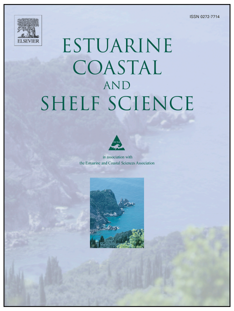

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ASSESSMENT OF SURF ZONE ZOOPLANKTON DYNAMICS IN A SOUTHWESTERN ATLANTIC SANDY BEACH: SEASONAL CYCLE AND TIDAL HEIGHT INFLUENCE

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Abstract

Surf zones of sandy beaches are poorly studied in comparison to estuarine and continental shelf waters, specifically because of the difficulties experienced in sampling in high-energy environments. The zooplankton of these areas, therefore, has received less attention than that in other coastal systems. The aim of this study was to investigate the seasonal patterns and tidal height effects (high tide/low tide) on the surf zooplankton community in a temperate southwestern Atlantic sandy beach. We also aimed to evaluate the influence of some environmental variables (water temperature, salinity, chlorophyll-*a*, suspended particulate matter and particulate organic carbon) on the community structure and to compare the surf community to nearby coastal zone (< to 50 m). Sampling was carried out from September 2009 to November 2010, with a monthly frequency during autumn-winter and bi-monthly during spring-summer. All samples were collected in a fixed station during high and low tide, using a conical net with a 300 µm mesh size. The net was hand-pulled parallel to the cost across 200 m, for 15-20 minutes. Surf waters hosted a very rich zooplanktonic community that were numerically dominated by crustaceans (30-99% of total abundance), especially two calanoid copepods: *Acartia tonsa* and *Paracalanus parvus*. The apparent low phytoplankton production detected in surf waters would be compensated by large quantities of detritus and suspended matter that could be an alternative food source for copepods that inhabit surf waters. Total abundances exhibited a strong seasonal variation, ranging from 2.42 (Spring 2009) to 11076.9 ind. m^{-3} (Autumn 2010). The tidal height was not a significant source of zooplankton variation, probably other factors are more influential at this short-term time scale. Surf waters were inhabited by a typical zooplanktonic community, coexisting both estuarine and neritic organisms. Most of the observed species were similar to those described for coastal waters, but others like *A. tonsa* were practically restricted to this particular zone. Water temperature, in combination with suspended particulate matter and chlorophyll-*a,* explained the observed temporal zooplankton pattern. Results obtained in this study highlight the importance of the surf waters of sandy beaches and will be useful for further studies and/or monitoring programs conducted in similar high-energy, turbulent, and turbid ecosystems.

1. Introduction

Sandy beaches are highly dynamic environments that make up two-thirds of the world’s ice-free coastlines (McLachlan and Defeo, 2018). Nowadays, they are under great pressure due to the intense coastal development which include human recreational activities (tourism), pollution, mining, disruption of sand transport, and the development associated with the expanding of human populations (Defeo *et al*., 2009; McLachlan and Defeo, 2018). Additionally, global climate change has incorporated another dimension to worldwide modifications of shorelines (Defeo *et al*., 2009; Orlando *et al*., 2019). Sandy beaches provide a wide range of ecosystem services, many of which are essential to support human uses: sediment storage and associated buffering against extreme events, dynamic response to sea-level rise, breakdown of organic materials and pollutants, water filtration and purification, nutrient cycling, water storage and groundwater discharge, maintenance of biodiversity, nursery areas for diverse species and feeding-breeding habitats for endangered wildlife (Defeo *et al*., 2009). Despite their ecological and socio-economic importance and strong potential as indicator of coastal system state, sandy beaches are underrepresented in the scientific literature. Considering that over the past few decades, these systems have suffered an increasing anthropogenic pressure, the establishment of systematic monitoring programs has become increasingly critical in order to understand the impact of these alterations on the ecological processes and biodiversity.

Sandy shores consist of three entities -surf zones, beaches, and dunes- which are linked by the interchange of material (mainly sand) and together they comprise a single geomorphic system, the *littoral active zone* (McLachlan and Defeo, 2018). It is characterized by wave- and wind-driven sand transport and lies between the outer limit of wave effects on bottom stability and the landward limit of aeolian sand transport (McLachlan and Defeo, 2018). The *littoral active zone* also conform two different ecological systems: the marine beach/surf zone mainly influenced by wave energy and the terrestrial dune strongly influenced by wind energy. In the beach/surf zone ecosystem, the entire resident fauna is of marine origin. Additionally, the main exchanges of organic materials and nutrients are with the sea, the pathway for such exchanges being the surf zone (McLachlan and Defeo, 2018). Besides its importance in shaping the beach and in transporting materials, the water envelope of the surf zone supports a varied fauna of zooplankton and fishes (McLachlan and Defeo, 2018). Numerous studies have dealt with surf hyper and epibenthos (*e.g*. Dominguez Granda *et al*., 2004; Marin Jarrin and Shanks, 2011; Marin Jarrin *et al*., 2015, 2016) and larvae, juvenile and adult fishes (*e.g*. Strydom, 2003, 2007; Inoue *et al.*, 2008), but less attention has been paid to smaller zooplanktonic organisms (<20 mm) in spite of their importance as trophic intermediates. The difficulties experienced in working in high-energy surf zones have been indicated as the main reason for the lack of this information (McLachlan and Defeo, 2018).

Zooplankton has a crucial position in surf zones, functioning as a linkage between primary producers and higher trophic levels such as fishes and shrimps, in addition to its role as environmental indicator (Pinheiro *et al*., 2013; Oliveira-Santos *et al.*, 2016). It also represents a food source for filter-feeding benthic macrofauna, so changes in this community may have a severe impact on beach ecosystems (Defeo *et al*., 2009). Zooplankton spatial and temporal dynamics and their relationship with the hydrological variables has been extensively studied in several types of coastal systems (*e.g.* David *et al*., 2005; Marques *et al.*, 2007, 2009; Leandro *et al*., 2007), however, there have been very few studies in sandy beach surf zones (DeLancey, 1987; Avila *et al*., 2009; Costa *et al*., 2011; Pinheiro *et al*., 2011, 2013; Aboul-Ezz *et al.*, 2014; Oliveira-Santos *et al.*, 2016; Stull *et al*., 2016). Moreover, a very limited number of these studies provide estimates of abundance and/or biomass (McLachlan and Defeo, 2018) and most of them are focused on tropical and/or subtropical beaches (Avila *et al*., 2009; Costa *et al*., 2011; Pinheiro *et al*., 2011, 2013; Oliveira-Santos *et al.*, 2016). These studies evidenced that seasonal variation in precipitation and the associated changes in salinity, are the main factors influencing the tropical and subtropical zooplankton communities (Costa *et al*., 2011; Pinheiro *et al*., 2011). In other coastal zones located in temperate regions, however, water temperature has been shown to be the most important parameter affecting the distribution and abundance of zooplankton (*e.g.* Marques *et al*., 2009). Planktonic organisms in coastal zones are also subject to tidal and diurnal environmental variability (*e.g.* Marques *et al*., 2009), which are correlated to changes in wave height, beach slope and light availability (Marin Jarrin and Shanks, 2011). Given their importance in surf zone ecosystems, understanding the zooplankton community structure at different temporal scales and how the environmental variables control their variation is essential for a correct interpretation of the ecology of these coastal waters.

The purpose of the present study was therefore to examine the seasonal patterns and tidal height effects on the surf zone zooplankton community in a temperate southwestern Atlantic sandy beach. The specific aims were (*i*) to describe the taxonomic composition and the abundance pattern of the zooplankton at seasonal and tidal scales, (*ii*) to evaluate the influence of physico-chemical variables on the community structure and finally, (*iii*) to compare the zooplankton communities from the surf waters and those for the nearby coastal zone (< to 50 m).

2. Materials and methods

2.1 Study area

The southern coast of Buenos Aires Province, Argentina, is an open and straight E-W oriented shoreline (Figure 1). Monte Hermoso (MH) (38º59' S, 61º06' 'W) is a dissipative sandy beach characterized by a low slope and backed by extensive sand dunes (*e.g.* Delgado *et al.*, 2012; 2017) (Figure 1). The area has a mesotidal regime with semidiurnal tides and a tidal amplitude that varies from 2.33 to 3.35 m for neap and spring conditions, respectively (Servicio de Hidrografía Naval, 2009). The mean significant wave height oscillates between 0.25 and 1.5 m, associated with significant wave periods between 1 and 16 seconds, with maximum heights occurring in spring and minimum ones in winter (Delgado *et al*., 2012).

MH coastal waters are temperate (6.1-22.9 °C), relatively high saline (33.5-36), and highly turbid (24-64 NTU), with pronounced seasonal variability and homogeneity of the water column all year round (Delgado *et al*., 2017). MH inner shelf is affected by the Bahia Blanca Estuary (BBE) plume (38° 45′-30° 40′ S; 61° 45′-62° 30′ W) and consequently, it is highly vulnerable to the seasonal and interannual dynamics of this estuary (Delgado *et al*., 2017). The BBE is a shallow, funnel shaped system, orientated NW/SW. It comprises a dense arrangement of meandering channels and islands, surrounded by extensive intertidal mudflats and marshes (Perillo and Piccolo, 1991). The BBE is considered a source of saline waters because of the relative low fluvial input (~2 m^3 s^1), the presence of salt flats, and the restricted water circulation (Perillo and Piccolo, 1991). Thus, high saline and turbid waters provided by the estuarine plume deflected towards MH coastal waters, creating a highly complex oceanographic and ecological regional ecosystem (Delgado *et al*., 2017).

The region has a temperate climate characterized by warm summers, cold winters, and moderate springs and autumns. Mean air temperatures oscillate between 14 and 20 °C and the annual mean precipitation is 650 mm (Campo de Ferreras *et al*., 2004). The prevailing wind directions are from the N, NW and NE but the strongest winds come from the S, SE and SW, especially in spring and summer, with mean speeds fluctuating between 22 and 24 km h^{-1} (SMN, 1992).

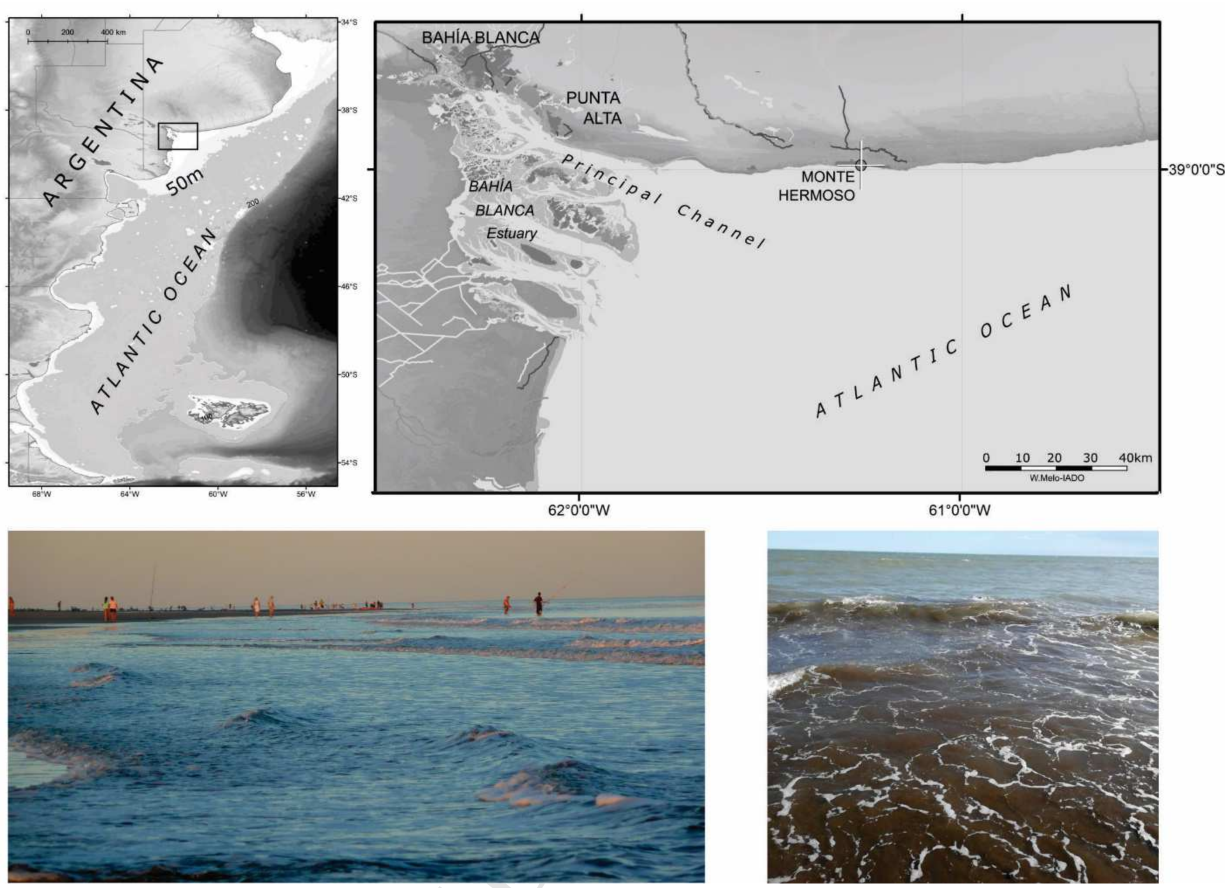


Figure 1. General location and map of the study area (top), the surf zone of Monte Hermoso sandy beach (bottom). Also noted in the map is the Bahia Blanca Estuary, the second largest estuarine system in Argentina, South America.

2.2 Field sampling

The surf zone waters of MH sandy beach were sampled on 16 occasions from September-2009 to November-2010. For most dates, sampling frequency was monthly (September 2009, October 2009, January 2010, March 2010, May 2010, June 2010, August 2010 and November 2010). During most of the austral spring-summer months, that is November 2009, December 2009, February 2010 and October 2010, sampling was done fortnightly (hereafter mentioned as Month-I and II). No field data for April 2010, June 2010 and September 2010 are available as no samples were taken due to difficult weather conditions. Field sampling was conducted at a fixed station (38º 59' 22.8'' S-61º 18' 42.1'' W) in waters ranging from 0.7 to 1.2 m at high (HT) and low tide (LT), always during the daylight hours. Zooplankton samples were collected by pulling a conical-cylindrical net (300-µm mesh) parallel to the coast across 200 m (15-20 minutes). The net was equipped with a *General Oceanic*® flow meter. Samples were immediately preserved in a 4% buffered formaldehyde solution. The mesh size used certainly under-estimates the copepod early life stages and smaller organisms. Thus, mainly larger copepodites and adult copepods are considered in this study which should be discussed with some caution. Surf zone water temperature, salinity and pH were measured *in situ* using a digital multisensor *Horiba U-10*® (0.5 m depth). At the same time, water samples for determination of chlorophyll-*a* (Chlo-*a*), phaeopigments, particulate organic carbon (POC) and suspended particulate matter (SPM) were collected from surf waters and transported to the laboratory in dark and cooled conditions.

2.3 Laboratory analysis

For zooplankton analysis, samples were rinsed to remove the formaldehyde and examined under a stereoscopic microscope to identify the organisms to the lowest possible taxon level. According to the lifetime spent as a planktonic form, the organisms were grouped into holoplankton (those living their entire life cycle in the water column), meroplankton (spend only a portion of their early life in the plankton) and adventitious plankton (organisms that occur only circumstantially in the water column; Raymont 1980). Most holoplanktonic forms were identified to species level as well as the gelatinous plankton. Meroplanktonic larvae and benthic or littoral forms were associated to family, order, or class. When more than 200 individuals from each dominant taxon were present, samples were subsampled (1/10). When these taxa occurred in the sample with less than 200 individuals, counting was completed on the entire sample. A taxon was considered ‘not dominant’ when the estimated abundance in the first one-eighth of the counting chamber was < than 25 individuals. Zooplankton abundances were expressed as number of individuals per cubic meter (ind. m^{-3}). Taxon richness was considered as the total number of taxa present in each zooplankton sample.

The Chlo-*a* concentration (µg L^{-1}) was determined spectrophotometrically according to APHA (1998). Water samples (250 ml) were filtered through Whatman GF/C membranes, which were immediately frozen and stored at -20 °C. Pigment extraction was done in 90 % acetone for 24 h, placing the tubes in a fridge and in darkness. Phaeopigments concentration was determined using the equations of Lorenzen (1967). For spectrophotometrically POC determination (mgC m^{-3}), water samples (500 ml) were filtered through previously muffled 1.2 µm Whatman GF/C filters, and the filters with the retained material were frozen and stored at -20 °C until determination (Strickland and Parsons, 1968). SPM (mg L^{-1}) was determined gravimetrically filtering 250 ml of water on pre-combusted and weighed GF/F filters. Thereafter, the filters were dried at 60 ºC to constant weight for the estimation of SPM concentrations. Further details related to the analysis of the physico-chemical data can be found in Menéndez *et al.* (2016).

2.4 Data analysis

2.4.1 Univariate analysis

Univariate analyses were performed using water temperature, salinity, Chlo-*a*, phaeopigments, SPM, POC, total zooplankton abundance and species richness as response variables, and seasons (austral spring 2009, autumn, winter, summer, spring 2010) and tidal heights (HT, LT) as explanatory ones (including their interaction), by means of a Two-way Analysis of Variance (ANOVA) and Tukey post-hoc comparisons tests. For each single variable, the distribution was visually assessed by means of Q-Q plots and the homogeneity of variances was evaluated using Levene's test. In order to suffice the normality and homogeneity of variances assumption, natural logarithmic transformation was applied for SPM, POC, phaeopigments and total zooplankton abundance. In order to assess the seasonal patterns, we defined season as a main factor by treating monthly or bi-monthly samples within a season as replicates. The effect of tidal height was not significant for any variable (two-way ANOVA single term, *p*-values ranged between 0.29 and 0.98, two-way ANOVA interaction term with season, *p*-values ranged between 0.41 and 0.99); hence it was discarded from the models and a one-way ANOVA was performed comparing the seasons using the tidal heights as replicates.

2.4.2 Multivariate analysis

Multivariate analyses were performed in order to explore the zooplankton community structure and consisted of Non-metric Multidimensional Scaling (nMDS), Cluster Analysis and Similarity Percentages (SIMPER). Samples corresponding to each date (monthly or fortnightly frequency) and tidal height (LT and HT) were mapped nonlinearly onto the two-dimensional ordination space by means of a nMDS. Before applying nMDS, a standardization of each sample by its total abundance and a fourth root transformation were applied to abundance data in order to reduce its dispersion (Legendre and Gallagher, 2001). The ordination of samples in the nMDS was based on Bray-Curtis distance, and the nMDS was supported by a cluster analysis with the same transformation, standardization and distance using a hierarchical agglomerative algorithm with complete linkage. The performance of the ordination was evaluated by a monotonic regression Stress function and a square correlation between fitted values and ordination distances. The 30% most-frequent taxa were incorporated in the ordination plot. In order to identify the main environmental variables affecting the community structure, an indirect approach was applied as an exploratory tool, where taxa data were not constrained by environmental data in the nMDS (Ramette, 2007). Environmental variables were adjusted to the nMDS ordination using vector fitting and those variables that showed a significant correlation were incorporated in the ordination plot. This analysis was also complemented by a Similarity Percentage (SIMPER) test determining the main contribution of the species to the formation of the groups. This analysis breaks down the contribution of each species to the observed similarity between samples. Also, the effect of season on zooplankton community structure was analyzed by means of a Permutational Multivariate Analysis of Variance (PERMANOVA, 999 iterations). All analyses were performed in R (R Core Team 2017) using packages *vegan* (Oksanen, 2018) and *ggplot2* (Wickham, 2009).

3. RESULTS

3.1 Surf zone environmental conditions

Water temperature in MH surf waters ranged from 12.4 ± 1.64 (± SD, winter 2010) to 22.9 ± 1.16 ºC (summer 2009) and varied significantly between seasons ($F_{(4,22)}$= 7.92, $p<0.001$) (Table 1). There were no significant differences in salinity or pH between seasons ($F_{(4,27)}$= 1.4, p= 0.258; $F_{(4,27)}$= 0.9, p= 0.426), averaging 33.9 ± 0.9 (range= 33 - 36.7) and 8.02 ± 0.04 (range= 7.68 - 8.36), respectively (Table 1). SPM concentrations varied from 28.13 ± 1.26 (spring 2009) to 108.5 ± 1.35 mg L^{-1} (spring 2010) and revealed a marked seasonal variation ($F_{(4,27)}$= 3.2, $p<0.05$) (Table 1, Figure 2). The amounts of POC were high and quite fluctuating (mean ± SD= 1469.8 ± 1363.8) but they did not show significant differences among seasons ($F_{(4,21)}$ = 0.8, p= 0.527). Mean Chlo-*a* was 4.28 ± 2.48 µg L^{-1} (range = 0.05 - 9.16 µg L^{-1}). Phaeopigments were quite variable, ranging from 1.23 ± 1.23 to 2.57 ± 1.23 µg L^{-1} (Figure 2). None of these variables showed significant differences between seasons ($F_{(4,21)}$= 2.7, p= 0.059; $F_{(4,21)}$= 2.1, p= 0.115 for Chlo-*a* and phaeopigments, respectively) (Table 1). The effect of tidal height was not significant for any variable (two-way ANOVA single term, p-values ranged between 0.29 and 0.98, two-way ANOVA interaction term with season, p-values ranged between 0.41 and 0.99).

Table 1. Mean values (±SD) per season of the environmental variables measured in surf zone waters of MH sandy beach. p value according to ANOVA results is also shown. Levels with the same letter do not differ significantly (p < 0.05) according to Tukey tests performed on variables where ANOVA resulted significant. SPM: suspended particulate matter. POC: particulate organic carbon.

Variable	Spring 2009	Summer 2009	Autumn 2010	Winter 2010	Spring 2010	*p*-value ANOVA
Temperature (°C)	16.77a ± 1.04	22.89b ± 1.16	16.63a ± 1.64	12.4a ± 1.64	17.28a ± 1.34	< 0.001
Salinity	33.36 ± 0.56	34.85 ± 0.63	35.5 ± 0.89	34.73 ± 0.89	34.45 ± 0.72	> 0.25
pH	7.95 ± 0.06	7.98 ± 0.06	8.1 ± 0.09	8.1 ± 0.09	8.1 ± 0 .7	> 0.4
SPM (mg L^{-1})	28.13a ± 1.26	48.53ab ± 1.3	50.35ab ± 1.45	36.6ab ± 1.45	108.5b ± 1.35	< 0.05
Chlo-*a* (µg L^{-1})	2.77 ± 0.89	3.22 ± 0.89	4.68 ± 1.1	6.99 ± 1.1	4.77 ± 0.89	< 0.1
Phaeopigments (µg L^{-1})	1.23 ± 1.23	1.28 ± 1.23	1.72 ± 1.29	1.87 ± 1.29	2.57 ± 1.23	> 0.1
POC (mgC m^{-3})	126.1 ± 4.9	794.9 ± 4.9	41.2 ± 7.1	816.8 ± 7.1	2168.9 ± 4.9	> 0.5

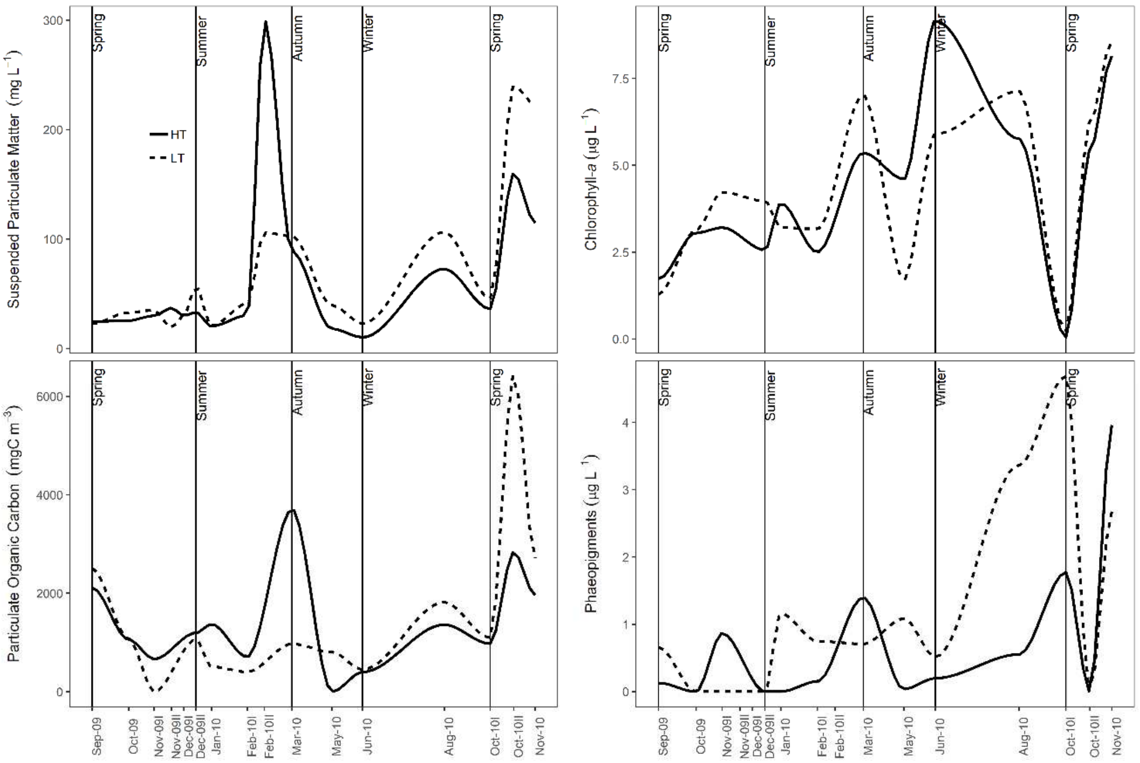


Figure 2. Temporal variations of suspended particulate matter (SPM), particulate organic carbon (POC), chlorophyll-*a* (Chlo-*a*) and phaeopigments concentrations during high (HT) and low tide (LT) in the surf zone of Monte Hermoso sandy beach.

3.2 Surf zooplankton composition and abundance: seasonal patterns

The zooplankton community was represented by a total of 49 identifiable taxa, including species, genera and in some cases higher taxa (Table 2). The overall specific richness was clearly underestimated considering that some organisms were only identified to genus or higher level (mainly meroplankton and adventitious taxa). The holoplankton fraction represented 30.61% of the total taxa observed whereas the remaining percentage corresponded to meroplankton (42.85%) and adventitious fraction (26.53%) (Table 2). Copepoda (7) and Cnidaria (7) were the most important groups in terms of number of taxa. Within holoplankton (15 taxa), Mysidacea, Chaetognatha, Apendicualaria, and Decapoda were also observed. The meroplankton fraction (21 taxa) included some medusae, decapod zoeae, gastropod veligers, benthic polychaete nectochaets and fish eggs and larvae, among others. Adventitious plankton (13 taxa) was mainly represented by several crustacean taxa (Isopoda, Amphipoda, Cumacea, and Ostracoda) and foraminiferans (Table 2). Taxon richness showed significant differences among seasons $F_{(4,26)}= 3.37$, $p<0.05$), being the spring 2009 significantly higher than spring 2010 (Tukey test $p<0.05$, Figure 3). However, there were no significant differences in the number of taxa between differents tidal heights ($F_{(1,26)}= 3.68$, $p= 0.066$).

Table 2. Mean abundance (ind. m^{-3}) per season of each taxon registered during the sampling period. Horizontal lines separate holoplankton (top), meroplankton (middle) and the adventitious fraction (bottom).

Group	Taxon	Spring-2009	Summer	Autumn	Winter	Spring-2010
Copepoda	*Acartia tonsa*	2.88	157.67	5715.44	497.87	526.04
Copepoda	*Paracalanus parvus*	24.70	13.70	17.44	280.45	624.06
Copepoda	*Ctenocalanus vanus*	1.39	2.11	2.61	0	0
Copepoda	*Calanoides carinatus*	14.21	0	0.31	0.03	18.69
Copepoda	*Labidocera fluviatilis*	1.44	0.72	0	1.49	1.80
Copepoda	*Euterpina acutifrons*	0.10	0.01	0	2.46	0.24
Copepoda	*Oithona nana*	0.02	0	0	0	0
Cnidaria	*Liriope tetraphylla*	0.05	0	0	4.36	0
Mysidacea	*Neomysis americana*	0.02	0.02	0	0.91	0.04
Mysidacea	*Arthromysis magellanica*	0.10	0.01	0.41	0	36.44
Decapoda	*Peisos petrunkevitchi*	0	0	0	0	3.85
Chaetognatha	*Parasagitta friderici*	0.09	0.91	2.65	0.98	391.83
Chordata	Apendicularia	22.64	0.15	0.56	8.11	0
Decapoda	*Alpheus puapeba* larvae	0	0.15	0	0	0
Decapoda	*Artemesia longinaris* larvae	8.06	0	0	2.11	0
Cnidaria	*Gossea brachymera*	0	0.08	0	0	0
Cnidaria	*Turritopsis nutricula*	0	0.08	0	0	0
Cnidaria	*Eucheilota ventricularis*	0.16	0.22	0	0	0
Cnidaria	*Clytia* spp.	0.07	1.02	0	0	0
Cnidaria	*Obelia* spp.	0.35	5.54	0	0	0
Cnidaria	Leptomedusae non id.	0	0	14.06	0	0
Decapoda	*Pinnixa* spp. larvae	0.06	0.11	0	0	0
Decapoda	*Corystoides chilensis* larvae	0.03	0.11	0	0	0
Decapoda	*Pachycheles* spp. larvae	0.17	0.22	0	0	0
Decapoda	Grapsidae larvae	0.32	1.05	0	0	0.49
Chordata	Ascidiacea larvae	0	0.15	0	0	0
Mollusca	Bivalvia larvae	0.03	6.32	0.71	0	5.32
Mollusca	Gastropoda larvae	0.06	0	0	0	0
Annelida	Polynoidae larvae	0.21	0.03	0	0	0
Annelida	Spionidae larvae	0.02	0.07	0.05	0.09	0.08
Annelida	Polychaeta larvae	0.05	0.06	0	0.41	0.02
Echinodermata	Ophiuroidea larvae	0	0.01	0.05	0	0
Echinodermata	Echinoidea larvae	0.05	0	0	0	0
Cnidaria	Ceriantharia larvae	0	1.36	4.74	0.24	0.16
Chordata	Teleostei eggs	18.14	0.16	0.33	0.03	1.33
Chordata	Teleostei larvae	0.94	0	0.21	0	0.72
Isopoda	Serolidae	0.07	0.56	0	0.19	0.01
Isopoda	Chaetilidae	0	0.08	0	0	0
Isopoda	Ancinidae	0.02	0.08	0	0	1.23
Isopoda	Idoteidae	0.04	0.01	0	0	0
Amphipoda	Oedicerotidae	0.36	0.56	0.33	0.20	1.02
Amphipoda	Lilljeborgidae	0.04	0	0	0	0
Amphipoda	Phoxocephalopsidae	0.04	0	0.19	0	0
Amphipoda	*Monocorophium insidiosum*	0.03	0.13	1.02	0	0
Amphipoda	Amphipoda non id.	0.10	0.11	0.84	0.72	0.32
Amphipoda	Caprellidae	0.01	0.01	0	0	0
Cumacea	Cumacea	0.09	0.04	0.18	0.03	0
Foraminifera	Foraminifera	0.56	0.04	0.11	0	0
Ostracoda	Ostracoda	0.01	0	0	0	0

Total zooplankton abundance exhibited strong seasonal variation, being the result of differential contributions of several taxa (Figure 3 and 4, Table 2). Total abundances varied between 2.42 and 11076.9 ind. m^{-3}, with an average of 1201.9 ± 2739.6 ind. m^{-3} (Figure 3). Season was a significant source of variation ($F_{(4,27)}$= 5.22, p<0.05), whereas differences in total zooplankton abundance between HT and LT were not significant ($F_{(1,22)}$= 0.28, p= 0.6). Total zooplankton showed a major peak during early autumn 2010 and others of less magnitude in winter and spring 2009 and 2010. In the remaining dates, abundances ranged between 2.42 and 798.38 ind. m^{-3} (Figure 3).

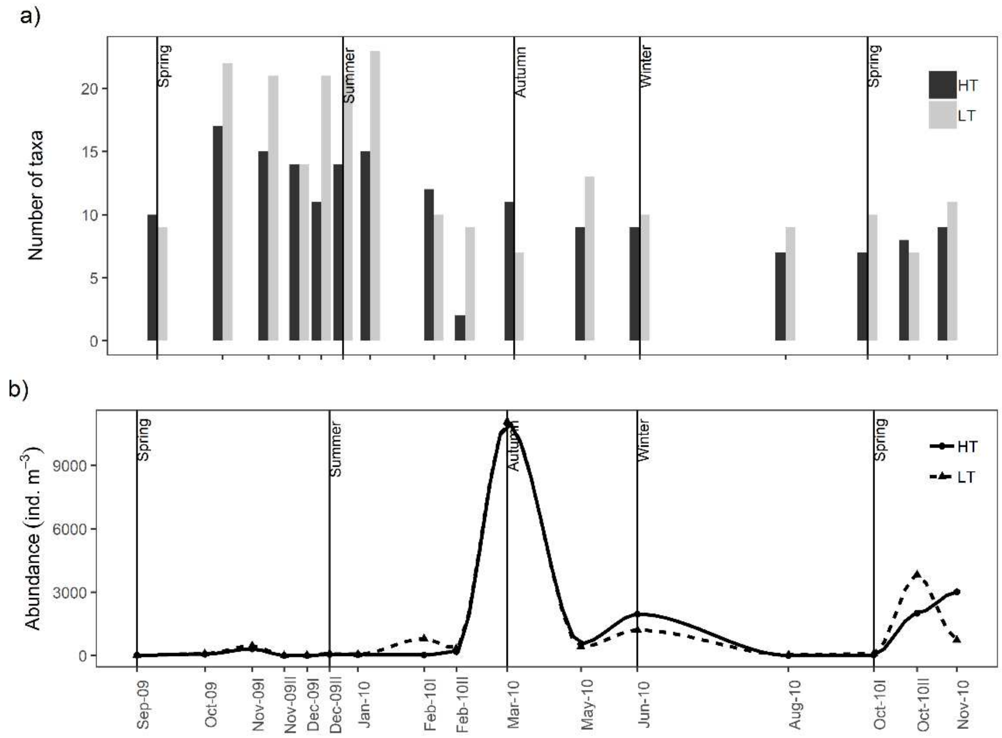


Figure 3. Number of taxa (a) and zooplankton total abundance (smoothed line made with loess function) (b) during the study period in the surf zone of Monte Hermoso sandy beach. LT: low tide. HT: high tide.

Holoplankton (21.79 and 99.94% of total zooplankton abundance) was the best represented fraction and Copepoda the most abundant group. The dominant copepod species were in the Calanoid class, mainly the estuarine *Acartia tonsa* and the neritic *Paracalanus parvus* (up to 99.2 and 48.3% of the total abundance, respectively). The former was present throughout the study period and constituted the bulk of zooplankton observed during autumn 2010, especially in March (99.2%) (Figure 4, Table 2). *A. tonsa* also dominated in summer and winter 2010, with abundances up 1273.81 ind. m^{-3}. *P. parvus* was registered in almost all sampling dates, and maximum abundances were registered in winter and spring 2010 (up to 635.47 and 1420.9 ind. m^{-3}, respectively). In spring 2010, particularly in October 2010-II, it was the dominant copepod species (1409.6 ± 15.9 ind. m^{-3}), although high abundances of *P. friderici* were also detected (~2300 ind. m^{-3}). Lower densities of *Calanoides carinatus* were registered in spring 2009 and 2010 (up to 70 ind. m^{-3}), coinciding with *P. parvus* maxima (Figure 4, Table 2). Meroplankton constituted 0.05-66.66% of total zooplankton abundance and was abundant principally in spring 2009 and summer 2010. Medusae were common in surf waters, especially in warm seasons, being *Obelia* spp. and a non-identified Leptomedusae the most abundant (up to 33.6 and 52 ind. m^{-3}, respectively). Teleostei eggs (0.09-110.22 ind. m^{-3}) and Bivalvia larvae (0.05-22.86 ind. m^{-3}) were also important in spring 2009 and summer 2010, respectively. The adventitious plankton comprised up to 34.5% of the total zooplankton abundance and most of the taxa were found sporadically.

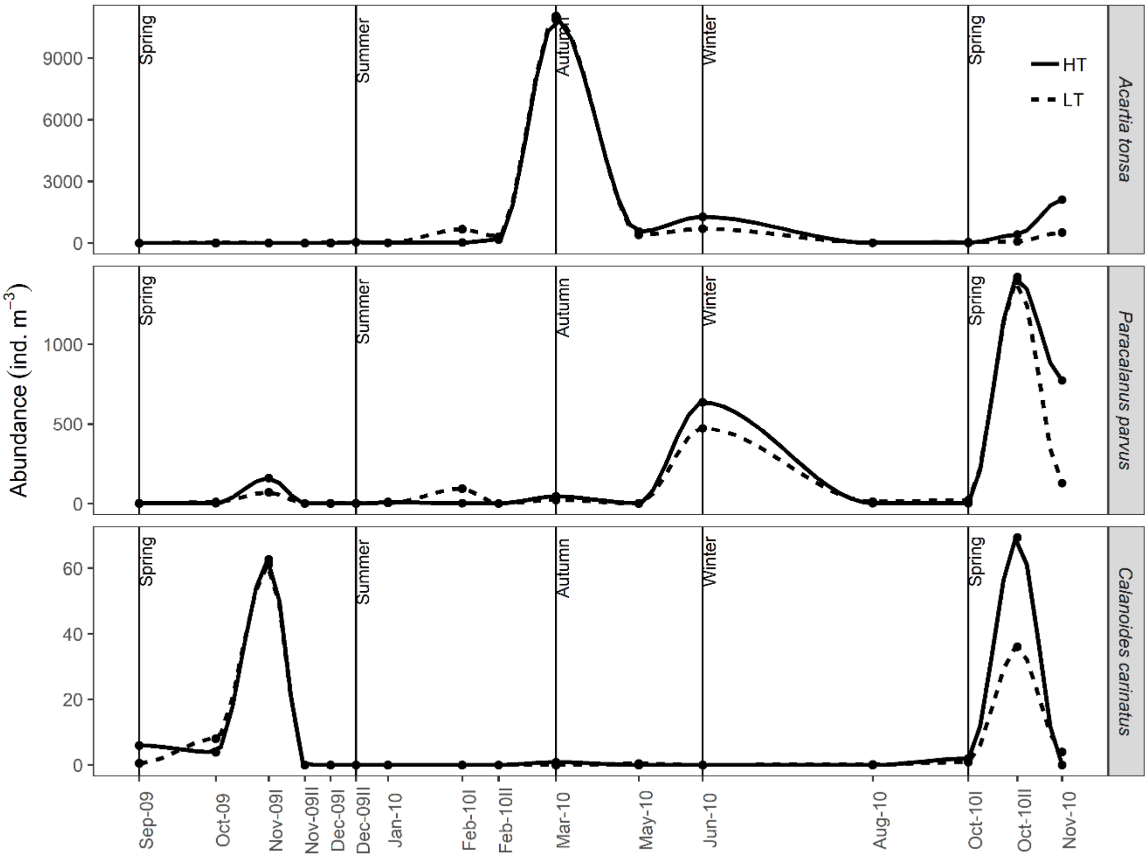


Figure 4. Temporal variation of the main copepods' species: *Acartia tonsa*, *Paracalanus parvus* and *Calanoides carinatus* during high and low tide (HT, LT) in the surf zone of Monte Hermoso sandy beach. Note different scales in the abundance axis.

3.3. Relationship between surf zooplankton and environmental conditions

The nMDS enabled the ordination of the samples in a two-dimensional space in which four different groups were identified (stress= 0.20, Shepard diagram linear fit R^2= 0.77) (Figure 5). These groups mainly represented seasonal changes in the zooplankton community structure. In addition, Cluster Analysis supported the formation of these groups (Pearson Correlation with Cophenetic Matrix, r= 0.71, *p*<0.001), which were clustered at a dissimilarity level of 58%. Group 1 included austral spring 2009 samples. Group 2 represented austral late-spring 2009/summer samples whereas group 3 was formed by late-summer/autumn samples. Finally, group 4 represented austral winter/spring 2010 samples. In the nMDS plot, nine of the fifteen 30%-most frequent taxa showed a significant fit on the ordination space (taxa with correlation significance higher than 0.3 were removed from the analysis). According to this analysis, group 1 was also associated with high abundances of Teleostei eggs (r^2= 0.6, p< 0.01) and *C. carinatus* (r^2= 0.67, p<0.01). Larvae of *A. longinaris* (r^2= 0.39, p<0.01), apendicularians (r^2= 0.16, p= 0.057) and *C. vanus* (r^2= 0.32, p<0.01) were also associated to this group. Group 2 was represented by the copepod *L. fluviatilis* (r^2= 0.21, p<0.05), the amphipod Oedicerotidae (r^2= 0.5, p<0.01) and larvae of Grapsidae (r^2= 0.51, p<0.01), Bivalvia (r^2= 0.31, p< 0.01) and Ceriantharia (r^2= 0.17, p= 0.06). *A. tonsa* (r^2= 0.66, p<0.01) was strongly associated to group 3 in which it dominated and showed a marked peak. Finally, *P. friderici* was weakly associated to group 4 (r^2= 0.09, p= 0.25). PERMANOVA analysis also supported that the structure of zooplankton community in MH surf waters varied significantly among seasons ($F_{(4,27)}$= 4.31, R^2= 0.39, p<0.01).

Considering the results of the SIMPER analysis, the estuarine copepod *A. tonsa* was typical in all groups but dominated widely in group 3 (Table 3, Figure 5). This species also dominated in groups 2 and 4 although with lower abundances (Table 3). *P. parvus* was typical in groups 1, 2 and 4, but its abundance was greater in group 4. Considering that *A. tonsa* and *P. parvus* were generally found in all seasons/groups, the differences among groups seemed to be mainly the result of variations in their relative abundance. However, there were clear differences between groups for the rest of the taxa driven by a different zooplankton composition. The most important discriminating species were *C. carinatus* (contribution= 8.47%) for groups 1-2 (Average Dissimilarity= 63.44); *C. carinatus* (9.42%), *A. tonsa* (9.30%) and Teleostei eggs (8.98%) for groups 1-3 (75.17); *P. parvus* (7.28%) for groups 2-3 (65.37); Teleostei eggs (8.49%) for groups 1-4 (60.75); Grapsidae larvae (5.49%) and Teleostei eggs (4.97%) for groups 2-4 (60.06) and *P. parvus* (17.44%) for groups 3-4 (58.38).

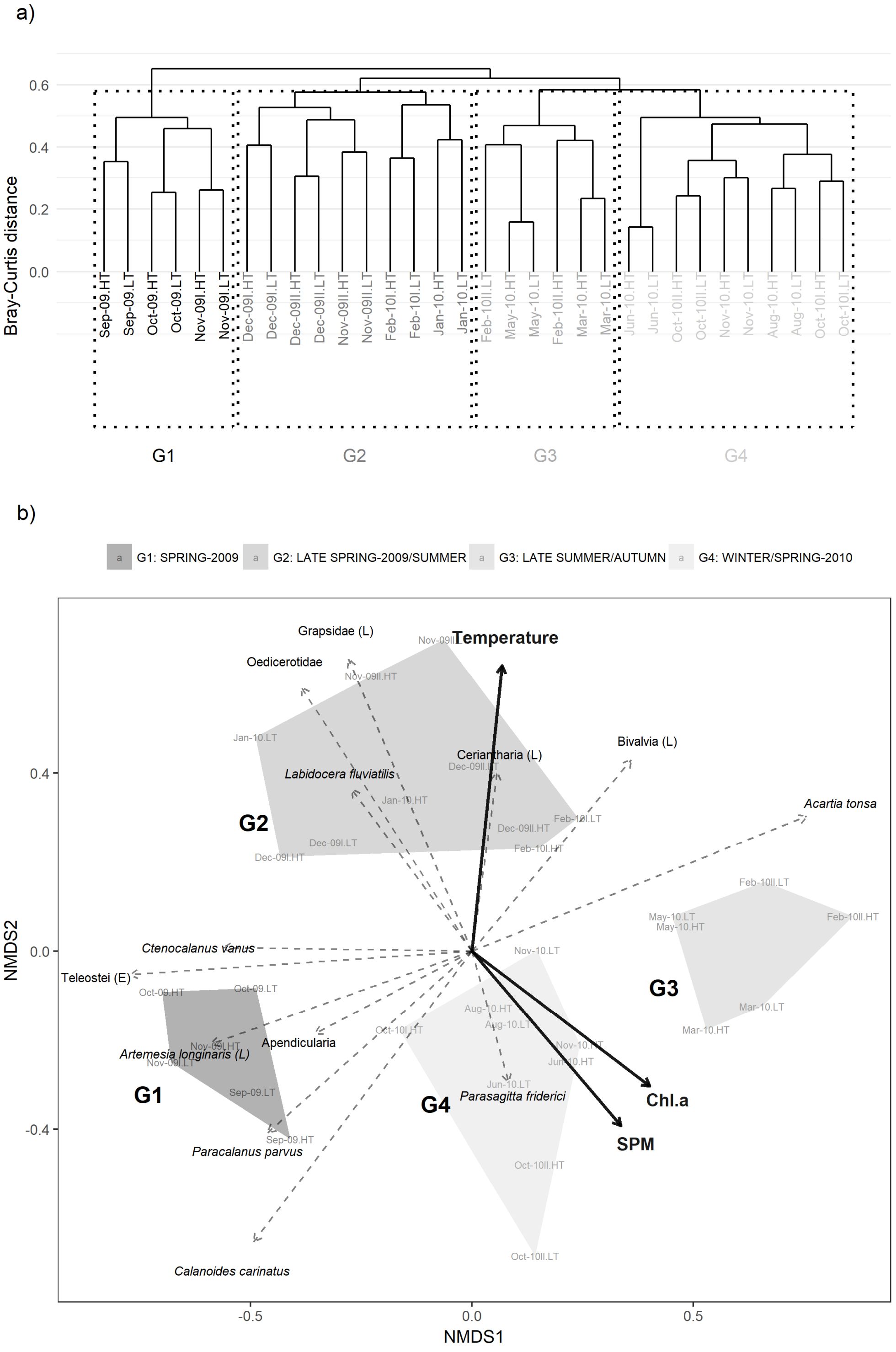


Figure 5. Cluster (a) and nMDS (b) plots showing the samples groups observed in the surf zone waters of Monte Hermoso sandy beach. Cluster groups obtained at a dissimilarity level of 58% were superimposed on the nMDS plot. The different groups are separated by polygons in different grey scale. G: group. HT: high tide. LT: low tide. SPM: suspended particulate matter. Chlo-*a*: chlorophyll-*a*. (L): larvae.

The vector fitting analysis of environmental variables showed that water temperature (r^2= 0.42, p<0.01), SPM (r^2= 0.27, p<0.05) and Chlo-*a* (r^2= 0.25, p<0.05) were significantly correlated to the ordination configuration (Figure 5). Thus, temperature highlighted seasonal differences in the community structure between samples, with the highest values during late-spring 2009/summer (group 2) and the lowest ones in winter/spring 2010 (group 4). SPM and Chlo-*a* were strongly correlated and presented higher values during late autumn/winter samples (group 4) than during late spring-2009/summer (group 2).

Table 3. SIMPER procedure (cut-off 50%) for zooplankton abundances per group determined by the Cluster/nMDS analyses, showing taxon percentage contribution to the average similarity within groups. In bold letters, the main similarity contribution percentages.

Taxa	**Group 1** (55.58)	**Group 2** (51.59)	**Group 3** (51.20)	**Group 4** (58.22)
Acartia tonsa	10.29	**20.94**	**28.47**	**70.76**
Paracalanus parvus	16.49	13.2	**20.09**	5.57
Calanoides carinatus	**17.38**	-	-	-
Ctenocalanus vanus	10.12	-	11.73	-
Obelia spp.	-	-	13.39	-
Clytia spp.	-	-	6	-
Teleostei (E)	**17.52**	5.63	3.95	-
Grapsidae (L)	-	12.56	-	-
Oedicerotidae	4.29	12.02	-	2.23
Artemesia longinaris (L)	7.18	-	-	-
Bivalvia (L)	-	4.88	1.94	9.35

4. DISCUSSION

4.1 Surf zooplankton composition and abundance: seasonal patterns

Analysis of zooplankton community in MH surf zone waters indicated a strong seasonal variation as a result of the differential contribution of several taxa. Despite of the perceived severe hydrodynamic conditions, surf waters hosted a very rich zooplanktonic community, mainly composed by organisms typical of both estuarine and neritic temperate waters. A seasonal sucession of dominat taxa was evident throughout the study period, especially due to pulses of abundance variation of holoplanktonic taxa and to a lesser extent of meroplanktonic organisms. As expected, the most abundant and diverse holoplanktonic taxa were the calanoid copepods and therefore, total zooplankton abundances reflected quite well the seasonal variation of the copepod populations. This group comprised 21-99% of total zooplankton, a usual contribution for marine coastal areas all over the world (*e.g.* David *et al*., 2005; Leandro *et al*., 2007; Marques *et al.*, 2007). Particularly in surf zone waters, these crustaceans also contribute with most of the zooplankton biomass and diversity (Costa *et al*., 2011; Pinheiro *et al*., 2013; Oliveira Santos *et al.*, 2016; Stull *et al*., 2016). In the case of meroplankton, medusae, benthic invertebrates' larvae and Teleostei eggs were the most important contributors, especially in warmer seasons. This is not surprising considering that gelatinous plankton are more abundant during the austral spring and summer conditions (Schiariti *et al.*, 2018) and that the BBE and neighboring inner shelf region has a high hydromedusae diversity, greater than other larger zones along the temperate SW Atlantic Ocean (Dutto *et al.*, 2017). On the other hand, the breeding patterns of benthic organisms may have contributed to the observed seasonality, which has already been reported in other coastal and estuarine waters (*e.g.* Marques *et al.*, 2009; da Costa *et al.*, 2011). Fish eggs were particularly abundant in the austral spring 2009 which can be related to a combination of responses between fish communities and physical factors, such as dispersion by local currents. Finally, the adventitious plankton abundances never exceeded 0.6 ind. m^{-3} indicating that despite the turbulence generated by the waves breaking, benthic organisms remain near the bottom layer at least during the daylight hours. Only the amphipod Oedicerotidae evidenced a seasonal pattern, being more abundant in the austral late spring-summer months.

From a quantitative point of view, the most abundant taxa were *A. tonsa* and *P. parvus*. The former had an important peak in late summer/autumn, and this could be related in part to the large quantities of detritus occurring in this season. This eurytopic copepod may reach very high abundances in waters containing high concentration of particulate organic matter (Marques *et al*., 2007), displaying an important degree of tolerance for environmental change (*e.g.* Marques *et al*., 2007). *A. tonsa* has a cosmopolitan distribution and is a widespread species in estuaries of Europe and America (*e.g.* Mouny and Dauvin, 2002; Hoffmeyer, 2004; David *et al*., 2005; Marques *et al.*, 2007). In the nearby estuary, *A. tonsa* is found throughout the year with maximum abundances during the austral summer and minimum ones during winter, when temperature decreases, and the environment becomes unfavorable for the species. Between June and October, this species coexists with the invasive copepod *Eurytemora americana* in a competitive relationship (Hoffmeyer, 2004). In MH surf waters, however, *A. tonsa* coexist with *P. parvus*. This latter species was present most of the year in surf waters and was very important in June 2010 and October 2010-II. This small-sized copepod is a neritic species widely distributed in many temperate and tropical regions (*e.g.* Bowman, 1971; Liang and Uye, 1996), particularly in surface waters between 0 and 100 m. It is also well represented in the copepod assemblages of the inner shelf of Argentine Sea between 34° and 41°S (Cepeda *et al*., 2018).

Studies conducted in other sandy beaches mentioned the presence of *A. tonsa* (Avila *et al.*, 2009; Stull *et al*., 2016) and *P. parvus* (Avila *et al.*, 2009) in surf waters, although only the former as numerically important. Additionally, some other Paracalanidae species like *Paracalanus quasimodo* and *Paracalanus aculeatus* are common and can dominate surf waters of Brazilian beaches (Avila *et al.*, 2009; Costa *et al*., 2011; Pinheiro *et al*., 2011, 2013). The bentho-pelagic *E. acutifrons* has been also reported in surf waters of Ajuruteua beach in Northern Brazil, but as dominant taxon (Costa *et al*., 2011; Pinheiro *et al*., 2011, 2013). This was related to the high concentrations of SPM and to the resuspension of the organisms due to the energetic conditions of the surf waters (Pinheiro *et al*., 2013). *C. vanus* has also been reported as abundant in Tramandaí Beach in Southern Brazil (Avila *et al.*, 2009). In the SW Atlantic, *C. carinatus* is a marine cold-water species mainly related to cold and nutrient-rich upwelled waters (Lopes *et al*., 1999) and to local upwelling events (Ramírez and Sabatini, 2000).

4.2 Relationship between surf zooplankton and environmental conditions

Coastal systems in temperate zones regularly exhibit spatio-temporal gradients, both in environmental variables and zooplankton assemblages, because of their tight physical-biological coupling (Marques *et al*., 2006). In this work, water temperature in combination with SPM and Chlo-*a* were closely correlated with zooplankton community structure. The well-defined temporal gradient is a common feature of other temperate coastal systems, where most of the environmental variability is attributed to a strong regional seasonality, and temperature is the main variable determining monthly zooplankton species composition and abundance (*e.g.* David *et al*., 2005; Leandro *et al*., 2007; Marques *et al*., 2009; Modéran *et al*., 2010). Temperature has already been mentioned as the most important environmental factor determining species' seasonal distribution (Marques *et al*., 2009). However, there are very few studies that consider the spatio-temporal zooplankton dynamics and its association with environmental variables in surf zones worldwide. Aboul Ezz *et al*. (2014) also related the zooplankton variability in Matrouh Beaches (Mediterranean Sea, Egypt) to seasonal changes in water temperature, especially for Copepoda group. Additionally, these authors stated that some species like *Oithona nana* were spatially controlled by local salinity variations. In surf waters of Brazilian beaches, zooplankton abundances correlated with precipitations levels, wich affected salinity through variations in the fluvial discharge (Avila *et al.*, 2009; Costa *et al.*, 2011; Pinheiro *et al.*, 2011, 2013). However, variations in temperature tend to have little effect on them (Costa *et al.*, 2011). Changes in salinity were not significant during the present study, hence, they had little effect on zooplankton community.

Chlo-*a* concentrations in surf waters were higher than those registered in the adjacent continental shelf (Delgado *et al*., in press). These authors reported values between 0.5 and 2.85 µg L^{-1} (mean= 1.8 µg L^{-1}) for stations located in the inner shelf offshore MH beach. Therefore, food supply accessible to zooplanktonic organisms is apparently higher in surf than in nearby ocean waters, explaining in part the registered zooplankton abundances. However, Chlo-*a* was very low compared with other beach systems in which surf-diatom accumulation occur and concentrations can reach up to 1700 µg L^{-1} (*e.g.* Rörig and Garcia, 2003; Odebrecht *et al.*, 2010). In MH surf waters, the low phytoplankton biomass as Chlo-*a* in combination with high amounts of particulate matter, could be more appropriate to explain the high zooplankton abundances observed. The strong local hydrodynamic -turbulence generated by the waves when they brake would be responsible for the high concentrations of SPM and turbidity of the water column. So, the surf zone can be thought as a physically dynamic environment that may drive closely coupled trophic interactions among surf zone habitants. Accordingly, Stull *et al.* (2016) suggested that the turbulence increases the encounter rates between small-consumers and small-preys, motivating a strong coupling between phytoplankton production and zooplankton and as a consequence, between zooplankton and their predators.

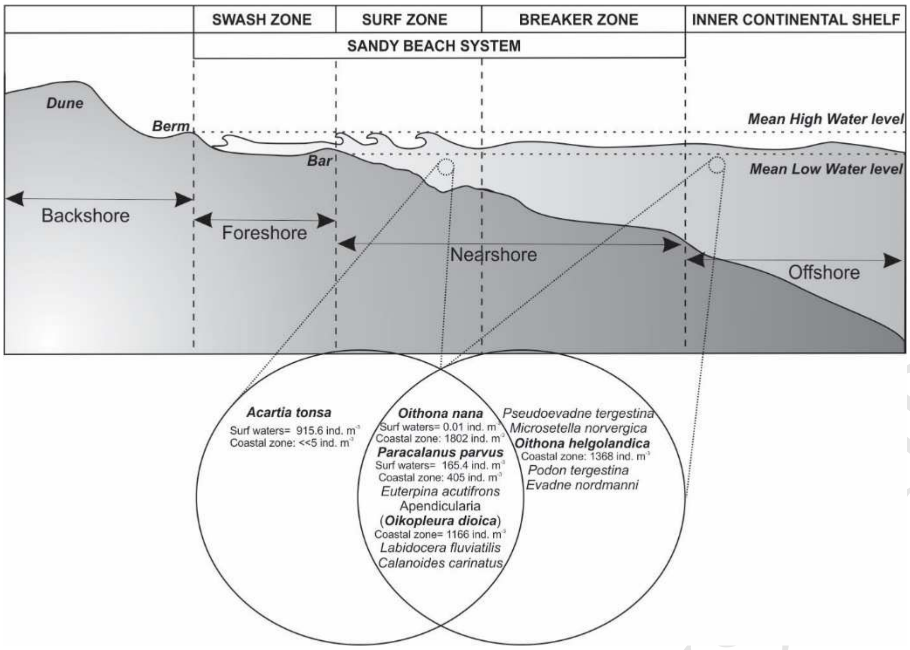
Additionally, POC values were high in MH surf waters. It has been suggested that most of C source present in surf zones is in the form of detritus (55-85%) and non-live material (13-43%), and not as live fraction (phytoplankton) (Talbot and Bate, 1988). In other coastal zones like estuaries, many researchers have noted the paradox between high copepod biomass with a large quantity of suspended matter and low phytoplankton production (David *et al*., 2005). This suggests the possible use of detritus as a food source for copepods (*e.g.* Roman, 1984; Irigoien and Castel, 1995; Richoux and Froneman 2008). Roman (1984) showed that the ingestion rate of *A. tonsa* on detritus (alone and mixed with algae) increased over the range of concentrations tested. Further, Roman *et al*. (2001) suggested that the ability of some copepod species to ingest detritus allows them to prosper in areas of maximum turbidity. In the Kariega Estuary, South Africa, Richoux and Froneman (2008) revealed that zooplankton used both phytoplankton and detritus as food. Particularly in the BBE, Diodato and Hoffmeyer (2008) stated that when phytoplankton and microzooplankton are scarce in the estuary, suspended matter and detritus become the main food of plankton, especially for *A. tonsa* and benthic filter-feeding consumers. Results of the present study indicate that in surf waters of this sandy beach, adjacent to the BBE, suspended matter and detritus could also be an alternative food source for zooplanktonic organisms, instead of phytoplankton.

4.3 Comparison between surf- and inner continental shelf zooplankton communities

In surf waters of beaches, a question arises: is the zooplankton community similar to that observed in nearby coastal waters (< 50 m depth)? or is it a different one, completely adapted to the particular conditions (high turbulence and turbidity)?. For the southern coastal area of Buenos Aires province (38-41° S), Marrari *et al*. (2004) described the zooplankton community as dominated by the copepods *L. fluviatilis*, *C. vanus*, *Paracalanus* spp., *E. acutifrons*, O. nana, *C. cf. carinatus*, and the cladoceran *Evadne nordmanni* (Figure 6, provided as supplementary material). Most of these taxa are small, omnivorous and fast-reproducing organisms, better adapted to warmer, variable and less productive coastal areas in comparison with middle shelf waters. Meroplanktonic larvae (decapod, bivalve) and medusae are also found in coastal waters, consistent with their dependence on benthic phases (Marrari *et al*., 2004). Viñas *et al*. (2013) included *O. nana*, *O. helgolandica* and *P. parvus* as dominant copepods in the coastal region between 38° and 40° S (Figure 6). Copepods smaller than one millimeter are mentioned as numerically dominant; however, the nets employed in the present study underestimated this fraction. *E. nordmanni* and *Podon polyphemoides* and the appendicularian *Oikopleura dioica* were also registered as dominant in the coastal zone < to 50 m depth (Viñas *et al*., 2013) (Figure 6). The dominance of *A. tonsa* can be related to the proximity of the BBE, however, it is clear that its higher abundances are restricted to these turbulent and turbid waters because it has not been practically mentioned for nearby coastal waters < to 50 m. Conversely, this copepod dominates in the Rio de la Plata estuary but also in the Argentine inner shelf as far as 51°S (Marrari *et al*., 2004; Viñas *et al*., 2013; Derisio *et al*., 2014). A gradual decrease in their relative abundance can be observed across shelf coinciding with a reduction of estuarine influence (Cepeda *et al*., 2018). More experiments and samplings are evidently necessary to understand why *A. tonsa* distribution is restricted to surf waters in the southwestern coast of Buenos Aires Province. Even though most of the taxa registered in MH surf zone are also mentioned for the inner shelf waters, the surf community is dominated by the estuarine copepod *A. tonsa* whose local distribution is practically restricted to this zone. Therefore, our results also show that in surf waters, estuarine and neritic species coexist, evidencing the connection between these ecosystems.

In conclusion, the present study provides evidence that MH sandy beach surf zone hosts a very rich zooplanktonic community which shows a strong seasonality and is numerically dominated by crustaceans, especially two calanoid copepods: *A. tonsa* and *P. parvus*. Other planktonic forms such apendicularians, mysids, chaetognaths and shrimps are sporadically important in these waters. Meroplankton abundance is low in relation to holoplankton and is mainly represented by some medusae species but also by benthic invertebrate larvae, and fish eggs. Despite the turbulent conditions in surf waters, the adventitious component is very scarce. Surf waters are inhabited by a typical zooplanktonic community, with some species similar to those registered in coastal waters, and others like *A. tonsa* practically restricted to this particular zone. The present results also show that in surf waters, estuarine and neritic species coexists, evidencing the connection between both ecosystems. Water temperature in combination with SPM and Chlo-*a,* explain the observed zooplankton seasonal pattern. The apparent low phytoplankton production detected in surf waters would be compensated by large quantities of detritus and SPM, which could be an alternative food source for copepods that inhabit these waters. These results can be considered for further studies and/or technical programs conducted in a similar high-energy, turbulent and turbid beach ecosystem.

Figure 6 (supplementary material). Typical profile of a sandy beach ecosystem and the adjacent inner shelf waters. Averagae abundance (ind. m^{-3}) of the main zooplanktonic species that characterize MH surf zone (our data) and waters of the southern coastal area of Buenos Aires Province (38-41° S), Argentina (based on data by Marrari *et al.*, 2003 and Viñas *et al.*, 2013). In bold are represented the most abundant species.



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