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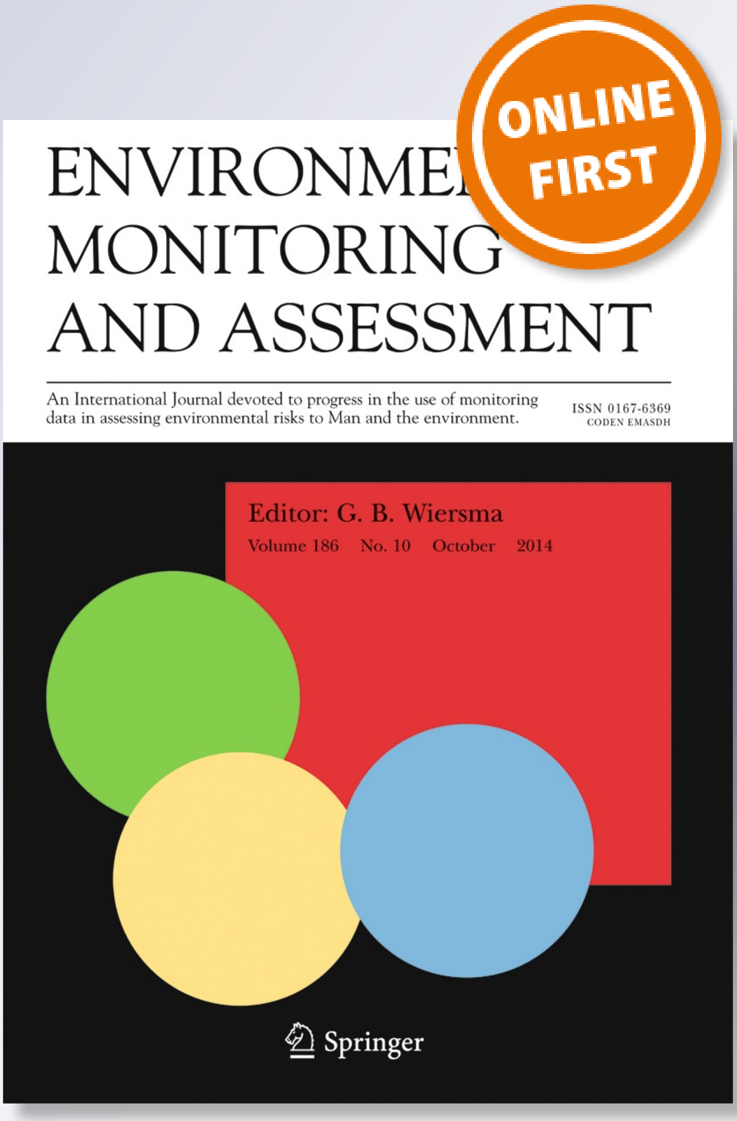
Environmental Monitoring and Assessment
An International Journal Devoted to Progress in the Use of Monitoring Data in Assessing Environmental Risks to Man and the Environment

ISSN 0167-6369

Environ Monit Assess
DOI 10.1007/s10661-014-4032-y



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Received: 9 May 2013 / Accepted: 1 September 2014

Abstract This study focused on the seasonal and spatial analysis of the mesozooplankton community in a human-impacted subantarctic bay in Argentina and aimed to detect assemblages associated with environmental variability. Mesozooplankton samples and environmental data were obtained in the Ushuaia Bay (UB) seasonally, from August 2004 to June 2005, and spatially, from coastal (more polluted), middle (less influenced) and open sea water (free polluted) sampling stations. Remarkable seasonal changes on the mesozooplankton community were observed. Nitrogenated nutrients, chlorophyll *a*, salinity and temperature were the prevailing environmental conditions likely associated with the different mesozooplankton assemblages found in the bay. The copepods *Eurytemora americana*, *Acartia tonsa*, *Podon leuckarti* and Nematoda were particularly observed on the northwest coast of the bay, characterized by the highest level of urban pollution, eutrophicated by sewage and freshwater inputs from the Encerrada Bay which is connected to it. The stations situated in the northeast area, mostly influenced by freshwater input from rivers and glacier melting, showed low mesozooplankton abundances and an important contribution of adventitious plankton. The copepods *Ctenocalanus citer*, *Clausocalanus brevipes* and *Drepanopus forcipatus* were mostly observed at the stations located near the Beagle Channel, characterized by open sea and free polluted waters. Our findings suggest that the variations observed in the mesozooplankton assemblages in the UB seem to be modulated by environmental variables associated with the anthropogenic influence, clearly detected on the coast of the bay. Certain opportunistic species such as *A. tonsa* and *E. americana* could be postulated as potential bioindicators of water quality in subantarctic coastal ecosystems.

Keywords Environmental variable changes · Nutrient enrichment · Sewage · Multivariate analysis · Mesozooplankton dynamics · Subantarctic bay

Introduction

Coastal marine areas, typically of considerable ecological, economic and social importance (Calbet et al. 2001), are impacted by a number of physico-chemical factors that affect the functioning of the planktonic community (Siokou-Frangou et al. 1998; Uriarte and Villate 2004). Fluctuations of these factors are more evident in coastal areas than in the open sea (Leandro et al. 2007; Li et al. 2006) and are enhanced by the influence of human activities (Valiela 1995). Owing to the global increase in human settlements along coasts (Small and Nicholls 2003), coastal systems have been subject to increasing levels of anthropogenic disturbance, generally leading to changes in the dynamics of

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local food webs and subsequently in the whole ecosystem (Chang et al. 2009; Silva et al. 2004; Uye 1994).

One of the most common forms of coastal pollution is organic enrichment (Valiela 1995), and studies on phytoplankton and zooplankton community changes related to it have been conducted in many coastal marine systems (Biancalana et al. 2012a; Chang et al. 2009; Silva et al. 2004, Park and Marshall 2000; Zervoudaki et al. 2009). Decreases in mesozooplankton biomass and abundance were one of the consequences of increasing eutrophication in the Suape Bay (Brazil) (Silva et al. 2004) and in the Chesapeake Bay (EE.UU.) (Park and Marshall 2000). In addition, changes in zooplankton composition have been related to increases in nutrient input in the Uchiumi and Fukuura bays (Japan) (Chang et al. 2009).

The zooplankton of coastal ecosystems plays a significant role in determining the quality of the ecosystem (Uriarte and Villate 2004; Uye 1994) and represents an excellent indicator of environmental deterioration due to anthropogenic influence (Smith et al. 1999; Uriarte and Villate 2004; Thompson et al. 2007). Bioindicators of environmental quality are commonly found among copepod species, and those belonging to the *Acartia*, *Eurytemora*, *Paracalanus* and *Oithona* genera have been especially associated with human disturbance and eutrophication in coastal marine areas (Caulleaud et al. 2009; Chang et al. 2009; Bianchi et al. 2003; Uye 1994).

Ushuaia City and its surroundings have undergone considerable population growth during recent years, as well as the whole of the Tierra del Fuego region. This has led to a marked increase in industrial and domestic sewage which even today is discharged untreated into the Ushuaia Bay (UB). A differentiation has therefore developed between coastal areas, directly impacted by anthropogenic activities, and remotes areas connected to open waters, such as the Beagle Channel. Several deleterious effects on coastal water quality have been observed as a consequence of the uncontrolled development of Ushuaia City and the industrial zones (Amin et al. 2010; Gil et al. 2011; Torres et al. 2009). A linkage between nutrient enrichment, particularly by inorganic nitrogen and phosphate, and anthropogenic and natural driven impacts (e.g. urban discharge, river and thawing inputs) has been reported by Amin et al. (2010) and Gil et al. (2011).

Several studies on mesozooplankton community structure have been carried out in the Magellan region, including the Magellan Strait, the Atlantic coast of Tierra del Fuego, fjords and channels of southern Chile and the Beagle Channel (Mazzocchi and Ianora 1991; Antezana 1999; Lovrich 1999; Sabatini et al. 2001; Thatje et al. 2003; Chiesa et al. 2005). Descriptive ecological information such as the composition and abundance of the mesozooplankton community of the UB was previously provided by Fernández-Severini and Hoffmeyer (2005) and Biancalana et al. (2007). Only two works studied the seasonal dynamics of the mesozooplankton biomass and metazooplankton related to temperature, salinity and chlorophyll *a* in the UB (Biancalana et al. 2012b; Aguirre et al. 2011), but there are no studies in the bay on the evaluation of the impact by different sources of variation (e.g. natural and anthropogenic derived) on the mesozooplantkon community and how it would respond seasonally and spatially.

To evaluate the changes in the dynamics of the plankton community associated with natural environmental variables and anthropogenic perturbations, an annual driven research over a spatial scale is required. Thus, the aims of the present study were to (i) analyse the seasonal and spatial variability of the mesozooplankton community in the UB in terms of composition, abundance and diversity; (ii) evaluate the mesozooplankton dynamics in relation to environmental variables; and (ii) determine mesozooplankton assemblages associated or not with anthropogenic disturbance in the UB.

Materials and methods

Study area

The UB is located on the northern coast of the Beagle Channel (54° 79′ S–68° 22′ W) in southern Argentina (Fig. 1). It has a depth of nearly 30 m in the western zone to 100–170 m in the eastern zone near the Beagle Channel. UB has a consolidated soft-bottom surface with stones and shells (Biancalana et al. 2007) and current velocities of 5.5 to 16.3 cm s^{-1} (Balestrini et al. 1990).

Salinity ranges from 15 to 32, depending on seasonal melting processes during the austral spring and summer (Amin et al. 2010). Low salinities during the austral warm season are a direct consequence of freshwater input from thaw and stream and river runoff (Amin et al. 2010). Temperature shows a seasonal trend ranging from −7 °C in July to 14 °C in January (Gil et al. 2011). Chlorophyll *a* ranges from 0.01 to 4.1 mg m^{-3} in winter and in spring, respectively (Amin et al. 2010).

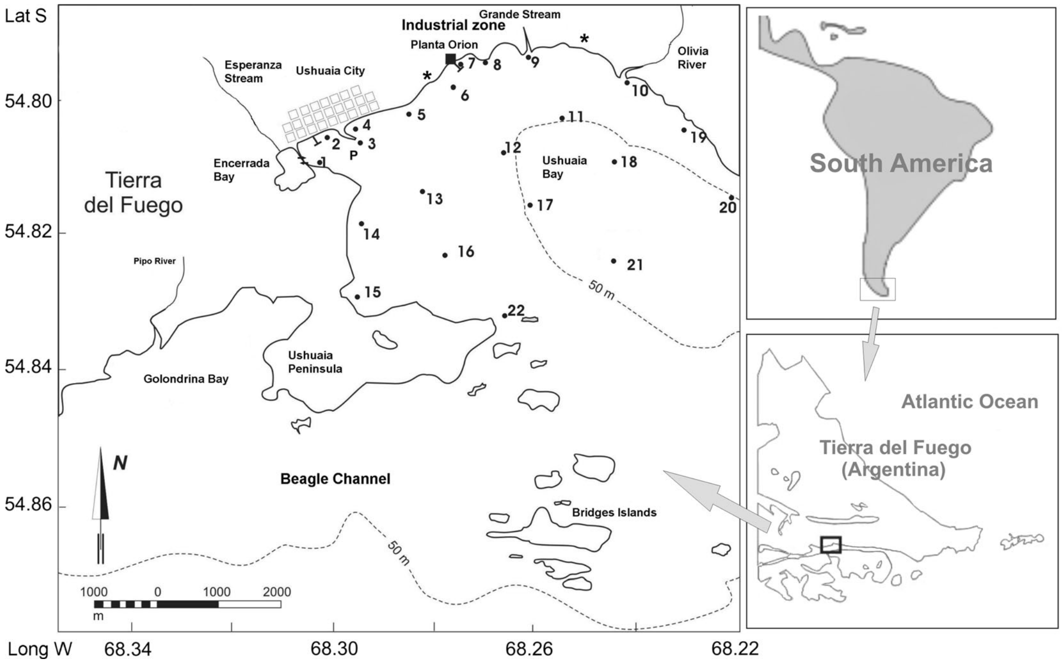

Fig. 1 Study area and sampling stations in Ushuaia Bay. *P* commercial port, *asterisk* wastewater outfalls (storm, sewage and/or industrial)

Dissolved oxygen ranges from 10.61 in winter to 14.87 mg L^{-1} in summer, reflecting well-oxygenated conditions throughout the year (Amin et al. 2010).

Sampling survey

To study the mesozooplankton community and its relation to anthropogenic impact, sampling was carried out at 22 stations including coastal and middle ones and those connected to the Beagle Channel (Fig. 1). The description of each sampling station in terms of anthropogenic influence is described in Table 1. Four seasonal field sampling campaigns were performed in late winter (26 August 2004), late spring (09 December 2004), late summer (03–04 March 2005) and late autumn (15 June 2005). Due to the difficulty of the sailing condition in the cold season, only 15 of the 22 stations (1 to 16 except 15) were sampled during late winter. All 22 stations were sampled for the remaining seasons. At each station, one mesozooplankton sample was collected by means of oblique hauls using a plankton net of 200 μm mesh from close to the bottom up to the surface, aboard a motor boat at a speed of 2 knots during 5 min. A General Oceanics® digital flowmeter was used to calculate the volume of filtered seawater. Samples were preserved in 4 % formalin (Boltovskoy 1981). Mesozooplankton was qualitatively and quantitatively analysed under a Wild M5 stereomicroscope. Total samples were counted and mesozooplankton abundance was expressed as individuals per cubic meter (ind. m^{-3}).

Surface water temperature and salinity were measured in situ at the time of each tow using a multiparameter probe sensor (HORIBA® U-10). Additionally, surface water samples were obtained by a Van Dorn bottle to determine inorganic nutrients (nitrate and nitrite (N+N), ammonium, phosphate and silicate), chlorophyll *a* and phaeopigments. Chemical determinations were carried out by the Chemical Oceanography and Water Pollution Laboratory at CENPAT-CONICET (Puerto Madryn, Chubut) following internationally validated methods (APHA 1980). Environmental data of the UB were provided by M. Gil.

Statistical analysis

Seasonal comparisons of mesozooplankton abundance and diversity were done using one-factor analysis of variance. Abundance data were log (X+1) transformed to comply with ANOVA assumptions. In order to determine differences in abundance among the seasons, least significant differences (LSD) tests were applied (Zar 1996). Specific diversity and dominance were calculated using the Shannon-Wiener (H') and Simpson (λ)

Table 1 Description of sampling stations in the Ushuaia Bay

Sampling stations	Sampling locations	Station characteristics
1	C	Untreated urban discharges (north-west). This station is located near the connection of Encerrada Bay (EB) with Ushuaia Bay. EB received different inputs from natural and anthropogenic sources (e.g. Buena Esperanza)
2		Yacht Club (north-west). This station receives the influence of water coming from EB
3 4		The commercial port area (north-west). Both stations are influenced by water coming from EB
5 6		The industrial zone (north). These stations receive wastewater outfalls (storm/sewage and industrial discharges)
7		Plant Orion (north-east). Pollution associated with port activities and fueling operations (oil charging)
8		This station is influenced by the industrial zone and Grande Stream (north-east)
9		Grande River (north-east). Near industrial zone and influenced by urban settlements along its course
10		Oliver River (north-east). Natural input
11 12 13	M	Stations located in the centre of the bay. These stations are influenced by the water coming from the urban and industrial zone
14 15	C	Coastal stations with influence of water coming from the urban zone (north-west)
16 17 18	M	Stations located in the centre of the bay and more influenced by water coming from the Beagle Channel
19 20 21 22	BC	Low anthropogenic influence

C coast, *M* middle, *BC* Beagle Channel connection

indexes (Pielou 1975). All these analyses were performed using a PRIMER® 5 package and SPSS®.

Seasonal and spatial variations of mesozooplankton as well as mesozooplankton assemblages for each season were shown by multidimensional scaling (MDS) after transforming abundance values by means of log (X+1). MDS were built using Bray-Curtis similarities and the average linkage technique. MDS plots for each season were performed in order to determine similarities between stations taking into account the biological data (e.g. composition and mesozooplankton abundance). Mesozooplankton assemblages revealed by MDS were drawn on the Ushuaia Bay map using Surfer® 8 software. Similarity percentages analyses (SIMPER) were used to identify those taxa contributing most to similarities within groups. Analysis of similarities (ANOSIM) was applied to detect significant differences between seasons, spatial groups of stations and mesozooplankton groups for each season (Clarke and Warwick 1994). These analysis were performed using PRIMER® 5 package.

A canonical correspondence analysis (CCA) was applied in order to analyse the relationship between mesozooplankton composition and environmental variables, using CANOCO 4.0 (ter Braak 1986; Leps and Smilauer 2003). To test the significance of all canonical axes, 499 unrestricted permutations were conducted using the Monte Carlo test. A forward selection process was used in order to identify the most important environmental variables associated with mesozooplankton composition. The significance of each environmental variable was evaluated using the Monte Carlo permutation test (α=0.05) (Leps and Smilauer 2003).

Results

Environmental variables

Surface water temperature showed a seasonal trend reaching the lowest value in late winter (5.24± 0.09 °C) and the highest value in late spring (10.63± 0.34 °C). Salinity showed lower values particularly in the coastal area in late spring and late summer, with the lowest value at station 8 in late spring (17.28) and the highest in late winter and late autumn (31.23±0.05 and 31.12±0.10, respectively) (Fig. 2). The N+N concentration varied between 0.66±2.97 and 13.36±0.27 μM during late spring and late winter, respectively. Maximum values of N+N were detected at coastal stations, the highest value being recorded at station 2 in late winter (15.67 μM, Fig. 3). The same seasonal trend was observed for phosphate, whose values ranged from 0.33±0.02 to 1.40±0.05 μM in late spring and late winter, respectively. The maximum value of phosphate

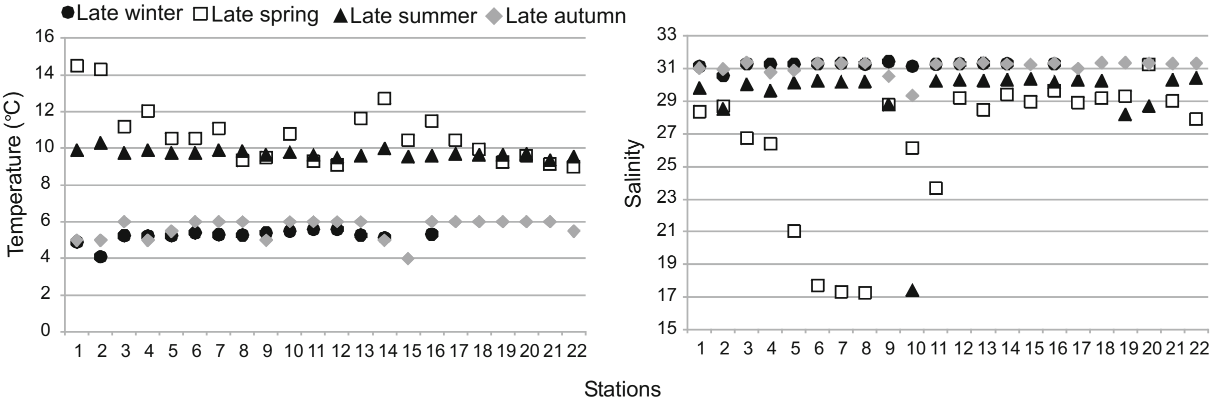

Fig. 2 Temperature (°C) and salinity spatial variation in Ushuaia Bay in each season

was 2.23 µM and recorded at station 4 in late autumn (Fig. 3). Lower ammonium values were registered in late spring (1.78±0.20 µM) and higher values in late autumn (4.34±1.65 µM) and two maximum of 28.14 and 28.58 µM were recorded at station 2 in late summer and station 1 in late autumn, respectively (Fig. 3). Silicate values ranged between 5.07±0.71 and 8.15±0.79 µM in late summer and late autumn, respectively. The highest value of silicate of 21.56 µM corresponded to station 16 in late autumn (Fig. 3). Chlorophyll *a* showed lower values in late winter and late autumn (0.71±0.14 and 0.31±0.02 µg L^{-1}, respectively) and higher values in late spring and late summer (3.39±0.25 and 11.13±0.89 µg L^{-1}, respectively). The maximum value of chlorophyll *a* was 21 µg L^{-1}, recorded at station 1 in late summer (Fig. 3). Phaeopigments varied from 0.15±0.04 µg L^{-1} in late spring to 1.02±0.46 µg L^{-1} in late summer and showed the highest value at station 2 in late summer (9.45 µg L^{-1}, Fig. 3).

Mesozooplankton seasonal and spatial patterns

Mesozooplankton mean abundance ranged from 16.85 in late winter to 425.81 ind. m^{-3} in late summer (Fig. 4). Significant differences in mesozooplankton abundance were found between late winter and the other seasons, and late autumn was significantly different to late spring and late summer (ANOVA $F=18.90$, $p<0.05$, LSD test, $p<0.05$). The Shannon-Wiener diversity index was lower in late autumn and late winter ($H'=2.36$ and $H'=2.47$, respectively) than in late spring and late summer ($H'=2.82$ and $H'=2.89$, respectively) (Fig. 4). The dominance index diminished in late spring and late summer and increased in late winter and late autumn. ANOVA revealed significant differences in the mean diversity between the seasons ($F=3.92$, $p<0.05$). Significant differences in diversity were detected between cold (late winter and late autumn) and warm (late spring and late summer) seasons (LSD test, $p<0.05$). A seasonal distribution of mesozooplankton abundance and composition was revealed by the MDS (stress=0.14) (Fig. 5). Five groups were formed due to shared taxa between them, and seasonal significant differences in the mesozooplankton community structure were detected (ANOSIM global $R=0.824$, $p=0.001$) (Fig. 5).

Ctenocalanus citer, *Oithona similis*, *Clausocalanus brevipes* and *Drepanopus forcipatus* were the most abundant copepods in late winter and late autumn (Figs. 4 and 6). *C. citer* dominated in late winter, accounting for 42.53 % of total abundance, followed by *O. similis* and larvae of the decapod *Munida gregaria* (18.11 and 13.94 %, respectively) (Fig. 4). *O. similis* (25.49 %) dominated in late autumn, followed by *C. brevipes* (17.92 %) and *D. forcipatus* (14.27 %) (Fig. 4). In late winter, *C. citer* and *O. similis* were observed at all the stations, with a higher abundance at stations 3 (26.32 ind. m^{-3}) and 4 (12.60 ind. m^{-3}) (Fig. 6). In late autumn, *C. brevipes* and *D. forcipatus* were found mostly at the stations close to the Beagle Channel, showing their highest abundances at stations 19 (294.26 ind. m^{-3}) and 22 (111.68 ind. m^{-3}) (Fig. 4). *Podon leuckarti*, *A. tonsa* and *Obelia* sp. were abundant in late spring and late summer (Figs. 4 and 6). *P. leuckarti* was detected in higher abundances (37.70 %) in late spring, followed by *Obelia* sp. (13.92 %). *A. tonsa* was dominant in late summer, with a relative abundance of 30.04 % (Fig. 4). *P. leuckarti* and *Atylus* sp. were also abundant in late summer (23.26

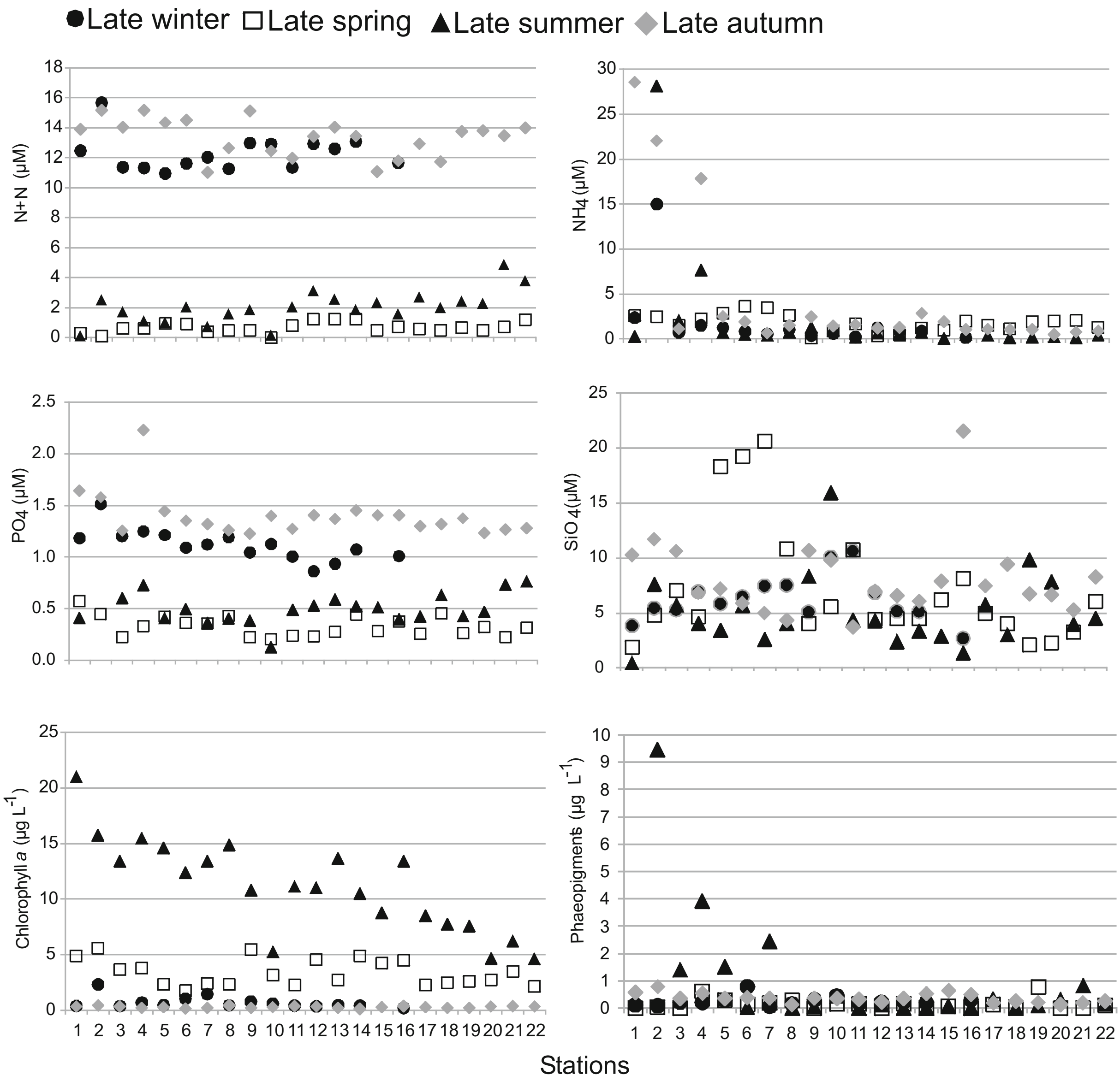

Fig. 3 Environmental variables: N+N (nitrite+nitrate—µM), NH_4 (ammonia—µM), PO_4 (phosphate—µM), SiO_4 (silicate—µM), chlorophyll *a* (µg L^{-1}) and phaeopigments (µg L^{-1}) in Ushuaia Bay in each season

and 8.39 %, respectively) (Fig. 4). *P. leuckarti* was observed at all the stations, with its maximum abundance value at station 17 (678.21 ind. m^{-3}) in late spring (Fig. 6). In late summer, *P. leuckarti* and *A. tonsa* were mostly observed at the coastal stations and their maxima were found at station 14 (1,023 and 1,209 ind. m^{-3}, respectively) (Fig. 6). *Eurytemora americana* accounted for up to 2 % of total abundance and was associated with the coastal stations in all the studied seasons (Figs. 5 and 6) with a maximum abundance at station 14 (138.39 ind. m^{-3}) (Fig. 6).

The spatial variation of taxa number, mean mesozooplankton abundance, diversity and dominance is shown in Fig. 7. The highest mean abundance of mesozooplankton was observed at station 14 (662.06 ind. m^{-3}) and the lowest at station 10 (51.27 ind. m^{-3}). In general, higher abundances were found at the coastal stations, with low diversity and high dominance, e.g. in stations 2 and 15 (Fig. 7). Two groups were revealed by the MDS (stress=0.13) due to the differences on mean mesozooplankton abundance, diversity and

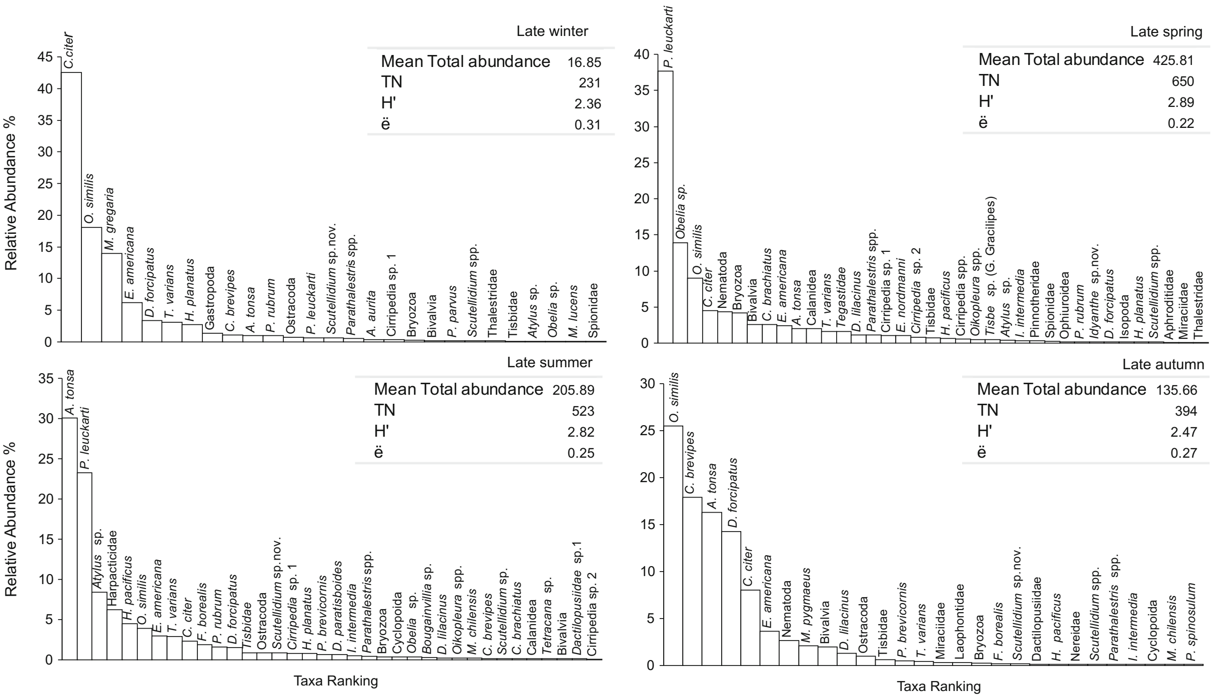

Fig. 4 Mesozooplankton relative abundance (*bars*), mean total abundance (ind. m^{-3}), total number of taxa (*TN*), mean diversity (*H'*) and mean dominance (λ) in Ushuaia Bay in each season. Only taxa with relative abundance >0.016 % were included in the graphic

dominance (ANOSIM global R=0.931, p=0.001), showing the stations related with the water coming from the urban zone (stations 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14 and 15) and those associated with the Beagle Channel waters (16, 17, 18, 19, 20, 21 and 22) (Fig. 7).

Multivariate analysis of the mesozooplankton community

Four groups (I, II, III and IV) were determined at 50 % of similarity in late winter (MDS stress=0.08, Fig. 8). Three taxa accounted for up to 67.78 % of similarity in

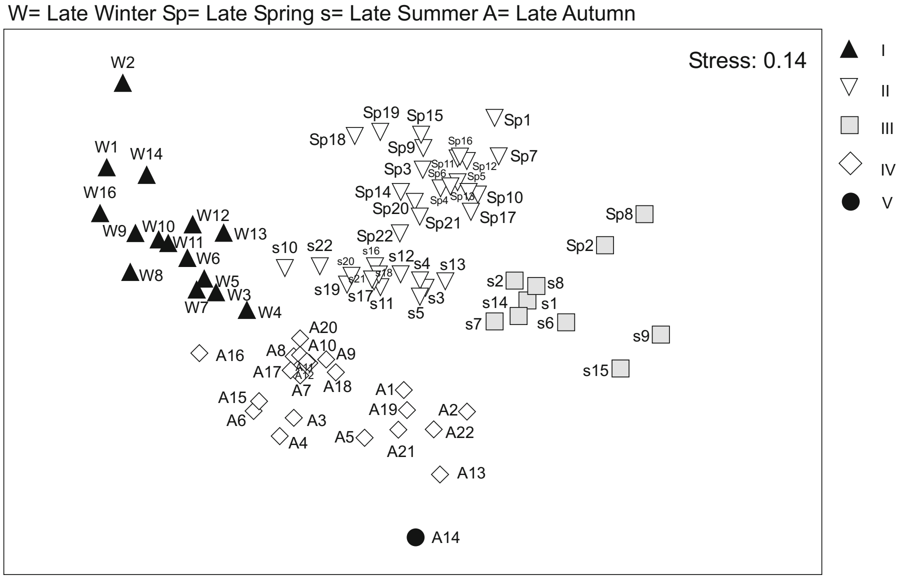

Fig. 5 MDS plot for seasonal mesozooplankton assemblages sampled in Ushuaia Bay

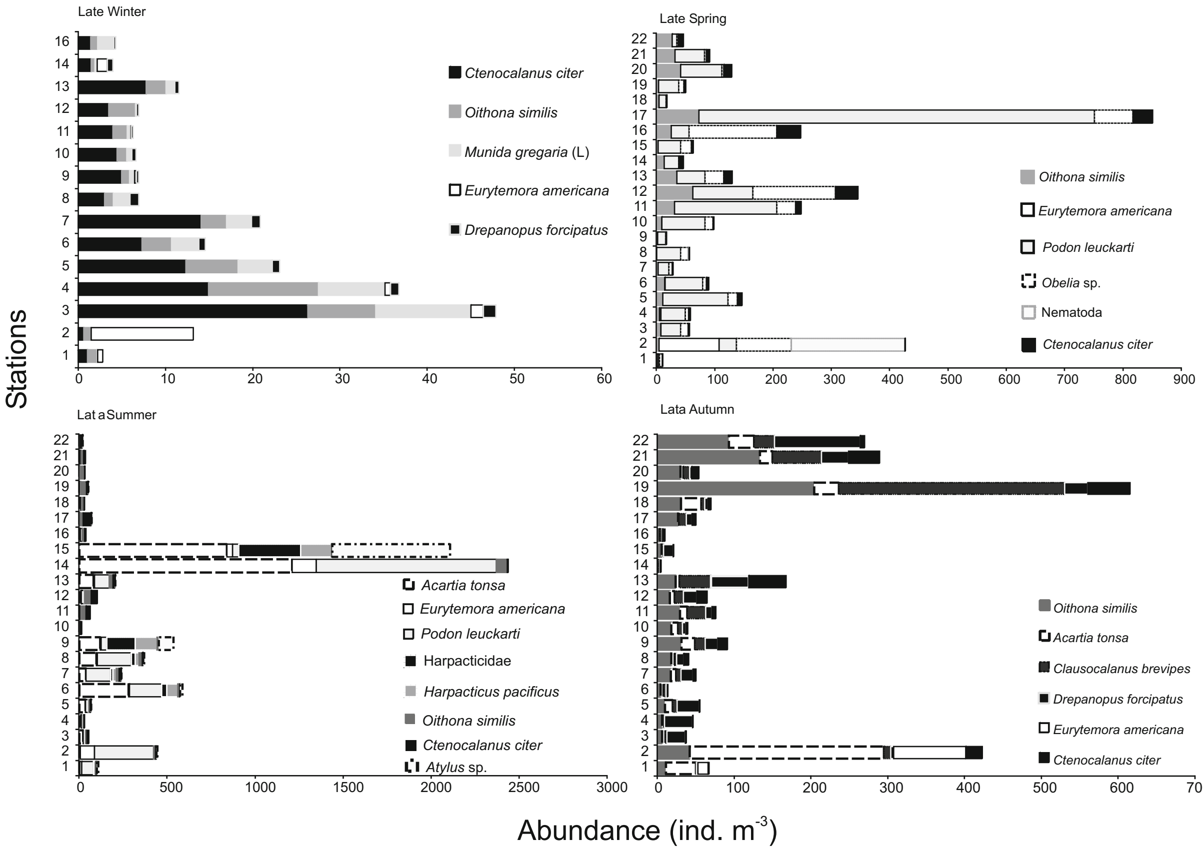

Fig. 6 Spatial variation of the main taxa abundance in Ushuaia Bay in each season

group I (SIMPER test, 61.19 % average similarity), namely *O. similis* (25.35 %), *C. citer* (22.51 %) and *E. americana* (19.90 %) (Table 2). Group II was formed by only one sampling station (station 14) and differed from the remaining groups by the low abundance of the taxa (Table 3). Three taxa-*C. citer* (33.05 %), *O. similis* (21.85 %) and *M. gregaria* (15.10 %)-accounted for 69.99 % of similarity in group III (Table 2) (SIMPER test, 65.65 % average similarity). Group IV was made up of only one sampling station (station 4) and differed from the remaining groups by the high abundance of *C. citer* and *O. similis* (Table 3). Differences between groups were detected (ANOSIM global R=0.921, p= 0.001). These differences were given by the higher contribution of *E. americana* and the absence of *D. forcipatus* in group I (Table 3).

Four groups (I, II, III and IV) were performed at a similarity level of 48 % in late spring. The groups were visually discriminated by the MDS plot with a stress of 0.11 and statistically differenced by ANOSIM (global R=0.865, p=0.001) (Fig. 8 and Table 3). Groups I, II and III were made up of only one sampling station (stations 2, 8 and 1, respectively), and group IV was arranged by the remaining stations. This latter group (SIMPER test, 58.89 % average similarity) was mainly represented by three taxa which accounted for up to 43.73 % of similarity: *P. leuckarti* (20.47 %), *O. similis* (12.64 %) and *Obelia* sp. (9.33 %) (Table 2). The highest abundance of Nematoda and *E. americana* within group I contributed to the dissimilarity between this group and groups II, III and IV (56.92, 60.77 and 65.85 % of average dissimilarity, respectively) (Table 3).

Three groups (I, II and III) were determined at a 50 % of similarity level in late summer and the MDS provided an excellent representation (stress 0.07) (Fig. 8). Group I showed 64.77 % similarity, with three taxa accounting for 45.61 % of the similarity, *O. similis* (16.87 %), *C. citer* (14.86 %) and *A. tonsa* (13.88 %) (Table 2). Group II was determined by stations 9 and 15 (SIMPER

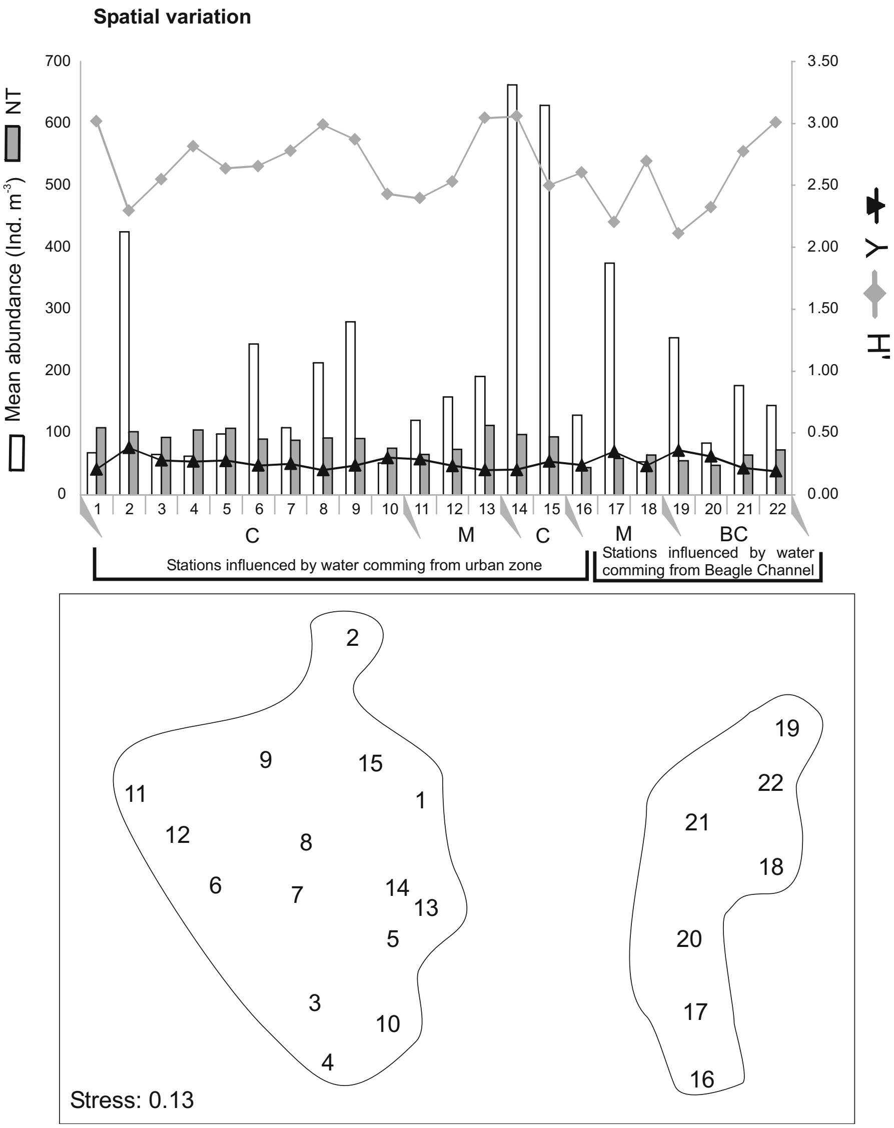

Fig. 7 The number of taxa (*NT—grey bars*), mean mesozooplankton abundance (*white bars*), diversity (*H'*) and dominance (λ) indexes spatial distribution in Ushuaia Bay. MDS plot for station assemblages sampled in Ushuaia Bay

test, 67.67 % average similarity), with the Harpacticidae family (8.29 % contribution) being the best represented taxon, followed by the copepods *Harpacticus pacificus* (7.87 %) and *A. tonsa* (7.80 %) (Table 2). Group III was constituted by six sampling stations (SIMPER test, 59.53 % average similarity) in which three taxa, namely *P. leuckarti* (17.09 %), *A. tonsa* (9.95 %) and *O. similis* (8.13 %), accounted for up to 35.17 % (Table 2). Differences between groups were statistically significant (ANOSIM global R=0.898, p=0.001) (Table 3). In group III, the high contribution of *P. leuckarti* to the total mesozooplankton abundance along with the contribution of *A. tonsa* and *E. americana* was mainly responsible for the dissimilarity between this group and groups I and II (58.07 and 52.54 % average dissimilarity, respectively) (Table 3).

Four groups (I, II, III and IV) were determined at a 50 % of similarity level in late autumn. The four groups were arranged by MDS with a stress of 0.13 (Fig. 8) and statistical differences among them were detected (ANOSIM global R=0.905, p=0.001) (Table 3). Group I was determined by station 14 only, and the most

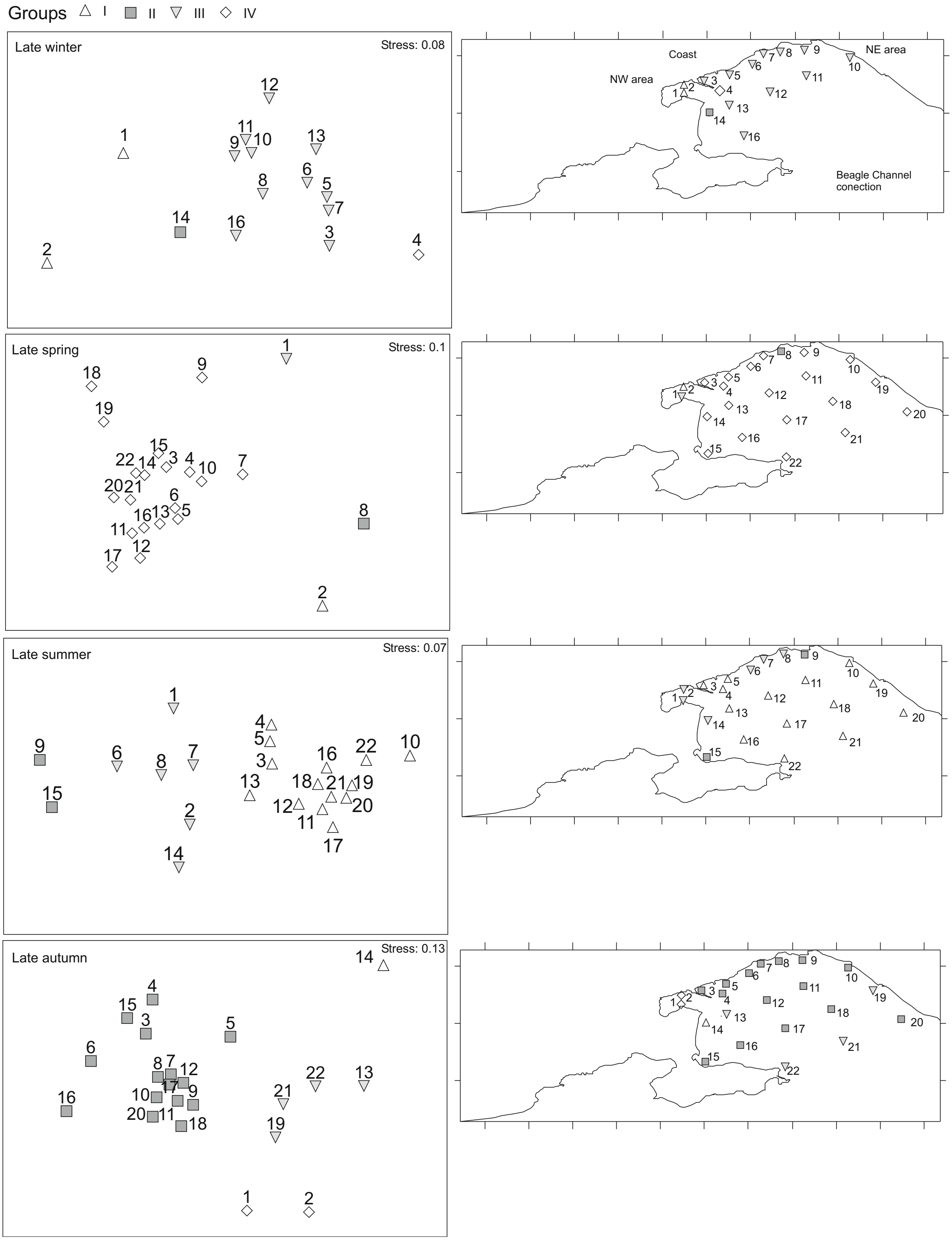

Fig. 8 MDS plot and maps showing the station groups in Ushuaia Bay in each season

Table 2 SIMPER analysis for mesozooplankton assemblages determined by MDS considering each season: average similarity percentage (%) and main taxa contribution percentage (%). Groups formed by one station are not represented

	Groups		
Late winter	II	III	
Average similarity (%)	61.19	65.65	
Main taxa contribution (%)	*O. similis* (25.35 %)	*C. citer* (33.05 %)	
	C. citer (22.51 %)	*O. similis* (21.85 %)	
	E. americana (19.90 %)	*M. gregaria* (15.10 %)	
Late spring	IV		
Average similarity (%)	58.89		
Main taxa contribution (%)	*P. leuckarti* (20.47 %)		
	O. similis (12.64 %)		
	Obelia sp. (9.33 %)		
Late summer	I	II	III
Average similarity (%)	64.67	67.77	59.53
Main taxa contribution (%)	*O. similis* (16.87 %)	Harparticidae (8.29 %)	*P. leuckarti* (17.09 %)
	C. citer (14.86 %)	*H. pacificus* (7.87 %)	*A. tonsa* (9.95 %)
	A. tonsa (13.88 %)	*A. tonsa* (7.80 %)	*O. similis* (8.13 %)
Late autumn	II	III	IV
Average similarity (%)	62.52	66.11	54.84
Main taxa contribution (%)	*O. similis* (27.25 %)	*O. similis* (15.54 %)	*C. citer* (11.12 %)
	D. forcipatus (21.71 %)	*O. similis* (15.54 %)	*E. americana* (16.02 %)
	A. tonsa (16.05 %)	*D. forcipatus* (13.85 %)	*O. similis* (14.87 %)
	C. brevipes (15.12 %)	*C. citer* (11.12 %)	

important taxon within this group was *D. forciptus* (Table 3). Group II was made up by 68.18 % of the sampling stations (SIMPER test, 66.52 % average similarity), and four copepods species accounted for up to 80.12 % of similarity, namely *O. similis* (27.25 %), *D. forcipatus* (21.71 %), *A. tonsa* (16.05 %) and *C. brevipes* (15.12 %) (Table 2). Four taxa accounted for up to 54.55 % of similarity in group III (SIMPER test, 66.71 % average similarity): *O. similis* (15.54 %), *C. brevipes* (14.03 %), *D. forcipatus* (13.85 %) and *C. citer* (11.12 %) (Table 2). Group IV was represented by two sampling stations (1 and 2) (SIMPER test, 54.85 % average similarity), and three taxa accounted for up to 53 % of similarity: *A. tonsa* (22.10 %), *E. americana* (16.02 %) and *O. similis* (14.87 %) (Table 3). The difference between group I and groups II, III and IV (76.35, 61.50 and 62.73 % average dissimilarity, respectively) was given by the high contribution of *E. americana*, *A. tonsa* and *O. similis* in group I (Table 3).

Mesozooplankton assemblages and their relation to environmental variables

The CCA ordination between the environmental variables and mesozooplankton community is shown in Fig. 9. Temperature and phosphate were the environmental variables that best explained the observed community pattern in late winter (F=4.50, p=0.012 and F=2.82, p=0.002, respectively). In late autumn, the test of all canonical axes was significant (F=1.51, p=0.04), and ammonium (F=4.46, p=0.01) best explained the community pattern. During late spring, the overall canonical axis was significant (F=3.58, p=0.002), with temperature (F=5.33, p=0.008), salinity (F=5.21, p=0.004) and silicate (F=5.37, p=0.002) as the environmental variables which best explained the mesozooplankton pattern. In late summer, temperature (F=2.76, p=0.03), Chl *a* (F=2.49, p=0.038) and salinity (F=4.55, p=0.002) mainly explained the pattern, and all canonical axes were significant (F=1.88, p=0.004).

Table 3 SIMPER analysis for mesozooplankton assemblages formed by MDS considering each season: average dissimilarities (%) among groups and taxa mean abundance (ind. m^{-3}) in each group. ANOSIM results between discriminated groups in each season

Seasons	Taxa	Groups				Average dissimilarity (%)
		Mean abundance				
		I	II	III	IV	
Late winter (ANOSIM, global $R=0.921$, $p=0.001$)	*C. citer*	0.62	0.92	1.98	2.77	I–II, 52.13
	E. americana	1.49	0.79	0.10	0.48	I–III, 58.75
	O. similis	0.68	0.35	1.20	2.61	I–IV, 69.39
	M. gregaria	0.03	0.23	1.01	2.15	II–III, 47.09
	D. forcipatus	–	0.48	0.46	0.68	II–IV, 62.50
						III–IV, 52.22
Late spring (ANOSIM, global $R=0.865$, $p=0.001$)	*C. citer*	0.54	–	0.11	10.67	I–II, 56.92
	E. americana	103.35	–	2.37	0.16	I–III, 60.77
	O. similis	4.31	–	0.65	21.16	I–IV, 65.85
	P. leuckarti	29.61	41.45	2.42	86.16	II–III, 65.87
	Obelia sp.	94.20	12.92	4.41	27.31	II–IV, 65.53
	Nematoda	194.85	1.62	0.43	0.06	III–IV, 60.78
Late summer (ANOSIM, global $R=0.898$, $p=0.001$)	*A. tonsa*	15.27	479.83	273.43		I–II, 78.64
	E. americana	0.51	18.39	39.12		I–III, 58.07
	P. leuckarti	11.95	33.95	324.05		II–III, 52.48
	Haparticidae	0.31	256.71	10.74		
	H. pacificus	0.48	148.86	19.35		
	Atylus sp.	0.04	375.87	5.66		
Late autumn (ANOSIM, global $R=0.905$, $p=0.001$)	*A. tonsa*	0.83	7.19	21.60	146.05	I–II, 76.35
	B. brevipes	0.77	6.62	106.30	4.70	I–III, 61.50
	C. citer	0.36	4.45	37.59	11.31	I–IV, 62.73
	D. forcipatus	1.12	12.81	56.63	2.97	II–III, 55.74
	E. americana	0.53	0.02	–	53.50	II–IV, 59.92
	O. similis	0.95	16.80	113.64	26.51	III–IV, 53.88

Discussion

Changes in environmental variables

Seasonal changes on temperature are in agreement with previous studies (Amin et al. 2010; Gil et al. 2011). The decreasing trend in salinity is given by the large volume of freshwater input to the bay coming from the ice and snow melting during warm season. This phenomenon has been registered by Amin et al. (2010), Gil et al. (2011) and Torres et al. (2009).

Inorganic nutrients, especially nitrate, phosphate and silicate, can be extremely high in the UB during thawing periods and rainy seasons (Amin et al. 2010; Gil et al. 2011). In our results, nutrients showed the highest values in late winter and late autumn and the lowest values in late spring and late summer. This could be the result of freshwater that is incorporated to the coastal system after running across the dense wood and large peatlands, together with inputs coming from the Ushuaia City, and a low biological activity.

The northwest coast of the UB was found to be the most affected by organic matter and nutrient loading and showed the highest oxygen demand (Gil et al. 2011). This area receives incoming urban-derived water from the Encerrada Bay (Torres et al. 2009), which has three sewage discharges (Onas, Guaraní and Beban), and inputs from the Buena Esperanza Stream. The

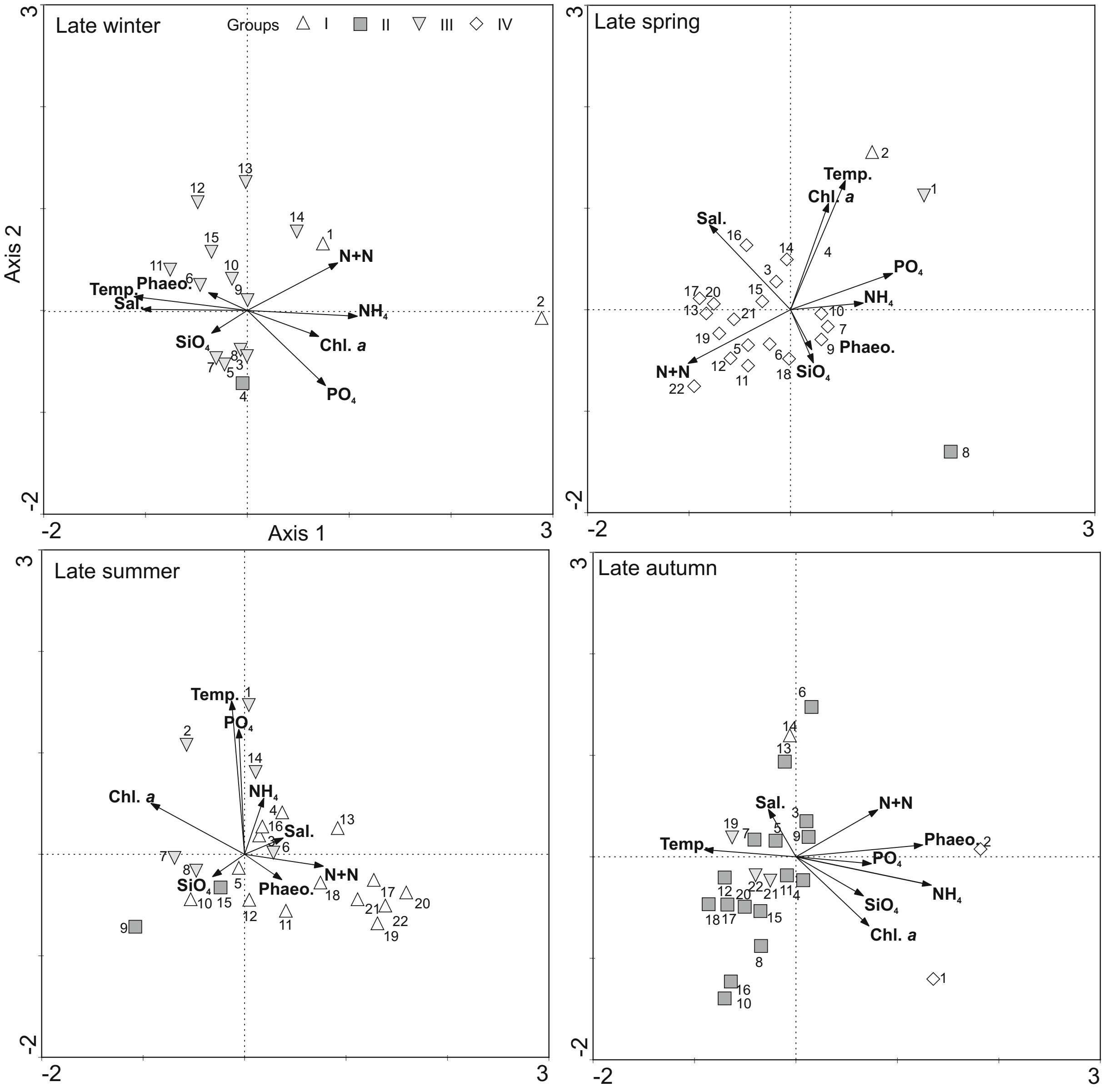

Fig. 9 Biplot of samples and environmental variables obtained from CCA on mesozooplankton taxa and environmental variables in Ushuaia Bay. *Temp.* temperature (°C), *Sal.* salinity, *Chl. a* chlorophyll *a* (μg L^{-1}), *Pheo.* phaeopigments (μg L^{-1}), *N+N* nitrite+nitrate (μM), *NH$_4$* ammonia (μM), *PO$_4$* phosphate (μM), *SiO$_4$* silicate (μM)

evaluation of the water quality from the Encerrada Bay by Torres et al. (2009) revealed maximum values of ammonium (320.8 μM), nitrate (40.7 μM) and phosphate (7.1 μM) during late winter. Accordingly, maximum values of ammonium in Buena Esperanza Stream (1,313.0 μM) and in Onas effluent (1,485.6 μM) were also detected during September (winter–spring) and the minimum in December (summer), coincident with the thawing period (Torres et al. 2009). In the present study, ammonium and phosphate were the variables that best explained the mesozooplankton pattern in late winter and late autumn, respectively. Furthermore, maximum concentrations of these nutrients were mostly observed at stations located on the northwest coast of the UB, especially stations 1 and 2 affected by untreated urban discharge from the Encerrada Bay. Silicate was the prevailing nutrient in Buena Esperanza Stream and in effluents carrying thawing water from the Martial glacier, which is enriched in wastewater from Ushuaia City (Amin et al. 2010; Gil et al. 2011; Torres et al. 2009). Natural tributaries such as Olivia River and Grande Stream located in the northeast area of the UB discharge large amounts of nutrients, particularly silicates and phosphates, derived from storm water and thaw outfall coupled with urban-derived waste (Amin et al. 2010).

An increase in chlorophyll *a* was observed during the warm season when nutrients were mostly available and temperature increased, while a decrease in the concentration of this pigment was found during the cold season. This seasonal pattern of chlorophyll *a* has been already observed in the bay by Amin et al. (2010), Aguirre et al. (2011) and Gil et al. (2011). The increase in chlorophyll *a* during the warm season is given by the increase in the phytoplankton growth favoured by high concentrations of nutrients and optimum temperature and light conditions. On the other hand, phaeopigments showed the lowest values during late spring and the highest during late summer. This may indicate an increase in primary productivity in late spring, followed by an increase in zooplankton grazing activity (Head and Harris 1992) during late summer. The maximum phaeopigment values were found at station 2 located on the northwest area of the UB, thus indicating potential zooplankton grazing in this station. These results are in agreement with Torres et al. (2009).

Mesozooplankton seasonal and spatial distribution

Mesozooplankton community pattern of the UB indicated a strong seasonal influence showing lower abundance and diversity during cold seasons and the inverse pattern in warm seasons. In the cold season, low temperatures, coupled with decreasing daylight hours, would produce a reduction in primary production. As a consequence, the mesozooplankton abundance and diversity may diminish. Inversely, high values of temperature, light and nutrient availability were the favourable conditions for the development of phytoplankton and macroalgae causing an increase in mesozooplankton abundance and production during the warm season in the UB. In agreement with our work, seasonal studies performed in different coastal areas found the same relationship between the increase of temperature and chlorophyll *a* and the subsequent increase of mesozooplankton abundance (Vieira et al. 2003; Mafalda et al. 2007).

The spatial MDS plot evidenced two groups of stations, one associated with water coming from the urban zone and the other with water related to the Beagle Channel. These groups could be differentiated by changes in the composition and contributions of the dominant species, which were associated with changes on environmental variables.

In the cold seasons, copepods like *C. citer*, *C. brevipes*, *D. forcipatus* and *O. similis*, typical species of subantarctic areas (Mazzocchi and Ianora 1991), were dominant. Also, the crab larvae *M. gregaria* contributed to the total abundance of mesozooplankton and was only found in late winter. This genus is commonly recorded during winter in this bay (Lovrich 1999). The copepod *C. citer* and the crab larvae *M. gregaria* would be adapted to conditions of low temperatures and relatively high salinities as those registered during late winter at coastal stations of the bay. In late autumn, *C. brevipes* and *O. similis* became more abundant and were mostly found in stations connected with the Beagle Channel.

A. tonsa and *P. leuckarti* were mainly found during the warm months being the dominant taxa in late summer and late spring, respectively. *O. similis* was also observed in low abundance during the warm season, together with *A. tonsa* and *P. leuckarti*. Increasing temperature along with high availability of food may favour the development of these species in agreement with previous findings (Uye and Fleminger 1976; Onbé et al. 1996; Berasategui et al. 2009, 2012). *E. americana* was observed during cold and warm months and was particularly associated with water coming from the urban zone (stations 1 and 2). *A. tonsa* and *E. americana* are copepod species typically associated with disturbed coastal areas (Avent 1998; Hoffmeyer et al. 2004; Biancalana and Torres 2011; Biancalana et al. 2012a, b; Dutto et al. 2012). In our study, both species were the dominant copepods at the coastal stations in the bay.

The Harpacticidae family, *H. pacificus*, *Obelia* sp. and *Atylus* sp. contributed most to the total mesozooplankton abundance during the warm season and were mostly observed in the coastal stations associated with urban perturbation. These groups, particularly harpacticoid copepods and amphipods, were found in close association with dense kelps dominated by *Macrocystis pirifera* during spring and summer (Adami and Gordillo 1999;

Biancalana and Torres 2011). The warm season's environmental conditions together with nutrient input are favourable to the development of *Macrocystis* forests in the coastal areas of southern California, Argentina and Chile (Hernandez-Carmona et al. 2001; Kühnemann 1970; Santelices and Ojeda 1984). It is known that *Macrocystis*, like other macroalgae, serves as substratum for a great number of organisms belonging to adventitious plankton (Adami and Gordillo 1999). This could be an explanation of the increase of mesozooplankton diversity despite the decrease in the mesozooplankton abundance in the coastal area of the UB.

Mesozooplankton response to environmental changes and anthropogenic perturbation

Zooplankton abundance and diversity distribution are directly and indirectly influenced by natural environmental variables and by anthropogenic perturbation (e.g. urban waste) (Albania et al. 2009; Li et al. 2006; Zervoudaki et al. 2009). Pollution and eutrophication processes, widely documented in the UB (Amin et al. 2010; Duarte et al. 2011; Gil et al. 2011; Torres et al. 2009), contributed indirectly to modulate the spatial distribution patterns of the mesozooplankton community in the bay.

In our study, stations 1 and 2 were the coastal stations mostly associated with the anthropogenic influence. These stations were located towards the west of the UB, which was the zone that showed the highest urban-type pollution. It was characterized by environmental conditions typically related to a certain degree of eutrophication, such as a high concentration of nutrients, high organic matter content and low salinities due to the confluence of sewage and freshwater contributions from the Encerrada Bay (Gil et al. 2011; Torres et al. 2009).

Nutrients, chlorophyll *a* and phaeopigments coming from the Encerrada Bay were found within the range of values for eutrophicated coastal environments (Kontas et al. 2004; Saunders et al. 2007). This is supported by the correlation of stations 1 and 2 with the first axis (CCA), positively correlated with chlorophyll *a*, nutrients, especially phosphate, and temperature during the warm season. Chlorophyll *a* and temperature were also negatively correlated with nitrogenated nutrients (N+N) in both seasons, thus indicating an increase in phytoplankton and macroalgae growth as a result of nutrient utilization. These favourable conditions may enhance the development of different mesozooplankton assemblages determined by stations 1 and 2 (groups I and III in late spring and group III in late summer), which were constituted by *E. americana* followed by Nematoda (late spring) and *A. tonsa* and *P. leuckarti* (late summer). It is noticed that *E. americana* was observed constituting the mesozooplankton assemblage of this zone (group I in late winter and late spring, group III in late summer and group IV in late autumn) in all the seasons.

Unlike in the other seasons, during late spring, a negative correlation between nitrogenated nutrients and ammonium was found, supporting the correlation of stations 1 and 2 with the first axis. This different trend could be explained by the variation in nitrogenated nutrients. Whereas the pattern of N+N concentration was constant along the study period, the ammonium concentration was consistently low in late spring, showing a marked variation in the other seasons, likely associated with the thawing period that produces the dilution of sewage (Torres et al. 2009).

A. tonsa, *O. similis* and *P. leuckarti* were found in the coastal stations located near the port of the UB, which is the area mostly subjected to urban pollution. Similar results were observed in the mesozooplankton community of two differently polluted areas in Saronikos Gulf in Greece (Siokou-Frangou et al. 1995). These authors found that the more polluted and eutrophic area was characterized by the dominance of few opportunistic species, great variations in zooplankton abundance and low diversity values. Similar patterns have been observed in the Gulf of Thessaloniki (Siokou-Frangou and Papathanassiou 1991), where high zooplankton abundances and low diversities typical of a disturbed zooplankton community were found. In addition, opportunistic copepods species belonging to the *Acartia*, *Podon* and *Oithona* genera were found at this eutrophicated gulf (Siokou-Frangou and Papathanassiou 1991).

Increases in temperature, photoperiod and radiation and decreases in salinity can favour the occurrence of both *A. tonsa* and *P. leuckarti* (Rosenberg and Palma 2003; Hoffmeyer et al. 2008). In particular, the coexistence of *E. americana*, *A. tonsa* and *P. leuckarti* at the coastal stations of the UB can be explained by differences in their feeding behaviors (Biancalana and Torres 2011), and their occurrence has been widely associated with polluted areas (Albania et al. 2009; Siokou-Frangou and Papathanassiou 1991; Siokou-Frangou et al. 1998; Uriarte and Villate 2004). Furthermore, *A. tonsa* has been proposed to be a reliable bioindicator of eutrophication (Bianchi et al. 2003).

E. americana and Nematoda were particularly observed in the northwest coast of the bay, suggesting that these taxa found appropriate environmental conditions for their development in this disturbed zone. *E. americana* is a well-adapted species to low temperatures and intermediate salinities (Sage and Herman 1772; Avent 1998), both of which are environmental conditions that prevail during the cold season in the UB. Nematoda was only detected at station 2 during late spring and contributed the most to the mesozooplankton abundance of the bay. Nematoda is known to be less sensitive to hypoxic or even anoxic conditions than copepods (Chen et al. 1999). Indeed, it was found in high densities near the Beagle Channel, associated with high concentrations of organic matter and detritus deposited in fine sediments (Chen et al. 1999). Additionally, fine sediment with high organic matter content (7.8 to 18.9 %) constituted the typical sediment of the Encerrada Bay (Torres et al. 2009). This may explain the occurrence of Nematoda in this disturbed bay.

The influence of freshwater input due to the proximity of the Grande Stream and Olivia River was observed towards the east of the UB, especially at station 8 in late spring and stations 9 and 15 in late summer, where a noticeable decrease in salinity and a high contribution of silicate were shown, corroborated by the strong negative correlation (CCA) between them. Stations 8 and 9, located near the Grande Stream, are influenced by industrial and urban inputs. Station 15, located in the west zone of the UB, constituted with station 9 a mesozooplankton assemblage (group II in late summer) and showed the same association with salinity and silicate, indicating that the mesozooplankton assemblage found was adapted to these environmental conditions. With the exception of station 15, stations 8 and 9 consistently showed low mesozooplankton abundances. The negative associations found between salinity and nutrients (mainly silicate) correlated with low mesozooplankton abundances, probably as a consequence of sewage and river runoff contributions. The same pattern, low mesozooplankton abundance associated with decreases in salinity and increases in nutrients, was shown in the Bilbao and Urdaibai estuaries (one with high pollution and the other with low pollution, respectively) in the Biscay Bay and was linked to the discharge of effluents, being the main source of coastal pollution (Uriarte and Villate 2004). Salinity is an indicator of different water masses closely related to the distribution of zooplankton (Marques et al. 2009). In our study, salinity seemed to be a significant factor in explaining the dynamics of the mesozooplankton, especially the spatial one.

The principal taxa that constituted the assemblages in the east coastal zone of the UB during the warm season were *Obelia* sp., the Harpacticidae family and the copepod *H. pacificus*. As we mentioned before, both the Harpacticidae family and *H. pacificus* were associated with *Macrocystis pyrifera* prairies (Pallares and Hall 1974; Webb and Parsons 1992). It is known that the typical environmental conditions during the warm season produce the growth of macroalgae forests (Kühnemann 1970), creating a greater availability of suitable microhabitats for the development of many taxa like harpacticoid copepods and amphipods. *A. tonsa* and *P. leuckati* were also observed constituting the mesozooplankton assemblage in the east stations of the UB during late spring and late summer, respectively. As we mentioned before, those species are likely to be adapted to disturbed areas.

According to a previous study (Gil et al. 2011), the stations closely related to the Beagle Channel showed less perturbed environmental characteristics than the stations located on the coast of the UB. The differences in terms of composition and mesozooplankton abundance between the disturbed coastal zone and the open sea could be due to variations in the environmental quality of the water column. In the open sea-related zone, associated with clean and cold waters coming from the Beagle Channel, the copepods *C. citer*, *C. brevipes* and *D. forcipatus* were found.

As it is well known, water circulation has a strong influence in the distribution and composition of zooplankton and this is especially detectable on coastal areas (Siokou-Frangou et al. 1995, 1998), where there is an exchange of water masses from deeper open sea areas towards shallower coastal ones and vice versa (Siokou-Frangou et al. 1998). Within the UB, there is a permanent and strong counterclockwise current displacement from the deeper area, which is close to the Beagle Channel, to the east, progressing with variable speeds ranging from 2.5 cm s^{-1} on the north coast to 5.5 and 16.3 cm s^{-1} in the centre and on the south coast (Balestrini et al. 1990). Water circulation appears to have an important influence on the observed pattern distribution of the mesozooplankton in the UB. As a consequence of the possible influence of the water circulation, species like *C. citer* and *C. brevipes*, which are closely associated with Beagle Channel waters, were found in low abundances in coastal assemblages during late autumn and late winter. Conversely, *A. tonsa* and *E. americana*, species highly related to coastal habitats, were also found in assemblages associated with the Beagle Channel.

Conclusions

This study showed variations in the mesozooplankton pattern distribution due to environmental factors associated with anthropogenic influence in a subantarctic bay. Our findings indicated that changes in the water quality by natural and anthropogenic forcings could lead to the existence of different mesozooplankton assemblages. A community dominated by the copepods *E. americana*, *A. tonsa* and Nematoda could be used as potential bioindicators of human disturbance and/or eutrophication processes, whereas a community dominated by the copepods *C. citer*, *C. brevipes* and *D. forcipatus* would indicate pollution-free waters.

Other factors different from anthropogenic derived ones such as seasonal driven changes in the plankton community and environmental variables, macroalgae prairie distribution, potential prey density patterns, wind influence and water mass circulation are also likely to contribute to the distributional pattern of the mesozooplankton community in the coastal area of the Ushuaia Bay. Further biological and environmental monitoring studies are suggested to follow the potential changes in the plankton community which may help provide ecosystem management tools.

Acknowledgments Funds were provided by FONCYT-ANPCyT (PICTR090/2002). We are grateful to (i) the staff of the Centro Austral de Investigaciones Científicas (CADIC-CONICET), (ii) the staff of the Centro Nacional Patagónico (CENPAT-CONICET) especially to Dr. M. N. Gil and Dr. J. L Esteves and (iii) to Dr. Erika Giarratano and Dr. Américo I. Torres for their collaboration and support during the sampling period. We are also grateful for the assistance of the research staff at the Deutsches Zentrum für Marine Biodiversitätsforschung, particularly the help of Dr. Grittae Veit-Köhler in determining the different harpacticoid species.

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