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Spatiotemporal variations of zooplankton community in a shallow tropical brackish lagoon (Sontecomapan, Veracruz, Mexico)

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Abstract

Background: We studied the relationships between zooplankton distribution and environmental and trophic factors (abiotic variables, nutrients, bacterial biomass, and chlorophyll pigments) from three sampling surveys carried out during the three hydrological seasons (rainy, dry, and norte) in a tropical coastal lagoon connected to the sea.

Results: Twenty eight (28) of the 54 taxa recorded were identified to species level, of which 3 genera of Cladocera were observed for the first time in the lagoon. Season-specific differences were highly significant. The overall zooplankton abundance was significantly higher during the dry season (157,000 ind.m⁻³) than those during the rainy and norte surveys (means of 11,600 and 16,700 ind.m⁻³ respectively). Copepoda (mostly nauplii) was the most abundant group (>83%) of total zooplankton abundance.

Conclusions: Multivariate (coinertia) and multilinear regression analyses showed that transparency, salinity, temperature, pH, and food availability (Chl *a*, *b*, and *c*) were the main determinants of zooplankton abundance, composition, and diversity, explaining the seasonal differences. The relatively low zooplankton density in the lagoon compared to other eutrophic lagoons is attributed to the combined effects of high water exchanges, low depth, and high transparency, which favor instability and vulnerability to UV effects and/or to visual predation.

Keywords: Sontecomapan; Zooplankton; Brackish lagoon; Shallow lagoon; Environmental factors

Background

Coastal lagoons are often considered as hot spots for biodiversity and are among the most productive ecosystems in the world due to higher nutrient inputs from their catchment basin. However, they are considered as one of the most affected environments by anthropogenic activities (Kemp and Boynton 2012). Increased anthropogenic activities may accelerate the eutrophication process leading to dystrophic crises and/or irreversible deterioration (Bartoli *et al.* 2001). These highly productive and vulnerable ecosystems are subjected to a strong variability at both spatial and temporal scale (Marinov *et al.* 2008) and need to be protected and managed rationally to continue to play their ecological and socio-economic role.

Zooplankton is considered as a sensitive tool for monitoring environmental changes in these lagoons because its sensitivity to trophic (Marcus 2004; Pinto-Coelho *et al.* 2005) and salinity conditions (Kibirige and Perissinotto 2003; Santangelo *et al.* 2007) and its considerable fluctuations induced by abiotic and biotic factors (Naumenko 2009). Zooplankton also constitutes one of the main subsystems in water bodies, transferring energy from autotrophic organisms or microzooplankton to higher trophic levels and regulating sedimentation and cycling of nutrients (nitrogen, phosphorus, carbon) (Eyre 2000; Eyre and McKee 2002; Lassalle *et al.* 2013). It also includes larvae of nektonic and benthic animals having a part of their life cycle in the plankton, and this meroplankton may be economically very important in coastal and lagoon waters (David *et al.* 2006; Kirby *et al.* 2008). Thus, any change in the composition and functioning of the zooplankton community affects the state of the whole ecosystem.

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The patterns and processes of zooplankton spatial and temporal distribution are thus important prerequisite for ecosystem modeling and rational management of coastal lagoons. Traditionally, plankton seasonality is assumed to be less prominent in low-latitude than in high-latitude environments due to the dampened fluctuations in both irradiance and temperature in the tropical zone. However, many tropical or sub-tropical aquatic ecosystems are sensitive to seasonal variations in hydrology due to annual cycles of precipitation; this seasonality occurs both directly through flushing and indirectly through hydrological effects on nutrient cycling by particle resuspension and run-off (De Senerpont *et al.* 2013).

In Mexico, 111 coastal lagoons have been registered (Contreras 1993); however, detailed studies on the zooplankton dynamics are still scarce. Some works confined to only one taxonomic group; for example, the distribution of freshwater rotifers are well documented (Rico-Martinez and Silva-Briano 1993; Nandini *et al.* 2008), as where copepods in coastal (Álvarez-Silva and Gómez-Aguirre 2000; Pantaleón-López *et al.* 2005; Álvarez-Cadena *et al.* 2009), marine, and inland waters (Suárez-Morales and Reid 1998; Suárez-Morales 2004; Suárez-Morales *et al.* 2011). Those studies that include the dynamics of the brackish zooplankton (Escamilla *et al.* 2001; Pantaleón-López *et al.* 2005; De Silva-Davila *et al.* 2006) usually omit the smaller taxonomic groups like rotifers. Until now, only two published papers are available at species level for rotifers and cladocerans from Mexican brackish waters (Mecoacan lagoon (Sarma *et al.* 2000) and Sontecomapan lagoon (Castellanos-Páez *et al.* 2005)). More recently, two works have been published about the rotifers diversity of inland saline waters contributing to 22 new records from Mexico (Wallace *et al.* 2005, 2008).

In summary, the importance of abiotic and biotic forces and that of the biophysical coupling in structuring planktonic communities has been demonstrated in many aquatic systems all over the world (Pinel-Alloul and Ghadouani 2007). However, the patterns and processes of zooplankton spatial and temporal distribution are poorly known in Mexican coastal lagoons.

The purposes of the present work were (1) to test whether the variability of abiotic (transparency, pH, salinity, temperature, etc.) and biotic (composition and abundance of microbial components) factors can significantly drive the seasonal and spatial patterns of zooplankton in shallow tropical coastal lagoons and (2) to contribute filling the knowledge gap about the zooplankton dynamics in Mexican lagoons.

Methods

The Sontecomapan lagoon is a tropical coastal lagoon located on the coast of Veracruz State, in the Gulf of

Mexico (18° 30' to 18° 34' N y 94° 47' to 95° 11' W) (Figure 1). The lagoon has an area of 12 km length and 1.5 km width with an average depth of 1.5 m and a maximum depth of 7 m at the mouth. It is permanently connected to the Gulf of Mexico. High spatiotemporal salinity fluctuation is recorded due to differential intrusion of freshwater and seawater. There are three hydrological seasons: rainy, dry and 'norte' (strong winds from the North). During the rainy season (June to October), the lagoon receives a continuous freshwater inflow from small rivers. In contrast, at the peak of the dry season (January to May), the lagoon shows marine salinities. During the norte season (November to December), the lagoon displays intermediate conditions and behaves like a brackish water body (Aké-Castillo and Vázquez 2008, 2011).

Three sampling surveys, covering a network of 10 stations having different characteristics (see Figure 1, Table 1) were realized in March (26 to 29), June (11 to 14), and November (19 to 22) 2010 corresponding to dry, rainy, and norte seasons, respectively. During each survey, the ten stations were sampled one time for environmental variables, bacterial abundance, chlorophyll concentration, and zooplankton. All sampling and measurements were performed during the day (between 9:00 a.m. and 04:00 p.m.).

Sediment composition

The percentage of sand, silt, and clay in the inorganic fraction of sediments was measured according to the standard Bouyoucos procedure. First, the samples were treated with sodium hexametaphosphate to complex Ca^{2+} , Al^{3+} , Fe^{3+} , and other cations that bind clay and silt particles into aggregates. The density of the soil suspension was determined with a hydrometer calibrated to read in grams of solids per liter after the sand settles down and again after the silt settles (Bouyoucos 1962). The organic matter content was determined by standard method (Walkey and Black 1934).

Water column abiotic variables

The transparency was measured using a Secchi disk. Water samples were collected at two levels (near the bottom and in subsurface) with a Van Dorn bottle. Several measurements were made immediately after the collection: temperature and pH were measured with a portable pH meter Centronics model 49 (± 0.01) (Centronics, Hudson, New Hampshire, USA), salinity with a portable refractometer (Speer 300011, Speer, Scottsdale, AZ, USA) and concentration of dissolved oxygen was determined using the Winkler method (Strickland and Parsons 1972). Subsamples were preserved at -11°C for subsequent analyses of nutrients [phosphate (PO_4^{3-}), ammonium (NH_4), nitrite (NO_2), and nitrate (NO_3)], according to standard Hach protocols 8190, 10023, 10205, and 8192, respectively.

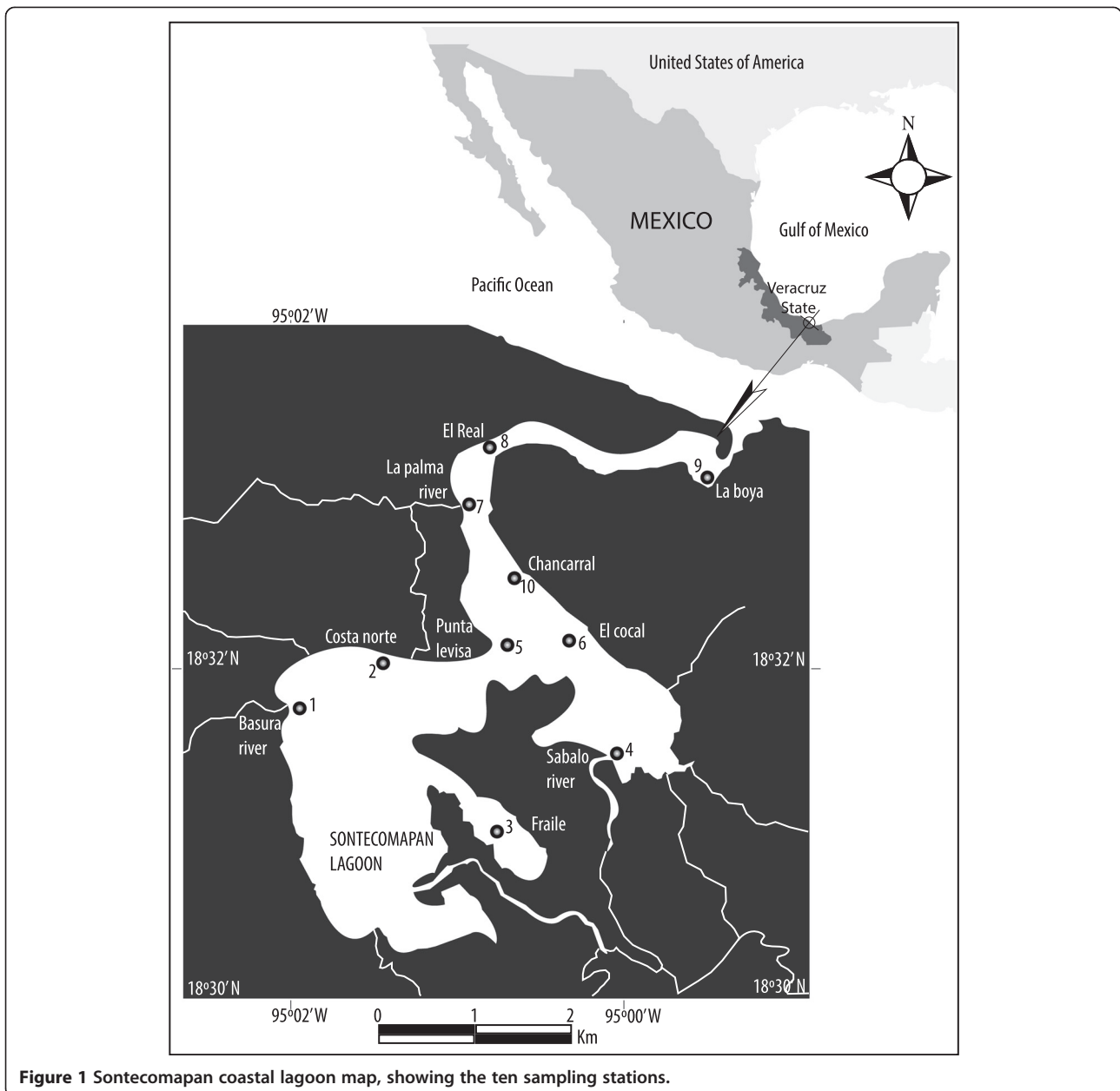


Figure 1 Sontecomapan coastal lagoon map, showing the ten sampling stations.

Biotic variables

In order to determine the bacterial abundance and biomass, samples of 10 ml were preserved with formaldehyde borate-buffered (2% final concentration) and stored in dark at 4°C. From each sample, 1 ml were stained in the dark with 4,6-diamidino-2-phenylindole (DAPI; 1.8 mg l⁻¹ final concentration) (Porter and Feig 1980) and filtered on 0.22 mm black polycarbonate filters. The filters that contain the samples were mounted on slides and stored frozen until analysis. The bacterial enumeration was done using the photomicrographies taken under UV excitation in an Olympus BX-50 epifluorescence microscope (Olympus Corporation, Shinjuku-ku, Japan) and a Lumenera camera

(Ottawa, ON, Canada). For each filter, 20 random fields of 250 μm⁻² were analyzed in the Image Pro Plus 7.1. All cells were counted and measured to calculate cell volumes (μm³) and then were converted to cell carbon (pg C cell⁻¹) using conversion carbon of 0.35 pg C μm³ for heterotrophic bacteria (Bjørnsen 1986). The carbon biomasses were estimated by multiplying the cell carbon by their abundances.

To analyze the photosynthetic chlorophyll pigment (Chl *a*, *b*, *c*₁, and *c*₂), 1 l water (previously filtered through 64 μm net) was passed through a glass fiber filter (GF/C Whatman, Maidstone, UK). At the end of the filtration, 0.2 ml of MgCO₃ suspension was added to the final few

Table 1 Geographic location of sampling sites, median composition of the sediment, and coefficient of pollution

Number	Station	Type	Depth (cm)	% Organic matter	% Silts and clays	% Sands	Coefficient of pollution
1	Río Basura	1	77	8.3 ± 8.8	36 ± 31.2	46 ± 0	1.79
2	Costa Norte	2	80	0.4 ± 0.2	7.3 ± 1.2	92.7 ± 1.2	1.94
3	El Fraile	2	88	3.5 ± 2.4	55.3 ± 5.8	44.7 ± 5.8	3.36
4	El Sábalo	1	240	ND	ND	ND	ND
5	Punta Levisa	2	47	4.6 ± 4.4	16.7 ± 1.2	83.3 ± 1.2	3.26
6	El Cocal	2	171	ND	ND	ND	ND
7	La Palma	1	103	0.6 ± 0.6	12 ± 0	88 ± 0	1.07
8	El Real	3	255	0.1 ± 0.1	9.3 ± 8.1	86 ± 0	2.46
9	La Boya	3	124	1.8 ± 0.4	21.3 ± 1.2	78.7 ± 1.2	0.81
10	El Chancarral	3	105	1.6 ± 0.6	24 ± 0	76 ± 0	2.16

Type 1 stations have direct input of freshwater, type 2 without direct input of freshwater, and type 3 are those with a strong marine influence. The values correspond to the average ± standard deviation.

milliliters to prevent the pigment deterioration and stored for a few hours in a dark and cool place (4°C).

The chlorophyll pigments extraction was done following the method of Vernick and Hayward (1984), and the calculations for determination of chlorophyll was made according to the equations of Jeffrey and Humphrey (1975).

Zooplankton

The zooplankton was collected using a cylindro-conical net (64 µm in mesh opening size, 30 cm in mouth diameter, and 1 m in length). Samples were preserved with 4% formalin. Species identification was made according to Koste (1978) and Segers (1995) for rotifers and Rose (1933), Tregouboff and Rose (1957), Carli and Crisafi (1983), Suárez-Morales and Elías-Gutiérrez (2000), Suárez-Morales (2004), and Razouls *et al.* (2005–2013) for copepods and other taxonomical groups. The taxa were identified and counted under an optical microscope Olympus BMX50 and dissecting microscope Nikon SMZ500 (Nikon, Chiyoda, Tokyo, Japan), respectively. Zooplankton densities, expressed as numbers per cubic meter, were calculated by dividing the number of organisms estimated in each sample by the volume of water filtered in the field (cylinder defined by the net opening area and the length of the drag). The taxonomic diversity was estimated using the Shannon index calculated without taking in account the copepod nauplii, which included miscellaneous species.

Data processing

Two-way analyses of variance (ANOVAs, with a general linear model) were performed to test the effects of sampling survey (dry season, rainy season, and norte), stations, and their interactions on the biotic and abiotic parameters and on zooplankton. 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 distribution. Relationships were tested between zooplankton parameters (total abundance, abundances of the main groups, and species), abiotic (transparency, temperature, salinity, oxygen), and biotic (bacterial abundance and biomass, chlorophyll *a*, *b*, and *c*) parameters.

The spatial and seasonal variability of environmental variables and zooplankton communities was assessed using multivariate analysis after data transformation (log + 1). To avoid the effects of underrepresentative species, a procedure was used to select taxa from the faunistic list based on their contribution to the population diversity as expressed by the Shannon diversity index (Lam-Hoai *et al.* 2006). Only those taxa making a contribution to the index higher than 0.6% were considered (e.g., 28 taxa over the 54 identified). For environmental variables, mean bottom subsurface values were considered, and additionally, we considered the difference between bottom and surface values for salinity and oxygen as proxy for stratification status.

The analysis was realized using two data sets: the first one featured the abundances of zooplankton taxa and the second one the environmental and trophic variables. Factorial correspondence analysis (FCA) and principal component analysis (PCA) were performed on these two data sets, respectively. The results of the two analyses were associated through a coinertia analysis (Doledec and Chessel 1994). Analyses were performed using ADE4 software (Thioulouse *et al.* 1997).

Results

Sediment composition

The Sontecomapan lagoon shows a high variability of sediment composition (Table 1). There was an important variation of the percentage of organic matter

content (OM). Station 8 presented the lowest OM percentage (0.1%) and could be classified as extremely poor according to Walkey and Black (1934) classification. It was followed by stations 2 (0.4%) and 7 (0.6%) typified as very poor and poor, respectively, whereas stations 9 (1.8%) and 10 (1.6%) reached medium contents. Station 3 (3.5%) was considered as very rich, and stations 1 (8.3%) and 5 (4.6%) as extremely rich in organic matter.

The mineral fraction was dominated by sands in stations 2, 5, 7, 8, 9, and 10 (>75%), while fine fractions (silts and clays) were relatively important in stations 1 (36%) and 3 (55%).

Water column abiotic variables

Statistical descriptors and seasonal (survey) variations for environmental parameters are shown in Table 2. Mean bottom surface values were considered.

Water transparency varied between 25 to 380 cm representing 19% to 100% of the total water column depth, but, despite high variability, showed no significant difference between stations or surveys (ANOVA, $p > 0.05$).

Temperature varied between 23.2°C and 28.6°C and displayed significantly higher values during the rainy season than during the two other surveys (ANOVA, $p < 0.05$) but showed no significant difference between stations ($p = 0.78$).

Table 2 Variations in environmental parameters

Variables (symbols, unit)	Dry (mean ± SD)	Rainy (mean ± SD)	Norte (mean ± SD)
Depth (cm)	110.7 ± 70.2 (35 to 280)	157.5 ± 100.2 (24.6 to 380)	118.6 ± 91.8 (30 to 320)
Transparency (cm)	69.8 ± 29.2 (31 to 115)	82.5 ± 106.7 (24.6 to 380)	44.8 ± 25.5 (25 to 100)
Temperature (°C)	24.8 ± 1.0 (23.4 to 27)	26.4 ± 1.2 (24.6 to 28.6)	24.7 ± 1.3 (23.2 to 27.3)
Salinity	17.9 ± 9.9 (4 to 32)	10.4 ± 3.7 (2.4 to 14)	11 ± 8.6 (2 to 27)
pH	7.3 ± 0.4 (6.61 to 7.7)	7.2 ± 0.3 (6.7 to 7.74)	8.1 ± 0.6 (7.05 to 8.98)
Dissolved oxygen (O ₂ m l ⁻¹)	5.6 ± 0.5 (4.9 to 6.5)	4.8 ± 1.3 (2.52 to 6.5)	4.8 ± 1.2 (2.6 to 6.45)
Nitrites (NO ₂ mg l ⁻¹)	0.00 ± 0.0 (0.00 to 0.045)	0.005 ± 0.006 (0.00 to 0.02)	0.014 ± 0.008 (0.004 to 0.03)
Nitrates (NO ₃ mg l ⁻¹)	0.100 ± 0.1 (0.00 to 0.4)	1.210 ± 1.021 (0.0 to 3.0)	0.028 ± 0.031 (0.01 to 0.11)
Ammonium (NH ₄ (mg l ⁻¹))	0.6 ± 0.4 (0.12 to 1.2)	0.093 ± 0.057 (0.0 to 0.22)	0.036 ± 0.023 (0.02 to 0.09)
Phosphates (PO ₄ ⁻ mg l ⁻¹)	0.2 ± 0.1 (0.12 to 0.3)	1.731 ± 2.5 (0.22 to 7.2)	1.867 ± 2.811 (0.08 to 6.84)
Bacterial density (BD (cells.ml ⁻¹ × 10 ⁶))	2.9 ± 2.1 (0.67 to 8.3)	3.8 ± 1.8 (1.3 to 6.9)	4.5 ± 1.3 (2.6 to 6.72)
Bacterial biomass (BBM (µg.C.m ⁻³))	2.6 ± 0.9 (1.2 to 3.8)	2.7 ± 1.4 (0.7 to 4.5)	4.3 ± 2.1 (1.8 to 9.3)
Chlorophyll a (CHLA (mg l ⁻¹))	1.2 ± 0.5 (0.5 to 1.9)	3.8 ± 3.9 (0.05 to 18.3)	0.7 ± 0.5 (0.06 to 1.6)
Chlorophyll b (CHLB (mg l ⁻¹))	0.5 ± 0.7 (0.1 to 2.4)	1.4 ± 1.3 (0.24 to 4.1)	0.8 ± 0.6 (0.07 to 1.9)
Chlorophyll c (CHLC (mg l ⁻¹))	4.0 ± 3.4 (0.2 to 9.6)	1.4 ± 1.3 (0.21 to 4.4)	0.3 ± 0.3 (0.004 to 0.9)

Numbers in body are mean ± standard deviation (SD), and ranges are enclosed in parentheses.

Salinity varied between 2 and 32 according to the stations and the surveys (Figure 2A). It displayed significantly higher mean value during the dry season (17.9) than during the rainy (10.4) and the norte (11) surveys (ANOVA, $p < 0.05$). There was a high variability between stations, with lowest values always recorded at station 1 (Figure 2A). Difference between surface and bottom salinity varied between 0 and 32 (Figure 2B) and displayed no significant variation between stations or surveys (ANOVA, $p > 0.05$). However, very high values (>15) occurred at stations 2 and 7 during the dry season and at stations 3, 6, and 9 during the norte survey.

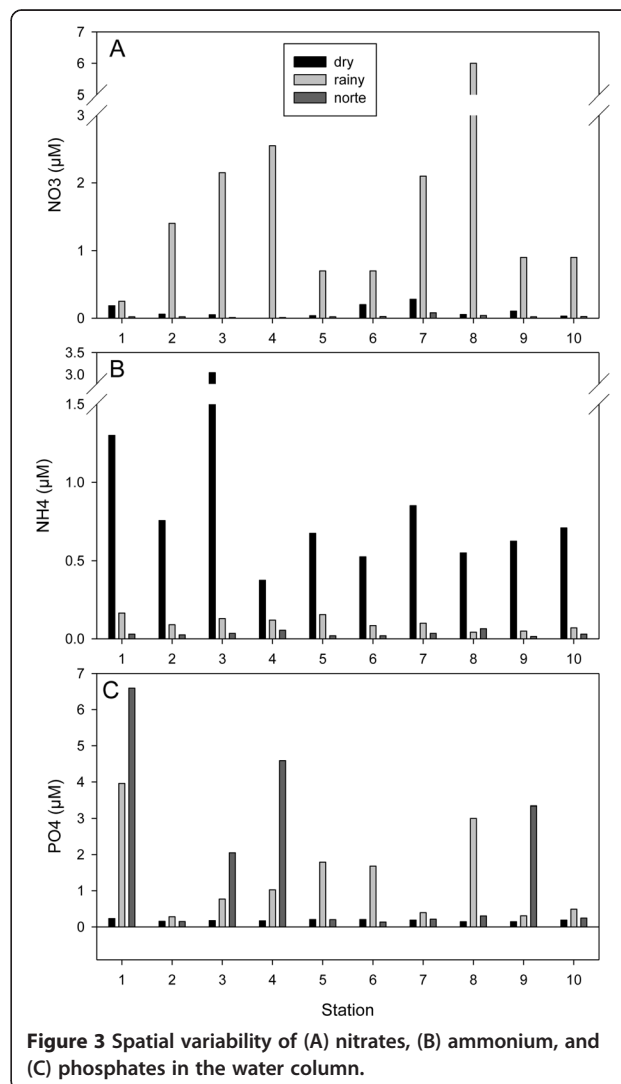
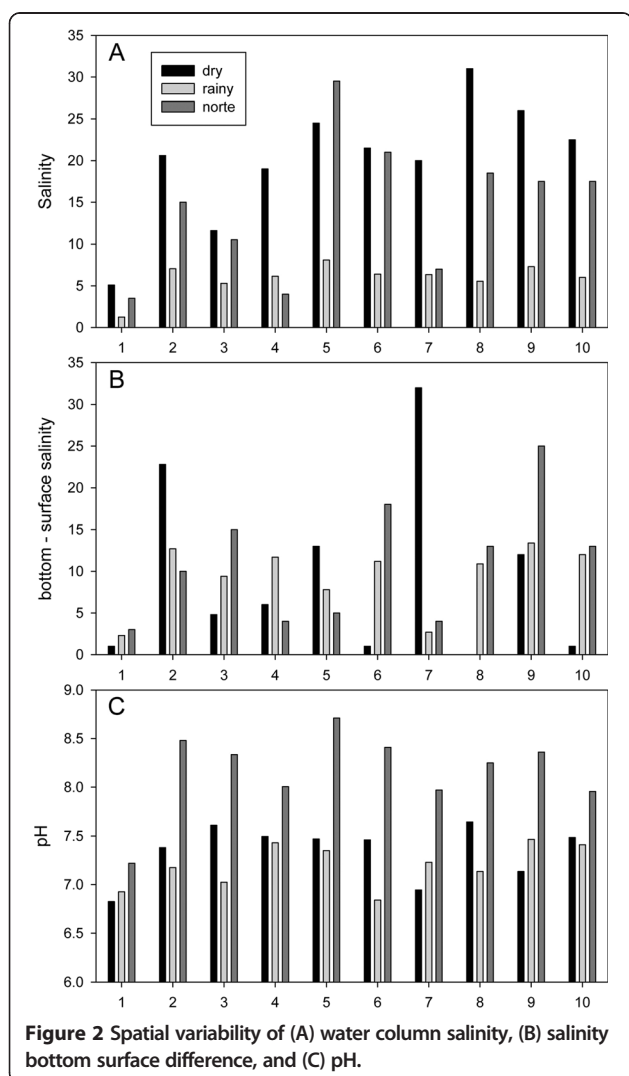
The pH varied between 6.61 and 8.98 and was significantly higher during the norte survey than during the two other ones (ANOVA, $p < 0.05$). Besides, mean pH values at stations 1 and 7 were significantly lower than at the other stations (Figure 2C).

Dissolved oxygen varied between 2.52 and 6.5 mg l^{-1} (Table 2) with difference between surface and bottom

values ranging between 0.1 and 3.8 mg l^{-1} . None of these variables displayed significant variation between stations or surveys (ANOVA, $p > 0.05$).

Nitrites displayed very low values ranging from 0 to 0.03 mg l^{-1} and showed no significant difference between surveys (ANOVA, $p > 0.05$) (Table 2). Nitrates showed significant higher values during the rainy season (mean = 1.21 mg l^{-1} , with values up to 3 mg l^{-1}) than during the two other surveys ($<0.3 \text{ mg l}^{-1}$) (Figure 3A). In contrast, ammonium concentration was significantly higher during the dry season (mean = 0.6 mg l^{-1} , with values up to 1.2 mg l^{-1}) than during the two other surveys ($<0.1 \text{ mg l}^{-1}$) (Figure 3B). None of these nitrogen nutrients displayed significant difference between stations.

Phosphate concentration was significantly lower during the dry season ($<0.2 \text{ mg l}^{-1}$) than during the two other surveys (mean = 1.73 and 1.87 mg l^{-1} in the rainy and norte seasons, respectively), but these differences were mainly linked to stations 1, 3, 4, 8, and 9 while very



low values were observed at stations 2, 7, and 10 during the three surveys (Figure 3C).

Biotic variables

Bacterial density and biomass ranged from 0.67 to 8.3×10^6 cell ml^{-1} and from 0.7 to $9.3 \mu\text{g.C.m}^{-3}$, respectively. They were significantly higher during the norte survey than during the two other ones (ANOVA, $p < 0.05$), while there was no significant difference between stations.

Except at station 1, chlorophyll *a* content was the highest (up to $18.3 \mu\text{g l}^{-1}$) during the rainy survey and lowest (up to $1.6 \mu\text{g l}^{-1}$) during the norte (Table 2, Figure 4A). Chlorophyll *b* showed no significant difference between stations or surveys (ANOVA, $p > 0.05$). However, stations 1 to 4 displayed lower chlorophyll *b* values during the rainy survey than during the two other ones, while a reverse trend was observed at stations 5 to 9 (Figure 4B). Chlorophyll *c* displayed significantly higher values during

the dry season survey (mean = $4.0 \mu\text{g l}^{-1}$, with values up to $9.6 \mu\text{g l}^{-1}$) surveys than during the rainy and the norte surveys (mean = 1.4 and $0.3 \mu\text{g l}^{-1}$, respectively). Station-specific differences in chlorophyll *c* content was not significant (ANOVA, $p > 0.05$); however, chlorophyll *c* value was consistently lower at stations 2, 3, and 4 ($< 1 \mu\text{g l}^{-1}$, Figure 4C).

Zooplankton

Fifty-five zooplankton taxa were enumerated in the 10 stations during the 3 surveys (Table 3). They included 21 rotifers, 17 copepods (including miscellaneous nauplii) 3 cladocerans, 7 miscellaneous other holoplanktonic groups (ostracods, polychaetes, nematods, appendicularians, chaetognaths hydrachnida, and water mites), and 6 meroplankton taxa (polychaete, fish, chironomid, gastropod, bivalve, cirriped, and decapod larvae).

The number of taxa per sample varied between 2 (station 4, norte survey) and 24 (station 2, dry season survey) (Figure 5A) and was significantly higher during the dry and rainy surveys than during the norte survey, while no significant difference was recorded between stations.

Shannon diversity index varied between 0 and 3.8 bit ind^{-1} and was significantly higher during the dry and rainy surveys than during the norte survey (Figure 5B). It was also significantly lower at stations 3 and 4 than in all other stations.

Total zooplankton abundance varied between 280 and $1,300,000 \text{ ind.m}^{-3}$ (Figure 5C) and showed no significant difference between stations or surveys (ANOVA, $p > 0.05$). However, stations 7, 8, and 9 always displayed very low abundances ($< 3,600 \text{ ind.m}^{-3}$) while stations 4, 6, and 10 during the dry season survey and station 3 during the norte survey displayed the highest abundances ($> 60,000 \text{ ind.m}^{-3}$).

Copepods were the most important group representing 31.1% to 99.7% of the total zooplankton abundance and nauplii (25.3% to 99.5%) mainly contributed to this dominance (Table 3).

The top two highly abundant copepod species were *Acartia tonsa* and *Oithona nana*, which were present in more than 80% of the samples and represented up to 100% and 77% of the non-naupliar copepod abundance, respectively. *Paracalanus aculeatus* (43% occurrence and up to 37% abundance), *Euterpina acutifrons* (20% and up to 3%), and *Pseudodiaptomus* sp. (17% and up to 29%) were also rather well represented while the other species were scarce ($< 10\%$ occurrence).

Other holoplanktonic organisms were less important, rotifers, cladocerans, and miscellaneous other groups representing less than 19%, 2%, and 37% of the total zooplankton abundance, respectively.

Among rotifers, only one species, *Brachionus plicatilis*, was present in more than 50% of the samples. *Lecane bulla*

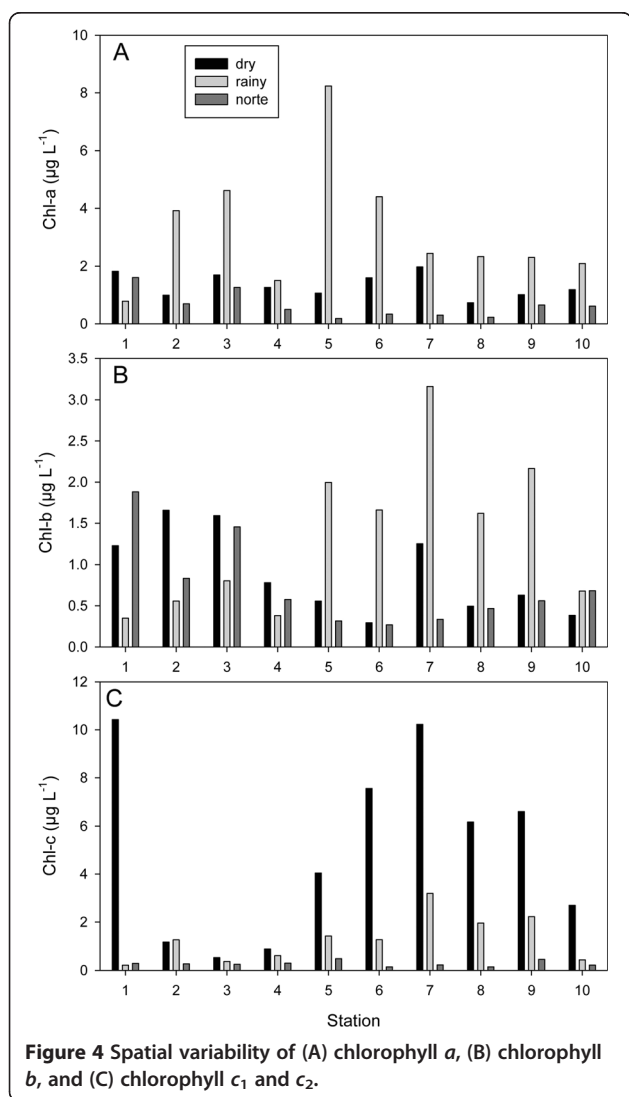


Table 3 Seasonal abundances and abundance percentage of the zooplanktonic taxa identified

	Symbol	DRY	RAINY	NORTE	% Abundance		
		(ind.m ⁻³ ± SD)	(ind.m ⁻³ ± SD)	(ind.m ⁻³ ± SD)	Dry	Rainy	Norte
Phylum Rotifera Cuvier, 1817							
Subclass Monogononta Plate, 1889							
Superorder Pseudotrocha Kutikova, 1970							
Order Ploima Hudson and Gosse, 1886							
Family Brachionidae Ehrenberg, 1838							
<i>Brachionus plicatilis</i> Müller, 1786	<i>RBp</i>	80.5 ± 222.2	0.5 ± 0.7		2.05	0.17	0.07
<i>Brachionus angularis</i> Gosse, 1851	<i>Rba</i>	0.1 ± 0.3	0.0 ± 0.1	0.0 ± 0.0	0.00	0.00	0.00
<i>Brachionus dimidiatus</i> Bryce, 1931	<i>RBd</i>	0.8 ± 2.4	0.0 ± 0.0	0.0 ± 0.1	0.02	0.00	0.00
<i>Keratella americana</i> Carlin, 1943	<i>RKa</i>	0.0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.00	0.00	0.00
<i>Keratella quadrata</i> (Müller, 1786) ^a	<i>RKq</i>	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.00	0.00	0.00
<i>Platylas quadricornis</i> (Ehrenberg, 1832)	<i>RPq</i>	1.1 ± 3.3	0.1 ± 0.1	0.0 ± 0.0	0.03	0.03	0.00
<i>Platyonus patulus</i> (Müller, 1786)	<i>RPP</i>	0.0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.00	0.00	0.00
Family Euchlanidae Ehrenberg, 1838							
<i>Euchlanis incisa</i> Carlin, 1939 ^a	<i>REi</i>	0.0 ± 0.0	0.1 ± 0.3	0.0 ± 0.1	0.00	0.03	0.00
<i>Euchlanis dilatata</i> Ehrenberg, 1832 ^a	<i>REd</i>	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.00	0.00	0.00
Family Lecanidae Remane, 1933							
<i>Lecane bulla</i> (Gosse, 1851)	<i>RLb</i>	1.5 ± 4.0	0.0 ± 0.0	0.6 ± 1.7	0.04	0.00	0.14
<i>Lecane quadridentata</i> (Ehrenberg, 1830)	<i>RLq</i>	0.5 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.01	0.00	0.00
<i>Lecane lunaris</i> (Ehrenberg, 1832)	<i>RLl</i>	0.0 ± 0.0	0.0 ± 0.1	0.0 ± 0.0	0.00	0.00	0.00
<i>Lecane nana</i> (Murray, 1913)	<i>RLn</i>	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.00	0.00	0.00
Family Lepadellidae Haring, 1913							
<i>Lepadella (Lepadella) donneri</i> Koste, 1972	<i>RLd</i>	0.0 ± 0.0	0.0 ± 0.1	0.0 ± 0.0	0.00	0.00	0.00
<i>Lepadella (Lepadella) patella</i> (Müller, 1773)	<i>RLp</i>	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.00	0.00	0.00
Family Mytilinidae Haring, 1913							
<i>Mytilina ventralis</i> (Ehrenberg, 1830) ^a	<i>RMv</i>	0.0 ± 0.0	0.0 ± 0.1	0.0 ± 0.0	0.00	0.00	0.00
<i>Mytilina bisulcata</i> (Luicks, 1912) ^a	<i>RMb</i>	0.5 ± 1.6	0.0 ± 0.0	0.0 ± 0.0	0.01	0.00	0.00
Family Synchaetidae Hudson and Gosse, 1886							
<i>Synchaeta oblonga</i> Ehrenberg, 1832 ^a	<i>RSo</i>	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0	0.00	0.07	0.00
<i>Synchaeta bicornis</i> Smith, 1904 ^a	<i>RSb</i>	0.0 ± 0.0	0.3 ± 0.5	0.0 ± 0.0	0.00	0.10	0.00
Family Trichotriidae Haring, 1913							
<i>Trichotria tetractis</i> (Ehrenberg, 1830) ^a	<i>RTt</i>	0.1 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.00	0.00	0.00
Superorder Pseudotrocha Kutikova, 1970							
Order Flosculariaceae Haring, 1913							
Family Testudinellidae Haring, 1913							
<i>Testudinella patina</i> (Hermann, 1783) ^a	<i>RTP</i>	0.3 ± 0.7	0.0 ± 0.1	0.0 ± 0.1	0.00	0.00	0.00
Subphylum Crustacea							
Class Branchiopoda							
Order Cladocera							
<i>Chydorus</i> sp. ^a	<i>CCh</i>	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.00	0.00	0.00
<i>Ceriodaphnia</i> sp. ^a	<i>CCd</i>	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.00	0.00	0.00
<i>Penilia avirostris</i> (Dana, 1849) ^a	<i>CP</i>	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.00	0.00	0.00

Table 3 Seasonal abundances and abundance percentage of the zooplanktonic taxa identified (Continued)

Class Maxillopoda								
Subclass: Copepoda								
Non identified nauplii	Cna	2952 ± 7647	249 ± 294	393 ± 552	75.2	85.6	94.4	
Superorder Gymnoplea								
Order Calanoida								
Family Acartiidae								
<i>Acartia tonsa</i> Dana, 1852	CA _t	54.5 ± 120.6	7.7 ± 19.8	0.5 ± 0.7	1.39	2.65	0.12	
Family Centropagidae								
<i>Centropages velificatus</i> (Oliveira, 1947)	CC _v	0.0 ± 0.0	0.4 ± 1.1	0.0 ± 0.0	0.00	0.14	0.00	
Family Paracalanidae								
<i>Paracalanus aculeatus</i> Giesbrecht, 1888	CP _a	5.4 ± 10.3	0.9 ± 1.0	0.2 ± 0.6	0.14	0.31	0.05	
Family Clausocalanoidea								
<i>Phaenna</i> sp. ^a	CHP	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0	0.1	0	
Family Temoridae								
<i>Temora turbinata</i> (Dana, 1852)	CT _t	0.1 ± 0.3	0.1 ± 0.1	0.0 ± 0.0	0.00	0.00	0.00	
Family Pseudodiaptomidae								
<i>Pseudodiaptomus</i> sp.	CP _d	0.1 ± 0.2	0.3 ± 0.5	0.0 ± 0.1	0	0	0	
Superorder Podoplea								
Order Cyclopoida								
Family Cyclopidae								
<i>Mesocyclops</i> sp.	CM _c	0.0 ± 0.0	0.0 ± 0.1	0.0 ± 0.0	0.00	0.03	0.00	
Family Oithonidae								
<i>Oithona nana</i> (Giesbrecht, 1892) ^a	CO _n	685.7±	20.3±	2.3±	0	0.1	0	
<i>Oithona</i> sp.	CO _{sp}	0.0 ± 0.0	0.9 ± 2.8	0.0 ± 0.0	0	0.2	0	
Family Corycaeidae								
<i>Corycaeus</i> sp.	CC _y	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0	0.3	0	0	
Family Oncaeiidae								
<i>Oncaea venusta</i> Philippi, 1843.	CO _v	0.0 ± 0.0	0.5 ± 1.6	0.0 ± 0.0	0	0	0.2	
Order Harpacticoida								
Family Tachidiidae								
<i>Euterpina acutiformis</i> Dana, 1852	CE _a	11.5 ± 32.5	0.1 ± 0.2	0.0 ± 0.0	0.1	0.5	0	
Family Tisbidae								
<i>Tisbe</i> sp. ^a	CHT	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0	0.1	0.1	0	
Other Harpacticoida								
<i>Canuella</i> sp. ^a	CHC	0.0 ± 0.1	0.0 ± 0.0	0.7 ± 2.0	0	0	0	
Unidentified 1	CH1	4.0 ± 5.1	1.6 ± 1.7	0.2 ± 0.3	0	0	0	
Unidentified 2	CH2	0.4 ± 1.1	0.0 ± 0.1	0.0 ± 0.0	0	0	0	
Other Zooplankters								
Ostracods	Osp	4.5 ± 12.2	0.3 ± 0.4	0.0 ± 0.0	3	6	0	
Appendicularia	Asp	0.0 ± 0.0	0.5 ± 1.0	0.0 ± 0.0	0	5	0	
Polychaeta (larvae)	Plv	15.1 ± 33.0	1.0 ± 1.2	1.0 ± 1.2	7	7	8	
Polychaeta (adults)	Psp	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.1	0	2	2	
Nematoda	Nsp	0.4 ± 0.5	0.7 ± 1.3	0.0 ± 0.0	4	7	0	
Chironomid larvae	Chlv	0.0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	1	1	0	
Hydrarachnidae	Hda	0.0 ± 0.0	0.02 ± 0.05	0.0 ± 0.0	0	0.03	0	

Table 3 Seasonal abundances and abundance percentage of the zooplanktonic taxa identified (Continued)

Watermite	Wtm	0.1	0.1 ± 0.2	0.0 ± 0.0	2	4	2
Chaetognatha	Chsp	0.0 ± 0.1	0.1 ± 0.2	0.0 ± 0.0	1	1	0
Gasteropod larvae	Glv	29.5 ± 38.1	0.8 ± 1.0	16.2 ± 25.4	7	8	8
Cyrripeda larvae	Cyl	73.8 ± 223.8	3.8 ± 4.9	0.9 ± 1.5	8	9	6
Bivalve larvae	Blv	1.8 ± 5.6	0.0 ± 0.1	0.4 ± 1.3	4	2	1
Decapod larvae	Dlv	0.4 ± 1.1	0.0 ± 0.1	0.0 ± 0.1	3	2	1
Fish larvae	Flv	0.2 ± 0.4	0.1 ± 0.2	0.0 ± 0.0	2	3	2

Seasonal (survey) values of mean abundances (±standard deviation, SD) and of abundance percentage of the zooplanktonic taxa identified. The symbols used for the multivariate analysis are shown in the second column. ^aSpecies or genera recorded for first time in the lagoon.

(23%), *Synchaeta oblonga* (17%), *Testudinella patina* (17%), *Platyas quadricornis* (13%), and *Synchaeta bicornis* (13%).

Cladocerans were represented by one marine species (*Penilia avirostris*) and two freshwater (*Chydorus* sp. and *Ceriodaphnia* sp.) species.

The other holoplankton with an occurrence frequency >10% were nematods (37% occurrence), ostracods (30%),

hydrachnids (27%), water mites (23%), and appendicularians (17%).

Meroplankton was present in all samples, except at station 10 during the rainy survey, and represented up to 19% of the total zooplankton abundance. It was mainly represented by cirriped, gastropod, and polychaete larvae (>70% occurrence). Decapod (23% occurrence), chironomids (20%), bivalve (13%), and fish (7%) larvae were less represented.

The relative percentages of copepods, rotifers, and meroplankton showed no significant difference between stations or surveys (ANOVA, $p > 0.05$). The percentage of other holoplanktonic groups was significantly higher during the rainy survey than during the two other ones ($p = 0.046$), but this was mainly due to the relative importance of appendicularia and nematoda (14% to 37%) at stations 7, 8, and 9 where they compensated relatively low percentages of copepods (36% to 78%).

Multiple regression analysis

When considering the whole data set for the three surveys ($n = 30$), the water transparency had positive effects on diversity (Shannon index), but had negative relationships with total zooplankton, copepods, copepod nauplii, and *A. tonsa* (Table 4). Temperature had positive effects on marine rotifers (*B. plicatilis* and *S. bicornis*). Salinity had positive effects on total zooplankton, *A. tonsa*, and marine rotifers. pH had negative relationships with the number of taxa per sample, *A. tonsa*, and freshwater rotifers. Contrasted effects were shown for the three different chlorophyll forms (*a*, *b*, and *c*). Chlorophyll *a* had positive effects on copepod, copepod nauplii, and *A. tonsa*. Chlorophyll *b* had positive effects on taxonomic richness (number of taxa) and on freshwater rotifers but negative effects on abundances of total zooplankton, copepods, nauplii, and *A. tonsa*. Chlorophyll *c* had negative relationship with freshwater rotifers. When considering the three surveys separately ($n = 10$), most of the preceding relationships were not significant (Table 4).

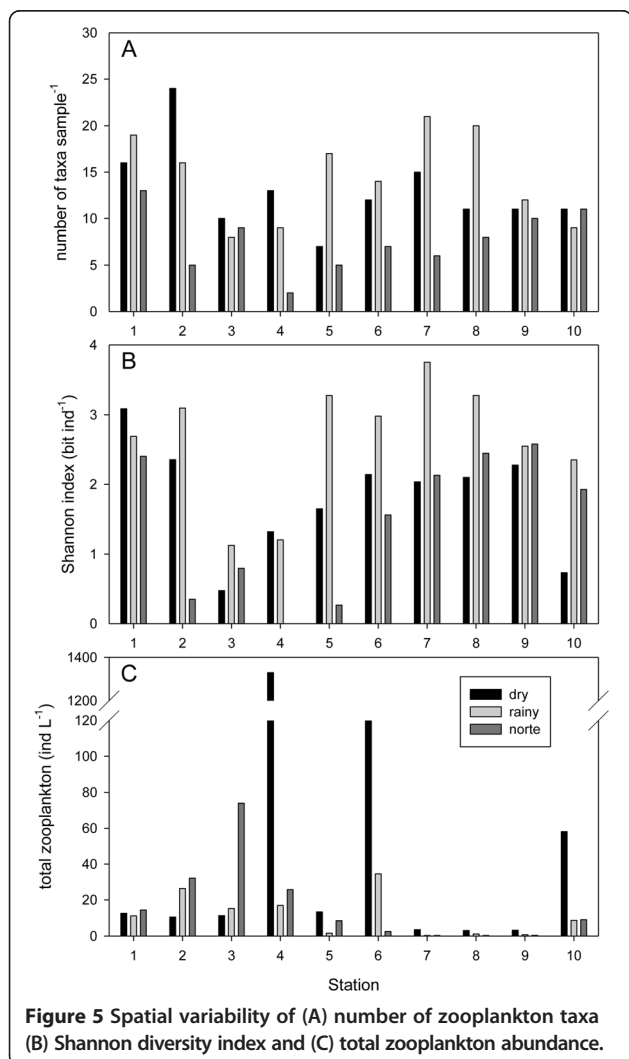


Figure 5 Spatial variability of (A) number of zooplankton taxa (B) Shannon diversity index and (C) total zooplankton abundance.

Table 4 Equation parameters of the multiple linear regression models

	Grouped data (n = 30)		Dry season survey (n = 10)		Rainy season survey (n = 10)		Norte season survey (n = 10)	
	Beta	<i>p</i>	Beta	<i>p</i>	Beta	<i>p</i>	Beta	<i>p</i>
Number of taxa	$R^2 = 0.62; p = 0.0002$		$R^2 = 0.21, p = 0.180$		$R^2 = 0.12; p = 0.267$		$R^2 = 0.19; p = 0.196$	
Intercept	225.30 ± 66.40	0.003	55.09 ± 91.50	0.566	143.41 ± 119.32	0.269	59.93 ± 0.83	0.434
Chlorophyll b	22.54 ± 5.26	0.000	22.09 ± 12.70	0.126	13.68 ± 8.95	0.170	11.02 ± 10.36	0.323
pH	-166.17 ± 45.60	0.002	-51.98 ± 98.05	0.612	-146.16 ± 130.97	0.301	-46.33 ± 60.83	0.471
Diversity	$R^2 = 0.44; p = 0.0025$		$R^2 = 0.41; p = 0.180$		$R^2 = 0.00; p = 0.72$		$R^2 = 0.06; p = 0.245$	
Intercept	6.07 ± 2.46	0.022	-0.65 ± 0.46	0.194	0.44 ± 0.27	0.146	-0.43 ± 0.63	0.507
Transparency	0.39 ± 0.13	0.005	0.59 ± 0.25	0.046	0.06 ± 0.15	0.710	0.48 ± 0.38	0.245
Zooplankton	$R^2 = 0.40; p = 0.011$		$R^2 = 0.16; p = 0.291$		$R^2 = 0.54; p = 0.055$		$R^2 = 0.76; p = 0.026$	
Intercept	5.88 ± 13.63	0.671	12.39 ± 3.97	0.021	4.94 ± 1.13	0.005	11.60 ± 3.10	0.010
Transparency	-3.23 ± 0.74	0.000	-3.10 ± 1.74	0.125	-0.63 ± 0.70	0.402	-5.32 ± 1.64	0.017
Chlorophyll b	-3.22 ± 1.11	0.009	-3.82 ± 2.67	0.203	-3.82 ± 1.12	0.015	-0.68 ± 2.48	0.793
Salinity	1.45 ± 0.60	0.024	-1.11 ± 1.47	0.476	1.45 ± 1.27	0.296	0.79 ± 0.77	0.344
Copepods	$R^2 = 0.39; p = 0.012$		$R^2 = 0.20; p = 0.255$		$R^2 = 0.74; p = 0.010$		$R^2 = 0.63; p = 0.029$	
Intercept	17.93 ± 7.62	0.028	9.85 ± 3.49	0.030	5.33 ± 0.97	0.002	13.12 ± 3.30	0.007
Transparency	-3.27 ± 0.78	0.000	-3.15 ± 1.73	0.118	-0.79 ± 0.61	0.242	-5.53 ± 1.73	0.019
Chlorophyll b	-3.97 ± 1.20	0.003	-3.81 ± 2.42	0.166	-4.78 ± 0.95	0.002	-7.50 ± 6.97	0.323
Chlorophyll a	3.03 ± 1.09	0.012	3.14 ± 3.55	0.411	2.26 ± 0.89	0.044	6.06 ± 6.42	0.382
Nauplii	$R^2 = 0.38; p = 0.015$		$R^2 = 0.21; p = 0.249$		$R^2 = 0.66; p = 0.022$		$R^2 = 0.75; p = 0.031$	
Intercept	15.03 ± 7.89	0.071	8.61 ± 3.60	0.054	4.05 ± 1.15	0.013	11.55 ± 3.39	0.014
Transparency	-3.39 ± 0.81	0.000	-3.39 ± 1.78	0.106	-1.00 ± 0.72	0.216	-5.55 ± 1.78	0.020
Chlorophyll b	-3.96 ± 1.24	0.004	-3.77 ± 2.50	0.181	-4.70 ± 1.12	0.006	6.59 ± 6.60	0.357
Chlorophyll a	2.87 ± 1.13	0.019	3.10 ± 3.67	0.430	2.12 ± 1.05	0.091	-8.00 ± 7.17	0.307
<i>Acartia tonsa</i>	$R^2 = 0.52; p = 0.001$		$R^2 = 0.00; p = 0.577$		$R^2 = 0.10; p = 0.445$		$R^2 = 0.00; p = 0.831$	
Intercept	14.27 ± 5.38	0.015	47.35 ± 47.53	0.376	-4.06 ± 20.21	0.851	-1.96 ± 5.87	0.755
Salinity	1.72 ± 0.44	0.001	-4.42 ± 3.69	0.296	-1.68 ± 2.08	0.465	0.23 ± 0.42	0.610
Chlorophyll a	2.23 ± 0.72	0.005	-3.97 ± 2.92	0.245	2.78 ± 1.54	0.145	0.23 ± 2.39	0.929
Chlorophyll b	-2.16 ± 0.77	0.011	1.97 ± 5.37	0.732	-1.53 ± 1.21	0.276	0.57 ± 2.62	0.840
pH	-14.00 ± 5.57	0.020	-44.55 ± 44.90	0.377	6.42 ± 23.21	0.796	1.98 ± 5.96	0.757
Transparency	-1.22 ± 0.52	0.028	2.46 ± 2.13	0.312	-0.60 ± 0.81	0.500	-0.14 ± 0.67	0.847
Marine Rotifers	$R^2 = 0.30; p = 0.033$		$R^2 = 0.22; p = 0.170$		$R^2 = 0.56; p = 0.022$		$R^2 = 0.00; p = 0.528$	
Intercept	-31.44 ± 17.10	0.080	-90.35 ± 58.55	0.167	81.78 ± 22.95	0.009	-24.28 ± 26.44	0.389
Salinity	2.04 ± 0.79	0.017	3.90 ± 2.35	0.140	2.76 ± 1.56	0.120	16.65 ± 18.37	0.395
Temperature	25.31 ± 12.19	0.050	61.63 ± 41.21	0.178	-57.75 ± 16.62	0.010	1.22 ± 1.10	0.303
Feshw. rotifers	$R^2 = 0.50; p = 0.003$		$R^2 = 0.69; p = 0.018$		$R^2 = 0.00; p = 0.726$		$R^2 = 0.76; p = 0.008$	
Intercept	50.94 ± 15.57	0.004	53.31 ± 30.04	0.126	22.52 ± 22.41	0.354	10.25 ± 8.45	0.270
Chlorophyll b	4.39 ± 1.23	0.002	3.17 ± 3.29	0.372	1.04 ± 3.43	0.772	5.06 ± 1.44	0.013
pH	-30.40 ± 11.39	0.015	-54.96 ± 31.01	0.127	-24.07 ± 24.62	0.366	-11.59 ± 8.67	0.230
Chlorophyll c	-1.79 ± 0.79	0.036	-3.18 ± 1.40	0.064	0.11 ± 3.36	0.974	1.21 ± 3.73	0.757

Equation parameters of the multiple linear regression models using forward stepwise method explaining the variations of the main zooplankton parameters. Significant *p* values (*p* < 0.05) are in bold characters.

Multivariate analysis (coinertia)

The first factorial plane of the coinertia analysis explained 57% of the variance, of which 34% were attributed to the first axis and 23% to the second.

In both 'environment' and 'zooplankton' structures, axis 1 showed a distinction between the rainy season (R1 to R10 but particularly R8) and the two other surveys (N and D) (Figure 6A). R samples were characterized by high NO_3 , NO_2 temperature, transparency, depth, and chlorophyll *a* values (Figure 6B). They were also associated with several taxa: *Appendicularia*, *Oncaea venusta*, *Corycaeus* spp., *S. oblonga*, and *S. bicornis* (Figure 6A). N and D samples were correlated with environmental (NH_4 , salinity, pH, bacterial biomass) and zooplankton variables (*L. quadridentata*, *L. bulla*, *T. patina*, *P. quadricornis*, gastropod larvae). The second axis mainly opposed the N samples (particularly N1) to the D samples (except D2 and D3) (Figure 6D). The N samples were characterized by high PO_4 and chlorophyll *b* values, by high oxygen gradients (d Oxy), and by harpacticoid

copepod (*Canuella* sp.). The D samples were characterized by high salinity, depth, transparency, and chlorophyll *c* values and by coastal marine or brackishwater zooplankton taxa: *A. tonsa*, *P. aculeatus*, *E. acutifrons*, *B. plicatilis*, and polychaete larvae.

Discussion

Environmental and trophic context

Our study highlighted high time and space variability of abiotic and biotic variables in the Sontecomapan lagoon. This can be linked to the shallowness of the lagoon (up to 7 m in the main channel and 0.4 to 2.5 m for the sampled stations in our study) and to the high influence of permanent exchanges with the ocean and of seasonal freshwater inflows. The exchanges with the ocean through the permanently opened pass are conditioned by tidal influence which must be important, as tidal amplitudes were 1.03, 0.87, and 0.83 m during the dry, rainy, and norte surveys, respectively (tablademareas.com 2013). Despite no data is available on the residence time, we can suppose

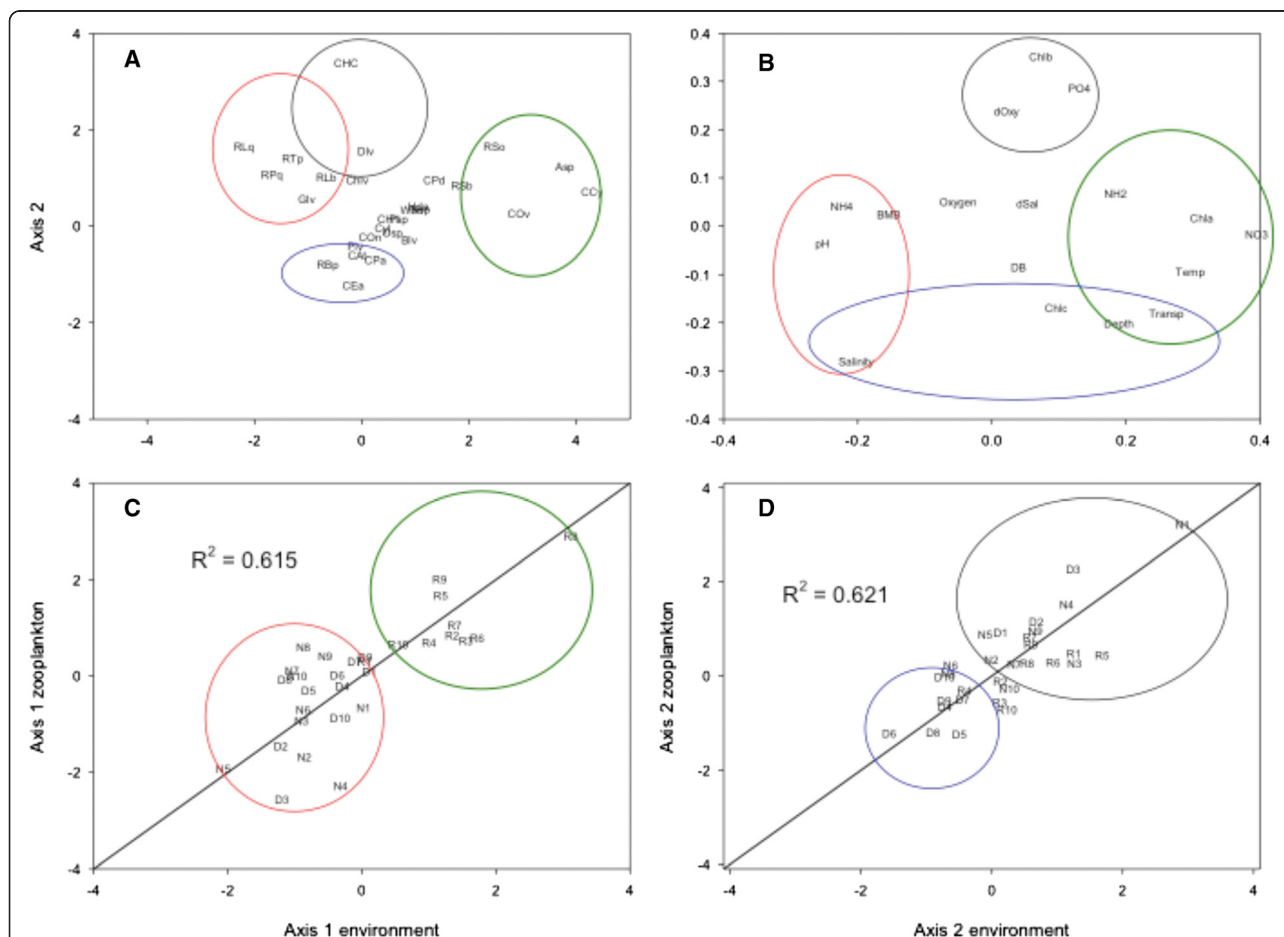


Figure 6 Co-inertia analysis. Ordination on the plan (1, 2) of taxa (A) and environmental variables (B) and plots of the sampling points on the first (C) and second (D) axes of the two systems. The line represents the equality between the coordinates on the two systems. Symbols are in Tables 2 and 3. dSal and dOxy are salinity and oxygen differences between surface and bottom. Symbols of sampling points the letters N, R, or D (for norte, rainy, or dry surveys) followed by the station number.

that the water renewal linked to tidal-driven exchanges was globally important in the major part of the lagoon, as suggested by the low percentages of organic matter and fine particles (silt and clays) in the sediment, except at station 3 situated in a slack water zone (see Figure 1).

The fresh water inflow comes mainly from three small rivers (La Palma, Basura, and Sabalo), and despite no data is available on their flows, we can consider that their influence is seasonally important as we observed significant salinity decrease during the rainy survey. Besides these, freshwater inputs presumably provoked important nitrate increase during the rainy season and local pH decrease near the mouth of the rivers, down to <7 at stations 1 and 7 (Basura and La Palma rivers).

Tidal exchanges with the ocean and seasonal fresh water inputs in this shallow lagoon explain the high variability in abiotic and biotic variables thus causing season-specific differences. During the rainy survey (June), high nutrient concentrations (mainly NO₃) probably stimulated phytoplankton production explaining the high chlorophyll *a* concentration. During the dry and norte surveys, high salinity and pH illustrated the resalinization of the lagoon linked to the scarcity of freshwater inputs. During the dry season survey, high ammonium concentration and high bacterial biomass suggested remineralization processes through the microbial loop and the excretion of planktonic organisms. At this period, high chlorophyll *c* concentration also suggested a specific phytoplankton community characterized by chrysophytes, cryptophytes, diatoms, and dinoflagellates according to the diagnostic for phytoplankton functional groups in natural estuarine and coastal communities (Paerl et al. 2003). In contrast, norte season was characterized by higher PO₄ values (and thus lower N/P ratios), perhaps explaining another phytoplankton community as suggested by higher chlorophyll *b* values characterized more by euglenophytes and prasinophytes (Paerl et al. 2003). Aké-Castillo and Vázquez (2008) have recorded 179 phytoplankton taxa (mainly diatoms and dinoflagellates) in the Sontecomapan lagoon and the three rivers draining into it. They also found peaks of phytoplankton abundance (2,226.47 cell ml⁻¹) during the rainy season.

In a complex lagoon system, the variability of the nutrient concentration and composition may also result from the diversity of the input sources. In Sontecomapan, only the litterfall of mangrove forest (*Rhizophora mangle*) represents significant loads of organic matter available for decomposition (1.1 Kg.m⁻²) (Aké-Castillo et al. 2006) and which may contribute to phytoplankton dynamics (Aké-Castillo and Vázquez 2008). But nutrients are cycled by a variety of biogeochemical processes (Eyre 2000; Eyre and McKee 2002), where bacteria are key in controlling the trophic linkages in aquatic ecosystems (Bianchi 2007).

Nevertheless, in terms of environmental conditions, the three study periods in Sontecomapan can be distinguished either on salinity conditions or on the basis of the nutrient and trophic status leading to different phytoplankton assemblages and thus different trophic condition for zooplankton.

Composition and abundance of zooplankton

This was the first complete study dealing with all the zooplankton groups in Sontecomapan. The taxonomic composition described in the present work is typical of brackish water zooplankton assemblages (Ferrari et al. 1982; Arfi et al. 1987; Étile et al. 2009). It has also similar characteristics with other Mexican coastal lagoons of the Yucatan Peninsula on the Gulf of Mexico (Chelem lagoon, Escamilla et al. 2001; Bojorquez lagoon, Álvarez-Cadena et al. 1996; Nichupté lagoon, Álvarez-Cadena et al. 2007). All these studies in Caribbean Mexican lagoons reported the dominance of copepods and *A. tonsa*, probably due to wider mesh size of zooplankton nets (200 or 330 vs. 64 µm in this study) neither the importance of *Oithona* species or the occurrence of rotifers was dealt.

Between the identified groups of zooplankton, the rotifers were the most diverse (21 species belonging to 8 families), due to the fresh water influence in the lagoon. Contrastingly, this phylum represented only 3.7% of the freshwater species reported for the neotropical region (Segers 2008) and 5.7% of total species recorded from Mexico (Benitez Diaz-Mirón, unpubl. data). The rotifer richness in Sontecomapan in the present study is low compared to the 250 species expected in tropical freshwater bodies (Segers 2008). It is also low as compared to the 60 species reported previously for the Sontecomapan lagoon (Castellanos-Páez et al. 2005). Besides, we found only 12 species of this previous investigation, while we reported 9 species for the first time in the lagoon, changing the current rotifer inventory to 69 species. This rotifer taxa richness is higher than the 37 taxa reported by (Sarma et al. 2000), in another brackish lagoon in Mexico (Mecoacan, Tabasco). In this lagoon, these authors reported only one cladoceran species (*Moina minuta*) which is also lower than the three cladoceran species identified in our study (*Ceriodaphnia* sp., *Chydorus* sp., and *P. avirostris*).

After the rotifers, the copepods were the most diverse group in our study, 15 free living copepods taxa were identified (see Table 3), of which 4 are recorded for the first time in coastal lagoons of the state of Veracruz (*O. nana*, *Canuella* sp., *Phenna* sp., and *Tisbe* sp.), according to the list of 23 species by Álvarez-Silva and Gómez-Aguirre (2000). Around 100 freshwater and 479 marine copepod species have been determined in Mexican waters (Elías-Gutiérrez et al. 2008). The number of brackish species is still very small, as most studies about brackish

copepods were oriented towards the description of new species or first records (Barranco-Ramírez and Gómez 2001; Gómez 2006; Morales-Serna and Gómez 2008) or to inventories of host-parasite copepods (Morales-Serna et al. 2012).

The most abundant copepods identified in the present work, *A. tonsa* (Dana), is a calanoid copepod species having a cosmopolitan distribution, being the dominant copepod in many subtropical and temperate coastal marine and estuarine areas (Peck and Holste 2006). As in our study, it has been often found coexisting with *O. nana* (Richard and Jamet 2001; Delpy et al. 2012).

Low zooplankton densities were also reported for other shallow Mexican Caribbean lagoon by Álvarez-Cadena et al. (1996) and Escamilla et al. (2001).

To explain these low zooplankton densities, different hypotheses can be advanced on the light of our results. A first hypothesis is linked to the instable conditions for zooplankton related to high variability of environmental and trophic conditions associated to the shallowness of the lagoon and the combined influence of freshwater and marine inputs (see Discussion above). Accordingly, several studies have shown negative impacts of disturbance or instability of hydrological, abiotic, and trophic conditions on zooplankton (Eckert and Walz 1998; Gascon et al. 2007). A second hypothesis is linked to the negative correlations between transparency and total or more abundant (nauplii, copepods, *A. tonsa*) zooplankton suggested (i) negative effect to the UV radiation (Leech and Williamson 2001) and (ii) vulnerability of zooplankton to visual predation (Williamson et al. 2011). This should be particularly problematic in very shallow ecosystems, such as Sontecomapan, where transparency reach up to the bottom in most situations and, scarcity of vegetation (submerged or floating macrophytes), imply lack of refuges for zooplankton against these threats. In contrast, some of the highest zooplankton densities ($>3,000,000 \text{ ind.m}^{-3}$) reported for tropical coastal lagoons were observed in Imboassica Lagoon (Brazil), which is a turbid ecosystem with a highly macrophyte colonized littoral zone (Kozłowski-Suzuki and Bozelli 2004). Besides, the scarcity of cladocerans in the Sontecomapan lagoon (only three species and $<2\%$ abundance) agree with the hypothesis of negative impact of light conditions. In laboratory experiments, cladocerans (*Daphnia* spp.) were shown to be less UV-tolerant than copepods or rotifers regardless of the UVR transparency of their source lake (Leech et al. 2005). Additionally, cladocerans have been shown to be very sensitive to visual predation (Vinyard 1980; Ramcharan et al. 2009).

Factors controlling zooplankton community

In this study, the relationship between biotic or abiotic conditions and zooplankton clearly appeared in the

multiple regression analysis (see Table 4) and in the coinertia analysis, which discriminated the three seasons on the basis of both environmental and zooplankton data sets (see Figure 6). The biotic processes in aquatic ecosystems could be acting separately or in tandem with abiotic forces in structuring planktonic communities at scales relevant to organisms, populations, and ecosystems (Gal et al. 2013).

As suggested by the results of the multivariate analysis, transparency (associated with salinity) probably drove the differences observed between zooplankton communities during the dry and norte surveys. Taxa of marine origin were associated to the more transparent waters during the dry season, while meiobenthic forms (the harpacticoid copepod *Canuella* sp) characterized the zooplankton during the more turbid norte survey. At this period, the presence of meiobenthic organisms in the plankton can be explained by the occurrence of strong winds driving wind resuspension of sediment and the mixing of meiobenthic forms with the plankton as also observed in other shallow coastal ecosystems (Lawrence et al. 2004).

The role of pH in structuring the seasonal variations of zooplankton clearly appeared in the coinertia analysis through its tight relationships with the community characterizing the norte and dry surveys. The pH was also negatively correlated to the taxonomic richness or to the abundance of *A. tonsa* and freshwater rotifers. The sensitivity of freshwater rotifers to high pH values has been evidenced in several studies (Bērziņš and Pejler 1987). Only few studies examined the relationships between pH and copepod species. Similar to our results, Chew and Chong (2011) found negative relationship between pH and several estuarine *Acartia* species.

Temperature showed significant positive relationships with abundance of marine rotifers. The positive influence of temperature on zooplankton in temperate conditions is well documented [e.g., meta-analyze in Sweden waterbodies (Bērziņš and Pejler 1989)], but in tropical areas, due to the lower range variation, the role of temperature is less evident despite increases in zooplankton abundance during the warmest periods have been also documented (Azevedo and Bonecker 2003; Kâ et al. 2012).

The role of salinity also appeared as driving the differences between the three seasonal surveys as well as through positive correlations with *A. tonsa* and marine rotifers. The highest salinity occurred during the dry survey when the zooplankton community was characterized by organisms such as the copepods *Acartia tonsa*, *P. aculeatus*, *E. acutifrons*, the rotifer *B. plicatilis*, and polychaete larvae which are very common in coastal oceanic areas or in coastal lagoons (David et al. 2007). *Acartia* and *Paracalanus* species as well as *E. acutifrons* generally

constitute the bulk of the copepod community in most coastal lagoons (Carli and Crisafi 1983). Populations of *A. tonsa* persist in both coastal marine waters as well as within estuaries having low salinity [e.g., 4 psu, Gulf of Finland, Baltic Sea (Katajisto et al. 1998)]. They can be also abundant in coastal lagoons within a wide salinity range [e.g., 5 to 36 psu; Berre Lagoon, south of France, Mediterranean (Delpy et al. 2012)], despite that it was demonstrated that this species shows high mortalities responding to high changes of salinity [>10 to 15 psu (Cervetto et al. 1999)]. The role of salinity in shaping rotifer communities has also been demonstrated (Malekzadeh Viayeh and Špoljar 2012).

The role of phytoplankton abundance and composition in structuring the zooplankton community appeared in the coinertia analysis through the association of the different forms of chlorophyll (*a*, *b*, and *c*) with the zooplankton communities of the three seasonal surveys. It was also evidenced in the regression analysis through (i) the positive relationships between chlorophyll *a* and copepods, nauplii, or *A. tonsa*, (ii) the relationships of chlorophyll *b* with total zooplankton, copepods, nauplii, or *A. tonsa* (<0) and with taxonomic richness, diversity or freshwater rotifers ($>$), and (iii) the negative relationship of chlorophyll *c* with rotifers.

Negative or positive correlations between zooplankton parameters and the different forms of chlorophyll (*a*, *b*, or *c*) suggest the importance of phytoplankton composition and abundance for the distribution and abundance of zooplankton. Variations in the proportion and abundance of edible and inedible (or toxic) phytoplankton food particles are known to drive variations in zooplankton composition and abundance (Pont 1995). Here, the clear seasonal variations of the chlorophyll forms (Figure 4) reveal variations in phytoplankton assemblages and thus variations in food composition and abundance for herbivorous zooplankton.

High chlorophyll *a*, the most common pigment contained in all photosynthetic algae and cyanobacteria (Paerl et al. 2003), reflects abundance of the most edible phytoplankton forms for zooplankton, such as chlorophytes and diatoms. Its positive relationship with *A. tonsa* and copepod nauplii suggests a clear food dependence for copepods in Sontecomapan. Food dependence of copepods (and *Acartia* species) has been observed in other eutrophic coastal lagoons (Cervetto et al. 1993; Pagano et al. 2003). The association of high chlorophyll *a* with appendicularians during the rainy survey (coinertia analysis, Figure 6) also reflects the high feeding efficiency of these organisms on phytoplankton (up to almost 1 L ind⁻¹ day⁻¹) (Fernandez et al. 2004; Lombard et al. 2009). Besides, the association of appendicularians with *O. venusta* and *Corycaeus* spp. can be explained by the feeding behavior of these two cyclopoid copepods, which can use small

particles aggregated on settling appendicularian houses (Turner 2004).

Negative relationships between chlorophyll *b* or chlorophyll *c* and zooplankton (see Table 4) may reflect importance of inedible or toxic forms in the available phytoplankton. Chlorophyll *c* (and particularly the forms *c*₁ and *c*₂ considered in this study) is characteristic of dinoflagellates and diatoms, of which several species may be toxic to zooplankton (Granéli and Turner 2006). However, the absence of concomitant data on phytoplankton composition does not allow us to draw further conclusion.

The partial regression analysis did not show any direct relationship between zooplankton parameters and the bacterial biomass. Bacteria can be punctually an alternative direct or indirect carbon source for the zooplankton, mainly for the rotifers (Agasild and Nöges 2005), as observed in other windy and shallow ecosystems. In a shallow subtropical bay in Florida, wind events were shown to inject dissolved and particulate benthic materials into the water column, where they directly stimulated the bacterioplankton, phytoplankton, and zooplankton community (Lawrence et al. 2004). It has been observed that *B. plicatilis* can consume up to 36% of the bacterial production while only $<1\%$ can be harvested by the metazooplankton when copepods are dominant (Bouvy et al. 1994). Generally, the bacterioplankton is not associated positively to the copepods due to their low feeding efficiency on small particles. Nevertheless, small cyclopoid nauplii (such as *O. nana*) have been shown to ingest (and prefer) very small particles [2 to 5 μm , (Böttjer et al. 2010)] and thus can represent an important trophic link between the classical and microbial food webs.

Conclusions

Our study highlighted spatiotemporal variability in zooplankton abundance and composition in relation to high variability of abiotic and trophic context in the Sontecomapan Lagoon. Spatial patterns could not be detected for most variables, but clear differences were recorded among the three seasons. These differences were mainly explained by water transparency, salinity, temperature, pH, and food availability (Chl *a*, *b*, and *c* as proxy for phytoplankton abundance and composition), which can be considered as the main structuring forces for the zooplankton in the lagoon.

Combined effects of high water exchange, low depth, and high transparency may explain the relatively lower zooplankton density in the lagoon (compared to other eutrophic lagoons) by favoring instability and vulnerability to UV effects and/or to visual predation.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

MIBDM, MECP and GGM conceived and designed the study. MIBDM and GGM participated in the field sampling and carried out the laboratory analysis. MECP helped in drafting the manuscript. GGM supported the taxonomic determinations of rotifers. MJFG provided advice for bacterial quantification. MP participated in the taxonomic identification of copepods, analysis of data and drafting the manuscript. All authors read and approved the final manuscript.

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