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Non-limiting food conditions for growth and production of the copepod community in a highly productive upwelling zone

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ABSTRACT

Zooplankton production is critical for understanding marine ecosystem dynamics. This work estimates copepod growth and production in the coastal upwelling and coastal transition zones off central-southern Chile ($\sim$35 to 37°S) during a 3-year time series (2004, 2005, and 2006) at a fixed shelf station, and from spring-summer spatial surveys during the same period. To estimate copepod production (*CP*), we used species-biomasses and associated C-specific growth rates from temperature dependent equations (food-saturated) for the dominant species, which we assumed were maximal growth rates (g_{max}). Using chlorophyll-a concentrations as a proxy for food conditions, we determined a size-dependent half-saturation constant with the Michaelis-Menten equation to derive growth rates (*g*) under the effect of food limitation. These food-dependent C-specific growth rates were much lower (<0.1 d^{-1}) than those observed in the field for the dominant species, while g_{max} for same species, in the range of 0.19–0.23 d^{-1} better represented the necessary growth to attain observed adult sizes of at least two copepods, *Paracalanus* cf. *indicus* and *Calanus chilensis*. Copepod biomass (*CB*) and rates of maximal copepod production (CP_{max}) obtained with g_{max} were higher in the coastal upwelling zone (<50 km from shore), and correlated significantly to oceanographic variables associated with upwelling conditions. Both CP_{max} and g_{max} exhibited negative trends at the fixed station from 2004 to 2006 in association with increased duration of upwelling in the latter year. Annual CP_{max} ranged between 24 and 52 g C m^{-2} y^{-1} with a mean annual P/B ratio of 7.3. We concluded that interannual variation in copepod production resulted from factors and processes regulating copepod abundance and biomass in the absence of bottom-up control, allowing copepods to grow without limitation due to food resources.

1. Introduction

Variability in biological production of lower trophic levels is critical for understanding the dynamics of marine ecosystems (Mann and Lazier, 1991). In this framework, zooplankton is a key component considering their ecological role in capturing, retaining and transferring freshly produced phytoplankton-carbon to higher trophic levels (Poulet et al., 1995; Kimmerer et al., 2007). There have not been many studies targeting secondary zooplankton production and its time-space variability, making it difficult to assess the role of zooplankton in controlling or limiting biological production of higher trophic levels, including fish, mammal and seabird populations (Aebischer et al., 1990; Richardson and Verheye, 1999; Beaugrand et al., 2003; Castonguay et al., 2008).

Secondary zooplankton 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). However, there is no single and simple method to estimate zooplankton production and growth rates. Rather several approaches have been applied that yield different results. Daily estimates of production can vary substantially when comparing mathematical models with enzymatic approaches (Avila et al., 2012) and significant deviations can occur with artificial cohort methods (Lin et al., 2013). Moreover, most of the methods traditionally used are logistically difficult to apply to characterize space-time variations in these rates (Sastri et al., 2013).

There have been several attempts to develop theoretical and empirical relationships between zooplankton production and the factors known to affect their growth. Temperature has been reported as a fundamental factor influencing copepod growth (Huntley and Lopez, 1992; McLaren, 1995; Escribano et al., 2014), while body size is also considered a fundamental driver for animal growth, considering that growth, like any other physiological rate, is controlled by body size (allometric effects) (West et al., 1997). In

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Nomenclature

g	Copepod growth rate (d^{-1}), calculated under food-limited conditions
g_{max}	Maximal copepod growth rate (d^{-1}), calculated under food-saturation conditions
CB	Copepod biomass ($mg\ m^{-3}$)
CP	Copepod production ($mg\ C\ m^{-3}\ d^{-1}$), calculated by multiplying CB by g
CP_{max}	Maximal copepod production ($mg\ C\ m^{-3}\ d^{-1}$), calculated by multiplying CB by g_{max}

fact, both temperature and body size are the basis for the metabolic theory of ecology (Brown et al., 2004), which proposes that animal growth is predictable from body size and environmental temperature. Other studies have provided evidence that food resources limit zooplankton growth (Hirst and Lampitt, 1998; Vargas et al., 2010).

To calculate secondary production it is necessary to have reliable estimates of in situ growth rates of the species that makes up the bulk of zooplankton biomass. As mentioned above, the weight or C-specific growth rate (g) is related to temperature, food conditions, and body size, but in most cases direct estimates of g show no relationship, or only a weak one, to these factors (Lonsdale and Levinton, 1985; Chisholm and Roff, 1990; Hutchings et al., 1995). The relationship may also depend on the taxonomic group being considered (Hirst and Bunker, 2003).

Zooplankton production in the eastern south Pacific has received very little attention. In this region, the Humboldt Current System (*HCS*) is one of the Eastern Boundary Currents (*EBC*s) known for its high level of biological productivity (Mann and Lazier, 1991), attributed to the high levels of primary production in the coastal zone ($>10\ gC\ m^{-2}d^{-1}$) sustained by wind-driven upwelling (Daneri et al., 2000; Montero et al., 2007). Copepods and euphausiids dominate zooplankton biomass in the *HCS* off Chile (Escribano et al., 2007; Riquelme-Bugueño et al., 2012), although there have been few studies on zooplankton production. 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) 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 are sometimes highly abundant in this region, the bulk of zooplankton biomass in the coastal upwelling zone is dominated by copepods, specifically small (<2 mm) copepods (Escribano et al., 2007). Hence, the latter may well reflect the dynamics of entire zooplankton biomass and production in the southern area of the Humboldt Current (Huggett et al., 2009). Around ten copepod species comprise $>90\%$ of total numerical abundance (Escribano et al., 2007; Escribano et al., 2012), including the small calanoid *Paracalanus* cf. *indicus*, which reproduces continuously throughout the year in the regions off northern and central-southern Chile, 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). The cyclopoids *Oithona similis, Oithona nana*, *Triconia conifera,Triconia media*, and *Corycaeus typicus* are also abundant (Hidalgo et al., 2010). Larger (>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 *Rhincalanus nasutus* and *Eucalanus* spp, including *Eucalanus inermis* and *Eucalanus hyalinus* (Castro et al., 1993; Hidalgo et al., 2010).

In this work, we first estimated growth rates (g) of the dominant copepod species found in the coastal upwelling zone off central-southern Chile using the general equations described by Hirst and Bunker (2003) that relate g to temperature and body size under food-saturation conditions. We then added a potential food-quantity effect by calculating a size dependent half-saturation constant derived from the Michaelis-Menten equation. Finally, we used these species-dependent growth rates to calculate copepod biomass production and its time-space variability in the coastal upwelling and coastal transition domains. We therefore provide: (a) first estimates of copepod community production in the Humboldt Current, (b) insights to elucidate whether growth of the copepod community is food-limited in this highly productive upwelling system, and (c) new understanding about factors causing time-space variability in copepod growth and production.

2. Methods

2.1. Field studies

Copepod abundance estimates were obtained monthly from a 3-year time series (January 2004 to December 2006) at the fixed shelf Station 18 (36°30'S–73°15'W, ~30 km from the coast) off Concepción (Fig. 1). Spatial surveys were conducted in the spring-summer of the same years to sample the area between the coastal and coastal transition zones (up to 180 km from the coast)off central-southern Chile (35–39°S). The spatial cruise in 2004 was carried out from January 14 to 21, completing a grid of 21 stations. The cruise in 2005 was from December 7 to 15, with a grid of 17 stations. Finally, the 2006 cruise was from November 10 to 25, with a grid of 22 stations. Fig. 1 illustrates the sampling stations for the spatial cruises.

The time series zooplankton sampling at Station 18 employed a 1 m^2 Tucker trawl net equipped with 200 μm mesh nets and a calibrated flowmeter. The net was trawled from 80 m deep to the 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 a fourth) was frozen at −20 °C for zooplankton biomass, and the rest of the sample was fixed with formalin at 10%. In this study the fraction fixed with formalin was used to study the copepod community.

Along with zooplankton sampling, environmental conditions at Station 18 were assessed by vertical profiles of a CTDO profiler deployed down to 85 m. Continuous profiles of temperature, salinity, dissolved oxygen and fluorescence were obtained, along with discrete water samples with an oceanographic carousel at 9 depths to estimate chlorophyll-a (*Chl-a*) concentrations, nutrients and dissolved gases. Details on methods and measurements for the time series study can be found in Escribano and Schneider (2007) and Escribano and Morales (2012). In addition, to assess upwelling conditions during the time series, wind data were obtained from a meteorological station (shown in Fig. 1). Data were available only from August 2004 to the end of the time series. Wind speed and direction were measured every 5 min and vectors averaged for every hour to assess wind forcing and estimate an upwelling index: