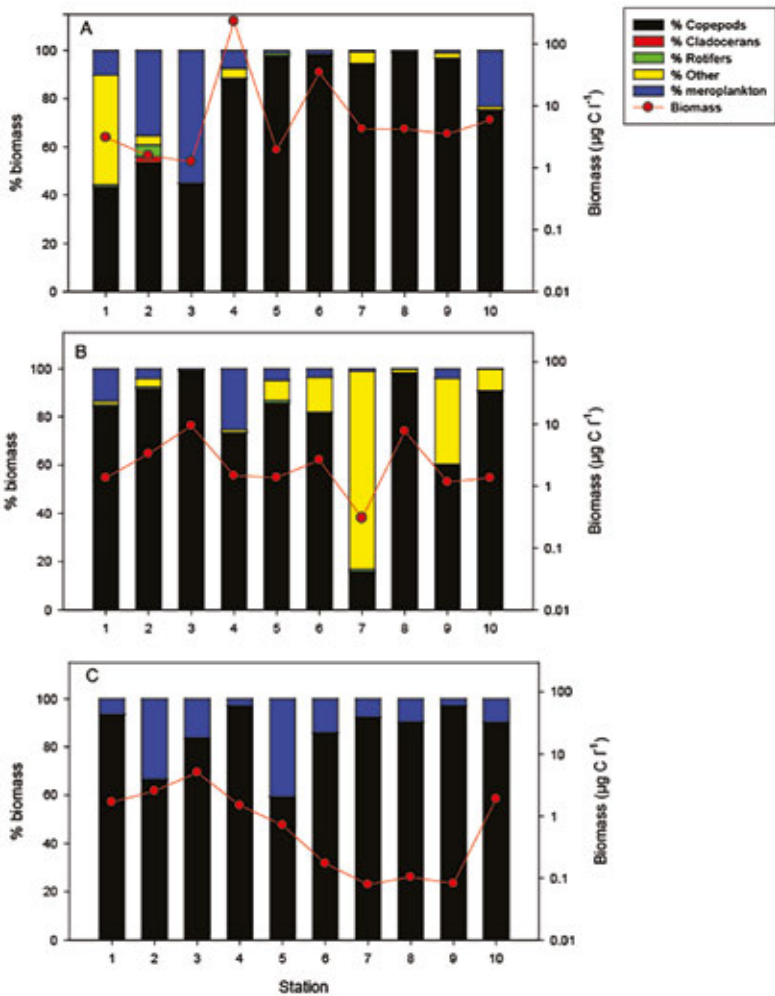
Figure 2. Variations for total zooplankton biomass and for biomass percentages of the main zooplankton taxonomic groups during the dry (A), rainy (B) and north wind (C) seasons.
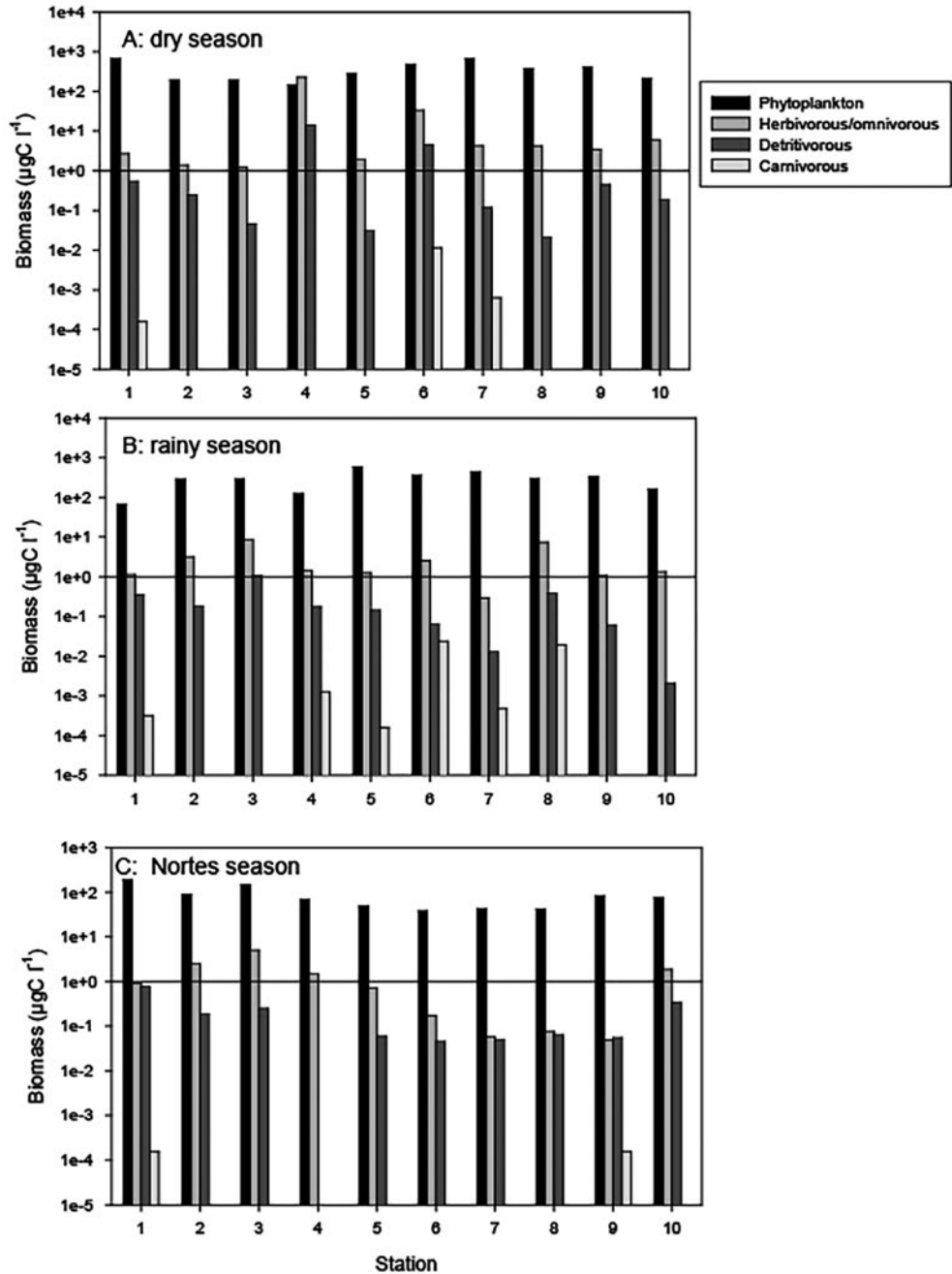
Figure 3. Variations for phytoplankton biomass and for the main zooplankton trophic groups during the dry (A), rainy (B) and north wind (C) seasons.
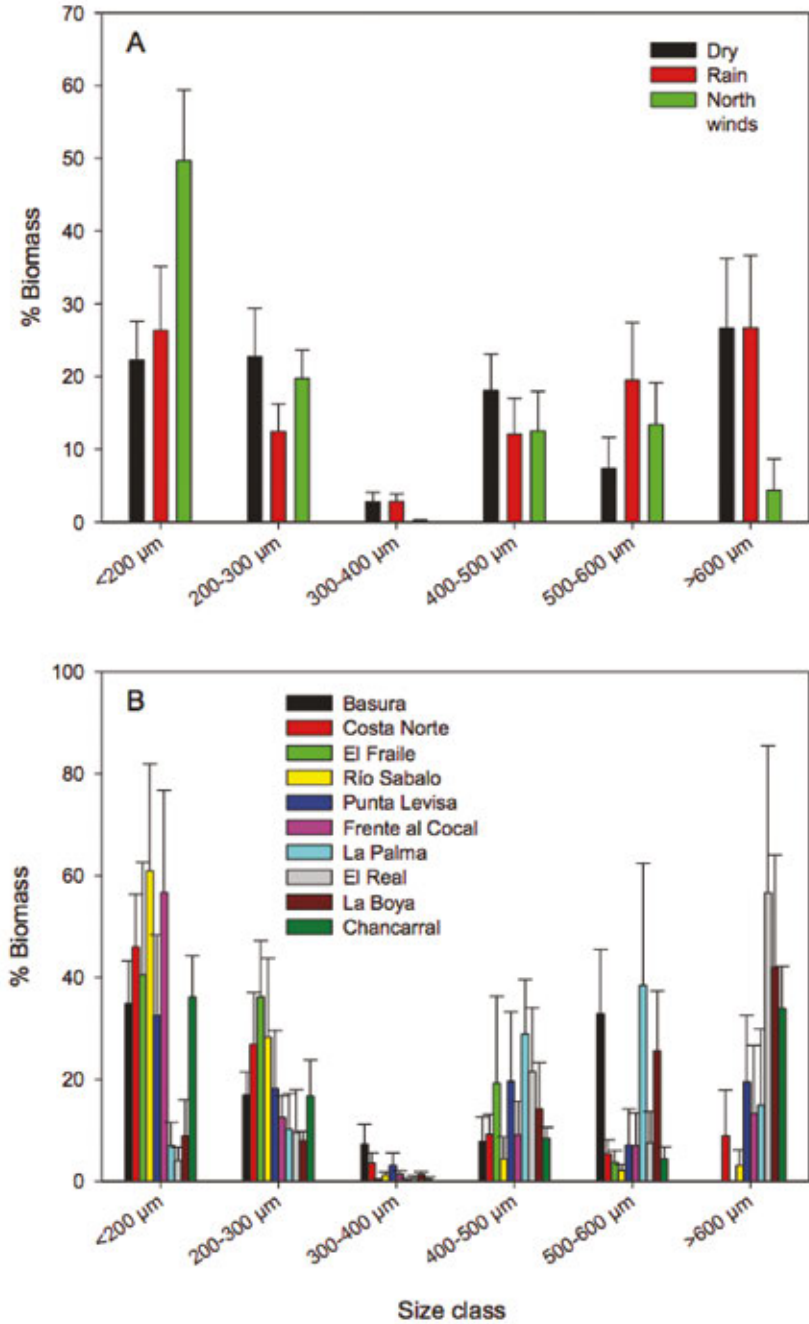
Figure 4. Variation for biomass percentage of the six zooplankton size-classes: mean values per season (A) and sampling station (B).

If we exclude the abnormally very high value at station 4 during the dry season, the zooplankton grazing pressure varied between 0.1 and 46 μgC l^{-1} d^{-1} (mean = 4.9 ± 1.6 μgC l^{-1} d^{-1}) which represented 0.1 to 9.8% of the phytoplankton stock removed daily (mean = 2.0 ± 0.4% d^{-1}; Fig. 5). The grazing pressure was significantly higher during the dry season than during the north wind season (ANOVA, p=0.042) but did not differ significantly between sampling stations. It was significantly correlated to the phytoplankton biomass (r=0.585; p=0.001) suggesting that bottom-up control prevailed.
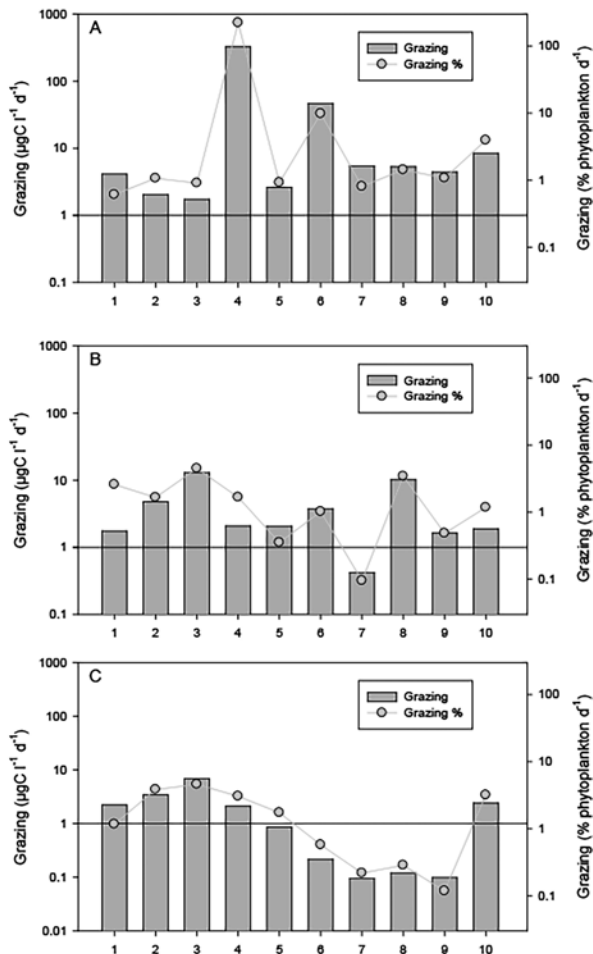

Figure 5. Variations for zooplankton grazing and % grazing impact during the dry (A), rainy (B) and north wind (C) seasons.

Table 2. Equation parameters of the multiple linear regression models, significances and partial correlation coefficients

	Beta			p	Partial correlation
Zooplankton biomass, R^2 = 0.048; p<0.0072					
Intercept	1.005	±	5.072	0.845	
Temperature	-1.448	±	3.639	0.694	-0.083
Salinity	0.027	±	0.219	0.903	0.026
Phytoplankton	0.699	±	0.185	0.001	0.619
Fish larvae	-0.886	±	0.382	0.029	-0.436
Decapod larvae	0.120	±	1.292	0.927	0.019
Phytoplankton biomass, R^2 = 0.49; p<0.028					
Intercept	-1.427	±	0.665	0.044	
Temperature	0.288	±	0.216	0.197	0.279
Salinity	0.034	±	0.249	0.892	0.030
NH_4	2.618	±	1.024	0.018	0.487
Nox	0.581	±	0.402	0.163	0.301
PO_4	-0.153	±	0.349	0.665	-0.095
N/P	-0.595	±	0.396	0.148	-0.312
Herbivorous	0.122	±	0.170	0.481	0.155

The multiple regression model for zooplankton (R^2 = 0.48; p<0.0072) shows that the variability of the zooplankton biomass is positively related to phytoplankton and negatively related to fish larvae whereas temperature and salinity do not enter significantly into the model. This suggests coupled bottom-up (phytoplankton) and top-down (with fish-larvae as predator index) controls of the zooplankton biomass.

The multiple regression model for phytoplankton (R^2 = 0.49; p<0.028) suggests bottom-up control of phytoplankton biomass with NH_4^+ contributing significantly (p=0.018), whereas top-down control (with herbivorous biomass as a proxy) has no significant effect (Table 2).

Principal component analyses (PCA)

The first factorial plane of PCA on biomass percentages of zooplankton taxonomic and trophic groups explained 65% of the variance of which 37.5% were attributed to the first axis and 27.5% to the second (Fig. 6). The first axis opposes most sampling points of the dry season, characterized by high zooplankton and phytoplankton biomasses and by high

percentage of non-copepod holoplankton (others), to the sampling points of the north wind season, characterized by lower plankton biomass and importance of meroplankton and detritivorous organisms.
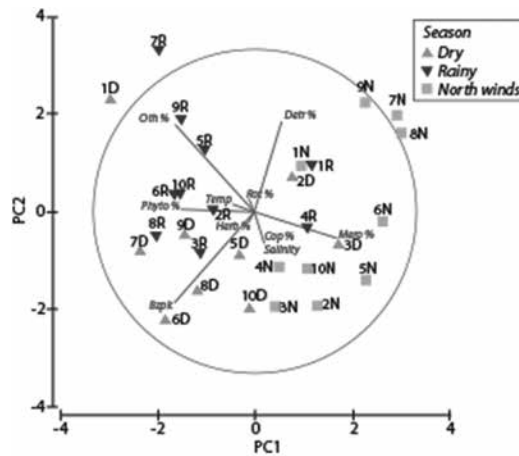

Figure 6. PCA on biomass percentages of zooplankton groups and trophic categories with zooplankton and phytoplankton biomass, temperature and salinity as additional variables: plot of vector variables and stations with color-code according to seasons.

The first factorial plane of PCA on biomass percentages of zooplankton size classes explained 63% of the variance of which 40.1% were attributed to the first axis and 23.0% to the second (Fig. 7). The first axis opposes almost all sampling points of the north wind season, characterized by abundance of smaller size-classes ($<300\,\mu$m), to sampling points of the two other surveys (Dry and Rainy), characterized by larger sizes and higher total biomass. The second axis mainly shows spatial opposition during the north wind season between stations close to the ocean (stations 7, 8 and 9) characterized by larger size classes (500-600 μm) and stations of the central part of the lagoon (stations 2, 3, 4, 5 and 6) characterized by small organisms (100-200 μm).

Discussion

Low zooplankton biomass in Sontecomapan compared to other coastal lagoons

Simultaneous data on phyto- and zooplankton biomass of coastal lagoons are rather scarce, thus it is difficult to compare our data to that from other sites of the world. How-

ever, the zooplankton biomass in Sontecomapan (0.1 to 34 mg C m^{-3}; mean = 3.5 mg C m^{-3}) appears very low compared to literature data. From several studies we could summarize in Table 3, Sontecomapan is the poorest in terms of zooplankton biomass despite the fact that its phytoplankton level is in the range of the other studies. Zooplankton biomass reported in this study is one magnitude lower than the second poorest lagoon in the list (Ebrié lagoon, Ivory Coast; Pagano & Saint Jean, 1994) and more than 100 times lower than those reported in NW Mediterranean lagoons (Lam Hoai & Rougier, 2001; Badosa *et al.*, 2007). Also, it is far poorer than the other Mexican coastal lagoons for which zooplankton biomass were reported, either from the Atlantic coast (Alvarado lagoon; Cruz-Escalona *et al.*, 2007) or the Pacific coast (Huizache-Caimanero Lagoon; Zetina-Rejón *et al.*, 2003).
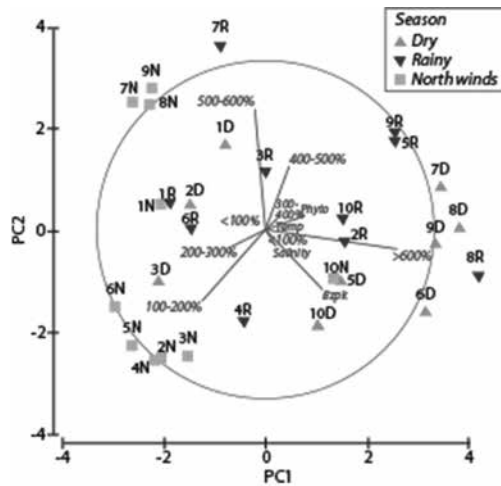

Figure 7. PCA on biomass percentages of zooplankton size classes with zooplankton and phytoplankton biomass, temperature and salinity as additional variables: plot of vector variables and stations with color-code according to seasons.

Another characteristic of Sontecomapan is the very low zooplankton/phytoplankton biomass ratio (1.4%), the lowest reported in Table 3. This low ratio may arise from (i) poor (or inefficient) transfer between the first trophic levels in the pelagos and/or (ii) strong predation pressure by zooplanktophagous organisms. The second hypothesis seems realistic due to high water transparency, favoring visual predation for example from juvenile fish forms (Benítez-Díaz Mirón *et al.*, 2014). Besides, this low biomass ratio is comparable to the one reported by Pagano & Saint Jean (1994) in another Atlantic tropical lagoon (Ebrié lagoon; W Africa) where it was shown that the low zooplankton

biomass compared to phytoplankton was mostly due to strong predation pressure by an important mysid (*Rhopalophthalmus africana*) population (Kouassi *et al.*, 2006).

Zooplankton biomass size-structure in Sontecomapan suggests top-down control by fish

The size spectrum is considered as a key indicator of the zooplankton assemblages dynamics (Krupica *et al.*, 2012). It also reflects the status of the zooplankton community in relation with trophic bottom-up and top-down forcing (Hall *et al.*, 1976; Pace, 1986), and has been shown to be a good indicator of the fish community structure (Mills *et al.*, 1987). Any changes in zooplankton size-structure, may thus reflect changes in the ecosystem structure and functioning in relation with environmental context modification, driven by climatic change and/or anthropogenic pressure (Brucet *et al.*, 2010). In Sontecomapan, the biomass size-structure is, in average, dominated by small organisms in the size-class of <200 μm (up to 97% of the total biomass, with mean of 33 $\pm$ 5%), including mostly rotifer species. This dominance of small organisms may reflect strong predation pressure from larvae or juvenile fish on larger zooplankton organisms, particularly in the 300-600 μm size range, which includes calanoids like *Acartia tonsa,* and harpacticoid copepods like *Euterpina acutifrons* and *Tisbe* spp. (Table 1). Such top-down control by fish on Sontecomapan zooplankton is also suggested by the results from the multiple linear-regression analysis showing a significant negative relationship between zooplankton biomass and fish larvae. The mullet *Mugil cephalus* well represented in the lagoon may exert a strong predation pressure on these copepods as its larvae eat zooplankton almost exclusively (Eda *et al.*, 1990) and its younger stages are known to prey on copepods near the sediment during the day (Eggold & Motta, 1992), when copepods migrate close to the bottom. Besides, mugilids have been shown to play a key role in shallow lakes by removing sediment (and indirectly nutrients) and large zooplankton, most likely influencing the dominance of smaller forms like rotifers (Oltra *et al.*, 2001; Blanco *et al.*, 2003). Catfish *Cathorops aguadulce,* well represented in Sontecomapan lagoon as well as in other coastal lagoon of the Gulf of Mexico, was also shown to spawn in different habitats of the lagoons using the seagrass/mangrove system as a nursery area. This suggests an important larval density of *Cathorops aguadulce* in Sontecomapan, probably exerting strong predation on zooplankton. High predation may be also exerted by their juvenile and adult stages which showed great percentages of copepods in their diet (87% and 47% of total prey numbers respectively) at Téminos Lagoon, Mexico (Yáñez-Arancibia & Lara-Domínguez, 1988).

In this study, we observed spatial and temporal changes on the zooplankton size-structure in Sontecomapan. In terms of seasonal variations, the dominance of small organisms was more accentuated during the north wind season mainly due to depletion of the largest size-class (>600 μm) compared to the other seasons (Fig. 4). This

seasonal variation in zooplankton size-structure may be linked to fish breeding cycles, leading to seasonal variation of the predation pressure from fish larvae on large calanoid copepods such as *Paracalanus aculeatus, Temora turbinata* and *Centropages velificatus*, which make the bulk of the largest zooplankton size-class (Table 1). For example, it was shown in Términos Lagoon (Mexico) that *Arius melanopus* carried seasonal migrations for reproduction and feeding with a peak spawning period just before the north wind season (Yáñez-Arancibia & Lara-Domínguez, 1988). Spatially, the dominance of small organisms was permanent in the central and southern part of the lagoon, but disappeared in the channel communicating with the ocean (stations 7, 8 and 9), where the size-distribution was shifted towards large organisms with a significant increase of the largest size-class (>600μm) as compared with the other stations. This may correspond to variations of zooplankton composition linked to marine water influence, with rather stable salinity conditions in the central and southern part of the lagoon contrasting with tidal influence in the northern part driving inputs of marine coastal species as *Paracalanus aculeatus, Temora turbinata* and *Centropages velificatus* in the channel and rotifers collapse due to high salinity pulses.

Trophic controls of phyto- and zooplanktons

If a top-down control on zooplankton by fish predation is suggested by biomass ratio analysis and the size-structure (see discussion above), our regression analysis also shows clearly that the zooplankton biomass is positively related to phytoplankton suggesting a bottom-up control linked to food (phytoplankton) limitation. Such food limitation, despite the rather high chlorophyll level (Table 3) may result from inedibility of a large part of phytoplankton. In Sontecomapan during the study period, high concentration of chlorophyll c with importance of *c1* and *c2* forms (Benítez-Díaz Mirón *et al.*, 2014) suggested large proportion of dinoflagellates and diatoms, from which several species may be toxic to zooplankton (Granéli & Turner, 2006), also, blooms of diatoms (*Skeletonema* spp., *Cyclotella* spp. and *Chaetoceros holasticus*) and dinoflagellates (*Peridinium* spp., *Prorocentrum cordatum*) have been reported (Aké-Castillo & Vázquez, 2008).

   The multiple regression model for phytoplankton suggests a bottom-up control of phytoplankton biomass linked to nitrogen limitation (NH_4^+) as also suggested by the overall low N/P nutrient ratio in the lagoon (6.4±1.5), much lower than the Redfield ratio. Aké-Castillo & Vázquez (2008) also pointed out the importance of bottom-up effects on phytoplankton in Sontecomapan with clear seasonal and spatial variations linked to organic matter mineralization introduced by mangrove litter.

Table 3. Mean and range values comparison of phytoplankton and zooplankton biomass with literature data on other coastal lagoons

Name	Location	Phytoplankton (P) mg C m^{-3}			Zooplankton (Z) mg C m^{-3}			Z/P (%)	Reference
		mean	min	max	mean	min	max	mean	
Thau	France (NW Mediterranean)	**150**	100	250	**1000**	205	3550	**667**	1
La Pletera	Spain (NW Mediterranean)	**790**	214	2239	**498**	54	1994	**63**	2
Ochkeul	Tunisia (SW Mediterranean)	**19**	1	34	**69**			**367**	3
Ebrié	Ivory Coast (SE Atlantic)	**2100**	776	3160	**36**	8	80	**2**	4
Huizache	Mexico (NW Atlantic)	**885**			**265**			**30**	5
Alvarado	Mexico (NE Pacific)	**207**			**184**			**89**	6
Sontecomapan	Mexico (NW Atlantic)	**250**	38	674	**3.5**	0.1	34.4	**1.4**	This study

References: 1 = Lam Hoai & Rougier (2001), 2 = Badosa *et al.* (2007), 3 = Casagranda & Boudouresque (2010), 4 = Pagano & Saint (1994a)

On the other hand, top-down control by herbivorous organisms on phytoplankton would be non-significant as shown by the regression analysis. Besides, our grazing estimates show that the grazing pressure from herbivorous zooplankton on phytoplankton is rather low, representing only 0.1 to 9.8% of the phytoplankton stock removed daily.

Conclusion

In Sontecomapan, the low zooplankton abundance is related to strong predation by larval and juvenile fish, while the food selectivity of herbivorous zooplankton would lead to a low exploitation of the phytoplankton production, and thus to reduced zooplankton stocks. This should foster the sedimentation of ungrazed dead cells and the accumulation of organic matter at the bottom that could lead to the lagoon's silting up and anoxia events. This tendency also favored by the use of fertilizers and pesticides, and associated eutrophication, would cause a degradation of the ecosystem structure and functioning, however, the high rate of water exchange with the ocean and the resulting low water renewal time in the lagoon should preserve the lagoon from these degrading trends, with the exception of the confined areas that must be surveyed and monitored with priority.

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