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Distribution of carnivorous gelatinous zooplankton in the upwelling zone off central Chile (austral spring 2001)

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The distribution of gelatinous carnivorous zooplankton off central Chile (35–37°30′S) was assessed during upwelling conditions in spring 2001 using stratified zooplankton sampling. The hydromedusa *Liriope tetraphylla* (54.2 ind. m^{-2}), siphonophore *Sphaeronectes gracilis* (16.5 ind. m^{-2}) and ctenophore *Pleurobrachia bachei* (52.1 ind. m^{-2}) were the most abundant species. A strong horizontal density gradient and the presence of low dissolved oxygen waters (<1 mL^{-1}) nearshore, characteristics of upwelling conditions in eastern boundary regions, occurred throughout the cruise. Two groups of gelatinous carnivorous zooplankton were identified associated with the density front structure: one located coastward from the front (*Sphaeronectes gracilis*, *Euphysa aurata* and *Beroe cucumis*) and another located seaward from the front (*Liriope tetraphylla*, *Pleurobrachia bachei*, *Abylopsis tetragona* and *Thalassocalyce inconstans*). The most abundant species occurred more frequently in well-oxygenated waters; however, high abundances (10–100 ind. 100 m^{-3}) were also observed in suboxic waters (<1 mL O_2 L^{-1}). A significant relationship was detected between the depth of the centroids of the most abundant species and the depths of the suboxic waters, suggesting that the depth of the suboxic seawaters determines their mean vertical distribution. The ability of gelatinous carnivorous zooplankton to withstand a wide range of oxygen concentrations seems to be an important adaptation in coastal upwelling areas because oxygen conditions vary widely, over both small time and spatial scales.

KEYWORDS: gelatinous zooplankton; suboxic waters; density front; *Liriope tetraphylla*; vertical distribution

INTRODUCTION

Carnivorous gelatinous zooplankton are some of the most important zooplankton groups in the pelagic food webs due to their great voracity and their rapid population growth that result in extensive seasonal blooms (Pagès *et al.*, 2001; Graham *et al.*, 2001; González *et al.*, 2004). Several studies describe their distribution and taxonomic variability during the high abundance seasons (Gibbons and Buecher, 2001; Thibault-Botha *et al.*, 2004; Palma and Apablaza, 2004; Sanvicente-Añorve *et al.*,

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2007). Although the association between groups of gelatinous species and water masses (Pagès *et al.*, 2001; Palma and Silva, 2006), estuarine frontal zones (Wang *et al.*, 1995) and fjords (Gorsky *et al.*, 2000; Hosia and Båmstedt, 2007) has been described, there is still limited information for some zones where limiting factors on zooplankton distribution [e.g. oxygen minimum layers (OMLs)] occur periodically.

The coastal zone off central Chile is an important upwelling area in the southernmost part of the Humboldt Current System where high primary production rates occur in the austral spring and summer (up to 10 g C m^{-2} day^{-1}, Daneri *et al.*, 2000; Montero *et al.*, 2007). The high seasonal production supports important microzooplankton, mesozooplankton and ichthyoplankton communities (Morales *et al.*, 2007; Landaeta *et al.*, 2008) that achieve high growth rates, especially in spring (Hernández and Castro, 2000). Studies in this area have examined the distribution of gelatinous predators and their potential prey (early life stages of marine fishes such as anchovy), revealing a spatial mismatch between both groups (Castro *et al.*, 2000; Castro, 2001), particularly in late winter when anchovy spawning peaks. In other areas of the Humboldt Current, such as off northern Chile, the presence of an OML ($<$1 mL L^{-1}) near surface waters during the upwelling season has been shown to affect the vertical distribution of several gelatinous taxa (Giesecke and González, 2004; Palma and Apablaza, 2004). For central Chile, however, the relationship between upwelling events and the spatial distribution of the most abundant species of gelatinous predators has yet to be assessed.

Physical processes play a key role in the aggregation and distribution of zooplankton in the ocean (Ulloa *et al.*, 2004). Temperature and salinity gradients are typical in coastal transition zones, fjords and estuarine areas where the effects of these oceanographic features on zooplankton distribution may be pronounced (Graham *et al.*, 2001). Thus, mesoscale oceanographic processes produce drastic changes in the physical and chemical properties of the water column that are reflected in similar micro- and mesoscale variations in the distribution of gelatinous taxa (Pagès and Gili, 1991; Gibbons and Buecher, 2001).

The main objective of this study was to determine the distribution patterns of gelatinous zooplankton off central Chile in spring, the season when the OML, typically assumed to be a limiting factor for the distribution of many zooplankters, starts to rise in the water column as a result of coastal upwelling. We tested the hypothesis that horizontal density gradients and the vertical distribution of oxygen concentrations in the water column generated by coastal upwelling affect the abundance and distribution of carnivorous gelatinous organisms off central Chile. The approach was, thus, to assess the vertical and horizontal distribution and abundance of the most abundant gelatinous carnivorous zooplankters and their relationship with environmental factors, particularly oxygen, in the austral spring 2001.

METHOD

Study area

The area studied was located in the southern part of the Humboldt Current System (35°0′S, 72°18′W–36°55′S, 73°40′W). In the northern half of the study area, the continental shelf is relatively narrow (∼30 km offshore) (Fig. 1). Around 36°S, the wide Itata Canyon interrupts the continental shelf. South of this canyon, the shelf widens to a maximum of 90 km offshore (Itata Terrace) until it is interrupted again by the narrow but deep Biobio Canyon at 36.9°S. Prevailing winds over the entire area in the austral spring and summer are south-westerlies and favour coastal upwelling. Winds reverse to northerlies and north-westerlies in the austral autumn and winter (Arcos and Navarro, 1986). During the austral spring–summer, cold (11°C), high salinity

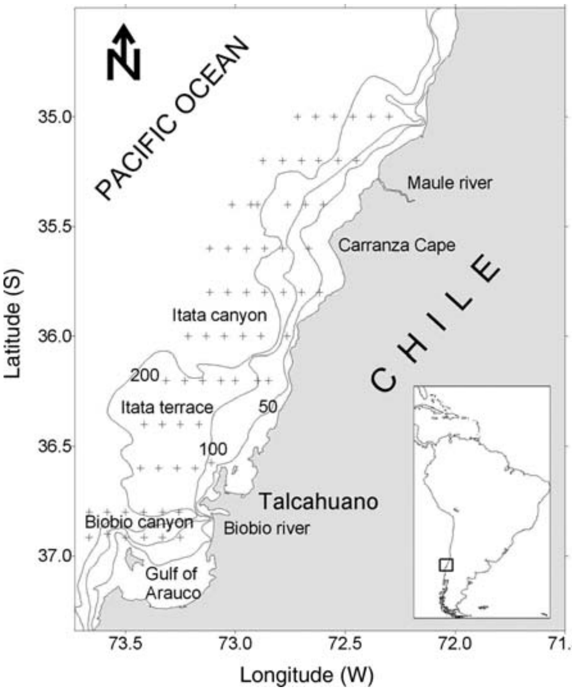

Fig. 1. The surveyed area and location of the sampling stations (dark circles), indicating the bathymetry (m).

(34.5), low oxygen (<1 mL L^{-1}) and nutrient rich Equatorial Sub-Surface Waters (ESSW) shoal over the continental shelf (Sobarzo and Djurfeldt, 2004), favouring high primary and secondary production due to the high nutrient input to the photic zone (Daneri *et al.*, 2000; Vargas *et al.*, 2007) that sustains the abundant pelagic (anchovy) and demersal (hake) fishes (Castro *et al.*, 2000; Landaeta and Castro, 2006).

Field and laboratory work

Between the 7th and 13th of November 2001, an intensive oceanographic cruise was carried out off central Chile, between 35 and 37°S, aboard the research vessel Abate Molina. The sampling grid consisted of 11 transects with six or seven stations on each, from nearshore (2 nautical miles, nmiles) up to 40 nmiles offshore. At each station, hydrographic casts were carried out from the surface to near bottom or to a maximum depth of 250 m, using a Seabird SB-19 CTD (Conductivity–Temperature–Depth profiler) equipped with an YSI Beckman oxygen sensor. Oblique tows of stratified zooplankton samples were collected with a 1 m^2 mouth Tucker trawl (300 µm mesh size) towed at 2–3 knots, equipped with a General Oceanic flowmeter mounted in the frame of the net to estimate the volume of seawater filtered. The sampled depths varied according to the distance from the coast: in nearshore areas, the sampled strata were 0–10 and 10–25 m deep; over the shelf they were 0–25, 25–50 and 50–100 m deep; and on the shelf break and seawards they were 0–50, 50–100, 100–150 and 150–250 m deep. Volume filtered ranged between 17 (in nearshore, shallow stations) and 598 m^3/tow (in the deepest and wider strata, 150–250 m, at the offshore stations). Mean volume filtered per strata in over 80% of the stations was 170 m^3/tow (standard deviation, SD = 52). The plankton samples were preserved in 4% formaldehyde buffered with borax.

In the laboratory, siphonophores, hydromedusae and ctenophores were identified using Pugh (Pugh, 1999), Bouillon (Bouillon, 1999) and Mianzan (Mianzan, 1999), respectively. In the case of siphonophores, we counted polygastric stages in Physonectidae and nectophores in Calycophorae. In the case of ctenophores, some of them were partially dissolved by the formaldehyde; these were enumerated by counting gastric bulbs. All specimens collected were counted under a Nikon stereomicroscope, in a range of fraction of 1–1/8 depending on the abundance of organisms in each sampler. The counts were standardized to individuals per m^2 for the horizontal distribution plots and to individuals per 100 m^3 for the vertical distribution diagrams.

Data analysis

Horizontal sections of seawater density (sigma-t) at 10 m depth and at the depth of low dissolved oxygen (<1 mL L^{-1}) were constructed using kriging as the interpolation method. Wind data were obtained from the meteorological station at Carriel Sur Airport (36°46′S, 73°04′W) for November 2001. These data were used to estimate the coastal upwelling index (CUI, Bakun, 1973) as: $\mathrm{CUI} = M/\rho_a * 100$, where ρ_a is seawater density in kg/m^3 and M is the Ekman transport defined by the quotient between the wind stress (τ) and the Coriolis parameter (f), $M = \tau/f$.

Stations were classified as neritic or oceanic according to their location over or beyond the continental shelf (~200 m depth isobath). To describe the spatial variability of the gelatinous community structure, a series of diversity indices were calculated for each station (Shannon–Wiener index H', Simpson index $1-\lambda$, Pielou index, J'). To compare the values of the diversity indices obtained between the neritic and oceanic stations, unpaired *t*-tests were run. Prior to the analyses, the assumption of normality and homogeneity of variance was tested using Kolmogorov–Smirnov test and Levene's test, respectively. If statistical differences were detected in the homogeneity of variances, a Mann–Whitney *U*-test was utilized.

In order to characterize the vertical distribution of the gelatinous carnivorous zooplankton in November 2001, the centre of mass of each species profile at each station (centroid, CD) was calculated for each species at each station as:

$$\mathrm{CD} = \frac{\sum(p_k x z_k)}{\sum p_k}$$

where p_k is the number of organisms in stratum k, and z_k is the mean depth of stratum k. For each species, least square linear regressions were then carried out between the centroids and the depths of the shallower limit of suboxic waters (<1 mL L^{-1}) at all stations. Also, the non-parametric statistic (Mann–Whitney *U*-test) was used to compare the distribution of the gelatinous taxa between the shelf and oceanic areas.

To identify relationships between the abundance of gelatinous zooplankton and the suite of predictors describing the environment, we used the following modelling approach. As the relationships are likely to be non-linear, we first used a generalized additive model (GAM) approach. The additive model extends the linear model by allowing the linear functions of the predictors to be replaced by smooth functions of these predictors (Agenbag *et al.*, 2003).

Table I: A summary of the parameters used in the GAM

Type	Parameter	Explanation	Units	Mean ± SD	Range (min, max)
Response	Abundance *E. aurata*	Abundance	Ind. 100 m^3	5 ± 7	0–24
	Abundance *L. tetraphylla*	Abundance	Ind. 100 m^3	23 ± 27	0–598
	Abundance *S. gracilis*	Abundance	Ind. 100 m^3	21 ± 12	0–406
	Abundance *M. atlantica*	Abundance	Ind. 100 m^3	3 ± 3	0–17
	Abundance *A. tetragona*	Abundance	Ind. 100 m^3	9 ± 10	0–149
	Abundance *P. bachei*	Abundance	Ind. 100 m^3	16 ± 13	0–349
	Abundance *B. cucumis*	Abundance	Ind. 100 m^3	5 ± 4	0–738
Predictor	Temperature		°C	10.94 ± 0.92	9.30–14.94
	Salinity		Non unit	34.44 ± 0.16	33.21–34.63
	Dissolved oxygen		mL O_2 L^{-1}	1.95 ± 1.8	0.20–9.66

The general form of the linear model is:

$$\Upsilon = \alpha + \sum \beta X_i + \varepsilon$$

and the replacement is:

$$\Upsilon = \alpha + \sum f_i X_i + \varepsilon \qquad (1)$$

where Υ is the response, X_i is the predictor, α and β are the parameters and ε error. The f_i is generally unknown and is estimated using smoothing (adjustment) based on the data dispersion (MathSoft, 2001). The preliminary form (scatterplot smoothers) enables the description of the relationship between the response variable and a predictor for each species, without imposing an a priori shape, in contrast to linear modelling where a specific functional relationship has to be defined. In this research, we used least-squared weighted smoothers (loess) to estimate these non-parametric functions. For the GAM analyses, the oceanographic data used corresponded to the values of the different variables (temperature, salinity and oxygen) at the mean depth of the stratum sampled for zooplankton (Table I).

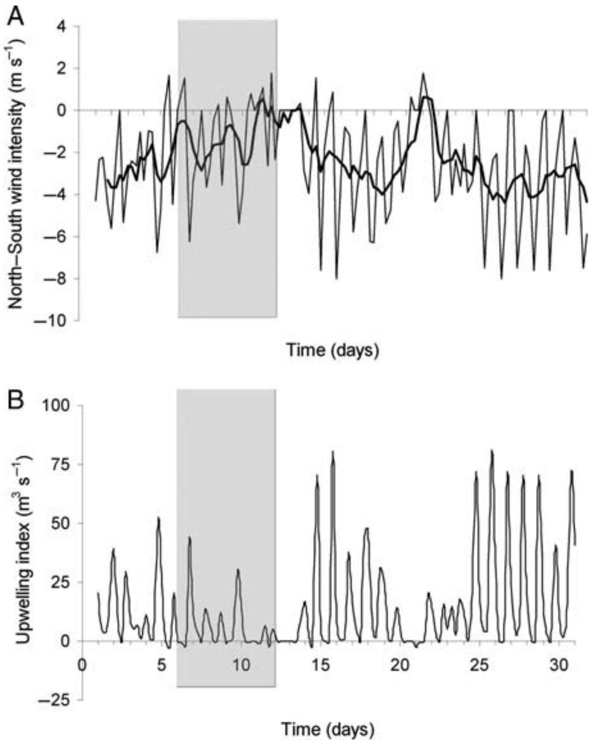

Fig. 2. (**A**) Alongshore wind intensity (m s^{-1}) and (**B**) upwelling index (CUI, m^3 s^{-1}) for November 2001 off the Talcahuano area, central Chile. Solid, bold line corresponds to a 24-h moving average. Grey bars indicate the sampling date.

RESULTS

Physical setting

Wind data showed that southerly winds dominated throughout most of November and also indicated three events of stronger winds lasting about 5–7 days each. The peak intensity of 8 m s^{-1} (Fig. 2A) occurred on the 15th of November. The wind direction and intensity led to coastal upwelling, indicated by CUI values as high as 80.8 m^3 s^{-1} per 100 m of coastline (Fig. 2B). During the cruise, although the southerly winds fluctuated in intensity every ca. 3 days, the general trend was towards a decreased intensity up to the final days of the cruise when northerly winds occurred. This change in wind direction and intensity produced a lower CUI and relaxation of the upwelling event (Fig. 2B).

The horizontal distribution of sea water density at 10 m depth (Fig. 3A) indicated the upwelling of denser (>26 units of sigma-t) parcels of water near the coastline, mainly in the north zone of the area surveyed, and the presence of a density front over the shelf break off Carranza Cape. Over most of the area surveyed, isopycnals followed the bathymetry of the shelf break (200 m) except over the Itata Terrace where strong horizontal density gradients were much closer to shore. In the centre of the Terrace and closer to the shelf break, the

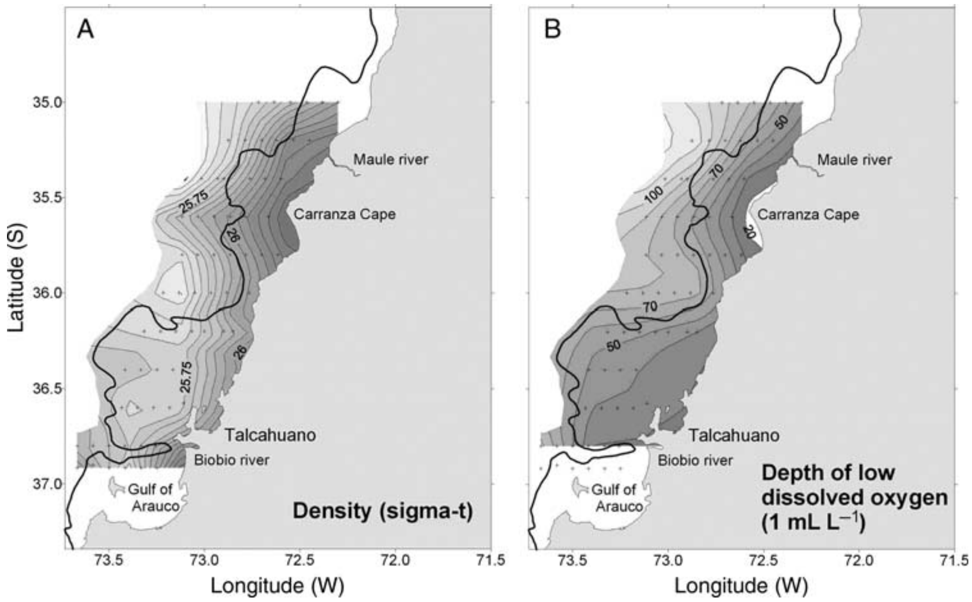

Fig. 3. Contour plots of (**A**) seawater density (sigma-t) at 10 m depth and (**B**) depth of suboxic waters (<1 mL L^{-1} dissolved oxygen) in November 2001 off central Chile. Solid bold line corresponds to the shelf break (200-m depth isobath).

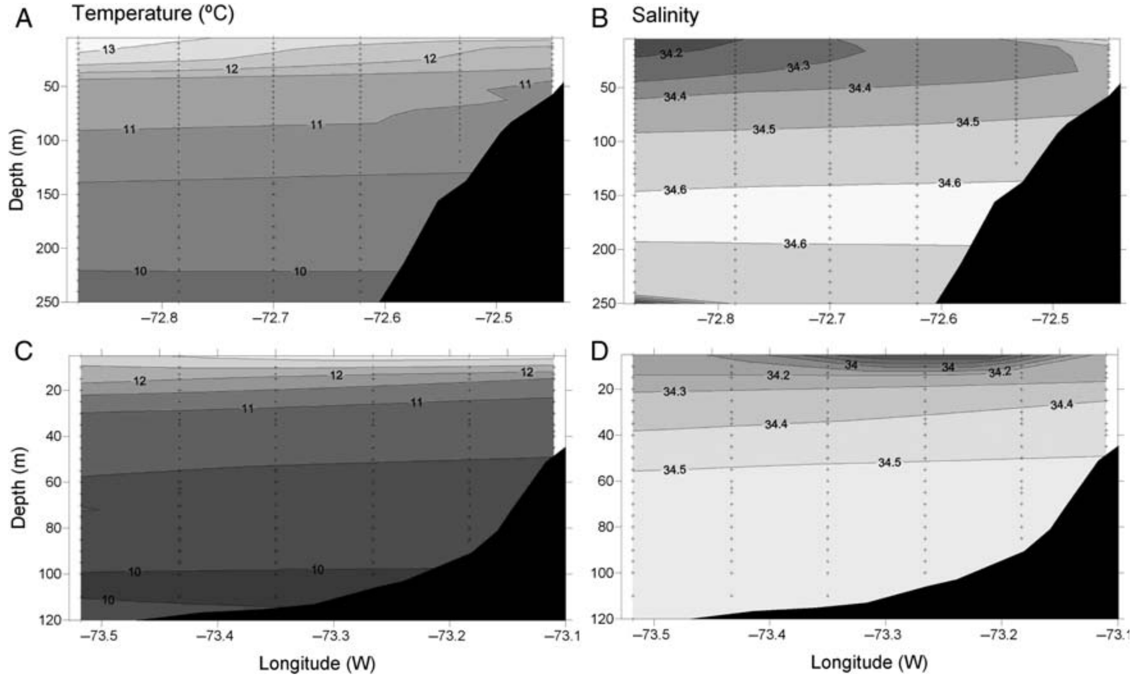

Fig. 4. Cross-shelf vertical sections of temperature (°C) and salinity off Carranza Cape (**A** and **B**, respectively) and over the Itata Terrace (**C** and **D**, respectively), carried out during 9th and 11th of November, respectively.

horizontal gradient in the density field was less pronounced (Fig. 3A). The depth of seawater with 1 mL L^{-1} of dissolved oxygen (Fig. 3B) followed the contours of the shelf break and the horizontal density field. The depth of low dissolved oxygen water was shallower in the vicinity of Carranza Cape (∼30 m deep) and within Concepcion Bay, indicating an intrusion of suboxic waters near the coast, an intrusion that in some areas over the Itata Terrace may also have extend further offshore (i.e. 20 nmiles offshore) where the suboxic (<1 mL O_2 L^{-1}) waters were at ca. 30–40 m deep. In the middle of the study area, there was a deepening of low oxygen waters over the Itata Canyon (Fig. 3B).

Vertical sections across the shelf off Carranza Cape (northern zone of the study area) and over the Itata Terrace (southern zone) are shown in Fig. 4. In the northern area, the nearshore ascent of cold (i.e. the 11°C isotherm) and saline (>34.4) waters indicates moderate coastal upwelling (Fig. 4A and B). Warmer (>13°C) and less salty (<34.2) waters were located offshore in the shallower layer. Further south, over the Itata Terrace, a well-stratified water column, a strong thermocline and a halocline were observed from the surface down to ca. 30 m depth (Fig. 4C and D), shallower than the depth of low dissolved oxygen water (<1 mL L^{-1}, Fig. 3B). A thin ($\sim$10 m thick), lower salinity water parcel was observed in the middle of the longitudinal section across the Itata Terrace (Fig. 4D), probably originating in the Biobio River.

Composition of the gelatinous zooplankton community

A total of 29 species (15 hydromedusae, 11 siphonophores and 3 ctenophores) were collected throughout the survey area. The most abundant species by taxonomic group (Table II) were *Liriope tetraphylla* and *Euphysa aurata* (hydromedusae); *Sphaeronectes gracilis*, *Abylopsis tetragona* and *Muggiaea atlantica* (Siphonophora); and *Pleurobrachia bachei* (ctenophore). The most frequent taxa were *L. tetraphylla*, *S. gracilis* and *P. bachei*, which were present at more than 95% of the total number of stations sampled ($n = 57$).

Except for the hydromedusae *Sarsia eximia* and *Eirene* sp., which did not occur in oceanic waters, and for *Bougainvillia* sp., which did not occur in the neritic area, all other species occurred in both neritic (over the continental shelf, $n = 35$ stations) and oceanic (off the continental shelf, $n = 22$ stations) zones. Seaward from the continental shelf, the most abundant and frequent species were *L. tetraphylla* (medusa, 54 ind. m^{-2} and 100%, respectively), *A. tetragona* (siphonophore, 26 ind. m^{-2} and 100%) and *P. bachei* (ctenophore, 32 ind. m^{-2} and 100%). Over the continental shelf, the most abundant species were *L. tetraphylla* ($\sim$12 ind. m^{-2}), *S. gracilis* ($\sim$17 ind. m^{-2}) and *P. bachei* ($\sim$10 ind. m^{-2}); these species were also the most frequent in this zone (94, 94, and 91%, respectively) (Table II).

Although the oceanic area exhibited a higher number of species per station, higher total abundance of individuals per station and lower dominance indices compared with the neritic stations (Table III), the differences were not statistically significant between areas (H': unpaired t-value $= -1.9$, $P = 0.063$; J': unpaired t-value $= 0.86$, $P = 0.079$; $1-\lambda$: $U = 364$, $P = 0.945$).

Distribution of gelatinous zooplankton

Different horizontal distributions were observed in the gelatinous zooplankton off central Chile (Fig. 5). In general, the three groups analysed (hydromedusae, siphonophores and ctenophores) exhibited higher abundances over and to the north of the wide Itata Canyon. Among hydromedusae, the small *Liriope tetraphylla* was more abundant (up to 604 ind. m^{-2}) to the west of the density front than over the continental shelf (less than 50 ind. m^{-2}) (Mann–Whitney U-test, $U = 174$, $P < 0.001$) (Fig. 5). Some hydromedusae were evenly distributed over and beyond (west) the shelf, such as *Euphysa aurata* ($U = 112$, $P = 0.290$) and *Rophalonema vellatum* ($U = 97$, $P = 0.382$). *Sarcia eximia* and *Eirene* sp. (not shown) were only present in neritic waters off the Itata Terrace (36°12′S). Among siphonophores, the abundant *Sphaeronectes gracilis* and less abundant *Muggiaea atlantica* were evenly distributed over the shelf and offshore (*S. gracilis*: $U = 307$, $P = 0.227$; *M. atlantica*: $U = 102$, $P = 0.499$). *Abylopsis tetragona* was significantly more abundant offshore, over the shelf break and over the Itata Canyon, and less abundant in shelf waters ($U = 90$, $P < 0.001$). Among ctenophores, the very abundant *Pleurobrachia bachei* and *Thalassocalyce inconstans* were also significantly more abundant offshore, over the shelf break and over the Itata Canyon, with lower abundances over the shelf (*P. bachei*: $U = 178$, $P = 0.002$; *T. inconstans*: $U = 26$, $P = 0.023$). *Beroe cucumis*, in turn, was evenly distributed over and beyond the shelf ($U = 239$, $P = 0.750$).

Figure 6 shows the vertical distribution of some of the most abundant species (*L. tetraphylla*, *S. gracilis*, *P. bachei* and *A. tetragona*) in transects located off Carranza Cape (northern zone) and over the Itata Terrace (southern zone). In all cases, abundances were higher and distributed over a wider inshore–offshore area and over a wider depth range (down to the maximum strata sampled, 150–250 m) in the northern zone. In the southern zone, there were fewer individuals and these were distributed deeper at the nearshore stations (down to the deepest strata sampled: 75–100 m) than at the offshore stations (only in the shallower strata sampled: 0–50 m). In the northern zone, the OML (<1 mL L^{-1}) was deeper (100–120 m) than in the southern area (35–40 m deep), and some individuals of these four species were present in this layer, although most were found in well-oxygenated waters

Table II: Mean abundance (ind. m^{-2}), standard deviation (SD), frequency of occurrence (%) and maximum density (ind. 100 m^{-3}) of gelatinous carnivorous zooplankton at all sampled stations off central Chile in November 2001

	Neritic ($N = 35$)				Oceanic ($N = 22$)			
	Mean abundance (ind. m^{-2})	SD	Frequency (%)	Max density (ind. 100 m^{-3})	Mean abundance (ind. m^{-2})	SD	Frequency (%)	Max density (ind. 100 m^{-3})
Hydromedusae								
Liriope tetraphylla	11.77	25.96	94.3	162	54.20	126.91	100.0	598
Euphysa aurata	4.81	13.25	57.1	283	1.94	3.84	63.6	24
Ectopleura dumortieri	1.27	2.65	57.1	47	1.97	3.63	50.0	23
Rhopalonema velatum	1.98	3.19	51.4	29	2.96	4.85	59.1	37
Haliscera conica	2.11	4.02	40.0	57	2.72	3.06	72.7	221
Clytia sp.	1.06	3.67	28.6	44	0.73	1.00	54.5	4
Cunina globosa	0.17	0.38	25.7	3	0.32	1.36	13.6	1
Leuckartiara octona	0.19	0.54	22.9	11	0.09	0.22	18.2	2
Solmaris sp.	0.02	0.08	5.7	1	0.15	0.28	31.8	37
Calycopsis sp.	0.01	0.07	5.7	2	0.12	0.55	4.5	5
Solmissus marshalli	0.19	0.47	20.0	7	0.29	0.86	22.7	3
Bougainvillia sp.	0.00	0.00	0.0	0	0.06	0.16	13.6	1
Pegantha clara	0.05	0.18	11.4	3	0.17	0.40	22.7	2
Sarcia eximia	0.14	0.54	8.6	7	0.00	0.00	0.0	0
Eirene sp.	0.01	0.07	2.9	2	0.00	0.00	0.0	0
Total	23.83				65.64			
Siphonophore								
Sphaeronectes gracilis	16.54	23.31	94.3	398	18.07	14.76	100.0	406
Sphaeronectes fragilis	1.44	4.20	17.1	22	3.64	4.06	68.2	24
Bassia bassensis	0.45	1.29	31.4	16	1.00	2.45	22.7	18
Lensia sp.	1.11	2.34	48.6	22	0.26	0.47	27.3	3
Agalma elegans	0.58	0.95	51.4	13	3.83	6.95	72.7	57
Muggiaea atlantica	2.15	3.97	51.4	120	1.38	2.12	59.1	17
Abylopsis tetragona	3.18	9.47	65.7	79	26.11	40.03	100.0	149
Rosacea sp.	0.65	1.40	34.3	11	1.01	1.29	63.6	7
Rhyzophysa sp.	0.04	0.18	5.7	117	0.32	0.77	22.7	26
Amphicaryon acaule	0.02	0.09	5.7	1	0.20	0.54	22.7	148
Vogtia spinosa	0.01	0.07	2.9	1	0.08	0.36	4.5	111
Total	26.16				56.03			
Ctenophore								
Pleurobrachia bachei	9.90	12.57	91.4	1183	32.61	52.13	100.0	349
Beroe cucumis	5.10	10.99	65.7	1150	4.76	3.71	100.0	738
Thalassocalyce inconstans	0.35	1.12	31.4	115	0.87	1.25	50.0	184
Total	15.02				38.22			

N, number of stations.

Table III: Mean value and diversity indices calculated for neritic (over the continental shelf) and oceanic (off the shelf) stations

	S	N	H'	J'	$1-\lambda$
Neritic stations	2–16	1–276	1.68 (0.56–2.33)	0.75 (0.50–0.95)	0.78 (0.66–0.98)
Oceanic stations	6–19	43–1026	1.85 (1.38–2.27)	0.72 (0.44–0.83)	0.79 (0.58–0.87)

S, number of species; *N*, number of specimens (individuals x m^{-2}); *H′*, Shannon–Wiener index of diversity; *J′*, Pielou index of dominance; $1-\lambda$, Simpson index of diversity.

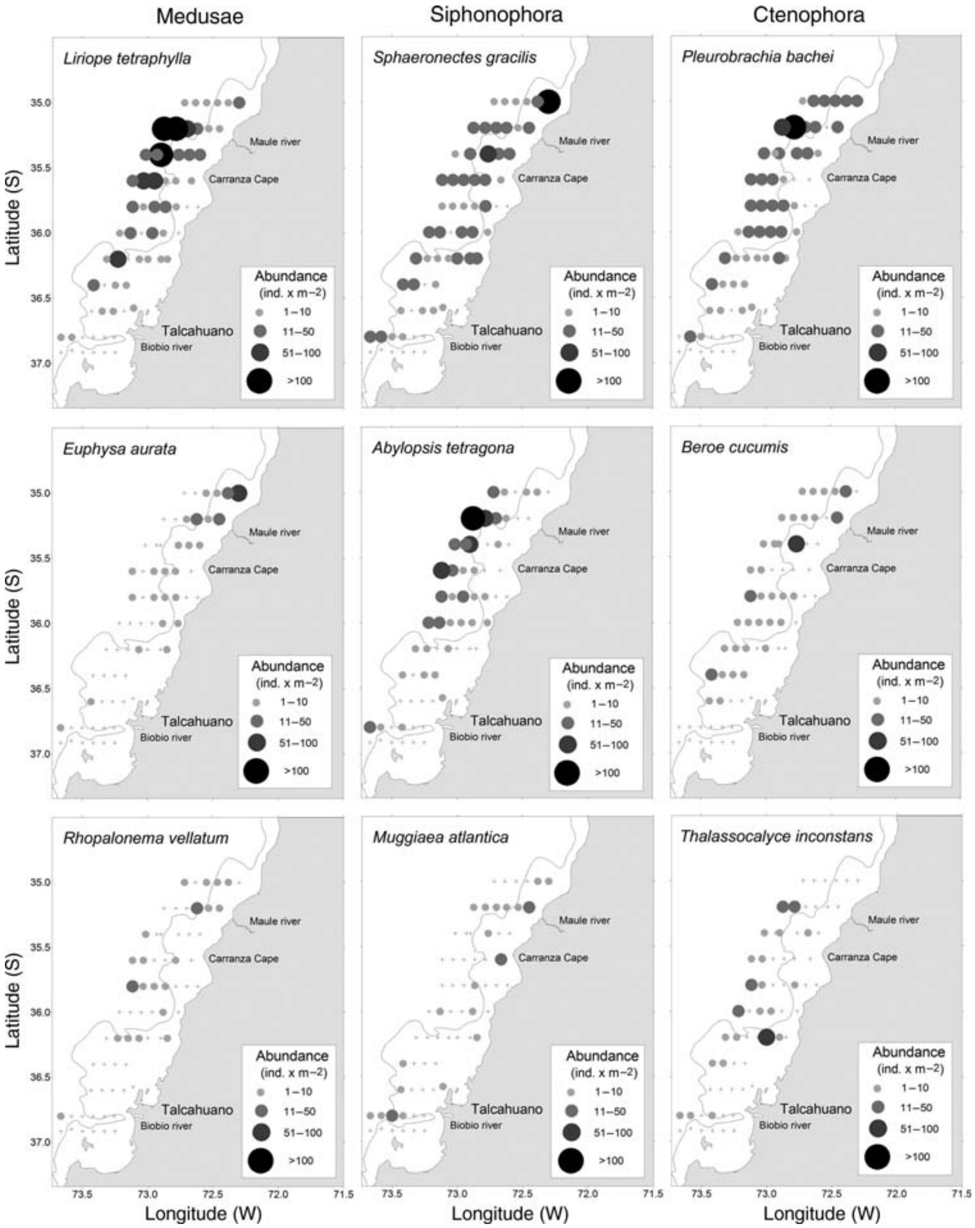

Fig. 5. Horizontal distribution of the integrated abundance (ind. m^{-2}) of gelatinous carnivorous zooplankton in November 2001.

(>1 mL L^{-1}). In the southern zone, however, the individuals of these four species were more evenly distributed in both the well-oxygenated and oxygen-depleted waters, although their abundances were much lower than in the northern area.

The relationship between the density (ind. 100 m^{-3}) of the most abundant species and oxygen concentrations in the water column indicated that, although these species were located in waters with the entire range of oxygen concentrations, in both areas, most individuals were located in well-oxygenated waters with temperatures above 10.5°C (Fig. 7). High abundances of individuals were present in both low-oxygen and oxygenated waters, both during the day and at night. Accordingly, it was not possible to detect differences in either area between day and night in terms of the type of residence water (shallow, well-oxygenated waters v/s deeper and low-oxygen waters), which could indicate potential vertical migrations between water types.

To further explore whether a relationship existed between the dissolved oxygen concentrations and the vertical distribution of the most abundant species, we

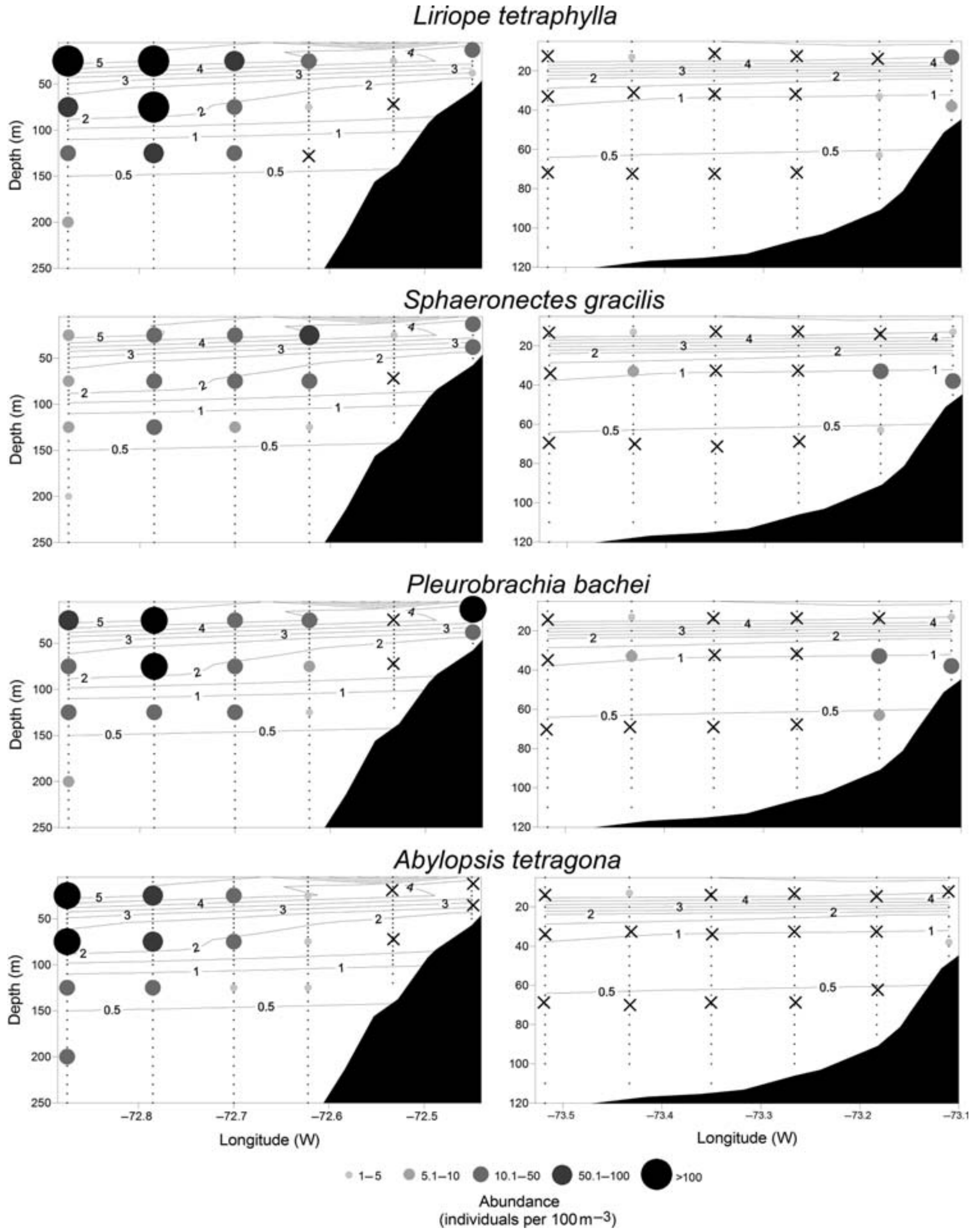

Fig. 6. Vertical distribution of gelatinous carnivorous zooplankton (ind. 100 m^{-3}) in November 2001, in relation to the vertical distribution of dissolved oxygen (mL L^{-1}) in the water column off Carranza Cape (left) and over the Itata Terrace (right).

plotted the depth of their centroids at each station (i.e. the weighted depth distribution for a given taxon at each station) and the depth of the suboxic layer (1 mL L^{-1}) throughout the entire sampled area (Fig. 8). Our results show that centroids were more frequently located at shallower depths than those of suboxic waters (circles located below the dashed line in Fig. 8). Moreover, the linear regressions showed a significant relationship between centroid depths and the depths of the suboxic waters (<1 mL L^{-1} of dissolved oxygen) for the four most abundant taxa (r^2 for *L. tetraphylla* = 0.47; *A. tetragona* = 0.4; *M. atlantica* = 0.34; *S. gracilis* = 0.3; *P. achei* = 0.25), suggesting that the depth of the suboxic seawaters might influence the mean vertical distribution of the most abundant gelatinous predators in the upwelling area off central Chile.

GAM analyses showed a relationship between the most abundant species of gelatinous predators and oceanographic variables such as temperature, salinity and dissolved oxygen (Table IV). According to the

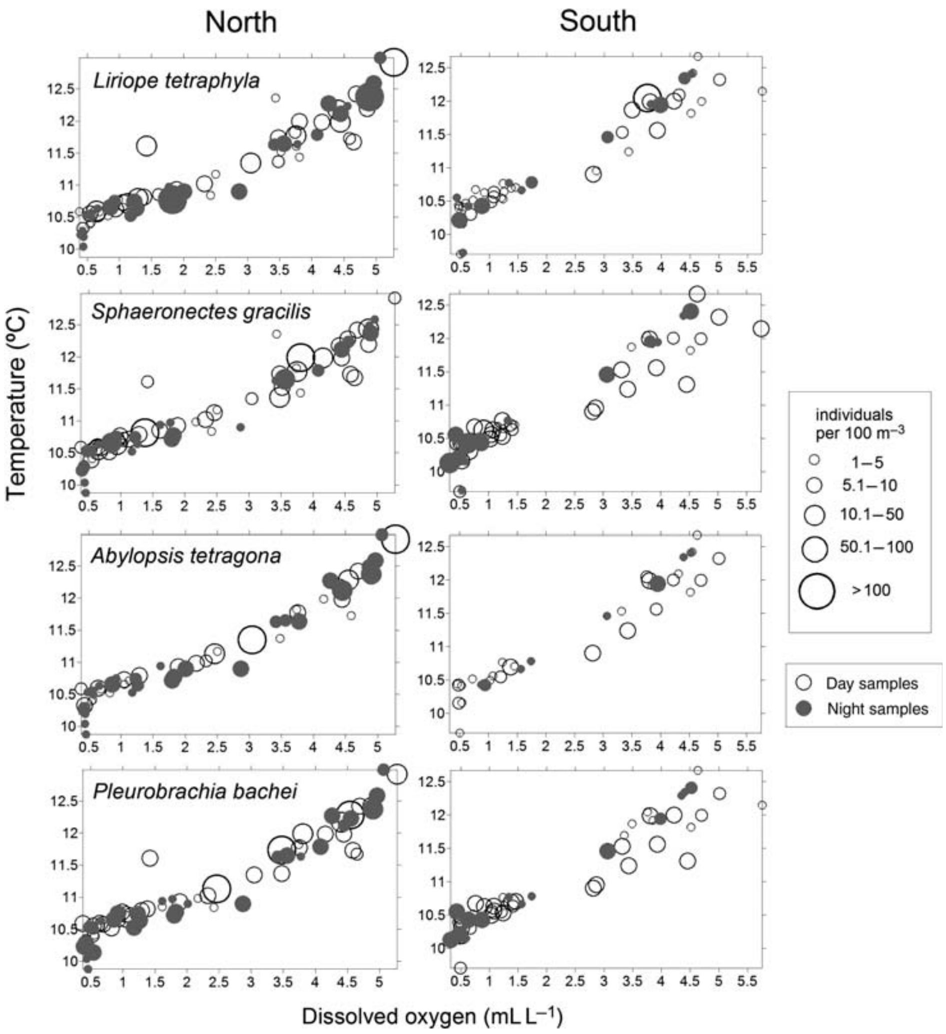

Fig. 7. Temperature and dissolved oxygen plots showing the abundance (ind. 100 m^{-3}) of different species of gelatinous carnivorous zooplankton in the northern and southern zones of the study area. White and grey circles indicate day and night sampling, respectively.

GAM results, the concentration of dissolved oxygen was not a significant factor in the abundance of most species and its effects were only significant on *M. atlantica* ($P = 0.03$). Temperature was significant in the abundance of *L. tetraphylla* ($P = 0.006$) and *A. tetragona* ($P = 0.0002$). As can be seen in Fig. 6, these species were more abundant at oceanic stations and in surface waters associated with higher temperatures in the sampling area (Fig. 4A), whereas salinity influenced the abundance of three species: *E. aurata* ($P = 0.05$), *S. gracilis* ($P = 0.0009$) and *A. tetragona* ($P = 0.01$).

In Fig. 7, the relationship between temperature and dissolved oxygen concentrations with standardized abundances of the most important species is presented. In general, the species analysed were present throughout the entire water column, regardless of the temperature or dissolved oxygen concentrations. For the northern region, abundances were higher than in the southern region, but neither condition was limiting for the distribution of these species.

DISCUSSION

Sudden changes in the abundance of gelatinous zooplankton may be due to rapid population growth (a bloom), mortality, sinking or a re-distribution of a stable population caused by oceanographic processes (Graham *et al.*, 2001). In the latter case, the presence of surface convergences such as upwelling or shelf-break fronts may accumulate zooplankton or separate different assemblages of gelatinous zooplankton (Sabatés *et al.*, 1989; Pagès and Gili, 1991; Buecher and Gibbons, 2000; Pagès *et al.*, 2001). The results presented in this

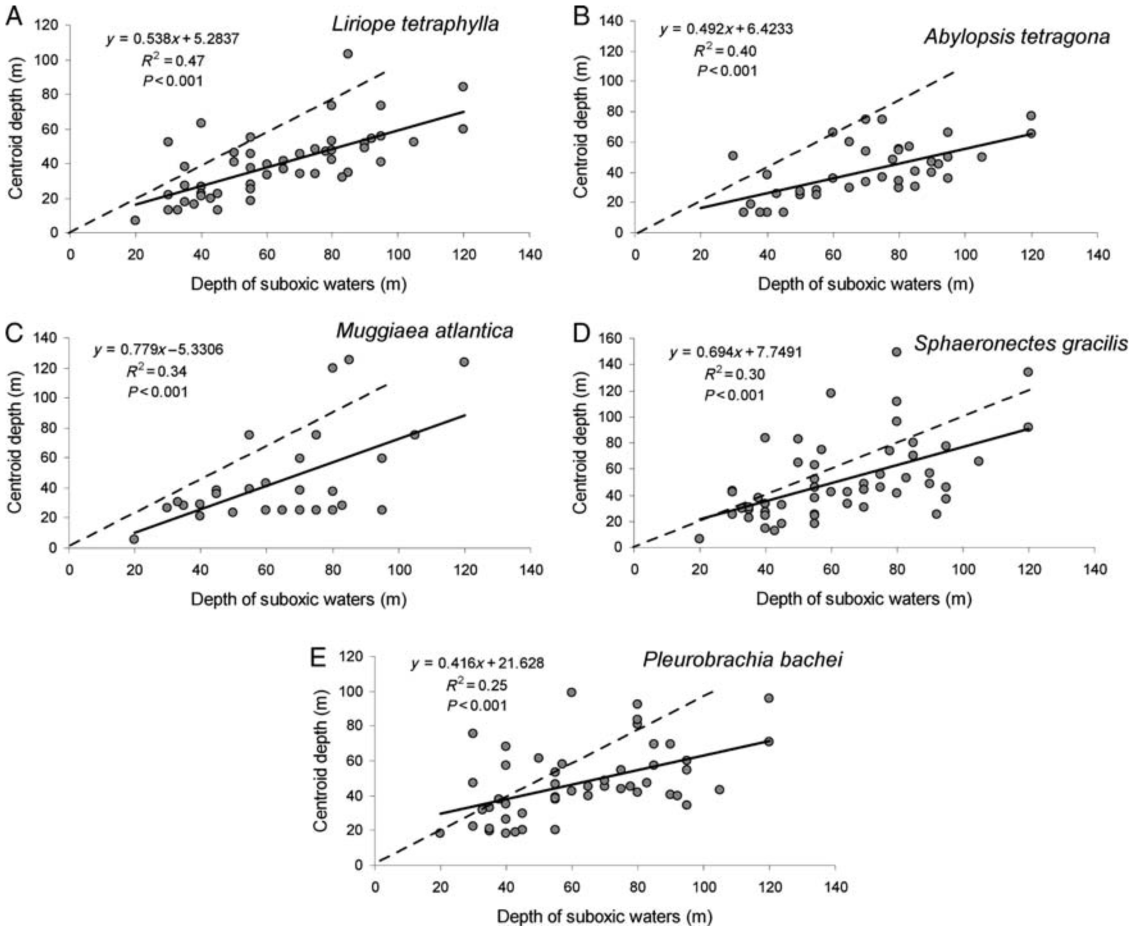

Fig. 8. Simple linear regression by least squares (black line) between centroid depth and depth of suboxic waters for (**A**) *Liriope tetraphylla*, (**B**) *Abylopsis tetragona*, (**C**) *Muggiaea atlantica*, (**D**) *Sphaeronectes gracilis* and (**E**) *Pleurobrachia bachei*. The dashed line indicates the level of equal depth.

Table IV: Generalized additive model (GAM) results for different species of gelatinous predators and oceanographic variables

	Temperature		Salinity		Dissolved oxygen	
Species	Chi-squared	*P*-value	Chi-squared	*P*-value	Chi-squared	*P*-value
Euphysa aurata	1.845	0.177	3.700	0.057	8.893	0.453
Liriope tetraphylla	7.720	0.006*	13.491	0.154	0.132	0.717
Sphaeronectes gracilis	1.762	0.187	30.535	0.001*	0.122	0.728
Muggiaea atlantica	0.161	0.689	15.319	0.094	18.647	0.036*
Abylopsis tetragona	35.536	0.000*	21.460	0.016*	0.188	0.665
Pleurobrachia bachei	1.166	0.282	10.550	0.317	0.113	0.738
Beroe cucumis	0.016	0.901	10.022	0.357	15.247	0.096

*Significant relationships (*P*-value $\leq$ 0.05).

study suggest a possible association between some taxa and the surface density front observed north of Carranza Cape (Fig. 3A). Some gelatinous taxa were more abundant on the seaward side of the front: *L. tetraphylla*, *P. bachei*, *A. tetragona* and *T. inconstans*. Others, such as *S. gracilis*, *E. aurata* and *B. cucumis*, were located in waters coastward from the front (Fig. 5). The distribution of *L. tetraphylla* and *A. tetragona* match their oceanic distributions reported in other studies in Chilean waters (Palma, 1977; Palma and Apablaza, 2004). For *L. tetraphylla*, De Souza *et al.* (de Souza *et al.*, 1996) established that swimming behaviour may be transiently affected by low salinities, which may negatively affect its presence in low salinity areas such as coastal areas near river mouths. Alternatively, other studies off the Chilean coast have regarded the ctenophore *P. bachei* as neritic, located in the first 50 m of the water column (Palma and Apablaza, 2004; Pavez *et al*., 2006) and associated with Sub-Antarctic Waters (SAAW), particularly off northern Chile (Pagès *et al*., 2001). The offshore presence of *P. bachei* in our study may have resulted from its advection from the coast in the Ekman layer during the upwelling season of spring 2001.

Other important drivers of the distribution of carnivorous gelatinous zooplankton are their life histories. While siphonophores and ctenophores are holoplanktonic, hydromedusae are mostly meroplanktonic with a polyp stage. For example, the holoplanktonic medusa of *Liriope tetraphylla* was dominant in both the neritic and oceanic zones, however the meroplanktonic hydromedusae of *Sarcia eximia*, whose hydroids are found in great abundance in coastal areas (Brinckmann-Voss, 1996), were only found at the neritic stations, where substrate for attachment was more easily found (Buecher and Gibbons, 2000).

Temperature has been identified as one of the most important factors in the distribution of gelatinous zooplankton (Gili *et al*., 1987; Palma and Rosales, 1995; Buecher and Gibbons, 2000). As is the case for the results presented here, more diverse gelatinous zooplankton assemblages have been recorded in the warmer (and lighter) waters of the Benguela upwelling ecosystem and dense aggregations of siphonophores and medusae were collected in the vicinity of a density front (Pagès and Gili, 1991). Our GAM analyses showed that the abundance of *A. tetragona* was influenced by water temperature. This species was more abundant in the surface layer at the oceanic stations (Fig. 6) where the temperatures were higher (Fig. 4), indicating SAAW displaced from the coast by the nearshore upwelling of Equatorial SubSurface Waters (ESSW). The positive relationship between this type of water and *A. tetragona* was recently described of central Chile by Palma and Silva (Palma and Silva, 2006) along a transect that covered a longitudinal gradient from South America to Easter Island in the south-central Pacific. In the northern Benguela system, Pagès and Gili (Pagès and Gili, 1991) found high abundances of these siphonophores in the density front formed by upwelling in the shallower layer (0–40 m). Therefore, the presence of upwelling events may affect the abundance, vertical and horizontal distribution of gelatinous zooplankton. For example, Gasca and Suárez (Gasca and Suárez, 1991) found that the local distribution and abundance of siphonophores were strongly influenced by upwelling, especially during the spring. Silguero and Robison (Silguero and Robison, 2000) detected changes in the vertical distribution of siphonophores (principally *Chuniphyes multidentata* and *Lensia conoidea*), coupled with the onset and cessation of upwelling events. More recently, Miglietta *et al*. (Miglietta *et al*., 2008) detected higher densities of hydromedusae during the upwelling season in the Tropical East Pacific.

Gelatinous zooplankton and dissolved oxygen concentrations

The potential relationship between the dissolved oxygen concentrations in the water column and the horizontal distribution of a number of gelatinous zooplankton species has been proposed previously (Giesecke and González, 2004; Apablaza and Palma, 2006; Escribano *et al*., 2007). However, given the high number of species these groups represent, no unique response pattern to this environmental variable has yet been identified. In other areas of the world, a similar conclusion has been reached: whereas some species seem to withstand hypoxia with relatively minor effects, for others, hypoxia tolerance ranges seem to be much narrower, leading to detrimental effects (Rutherford and Thuesen, 2005). According to Childress and Seibel (Childress and Seibel, 1998), three modes of adaptation to the oxygen minima have been proposed: (i) the development of mechanisms for the highly effective removal of oxygen from water, allowing an animal to regulate its rate of oxygen consumption down to low partial pressures; (ii) the reduction of metabolic rates so that the organism can live at lower oxygen partial pressures with a given set of uptake mechanisms; and (iii) the use of anaerobic metabolism to make up the difference between aerobic capacity and total metabolic demand. This could be on a sustained basis, during periods of increased demand due to higher activity or during transient periods spent in the OML by diel vertical migrators. For some gelatinous species, morphological characteristics seem to be important in terms of oxygen tolerance. Hydromedusae such as *Clytia* spp. and *Euphysa aurata*, for instance, have relatively narrow velar apertures that restrict seawater exchange between their subumbrellar cavities and the surrounding seawater. This morphological feature may produce a higher susceptibility to hypoxia, because these species need to expend more energy by swimming to ventilate the subumbrellar tissues at depths with low dissolved oxygen (Rutherford and Thuesen, 2005). Alternatively, many medusae are found in low-oxygen habitats ranging from the oceanic OML (Thuesen and Childress, 1994) to the “dead zone” of the Gulf of Mexico (Purcell *et al*., 2001).

In our study, species such as *S. gracilis* and *P. bachei*, which were previously reported above the OML in the well-oxygenated SAAW (Pagès *et al.*, 2001; Apablaza and Palma, 2006), were found both in oxygenated and in suboxic waters. Recent studies have demonstrated that ctenophores may survive anoxia for several hours. In fact, *P. bachei* has survival times of 2.8–6.0 h in anoxic waters and is known to reduce its oxygen consumption at very low oxygen partial pressures due to "their low metabolic oxygen demand and to the diffusion gradients that exist between the surrounding seawater, mesogleal gel and metabolically active tissues" (Thuesen *et al.*, 2005, p. 631). If this mechanism exists for *P. bachei*, then the presence of this species and others, both in well-oxygenated and in suboxic waters, should be no surprise, especially in coastal upwelling areas where oxygen conditions in the water column change abruptly.

In our study, most species occurred in both well-oxygenated and low-oxygen content waters. The overall vertical distribution of the different gelatinous zooplankton groups, however, showed that most individuals were located in well-oxygenated waters. Their maximum abundance in this type of water, along with the relationship detected between the depths of the centroids of the different species and the depths of the suboxic waters (<1 mL L^{-1} dissolved oxygen), suggest that the distribution of the gelatinous groups is not entirely independent of the environmental oxygen concentrations and also that the depth of the suboxic seawaters might determine the mean vertical distribution of the most abundant gelatinous predators in the upwelling area off central Chile. This relationship, which may have important implications for the functioning of the pelagic system in this area, had not been determined for gelatinous organisms before, probably due to the scarcity of previous stratified zooplankton sampling.

In summary, our results show that most gelatinous carnivorous zooplankton off central Chile are plastic organisms that occur in a wide range of hydrographic conditions (temperature, salinity and dissolved oxygen concentrations), although oxygen may determine their vertical distribution to some extent. The ability to tolerate fluctuating environmental conditions seems to be an important adaptation in coastal upwelling areas where variables such as oxygen concentration vary strongly, in both small spatial (meters) and time scales (hours, days), especially in spring and summer when optimal oxygen concentrations in the water column may be reduced to within only a few meters from the surface. This ability, coupled with a wide range of food items (Mills, 1995; Pagès *et al.*, 1996) and high growth and reproduction rates (Reeve and Walter, 1978; CIESM, 2001), might give these zooplankters significant advantages in a variable environment and may also explain why they could play an important role in the carbon pathway of these productive coastal areas.

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