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Review

Community response of zooplankton to oceanographic changes (2002–2012) in the central/southern upwelling system of Chile

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A B S T R A C T

A 10-year time series (2002–2012) at Station 18 off central/southern Chile allowed us to study variations in zooplankton along with interannual variability and trends in oceanographic conditions. We used an automated analysis program (ZooImage) to assess changes in the mesozooplankton size structure and the composition of the taxa throughout the entire community. Oceanographic conditions changed over the decade: the water column became less stratified, more saline, and colder; the mixed layer deepened; and the oxygen minimum zone became shallower during the second half of the time series (2008–2012) in comparison with the first period (2002–2007). Both the size structure and composition of the zooplankton were significantly associated with oceanographic changes. Taxonomic and size diversity of the zooplankton community increased to the more recent period. For the second period, small sized copepods (<1 mm) decreased in abundance, being replaced by larger sized (>1.5 mm) and medium size copepods (1–1.5 mm), whereas euphausiids, decapod larvae, appendicularian and ostracods increased their abundance during the second period. These findings indicated that the zooplankton community structure in this eastern boundary ecosystem was strongly influenced by variability of the upwelling process. Thus, climate-induced forcing of upwelling trends can alter the zooplankton community in this highly productive region with potential consequences for the ecosystem food web.

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1. Introduction

Zooplankton are considered to be a suitable indicator for assessing the impact of climate change-related environmental variability on the structure and functioning of global marine ecosystems (Roemmich and McGowan, 1995; Mackas et al., 2007; Chiba et al., 2015). This is because zooplankton populations and communities respond rapidly to the environmental variables affected by climatic changes (Richardson, 2008).

In the ocean, some of the variables most affected by climate change (temperature, water-column stratification, acidification, oxygenation, the quality and quantity of food resources) also interact with zooplankton (Daufresne et al., 2009; Doney et al., 2012). Increasing atmospheric temperatures cause the sea surface temperature to rise, and the development of a strong pycnocline reduces vertical mixing in the water column. This depletes the nutrients in the photic layer, thereby lowering primary production (Mann and Lazier, 1991; Doney, 2006) and affecting the entire marine food web (Landry and Kishi, 2013; Doney et al., 2012). However, the different regions of the ocean respond differently to such changes. For example, in eastern boundary current systems (EBCs) of the southern hemisphere, stronger southerly winds give rise to more active upwelling (Garreaud and Falvey, 2008; Belmadani et al., 2013), allowing more mixing in the water column and cooling the surface water, with uncertain consequences for primary production and zooplankton dynamics.

Among the EBCs, the coastal zone off Chile is one of the most productive marine ecosystems on Earth (up to 10–20 g C m^{-2} d^{-1}). Here, strong fisheries are sustained by the intense upwelling of cold, nutrient-rich, subsurface waters of equatorial origins (Escribano and Schneider, 2007; Thiel et al., 2007). Upwelling off central/southern Chile (30–40°S) experiences both seasonal (more intense in spring–summer) and strong intra-seasonal variation (alternating periods of active upwelling and relaxation) (Sobarzo et al., 2007; Pino-Pinuer et al., 2014). The upwelling period takes place between early September to March (austral spring–summer) and is characterized by strong southerly winds, resulting in the ascent of equatorial sub-surface water into the photic zone, increasing surface salinity and lowering surface temperature and oxygenation upon the ascent of the oxygen minimum zone (OMZ). During the months of April and August (austral autumn and winter) downwelling (non-upwelling) conditions prevails with weakening of southerly wind, low salinity water near surface due to rain and river runoff, highly oxygenated water in the upper layer (Escribano et al., 2009). The biogeochemical consequences of these upwelling variations include near-surface hypoxia events that occur during spring–summer when the OMZ rises (Paulmier and Ruiz-Pino, 2009), and changes in water column stratification resulting from heat-driven (i.e., solar) mixing in the water column and freshwater runoff (i.e., river discharge and/or precipitation) (Sobarzo et al., 2007). This variability in oceanographic conditions can heavily impact the zooplankton community in the coastal zone (Escribano et al., 2007; Hidalgo et al., 2012; González et al., 2015).

The zooplankton community off central/southern Chile is dominated by small (<1.5 mm) and medium-sized (1.5–3.0 mm) copepods (Hidalgo et al., 2010). Strong aggregations of the dominant euphausiid, *Euphausia mucronata*, occur occasionally, mainly by late summer/early autumn (Riquelme-Bugueño et al., 2012). The responses in the composition and diversity of copepods and euphausiids have been studied as a means to evaluate upwelling forcing in the zooplankton community (e.g. Escribano et al., 2007, 2012).

Automated analyses of digitized zooplankton samples offer an alternative approach that incorporates the entire zooplankton community structure and does not require taxonomic description at the species level, but instead it is related to major taxa and size composition. Although this approach may not provide a full description of the community composition, it should be considered as an useful tool to rapidly assess a large number of samples and obtain size and group structure. This automated analyses can thus be adopted by applying ZooImage (Grosjean and Denis, 2007) and it has been named as the "RAPID" (Research in Automated visual Plankton Identification) approach (Benfield et al., 2007).

Previous studies performed off central/southern Chile have used ZooImage to describe how oceanographic variations influenced the size structure of the zooplankton community. In a spatial study carried out in spring 2004, the zooplankton size spectrum (derived from ZooImage) was linked to cross-shelf oceanographic conditions. The steeper (offshore) slopes of the normalized size spectrum were related to lower diversity and abundance, whereas more gradual slopes (inshore) were related to more size classes and greater abundances (Manríquez et al., 2012). A temporal analysis of the zooplankton time series (2002–2005) at Station 18 off Concepción (36°S) showed a highly variable size spectrum. Slopes were less pronounced during active upwelling, indicating a more uniform distribution of size classes. In contrast, during non-upwelling periods, the zooplankton community was dominated by smaller size classes, with scarce large-sized zooplankton and steeper size-spectrum slopes (Manríquez et al., 2009).

Accordingly, intense upwelling can force responses in the zooplankton community. Therefore, the composition and size-structure of zooplankton in the coastal upwelling zone could reflect climate-induced changes in the upwelling process. In this work, we used a 10-year time series study at Station 18 off central/southern Chile and the RAPID approach to assess how the size structure and composition of the main meso-zooplankton community responded to variations and trends in upwelling intensity. We ultimately aimed to understand how zooplankton dynamics can be affected given a scenario in which global warming impacts wind-driven coastal upwelling.

2. Methods

2.1. Field studies

The COPAS research center initiated a time series study at a fixed station (Station 18) in the upwelling system off central/southern Chile (36°30, 80′S; 73°07, 75′W). Station 18 is located on the continental shelf about 30 km from the coast and 90 m deep (Fig. 1) and was used for a this study lasting from August 2002 to 2012.

Oceanographic data were obtained with two CTD autonomous profilers (SBE-25 and SBE-19 Plus) deployed down to 85 m depth. Additional water samples were collected with 10-L Niskin bottles at nine different depths for chemical and chlorophyll *a* (Chl *a*) analyses. See Sobarzo et al. (2007) for details on the CTD procedures and chemical and physical data.

Monthly zooplankton samples were collected by oblique hauls using a 1-m^2 Tucker trawl net (mesh size: 200 µm) equipped with a calibrated General Oceanics flowmeter. On occasions, during rough weather, samples were obtained with a 200-µm to 0.5-m opening WP2, towed vertically from 80 m to the surface. Our Tucker trawl net was equipped with three nets and an opening-closing mechanism activated by messengers, allowing us to take one integrated and two additional stratified samples. Pre-defined sampling depths were achieved in according to wire length and its corresponding inclination angle.

Zooplankton specimens were caught in each haul covering the 0–80 m layer and the 0–50 m and 50–80 m layers, such that we could also assess the zooplankton vertical distribution. These strata