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PRIMARY RESEARCH PAPER

Intra-seasonal variation of upwelling and its effects on copepod community structure off central/southern Chile (2002–2009)

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Abstract Copepods are major components of zooplankton in the Humboldt Current system. Here, intra-seasonal (monthly) variation of upwelling and its influence on the copepod community were assessed. Species abundances, species richness, diversity (Shannon–Wiener index) and dominance, were studied during four upwelling periods (2002–2009) at the Station 18 time series off of Concepción (36°S). Although 77 species were identified, most variability of the community structure was explained by few (<10) species. A negative trend in copepod abundance over the years was associated with lower oxygenation of the mixed layer. A generalized linear model test for relationships among community descriptors and environmental parameters (temperature, dissolved oxygen, chlorophyll, and water column stratification) revealed that diversity was positively correlated with stratification. Upwelling variation, reflected in alternate periods (active and relaxed), characterized two distinct communities during the spring–summer. The study concludes that upwelling interacts with copepod populations by changing stratification, and temperature and oxygenation gradients. The study also suggests that greatly increased upwelling may negatively impact copepods by reducing oxygenation, cooling down the mixed layer and causing more advection. The same mechanisms may be operating in other systems, and thus this study provides clues on how zooplankton communities can respond to climate-induced variation of upwelling.

Keywords Copepods · Chile · Upwelling · Intra-seasonal variation · Community structure

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Introduction

The Humboldt Current system (HCS) is one of the large marine ecosystems of the world's ocean, extending for 5000 km from near the equator to 40°–45°S in southern Chile. Wind-driven coastal upwelling off Peru and Chile drives high biological production. The HCS is subjected to distinct upwelling regimes along the Chilean coast, from year-round intermittent upwelling in northern Chile (18°–30°S) (Thomas et al., 2001) to strongly seasonal upwelling concentrated during the austral spring–summer in central/southern Chile (Sobarzo et al., 2007a). As a consequence, primary production and phytoplankton blooms exhibit irregular pulses at any time of the year in northern Chile, whereas in central/southern Chile a strong phytoplankton bloom develops at the spring, prevailing throughout the summer (Montero et al., 2007).

Pelagic copepods are the main phytoplankton grazers in central/southern Chile, and they appear abundant at any season, although they become more concentrated in the upwelling zone during the spring–summer period (Escribano et al., 2007). During this upwelling period, phytoplankton blooms are dominated by chain-forming diatoms, and copepods exhibit enhanced growth. The copepod community is comprised of a group of small-sized species (<2 mm in body length) which dominate most of the year. These include the calanoids *Paracalanus* cf. *indicus* and *Acartia tonsa*, and the cyclopoid *Oithona similis*, and also a smaller number of large-sized calanoids, such as *Calanoides patagoniensis* and *Rhincalanus nasutus* which become abundant during early spring (Castro et al., 1993; Hidalgo et al., 2010). Small copepods exhibit nearly continuous reproduction year round with many generations per year (Escribano et al., 2013), whereas larger-sized copepods have a seasonal life cycle, dominating during spring in the upwelling zone (Peterson et al., 1988; Castro et al., 1993).

During the spring–summer in central/southern Chile, the upwelling process is not regular and strong variation in upwelling intensity occurs from the synoptical to event time scales (Sobarzo et al., 2007b). Therefore, either active or relaxed phases of upwelling can be found in observations over a monthly scale. We here define this as intra-seasonal variation. Intra-seasonal variation of upwelling can substantially modify the physical and chemical conditions of the water column. Wind stress can alter water column structure, turbulence, depth of the mixed layer, and advective forces (Sobarzo et al., 2007a). Furthermore, in the coastal zone off Chile, presence of an intense oxygen minimum zone (OMZ) with oxygen-deficient water (<0.5 ml O_2 l^{-1}) (Paulmier & Ruiz-Pino, 2009) can also vary with upwelling. During the spring–summer, the upper limit of this OMZ can reach up to the photic layer (<30 m) during active upwelling, or descend below 60 m during periods of convergence (downwelling) (Morales et al., 1999). Variation in vertical mixed and advection may also strongly modify temperature and salinity gradients in the water column (Paulmier & Ruiz-Pino, 2009).

All physical and chemical alterations taking place in the water column, as forced by intra-seasonal variation of upwelling, may differentially impact copepod populations. For example, levels of tolerance to low oxygen levels are species-specific (hypoxia) (Seibel, 2011). Also, depending on size-structure, advection may differently affect spatial distribution of populations (Morales et al., 2010), and the temperature gradient may exert a direct effect on development and growth of cohorts with species-dependent responses (Escribano et al., 2013). All these effects may impact the structure of the copepod community, in terms of abundance, species composition, and size structure. Although seasonal effects of upwelling have been well described for copepod populations in this region (Castro et al., 1993; Escribano et al., 2007; Hidalgo & Escribano, 2007), there are no studies focusing on intra-seasonal variability. This information can be relevant for understanding processes structuring the plankton community in upwelling zones, and also responses of the upwelling systems to changes in upwelling regimes driven by climate forcing and global warming. In this work, based on a time series study carried out off central/southern Chile, we examine the influence of upwelling variation on copepod community structure during austral spring–summer periods and test the hypothesis that intra-seasonal variation in copepod community structure is associated with changes in the water column forced by the upwelling process.

Methods and materials

The coastal upwelling zone of central/southern Chile comprises a region of about 600 km, between 33° and 39°S off Chile where there is a continental shelf of about 50 km wide. Off Concepción (36°S), a time series study at the fixed Station 18 has continued since initiation in August 2002 (Escribano & Schneider, 2007). This station is located at 36°30.80′S, 73°7.75′W and has a depth of ca. 90 m (Fig. 1). Zooplankton samples along with oceanographic data have been obtained on a monthly basis at Station 18, most of the time with a 1 m^2 Tucker Trawl net equipped with 200 μm mesh size net. This net was deployed down to 80 m and trawled for about 20 min to obtain a water column integrated sample for the 0–80 m stratum. Samples were preserved in 10%

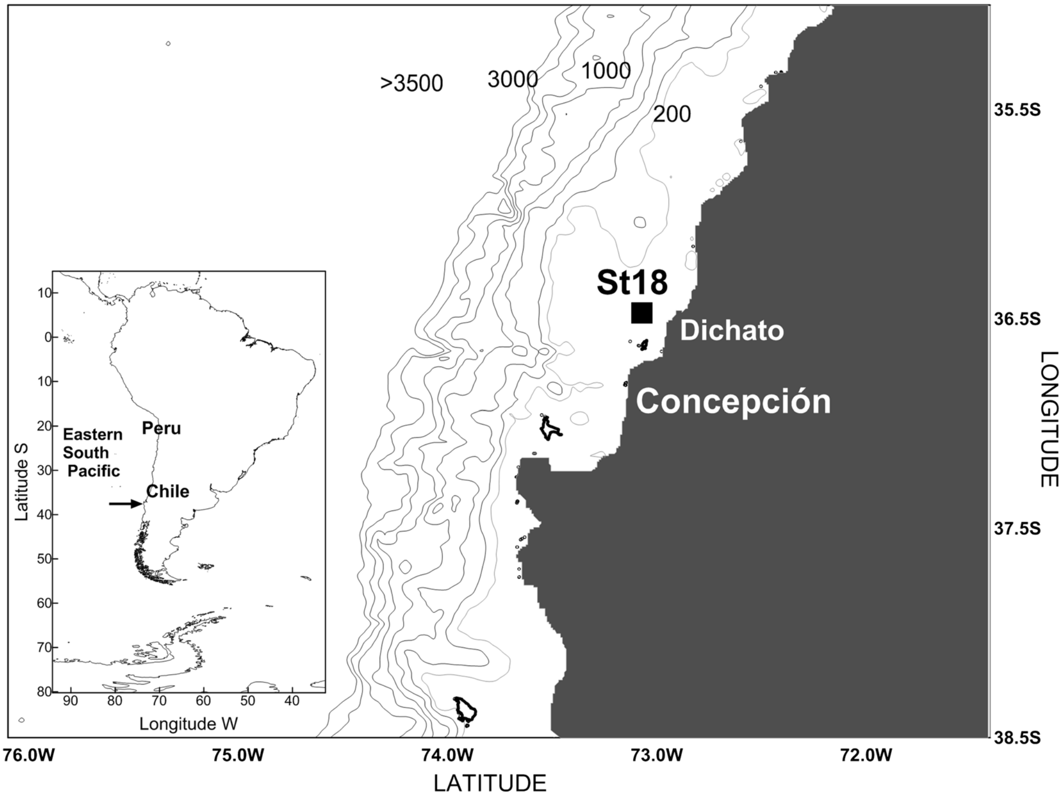

Fig. 1 The coastal upwelling zone off central/southern Chile showing location of Station 18 where the time series study of zooplankton and upwelling variability has been carried out since August 2002

formalin for later analysis. Occasionally, during rough weather conditions, a vertical 0.5 m opening diameter WP2 net was deployed down to 80 m to obtain a water column integrated sample. More details on sampling are provided in Escribano et al. (2007).

After the earthquake and tsunami that affected the central/southern region of Chile on 27 February 2010, destroying the Marine Biology Station at Dichato (Escribano & Poulet, 2010), many zooplankton samples of the time series were lost. However, some of them had been previously analyzed for copepod species and others were recovered. For this study, data and samples for complete series of spring–summer conditions (September–March) were available for the years 2002–2003, 2003–2004, 2004–2005, and 2008–2009.

Copepod species composition involved identifying all species represented by copepodite stages, usually from stage C3 to adult. Nauplii and younger stages C1 and C2 were not identified to the species level. The complete list of identified species for the region is available in Hidalgo et al. (2010).

Oceanographic conditions at Station 18 were assessed using autonomous profilers, CTD SeaBird SBE-25 or SBE-19 plus, equipped with calibrated oxygen and fluorometer sensors. Water samples for dissolved oxygen (DO) and chlorophyll-a (Chla) concentrations were obtained with a 12 Niskin bottle Rosette deployed to 80 m sampling nine discrete depths. DO was measured with a modified Winkler method and Chla with a Turner design fluorometer. More details on Chla and DO measurements are described in Morales & Anabalón (2012) and Montero et al. (2007).

Monthly data of copepod species abundance were selected for the months of September–March of the following year, thus constituting four upwelling periods: (1) 2002–2003, (2) 2003–2004, (3) 2004–2005, and (4) 2008–2009. For the second period (2003–2004), only the months of September–January were available. Then for each month, we calculated the community descriptors, species richness, abundance, diversity and dominance indices with PrimerV.6.0 program.

Oceanographic variability was assessed in terms of temperature, salinity, water density, DO and Chla. Other derived oceanographic parameters were depth of the mixed layer (Z_{mix}), estimated from the density gradient, and mean temperature of the mixed layer (T_{mix}). Also, a stratification index was estimated as the potential energy anomaly (*PEA*) described by Bowden (1983), such that

$$\Phi = \frac{1}{H} \int_{-H}^{0} (\rho m - \rho) g z \mathrm{d}z,$$

where Φ represents a stratification index, measured as J m^{-2}, H = height of water column, ρm = average density of the water column (kg m^{-3}), ρ = density of seawater (kg m^{-3}), dz = depth variation (m), and g = acceleration of gravity (m s^{-2}). The level of hypoxia was assessed by estimating depth of upper limit of the OMZ, assumed as the depth of both 1.0 and 0.5 ml O_2 l^{-1} and also by calculating mean oxygen concentration of the mixed layer ($O_{2_{mix}}$).

Generalized linear models (GLM) were applied to assess whether intra-seasonal variation in oceanographic conditions and community descriptors were statistically significant. This method also allowed us to test the effect of oceanographic variables on community descriptors. For this analysis, periods and months were considered as categorical variables and oceanographic variables along with community descriptors as continuous ones. The study covered four upwelling periods over 4 years. There were 7 monthly samples (one per month) within each series and thus four replicates (one per year) for each month. Therefore, the GLM model had two levels: period and months. GLM was applied on log-transformed variables (both oceanographic and biological) as to normalize data. Significant relationships between community descriptors and oceanographic variables were also explored and described by a linear regression model of log-normalized variables, and tested with ANOVA.

In order to assess whether intra-seasonal variation of upwelling could affect the copepod community, we applied the K-means analysis (Wilkinson, 1990) to divide all sampling months into two distinct groups: upwelling (active) versus downwelling (relaxed) conditions. K-means analysis used all oceanographic variables to generate two groups of data, such that the variance between groups was maximized and variance within groups minimized. This method also allowed us to identify which oceanographic variables characterized active versus relaxed periods of upwelling. Thereafter, a cluster analysis using the Bray–Curtis index of similarity was constructed as to explore whether these two distinct conditions were associated with different copepod communities. Principal component analysis (PCA) was used to identify which species explained the variability in community structure. PCA was applied over normalized residuals. In addition, the association of the copepod community structure with environmental variability was explored with a non-metric multidimensional scaling (NMDS). All these analyses were performed with PRIMER-V6 following procedures described by Clarke & Warwick (2001).

Results

Oceanographic conditions

Variability in water column properties was examined for each upwelling period separately, since they do not represent a time series but can be considered as independent observational periods. For each period, intra-seasonal variation can be assessed by looking at monthly profiles of oceanographic variables (Fig. 2). There was considerable variability in vertical structure of temperature. This variability affected the whole water column, but the pattern of variation changed among periods and most variability occurred in the upper mixed layer. Surface temperatures ranged between 12 and 14°C and December tended to be warmer, although the first period conditions remained colder and more mixed in all months (Fig. 2). Salinity showed a more pronounced pattern, characterized by lower surface salinity at early spring (September), related to rainy conditions and more runoff after late winter, whereas by mid- and late-summer salinity was more homogenous in the water column. Dissolved oxygen also exhibited a seasonal pattern with more oxygenated conditions at early spring and presence of low oxygen water (<1 ml O_2 l^{-1}) within the upper 50 m as the upwelling season progressed by December–February (Fig. 2). Maximum peaks of Chla reached values >10 mg m^{-3} in the mixed layer, usually concentrated by mid spring (October) and early January (January). Meanwhile, water column

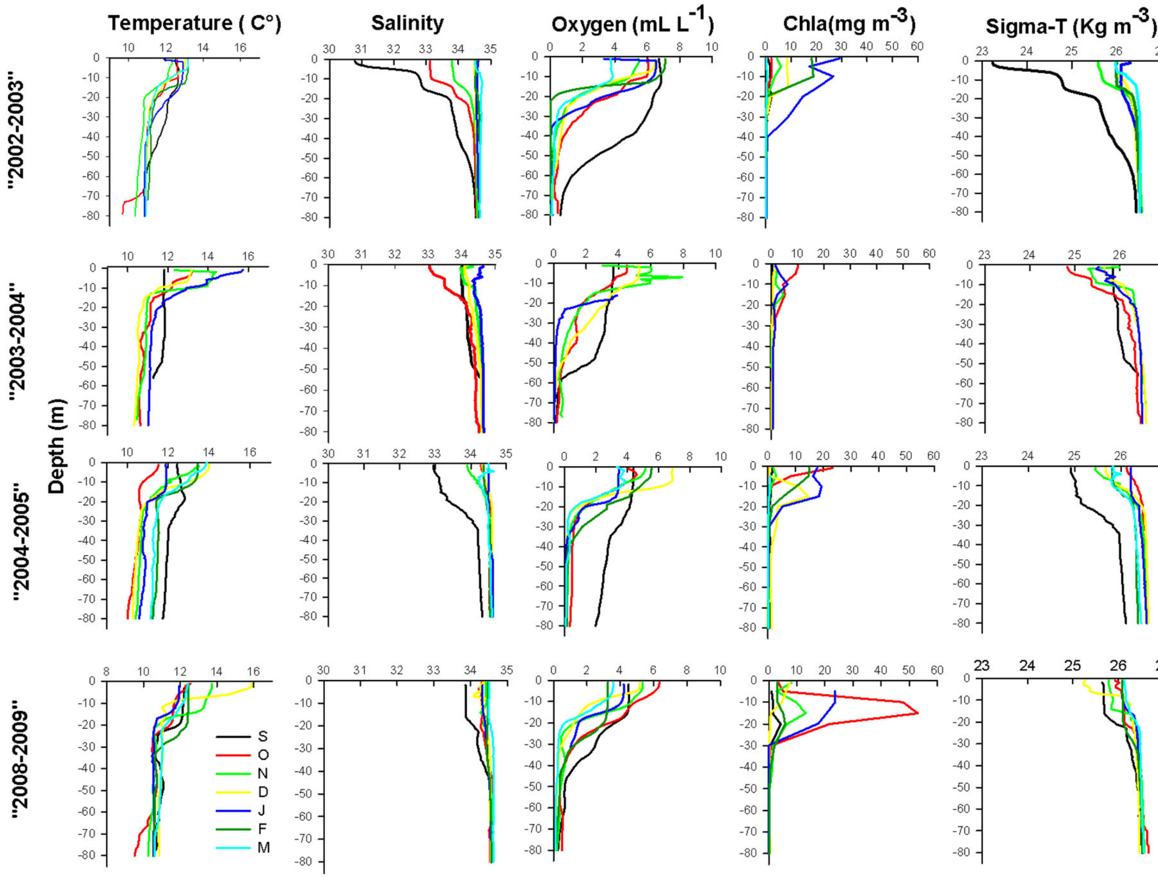

Fig. 2 Vertical profiles of oceanographic variables at Station 18 off central/southern Chile for four upwelling periods (during 2005 and 2009). Profiles represent monthly CTD casts. Each upwelling period covers the months September (*S*), October (*O*), November (*N*), December (*D*), January (*J*), February (*F*) and March (*M*)

stratification tended to decrease from a highly stratified condition in early spring (less surface salinity) to more mixing during the summer upon more upwelling, although this pattern varied among periods (Fig. 2).

Variability among seasonal periods was examined according to derived conditions from the vertical profiles (Fig. 3, with period averages over all years summarized in Table 1). Mean temperature of the mixed layer remained between 12 and 13°C and did not show any clear trend. Mean depth of the mixed layer (Z_{mix}) showed high variability, generally being deepest at the start of spring (September) and deepening in January–February before shoaling again at the end of summer (March). Nevertheless, the index of the degree of water column stratification (*PEA*) exhibited a clear decreasing trend from September–March. There was also a clear trend to shoaling of the OMZ paralleling decreased stratification of surface conditions from the first to the last period (Table 1). Likewise, oxygenation of the water column tended to diminish toward late summer. An exception to the seasonal trends in oxygenation and stratification was 2003–2004, when more oxygenated conditions prevailed during the spring–summer and there was no trend to decreased stratification, despite shoaling of the OMZ (Fig. 3).

Copepod community structure

During the study, a total of 77 species were identified and counted, of which six species accounted for more than 90% of total abundance. The dominant species was the small calanoid *Paracalanus* cf. *indicus* (>50%) having a mean abundance greater than 560 individuals m^{-3} (Table 2).

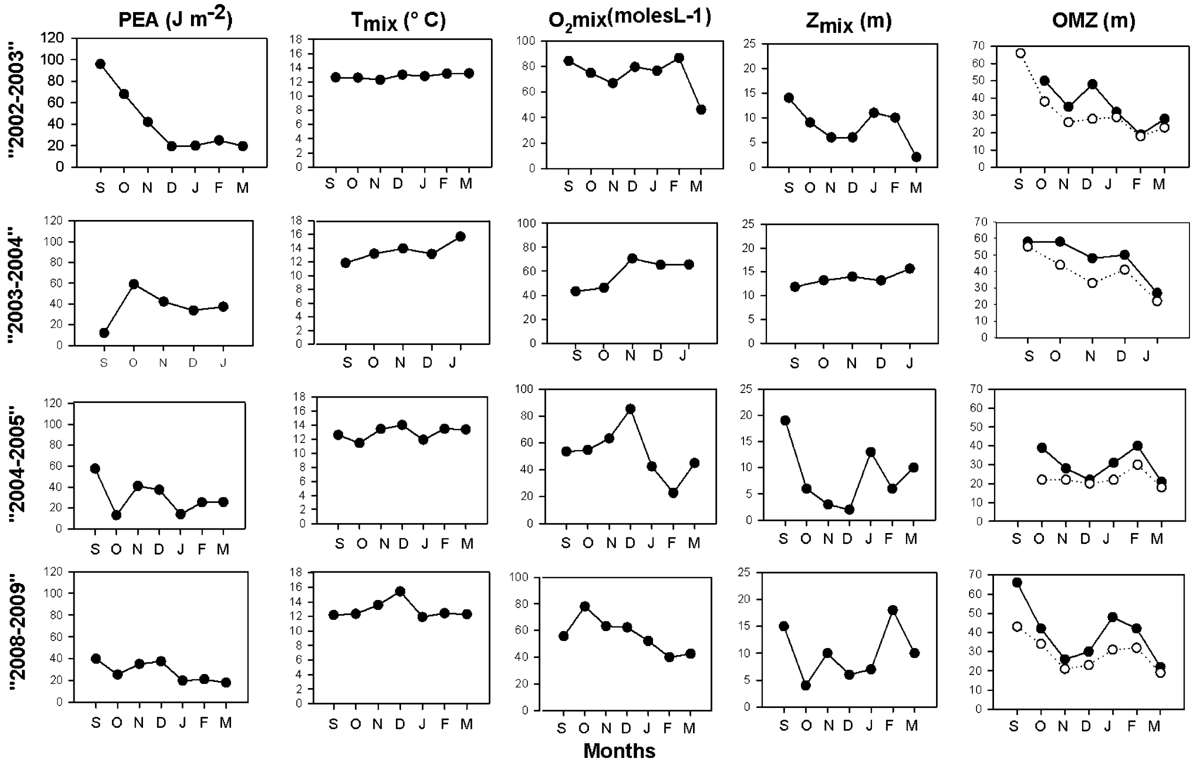

Fig. 3 Intra-seasonal variation (monthly) in water column stratification (PEA), temperature of the mixed layer (T_{mix}), oxygenation of the mixed layer ($O_{2_{mix}}$), depth of the mixed layer (Z_{mix}) and depth of the oxygen minimum zone (OMZ) during four upwelling periods at Station 18 off Concepción, Chile during the time series study 2002–2009. *Filled circles* and *open circles* for OMZ represent depth of the OMZ at 1 ml O_2 l^{-1} and 0.5 ml O_2 l^{-1}, respectively

Table 1 Monthly means (±SD) of oceanographic conditions at Station 18 off Concepción, Chile for the upwelling period (spring–summer) during four different years (2002, 2003, 2004 and 2009)

Months	Z_{mix}(m)	OMZ (m)	T_{mix} (°C)	$O_{2_{mix}}$ (moles m^{-3})	O_2 (ml l^{-1})	PEA (J m^{-2})	Chl *a* (mg m^{-3})
September	19.5 ± 7.3	46.5 ± 18.8	12.3 ± 0.4	59.2 ± 17.6	5.0 ± 1.7	51.3 ± 35.1	1.4 ± 0.3
October	5.2 ± 3.0	34.5 ± 9.3	12.4 ± 0.7	63.5 ± 15.5	5.3 ± 0.9	41.3 ± 26.2	6.3 ± 3.1
November	7.0 ± 3.2	25.5 ± 5.5	13.3 ± 0.7	66.0 ± 3.5	5.3 ± 0.4	40.01 ± 3.3	3.6 ± 1.8
December	4.3 ± 2.1	28.0 ± 9.3	13.9 ± 1.1	73.2 ± 11.1	5.9 ± 0.9	32.0 ± 8.6	4.1 ± 3.8
January	12.6 ± 0.3	26.0 ± 4.7	13.1 ± 1.8	59.2 ± 13.0	4.7 ± 1.3	22.8 ± 10.1	15.1 ± 8.5
February	11.3 ± 6.1	26.7 ± 7.6	13.0 ± 0.5	49.8 ± 33.1	5.3 ± 1.9	23.8 ± 2.2	8.9 ± 5.8
March	7.3 ± 4.6	20.0 ± 2.7	12.0 ± 0.5	44.6 ± 1.9	3.6 ± 0.1	21.1 ± 3.4	1.9 ± 2.2

Z_{mix} depth of the mixed layer, *OMZ* depth of the oxygen minimum zone (1 ml O_2 l^{-1}), T_{mix} mean temperature of the mixed layer, O_{2mix} mean oxygen of the mixed layer, O_2 mean surface oxygen, *PEA* water column stratification, *Chla* mean surface concentration

Community descriptors (such as) total abundance (*N*), species richness (*R*), Shannon–Wiener diversity (HS), and dominance (*J*) showed substantial variability both within and between years (Fig. 4; Table 3). Through months *N* showed important changes, usually with lower values in early spring compared to late spring or summer, but then either increasing or decreasing through the upwelling season. *R*, *HS*, and *J* did not show important changes or trends among periods, and intra-seasonal variation was also unclear (Fig. 4).

Table 2 Dominant copepod species in the coastal upwelling zone off central/southern Chile as found during upwelling periods at Station 18 off Concepción, during 2002–2009

Species	*N* (Ind. m^{-3})	Relative abundance (%)
Paracalanus cf. *indicus*	568.8 ± 845.34	52.8
Calanoides patagoniensis	208.1 ± 560.46	19.3
Oithona similis	161.2 ± 173.07	15.0
Acartia tonsa	41.6 ± 103.20	3.9
Drepanopus forcipatus	20.6 ± 55.26	1.9
Oithona setigera	10.8 ± 27.49	1.0

These species were present with at least 1% of relative abundance from the entire copepod community. Abundance was estimated from monthly sampling in the 0–80 m layer. Mean abundances (*N*) ± SD are shown. Relative abundances are from all data combined

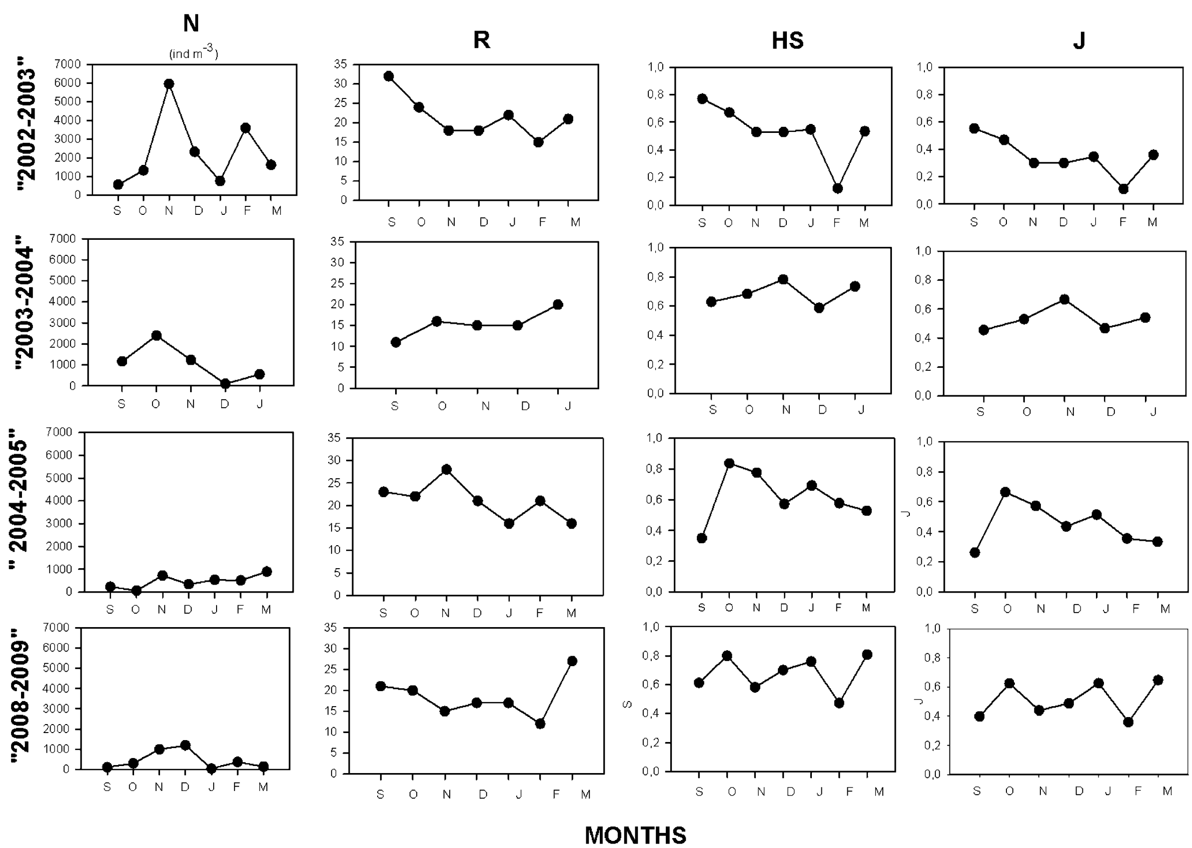

Fig. 4 Intra-seasonal variation (monthly) in abundance (*N*), species richness (*R*), species diversity (HS) and dominance (*J*) of the copepod community at Station 18 off Concepción, Chile during four upwelling periods at Station 18 off Concepción during the time series study 2002–2009

Environmental influences on copepod community structure

Because of the strong intra-seasonal changes in depth of the mixed layer (Z_{mix}) and depth of the upper boundary of the oxygen minimum zone (OMZ), it was thought that copepod abundance (*N*) and species richness (*R*) could be affected by such oceanographic variability. Changes in these descriptors associated with Z_{mix} and OMZ are illustrated in Fig. 5. When

Table 3 Monthly means (±SD) of descriptors for copepod communities from the coastal upwelling zone off central/southern Chile, estimated for four upwelling periods (spring–summer) at Station 18 off Concepción, during 2002–2009

Months	N (Ind. m^{-3})	R	J	HS
September	512.2 ± 472.3	21.8 ± 8.6	0.4 ± 0.1	0.6 ± 0.2
October	1018.7 ± 1064.7	20.5 ± 3.4	0.6 ± 0.1	0.8 ± 0.1
November	2228.2 ± 2496.1	19.0 ± 6.2	0.5 ± 0.2	0.7 ± 0.1
December	987.1 ± 1001.8	17.8 ± 2.5	0.6 ± 0.1	0.6 ± 0.1
January	469.3 ± 300.0	18.8 ± 2.8	0.5 ± 0.1	0.7 ± 0.1
February	1492.1 ± 1824.0	16.0 ± 4.6	0.3 ± 0.1	0.4 ± 0.2
March	881.9 ± 736.2	21.3 ± 5.5	0.4 ± 0.0	0.6 ± 0.2

N numerical abundance, *R* species richness, *J* dominance index from Pielou index and *HS* Shannon–Wiener index

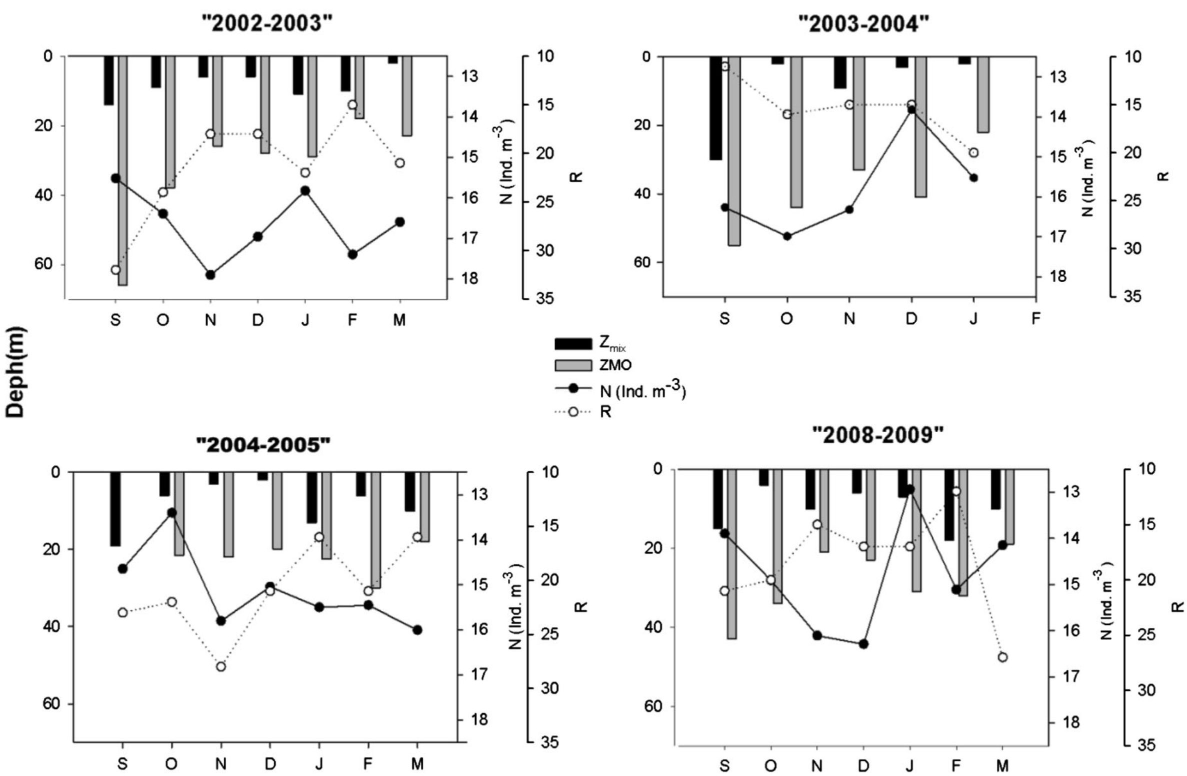

Fig. 5 Monthly fluctuations in abundance (N) and species richness (R) of the copepod community along with depth of the mixed layer (Z_{mix}) and depth of the oxygen minimum zone (OMZ) during four upwelling periods at Station 18 off Concepción, Chile during the time series study 2002–2009

Z_{mix} and OMZ deepened or shoaled the responses in N and R varied in irregular patterns. It seemed that deeper Z_{mix} and OMZ favored higher values of N and R and this is the most frequent response, although it did not occur in all situations (Fig. 5).

All derived oceanographic indices and community descriptors were tested for upwelling period and monthly effects by the GLM model. Significant period and month effects were found in some oceanographic conditions and only in the community descriptor

Table 4 General linear model (GLM) applied to oceanographic conditions and copepod community descriptors in the coastal upwelling zone off central/southern Chile estimated for four upwelling periods at Station 18 off Concepción, during 2002–2009 as to test the effect of upwelling period and sampled month

Dependent variable	Effect	DF	*F*	*P*
O_2	Period	1, 24	7.163	0.013**
O_{2mix}	Period	1, 24	5.161	0.032**
	Month	1, 24	4.953	0.036**
PEA	Month	1, 24	4.781	0.039**
Salinity	Month	1, 24	4.336	0.048**
Chl *a*	Month	1, 24	7.513	0.011**
N	Period	1, 24	13.850	0.001***
R	*PEA*	1, 24	6.389	0.018**

Only significant effects are shown. Oceanographic and copepod variables were log-normalized prior to GLM application

O_2 mean surface oxygen, O_{2mix} mean oxygen of the mixed layer, *PEA* water column stratification, *Chla* mean surface concentration of chlorophyll-a, *N* copepod abundance, *R* species richness, *DF* degrees of freedom, *F* Fisher's statistics

** Significant effects ($P < 0.01$), *** Highly significant effects ($P < 0.001$)

N (Table 4). GLM also showed a significant effect of stratification (*PEA*) on species richness (*R*) (Table 4). To illustrate intra-seasonal (monthly) effects on oceanographic variables, these significant conditions were plotted throughout the upwelling season, so that patterns become clearer. For instance, the maximum peak of Chla is reached by mid-summer (January) (Fig. 6A). Stratification clearly and significantly decreases as upwelling progresses (Fig. 6B). Salinity increases from early spring becoming stabilized during the summer (Fig. 6C). Oxygenation of the mixed layer increases slightly from early to late spring, but then it decreased again during the summer months (Fig. 6D).

The negative trend in copepod abundance (*N*) from the first to the last period was associated with a decreased oxygenation of the mixed layer and this is clearly illustrated in Fig. 7. This was consistent with significantly decreased values of *N* and oxygen through the years as shown in Table 4. Independently from upwelling periods or sampling month, the species richness (*R*) was positively associated with water column stratification as shown in Table 4 and as illustrated in Fig. 8. Although the positive correlation

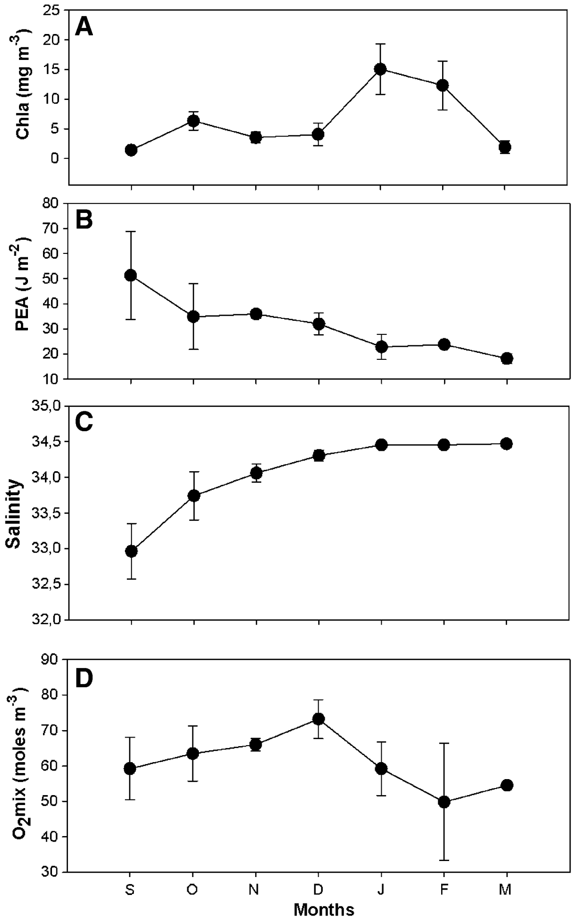

Fig. 6 Monthly variation in phytoplankton biomass (Chl *a*, **A**), water column stratification (PEA, **B**), Salinity (**C**) and oxygenation of the mixed layer ($O_{2_{mix}}$, **D**) during the upwelling period (September–March) at Station 18 off Concepción, Chile during the time series study 2002–2009. *Vertical bars* are standard deviations

seemed driven by few points, this is statistically significant ($P < 0.05$).

K-means analysis applied on the oceanographic variables resulted in two groups that differed significantly in surface salinity and water column stratification (*PEA*). The first group contained 12 months and the second one 14 months. Mean salinity was 33.98 ± 0.570 and 34.08 ± 0.729 for the first and second group, respectively. *PEA* was 39.8 ± 15.16 J m^{-3} and 29.1 ± 21.46 J m^{-3} for group 1 and group 2, respectively. Therefore, group 1 having less salinity and more stratification was assumed as representing months with downwelling conditions, while group 2 with higher surface salinity

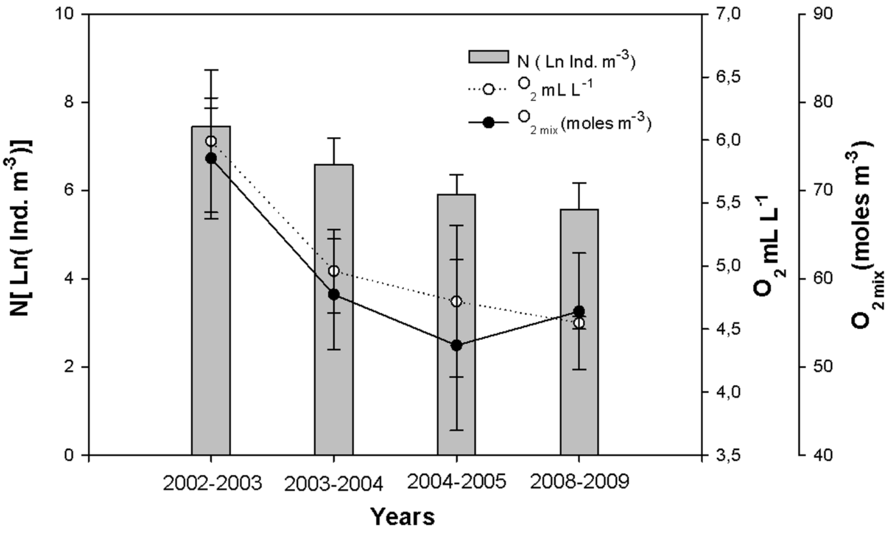

Fig. 7 Annual means (upwelling period) of copepod abundance (*N*), surface oxygen (O_2) and oxygen of the mixed layer ($O_{2_{mix}}$). Data are from monthly sampling (September–March) at Station 18 off Concepción, Chile during the time series study 2002–2009. *Vertical bars* are standard deviations

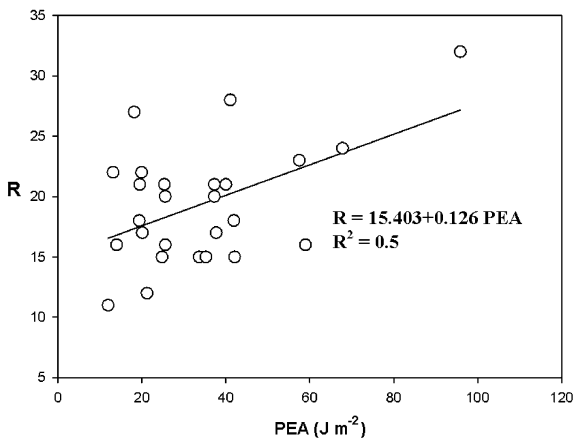

Fig. 8 The relationship between species richness (*R*) and water column stratification estimated as potential energy anomaly of the water column (PEA) of the copepod community at Station 18 off Concepción, Chile during the time series study 2002–2009. The regression equation was highly significant ($P < 0.01$)

and less stratified conditions represented upwelling conditions. These two groups were thereafter used for comparing copepod communities representing these two conditions.

Cluster analysis applied to the species matrix (all species), based on Bray–Curtis similarity distance, also divided copepod communities into two principal groups (with two outliers). The first group contained 14 sampled communities of which 10 were from downwelling conditions. The second group contained 10 sampled communities, of which eight were from upwelling conditions (Fig. 9A). Furthermore, a multidimensional plot showed that only a few species (<10) were significantly associated with up- or downwelling conditions, and so representing distinct communities (Fig. 9B).

Discussion

Zooplankton in upwelling zones vary strongly over the spatial mesoscale (Peterson, 1998; Morales et al., 2010), and it is difficult to account for such variability by observing a fixed station. This issue was discussed in a previous work, based on the same time series study (Escribano et al., 2007). In that respect, the length of the time series becomes important to compensate for the lack of spatial coverage, but it should be kept in mind that seasonal and intra-seasonal patterns may be subject to bias due to spatial effects. In our study, we covered four upwelling periods from different years, allowing replication of that cycle, and hence some of this error may have been addressed.

The strong seasonality of upwelling in this region was somewhat reflected in the analysis of our oceanographic data. For example, winter conditions were still present by early spring with more stratification due to rain and run-off (Sobarzo et al., 2007a), and a more oxygenated mixed layer, as expected for winter conditions (Sobarzo et al., 2007a). Upwelling could reach maximal intensity by mid-summer, characterized by less stratified conditions, high Chla

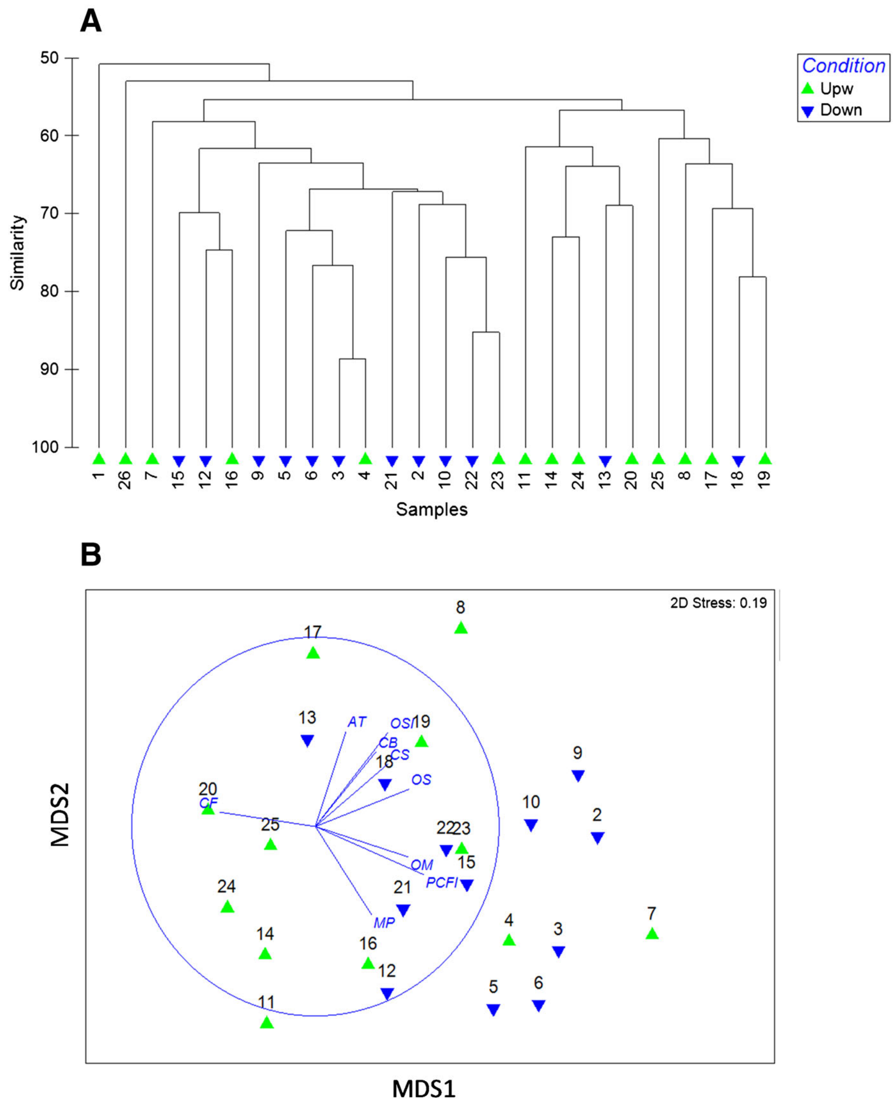

Fig. 9 **A** Cluster analysis of the copepod community at Station 18 in the coastal upwelling zone off central/southern Chile associated with two oceanographic conditions: active upwelling (*Upw*) and downwelling (*down*). The Bray–Curtis similarity distance was applied for grouping samples derived from each condition. **B** Multidimensional analysis of the copepod community associated with the two upwelling conditions. The species significantly associated with the upwelling conditions were *Paracalanus* cf. *indicus* (*PCFI*), *Acartia tonsa* (*AT*), *Oithona similis* (*OS*), *Calocalanus styliremis*, *Centropages brachiatus* (*CB*), *Clausocalanus furcatus* (*CF*), *Oncaea media* (*OM*), *Microcalanus pygmaeus* (*MP*). The *circle* defines the limit for complete correlation ($r = 1.0$). Each point represents a monthly sample

(>5 mg m^{-3}) and a shallow (<30 m) OMZ, and then gradually diminished toward late summer (March). Therefore, part of the observed intra-seasonal variation was due to initiation and termination of the upwelling period. However, throughout the upwelling season, there were strong monthly fluctuations in oceanographic variables, because the upwelling process behaved in pulses. Undoubtedly, monthly observations can miss some variability for shorter time scales. For example, wind stress may respond to event scales (3–7 days), causing variation within and between inertial periods (Sobarzo et al., 2007b). However, how relevant is such variation for copepod populations is unknown. In this region, dominant copepods exhibit generation times extending from 15 days to about 40 days (Hidalgo & Escribano, 2007; Escribano et al., 2013), and thus some of this variability may be integrated over a longer time scale (>20 days).

Monthly variation in upwelling can indeed affect copepod populations by modifying temperature gradients, oxygenation, food resources, mixing and advection. Temperature can strongly affect development, growth and generation times (Escribano et al., 2013), whereas oxygenation can affect copepod physiology (Seibel, 2011) or population distribution and survival (Wishner et al., 2013). The impact of variability in food resources is still a matter of controversy. Although, in terms of food quantity, it has been suggested that copepod growth and production is not limited by food in this highly productive upwelling system (Escribano et al., 2013). Meanwhile, variability in food quality may strongly affect copepod reproduction and recruitment (Vargas et al., 2006; Poulet et al., 2007). Both, food quantity and quality vary extensively in the upwelling zone on a monthly basis (Morales &Anabalón, 2012), therefore, it is likely that copepods might respond to such variation. Finally, mixing and advection, modulated by upwelling intensity, are certainly important factors affecting copepod populations (Peterson, 1998). Advective forces can mix cohorts, affecting population growth (Peterson, 1998), and also can cause substantial offshore export (Morales et al., 2010) reducing the community over the continental shelf. The fate of offshore export is unknown, but it can be considered as a population loss, at least for the upwelling system.

Changes in copepod abundance and community structure may reflect a combination of factors. In this respect, the most noticeable change occurred with copepod abundance. Through the upwelling season, fluctuations in abundances and community composition may relate to population cycles. This because peaks of abundances vary over a 20–35 days for most abundant species (Hidalgo & Escribano, 2007). Nevertheless, the significant negative trend in abundance from the first (2002) to the last (2009) period (Table 4) might reflect a more general trend of decreasing abundance of zooplankton in the Chilean upwelling zone during the last 2 decades (Escribano et al., 2012), apparently linked to incremented upwelling (Bakun et al., 2010). In our analysis, it seems that more upwelling was also linked to less oxygenation of the mixed layer which could negatively impact copepod abundance, as shown in Fig. 7. Nevertheless, species responded differently to changing conditions. For instance, *P.* cf. *indicus* which was the numerically dominant copepod responded to increased upwelling by decreasing their abundance through the years, and two other species *Oncaea media* and *Microcalanus pygmaeus* responded similarly. These are all small-sized species (<1.5 mm) which are now viewed as the dominant species of the copepod community in this region (Hidalgo et al., 2010). Since *P.* cf. *indicus* dominated the community and seemed highly sensible to altered upwelling condition (less oxygenation), this species could explain most of the variation shown by the whole copepod community. Other species responding to upwelling versus downwelling changes were *Acartia tonsa* and *Oithona similis*. These copepods were also greatly affected by incremented upwelling, diminishing their abundances through time, and they are also small-sized and abundant copepods for the region, so that their changes in abundance are reflected in total copepod biomass and abundance. The large sized (>2.5 mm) *Calanoides patagoniensis* is an abundant component of the copepod community, but this species did not show a clear response to upwelling variation. However, in a long-term analysis for the same time series, it was shown that such species have been gradually diminished in the upwelling zone and apparently replaced by the medium size copepod *Drepanopus forcipatus* (Pino-Pinuer et al., 2014).

The significant association between diversity (species richness) and water column stratification suggests some of the key processes controlling community structure. More stratified conditions were found at the end of winter in this region, when low salinity water prevailed at the upper 20 m layer. Under these conditions, the number of species increases, but with low abundances. As the upwelling season progressed species richness usually diminished, but then some species dominated, with increasing abundance of species such as *Paracalanus* cf. *indicus*. Changes in stratification modified vertical gradients in temperature, oxygen, and food aggregation, and such combined effects can affect copepod community structure.

The dynamics of the copepod community structure seems linked to upwelling variability. Over annual and seasonal scales, life cycles of copepods are coupled to upwelling regimes (Peterson 1998; Hidalgo & Escribano, 2007; Escribano et al., 2013). We have now revealed that in shorter time scales, such as intra-seasonal one, upwelling can also impact the community structure. Therefore, the issue of altered upwelling regimes due to climate variability (Garreaud & Falvey, 2009; Belmadani et al., 2013) becomes very relevant for zooplankton dynamics. The decreasing populations, perhaps due to poor survival under enhanced hypoxia (Wishner et al., 2013), or increasing population losses under more advective conditions, are some of the consequences driven by increased upwelling, which may explain the negative interannual trend in zooplankton biomass (Escribano et al., 2012).

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