# Copepod community response to variable upwelling conditions off central-southern Chile during 2002–2004 and 2010–2012

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ABSTRACT: Community structure of pelagic copepods inhabiting the coastal upwelling zone of central-southern Chile was compared between the periods 2002–2004 and 2010–2012. For both periods, 74 copepod species were identified; the Order Calanoida accounted for 68% of the total abundance. Numerically dominant species (ca. 80% of total abundance) were *Paracalanus* cf. *indicus*, *Oithona similis*, *Calanoides patagoniensis*, *Drepanopus forcipatus* and *Acartia tonsa*. Multivariate analyses showed that from the first period (2002–2004) to the second period (2010–2012), there were significant changes in the abundance of some species, the order of dominance and community size structure, although no significant changes in species richness and diversity indexes were found. The dominant species, *Paracalanus* cf. *indicus*, was numerically replaced by *Drepanopus forcipatus* in 2010–2012. There was also a significant decrease in total abundance of copepods during 2010–2012. The assessment of oceanographic variables revealed that colder and saltier conditions prevailed during 2010–2012, accompanied by a greater stratification of the water column because of increased upwelling intensity. Our findings suggest that increasing upwelling has been an important factor for causing changes in the copepod community structure during the past decade.

KEY WORDS:  Coastal upwelling · Copepods · Chile · Community structure · Climate change

## INTRODUCTION

Eastern boundary currents (EBCs) are dynamic ecosystems that can strongly vary in their physical and chemical properties over temporal and spatial scales (Freón et al. 2009). EBCs usually cover extensive latitudinal gradients, exhibit strong seasonal and interannual variability, and can be subjected to large-scale inter-decadal variability, regime shifts, and El Niño Southern Oscillation (ENSO) variability (Chavez et al. 2003, Cahuin et al. 2009).

In the eastern South Pacific, the EBC is known as the Humboldt Current System (HCS). This is a large marine ecosystem with an extensive coastal up- welling zone (ca. 40° latitude), directly influenced by the high pressure center of the Pacific anticyclone, which causes strong SW winds, inducing persistent coastal upwelling along the coasts of Chile, Peru, and Ecuador (Thomas 1999).

EBC systems are affected by anthropogenic global warming (Garreaud & Falvey 2009). As a consequence, increased coastal upwelling, induced by intensification of S and SW winds, may be expected, causing the prevalence of colder conditions (Bakun et al. 2010). This effect has also been described for the Benguela system (Santos et al. 2012). Furthermore, the HCS is characterized by the presence of a subsurface oxygen minimum zone (OMZ) (Paulmier

& Ruiz-Pino 2009), and this hypoxic layer may become shallower upon increased upwelling. These long-term changes in the physical-chemical environment of the HCS are expected to affect diversity and productivity (Hoegh-Guldberg & Bruno 2010).

At lower trophic levels, zooplankton is a group that may be altered by climate change (Richardson 2008). Several studies have shown long-term changes in community structure, diversity and abundance of various zooplankton groups from different regions of the world. These changes have been related to climate variability (Beaugrand et al. 2002, Richardson 2008, Mackas & Beaugrand 2010). Therefore, zooplankton can be used as a sentinel group reflecting changes in the marine ecosystem and providing early evidence of biological response to climate variability (Hays et al. 2005).

Biomass and abundance of copepods are correlated to upwelling variation in the HCS (Ayón et al. 2008, Escribano et al. 2012), but it is unclear how this group will respond to gradually increasing upwelling. Although more upwelling may promote a higher primary production by increasing nutrient inputs to surface water (Bakun et al. 2010), copepods might not be able to utilize the surplus of phytoplankton biomass if food spectra have been modified. Also, the complexity of the food web dynamics in the upwelling zone, characterized by a seasonal interplay between a microbial food web and phytoplankton–herbivores food chain for C transfer (Vargas et al. 2007), may not ensure more secondary production. Increased upwelling may have further implications, such as increased offshore advection and more hypoxic conditions, both of which can negatively impact copepod populations (Peterson 1998, Donoso & Escribano 2013, Wishner et al. 2013). Alterations may be reflected in changes in abundance of some species, in total abundance, in diversity indices or in the order of dominance.

Copepods in the Humboldt Current are dominated by medium-size and small species (1.0 to 2.5 mm in prosome length) (Hidalgo et al. 2010), and they exhibit year-round reproduction and annual cycles strongly associated with upwelling variability (Escribano et al. 2007, 2012, Hidalgo & Escribano 2007).

In this study, we compared the abundance, diversity and dominance of copepod species in an upwelling zone off Chile between 2 periods: 2002–2004 and 2010–2012. These 2 periods represent conditions for potential changes taking place after a decade of sampling in the coastal upwelling zone off central-southern Chile through the COPAS Time Series Study of Concepción at Stn 18 (Escribano & Morales 2012). Our study aimed at examining the consequences for the copepod community as a result of increased wind-driven upwelling in recent years.

## MATERIALS AND METHODS

### Zooplankton sampling and oceanographic measurements

The upwelling region of central-southern Chile (30 to 40° S) corresponds to the southern portion of the Humboldt Current System in the eastern South Pacific (Fig. 1). Off Concepción (36° 30′ S), we have maintained a time series study from August 2002 to the present at Stn 18 (36° 30.80′ S, 73° 7.75′ W), which was initially sampled every 15 d (2002 to 2003), and monthly thereafter (Escribano & Morales 2012). This station is located over the continental shelf ~20 km from the coast at a depth of ~90 m (Fig. 1).

At Stn 18, chemical, physical and biological conditions of the water column are assessed with autonomous profilers, CTD SBE-25 and SBE-19 Plus, attached to a SeaBird SC-32 rosette for water sampling. The collected data include temperature, salinity and pressure. CTDs are also equipped with calibrated oxygen sensors and fluorometers. CTD casts are averaged at a 1 m resolution from surface to 85 m. Water samples, either with the rosette or with 10 l Niskin bottles, are obtained at 9 depths from surface to 85 m, and they are used to measure chlorophyll a (chl a) by fluorometric methods, as described by Anabalón et al. (2007), and dissolved oxygen by the micro-Winkler technique as described by Montero et al. (2007).

Since 2002, zooplankton samples have been collected by oblique hauls for 3 depth strata: 80–0 m, 80–50 m and 50–0 m. For this, a 1 m$^2$ Tucker Trawl net fitted with 200 µm mesh size and equipped with a calibrated flowmeter is used. On occasions, day and night samples have been carried out on the same sampling day, and some samples (0–80 m) were also obtained with a 200 µm 0.5 m opening WP2 during rough weather conditions. For this study, we have used integrated samples of the 0–80 m stratum collected during daylight.

After collection, zooplankton samples were immediately preserved onboard with a solution of 4% neutralized formalin. We identified and counted all species of copepods. Highly concentrated samples were fractionated up to a minimum of 25% of the total sample for taxonomic analysis. The species were identified with stereomicroscopes Nikon SMZ 1000 and Leica DM500.
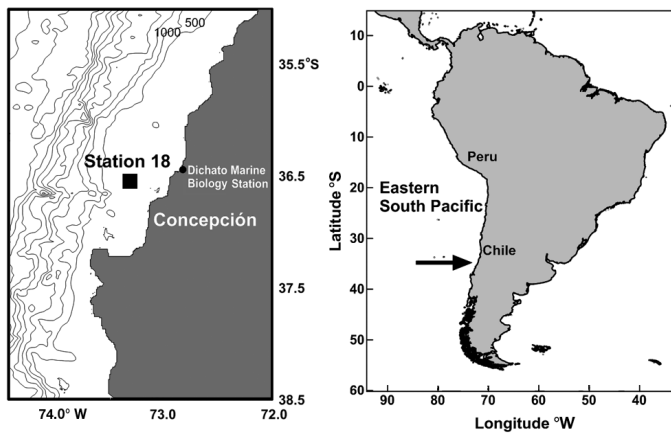
Fig. 1. Eastern South Pacific and coastal upwelling zone off central-southern Chile, illustrating the location of Stn 18, where the COPAS time series study has been carried out since 2002. The 500 and 1000 m isobaths are shown

## Data analysis

For this study, we used copepod data from 2 distinct periods for 2 consecutive years each, after 10 years of the Time Series Study. Period 1 is from August 2002 to August 2004. The second period included samples from August 2010 to August 2012. Samples collected from 2004 to 2010 were largely lost when a tsunami destroyed the Marine Biology Station in 2010.

Oceanographic conditions between periods were compared mostly by considering changes in temperature, salinity and density at 10 m depth, where most dominant copepods are (Escribano et al. 2007), as the phyto- and microzooplankton provide an adequate nutritional environment for copepods (Iriarte et al. 2000, Anabalón et al. 2007), and most of the environmental variation occurs in the mixing layer. Oxygen conditions and chlorophyll *a* concentration of the water column were also considered at 10 m depth. In addition, we estimated the depth of the OMZ, defined as the depth at which oxygen levels attain 1 ml $O_2$ $l^{-1}$.

The monthly stratification index ($\Phi$) of the water column was derived from temperature, salinity and density (Sigma-T) for the upper 50 m layer as described by Bowden (1983), such that:

$$\Phi = \frac{1}{H} \int_{-H}^{0} (\rho m - \rho) gz \, dz \qquad (1)$$

where $\Phi$ is the stratification index (J $m^{-2}$), $g$ is the acceleration of gravity (9.8 m $s^{-2}$), $H$ is the depth of the water column (50 m), $\rho$ is water density (kg $m^{-3}$) at depth $z$ (m), and $\rho m$ is the average density of the water column (0 to 50 m).

Upwelling variability in the region was examined from monthly upwelling indices estimated by the National Oceanic and Atmospheric Administration (NOAA) from the Project NCEP/NCAR Division of Physical Sciences, derived for 36°S off the Chilean coast as the Bakun index (Bakun 1973). We complemented this information with meridional wind data computed from 2 data assimilating type models NCEP/FNMOC (NOAA), centered near Stn 18.

Analysis of copepod data involved the calculation of numerical abundance of species standardized to ind. $m^{-3}$, and relative abundance and occurrence were estimated as percentages. Changes in the copepod community were assessed using the descriptors species richness (R), numerical abundance (N), dominance (relative abundance) and diversity was estimated with the Shannon-Wiener index ($H'$), defined as follows:

$$H' = -\ln \Sigma p_i (p_i) \qquad (2)$$

where $p_i$ is the proportion of individuals of a species $i$ to the total of individuals ($n_i$/N), $n_i$ is the number of individuals of the species $i$, and N is the total number of individuals in the sample. To incorporate a copepod size effect on the diversity index, a modified $H'$ index was also calculated. For this, an $H'$s index was standardized by the average size of adult stages of the species present in the corresponding sample. This size-weighted $H'$s index has been suggested to better represent copepod diversity in highly advective ecosystems (Hidalgo et al. 2012). Size structure of the copepod community was also examined by distinguishing size classes and their abundances; 4 classes were distinguished using total body length: <1 mm, 1–2 mm, 2–3 mm and >3 mm. We obtained direct measurements of body length of at least 30 adult female individuals (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m515p083_supp.pdf) for rare species, measurements were complemented with data from Mauchline et al. 1998).

We used multivariate analyses to explore changes in copepod community structure between the 2 periods. From a density matrix with the abundance of each copepod species (ind. $m^{-3}$), the data were square-root transformed to normalize the variance while preserving distances among low values (Field et al. 1982), and cluster analysis was used to identify changes in natural groupings in samples based on their abundance similarities. The Bray-Curtis similarity measure and group average linkage method were used (Clarke & Warwick 2001). The SIMPER test was used to examine the contribution (%) of each cope-

pod species to average resemblances between sample groups. Principal component analysis (PCA) was used to identify which physical variables explained the environmental variability. PCA was applied over normalized residuals. In addition, the association of the copepod community structure with environmental variability was determined from a non-metric multi-dimensional scaling (NMDS) and stepwise-multivariate correlation analysis (BEST). NMDS was plotted as scatter-plots for taxonomic data, and the environmental data were then overlaid as gradients. These gradients are represented as vectors whose direction indicates the increment of the attribute or variable, and the length corresponds to the degree of correlation; i.e. short arrows mean low correlations and weak relationships between environmental variables and the NMDS space. The BEST test selects environmental variables 'best explaining' community pattern by maximising a rank correlation between their respective resemblance matrices. The BVSTEP algorithm (permutational stepwise) was used. Finally, an analysis of similarities (ANOSIM, 999 permutations) was performed over the community structure dataset to test hypotheses for differences between samples from different periods. All these analyses were performed using PRIMER v6 software (Field et al. 1982, Clarke & Warwick 2001, Clarke & Gorley 2006).

## RESULTS

### Oceanographic conditions

Seasonality of upwelling became clear from CTD data, in all oceanographic variables. Near surface temperature (10 m depth) shows the differences between upwelling (spring-summer) and non-upwelling seasons (autumn-winter). The annual mean (±SD) temperature was 12.9 ± 0.9 and 12.7 ± 1.2 for Periods 1 and 2, respectively. The maximal temperature at 10 m was 15.7°C during March for Period 1, whereas in Period 2, the greatest temperature was 15.8°C in January. The coldest conditions were also found during the spring-summer months upon increased upwelling with temperatures <11.5°C at 10 m depth in both periods. Temperatures of the water column were 11.6 ± 0.6 for Period 1 and 11.4 ± 0.7 for Period 2, where the lowest mean temperatures were also found in the spring-summer season in both periods (Fig. 2a).

Salinity showed a similar annual cycle for both periods, with much lower salinity in winter associated with the rainy season and increased river dis-charge, contrasting with higher salinity in periods of active upwelling (Fig. 2b). Salinity was 33.8 ± 0.7 and 34.0 ± 0.6 in Periods 1 and 2, respectively; a highly significant greater salinity in Period 2 was confirmed by a $t$-test ($t_{(2),42} = 8.86$, $p < 0.01$). Mean salinity for the entire water column (0–80 m) was 34.3 ± 0.2 and 34.4 ± 0.2 for Periods 1 and 2, respectively. These means also differed significantly ($t_{(2),41} = 6.68$, $p < 0.01$; see the supplement at www.int-res.com/articles/suppl/m515p083_supp.pdf.

Dissolved oxygen (DO) also exhibited a seasonal pattern (Fig. 2c), characterized by sharp decreases during the spring-summer after nearly saturated conditions (5 to 6 ml $O_2$ $l^{-1}$) during the winter. DO was 5.4 ± 1.1 ml $O_2$ $l^{-1}$ and 5.2 ± 1.0 for Periods 1 and 2, respectively. These values of DO did not differ significantly ($t_{(2),42} < 1.86$, $p > 0.05$).

Concentration of chl $a$ showed a marked seasonal pattern, characterized by a maximum concentration in the spring-summer seasons, but also showed marked changes between periods (Fig. 2d). During the upwelling season (spring-summer), the mean chl $a$ level was 4.9 ± 6.7 mg chl $a$ $m^{-3}$ for Period 1 and 4.9 ± 5.8 for Period 2. By contrast, in the non-upwelling season (autumn-winter), chl $a$ was 1.9 ± 2.8 mg $m^{-3}$ and 1.5 ± 2.1 mg $m^{-3}$ at 10 m depth for Periods 1 and 2, respectively. Chl $a$ values did not differ significantly between periods ($t_{(2),42} < 1.86$, $p > 0.05$).

When upwelling conditions for both periods were compared through the regional upwelling index of Bakun (1973), the seasonal regime of upwelling intensity became clear, although there were no apparent differences between periods (Fig. 2e). However, water column stratification was clearly different between periods, revealing that during the most recent period (2010–2012), mixed, less-stratified conditions prevailed compared to the period 2002–2004 (Fig. 2f). The seasonal pattern of Φ also showed that stratification was greater during the winter, and this is caused by low salinity water at the surface after rainfall and river runoff. The annual cycle of depth of the OMZ also shows a clear seasonal pattern characterized by a very shallow (<50 m) OMZ in the spring-summer in both periods, and the OMZ was much shallower during the more recent period (Fig. 2g).

### Species composition

The copepod community for both study periods was represented by 74 species belonging to 4 orders, 29 families and 41 genera. The Order Calanoida was the most representative with 67.6% of total species,
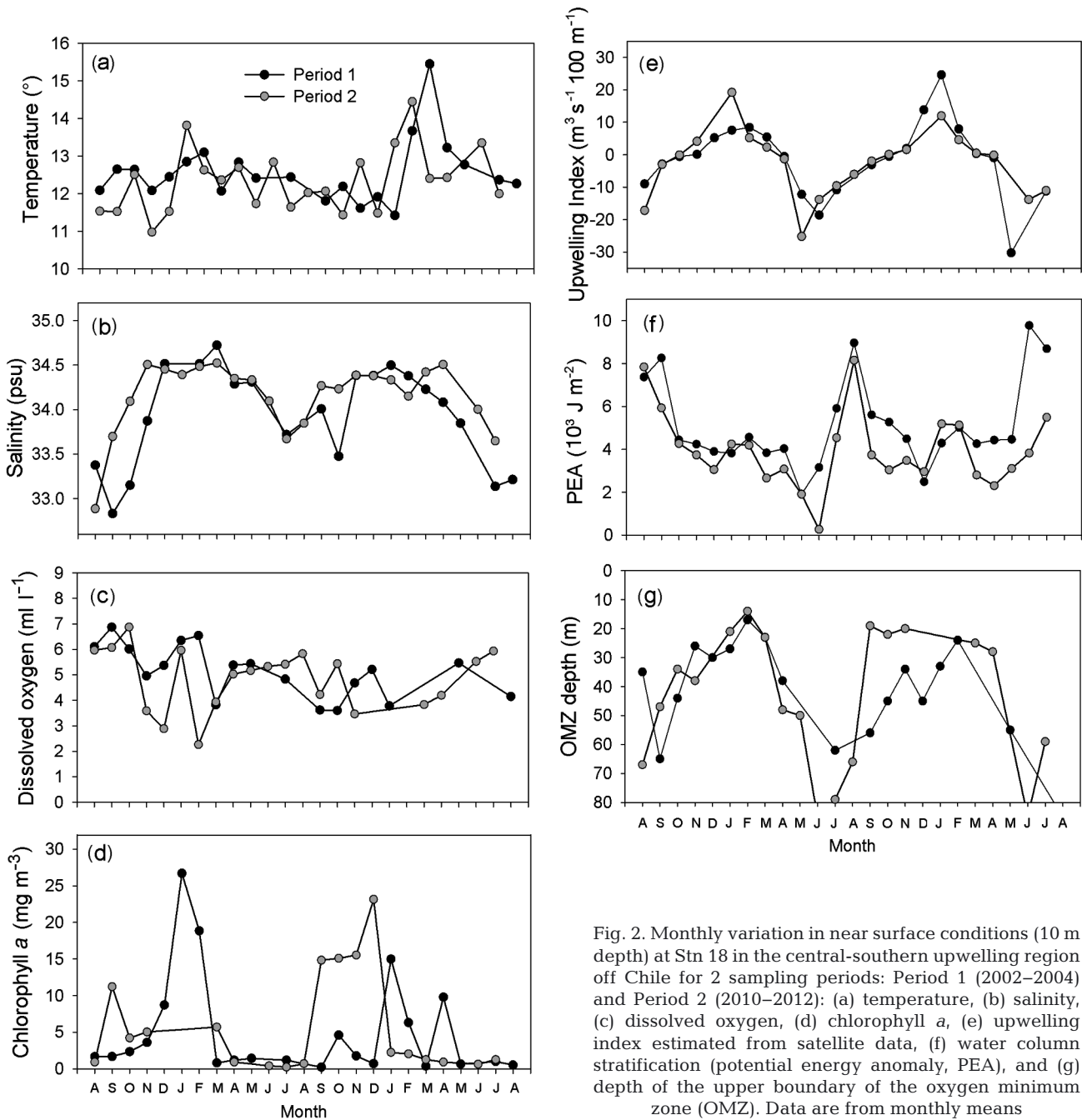
Fig. 2. Monthly variation in near surface conditions (10 m depth) at Stn 18 in the central-southern upwelling region off Chile for 2 sampling periods: Period 1 (2002–2004) and Period 2 (2010–2012): (a) temperature, (b) salinity, (c) dissolved oxygen, (d) chlorophyll *a*, (e) upwelling index estimated from satellite data, (f) water column stratification (potential energy anomaly, PEA), and (g) depth of the upper boundary of the oxygen minimum zone (OMZ). Data are from monthly means

followed by the Order Cyclopoida with 16.2% and the Orders Harpacticoida with 8.1% and Poecilostomatoida with 8.1%. The complete list of species is provided in the Supplement.

Numerically dominant species, representing >1% of total abundances in either period, are shown in Table 1. These species were also present throughout the year in the upwelling zone, with frequency of occurrence >60% (Table 1). During Period 1, there was a total number of 58 species of copepods, of

which 53 were identified to species and 5 to genus level (see the supplement). In this period, *Paracalanus* cf. *indicus*, *Calanoides patagoniensis*, *Oithona similis* and *Acartia tonsa* were the dominant species, representing >90% of the total copepod community. *P.* cf. *indicus* was the most abundant species (Table 1, Fig. 3), representing 60% of the abundance of copepods in this period. During Period 2, a total of 55 species were found, all of them identified to species level. *Drepanopus forcipatus*, *O. similis*, *C. pata-*

Table 1. Numerically dominant species (>1% of total abundance) of copepods found at Stn 18 in the coastal upwelling zone. Data are from monthly samples for August 2002 to August 2004 (Period 1) and August 2010 to August 2012 (Period 2). The complete list of identified species and their abundances are provided in the Supplement (at www.int-res.com/articles/suppl/m515p083_supp.pdf); n is the mean abundance, and *f* represents the frequency of occurrence

| Species | Period 1 | | Period 2 | |
|---|---|---|---|---|
| | n (ind. m$^{-3}$) | *f* (%) | n (ind. m$^{-3}$) | *f* (%) |
| *Paracalanus* cf. *indicus* | 755.6 | 100.0 | 41.7 | 95.2 |
| *Calanoides patagoniensis* | 220.2 | 95.7 | 68.4 | 76.2 |
| *Oithona similis* | 151.5 | 100.0 | 115.4 | 90.5 |
| *Acartia tonsa* | 58.1 | 100.0 | 24.9 | 85.7 |
| *Drepanopus forcipatus* | 34.5 | 100.0 | 138.2 | 90.5 |
| *Oithona setigera* | 16.7 | 100.0 | 7.7 | 81.0 |
| *Clausocalanus arcuicornis* | 7.3 | 82.6 | 29.6 | 71.4 |
| *Microcalanus pygmaeus* | 7.0 | 82.6 | 16.2 | 66.7 |
| *Pleuromamma gracilis* | 3.0 | 78.3 | 6.4 | 71.4 |

Table 2. Non-parametric Kruskal-Wallis test to compare the abundance of a dominant copepod species, and total copepod abundance between Period 1 (2002–2004), and Period 2 (2010–2012) at Stn 18 in the upwelling zone off Chile

| Variable | Period 1 Rank sum | Period 2 Rank sum | df | p |
|---|---|---|---|---|
| *Paracalanus* cf. *indicus* | 211.00 | 89.00 | 1 | <0.01 |
| Total abundance (n) | 187.00 | 113.00 | 1 | 0.03 |

*goniensis*, *P.* cf. *indicus*, *Clausocalanus arcuicornis*, *A. tonsa*, *Microcalanus pygmaeus* and *Microsetella norvegica* were the dominant species (>1%), making up >90% of copepod abundance. During this second period, there was a sharp decrease in the abundance of *P.* cf. *indicus*, which represented only 8% of the whole community and with abundance 1 order of magnitude lower (Table 1). In this period, *D. forcipatus* dominated (Table 1), accounting for 28% of the total copepod community. A Kruskall-Wallis test showed a significant decrease in abundance of *P.* cf. *indicus* and total abundance of copepods from Period 1 to Period 2 (Table 2).

*C. patagoniensis*, *A. tonsa* and *O. similis* had higher abundances during the first period, whereas *C. arcuicornis*, *M. pygmaeus* and *Pleuromamma gracilis* increased over 50% in their abundances during Period 2 (Fig. 3).

The highly dominant *P.* cf. *indicus* in Period 1 seem to increase during the spring-summer compared to winter months, but such a pattern is not clear during Period 2. Instead, there was an abrupt decrease in the spring (Fig. 4a). *C. patagoniensis* showed the same pattern in both periods, with a slight tendency to decrease by mid-winter (Fig. 4b). *O. similis* was present during all seasons with similar levels of abundance and no clear seasonal pattern (Fig. 4c). *A. tonsa* also decreased by the winter but exhibited strong variation in other months (Fig. 4d). Finally, *D. forcipatus* clearly increased in abundance during the autumn and early spring of Period 2, whereas in Period 1, this species varied sharply with no clear seasonality (Fig. 4e).

The annual cycle of species richness (*R*) showed the highest values during May for the first period and in August for the second period, in both cases under downwelling conditions, whereas much lower values were found during the spring-summer seasons
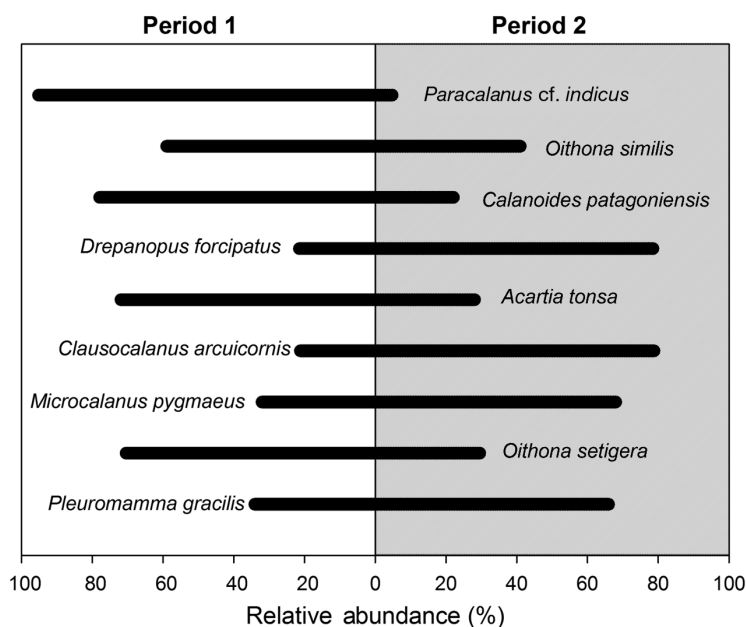


Fig. 3. Relative abundance of dominant copepod species at Stn 18 in the coastal upwelling zone off Chile for Period 1 (2002–2004) and Period 2 (2010–2012). Data are from monthly samplings
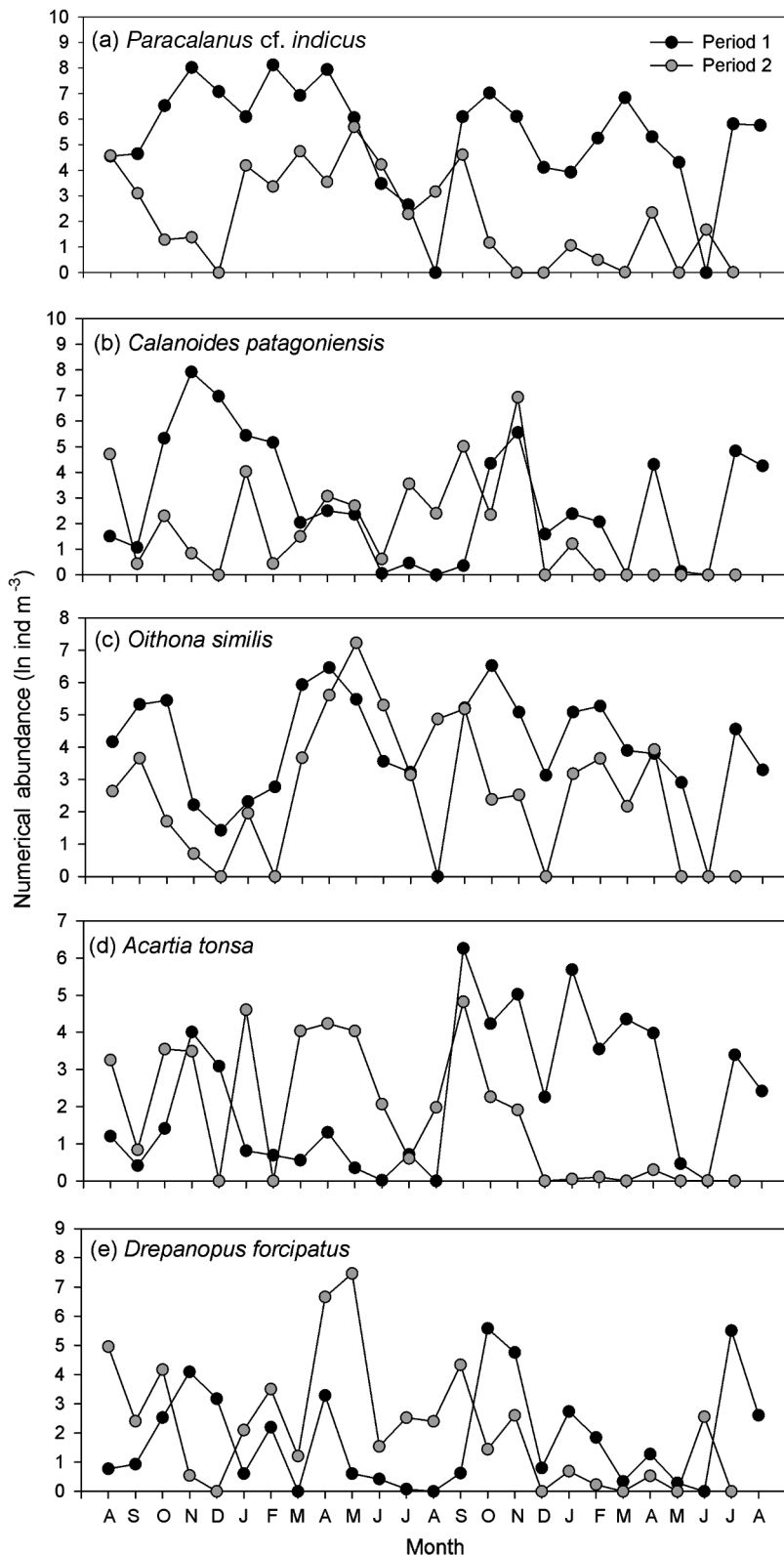
Fig. 4. Monthly variation in numerical abundance (ln-transformed data) of dominant copepod species at Stn 18 in the coastal upwelling zone off Chile during Period 1 (2002–2004) and Period 2 (2010–2012)

(Fig. 5a). Variability of the diversity index ($H'$) was unclear, although there was a slight tendency to increase in the winter and decrease in early spring (Fig. 5b), whereas the diversity index standardized by copepod size ($H's$) was more variable throughout the year, with a slight decrease in the spring and greater values by mid winter (Fig. 5c). Meantime, total copepod abundance (N) showed 2 major peaks in the spring and in the autumn in both periods and marked low values during the winter (Fig. 5d).

Eventual changes in community size structure were examined by grouping copepod abundances in 4 size classes (<1, 1–2, 2–3 and >3 mm). During the first study period, the small size class (<1 mm) was numerically dominant, contributing 72% to total abundance (Fig. 6a). Species belonging to this size class were *P.* cf. *indicus*, *O. similis*, *M. pygmaeus* and *Oncaea media*. By contrast, in the second study period, the mid-size class 2–3 mm dominated and small copepods decreased in abundance (Fig. 6b). This mid-size class was mostly represented by *D. forcipatus*.

To better characterize environmental changes from one period to another, the annual cycle was obtained from all data, and thereafter, monthly anomalies were derived for each period. Clear differences between periods became evident from temperature, salinity and stratification data (Fig. 7). For both sea surface temperature (Fig. 7a) and mean temperature of the water column (Fig. 7b), Period 2 became substantially colder for most of the year cycle, with negative anomalies for 9 and 10 mo, respectively. Period 2 also exhibited positive salinity anomalies both at the surface (Fig. 7c) and in the entire water column, especially during the spring (Fig. 7d). The water column during Period 2 was also more stratified for most of the year cycle (Fig. 7e).

Based on normalized oceanographic residuals (monthly anomalies), a PCA analysis was used to identify factors contributing to variability between periods. The first 2 principal components accounted for 67.6% of the variance, and
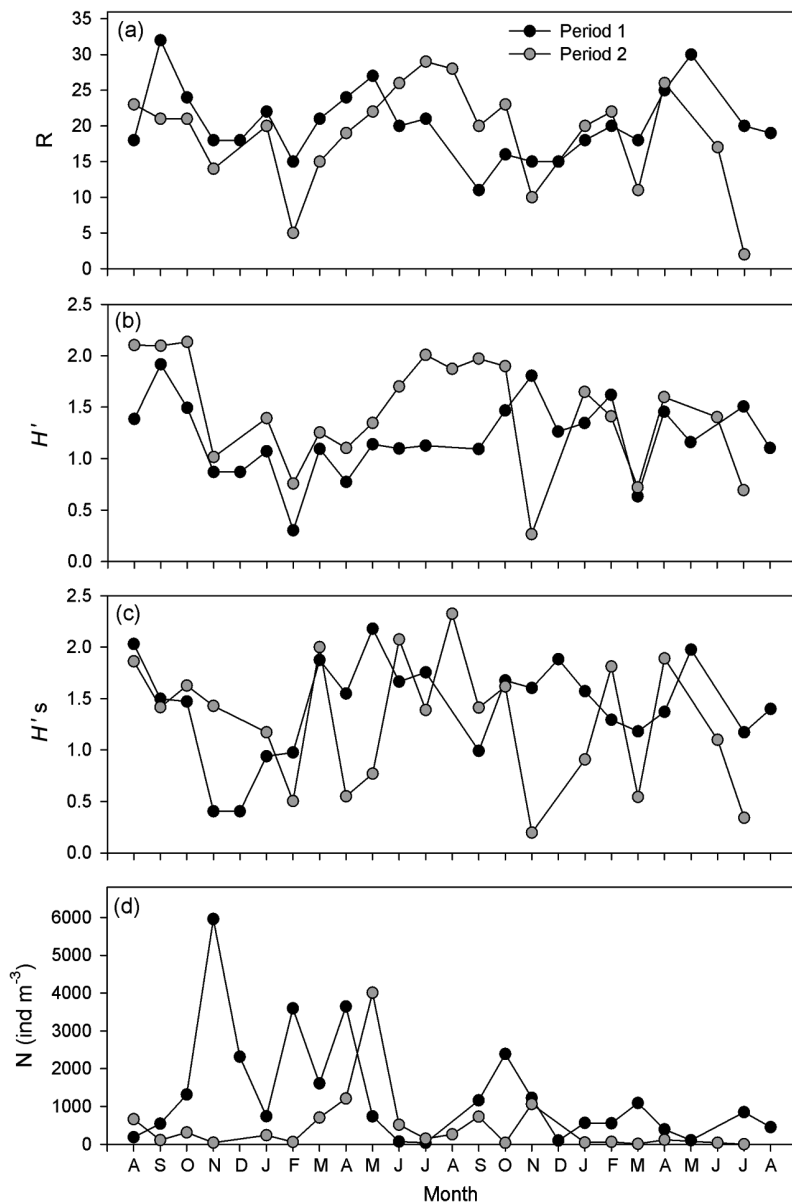
Fig. 5. Monthly variation of community descriptors of the copepod community at Stn 18 in the coastal upwelling zone off Chile for 2 comparative periods: Period 1 (2002−2004) and Period 2 (2010−2012). (a) Species richness (*R*), (b) Shannon-Wiener index (*H'*), (c) size-weighted Shannon-Wiener index (*H'*s), (d) copepod total abundance (N)
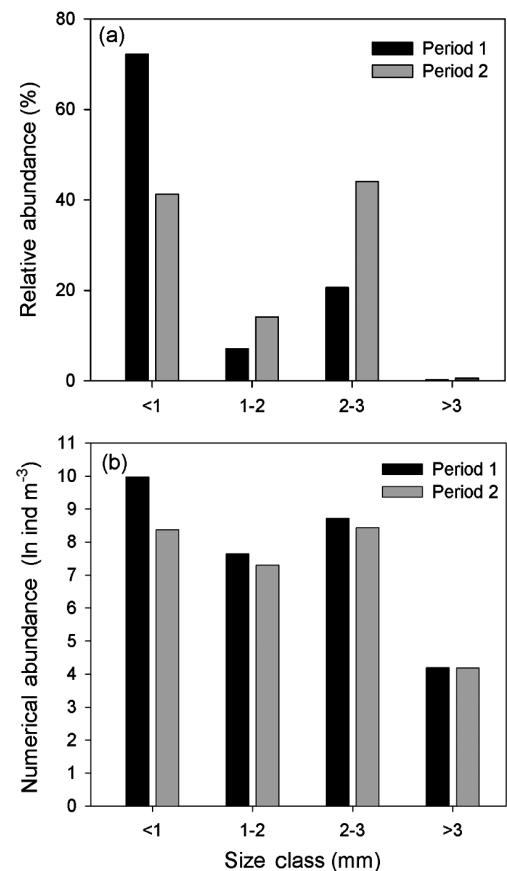


Fig. 6. Changes in size structure of the copepod community at Stn 18 in the coastal upwelling zone off Chile for Period 1 (2002−2004) and Period 2 (2010−2012) after comparing (a) relative abundance and (b) numerical abundance (ln-transformed means from monthly samplings). The 4 copepod size classes were assigned on the basis of adult total length of females

PC1 was associated with mean temperature of the water column and PC2 with stratification. These 2 factors accounted for most of the variability (Fig. 8).

Changes in community structure between periods were assessed with abundances of the 9 dominant species (from Table 2) and environmental residuals by using PCA and MDS analyses. Significant factors were filtered with r ≥ 0.4. Periods became clearly distinct from a NMDS plot, revealing that stratification, temperature, OMZ depth and upwelling index were the factors explaining the differences (Fig. 9). The difference between periods was highly significant (ANOSIM test, R = 0.236, p < 0.01). A cluster analysis using Bray Curtis similarity as distance also produced a clear segregation of 2 communities depending on sampling period with a similarity criterion >70% (Fig. 10). Moreover, a SIMPER test indicated that *P.* cf. *indicus* (27.1%), *O. similis* (19.2%) and *A. tonsa* (12.3%) were the greatest contributors to Period 1, whereas *O. similis* (19.0%), *D. forcipatus* (15.9%) and *A. tonsa* (15.5%) were the main contributors to variance in Period 2.

The influence of environmental changes from one period to another was examined using the non-parametric stepwise Biota/environmental matching test
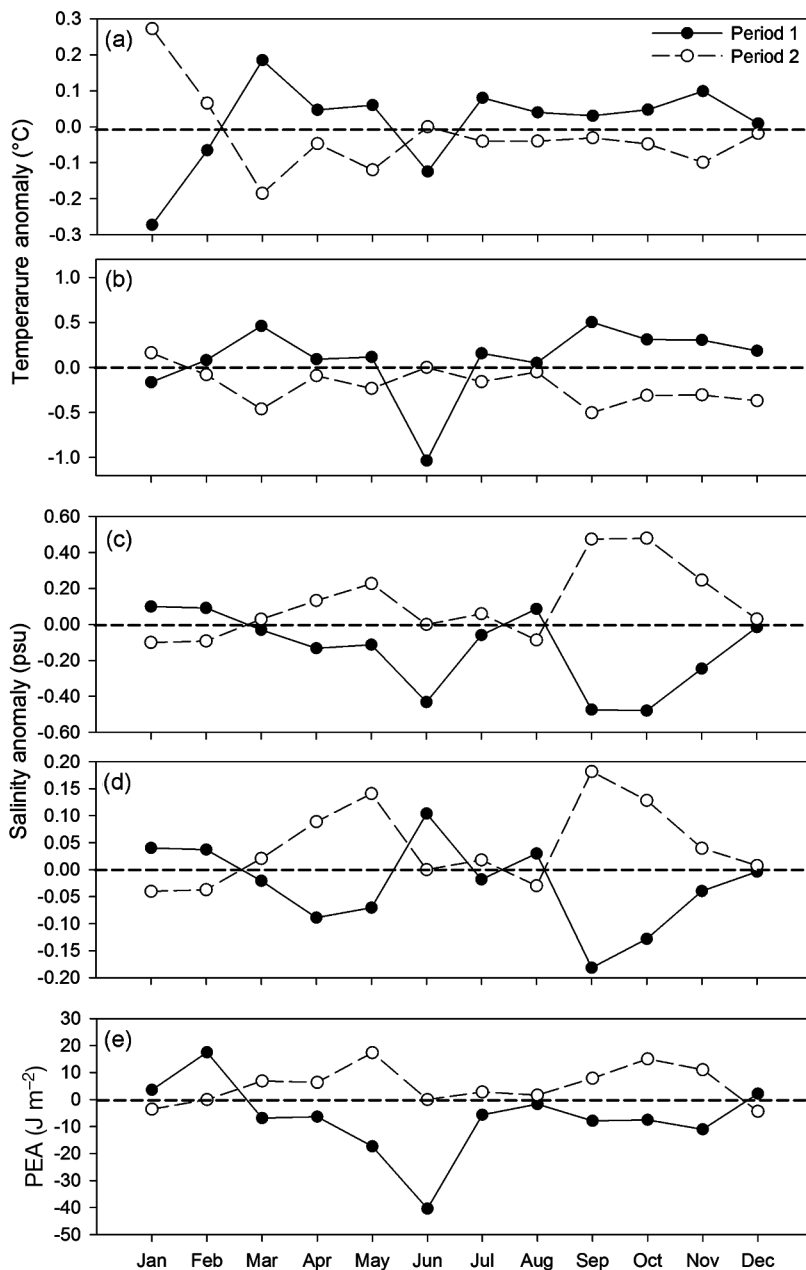
## DISCUSSION

For central-southern Chile, the evidence indicates that significant changes in the water column have occurred in the last 10 yr, resulting in a colder and saltier condition. This change has been induced by increased upwelling promoted by stronger southerly winds in the eastern South Pacific region in the last decades (Garreaud & Falvey 2009, Bakun et al. 2010). However, the NOAA regional upwelling index showed no differences between periods. This lack of differences in the Bakun index is explained in terms of spatial effects. The Bakun index is derived from geostrophic winds, which cannot have sufficient resolution in the coastal area (Bakun 1973) or under the conditions that occur at Stn 18, where increasing upwelling takes place. Therefore, a higher resolution analysis of wind data is required. In fact, wind data for both periods at 2 points near Stn 18 derived from NCEP/FNMOC models showed clear differences in meridional winds when comparing periods, suggesting strongly increased upwelling during the 2010–2012 period (see the Supplement at www.int-res.com/articles/suppl/m515p083_supp.pdf).

Previous studies that assessed seasonal variability of few or single species (Castro et al. 2007, Escribano et al. 2007) or covered a few years (Hidalgo et al. 2010, Escribano et al. 2012) showed strong seasonal variation of copepod abundances, but whether such patterns repeat every year remained uncertain. Indeed, our study shows that interannual variability can be greater than seasonal variability. Over a few years, changing environmental conditions in terms of temperature, salinity and stratification, in this case driven by changes in upwelling intensity, affect the structure of copepod communities, as has been shown in other regions of the world ocean. For example, in the northern California Current, a change from warm to colder conditions can affect the species



Fig. 7. Monthly anomalies of oceanographic variables at Stn 18 in the coastal upwelling zone off Chile for Period 1 (2002–2004) and Period 2 (2010–2012). (a) Near-surface temperature (10 m depth), (b) mean temperature of the water column (0–80 m), (c) near-surface salinity (10 m depth), (d) mean salinity of the water column (0–80 m), (e) water column stratification estimated as potential energy anomaly (PEA)

(BVSTEP) applied on dominant species matrix and the environmental residuals matrix. BVSTEP test was significant (Rho = 0.461, p < 0.05), and the variables accounting for this correlation were dissolved oxygen, upwelling index and stratification of the water column.
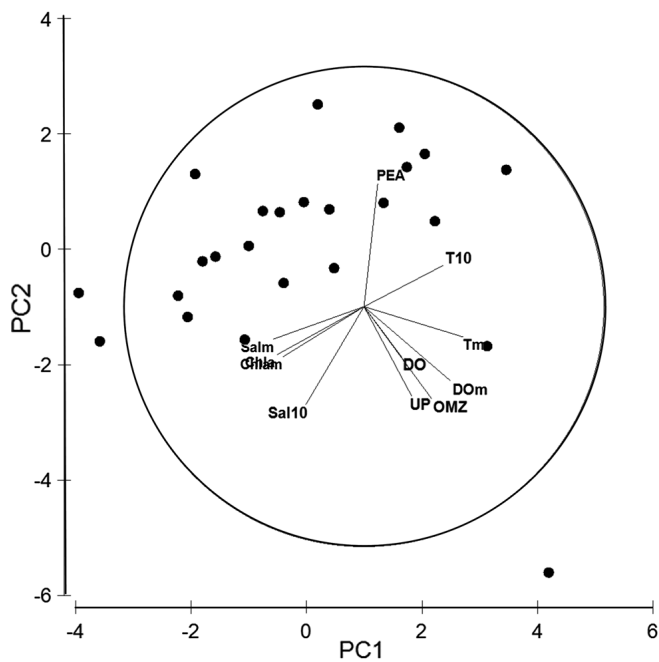
Fig. 8. Principal component analysis to assess oceanographic variation at Stn 18 in the coastal upwelling zone off Chile for Period 1 (2002–2004) and Period 2 (2010–2012). PEA: potential energy anomaly represents stratification, T10: temperature at 10 m depth, Tm: mean temperature of the water column, Sal10: salinity at 10 m depth, Salm: mean salinity of the water column, OMZ: depth of the oxygen minimum zone, UP: upwelling index, DO: dissolved oxygen at 10 m depth, DOm: mean oxygen of the water column, Chla: chlorophyll *a* at 10 m depth, Chlam: mean chlorophyll of the water column. Circle represents 95% confidence limit
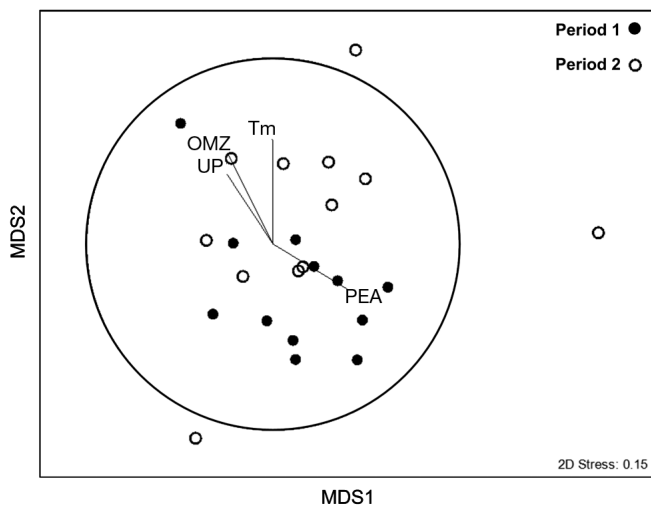


Fig. 9. Multidimensional analysis of the copepod community associated with oceanographic conditions and at Stn 18 in the coastal upwelling zone off Chile for Period 1 (2002–2004) and Period 2 (2010–2012). Plotted variables were filtered from a criterion of r = 0.4. See Fig. 8 for definitions

richness and the composition of the copepod community (Peterson et al. 2006). In the northern HCS, the zooplankton community, including copepods, can also respond to changing warm-cold conditions driven by El Niño/La Niña fluctuations (Aronés et al. 2009), and in the North Atlantic region there is a strong influence of changing hydrographic conditions on copepod diversity and abundance (Beaugrand et al. 2002).

Changes in the community structure of copepods from Period 1 to Period 2 were reflected in species abundance with consequences for the size structure. Some species increased towards the Period 2 (e.g. *Drepanopus forcipatus*), others reduced their abundance (e.g. *Paracalanus* cf. *indicus*), and other species were maintained in similar abundances (*Oithona similis*). The dominance of some species also changed between periods. *P.* cf. *indicus* was displaced by *D. forcipatus*. The latter is a species found in colder waters originated in the subantarctic or Antarctic regions. Therefore, this species could be signaling an increase in the proportion of sub-Antarctic waters in the study area. This region is subjected to the influence of subantarctic waters, equatorial and subtropical water in different proportions in the surface layer (<100 m), where copepods can be indicators of different water masses (Morales et al. 2010). This mixing of waters of different origins can be affected by changes associated with El Niño Southern Oscillation (ENSO) conditions, i.e. from a cold to a warm phase (El Niño and La Niña, respectively) (Escribano et al. 2004). However, NOAA data show that both study periods mainly represent either neutral or La Niña ENSO conditions; therefore, the observed changes in abundance and species replacement cannot be attributed to ENSO variability, and most likely, they have been induced by longer term changes in upwelling intensity (Bakun et al. 2010).

All species found in this study have been previously described for this region (Hidalgo et al. 2010, 2012, Morales et al. 2010, Escribano et al. 2012). Names of 3 species have been modified in recent years: *Pseudoamallothrix ovata*, *Pseudoamallothrix profunda* and *Scolecithricella bradyi*. The species names have been validated in the Global Registry of scientific names of marine species (WoRMS) (www. marinespecies.org).

We also found a decrease in total abundance of copepods for the more recent period, which is consistent with the decrease in *Paracalanus* cf. *indicus*. Previous studies have shown that >46% of total abundance of pelagic copepods in the HCS corresponds to *P.* cf. *indicus* (Hidalgo et al. 2010, 2012). This species
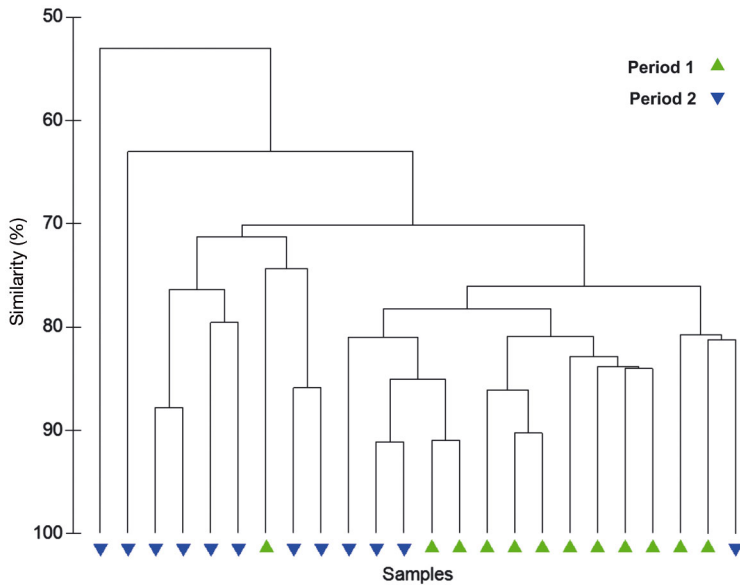
Fig. 10. Cluster analysis of the copepod community associated with oceanographic conditions and at Stn 18 in the coastal upwelling zone off Chile for Period 1 (2002–2004) and Period 2 (2010-12). Dominant species (>1% of relative abundance) were considered, and the Bray-Curtis similarity distance was applied for grouping samples derived from each period

could therefore account for a reduction of total abundance of copepods during the period 2002 to 2008 (Escribano et al. 2012). Declines of zooplankton have been observed in other time series in coastal upwelling areas (Roemmich & McGowan 1995), and these are suggested to be caused by physical forcing, such as changes in winds, thermocline depth, heat flux and temperature (Clarke & Lebedev 1999), although others postulate that pelagic fish predation on zooplankton can explain the zooplankton decline (Carrasco & Lozano 1989).

Distribution of zooplankton is strongly variable over time and space, and in upwelling waters, zooplankton distribution is highly aggregated (Peterson 1998, Morales et al. 2010). This strong aggregation can affect temporal observations of the water column when based on fixed stations. Despite these potential sources of errors for sampling, long-term studies based on fixed stations have proven useful to examine temporal trends in zooplankton (Mackas & Beaugrand 2010).

Although underlying mechanisms explaining the changes in community structure of copepods as a response to changing conditions are unclear, the evidence shows that alterations in water mass distribution and circulation patterns may be an important factor (Peterson et al. 2006). However, changes in the abundance of particular species can also be induced by direct influence of oceanographic factors, of which temperature (e.g. Ulloa et al. 2001) and probably food conditions must be considered as key ones. Oxygenation of the water column should also be considered as an important factor (Wishner et al. 2013). Copepod diversity correlates with depth of the OMZ (Hidalgo et al. 2012), suggesting that some species may not tolerate conditions of hypoxia, and therefore, their distribution seems affected by the ascent of the OMZ forced by upwelling (Wishner et al. 2013). More upwelling can cause increased hypoxia and hence alterations of the copepod community. In sum, there are top-down and bottom-up factors acting on copepod communities, forcing their composition, size structure and species diversity and abundance (Mackas & Beaugrand 2010). Both types of community control can be altered by modifications of the physical environment. In this regard, alterations of water mass distribution and circulation should be important processes altering the physical, chemical and biological environment (Peterson et al. 2006).

We conclude that increased coastal upwelling in the HCS may gradually and substantially modify the zooplankton community. This effect could also impact higher trophic levels, such as fish populations, for example by modifying the available food spectra. Early stages of fishes seem more sensitive to changing food conditions, and this can impact fish recruitment rates (Cahuin et al. 2009). Variability of some important fish populations in the HCS, such as jack mackerel, Chilean hake and the small, pelagic sardines and anchovies, might relate to some of these climate-associated impacts of upwelling on the biology of this highly productive marine ecosystem.

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