Growth and production of the copepod community in the southern area of the Humboldt Current System

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Abstract

Zooplankton production is a critical issue for understanding marine ecosystem dynamics.~~structure and dynamics, however, its time-space variations are mostly unknown in most systems.~~ In this study, estimates of copepod growth and production (CP) in the coastal upwelling and coastal transition zones off central-southern Chile (~35-37° S) were obtained ~~from annual cycles~~ during a 3-year time series (2004, 2005, and 2006) at a fixed shelf station, and from spring-summer surveys during the same years. To estimate copepod production (CP), we used published and unpublished C-specific growth rates (*g*) of dominant copepod species from previous studies in the same upwelling zone, and copepod biomasses assessed in our study. A preliminary analysis of compiled data of copepod growth (*g*) showed that ~~varied extensively among species and under variable environmental conditions; however,~~ *g*-values were not correlated to either ~~near surface~~ temperature or copepod size. Therefore, we used mean *g*'s of species and their corresponding biomasses to assess species production and added CP. Copepod biomass (CB) and CP were higher within the coastal upwelling zone (<50 km) and both decreased substantially from 2004 to 2006. Integrated a~~A~~nnual CP ranged between 24 and 52 g C m^{-2} year^{-1} with a mean annual P/B ratio of 7.3~~2.7~~. We estimated that CP could consume up to 60% of the annual primary production (PP) in the upwelling zone but most of the time was~~is~~ around 8%. Interannual changes in CB and CP values were associated with changes in the copepod community structure. Dominance of large-sized forms shifted to small-sized species~~, the dominance of large-sized forms replaced by small-sized species~~ from 2004 to 2006. This change was also accompanied by more persistent ~~and time extended~~ upwelling during the same season of each year~~al period~~. Extended upwelling may have caused large losses of CB from the upwelling zone due to ~~an~~ increased ~~in~~ offshore advection of coastal plankton. On a larger scale, these results suggest that climate-related impacts of

incremented~~asing~~ wind-driven upwelling in ~~coastal ~~upwelling systems may cause~~generate~~ a negative trend in zooplankton biomass.

Key Words: Copepods, Growth Rate, Humboldt Current, Biomass, Secondary Production

1. INTRODUCTION

Variability in biological production of lower trophic levels is a critical issue for understanding the dynamics of marine ecosystems of the world ocean (Mann and Lazier, 1991). In this context, zooplankton is a key component considering their ecological role in capturing, retaining and transferring freshly produced phytoplankton-carbon toward higher levels (Poulet et al., 1995; Kimmerer et al., 2007). Despite this wide recognition, there are not many studies targeting zooplankton secondary production and its time-space variability in the ocean, making difficult to assess the actual role of zooplankton in controlling or limiting biological production of high trophic levels, including fish, mammals and seabird populations (Aebischer et al., 1990; Beaugrand et al., 2003, Castonguay et al., 2008). Zooplankton secondary production is the total biomass produced by a population or community per unit of area or volume over a unit of time (Kimmerer et al., 2007), regardless the fate of such biomass (Winberg, 1971). There is, however, not a single and simple method to estimate zooplankton production and growth rates, but several approaches have been applied and different results obtained. For instance, daily estimates of production can vary substantially when comparing mathematical models with enzymatic approaches (Avila et al., 2012), or significant deviations can occur when applying artificial cohorts methods, as compared with metabolic approaches~~;~~ (Lin et al., 2013); even more, most of the traditionally applied methods are logistically difficult to apply as to characterize time-space variations in these rates (Sastri et al., 2013~~; Mitra et al., 2014~~).

In the case of copepods, the dominant components of zooplankton biomass in the oceans, there have been several attempts to develop theoretical and empirical relationships between zooplankton production and the factors known to affect their growth. For instance, temperature has been widely reported as a fundamental factor influencing copepod growth (Huntley and

L~~o~~ópez, 1992; McLaren, 1995; Escribano et al., 2014), while body size should also be considered as a fundamental driver on the basis that growth, as any other physiological rate, must be modulated by allometric effects (West et al., 1997). In fact, both variables have motivated the development of the metabolic theory of ecology (Brown et al., 2004) which proposes that animal growth is predictable from body size and environmental temperature. Meantime, other studies have provided evidence that food resources can often limit zooplankton growth (Hirst and Lampitt, 1998; Vargas et al., 2010~~09~~). Which one of these factors is more important, or upon which conditions, any of these effects are noticeable and can thus be used as a growth predictors are still open questions in pelagic ecology.

~~In order to obtain realistic estimates of zooplankton growth and production, specific approaches should be adopted for any particular condition or community but ~~O~~o~~ne of the critical problems for the calculation of secondary production is having reliable estimates of in situ growth rates of the species comprising the bulk of the zooplankton biomass in a given region or area. As mentioned above, weight or C-specific growth rate (*g*) has been related to temperature, food conditions, and body size, but in most cases direct estimates of *g* show no relation or ~~very ~~weak relationships with these factors (e.g. Lonsdale and Levinton, 1985; Chisholm and Roff, 1990; Hutchings et al., 1995).

These relationships may also depend on the taxonomic group being considered (Hirst and Bunker, 2003).

Zooplankton production has received very little attention in the eastern south Pacific. In this region, t~~T~~he Humboldt Current System (HCS) is one of the Eastern Boundary Currents (EBC´s) known by its high biological productivity (Mann and Lazier, 1991), attributed usually to the high levels of primary production in the coastal zone (>10 g C m^{-2}d^{-1}) sustained by wind-driven upwelling (Daneri et al., 2000; Montero et al., 2007). Copepods and euphausiids dominate the zooplankton biomass in the HCS off Chile (Escribano et al., 2007; Riquelme-Bugueño et al., 2012), however, very few studies on zooplankton production are available. Escribano and McLaren (1999) estimated secondary production for the dominant copepod *Calanus chilensis* in the upwelling region off northern Chile, and Vargas et al. (2010~~09~~) estimated growth and production of three copepod species in the upwelling region off central-southern Chile during an annual cycle. Riquelme-Bugueño et al. (2013) described the population dynamics and biomass production of the Humboldt Current "Krill", *Euphausia mucronata*, for the same region. Although euphausiids may occasionally become very abundant in this region, the bulk of zooplankton biomass in the coastal upwelling zone is dominated by copepods, and, more specifically, by small-sized (<2 mm) copepods (Escribano et al., 2007). Hence, the latter may well reflect the dynamics of the whole zooplankton biomass and production in the southern area of the Humboldt Current (Hugget et al., 2009). A group of about 10 copepod species comprises >90% of the total numerical abundance (Escribano et al., 2007; Escribano et al., 2012), including the small calanoid *Paracalanus* ~~cf~~Cf. *indicus*, which exhibits continuous reproduction throughout the year in the regions off northern and central-southern Chile, apparently with >20 generations a year (Escribano et al., 2014). Also included is the small calanoid *Acartia tonsa*, with multiple generations per year (Vargas et al., 2010~~09~~). The cyclopoids *Oithona similis* and *O. nana*, and the poecilostomadoids *Triconia conifera*, *T. media*, and *Corycaeus typicus* are also abundant (Hidalgo et al., 2010). Larger-sized (>2 mm) copepods are mainly represented by *Calanus chilensis* in the northern region and *Calanoides patagoniensis* in the central-southern region (Hidalgo et al., 2010), and~~,~~ occasionally, by *Rhyncalanus nasutus* and *Eucalanaus* spp, including *E. inermis* and *E. glacialis* (Castro et al., 1993; Hidalgo et al., 2010).

In this work, we first compiled published and unpublished (previous studies) data on ~~assessed~~ growth rates of the dominant copepod species found in the coastal upwelling zone off ~~central-southern~~ Chile, and assessed their relationships with temperature, under which their growth was measured, and with copepod body size. ~~during the spring-summer period and under time-space variations in environmental conditions, including temperature and food resources, which allowed us to test the influence of copepod size and temperature on the C-specific growth rate (g).~~ Secondly, we used these~~a~~ species-dependent *g* values and copepod biomass to calculate copepod ~~biomass~~ production and its ~~its~~ time-space variability in the domain of the coastal upwelling and coastal transition zones, thereby contributing to provide the first estimates of copepod community production in the Humboldt Current, and to understanding the factors causing time-space variability in copepod growth and production in this upwelling region.

2. METHODS

2.1. Field studies

Copepod abundance estimates were monthly obtained from a 3-years time series (January 2004 to~~-2005, and~~ December 2006) at a fixed shelf station (Station 18, ~36.5° S, ~~~-~~30 km from the coast) off Concepción.~~,~~ During the spring-summer of the same years, spatial surveys were conducted to sample ~~-including monthly samplings, and from spring-summer surveys during the same years (Table 1), with~~ the area~~stations~~ located between~~in~~ the coastal and the coastal transition zones (up to 180 km from the coast) off central-southern Chile (35°-39° S~~; Fig. 1~~). The spatial cruise in 2004 was carried out during 14-21 January completing a grid of 29 stations. In 2005 the cruise was performed during 7-15 December with a grid of 17 stations. Finally, the 2006 cruise took place during 10-25 November with a grid of 22 stations. Fig. 1 illustrates position of station 18 and sampling stations for the spatial cruises.

At Station 18 and during the spatial surveys, zooplankton sampling was performed using a 1 m^2 Tucker Trawl net equipped with 200 µm mesh size nets and a calibrated flowmeter. At the

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time series, the net was trawled from 80 m deep to surface, providing integrated samples; details on sampling procedures are described in Escribano et al. (2007). Samples were immediately split onboard with a Motoda splitter and a fraction (usually ¼) was frozen at -20° C for zooplankton biomass, and the rest of the sample was fixed with formalin 10%.~~Space variations in copepod abundance were assessed through spring- summer, oceanographic cruises covering the upwelling and the coastal transition zones (up to 180 km from the coast). The sampling grid varied slightly from year to year (Fig. 1 and Table 1).~~ During the~~se~~ spatial surveys, similar procedures as those of the time series study were applied to obtain hydrographic data and zooplankton samples. For zooplankton sampling, however, the Tucker Trawl equipment was deployed down to 200 m depth, or near bottom in shallower stations. CTDO casts and bottle samples were obtained at each station, together with chlorophyll–a (Chl-a) estimations in at least 7-9 depths in the upper 100 m layer~~depth~~ at each station. Continuous profiles of temperature were used to assess depth of the thermocline and derive mean temperature of the mixed layer, but thereafter temperature at 10 m depth was used to relate with CB and CP, as suggested in previous studies (Escribano, 1998), whereas Chla at 5 m depth was related to CB and CP, because Chla at this depth represents approximately the phytoplankton maximum at Station 18 (Morales and Anabalón, 2012).

To assess upwelling conditions during the time series, ~~In addition,~~ wind data were obtained from a meteorological station (shown in Fig. 1) since August 2004; speed and direction were measured every 5 min. and vector averaged for every hour as to assess wind forcing and estimate an upwelling index:

$$\tau = \rho \; cd \; V|V| \qquad (1)$$

where τ= wind stress (kg s m^{-2}), ρ= air density assumed as 1.2 kg m^{-3}, cd=is an empirical constant= 0.0013, and V is the alongshore component of the wind in m s^{-1}.

~~Station 18 represents an oceanographic time series study launched by COPAS Center (Escribano and Schneider 2007) and it includes rosette CTDO deployments and plankton monitoring. Zooplankton sampling was performed on a monthly basis using a 1 m^{2} Tucker Trawl net equipped with 200 µm mesh size nets and a calibrated flow meter; deployments from 80 m depth to surface provided integrated samples; details on sampling procedures are provided in Escribano et al. (2007).~~

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2.2. Copepod biomass and growth

Copepod biomass is needed to calculate secondary production. Biomass ~~estimates~~ for each species was~~e~~ obtained from mean weight estimates and length-weight relationships, available from the literature, for copepodid stages of same species~~(REFS)~~. For this purpose, we first calculated the mean body size of all copepodid stages for each species (Table 1~~2~~), and then we applied a length-weight regression to estimate mean weight (as dry weight). Length-weight regressions were obtained from literature (Chisholm and Roff, 1990; Hofcroft et al., 2002) and species biomasses were estimated as:

$$B_i = \sum_{i=1}^{N}(w_i n_i)0.4 \qquad (2)$$

where B_i is the species-i biomass (µg C m^{-3}), W_i and n_i are the mean dry weight (µg) and abundance (number m^{-3}) of the i-species and 0.4 is the conversion factor to µg C from dry weight (Escribano et al., 2007).

Several studies carried out in the last few years in the upwelling zone off Chile have provided estimates of in situ growth rates (*g*) of copepods for different copepodid stages and species (Table 1~~2~~). ~~Most of ~~T~~t~~hese studies have applied the molting rate method, by using artificial cohorts (review in Harris et al., 2000). We made use of this set of estimates to examine the influence of temperature and copepod size on growth and, from that, we attempted to develop an empirical equation to predict in situ *g*'s from these variables for each of the dominant species in the samples.

2.3. Data analyses

Copepod production for each species was estimated from their biomass and *g* values as to obtain total production, such that:

$$CP = \sum_{i=1}^{N}(B_i\, g_i) \qquad (3)$$

where CP = total copepod production (mg C $m^{-3}d^{-1}$), B_i= as defined above and g_i= C–specific growth rate (d^{-1}) for each i-species.

CP was calculated for each sampling station during the spatial cruises and each of the monthly samplings during the time series. CP integrated values in the water column ~~(trapezoidal method)~~ were obtained by multiplying by the sampling depth and, in the case of the time series, an integrated annual value was estimated by applying the trapezoidal method over the time axis. An estimate of the annual production/biomass ratio (P/B) was also obtained. For this, annual integrated CP and monthly mean biomass were used. Oceanographic data were all processed to construct spatial contours (cruises) and temporal contours (time series) and the ranges of temporal variation of temperature and Chla were derived for the mixed layer . Similar procedures were applied to copepod abundance, biomass and production as to identify space-time patterns. Relationships between *g* and temperature and body size were tested by linear and non-linear regression methods, and goodness-of-fit was tested by correlation, the determination index and ANOVA. Meantime, eventual associations among copepod variables and oceanographic factors were assessed by General Linear Models (GLM) and Stepwise Multiple Regression (1-step) applied on log-transformed data on copepod abundance, biomass and CP. GLM can test linear effects of multiple continuous variables (e.g. environmental) on single dependent responses, such as CB or CP. Influences of single or multiple variables are then tested with F-statistics. Meantime, Stepwise Multiple Regression can selectively remove non-significant variables and find the best fitted model to account for variation of the response variable (CB and CP in this case).

3. RESULTS

3.1. Oceanographic conditions

The three spatial surveys were carried out during the period of coastal wind-driven upwelling, as evidenced by the surface distributions of temperature and salinity (Fig. 2). During the 2004 cruise, recently upwelled waters (<13° C and salinity >34~~ psu~~) were found in the northern and central areas in the coastal band; the offshore extension of these waters in the central area indicated~~s~~ that there may have been one or more (sub) mesoscale eddies located in that area. Coastal upwelling activity was also observed during the 2005 cruise but colder waters (<12° C) with higher salinities were restricted to the nearshore, except for lower salinity water (~33) off and within the Arauco Gulf (~37° S). In the 2006 cruise, upwelling was concentrated in the northern area and restricted to a narrow coastal band (<40 km from shore) so that, in general, waters were less saline compared to 2004 and 2005. Upwelling conditions during the surveys were also evident from the surface distributions of dissolved oxygen (DO) and Chl-a concentration (Fig. 3). Remarkable differences in DO distribution among the cruises were found. In 2004, DO was within saturated levels (>5 mL L^{-1}) over most of the region, except in the central area which showed lower oxygenation (<4 mL L^{-1}) in a zonal band where higher salinities were detected, and an oversaturated zone (>6 mL L^{-1}) in the northern part, coinciding also with higher salinities (Fig. 2), together with high Chl-a levels (>8~~10~~ mg m^{-3}). During the 2005 cruise, oxygenation levels were lower (<5 mL L^{-1}) in the entire region and more so in the coastal zone where higher salinities were observed, except in area around the Arauco Gulf. Chl-a distribution was similar to that in 2004, with high levels in the nearshore area in the northern and central areas. In 2006, highly oxygenated conditions (>~~6~~5 mL L^{-1}) prevailed in most of study region, except in the coastal band. High levels of DO coincided with greater Chl-a concentrations in the entire region compared to 2004 and 2005 (Fig. 3, lower panel).

~~During the time series study, daily-integrated data of wind stress, and their monthly means, were estimated for the period from August 2004 to May 2007. Since data for the time series were available from January 2004 through December 2006, wind data were divided into two periods having the same number of days and same months as to assess whether upwelling conditions had~~

~~changed during these periods. There was a clear seasonality in upwelling favorable winds (T's with positive values), such that potential for upwelling initiated in August and remained favorable until April-May of each year, while downwelling conditions prevailed in the winter period between June to early August (Fig. 4). In the first period of the time series (2004-2005), there were 205 days favorable for upwelling (T >0) and downwelling was intense and persistent throughout early winter (May 2005) to late winter (August 2005). In the second period (2006-2007), there were 255 days favorable for upwelling and downwelling conditions in winter were less intense and persisted for a shorter time (~115 days) compared to the first period (Fig. 4).~~

At Station 18, the three annual cycles based on monthly sampling clearly revealed a seasonal pattern, characterized by an upwelling period (September-March) and a non-upwelling period (May-August) (Fig. ~~5~~4). Mean temperature a 10 m depth was 12.6 °C for the entire time series ranging between 10.6-14.5 °C. During the upwelling period, the ascent of cold waters (<12° C) reached~~s~~ a shallow depth (below 20 m), together with surface warming in the upper layer during the summer, whereas warmer waters (>13° C) prevailed below 30 m depth upon the non-upwelling period in winter (Fig. ~~5A~~4A). Upwelling also brings to the surface layer high salinity water (>34~~ psu~~) whereas a layer of freshwaters appears in winter such that higher stratification is generated due to increased river runoff (Fig. 4~~5~~B). During active upwelling~~ conditions~~, oxygen-deficient conditions dominated in shallow subsurface waters (<20 m depth) due to the shallowness of the oxygen minimum zone (OMZ) in the region. By contrast, the water column beca~~o~~me~~s~~ oxygenated down to near bottom during non-upwelling (Fig. ~~5C~~4C). The annual bloom of phytoplankton started~~s~~ in early spring (September-October), coinciding with the setup of upwelling, and Chl-a remained~~s~~ high until the end of summer in most cases. Mean Chla in the mixed layer (5 m depth) during the time series was 3.0 mg m^{-3} with a range of 0.01-46.3 mg m^{-3}.

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Seasonality of upwelling conditions was also clearly reflected in the upwelling index, estimated as wind stress (τ). This index was ranged between -54 and 34 (kg $s^{-1}m^{-2}$) and negative values dominated during the autumn-winter, whereas in the spring-summer most of the daily integrated values of τ resulted positive, indicating favorable winds for upwelling.

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3.2. Copepod growth rates

Several studies in the last few years have estimated *g* for dominant copepod species from the Chilean upwelling zone; most of them are based on laboratory studies ~~simulating~~ under a variety of temperature and food conditions representing those in the field from where animals were captured and, therefore, their results can be considered as~~represent~~ reliable estimates of copepod growth in nature~~g~~. A summary of estimates of *g* for different developmental stages and species, including body size of tested individuals, is provided in Table 1~~2~~. Because of potential allometric effects on growth rate, we attempted to develop a size-dependent model to predict *g* as a function of body size (Fig. 5~~6~~A). Although an apparent decrease in *g* with size is observed, no significant correlation between these two variables was found (P >0.05) after testing with different lineal (GLM) and non-linear models.

Since temperature has been established as an important factor affecting growth rate of copepods (Huntley and Ló~~o~~pez, 1992~~,~~; Gillooly et al., 2001), it has been suggested~~was thought~~ that this variable could be a suitable predictor of *g* under variable environmental conditions (e.g. Huntley and López, 1992; Lin et al., 2013). For all the available *g* estimates, we tested the influence of ~~in situ simulated~~ temperature under which g was estimated; ~~also,~~ no significant effects were found (P>0.05) after lineal (GLM) and non-lineal models (Fig. ~~6B~~5B). A combined model using both body size and temperature, as that described by Lin et al. (2013), did not result in a significant association~~differences~~ either. On this basis, mean values of *g* for some of the dominant species were thus calculated and used to estimate their specific production rates (Fig. ~~7~~6). In these analyses we did not include some species, such as *Oithona* spp., *Oncaea* spp., *Corycaeus* spp., *Pleurommama* sp. and *Centropages* sp., for which no estimates of g were available. For the~~o~~se species~~ in which no estimates of g were available~~, a grand mean of copepod growth rate, calculated from all available data (Table 1), ~~rate ~~was applied (mean ± SD: 0.27 ± 0.133 d^{-1}) for later estimates of CP.

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3.3. Copepod biomass and production

Copepod abundance (N), biomass (CB) and production (CP) were estimated as annual means for ~~both the spatial surveys and ~~the time series and mean values during the spatial surveys (Table 2~~3~~). In both cases, strong variability in N, CB and CP was observed (coefficient of variation:25-50%). Spatial variability of N relates to a greater aggregation of copepods in the upwelling zone and decreasing values towards the offshore (Fig. 7~~8~~). The highest values of CB and CP were also concentrated in the upwelling zone although there was a strong variation from year to year, with lower values in 2004 (Fig. ~~9~~8).

Copepod species in three size categories, in according to their total length: small (<1. 5 mm), medium (1.5 - 2.5 mm) and large (>2.5 mm), varied substantially from year to year (Table 3~~4~~). Small-sized species increased in abundance from 2004 to 2006, whereas large-size species tended to slightly decrease~~d~~ in 2006 compared to 2005, although they were scarce in 2004~~the same years~~. The distribution of these 3 size categories also varied from one year to another (Fig. 9~~10~~). Medium size species were absent in 2004 and large-sized species were more abundant in the upwelling zone, while small-sized species became more abundant in 2005 and even more so in 2006 and concentrated in the upwelling zone.

From the time series at Station 18, no seasonal pattern or trend in copepod abundance was detected (Fig. 10~~1~~A), as was the case for CB and CP (Fig. 10~~1~~B); in both cases, lower values were detected during 2006. Integrated annual CP at station 18 was 52.2 g C m^{-2} y^{-1}, 32.8 g C m^{-2} y^{-1} and 24.0 g C m^{-2} y^{-1} for 2004, 2005 and 2006, respectively. ~~From annual means of monthly integrated biomasses, the ~~A~~a~~nnual P:B ratios obtained were 7.1~~2.5~~, 7.4~~2.8~~ and 7.5~~2.9~~ for 2004, 2005 and 2006, respectively. The daily P:B ratio was, on average, 0.24. The variance of CB for each year, estimated from the coefficient of variation, was 16%, 27% and 24% for 2004, 2005 and 2006, respectively.

3.4. Environmental effects on biomass and production

Using the data from the spatial surveys, a stepwise multiple regression was applied to test the effect of year of sampling and oceanographic conditions on N, CB and CP. Copepod data were previously log-transformed and a 1-step function was applied. Significant differences among years in N and CP were found. Chla correlated positively with N, whereas Chla, DO and OMZ depth correlated with CP (Table 4~~5~~).

For the time series data, we used cross-correlations between copepod variables and oceanographic conditions (including temperature, Chl-a, DO, and OMZ depth) to test for eventual associations. Although all the oceanographic factors showed a seasonal pattern, characterized by upwelling and downwelling periods (Fig. ~~5~~4), copepod abundance, biomass and production did not but their monthly fluctuations are rather random (Fig. 10~~1~~). Therefore, it was not surprising that no significant correlations (P>0.05) between N, CB and CP and derived oceanographic variables were found.

4. DISCUSSION

The oceanographic conditions observed during this study are those expected from previous studies in the upwelling zone (Strub et al., 1998; Hidalgo et al., 2012; Morales and Anabalón, 2012) and the coastal transition zone (Letelier et al., 2009). The spatial surveys, conducted during spring-summer conditions, show that upwelling conditions prevailed in a coastal band along the study are of about 50 km width, coinciding with the isobath of 200 m (shown in Fig. 1). These conditions are characterized by colder, more saline and less oxygenated water. This coastal band constitutes the main habitat of a few dominant copepods species (Hidalgo et al., 2010), and as evidenced by their aggregation over the shelf (Fig. ~~8~~7). Dominant *Paracalanus* Cf. *indicus* and *Acartia tonsa* tend to concentrate in the nearshore, or upwelling zone, whereas larger size calanoids, such as *Calanus patagoniensis* and *Rhyncalanus nasutus* exhibit greater concentration offshore (Hidalgo et al., 2010). However, at times during intense upwelling the whole community can be advected offshore into mesoscale eddies (Morales et al., 2010). Therefore same species are~~, however,~~ present in the coastal transition zone although in lower abundances.~~, probably as a result of their~~ O~~o~~ffshore transport by mesoscale eddies (Morales et al., 2010), which are originated in the upwelling zone, can~~and~~ move plankton mostly in a westward direction (Hormazabal et al., 2013). Our findings however indicate that m~~M~~ost of the copepod production (CP) takes place in the coastal upwelling zone, where food resources (as represented by Chl-a) are also concentrated. Although, at times during the year Chla becomes low (<1 mg m^{-3}), even within the upwelling zone. In this respect, Chla itself should not considered as a suitable indicator for food resources for omnivorous copepods in this system, which are capable of efficiently use a heterotrophic diet when Chla is low (Vargas et al., 2006).

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If most CP occurs in the upwelling zone, Station 18 is therefore a suitable location to assess its temporal variability. Oceanographic variability there also clearly shows the upwelling signal (Sobarzo et al., 2007~~a~~; Montero et al., 2007; Morales and Anabalón, 2012). At this location, the copepod community has been well studied (Escribano et al., 2007;~~,~~ Hidalgo and Escribano, 2007), and even though some seasonal signals in abundance and age-structure of some species have been described (Castro et al., 1993;~~,~~ Hidalgo and Escribano, 2007), most populations can grow and reproduce throughout the year (Vargas et al., 2010~~09~~;~~,~~ Escribano et al., 2014). ~~, suggesting that CP is a process taking place year-round.~~

~~-~~It has been suggested that food conditions (quantity and quality) may be an important factor determining copepod growth and production (Huntley and Boyd, 1984; Hirst and Lampitt, 1998; Lin et al., 2013). However, evidence from field studies has shown weak correlations between growth rate of copepods and food conditions. In this regard, Hutchings et al. (1995) found no correlation between copepod growth rate and Chl-a in the Benguelas upwelling system, while Peterson et al. (1991) suggested little effects of food availability on copepod production during summer in Skagerrak (north sea). In our study, we found a significant correlation between copepod abundance and Chl-a during the spatial surveys. This positive correlation was also found between CP and Chl-a. It should be noted, however, that a significant correlation of copepod abundance and CP with Chl-a does not necessarily means that copepod growth~~CB~~ is being controlled by phytoplankton biomass. Copepod abundance and production~~CP~~ also correlated~~s~~ significantly with low oxygen and a shallow OMZ which, the same as for higher Chl-a levels, coincide in the zone were greater CP occurs. Thus, t~~T~~he question on whether CP can be controlled or limited by phytoplankton biomass cannot be answered from the spatial survey just because of spatial correlation. On the other hand, no correlation between Chl-a and CP was found in the time series data, and copepod abundance, CB and CP appeared uncoupled to the seasonal pattern of

Chl-a. Food conditions, in terms of quality, could also be considered as affecting copepod growth (Peterson et al., 1991). During the same spatial surveys, Morales and Anabalón (2012) showed that both nanoplankton and microplankton fractions as potential food resources for copepods were abundant, diverse and widely distributed over the upwelling zone, so that food limitation for copepodid growth seemed unlikely, at least over the upwelling zone. In the context of food effects on CP, in this upwelling system dominant small-sized copepod can prey on both autotrophic and heterotrophic components of the nano- and microplankton, being able to even shift their diet depending on the available food offer during the year cycle (Vargas et al., 2006). In the upwelling zone, the nanoplankton fraction remains high and diverse throughout seasons (Böttjer and Morales, 2007: Anabalón et al., 2007). It has therefore been suggested that copepods in this region can grow without food limitation year round (Escribano et al., 2014).

In our approach to estimate copepod production, the use of species-dependent growth rates may be justified on the basis that *g* is a physiological rate controlled by two processes, development rate (DR) and tissue accumulation. In fact, estimating DR is the most widely used approach to assess growth rate of copepods. DR has been widely studied in copepods (McLaren and Leonard, 1995; Heinle, 1969) and it is considered a species-dependent attribute (Heinle, 1969; Atkinson, 1994). Nevertheless, within species g may strongly vary (Runge and Roff, 2000) and the use of a constant *g* is certainly much more difficult to justify. In field and laboratory studies, *g* of copepods has been found to vary as a function of temperature (Huntley and Ló~~o~~pez~~s~~, 1992; Hirst and Bunker, 2003)~~)~~, food conditions (Checkley et al., 1980; Finlay and Roff, 2006) and body size (Hirst and Sheader, 1997), although size effects may not be reflected at the intra-specific level but among species (Banse, 1982; Peters, 1983). Temperature on the other hand may strongly affect g by accelerating or retarding the development of copepods (McLaren, 1995). It is therefore expected that *g* would correlate positively with temperature. From our oceanographic surveys, however, temperature seems to vary in a rather narrow range (~ 3~~11.5 - 13.5~~° C) in the mixing layer of the upwelling zone, where dominant copepods aggregate and whose ~~diel~~ vertical distribution is restricted by a shallow (<50 m) OMZ during the upwelling period (Escribano et al., 2009). Thus, because of its little variation within the upwelling zone of central/southern Chile, temperature may not be the key factor controlling *g*. Variation in temperature could also affect copepod size through its effect on development rate (Escribano et al., 2014), and thus affecting our biomass estimates. However, because of weak seasonal signal of temperature copepodid sizes do not follow a seasonal pattern in this region (Hidalgo and Escribano, 2007), and hence this potential effect remains uncertain.

It is important to consider that copepod production represents only a fraction of total secondary production for the upwelling zone. Our estimate of CP does not consider molt and egg production of copepods either, but only somatic biomass production. Also, estimates of CB and CP are mostly based on late copepodid stages, since early stages (nauplii, C1-C3) were not assessed since they are difficult to identify and some of them could be undersampled by the 200 µm net. The assessment of all stages for a given species is a complex task, and previous studies have shown a numerical dominance of late stages through the year cycle, due to rapid development of young stages and their greater mortalities (Hidalgo and Escribano, 2007; Escribano et al., 2014). Thus, biomass and production of young stages have not been accounted in our estimates, although because of their small biomasses and possibly less abundance this missing fraction may not be substantial.

Our estimates of copepod growth rates and production are comparable to values reported from other systems. Hutchings et al. (1995) found a CP in the range of 17 - 150 g C m^{-2}y^{-1} for the similar upwelling system of Benguelas, whereas Mackinnon and Duggan (2003) estimated a CP of 3.4 g C m^{-2}y^{-1} for subtropical water in north west Australia. Regarding the growth rate (*g*), Peterson et al.

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(1991) found a *g* of 0.1 d^{-1} for adults and about 0.27 d^{-1} for juveniles copepods, which is exactly the same mean value we found for the whole copepod community and Lin et al. (2013) reported a *g* in the wide range of 0.01 - 0.79 d^{-1} for medium size copepods from the east China sea. With respect to the bulk of zooplankton, in the time series at Station 18 total zooplankton biomass (TZB) was available for the same period, as published in Escribano et al. (2007). TZB shows more variability than copepod biomass (CB) (Fig. 11~~2~~A) and, on occasions, CB may account up to 96% of TZB although on average our estimate of CB represents nearly 40% of TZB. Meantime, monthly means of primary production (g C $m^{-2}d^{-1}$) in the same upwelling zone (Daneri et al., 2000) indicates that copepod production could take up to 60% of the C being produced by phytoplankton (winter 2004) although the mean conversion of PP into CP was about 8% (Fig. 11~~2~~B). This figure is in according with global mean estimates of the effect of mesozooplankton on PP (as the percent PP consumed per day: mode 6%, mean 23%) and decreases exponentially with increasing productivity (Calbet, 2001).

Recently, Escribano et al. (2012) and Pino-Pinuer et al. (2014) have described a negative trend in copepod biomass and abundance from the beginning of the time series at Station 18 (2002) to more recent years (2010 - 2012). Both works related this decrease in copepods with a gradual increment in upwelling intensity in the coastal zone off Chile upon increased southerly winds in the last decade (Garreaud and Falvey, 2009). In this study, CB and CP significantly decreased from 2004 to 2006 at Station 18, although this trend was unclear in the spatial surveys. Copepods are strongly subjected to offshore advection during upwelling (Peterson, 1998;~~,~~ Keister et al., 2009; Morales et al., 2010). When examining the spatial patterns of oceanographic conditions, it appears that in 2005 and 2006 the upwelling focuses were concentrated near the location of Station 18, judging by low oxygen water in that area (Fig. 3), as compared to 2004 when the upwelling focus was located farther from the nearshore. It is therefore likely that copepods populations were

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more subjected to offshore advection in 2005 and 2006. Most advective forces take place in the mixed layer (upper 50 m) and even though we obtained depth-integrated samples (0-200 m) most copepods, as indicated above, aggregate in this layer and thus being advected offshore.

Another possibility for lower biomass and production in 2005 and 2006 at Station 18 could be explained in terms of food-limitation for copepod growth, as suggested for other systems (e.g. Hirst and Lampitt, 1998). Nevertheless, we found no significant differences in phytoplankton biomass (as food indicator) among the three years. Also, primary production (PP) estimated monthly at Station 18 during the same period, showed that the annual cycle of PP almost repeated every year (Montero et al., 2007). ~~Furthermore, off Central/southern Chile, copepods can sustain their reproduction and growth throughout the year, despite the seasonal bloom of phytoplankton, by switching their diet from autotrophic preys to an omnivorous diet (Vargas et al., 2006). Therefore, it is unlikely that annual CP could be limited by food in this upwelling region.~~

Since copepods mostly concentrate in the Ekman layer (<50 m) during upwelling, as constrained by a shallow OMZ (e.g. Escribano et al., 2009), more offshore advection, upon increased upwelling, can cause biomass loss from the coastal zone. In fact, from our analysis of wind data we found~~showed~~ that favorable conditions for upwelling were more persistent (lasted longer) during the second part of the time series and hence promoting more export of CB to offshore areas. The upwelling index revealed that from year to year the number of days favorable for upwelling (-daily integrated τ >0) varied substantially during the upwelling season (September to March). The number of days having positive values of τ was greater in 2006 than in 2005 and 2004 (Fig. 12A) .

Active upwelling also promotes formation of mesoscale intra-thermocline eddies (Hormazabal et al., 2013) which can also enhance plankton export from the upwelling zone.

The effect of these physical processes would thus be reflected in lower CP at Station 18. In according to Keister et al. (2009), offshore advection from the upwelling zone constitutes an efficient mechanisms to transport carbon~~C~~ to oceanic regions. From the viewpoint of biological production of the upwelling system, however, this should be considered as a C loss. Over an annual basis, we estimated how much of the C produced by phytoplankton is converted into CP and CB, and the annual deficit in CP that biomass loss can cause due to more advection driven by increased upwelling. The impact of greatly incremented upwelling is shown in Fig. 12B~~3~~, which illustrate how combined factors and processes, such as upwelling conditions, CP, CB and primary production may have interacted during the time series as to cause a reduction in copepod production in the upwelling zone. This schema illustrates observed copepod production (CP) and biomass (CB) on an annual basis, as well as an estimate of expected CP (CPe) assuming a 8% of conversion efficiency of PP into CP. CPe remains constant because PP was assumed as constant also over an annual basis. Then the potential biomass loss due to incremented offshore advection in 2005 and 2006 is illustrated (Fig. 12B). It is important to stress that upwelling intensity may not significantly change from one year to another in average, but the length and continuity of the upwelling season can be the key process causing more biomass loss on an annual basis.

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~~Table 1~~

~~Summary of cruises and the time series study in the coastal upwelling region of Central/southern Chile to estimate copepod biomass and production in relation to upwelling conditions. Three spatial cruises were conducted (FIP 2004, 2005 and 2006) and a monthly time series study at the fixed Station 18.~~

~~**CRUISE**~~	~~**PERIOD**~~	~~**SEASONAL CONDITION**~~	~~**No. STATIONS**~~
~~FIP 2004~~	~~14 – 21 November~~	~~spring/upwelling~~	~~29~~
~~FIP 2005~~	~~7 – 15 December~~	~~summer/upwelling~~	~~17~~
~~FIP 2006~~	~~10 – 25 November~~	~~spring/upwelling~~	~~22~~
~~Time Series~~	~~Jan 2004 to Dec 2006~~	~~all seasons~~	~~Single (fixed)~~

Table 1~~2~~

C-specific growth rates and size ranges for different developmental stages of copepods from the coastal upwelling zone off Chile. Estimated growth rates (*g*) were obtained from the molting rate method applied under in situ simulated conditions of temperature. Satiating conditions of food were assumed. ~~Developmental stages are copepodids (C1 to C5) and adult females (AD ♀)~~ Estimates of g were obtained at the northern upwelling region of Chile (Nor) or at the southern region (Sou).

~~SPECIE~~	~~STAGES~~	~~SIZE RANGE~~	~~g~~	~~TEMP.~~	~~REFERENCE~~
		~~(mm)~~	~~(d^{-1})~~	~~(°C)~~	
~~*A. tonsa*~~	~~C1, C2, C3, C4,~~ ~~C5, AD ♀~~	~~0.53 – 1.33~~	~~0.248~~	~~12~~	~~Hidalgo P. (Unpublished data)~~
~~*C. patagoniensis*~~	~~C1, C2, C3~~ ~~C4, C5.~~	~~0.85 – 2.15~~	~~0.294~~	~~12~~	~~Hidalgo P. (Unpublished data)~~
~~*C. chilensis*~~	~~C1, C2, C3, C4,~~ ~~C5, AD ♀~~	~~0.94 – 2.45~~	~~0.214~~	~~12~~	~~Hidalgo P. (Unpublished data)~~
	~~C1, C2, C3, C4,~~ ~~C5, AD ♀~~	~~ND – 2.33~~	~~ND~~	~~15~~	~~Escribano R. et al. (1998)~~
	~~C1, C2, C3~~ ~~C4, C5.~~	~~0.61 – 1.96~~	~~ND~~	~~16.5~~	~~Escribano R. & I. McLaren (1999)~~
	~~AD ♀~~	~~2.55~~	~~ND~~	~~14.6~~	~~Ulloa et al. (2001)~~
	~~AD ♀~~	~~2.35~~	~~ND~~	~~18.5~~	

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Con formato: Fuente: 11 pto

Con formato: Fuente: 11 pto

Con formato: Interlineado: Doble

Con formato: Interlineado: Doble, Borde: Inferior: (Línea continua sencilla, Automático, 1.5 pto Ancho de línea)

~~*E. inermis*~~	~~AD ♀~~	~~4.77~~	~~0.193~~	~~16~~	~~Hidalgo et al. (2005)~~
~~*P. indicus*~~	~~C1, C2, C3, C4, C5, AD ♀~~	~~0.35 – 0.96~~	~~0.270~~	~~12~~	~~Yáñez et al. (2012)~~
~~*R. nasutus*~~	~~C1, C2, C3, C4, C5, AD ♀~~	~~1.45 – 5.88~~	~~ND~~	~~ND~~	~~Hidalgo P. (Unpublished data)~~

Specie	Stages	Size Range (mm)	*g* ± ~~s~~SD~~d~~ (d^{-1})	Temp. (°C)	Reference
A. tonsa	C1, C3, C5 (Nor)	0.53 – 0.87	0.22 ± 0.035	12	Hidalgo P. (Unpublished data)
	C1 to C5 (Nor) ND		0.20 ± 0.06	12	Hidalgo P. (Unpublished data)
	C1 to C5 (Sou) ND		0.25 ± 0.05	12	Hidalgo P. (Unpublished data)
	C1, C2, C4 (Sou)	0.53 – 0.73	0.093 ± 0.042	12	Vargas et al. (2010)
	C3 (Sou)	0.658	0.21 ± 0.01	13	Vargas et al. (2010)
C. patagoniensis	C1 to C5 (Sou)	0.85 – 2.15	0.29 ± 0.056	12	Hidalgo P. (Unpublished data)
C. chilensis	C1 to C5 (Nor)	0.61 – 1.96	0.27 ± 0.11	16.5	Escribano & McLaren (1999)
	C1 to C5 (Nor)	2.33	0.114	15	Escribano et al. (1998)
	C1 to C5 (Nor)	ND	0.21 ± 0.05	12	Hidalgo P. (Unpublished data)
	C1 to AD (Nor)	2.55	0.28	14.6	Ulloa et al. (2001)
	C1 to AD (Nor)	2.35	0.35	18.5	Ulloa et al. (2001)
E. inermis	C1 to AD (Nor)	4.77	0.193	16	Hidalgo et al. (2005)
P. Cf indicus	C1 to C5 (Nor)	ND	0.24 ± 0.07	12	Hidalgo P. (Unpublished data)
	C1 to C5 (Sou)	ND	0.27 ± 0.04	12	Hidalgo P. (Unpublished data)
	C2 (Sou)	0.427	0.13	14	Vargas et al. (2010)
	C2 (Sou)	0.427	0.25 ± 0.064	13	Vargas et al. (2010)
	C3 (Sou)	0.593	0.29 ± 0.072	13	Vargas et al. (2010)
	C3 (Sou)	0.593	0.35 ± 0.03	14	Vargas et al. (2010)
	C4 (Sou)	0.725	0.053 ± 0.006	12	Vargas et al. (2010)
	C1 to C5 (Nor)	0.35 – 0.84	0.23 ± 0.11	12	Yáñez et al. (2012)
	C1 to C5 (Sou)	0.35 – 0.84	0.3 ± 0.15	12	Yañez et al. (2012)
R. nasutus	C1 to AD	1.45 – 5.88	ND	ND	Hidalgo P. (Unpublished data)

Con formato: Superíndice

Table 2~~3~~

Estimated copepod abundance (N), copepod biomass (CB) and copepod production (CB) from the coastal upwelling zone of Central/southern Chile, based on spatial cruises ~~(FIP)~~ and a time series study at Station 18. Mean ± SD are shown. n represent the number of stations for each spatial~~FIP~~ cruise and the number of sampled~~s~~ months for each year, respectively.

	~~SPATIAL SURVEYS~~				~~TIMES SERIES~~			
~~YEAR~~	~~N (Ind/m^{-3})~~	~~CB (mgC m^{-2})~~	~~CP (mgC m^{-2} d^{-1})~~	~~n~~	~~N (Ind/m^{-3})~~	~~CB (mgC m^{-2})~~	~~CP (mgC m^{-2} d^{-1})~~	~~n~~
~~2004~~	~~50 ± 76~~	~~449 ± 65~~	~~12 ± 17~~	~~22~~	~~435 ± 337~~	~~711 ± 577~~	~~164 ± 128~~	~~9~~
~~2005~~	~~219 ± 262~~	~~773 ± 1412~~	~~193 ± 351~~	~~17~~	~~199 ± 306~~	~~281 ± 451~~	~~65 ± 99~~	~~10~~
~~2006~~	~~364 ± 778~~	~~515± 1138~~	~~130 ± 288~~	~~22~~	~~215 ± 178~~	~~279 ± 276~~	~~67 ± 65~~	~~12~~

Spatial Cruises

Year	N (Ind m^{-3})	CB (mg C m^{-2})	CP (mg C m^{-2} d^{-1})	n
2004	49.5 ± 75.97	449 ± 65.27	11.5 ± 16.75	22
2005	219.0 ± 261.50	772.6 ± 1412.08	192.8 ± 351.18	17
2006	364.0 ± 778.29	515.0 ± 1137.78	130.4 ± 287.79	22

Time Series

Year	N (Ind m^{-3})	CB (mg C m^{-2})	CP (mg C m^{-2} d^{-1})	n
2004	435.1 ± 336.90	711.0 ± 577.45	164.1 ± 127.99	9
2005	199.3 ± 306.08	281.1 ± 450.60	65.2 ± 99.36	10
2006	215.3 ± 177.73	279.2 ± 276.39	67.2 ± 64.56	12

N: abundance, CB: Copepod biomass, C P: Copepod production, n: sample size

Table 34

Copepod species classified by size ranges as found during the spatial cruises in the coastal upwelling zone of Central/southern Chile. Species abundance is shown as mean ± SD for each year.

Size	Specie	Abundance (n m^{-3})		
		2004	2005	2006
Small	*Acartia tonsa*	-	72.2 ± 5.90	60.0 ± 190.07
[< 1.5 mm]	*Corycaeus* spp	-	19.0 ± 33.36	5.3 ± 8.85
	Oithona similis	34.6 ± 49.62	23.8 ± 53.26	48.1 ± 60.20
	Oncaea spp.	-	8.6 ± 7.93	58.5 ± 190.62
	Paracalanus CF. indicus	33.5 ± 37.0	65.2 ± 60.99	180 ± 440.31
Medium	*Centropages* brachiatus	-	4.2 ± 4.97	3.0 ± 3.20
[1.5–2.5 mm]	*Pleuromamma* gracilis	-	8.0 ± 9.61	16.8 ± 27.49
Large	*Calanoides patagoniensis*	-	62.2 ± ND	62.3 ± 71.23
[> 2.5 mm]	*Calanus chilensis*	1.1 ± 2.41	90.2 ± 191.2	29.9 ± 76.04
	Eucalanus spp.	-	1.2 ± 1.29	-
	Metridia spp.	-	-	5.5 ± 13.54
	Rhyncalanus nasutus	2.6 ± 4.22	15.2 ± 32.56	5.9 ± 10.10

Table 4~~5~~

Results from a generalized linear model (GLM) to test the influence of oceanographic variability on copepod abundance (N) and copepod production (CP), estimated from spatial cruises carried out during upwelling conditions in the coastal upwelling zone off Central/southern Chile. Only significant (P<0.05) or nearly significant (0.05< P <0.10) are shown. *=Significant (P<0.05), **=Highly significant (P<0.01).

~~DEPENDENT VARIABLE~~	~~SOURCE VARIATION~~	~~t-value~~	~~P~~
~~N~~	~~Year~~	~~3.077~~	~~0.003~~
	~~Chla~~	~~1.772~~	~~0.082~~
~~C P~~	~~Year~~	~~2.845~~	~~0.006~~
	~~Chla~~	~~2.797~~	~~0.007~~
	~~DO~~	~~-1.816~~	~~0.075~~
	~~OMZ~~	~~2.182~~	~~0.033~~

Dependent variable	Source variation	t-value	p-value
N	Year	3.077	0.003**
	Chl–a	1.772	0.082
CP	Year	2.845	0.006**
	Chl–a	2.797	0.007**
	DO	-1.816	0.075

Con formato: Fuente: (Predeterminado) +Cuerpo

OMZ	-2.182	0.033*

Figure Captions

Figure 1: The coastal upwelling zone off Central/southern Chile in the eastern South Pacific showing the sampling stations for three oceanographic cruises carried out in 2004, 2005 and 2006 under upwelling conditions (spring-summer). The map also illustrate location of Station 18 were the monthly time series study was conducted during the same 3 years. Wind data to assess upwelling condition were obtained at the coastal Meteo Station.

Figure 2: Spatial distribution of nearly surface (5 m depth) temperature and salinity during the spring-summer cruises in 3 different years, illustrating upwelling conditions over the upwelling zone and the offshore area. The map shows the isotherms (°C) for temperature distribution and the color scale for salinity.

Figure 3: Spatial distribution of nearly surface (5 m depth) dissolved oxygen (DO) and Chlorophyll-a concentration (Chla) during the spring-summer cruises in 3 different years, illustrating upwelling conditions over the upwelling zone and the offshore area. The map shows the isolines (mg m^{-3}) for Chla distribution and the color scale for DO.

~~Figure 4: Time series of wind stress at the coastal zone of Central/southern Chile as to represent variability in upwelling conditions. Data are plotted as daily integrated values and monthly means. Positive values of wind stress represent upwelling favorable conditions and negative ones downwelling conditions. The time series divided into two periods resulted in different number of days favorable for upwelling.~~

Figure 4~~5~~: Time series of temperature (A), salinity (B), dissolved oxygen (C) and chlorophyll-a (D) at Station 18 of Central/southern Chile as observed from monthly data. Contours were constructed from CTD-O casts at 1 m resolution and Chl-a was measured at 9 depths from surface to 80 m. The salinity=34 isoline in B is noted to illustrate upwelling pulses. The red broken line in the DO contour illustrate the depth distribution of the upper limit of the oxygen minimum zone assumed as depth of 1 mL O_2 L^{-1}.

Figure 5~~6~~: Variability of growth rate (*g*) of copepods from the upwelling zone off Chile as a function of mean copepod size and temperature. *g* was estimated by the molting rate method under in situ temperature and copepod size represents the mean body size of all copepodid stage~~adult females~~ for each species. No significant relationship was found in either case (A or B). Data are from published and unpublished works summarized in Table 1.

Figure 6~~7~~: Variability of C-specific growth of copepod species from the coastal upwelling zone off Chile estimated by the molting rate method. Mean values and standard deviation (vertical line) are shown. Data are from two upwelling regions, Northern and Central/south of Chile, as described in Table 1~~.~~

Figure 7~~8~~: Spatial distribution of dominant copepods during the spring-summer cruises in 3 different years over the upwelling zone and the offshore area off Central/southern Chile. Total copepod abundance (N) was obtained from depth integrated zooplankton samples (0-200 m).

Figure 8~~9~~: Spatial distribution of copepod biomass (CB) and copepod production (CP) during the spring-summer cruises in 3 different years over the upwelling zone and the offshore area off Central/southern Chile. Open circles in 4 categories ~~of size~~ show CB distribution, whereas isolines and the color scale show the distribution of CP.

Figure 9~~10~~: Spatial distribution of copepods of 3 size categories: small (<1.5 mm), medium (1.5 - 2.5 mm) and large (>2.5 mm) during the spring-summer cruises in 3 different years over the upwelling zone and the offshore area off Central/southern Chile. Copepod abundance (N) was obtained from depth integrated zooplankton samples (0 - 200 m).

Figure 10~~1~~: Copepod abundance (A) and copepod production ~~(CP)~~ and biomass (B) during the time series study at Station 18 from monthly zooplankton sampling (0-80 m). Copepod production (CP) (line-scatter) and biomass (vertical bars) were estimated from mean size and mean C-content of copepodid stages of dominante ~~adult~~ species, and their associated growth rates.

Figure 11~~2~~: A) Time series of copepod biomass (CB) as related to total zooplankton biomass (TZB) at Station 18 off Central/southern Chile from monthly data. TZB is from Escribano et al. (2007). B) Time series of copepod production (CP) in relation to variability in primary production (From Daneri et al. 2000). Data are from monthly estimates of CP and PP.

Figure 12~~3~~: A) Time series of wind stress at a coastal station near Station 18 off Concepción illustrating upwelling variability for near 3 years. Daily integrated wind stress is shown, including monthly means and the number of days favorable for upwelling (wind stress>0) for each annual upwelling period (September to

March) indicated by the shaded areas. B) Conceptual model to illustrate the interaction among factors and processes determining the variability of copepod biomass and copepod production in relation to upwelling conditions in the coastal upwelling zone of Central/southern Chile during a 3 year time series study. CP=copepod production, CB=copepod biomass, PP=primary production, CPe= expected copepod production assuming a daily P/B ratio=0.25. Biomass loss ~~(shaded area)~~ represents the CB being exported from the upwelling zone upon ~~a~~ more extended periods of upwelling in 2005 and 2006 as shown in B)~~during the second part of the time series~~. This biomass loss due to increased offshore advection explains the reduction in CP as compared to CPe.

Fig. 1

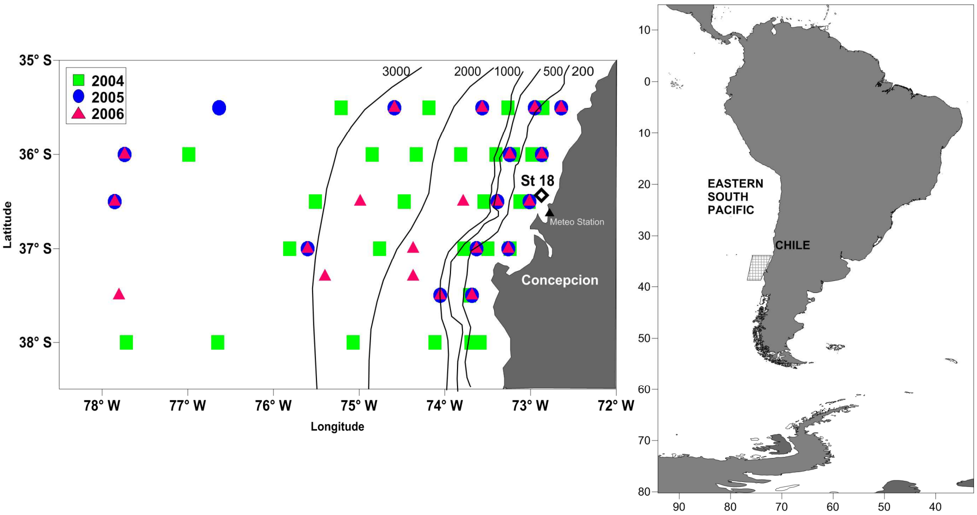

35° S
36° S
37° S
38° S
Latitude
2004
2005
2006
3000
2000
1000
500
200
St 18
Meteo Station
Concepcion
78° W
77° W
76° W
75° W
74° W
73° W
72° W
Longitude
10
0
10
20
30
40
50
60
70
80
EASTERN
SOUTH
PACIFIC
CHILE
90
80
70
60
50
40

Fig. 2

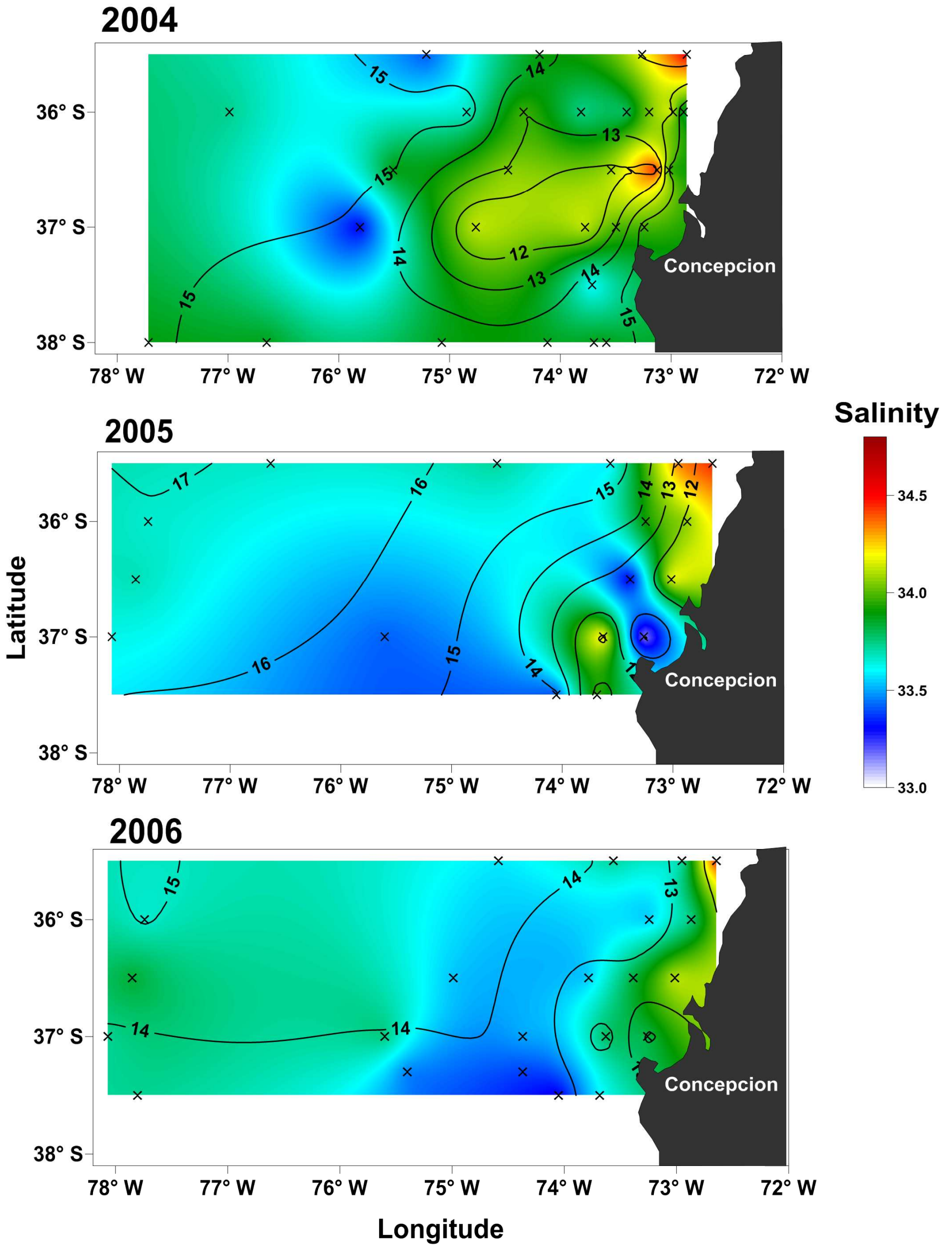

2004
2005
2006
Concepcion
36° S
37° S
38° S
78° W
77° W
76° W
75° W
74° W
73° W
72° W
15
14
13
12
16
17
Latitude
Longitude
Salinity
34.5
34.0
33.5
33.0

Fig. 3

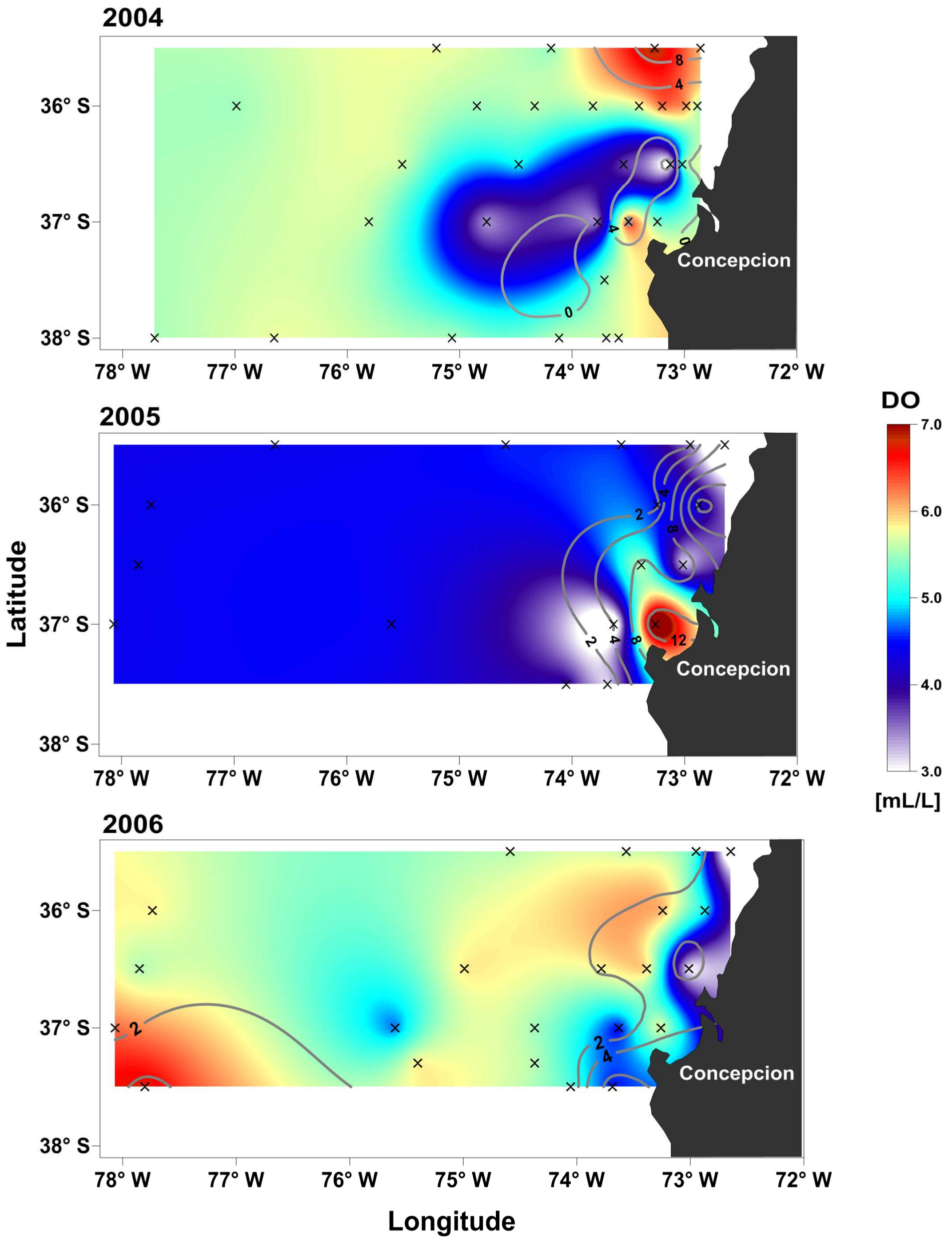

2004
2005
2006
36° S
37° S
38° S
78° W
77° W
76° W
75° W
74° W
73° W
72° W
Concepcion
8
4
0
12
2
Latitude
Longitude
DO
7.0
6.0
5.0
4.0
3.0
[mL/L]

Fig. 4

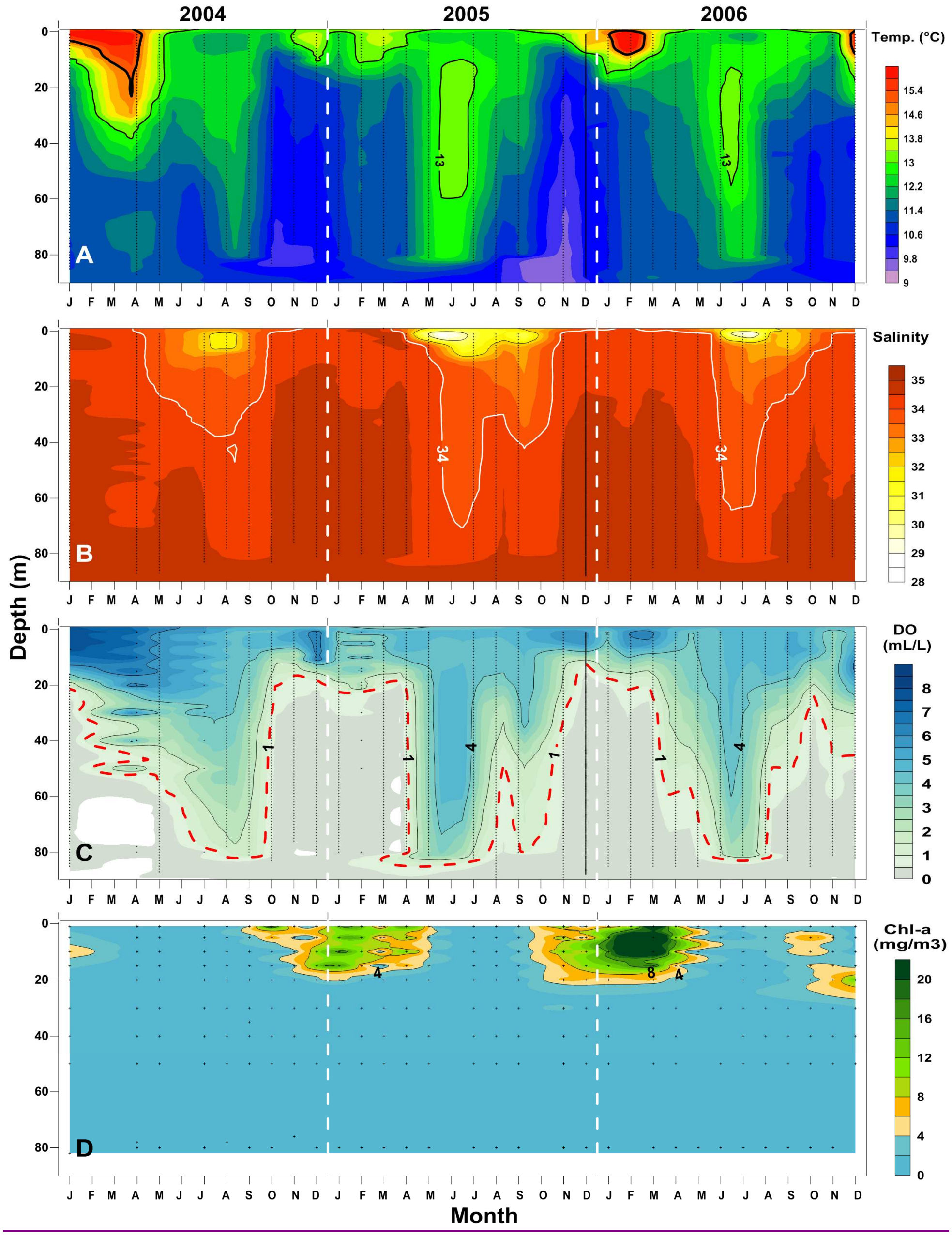

2004
2005
2006
Temp. (°C)
15.4
14.6
13.8
13
12.2
11.4
10.6
9.8
9
A
13
Salinity
35
34
33
32
31
30
29
28
B
34
DO (mL/L)
8
7
6
5
4
3
2
1
0
C
Chl-a (mg/m3)
20
16
12
8
4
0
D
Depth (m)
0
20
40
60
80
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
Month

Fig. 5

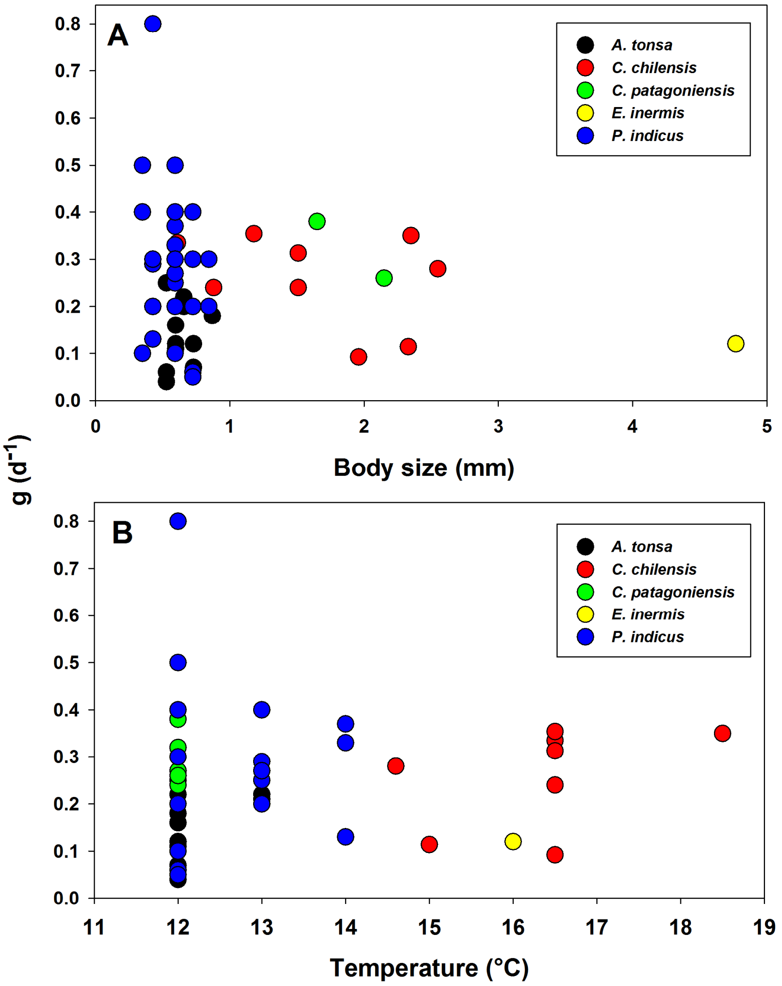

A
B
g (d^{-1})
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0
1
2
3
4
5
Body size (mm)
11
12
13
14
15
16
17
18
19
Temperature (°C)
A. tonsa
C. chilensis
C. patagoniensis
E. inermis
P. indicus

Fig. 6

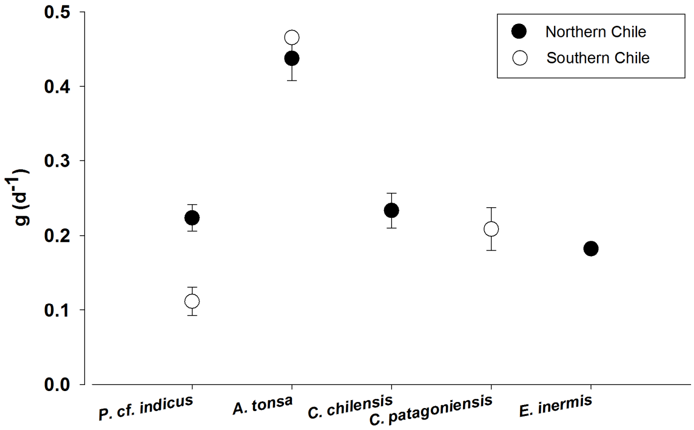

g (d^{-1})
0.5
0.4
0.3
0.2
0.1
0.0
Northern Chile
Southern Chile
P. cf. indicus
A. tonsa
C. chilensis
C. patagoniensis
E. inermis

Fig. 7

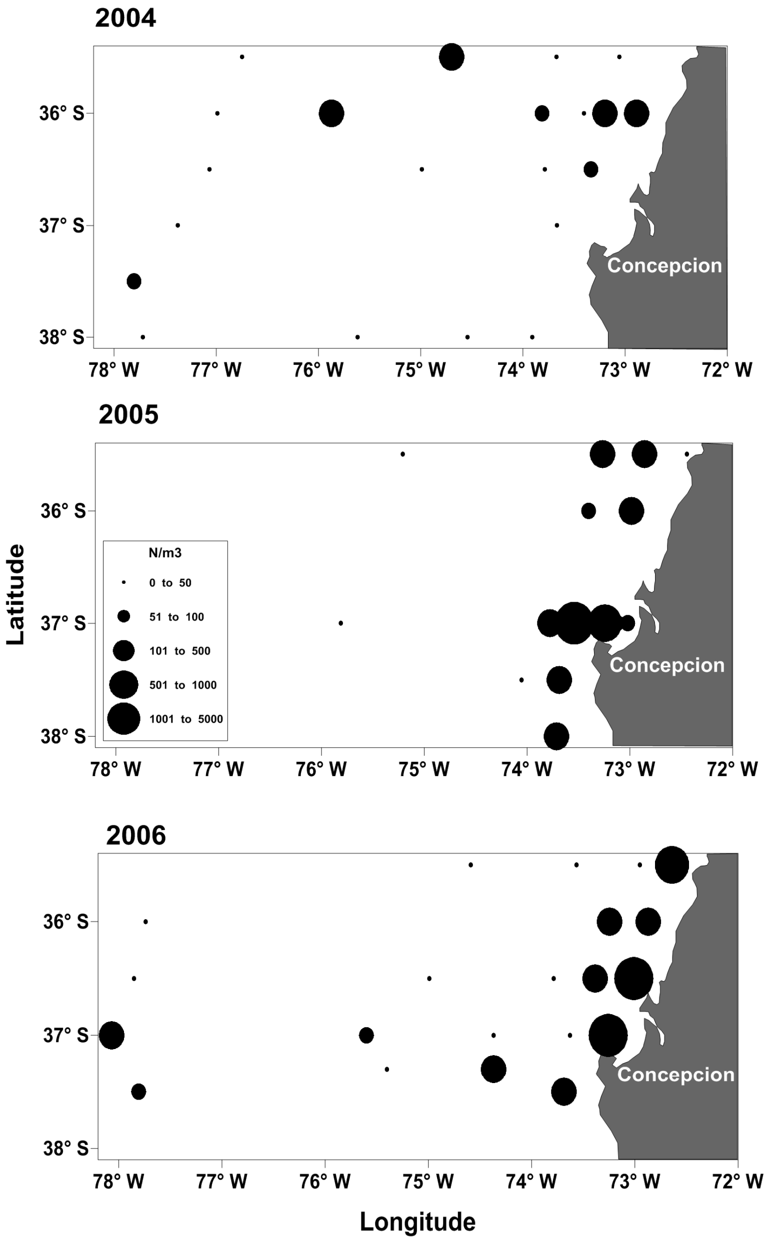

2004
2005
2006
36° S
37° S
38° S
78° W
77° W
76° W
75° W
74° W
73° W
72° W
Concepcion
Latitude
Longitude
N/m3
0 to 50
51 to 100
101 to 500
501 to 1000
1001 to 5000

Fig. 8

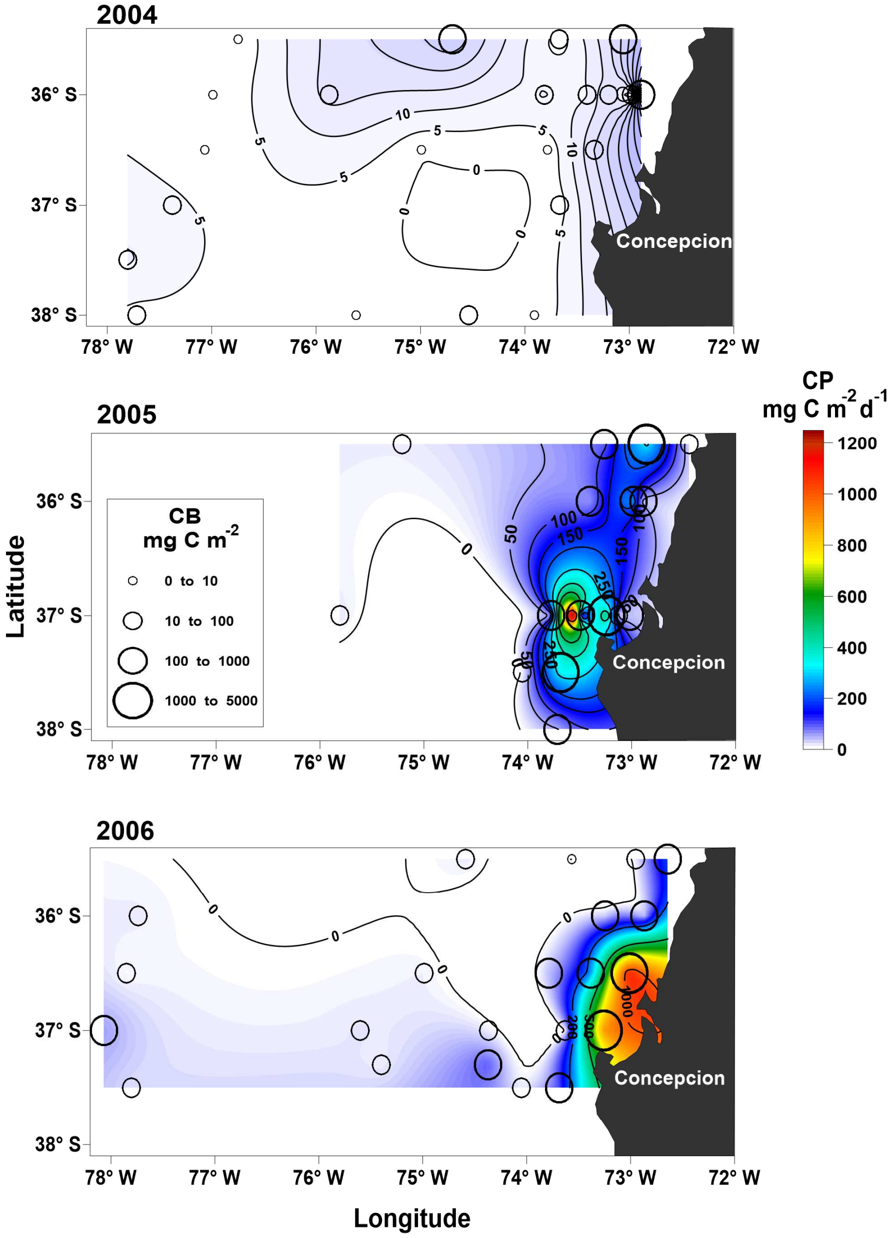

2004
2005
2006
36° S
37° S
38° S
78° W
77° W
76° W
75° W
74° W
73° W
72° W
Concepcion
Latitude
Longitude
CB
mg C m^{-2}
0 to 10
10 to 100
100 to 1000
1000 to 5000
CP
mg C m^{-2} d^{-1}
1200
1000
800
600
400
200
0

Fig. 9

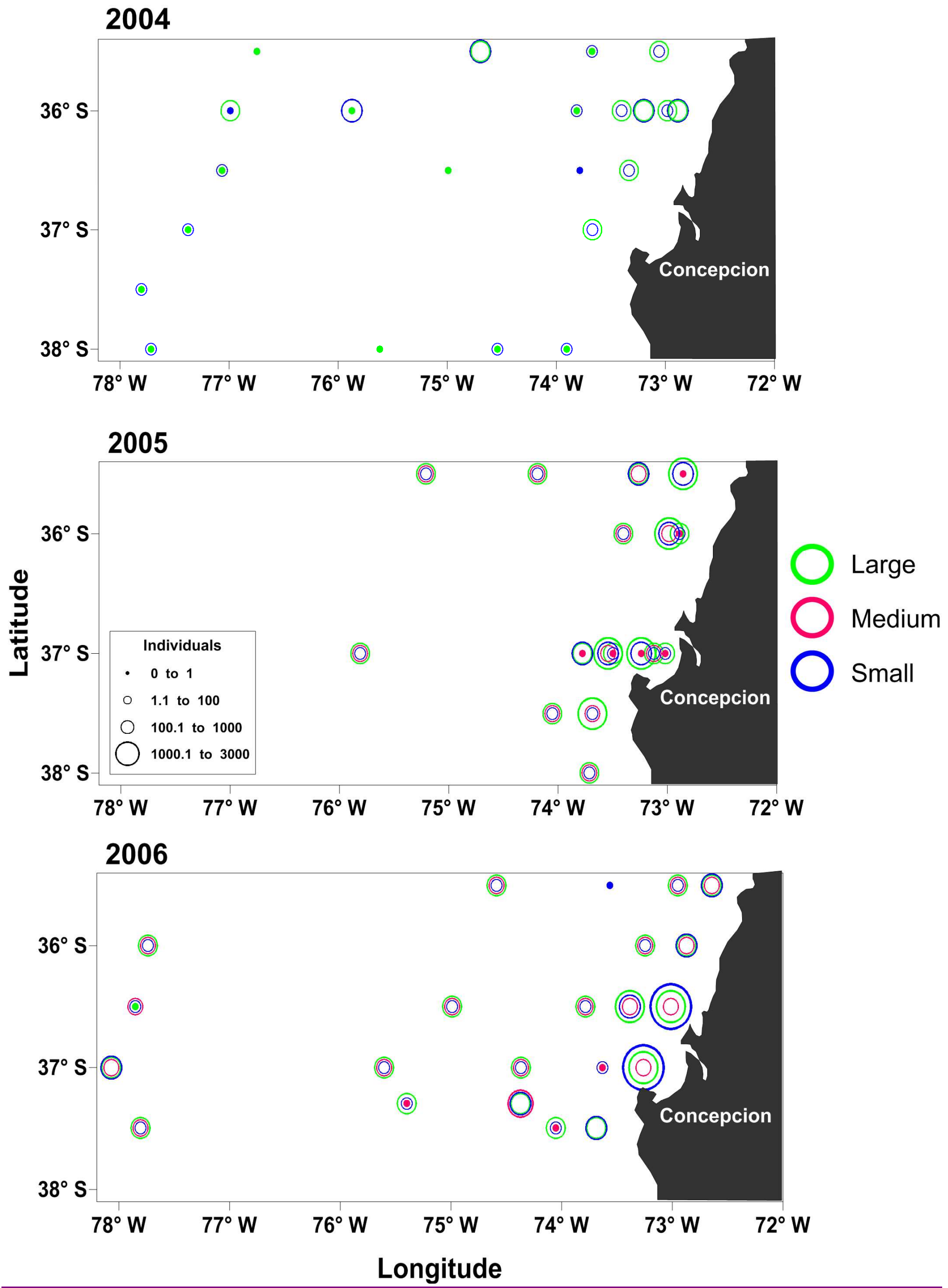
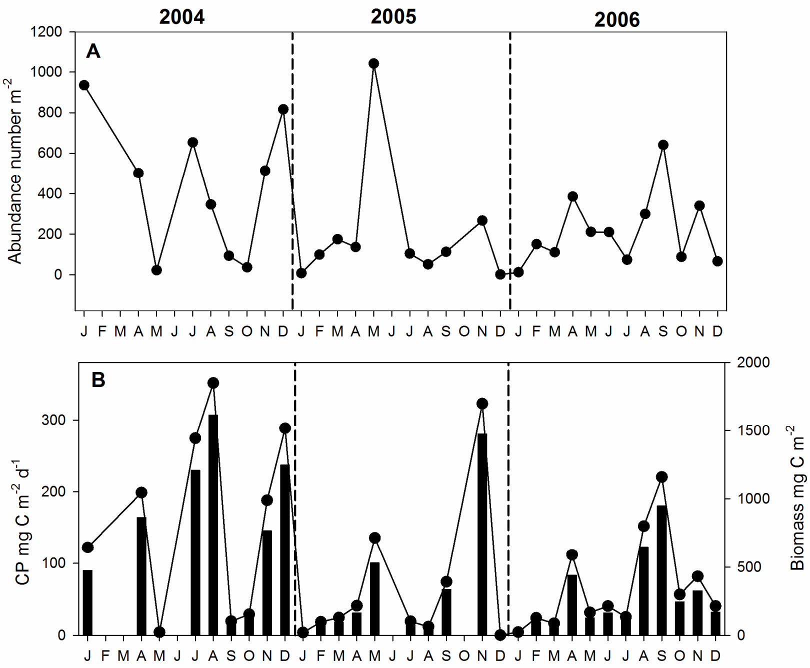

2004
36° S
37° S
38° S
78° W
77° W
76° W
75° W
74° W
73° W
72° W
Concepcion
2005
Latitude
Individuals
0 to 1
1.1 to 100
100.1 to 1000
1000.1 to 3000
Large
Medium
Small
2006
Longitude

Fig. 10



2004
2005
2006
A
Abundance number m^{-2}
1200
1000
800
600
400
200
0
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
B
CP mg C m^{-2} d^{-1}
300
200
100
0
Biomass mg C m^{-2}
2000
1500
1000
500
0
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D

Fig. 11

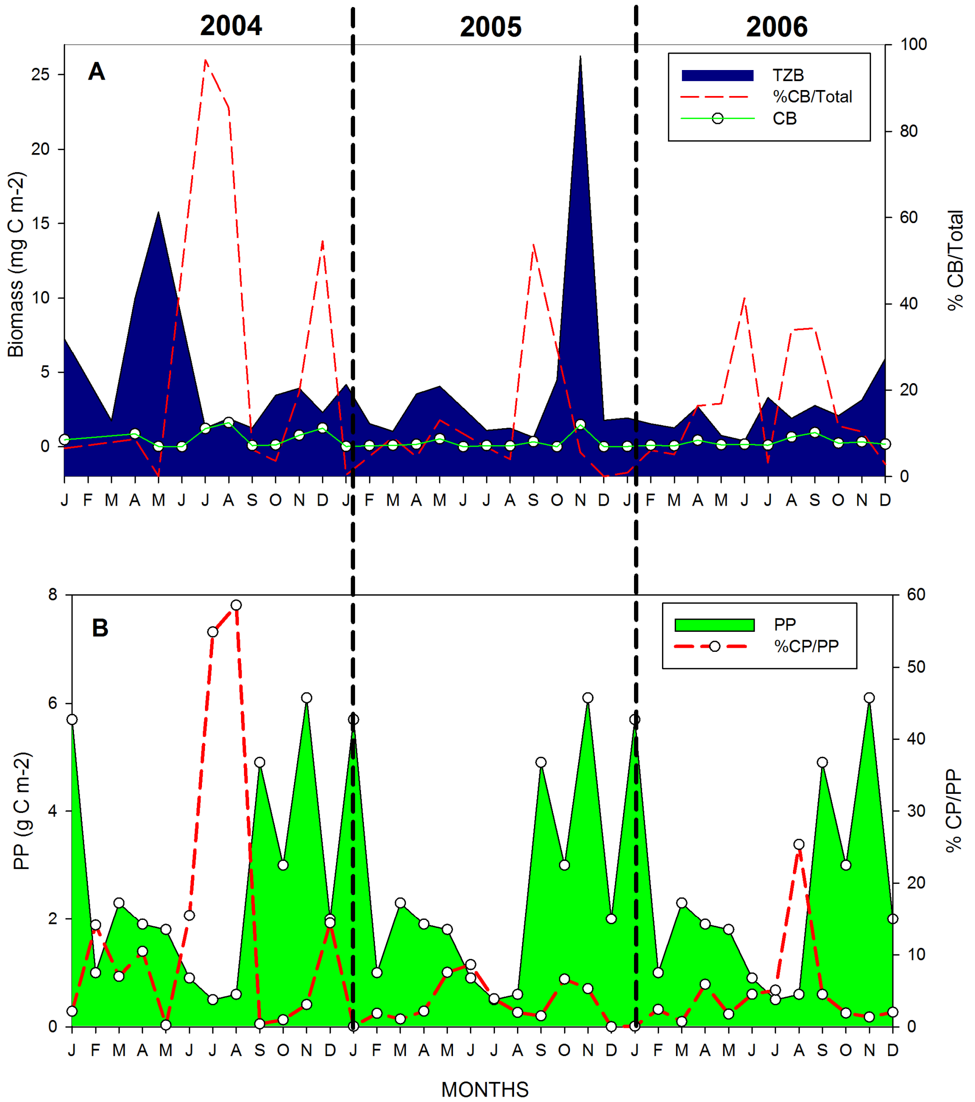
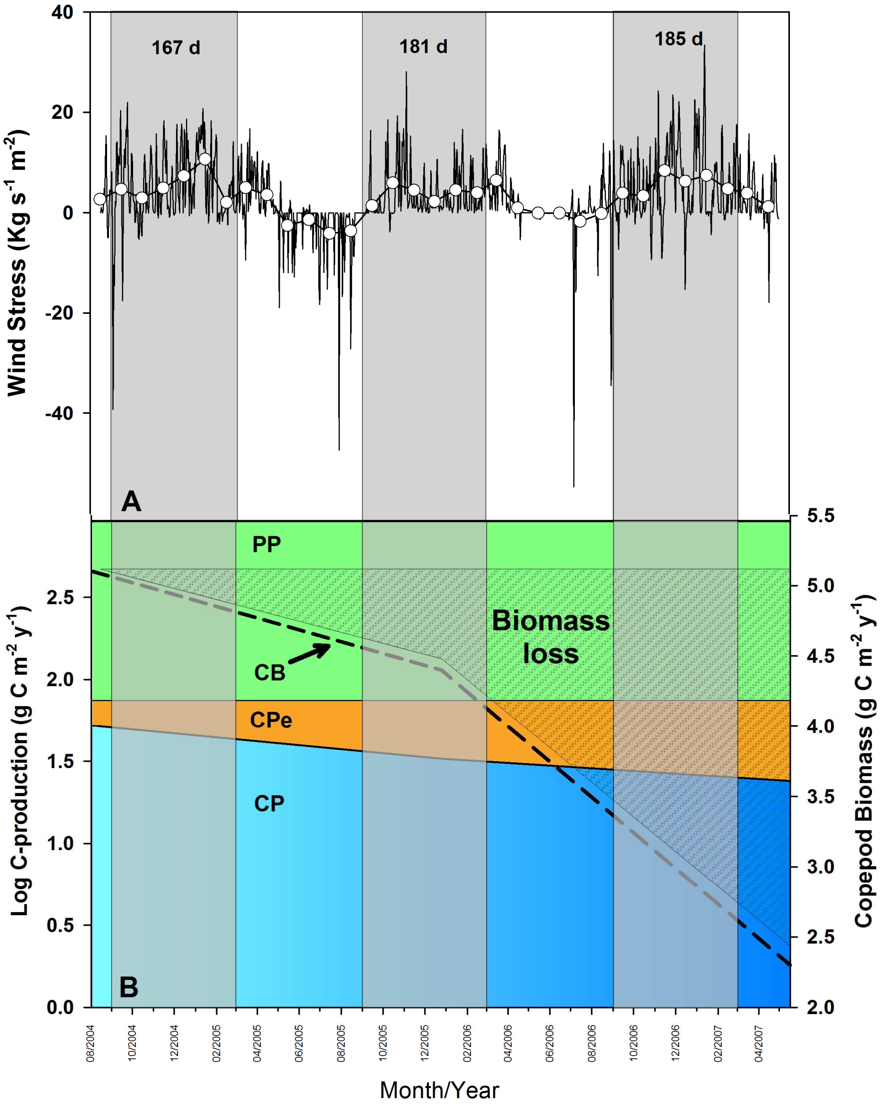

2004
2005
2006
A
TZB
%CB/Total
CB
Biomass (mg C m-2)
% CB/Total
25
20
15
10
5
0
100
80
60
40
20
0
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
B
PP
%CP/PP
PP (g C m-2)
% CP/PP
8
6
4
2
0
60
50
40
30
20
10
0
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
MONTHS

Fig. 12



A
B
167 d
181 d
185 d
Wind Stress (Kg s^{-1} m^{-2})
40
20
0
-20
-40
PP
CB
CPe
CP
Biomass loss
Log C-production (g C m^{-2} y^{-1})
2.5
2.0
1.5
1.0
0.5
0.0
Copepod Biomass (g C m^{-2} y^{-1})
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
08/2004
10/2004
12/2004
02/2005
04/2005
06/2005
08/2005
10/2005
12/2005
02/2006
04/2006
06/2006
08/2006
10/2006
12/2006
02/2007
04/2007
Month/Year