Spatio-temporal variability of zooplankton community structure and trophic processes off central Peru

Doctoral Thesis

By

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to my parents, Bernardo and Alicia for their unwavering support.

Thank you for believing in me.

Como un copo de nieve suspendido en el aire
Tus alas temblaban por el dolor y el esfuerzo
Pero eso no detuvo tu decisión de llegar
Tan lejos como el viento te quisiera llevar.

El tesón y la práctica perfeccionaron tu vuelo
Y al fin conseguiste el control interior
El balance en el ala y el rizo difícil
La barrera invertida y hasta dormir en el aire.

Richard Bach
Summary

The coastal upwelling ecosystems of the Humboldt Current are characterized by high biological production. This productivity originates in the lower trophic levels in response to the fertilization of the surface layers with nutrients that are brought to upper layers through wind-driven processes. Phytoplankton is mainly consumed mainly by zooplankton, which in turn is preyed on by small pelagic fishes. These groups of organisms are subject to large perturbations due to intrannual (seasonal) and interannual (El Niño Southern Oscillation ENSO) physical fluctuations in oceanographic conditions. The objective of this study was to describe and quantify the spatio-temporal variability in phyto-and zooplankton biomass, composition, and size class distribution off open shores (continental shelf off Callao) and inside a semi-enclosed bay (Independencia Bay) in central Peru. An exhaustive review of the published and grey literature on the Peruvian coastal upwelling ecosystem, focusing specifically on zooplankton studies, concluded that there were still several information gaps and more research effort was needed. The present study investigated the vertical distribution and migration mechanisms that the dominant the zooplankton taxa have developed in response to the variability of the oxygen minimum zone (OMZ). Additionally research was carried out into the processes and factors that determine changes in zooplankton grazing and egg production for the dominant copepod species Acartia tonsa and how these processes are related to the ENSO. Furthermore, I present an exhaustive review of the published and grey literature on the Peruvian coastal upwelling ecosystem.
The present study showed that the phytoplankton community underwent extreme changes in density and composition, with a huge change between different ENSO phases. Dinoflagellates, nanoflagellates, and diatoms dominated during 2006, including ENSO-neutral conditions in April 2006 and the moderate El Niño in July and August 2006. Diatoms dominated in 2007, including ENSO-neutral conditions in February and April 2007 and the strong La Niña event that impacted the area from May to August 2007. Zooplankton were found mostly aggregated at the nearshore, and in the well-oxygenated upper 20m layer during ENSO-neutral and La Niña conditions. During warm conditions, all zooplankton was more dispersed throughout the upper 50 m due to the expansion of the OMZ depth. *Acartia tonsa* was generally the most abundant species, but its population was strongly reduced during the 2006 EN event. The study showed that *A. tonsa* ingestion rates and prey selectivity were modulated by the availability of phytoplankton in this area. The trophic impact of *A. tonsa* on the primary production during the period studies was also very variable. This wide variation in the trophic impact was caused by the asynchronous variability of primary production, *A. tonsa* abundance and ingestion rates. The results of this research show that the zooplankton community off Central Peru is strongly influenced by physical conditions. The most visible changes were associated with intrannual (seasonal) and interannual (ENSO) cycles. One fundamental physical factor that influences zooplankton distribution is the spatial variability in OMZ depth.
Zusammenfassung


Resumen

Los sistemas de surgencia costera que se desarrollan en la Corriente de Humboldt presentan una alta productividad biológica que comienza en los niveles tróficos inferiores con la fertilización de las capas superficiales. El fitoplancton es consumido principalmente por el zooplancton y estos a su vez son consumidos por pequeños peces pelágicos. De esta manera el zooplancton cumple con una función de enlace entre los productores primarios y los pequeños pelágicos. Estos organismos deben enfrentar varios procesos y fuerzas físicas para mantener sus poblaciones y completar sus ciclos de vida en la zona costera del ecosistema. Con el propósito de conocer los mecanismos que las comunidades zooplanctónicas desarrollan para enfrentar estos cambios temporales y espaciales en la Corriente de Humboldt en la zona Central del Perú se desarrollo el presente estudio durante tres años, entre el 2005 y el 2007. Se analizó la distribución de las especies zooplanctónicas en la columna de agua y las estrategias que desarrollan para sobrevivir en la zona minima de oxigeno. Por ultimo se evaluó la importancia trófica del zooplancton, a través del estudio de las tasas de alimentación y producción de huevos de la especie más abundante *Acartia tonsa*. Además, se hizo una exhaustiva revision de la literatura gris y publicada sobre el sistema de surgencia costero Peruano.

El presente estudio mostró que la comunidad de fitoplancton presenta cambios substanciales en la densidad y composición entre las diferentes fases del ENOS (El Niño Oscilación del Sur). En condiciones normales y frías el sistema fue dominado por diatomeas pero cuando se presentó el ingreso de aguas calidas los dinoflagelados y nanoflagelados aumentaron sus abundancias y las diatomeas
disminuyeron drásticamente. En general el zooplancton se encontró en las estaciones cercanas a la costa y en las capas más superficiales por encima de los 20 m, cuando las condiciones imperantes son normales o frías, mientras que durante las situaciones cálidas la comunidad se encuentra más dispersa debido al aumento de la profundidad de la capa de mínima de oxígeno por debajo de los 50 m de profundidad. Aunque el mayor agregado de especies permanece restringido a las capas superficiales oxigenadas, algunas especies como *Eucalanus inermis* que fueron encontradas en mayores abundancias en las estaciones fuera de la costa, desarrollan migraciones verticales utilizando como barrera natural la capa mínima de oxígeno. La especie más importante durante el estudio fue *Acartia tonsa*, que se vio afectada por la intrusión de aguas calidas en la zona durante el El Niño moderado del 2006. Esta especie presentó marcadas diferencias interanuales en su abundancia, tasas de ingestión y selectividad. Además el impacto trófico de esta especies sobre la producción primaria fue muy variable durante el periodo de estudio. Esta gran variabilidad del impacto trófico se ocasionó por causa de la asincronía entre las variaciones de la producción primaria, de las tasas pastoreo, y de la abundancia de *A. tonsa*.

Los resultados de este estudio indican en términos generales que la comunidad de zooplancton esta fuertemente influenciada por las condiciones ambientales y que los cambios mas visibles se encuentran asociados a las variaciones estacionales y a las fluctuaciones anuales de los ciclos del ENSO. Uno de los factores físicos fundamentales que regulan la distribución de la comunidad en este sistema es la variabilidad espacial de la Zona Mínima de Oxígeno (OMZ).
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<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tr>
<td>ANOSIM</td>
<td>Analysis of Similarity</td>
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<tr>
<td>CCW</td>
<td>Cold Coastal Water</td>
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<tr>
<td>CENSOR</td>
<td>Climate Variability and El Niño Southern Oscillation: Implications for Natural Coastal Resources and Management</td>
</tr>
<tr>
<td>Chl-α</td>
<td>Chlorophyll α</td>
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<tr>
<td>CTW</td>
<td>Coastal Trapped Waves</td>
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<tr>
<td>CUEA</td>
<td>Coastal Upwelling Ecosystem Analysis</td>
</tr>
<tr>
<td>DVM</td>
<td>Daily Vertical Migration</td>
</tr>
<tr>
<td>EKW</td>
<td>Equatorial Kelvin Waves</td>
</tr>
<tr>
<td>EN</td>
<td>El Niño</td>
</tr>
<tr>
<td>ENSO</td>
<td>El Niño Southern Oscillation</td>
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<tr>
<td>ESD</td>
<td>Equivalent spherical diameter</td>
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<tr>
<td>ESW</td>
<td>Equatorial Surface Water</td>
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<tr>
<td>ESW</td>
<td>Equatorial Surface Water</td>
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<tr>
<td>EUC</td>
<td>Equatorial Undercurrent or Cromwell Current</td>
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<tr>
<td>EwE</td>
<td>Ecopath with Ecosim</td>
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<tr>
<td>e</td>
<td>Chesson electivity Index</td>
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<tr>
<td>H'</td>
<td>Shannon diversity</td>
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<tr>
<td>HCS</td>
<td>Humboldt Current System</td>
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<tr>
<td>ICANE</td>
<td>Investigacion Cooperativa de la Anchoveta y su ecosistema</td>
</tr>
<tr>
<td>IDVM</td>
<td>Inverse Daily Vertical Migration</td>
</tr>
<tr>
<td>IMARPE</td>
<td>Instituto del Mar del Peru</td>
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<tr>
<td>J</td>
<td>Pielou's evenness</td>
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<tr>
<td>LN</td>
<td>La Niña</td>
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<tr>
<td>MDS</td>
<td>Multidimensional scaling</td>
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<tr>
<td>MEI</td>
<td>Multivariate ENSO index</td>
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<tr>
<td>OML</td>
<td>Oxygen Minimum Layer</td>
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<tr>
<td>OMZ</td>
<td>Oxygen Minimum Zone</td>
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<tr>
<td>PaC</td>
<td>Panama Current</td>
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<tr>
<td>PCC</td>
<td>Peru Coastal Current</td>
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<tr>
<td>PCCC</td>
<td>Peru-Chile Counter-Current</td>
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<tr>
<td>PCUC</td>
<td>Peru Coastal Undercurrent</td>
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<tr>
<td>PDO</td>
<td>Pacific Decadal Oscillation</td>
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<tr>
<td>PI</td>
<td>Portion Ingested</td>
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<td>POC</td>
<td>Peru Oceanic Current</td>
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<tr>
<td>Pt</td>
<td>Percentage at the top oxygenated layer in relation to the total abundance per haul</td>
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<tr>
<td>PPC</td>
<td>Phytoplankton carbon</td>
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<tr>
<td>PUC</td>
<td>Poleward Undercurrent</td>
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<tr>
<td>SAW</td>
<td>Sub-Antarctic waters</td>
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<td>SST</td>
<td>Sea surface temperature</td>
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<td>SSW</td>
<td>Subtropical Surface Water</td>
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<td>t₀</td>
<td>Initial phytoplankton density and composition</td>
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<td>tₐ</td>
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<td>tₑ</td>
<td>Phytoplankton density and composition with copepods</td>
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<tr>
<td>TSW</td>
<td>Tropical Surface Water.</td>
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<tr>
<td>WMD</td>
<td>Weighted mean depth</td>
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<td>Zₒxy</td>
<td>Oxycline depth at 1 ml L⁻¹</td>
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<tr>
<td>Ztherm</td>
<td>Thermocline depth at 15°C</td>
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Chapter 1. Background and scope of thesis

This cumulative dissertation is essentially composed of four scientific papers as listed below. In addition, it includes a General Introduction, Methods and a Synoptic Discussion. This thesis was produced as a result of the cooperation between AWI and IMARPE in the context of CENSOR (Climate Variability and El Niño Southern Oscillation: Implications for Natural Coastal Resources and Management, www.censor.name), a multilateral project funded by the European Commission (INCO-FP6). It draws on major results of a sub-project (WP2) within CENSOR, which investigated pelagic-benthic processes off Peru and northern Chile. Additional funding for this thesis was provided by DAAD (Deutscher Akademischer Austausch Dienst) in the form of short-term fellowships.

The central objective of this thesis is to quantify and analyze the spatio-temporal variability in zooplankton biomass, composition, feeding activity, and secondary production in the highly productive Central Peruvian marine waters. The main emphasis is on the effect of the ENSO cycle (El Niño Southern Oscillation) on these key parameters, which regulate the productivity of marine system. Processes and factors that determine changes in zooplankton grazing and their relation to ENSO are quantified, analyzed, and discussed. These objectives are addressed in four scientific articles (Chapters 5.1 to 5.4) that have been already published or have recently been submitted to scientific journals. The specific objectives related to each of these articles are summarized below.

i) To summarize and review the current state of zooplankton research off Peru and identify important knowledge gaps.
ii) To quantify the abundance and composition of the zooplankton and identify seasonal and interannual changes in the zooplankton community structure at the continental shelf off Central Peru, and their relation to ENSO.

iii) To describe and analyze the vertical distribution and diel vertical migration of the zooplankton community at the continental shelf off Central Peru, during different ENSO phases.

iv) To evaluate the effects of ENSO on primary production, grazing rates, feeding selectivity, and egg production rates of the dominant copepod species in offshore shelf, nearshore shelf, coastal, and inshore bay habitats off Central Peru.

The history and current state of zooplankton research conducted in marine waters off Peru were analyzed and discussed in Chapter 5.1. This article reviewed zooplankton methodology, taxonomy, biodiversity, spatial distribution, seasonal and interannual variability, trophodynamics, secondary production, and modeling. These topics were analyzed and discussed in the context of ecological regime shifts to determine the responses of zooplankton to climatic variability (ENSO and multi-decadal). The co-authors and I undertook the idea of this review in the context of the CENSOR project, drawing on ideas in a previous short report from the Instituto del Mar del Peru (Guzman and Carrasco, 1996). I defined the conceptual premises of the review, took part in the search of available literature resources and wrote the summary of the results. This review was published in Progress in Oceanography 2008 (79): 238-255.
The idea of the article presented in Chapter 5.2 was to analyze changes in zooplankton distribution, composition, and abundance in relation to changes in environmental conditions, during different ENSO phases. It explored the effect of seasons, the ENSO cycle and the distance from the coast on zooplankton community structure. I originally developed, proposed and organized this zooplankton sampling program, within the context of a larger-scale sampling program at IMARPE known as the fixed station monitoring program. I carried out 50% of the sampling on board R/V OLAYA, while the other 50% was undertaken by technicians from IMARPE. I identified and quantified the species from all samples, with supervision of P. Ayón. I performed the analyses of the results and wrote the manuscript, with scientific and editorial help from Dr. R. Schwamborn. The final version of the manuscript took account of the comments and recommendations received from all the coauthors.

One conclusion of the review was that Peruvian zooplankton has a huge time series with a consistent methodology. However, the adaptation to life in the Oxygen Minimum Zone (OMZ) is still poorly understood. In this context, Chapter 5.3 describes and analyzes the vertical distribution and diel vertical migration of the zooplankton community at two stations on the continental shelf off Callao, Central Peru. I studied the different mechanisms, which the zooplankton displays in the water column and their response to changes in OMZ depth. This article was published in Helgoland Marine Research 2008 (62): 85-100. The authors are: Maria Isabel Criales-Hernandez, Ralf Schwamborn, Michelle Graco, Patrica Ayón, Hans-Jürguen Hirche, and Matthias Wolff. I developed the concept for this study and conducted all sampling with assistance of Dr. R. Schwamborn, P. Ayón, and several volunteers and technicians. I performed the identification and quantification of the species with
Finally, I studied the trophic link between phytoplankton and zooplankton, and its variability in relation to ENSO. These studies are still incipient in the Peruvian upwelling ecosystem (Chapter 5.1) and phytoplankton – zooplankton interactions in this area are still not well described. Furthermore, there are no previous studies on the effects of ENSO on primary and secondary production in this region. The article presented in Chapter 5.4 quantifies the grazing activity, feeding selectivity and egg production of the most abundant zooplankter (*Acartia tonsa*) at four stations in several habitats (offshore shelf, nearshore shelf, coastal area, inshore bay) off Central Peru during different El Niño Southern Oscillation (ENSO) phases in 2006 and 2007. I discussed how grazing activity, conversion efficiencies, and productivity by copepods have important consequences for the overall ecosystem. I performed all grazing experiments and analyzed all data from these experiments. Phytoplankton identification and counting was provided by “Area de Producción primaria” at IMARPE (Instituto del Mar del Peru). Additional data on primary production used in this study were provided by Dr. M. Graco, and data from egg production experiments were provided by P. Ayón. I wrote the manuscript with scientific and editorial help from Dr. H.-J. Hirche and Dr. R. Schwamborn. The final version of the manuscript takes account of comments and recommendations received from all co-authors. This manuscript has recently been accepted for publication in the *Journal Plankton Research*. 
In the synoptic Discussion (Chapter 6), the results of these articles are discussed. This chapter analyzes the importance of seasonal and interannual changes in environmental conditions on the composition and distribution of zooplankton in upwelling ecosystems and also evaluate the importance of trophodynamic interactions in the lower trophic levels.
Chapter 2. General introduction

The coastal zone of the Humboldt Current System (HCS) contains one of the world’s most productive aquatic ecosystems (Barber and Chavez, 1983). The phytoplankton bloom provide the food supply for the zooplankton, which in turn acts as a link in the trophic processes that sustain the largest single species fisheries of the world (Alheit and Niquen, 2004). HCS is characterized by a predominant northward flow of Surface Subantarctic Waters (SSW) toward the Equator, by an offshore Ekman transport, and coastal upwelling of cold, nutrient rich surface waters (Hill et al., 1998; Chavez and Barber, 1987; Pizarro et al., 2002). This system shows seasonal variability but also marked interannual (El Niño Southern Oscillation, ENSO) and inter-decadal oscillations (Pacific Decadal Oscillation (Chavez et al., 2003). Zooplankton is one of the most aggregated communities that inhabit the pelagic systems. Virtually all marine fish and invertebrate species spend at least one part of their life in the plankton. It is an important component of food webs. Furthermore, it is a good indicator of environmental changes (Batten and Welch, 2004; Hays et al., 2005; Hoof and Peterson, 2006).

My work focuses on the northern HCS, off the Central Peruvian coast. This area is characterized by strong and persistent wind-driven upwelling during the whole year, (Barber and Chavez, 1983; Nixon and Thomas, 2001; Pizarro et al., 2002). Peak biological productivity occurs between 5°S and 15°S, up to 100 Km offshore, where active upwelling sites are present (Calienes et al. 1985; Chavez et al., 1989; Nixon and Thomas, 2001; Pennignton et al., 2006). However, as in most of the HCS, productivity is strongly affected during El Niño events. El Niño has global
consequences (Siegert, et al., 2001; McPhaden et al., 2006), but changes are most drastic off northern Chile, Peru and Ecuador (Arntz and Fahrbach, 1991; Mullin, 1995; Cane, 2004; Chen and Cane, 2008).

2.1 The Humboldt Current system off Peru

The HCS extends along the western coast of South America from southern Chile (~42°S) to northern Peru (~5°S) and the Galapagos Islands (Hill et al., 1998). This ecosystem has been divided into four ecoregions, in accordance with climatic, oceanographic, and coastal morphological conditions, two of which two extend into Peruvian waters: (1) The Central Peru Ecoregion, which extends from 12°S to 5°S and (2) The Humboldtian Ecoregion, which extends from 12°S to 25°S and is characterized by a narrow shelf (Sullivan and Bustamante, 1999). Five areas of enhanced high upwelling and biological activity have been recognized inside the two ecoregions: (1) Paita, 5°S, (2) Punta Aguja, 6°S, (3) Chimbote, 9°S, (4) Callao, 12°S and (5) San Juan, 15°S (Zuta and Guillen, 1970) (Figure 1.2a).

Primary production throughout the year is on average 2.04 g C m\(^{-2}\) day\(^{-1}\) in the HCS as a whole and between 4 and 6.5 g C m\(^{-2}\) day\(^{-1}\) in Peru (Barber and Kogelschatz, 1990; Barber and Chavez, 1991). As a result, a rich secondary production develops in the upper layers and nearshore zones, but part of this material cannot be recycled near the surface, and sinks to increase an extensive Oxygen Minimum Zone (OMZ), which may reach close to the surface (up to only 20 m depth) at the shelf and upper slope (Arntz et al., 2006).
Coastal oceanographic conditions along the HCS are characterized by isotherms and isohalines in the upper ~100m tilted upward towards the coast, produced by upwelling. The temperature of water mass along the coast is constantly modified by the horizontal mixing of cold upwelling waters and ranges between 15°C and 19°C (Wyrtki 1966; Stevenson and Taft 1971; Enfield 1975). Four water masses can be distinguished in the coastal zone off Peru: Tropical Surface Water (TSW), Equatorial Surface Water (ESW), Subtropical Surface Water (SSW), and Cold Coastal Water (CCW) (Fig. 1.1b). The interaction of these water masses depends upon the interaction of the three fundamental currents that dominate the coastal waters off Peru (Fig 1.2b). The Peru Coastal Current (PCC) flows towards the equator, while the Peru-Chile Under-Current (PCUC) follows the shelf break towards the pole, and the Peru-Chile Counter-Current (PCCC) flows directly towards the south and veers to the west at around 15°S (Penven et al., 2005; Chapter 5.1, Fig. 1.1c). The flow of the PCC displays strong intrannual variability and is superimposed on mean seasonal patterns by the El Niño Southern Oscillation (ENSO) signal.

Figure 1.1 (a) Location of the Humboldt Current System; (b), schematic distribution of characteristic surface water masses, figure adapted from Ayón et al 2008 (c), overview of the surface and under currents in the eastern South Pacific that comprise the main flows of the HCS, Ayón et al 2008. The approximate locations for main upwelling areas for nutrient-rich waters are indicated (“X”). Adapted from Murphy (1937), Gunther (1936), Wyrtki(1963, 1967), Zuta and Guillen (1970), Tsuchiya, (1985), Lukas (1986), Huyer et al. (1991), Strub et al. (1998), Schneider et al., (2003), Penven et al. (2005),
Introduction

Croquette and Eldin, (2006), Kim et al. (2006), and Lucero et al. (2006), modified. Water masses in b: CCW: Cold Coastal Water and mixed waters under the influence of upwelled cold waters, SSW: Subtropical Surface Water, ESW: Equatorial Surface Water, TSW: Tropical Surface Water. Currents in c: EUC: Equatorial Undercurrent or Cromwell Current, PaC: Panama Current PCC: Peru Coastal Current, Chile-Peru Current, or Humboldt Current, PCCC: Peru-Chile Counter-Current, PCUC: Peru Coastal Undercurrent, Poleward Undercurrent (PUC), or Gunther Current, POC: Peru Oceanic Current, Oceanic Chile-Peru Current, or Oceanic Humboldt Current. Figure adapted from Ayón et al 2008

2.2 El Niño Southern Oscillation (ENSO)

The El Niño–Southern Oscillation (ENSO) cycle is a fluctuation between unusual warm (El Niño) and cold (La Niña) conditions in the eastern Pacific. It is the most prominent year-to-year climate variation on earth (Philander, 1999; McPhaden et al., 2006). ENSO itself consists of an unstable interaction between sea surface temperature (SST) and the atmospheric pressure field. It results in variations in winds, rainfall, thermocline depth, circulation, and ultimate in biological productivity, modifying the feeding and reproduction of fish, birds and mammals (Fiedler, 2002, Yusunaka and Hanawa, 2005, Penington et al., 2006) (Fig. 1.2). The ENSO fluctuation between warm and cold events exhibits considerable irregularity in amplitude, duration, temporal evolution, and spatial structure (McPhaden, 2006). Evidence exists that the longer-waved Pacific Decadal Oscillation (PDO) may be modulated by ENSO (McPhaden, 2006).

In general, the upwelling of cold, nutrient-rich waters is greatly reduced during El Niño events due to arrival of warm Equatorial Kelvin waves, causing a significant reduction in primary production, rise temperature, deeper thermocline, and an increase in dissolved oxygen (Wirtky, 1981; Arntz and Fahrbach, 1991; Arntz et
al., 2006). In consequence, a dramatic impoverishment occurs in the entire HCS of marine biological communities (Arntz and Fahrbach, 1996; Escribano et al., 2004), which are maintained during La Niña and ENSO-normal conditions by effective upwelling of nutrient-rich deep water (Arntz, et al., 2006). During La Niña the thermocline rises drawing macronutrients into the euphotic zone. Productivity and biomass increase around the equator, but micronutrients are limiting and may produce a low chlorophyll condition in the system (Ryan et al., 2002).

Geographically, the impact of El Niño and La Niña on the HCS is extended from the open ocean to the coast over the entire the Eastern Pacific off North and South America (McPhaden, 2006). Marked effects have been reported on pelagic as well as benthic communities (Arntz et al., 2006).

**Figure 1.2** Schematic diagram showing of the ENSO (El Niño Southern Oscillation) cycle. (a) Warm conditions El Niño, (b) Normal and (c) La Niña in the Pacific Ocean. The underlying blue layer denotes the relative depth of the thermocline. Decreased trade winds during El Niño allow the basin-wide slope of the Pacific Ocean to relax. Surface waters flow back to the west during El Niño and the thermocline is pushed downward (figure taken from [http://www.pmel.noaa.gov/tao/elNiño/el-Niño-story.html](http://www.pmel.noaa.gov/tao/elNiño/el-Niño-story.html)).
2.3 Zooplankton distribution in upwelling systems

Zooplankton populations display specific patterns of distribution in the HCS, which are related to changes in oceanographic conditions and processes i.e. OMZ, Ekman transport, and upwelling intensity. Low OMZ depth constrains the plankton population in a narrow region of shallow water, especially during intensive upwelling (Judkins, 1980; Smith et al., 1981; Chapter 5.3). Ekman transport has an effect on the zooplankton distributions across the coast. This variable causes cross-shelf advection and different assemblages of species can be identified from nearshore to offshore and along the latitudinal gradient from north to south (Santander, 1981; Smith et al., 1981; Thiel, et al., 2007; Chapter 5.1). Thus, active upwelling and relaxation periods affect biological processes and determine rates of primary production, which in turn produce changes in secondary production, specially in the nearshore areas (Escribano and Morales, 2004; Echevin, 2004).

Although the biodiversity of zooplankton varies along the coastal and cross-shelf, copepods are a major component of zooplankton and the dominant grazers of phytoplankton throughout the HCS (Gonzales et al., 2000; Calbet and Landry, 2004). Nearly 60 species of copepods have been identified in the coastal zone of Chile (Thiel et al., 2007), and 150 species of copepods were identified in the coastal zone of Peru (Chapter 5.1). Copepods occupy a key position in pelagic food webs. They transfer organic matter produced by the phytoplankton to higher trophic levels such as pelagic fish stocks, marine mammals, seabirds and finally humans (Lenz, 2000).
In addition, zooplankton can respond to changes in external forcing. Previous studies have found strong correlation between ENSO phases and diversity, abundance and distribution of some taxa (Santander and Carrasco, 1985; Escribano, et al., 2004; Chapter 5.1). During EN conditions, the usually dominant copepods (*Acartia tonsa*, *Paracalanus parvus*, and *Centropages brachiatu*s) are depleted and replaced by tropical species from equatorial regions (*Centropages furcatus* and cyclopoids)(Chapter 5.3; Aronés et al., 2009). In addition, there may be an increase in gelatinous species that could be preying upon meroplanktonic larvae and ichthyoplankton (Ayón et al, 2008)
Chapter 3. Study areas

3.1 Continental shelf off Callao

The shelf off Callao (12° S) is an open shore area located on the central Peruvian coast in the northern part of the HCS (Fig 3.1, 3.3). It is affected by strong upwelling, which persists for seven months between June to February (Zuta and Guillen, 1970; Zuta et al., 1978; Calienes and Guillen, 1981). A widening of the shelf is observed in this area (Carrasco and Lozano 1989). The Oxygen Minimum Zone (OMZ) here is the most intense in the world (Rossemberg et al., 1983; Arntz, et al., 1991) and is notably shallower than at other latitudes off Peru (Gutierrez et al., 2008). Modulations in the OMZ show significant temporal variability with periods between 30 and 50 days (Gutierrez et al., 2008).

Figure 3.1 Continental shelf off Callao, satellite photo from Google earth 2009, left, and photo during typical sampling procedure, right (photo taken by Maria Isabel Criales).

3.2 Independencia Bay

Independencia Bay (14°06’-14°20’S; 76°00’-76°18’W) is a large, shallow bay situated within the Paracas National Reserve, near Pisco, Peru. (Fig. 3.2, 3.3). It is a semi-enclosed bay containing two large islands, La Vieja and Santa Rosa. La Vieja
Island (5.6 km long and 2.4 km wide) occupies most of the southern half of the mouth of the bay, with the longer side parallel to the coast (Fig. 3.2, 3.3). This area is located in the Humboldtian ecoregion and is close to an upwelling site. Levels of primary production are high all year round, but with peaks between June to November (Vélez et al., 2005). The bay is characterized by low surface temperatures (14-18°C) and high nutrient levels mainly arising from the run-off from guano bird colonies on La Vieja Island, disturbance of organic-rich sediments, and coastal upwelling at the adjacent shelf. Characterized by high biodiversity and abundance of seabirds, it is considered as a key ecosystem in Peru and is the site of one of the country’s most important artisanal fisheries (Tarazona, et al., 1989; Taylor et al., 2008).

**Figure 3.2** Independencia Bay, satellite photo from Google Earth 2009 with sampling sites labeled (T6, T5, T8), left, and close up photo of La Vieja Island, Peru, where sites T6 and T5 are located, right, (photo taken by Maria Isabel Criales).
Figure 3.3 Map of the continental shelf off Callao and Independence Bay. Experimental and sampling stations from 2006 and 2007 are indicated. Bi-monthly sampling occurred at four stations off Callao (1, 2, 3 and 4), seasonal intensive sampling at two stations off Callao (2 and 5), and grazing experiments at three stations off Callao (at the IMARPE pier, not pictured, and stations 2 and 5) and one stations in Independencia Bay (T6).
Chapter 4 Synopsis of main methods employed

This chapter briefly describes the data sources and main methods used in this study. Detailed descriptions of the methods are found in the corresponding references.

4.1 Sampling and Experiments

Bimonthly sampling

I took samples of zooplankton every two months from February 2005 to December 2007 off Callao (Fig.3.1). For the sampling of zooplankton I performed oblique tows with a 60 cm of diameter Bongo net of 300 μm mesh size (Fig 4.1). I sampled at four stations along a transect off Callao perpendicular to the coast (Fig, 3.3, 4.1). Nets were equipped with calibrated flowmeters. To preserve all samples I used 4% formalin solution, buffered with sodium tetraborate. In the laboratory, I identified all copepod species were identified to the lowest taxonomic unit possible and counted them under a stereomicroscope.

Figure 4.1 Photos from oblique tows with Bongo net during typical sampling procedure off Callao (photos taken by Maria Isabel Criales)
**Seasonal intensive sampling (winter and autumn)**

I sampled zooplankton at two stations off Callao twice a year at two stations off Callao between 2006 and 2007. Station 2 (93 m deep) and Station 5 (176 m deep) were respectively located on the nearshore shelf and the offshore shelf, close to the shelf break (Fig. 3.3). I took the samples over 24 hours periods at both stations. I took vertically stratified tows every 3 hours with a multinet (Midi model, 50 x 50 cm mouth size, Hydro-Bios, Kiel) equipped with five 300-μm-mesh nets (Fig. 4.2). Each of the five nets had calibrated Hydro-Bios flowmeter, to later make individual estimates of filtered volume for each sample. Depth strata sampled with each net were: (1) maximum depth to 50 m, (2) 50–30 m, (3) 30–20 m, (4) 20–10 m, and (5) 10 m below the surface. I chose this sampling strategy was chosen to ensure a consistent sampling of the three main strata (oxygen minimum layer, oxycline, and upper layer) of the water column. At each station, I also took CTD profiles for temperature and conductivity data. Additionally, I sampled water samples were taken with a Niskin bottle to measure nutrient, chlorophyll *a* and oxygen measurements. In the laboratory, I identified all copepod species were identified to the lowest taxonomic unit possible and counted their abundances under a stereomicroscope.

**Figure 4.2** Photos from stratified tows with Multinet during typical sampling procedure off Callao (photos taken by Maria Isabel Ciales)
**Grazing experiments**

I carried out experiments to study mesozooplankton grazing *in situ* at four stations: three off Callao (at the IMARPE pier, and stations 2 and 5) and one in Independencia Bay (Fig. 3.3). I performed experiments in April, July, and August 2006, and in February, April, May and August 2007 (Fig. 4.3). For the *in situ* grazing experiments, I used the most abundant copepod species, *Acartia tonsa*. I calculated phytoplankton abundance and biomass in terms of density (cells ml⁻¹) and carbon biomass (μgC l⁻¹).

I measured cell dimensions to calculate cell volumes by assigning specific shapes to each taxa in order to estimate carbon content (Sun and Lui, 2003, Hillebrand et al., 1999). I used Frost’s equations (Frost, 1972) to calculate ingestion rates. Grazing rate estimates were expressed for individual organisms and in relation to biomass (μg C). I compared the composition of *A. tonsa* diets to the composition of the food offered, and used the Chesson selectivity Index (ε) to assess for food selectivity (Chesson, 1983; Schwamborn et al., 2004). I performed additional primary production and egg production experiments at stations 2 and 5 off Callao, simultaneous with the *in situ* grazing experiments. The results of these experiments allowed me to estimate gross efficiency, and observe the effect of grazing on primary production and its consequences of *A. tonsa* egg production rates.
Figure 4.3 Photos from primary production and grazing experiments. Steel basket used for *in situ* incubations, left, general set-up for grazing experiments onboard (photos taken by Maria Isabel Criales).

### 4.2 Data analysis

**Temporal and spatial dynamics in community structure**

For this section, I used the abundance data to determine potential changes in zooplankton communities. First, I built two separate Bray-Curtis Similarity matrices were built based on species abundance after appropriate transformation (ln x). I used these similarity matrices to perform cluster analyses by samples and by species, to test possible ruptures, abrupt changes in community structure, and the appearance of distinct communities appearing at different periods of time. Clustering was performed by group average linking (Grey et al, 1988). I also used ANOSIM (Analysis of Similarity) to test for significant differences (at \( \alpha = 0.05 \)) in community structure between sampling periods and stations (Clarke and Warwick, 1994).

**Vertical distribution and migration in relation to the OMZ**

To evaluate vertical distribution of zooplankton. I used two approaches: i) changes in weighted mean depth (WMD) (Roe et al., 1984 and Pillar et al., 1989) and ii) changes in the abundance percentage at the top oxygenated layer in relation to the total abundance per
haul ($P_{oxy}$). The top oxygenated layer corresponds to the Multinet strata sampled above the 1 ml l$^{-1}$ oxygen isopleths. The significance of differences in WMD and $P_{oxy}$ between day and night was tested to verify whether vertical migration occurred. Additionally, I used non-parametric test to evaluate daily diel vertical migration of species, and to compare vertical distribution of different life history stages. In addition, Spearman rank correlation analysis to assess the effect of the environmental conditions on the vertical distribution. Statistical tests were performed using Statistica 6.1

**ENSO effect on primary production, grazing rates, electivity and egg production of A. tonsa**

I used Spearman’s correlation analysis to test for significant relationships between several indicators of cell size (length along major axis, volume, equivalent spherical diameter ESD, and carbon content) and electivity ($\varepsilon$). I performed these test for the entire data set, and separately for each time period (EN 2006, LN 2007, Neutral 2006-2007), and for each taxonomic group (flagellates, silicoflagellates, dinoflagellates and diatoms). I also performed Mann-Whitney U-tests to evaluate significant differences in $\varepsilon$ between time periods (EN 2006 vs LN 2007) and taxonomic groups (dinoflagellates vs diatoms). I used Spearman’s rank correlation analysis to test for significant correlations between several variables, i.e. cell density, ingestion rates, and egg production. This analysis was used to verify how grazing and egg production by *A. tonsa* changed with food concentration and composition. Statistical analyses were performed with Statistica 6.1 and using the “R” language and environment (R Foundation for Statistical Computing).
Chapter 5. Results

5.1 Scientific contribution

Zooplankton research off Peru: A review

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ABSTRACT

A review of zooplankton studies conducted in Peruvian marine waters is given. After a short history of the development of zooplankton research off Peru, we review zooplankton methodology, taxonomy, biodiversity, spatial distribution, seasonal and interannual variability, trophodynamics, secondary production, and modelling. We review studies on several micro-, meso-, macro-, and megazooplankton groups, and give a species list from both published and unpublished reports. Three regional zooplankton groups have been identified: (1) a continental shelf group dominated by Acartia tonsa and Centropages haggloi; (2) a continental slope group characterized by myctophids, hiatellids, foraminifers and radiolarians; and (3) a species-rich oceanic group. The highest zooplankton abundances and biomasses were often found between 4-6°S and 14-16°S, where continental shelves are narrow. Species composition changes with distance from the shore. Species composition and biomass also vary strongly on short time scales due to advection, peaks of larval production, trophic interactions, and community succession. The relation of zooplankton to climatic variability (ENSO and multi-decadal) and fish stocks is discussed in the context of ecological regime shifts. An intermediate upwelling hypothesis is proposed, based on the negative effects of low upwelling intensity in summer or extremely strong and enduring winter upwelling on zooplankton abundance off Peru. According to this hypothesis, intermediate upwelling creates an optimal environmental window for zooplankton communities. Finally, we highlight important knowledge gaps that warrant attention in future.

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1. Introduction

The coastal upwelling ecosystem off Peru hosts the world’s largest single-species fisheries, which is sustained by wind-driven upwelling of nutrient-rich waters to the surface. Where phytoplankton bloom at the base of highly productive pelagic food webs (Bertrand et al., 2005; see also Pennington et al., 2006). Many zooplankton eat phytoplankton, and are in turn preyed upon by fish larvae and many adult planktonic fish. Conversely, certain zooplankton groups (e.g. medusae) also prey on fish eggs and larvae. Due to their intermediate position in the food web between primary producers and predators, zooplankton serves as a link between bottom-up climate-related control of phytoplankton and fish.

Here we present a short review of zooplankton research off Peru. We focused on mesozooplankton, microzooplankton, and microzooplankton, but left the extensive literature on Peruvian ichthyoplankton for a separate review. We build on the short review by Guzmán and Carrasco (1986) of IMARPE ichthyoplankton and zooplankton studies. Montecinos et al. (2006) and Pennington et al. (2008) provided overviews of biological-physical interaction processes off western South America, including several aspects of the Peruvian sector of the Humboldt Current System. More specific reviews of the Peruvian upwelling ecosystem were given by Arntz and Fahrbach (1991), Iturriaga and Arntz (2001) and Tanaka et al. (2003), but the main emphasis was on benthic communities and fisheries stocks and zooplankton were mentioned only briefly. An extensive review of zooplankton in the eastern tropical Pacific, however, was recently published by Fernández-Almario and Fárbeg-Lordía (2000), who focused on large-scale surveys in the eastern tropical Pacific (e.g., EASTROPAC). Our review provides an overview of the work conducted off Peru. In particular, we (1) provide an overview and hosts for comparison with other upwelling regions, and (2) summarizing all the literature available, much of which was found in unpublished reports and theses, and (3) identify gaps in our knowledge.

2. History of zooplankton research in Peru

Peruvian marine research was established in 1960 with the Instituto de Investigaciones de los Recursos Marinos (IMARPE) with the financial and technical support of FAO, which in 1964 changed its name to Instituto del Mar de Perú (IMARPE). IMARPE's
initial mission was to compile scientific information about Peru's fish stocks to provide a scientific base for management decisions. With time, effects affecting the stocks led to the realization that the scientific base had to be broadened to scale that were previously not regarded as necessary. This lesson was brought home by the catastrophic effects of El Niño on the anchoveta fishery and Peru's continued dependence on this single-species fishery (Dibb and Valliéva, 1981).

Early zooplankton work concentrated on taxonomy and horizontal distribution (Vásquez, 1987; Alvarado, 1972; Gómez, 1972), especially of euphausiids (Santander, 1967; Santander and Santolvo de Castillo, 1969) and appendicularians (Peraula, 1968). Additional work followed in the 1970s during the International Decade of Ocean Exploration, which coincided with the initial decade of the Law of the Sea. The Law of the Sea emphasized that nations have rights to their coastal resources, including the right of exploration and research (Angeles, 1981). Interest in the biological production in Peru's coastal waters was high due to the prosperous anchovy-meat industry.

The International program CUEA (Coastal Upwelling Ecosystem Analysis, 1972–1980) was developed to study the physical, chemical, and biological drivers within upwelling ecosystems. It compared the upwelling systems of Oregon, Baja California, Peru, NW Africa, and Somalia. CUEA was conceived following the "Anton Bruun" cruise off Peru in 1966 (e.g. Ryther et al., 1966; Ryther, 1967; Barber and Chavez, 1987). Under CUEA, interdisciplinarity and multiphase studies were conducted off Peru during the "Anton Bruun" expedition from March to October 1976 and March to May, 1977. Results were presented at a series of meetings (Barcelona, 1970; Investigations Pesquera 10, 1972; Marraruci, 1972; Tetuya 6, 1974; Kiel, 1975; Upwelling Ecosystems, 1978) and on the IOC (International Decade of Ocean Exploration) International Symposium on Coastal Upwelling in Kiel, 1975.

Several cruises of the Institute of Oceanology, Russia, were conducted in 1974 (Vinogradov, 1977) to study the pelagic communities of tropical regions and their zones of intense upwelling. The majority of the results are published in the journal Oceanology.

In 1975, the Pennzoil-German Program PROCPA (Programa Cooperativo Perúano-Alemán de Investigación Pesquera) was initiated, which lasted until 1985. Its main purpose was to support research in areas that could not be covered sufficiently by Peruvian scientists. Part of the program was the building of RV "Alexander Humboldt", which remains an important vessel in Peruvian fishery research in 1994, Germany funded time series sampling at stations off Paita and San José ("Fixed Coastal Stations Program"). Sampling at these stations is ongoing.

The bi-country project KANES (Investigación Cooperativa de la Archavetax y su Ecosistema) between Peru and Canada began in 1976 during severe changes in the fisheries. The goal was to identify causes of the recent decreases in the anchoveta population, with the goal of predicting events in this system on a time scale relevant to fishery management (Dibb and Valliéva, 1981). Results were published in Boletín Instituto del Mar del Perú-Callao, Vol. extracranio (1981). These interdisciplinary programs improved Peruvian field work and data analysis and also established collaborations between Peruvian and foreign scientists.

Table 1: Summary of the main types of zooplankton surveys off Peru.

<table>
<thead>
<tr>
<th>Program</th>
<th>Method</th>
<th>Comment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vertical net</td>
<td>several times per year since 1964. Stations located several times per year since 1964. Stations located over the whole marine area off Peru</td>
<td></td>
</tr>
<tr>
<td>Horizontal net</td>
<td>several times per year since 1964. Stations located over the whole marine area off Peru</td>
<td></td>
</tr>
<tr>
<td>Subsurface</td>
<td>several times per year since 1964. Stations located over the whole marine area off Peru</td>
<td></td>
</tr>
</tbody>
</table>

Table 1: Water masses found in surface waters off Peru.

<table>
<thead>
<tr>
<th>Water masses</th>
<th>Salinity</th>
<th>Temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical Surface Water (TSW)</td>
<td>&lt;33.5</td>
<td>&gt;20°</td>
</tr>
<tr>
<td>Equatorial Surface Water (ESW)</td>
<td>33.5-34</td>
<td>&gt;20°</td>
</tr>
<tr>
<td>Subtropical Surface Water (SSW)</td>
<td>35-35.5</td>
<td>18-22°</td>
</tr>
<tr>
<td>Cold Coastal Water (CCW)</td>
<td>34.8-35.5</td>
<td>14-18°</td>
</tr>
</tbody>
</table>

* Zita and Guillette, 1990.
3. Study area – water masses, currents, and upwelling

The distribution of planktonic organisms is dependent on currents and water masses. The waters off Peru are part of the Humboldt Current System (HCS), which dominates most hydrodynamic processes off Chile and Peru (Fig. 1; cite reviews in PRO vol 49). The Peru Coastal Current (PCC) flows equatorward, while the Peru–Chile Under-Current (PCUC) follows the shelf break towards the pole, and the Peru–Chile Counter-Current (PCCC) flows directly towards the south and veers to the west around 15°S (Ferreyra et al., 2005). The flow of the PCC is strongest in austral winter, when equatorward winds are maximal (Bakun and Nelson, 1981; Echevin et al., 2004a,b; Crochet et al., 2005). It carries colder and saltier upwelled water to the north where they eventually become part of the South Equatorial Current (SEC).

Many oceanographic features vary seasonally and interannually, especially during El Niño. During "average" years, and especially during La Niña events, the Peruvian shelf is dominated by Cold Coastal Water (CCW; see Table 1), which is strongly influenced by coastal upwelling. Under normal conditions, upwelled waters originate from the PCUC (Echevin et al., 2004a,b). This upwelling of nutrient-rich waters sustains one of the most productive ecosystems of the world, with zooplankton biomasses which are among the highest recorded for large marine ecosystems in lower latitudes (Fernández-Alamo and Farber-Lordia, 2006). Plumes of upwelled water may extend several hundred km offshore at the

![Fig. 1. Study area along the Peruvian coast showing zooplankton sampling stations covered since 1964 (Aypé et al., 2004, modified) (A), schematic distribution of characteristic surface water masses (b), and bathymetry with main currents (c). The approximate locations for main upwelling areas for nutrient-rich waters are indicated ("CC"). According to Gutiérrez (1998), Wyrtki (1963, 1967), Izzi and Guifré (1990), Tschiøen (1987), Hupe et al. (1989), Balbontín et al. (1996), Lebranch et al. (2000), Pearson et al. (2005) and Crochet et al. (2006), modified. Water masses in b: CCW, Cold Coastal Water; and mixed waters under the influence of upwelled cold waters; SSW, Subsurface Surface Water; ESW, Equatorial Surface Water; TSM, Tropical Surface Water. Currents in c: EUC, Equatorial Undercurrent; or Counter-Current; EAC, Equatorial Counter-Current; FUC, Fakawai Current; PCC, Peru Coastal Current, Chile-Peru Current, or Humboldt Current; PCCC, Peru-Chile Counter-Current; PCUC, Peru Coastal Undercurrent; Poleward Undercurrent (PUC), or Gulfstream Current; FOC, Peru Oceanic Currents, Oceanic Chile-Peru Current, or Oceanic Humboldt Current.](image-url)
Results

4. Research topics

4.1. Sampling and survey development

IMARPS has always focused on fisheries. Zooplankton samples were by a prototype of ichthyoplankton sampling, which was conducted on all surveys; best pelagic, demersal or hydrographic surveys. Between 1961 and 2006 ~ 150 surveys were carried out with more than 10,000 samples collected. Surveys covered up to 500 km from the coast between 3°30'S and 18°20'S, although over 95% of the samples were collected within 100 km of the coastline (Fig. 1). Two types of standard surveys for zooplankton sampling have evolved with time (Table 2):

1. In the Hensen Net Program, zooplankton data have been collected since 1964 on Pelagic Fish, Demersal Fish and Oceanographic Surveys, where a Hensen net (330 μm mesh, 60 cm diameter) has been towed vertically from 50 m to the surface. After removal of large zooplankters and ichthyoplankton, the zooplankton settlement volume is measured (Carrasco and Lazano, 1988; Ayón et al., 2004). The stations are located on a pre-defined meander-shaped transect covering the whole coastal area of Peru, although the cruise track was sometimes modified. Zooplankton samples were only taken at stations where echanges indicated fish were present and fish trolling should also be conducted. Since 1996, additional zooplankton sampling has been conducted where distance between travel positions was >20 km.

2. In the Fixed Coastal Stations Program, on transects perpendicular to the coast near Paita, San José and Callao, horizontal surface tows have been taken since 1964 with a WFS net (Working Party 2: UNESCO, 1969: 310 μm mesh, 50 cm diameter). Additionally, since 2004, oblique bongo net tows (60 cm diameter, 60 cm mesh size; Table 2) have been included.

During a limited project in 1996/1997, vertically stratified samples were taken with a closing net (200 μm mesh, 85 cm mouth diameter) were taken, usually from 100–30–25–10–0 m on two fixed stations near Callao (12°12.5′S, 77°13′W; Escudero, 2001) and Chimbote (09°20.4′S, 79°41.0′W). Since 2000, on Demersal Fish Surveys stratified samples have been taken with a multinet (Hydrobios, 330 μm mesh, 50 × 50 cm mouth size) from 200–150–100–50–10–0 m. More advanced sampling methods have been recently used during the International Cruises Program (CRID) that was started under the CENSOR project (Table 2, Section 4).

4.2. Biodiversity

In general, knowledge of the taxonomy of the zooplankton fauna is poor, considering the amount of work invested into sampling (Table 2) and the ecological and economic importance of these ecosystems (Koehl, 1983). Consequently, a few species of siphonophores collected by the US Steamer Albatross in 1904/1905; Santander et al. (1981: a,b) catalogued 3 siphonophore, 21 copepods, 35 amphipods, 8 echinoids, and 6 ctenophora species. Abante (2001) presented a list of 152 copepod species from 54 genera collected on 15 cruises between 3°30’S and 14° and 1980–2001. The zooplankton species in Table 4 were identified from the Fixed Coastal Stations Program since 1994, and since 1987 from material sampled in the Hensen Net Program. Previously existing keys have usually been used for identification, which often are based on material from other regions. Organisms have sometimes been mis-identified. For example, during the same expeditions the abundant Calanus species were called Calanus chiilensis (Sameoto, 1981) and C. australis (Santander et al., 1981b). Therefore, a careful taxonomic revision of the fauna of the southeast Pacific is required.

4.3. Spatial patterns

4.3.1. Horizontal distribution and abundance

Santander (1967) provided the first data on major taxa in surface samples from transects perpendicular to the coast between Callao and Chimbote (copepods, euphausiids, appendicularians, siphonophores, and praeodons). In 1987, Carrasco and Santander found that during normal conditions between 6°S and 12°S, copepods were the most abundant, followed by siphonophores, chaetognaths, polychaetes, euphausiids, and amphipods. Other studies have found that the main zooplankton groups off Peru were copepods, euphausiids, and chaetognaths (Ayón and Gác, 1996, 1997; Ayón and Arellano, 1997; Ayón et al., 1998; Ayón and Girón, 2004). Off Paita and San José, ca. 50% of the zooplankton were crustaceans, copepods being by far the most abundant group (Gutiérrez et al., 2005).

Santander (1981) studied the zooplankton in an important upwelling area from Pisco to San Juan, in autumn 1870 and 1877. She concluded that food quality and concentration were regulating the zooplankton composition, being low primary production associated to the dominance of eutrophic or carnivorous species, with less herbivorous species. Santander (1981), defined three major zooplankton groups: (1) continental shelf (dominated by A. tonka and C. hickmani); (2) continental slope (siphonophores, bivalves, foraminifera, and radiolaria); (3) oceanic group (Megrina major, Phronima gracilis, Sclerionic danse, Loricaria flavicornis, Euchareus marina, Euchareus bellus, Oithona plumifera, Calocalanus pavo, Temora stylifera, T. danaeoides, Hamniconus minor, Eucalanus peelei, Acrocalanus sp., Corycaeus sp., Oithona sp., Oncaea sp., Suphragia sp., Corycosus sp., Capella sp.) Sarmiento (1981) confirmed this species composition changes with distance from the shore, but noticed a high variability in species composition and biomass that can occur on daily time.

Planktonic ecosystems of the PCC under the influence of upwelled Cold Coastal Waters (CCW) differ markedly from the subtropical waters to the west by their high concentration of life (fish, birds, mammals, etc.) and by their huge biomass (Ayón et al., 2004). However, a recent analysis of historical data indicates that within the CCW, higher biovolumes are found offshore, prob-
<table>
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### Table 4


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- *Perissocopa setosa* | Paracas | Bamber, unpublished |
- *Perissocopa setosa* | Paracas | Bamber, unpublished |
- *Perissocopa setosa* | Paracas | Bamber, unpublished |
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- *Perissocopa setosa* | Paracas | Bamber, unpublished |
- *Perissocopa setosa* | Paracas | Bamber, unpublished |
- *Perissocopa setosa* | Paracas | Bamber, unpublished |

### Copepoda

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- *Acanthus derreti* | Paracas | Bamber, unpublished |
- *Acanthus derreti* | Paracas | Bamber, unpublished |
- *Acanthus derreti* | Paracas | Bamber, unpublished |
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- *Acanthus derreti* | Paracas | Bamber, unpublished |
- *Acanthus derreti* | Paracas | Bamber, unpublished |
- *Acanthus derreti* | Paracas | Bamber, unpublished |

### Ostracoda

- *Ostracoda* | Paracas | Bamber, unpublished |
- *Ostracoda* | Paracas | Bamber, unpublished |
- *Ostracoda* | Paracas | Bamber, unpublished |
- *Ostracoda* | Paracas | Bamber, unpublished |
- *Ostracoda* | Paracas | Bamber, unpublished |
- *Ostracoda* | Paracas | Bamber, unpublished |
- *Ostracoda* | Paracas | Bamber, unpublished |
- *Ostracoda* | Paracas | Bamber, unpublished |
ably due to stronger predation nearshore and low biovolumes in freshly upwelled water (Ayón et al., 2008). Also, there is a clear north-south pattern, with high biovolumes mainly between 4°S and 6°S and again poleward of 14°S. These high biovolume areas are characterized by a narrow continental shelf (18–28 km) (Samsander, 1981; Carrasco and Lozaro, 1981; Ayón et al., 2004). The high biovolumes in the north may be due to the influence of the ESW, which has larger species and higher diversity (Ayón, 1999).
than CCW. On the other hand, the number of abundant tropical species greatly decreases toward the coast. In the coastal areas under influence of CCW, large aerobic herbivores like Calanus australis and Eucalanus inconcisus may grow in mass (Geyink, 1973). Off northern and central Peru, euphausiids were less but the remaining mesozooplankton were more abundant (Gamber, 1936).

ENE alters mesozooplankton diversity, distribution, and abundance. An increase in diversity is caused by the intrusion of tropical species in the central and southern Peruvian coast (Santander and Carrasco, 1985; Carrasco and Santander, 1987; Carr, 2003). Work off northern Peru was done during ENE when the intrusion of warm waters with warm water species such as Centropages furcatus (Santander et al., 1981b; Aronés et al., 2001). The 1982/1983 EN caused an increase in zooplankton biomass, especially gelatinous species, and diversity (Santander and Carrasco, 1985). In contrast, there was a pronounced decrease in mesoplankton: larvae and ichthyoplankton in the coastal waters during EN.

Specific attention on the regional and seasonal distribution of certain taxonomic groups was given by Varela (1987), who identified ten species of siphonophores between 5°47' and 9°13' up to 260 km offshore, and by Castillo et al. (2004) and Castillo et al. (2007) who studied the distribution of 15 ostracod species. During the 1998 EN ostracod species shifted south and their distribution showed positive or negative correlations with salinity and distance to shore. Some species can be used as water masses indicators (Gómez, 1972; Geyink, 1973; Aronés, 2002; Castillo, 2004). Sandoval de Castro (1987) used chaetognaths as water mass indicators, with Sagitta bedoti, S. neglecta, S. perspicua, and S. pulchra associated in ESW, and S. ferus, S. regularis and Kiasirita pacifica in SSW. Carrasco and Santander (1987) showed that the copepods Centropages furcatus, Acrocalanus gracilis, and A. monacha were typical in ESW, while CCW species were Clausocalanus arcticus, Acartia tonsa, Oithona plumifera, Paracalanus parvus, Centropages brachionus, and Eucalanus inconcisus. A recent study conducted off northern Peru (Guzmán et al., 2005) recognized several copepod species as indicators of CCW: Acartia densa, Calanoides japonicus, Ichthyocalanus planulatus, Meisocrene clausil, and Oncorhynchus cancrivora. Abanto (2001) related the distribution of 135 copepod species to hydrographic data between 3°30' and 14°5' between 1980 and 1983. Samples are presented in Fig. 5. Thus, Acartia tonsa, Calanus australis, Clausocalanus sp., Paracalanus parvus are especially eurythermal and euryhaline and not water mass specific, while Sibogacinus cassiae, Sphygma larvata, Neocalanus acutus, and A. monacha were typical in ESW, while CCW species were Clausocalanus arcticus, Acartia tonsa, Oithuna plumifera, Paracalanus parvus, Centropages brachionus, and Eucalanus inconcisus. Recent study conducted off northern Peru (Guzmán et al., 2005) recognized several copepod species as indicators of CCW. During EN, Centropages furcatus shifts south and replaced the CCW species C. brachionus and Eucalanus inconcisus (Abanto, 2001). The shift between C. brachionus (pre-EN) and C. furcatus (EN) was also observed by Abanto (2001), who related hydrographic parameters to changes in microphytoplankton, mesozooplankton (volume, abundance, and species richness), Eucalanus and macrozoobenthos in surface samples collected between 1994 and 2004 on fixed stations off central Peru. They found notable changes in species composition and richness associated with the 1997/1998 EN.

4.3.2 Vertical distribution and migration

The vertical distribution of zooplankton is controlled by their nutritional and physiological requirements; therefore, the structure of the water column with its gradients of temperature and salinity is important. Furthermore, in the Eastern Tropical Pacific, a subsurface OMZ (Pennington et al., 2006) has a profound impact on the distribution of pelagic animals and limits the space available for aerobic life. The upper limit of the OMZ depth is often identified as the depth of 0.5 mg L⁻¹ (Frid et al., 2003) or 1 mg L⁻¹ (Hidalgo et al., 2005; Criales-Hernández et al., 2008) oxygen isopleth. In regions of coastal upwelling, hypoxic water can reach to within a few meters of the surface (Wyrtki, 1965; Juddles, 1980; Escobar et al., 2004). Not many studies have been conducted on the vertical distribution of zooplankton off Peru. Only during international cruises have closing nets, pumps and electronic plankton counters been used (Mackas et al., 1981). Juddles (1980) pumped samples down to 65 m at three stations at the shelf break, over the continental slope, and further offshore. The OMZ appeared to have been the single most important environmental factor structuring and modifying the vertical distribution of zooplankton over the shelf and slope off central Peru. Most mesozooplankton did not occur below the 0.1 mg L⁻¹ oxygen isopleth. Onshore shoaling of the OMZ resulted in high near-surface concentrations of mesozooplankton relative to offshore stations. Semenova et al. (1982) described the vertical and horizontal distribution of 37 mesozooplankton species along transects between 7°S and 15°S. Only two species were able to occupy the OMZ: Eucalanus inconcisus, which other species have shown can withstand 12 h of anoxia (Juddles, 1980; Boyd et al., 1980), and Euphausia superba (Antezana, 2002a). A thickening of the surface oxygenated layer occurs during EN, and is accompanied by increased vertical migration and habitat expansion for many zooplankton and fish species (Escobar et al., 2004).

Diel vertical migration (DVM) was first demonstrated off Peru by Antezana (1978, 2002a,b). He showed that larvae and juveniles of Euphausia superba are always in the surface layer, while the adults spend days in the OML and migrate to the surface at night. Smith et al. (1981b) studied the vertical migrations of three copepod families with a 5 m resolution (Oncoecita, Oithona, small Calanoida). The OMZ established a distinct lower boundary. During day-time, all three groups accumulated above the oxycline while at night, small Calanoida were always higher in the water column than Oncoecita. These daily excursions seemed sufficient to expose Oncoecita to onshore/poleward flow by day and offshore/equatorward flow at night. Restriction to the upper 20 m above the OMZ likely influences the onshore/oﬀshore distribution of species (Smith et al., 1981a). Boyd et al. (1980) observed that Eucalanus inconcisus, Calanus australis, and Centropages brachionus show different patterns of DVM inshore and offshore, not apparently related to the OMZ. All three species left the upper 5 m during the day inshore, but offshore they remained at the surface both to day and night, even though the surface oxygenated layer is thicker offshore. Santander et al. (1981a) found that many mesozooplankton can tolerate oxygen concentrations down to 0.5 mg L⁻¹, but concentrations <0.2 mg L⁻¹ have deadly effects on most taxa. They also found that Eucalanus inconcisus, Eucalanus frondisi, Oithona similis, amphipods, and oostacids occur mainly between 50 and 100 m, where the oxygen content was <0.5 mg L⁻¹. Using a closing net off Callao during three 48-hour experiments (2003), distinguished four types of migration, with species: (1) spending day at depth and coming to the surface during dusk and midnight; (2) non-migrating; (3) migrating several times each 24 h; and (4) reverse migrating, swimming up in the day and down at night, as in Eucalanus inconcisus. Environmental conditions modify the migrations, as O₂ concentrations <0.5 mg L⁻¹ were limiting for most taxa.

4.4. Time series: seasonality and interannual variability

Temporal variation of zooplankton abundance can occur as a result of both biological and physical processes. Biological variations occur at a time scale of weeks, associated with the life cycle of zooplankton organisms, and on a diurnal time scale associated with vertical migration. Physical variations can be seasonal and interannual, or also may occur as a result of onshore/offshore and alongshore advection, on a time scale of days. Changes in cross-shelf advection have been observed on a fixed station during 15 days of daily sampling (Smith et al., 1981a). During periods of surface
onshore flow, oceanic species were observed, while during offshore flow, coastal species dominated.

Seasonal variability is driven by changes in wind speed and direction, which affect upwelling intensity and coastal circulation. Anchovies and other species release larvae seasonally (Santander and Flores, 1983). Such spawning seasonality suggests that favourable pelagic conditions may also be seasonal. Upwelling off Peru is more intense in winter (Bakun and Nelson, 1991; Echevin et al., 2004a,b; Crockett et al., 2005; Arens et al., in press). Since primary and secondary production is supported by upwelling nutrient-rich upwelled cold water, maximum phyto- and zooplankton abundances should occur in winter. However, Ayón et al. (2004) found peak zooplankton volumes in spring, especially during the 1960s (Fig. 2). Zooplankton volumes were higher in spring except during the 60s when no seasonal trend was evident. Arens et al. (in press) analysed the seasonality of zooplankton abundance off Pata (Fig. 2). They generally found highest total abundances in spring and autumn, under moderate upwelling conditions. These observations may suggest that ‘intermediate-strength upwelling’ is favourable for zooplankton, with winter upwelling too strong and summer upwelling too weak. Although coastal upwelling was more intense in winter, zooplankton abundance off Pata was at minimum during winter, and thus displayed a positive correlation with temperature (Arens et al., in press). Studies off Chile have shown that intermediate monthly wind strengths, with alternating periods of upwelling and relaxation, may best sustain phytoplankton blooms off Chile (Echevin et al., 2004b) and successful recruitment of Peruvian pelagic fish stocks (Walsh et al., 1980; Mendelssohn and Blemenda, 1987; Curry and Roy, 1989). Similar concepts have also been called the “optimal environmental window” (Curry and Roy, 1989; Sugimoto and Takeda, 1988) or “optimal stability window” (Gargett, 1997). We suggest that the dome-shaped relationship between wind-induced turbulence and zooplankton biomass has an important influence on zooplankton productivity off Peru (Arens et al., in press), although the dominating mechanisms and processes are not yet clear. Curry and Roy (1989) suggested that strong winds decrease recruitment success by inducing turbulence that hampers the location of zooplankton prey by fish larvae off Peru. This idea is a restatement of “Lasker’s hypothesis” (Lasker, 1975; Lasker and Smith, 1977) which proposes that strong turbulent mixing (beyond an “optimum”) associated with strong wind and coastal upwelling destroys vertical stratification and the prey patchiness required for optimal larval feeding. Under the “optimal window” hypothesis, intermediate upwelling intensity supplies nutrients but below intensity levels where harmful processes become important, such as horizontal advection and the break-up of vertical aggregation layers.

On the other hand, recent studies suggest that aggregations of zooplankton and fish larvae can be formed by vertical currents (Francis, 1992; Genin et al., 2005). In this case increased vertical turbulence may increase predation intensity by aggregating organisms that are dispersed horizontally, but are able to maintain their depth, such as zooplankton and fish larvae (Hardy, 1936; Francis, 1992; Genin et al., 2005). Increased wind and turbulence could also require increased effort to maintain depth, thus leaving less energy for growth and reproduction (Kloppmann et al., 2002).

The negative effect of strong winter upwelling on zooplankton abundance may also be explained by (1) adverse losses, (2) shrinking habitat due to the rise of the hystoxine, or (3) mismatch among the species of zooplankton blooms off Chile (Echevin et al., 2004b) and successful recruitment of Peruvian pelagic fish stocks (Walsh et al., 1980; Mendelssohn and Blemenda, 1987; Curry and Roy, 1989). Similar concepts have also been called the “optimal environmental window” (Curry and Roy, 1989; Sugimoto and Takeda, 1988) or “optimal stability window” (Gargett, 1997). We suggest that the dome-shaped relationship between wind-induced turbulence and zooplankton biomass has an important influence on zooplankton productivity off Peru (Arens et al., in press), although the dominating mechanisms and processes are not yet clear. Curry and Roy (1989) suggested that strong winds decrease recruitment success by inducing turbulence that hampers the location of zooplankton prey by fish larvae off Peru. This idea is a restatement of “Lasker’s hypothesis” (Lasker, 1975; Lasker and Smith, 1977) which proposes that strong turbulent mixing (beyond an “optimum”) associated with strong wind and coastal upwelling destroys vertical stratification and the prey patchiness required for optimal larval feeding. Under the “optimal window” hypothesis, intermediate upwelling intensity supplies nutrients but below intensity levels where harmful processes become important, such as horizontal advection and the break-up of vertical aggregation layers.

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ENSO and multi-decadal shifts in global sea surface temperature (SST) shifts co-occur (Yasunaka and Hanawa, 2005). Although many other strong ENSO transitions occurred since the early 1960s, Yasunaka and Hanawa (2005) detected only two global SST regime shifts in this period, one in 1970–1971 (transition from EN to the strong 1970–1972 LN) and another one in 1996–1997 (transition from the strong 1994–1995 LN to DN conditions). Coincidentally or not, these ENSO-related global SST regime shifts mark the beginning collapse of the anchovy stock in the late 60s to early 70s, and onset of stock recovery in the mid 70s (vertical arrows in Fig. 2). The synchrony of the Peruvian zooplankton and anchovy data with statistically significant global SST regime shifts provide further support for the idea of strong links between regional-scale ecosystem changes and global-scale climate processes.

Zooplankton volumes and anchovy biomass show a similar pattern (Fig. 3), indicating that multi-decadal oscillations may be affecting both compartments of this ecosystem. There may be valid alternative explanations for the variations in anchovy biomass (e.g. overfishing in the late 60s), but the synchronicity of fisheries and zooplankton data in this and other regions of the Pacific strongly indicate a globally relevant ENSO-like multi-decadal oscillation pattern that is probably triggering these ecological regime shifts. However, there are also three remarkable differences between the time series of anchovy biomass and zooplankton volume: (1) the magnitude of the population collapse in the late 60s and early 70s is similar for both anchovy and zooplankton, but the subsequent recovery was much better for anchovies. Zooplankton never recovered 60s levels; (2) strong EN’s do not seem to affect zooplankton communities; there is no clear affect of even the strongest EN events on zooplankton volume; (3) the zooplankton collapse seems to have started 3 or 4 years earlier (in 1968) than for anchovy (in 71 or 72). If real, this association may prove to be a useful early indicator of ecosystem regime shifts. Modelling efforts and time series analyses have shown that mesozooplankton populations respond to subtle climatic signals, and could serve as indicators of climate change (Taylor et al., 2002).

A more recent regime shift in 1995 or 2000 apparently affected pelagic ecosystems in the north-eastern (Greene, 2002; Mäkynen et al., 2004; Litvak, 2005), north-western (Reibstedt and Kang, 2003; Tadokoro et al., 2005), and south-eastern Pacific (Araya et al. in press). This recent shift, which occurred following the 1997/1998 EN and perhaps during the strong 98/99 LN (Fig. 4), is still under discussion (Bond et al., 2001; Litvak, 2006; Gutierrez et al., 2007). An analysis of spatial distribution of anchovies and sardines off Peru also showed a dramatic shift after the 1997–1999 ENSO (Gutierrez et al., 2007). Although sardines were already declining and anchovies had been increasing in biomass before 1998, Gutierrez et al. (2007) concluded that “since 1998, we have been in a ‘full anchovy era’ with dramatically low levels of sardine in the HCS”. This may be related to an increase in copepod and euphausiids abundance, which at least off northern Peru, showed an abrupt increase after 1999 (Araya et al., in press, Fig. 4).

Ayón et al. (2004) and Aronés et al. (in press) demonstrated the importance of long-term zooplankton monitoring in upwelling areas, and confirmed that dramatic changes in pelagic ecosystems occur in the Southeast Pacific. Ayón et al. (2008) used a slightly extended data set (1961–2003) and applied a Generalized Additive Model (GAM) and Classification and Regression Trees (CART) to the zooplankton biovolumes as a function of time of day to examine
the effect of the diet cycle, other environmental factors, and biological interactions on biomasses. The CART results showed a strong negative impact of anchovy but not sardine biomass on zooplankton. Additionally, zooplankton biomass was higher offshore than on the shelf and was higher when SST was above 21.2°C for some years and months. GAB results corroborated the CART.

4.5. Pelagic macrocrustaceans (Euphausiacea and Decapoda)

Two pelagic macrocrustaceans are characteristic of the Peru-Venezuelan Current System (SVS): *Euphausia pacifica* (or krill); Escrichano et al., 2010; Antezana, 2006), and the gatalhead crab *Pleuropsis montesii* ("red crab", "squid lobster", "largostino colorado", or "tintorera"). These species can be very abundant (Antezana, 2002a,b; Bertrand et al., 2005) and thus likely interact with the even larger biomass of *Engyosoma ringeri* (Peruvian anchovy). Recent data even indicate that krill may be the main food source for adult anchovy (Espinoza and Bertrand, 2008). Many other predators, such as hake, also feed on these pelagic macrocrustaceans (Mejia et al., 1971, 1973, 1980). Although adults, juveniles, post-larvae and larvae of pelagic decapod shrimps are common in plankton catches in tropical and subtropical oceans (Luciférizidae, Sergestidae, Penaeidae, and Carideae; Cúulas and McGowan, 1994; Schwamborn et al., 1989; Schwamborn et al., 2001; Martin et al., 2005; Kottelat and Freire, 2006) and occur off Peru (Fernández-Álamo and Fábrer-Loza, 2006, Table 4), there is little information on these groups. Herrick and Estuar-Navarrete (1989) discussed the distribution of pelagic decapod shrimps in the Eastern Pacific, including offshore waters off Peru, but did not give biomass data for these groups off Peru.

Early euphausiids research focused on taxonomy (Santander, 1967; Santander and Sandoval de Castillo, 1969; Fonseca, 1982). Although sampling with Hensen nets is probably misses adults, euphausiids were nevertheless found to be very abundant, especially at night (e.g. Santander, 1981). Most euphausiids are captured as furcula and calyptopis larvae (Antezana et al., in press). Antezana (1978, 2002a,b) studied the distribution of *Euphausia pacifica* along the Peruvian and Chilean coasts and the vertical distribution of developmental stages in relation to the oxygen minimum layer (OML). All stages migrated downward during the day, adults migrating deeper than larvae and juveniles. He suggested that these ontogenetic and diel vertical distribution patterns reflect a predator avoidance strategy and may explain the success of this species, which may contribute up to 50% of total zooplankton biomass in the SVS.

The distribution of red crab extends from Chilean Island (47°S) off Chile to 7°S off Peru (Halg, 1955; Gutiérrez et al., 2008). Red crab individuals are larger in southern end of their range, where they are mostly benthic (Gallardo et al., 1993; Palma, 1994). Off northern Chile and Peru, red crab individuals are smaller and mostly pelagic (Gutiérrez et al., 2008), leading Rivera and Santander (2005) to consider the northern specimens a "dwarf" subspecies (*P. monodon pelagicus*). Most studies on *P. monodon* have been performed off Chile due to its importance for the fisheries in this region (e.g. Halg, 1955; Palma, 1976; Gutiérrez and Zúñiga, 1977; Bustos et al., 1982; Gallardo et al., 1981, 1984; Palma, 1984; Rivera and Santander, 2005). The biology of red crab in Peruvian waters is not well known (Segura and Castillo, 1996; Chimbote, 1999; Franco, 2003), perhaps because red crab have recently increased in biomass (Gutiérrez et al., 2008). *P. monodon* have been occasionally reported as abundant during the last 50 years, mainly off southern Peru. Older reports indicate that *P. monodon* was an important prey item of tunas during the 1930s and
According to Gutiérrez et al. (2008), P. monodon became highly abundant along the Peruvian coast after the 1987–1988 EN. Biomass ranged between 0.6 and 3.4 × 10^4 t from 1988 to 2005 (acoustic estimates in Gutiérrez et al., 2008) in upwelled nearshore waters where red crab are preysed on by seabirds, mammals, and fish (anchovy preys on red crab zoa). Gutiérrez et al. (2008) also found that P. monodon forage on fish eggs and larvae. Trophic interactions are likely to occur between krill, red crab, and anchoveta.

4.6. Mesoplankton

Mesoplanktonic larvae of benthic invertebrates (e.g., Decapoda, Ctenopoeida, Molukosa, Polyplacota) constitute an important fraction of the zooplankton, especially nearshore (Cruillas-Hernández et al., 2008). Although nearshore food supply may be ample, larvae have to cope with predation, advection, and benthic hypoxia. Important predators are planktivorous fishes and macrocrustaceans, which build up huge biomass in this region. Surface currents in coastal upwelling regions are, on average, directed alongshore or offshore and subsurface waters are anoxic, thus limiting any vertical migration (Shanks and Brink, 2005). Variability in currents exists at various scales, including the upwelling/relaxation cycles, EN and decadal cycles. Shallow-water invertebrates must be able to recruit from larvae retained nearshore or in bays, or, as postulated by Pielou (1977), follow an r-strategy and produce huge numbers of larvae, few of whom return to shore.

The mesoplanktonic larvae of many commercially important benthic organisms remain largely undescribed. The distribution of polycrabs larva has been described for two crabs in Bahía de Independencia (Mendo et al., 1989; Yamashiro et al., 1990). Increased survival and recruitment of larvae probably explain the dramatic population increases of the scallop Argopecten purpuratus that occur during EN. One explanation for “scullop outbreaks” is that larval survival increases with temperature (Wolff et al., 2006) and a thicker surface oxic layer, while another idea is that larval predators or competitors disappear from surface waters during EN (e.g., anchovy and crab larvae). Tarazona et al. (1988) studied the bivalve communities of the central Peruvian coast during the 1982–1983 EN. Abundance of bivalve larvae declined during peak EN months in 1983, but recovered immediately afterwards. The mesoplankton of Ancón Bay (11°46'S 77°11'W) and Independencia Bay (14°09'S 76°10'W) (Fig. 1) were compared by Tarazona et al. (1989), who found that polychaete larvae dominated Independencia Bay, while bivalve larvae dominated Ancón Bay. Experiments showed that in spite of small tidal amplitude (<1 m), tidal currents dispersed larvae. Scallop larvae may occur in high densities nearshore, specifically in Independencia Bay (M. Wolff, personal communication). Yamashiro et al. (1980) evaluated larval stocks in Independencia Bay. The mesoplankton was comprised of brachiuran zoa, brachiopods, gastropods, and polychaete larvae, together with young priapulids and euphausiids larvae. Tidal fluctuations in larval abundance were also observed. Macro-invertebrate settlement in this bay during the 1987–1988 EN has been described by Ramos et al. (1990) by determining recruitment to artificial substrates. Argopecten purpuratus only settled during EN, together with warm water turitiform gastropods. In contrast, the bivalve Hiatella arctica, the turitillarian Narugona sp., and the gastropod Geueria chilensis settled mainly during the preceding cold period. A third group, comprised by the bivalves Dicostea lamellosa, the echinoderm Epitrix kroyeri, and mytilid bivalves, settled only at the very onset of EN (March 1987). This EN-onset settlement peak may be related to unusually strong onshore currents associated with a month-long relaxation of upwelling, or to ecosystem changes. The appearance of unusual tropical species at the end of this EN were also noted (e.g. the bivalve Peria straminea and the gastropod Epitonium sp.). Further studies on macro-invertebrate settlement in Peruvian inshore ecosystems have recently been published by Pacheco and Garate (2005).

Larval development has been described for less than 10% of the decapod species that occur off Peru, mostly from other parts of the eastern Pacific (e.g., Coslow and Fagetti, 1967; Quintana, 1983; Ditir and Epifanio, 1984; Quinlan and Snelzer, 1986; Ríos and Martin, 1992; Río, 1992; Wohlfarth and Río, 1997). Although crab larval stages are generally found in zooplankton surveys, there are no species-specific data on decapod larval distributions off Peru. This is one of the focuses in the ongoing CENSOR project.

4.7. Trophodynamics and production of zooplankton

Dugdale and Goering (1970) first studied the trophic role of zooplankton in the Peruvian HCS. Their study of biological production in the Peru Coastal Current during a period of high diatom levels indicated grazing was not the principal source of loss of phytoplankton, with combined anchovy and zooplankton grazing at about 20% of the standing crop. They also suggested that the
anchovy were more important grazers than zooplankton, Beers et al. (1971) estimated the consumption by the zooplankton not to exceed 23% of the daily primary production.

During the cruises of the Institute of Oceanology in 1974, attempts were made to describe plankton community dynamics (Milhch, 1965) and to estimate zooplankton production (Shishkinda and Kshlyakov, 1977). Dirks (1985) measured the ingestion rates of Calanus australis under natural conditions and studied the content of the gut and fecal pellets. Milhch (1977) showed that the age structure of dominant copepod species on a transect across the shelf and an upwelling center and compared species number, biomass and species diversity (Milhch, 1977). Mint and Timofeyin (1985) studied the trophic structure of the crustacean community using mouthpart morphology. In nearshore areas, fine filter-feeders dominated. Over the shelf break area, they found a predominance of coarse filter-feeders and omnivores. Spatial variability in the zooplankton community was explained by the patchy distribution of local upwelling cells, which undergo characteristic changes depending on their age. Secondary production was from experiments following the fate of 15C-labelled phytoplankton and applying a mathematical simulation of a trophic model (Shishkinda and Kshlyakov, 1977). According to Feiga et al. (1977) excess production on the shelf is utilized in a 200-300 km band of offshore water.

Measurements of grazing and excretion rates of copepods and qualitative descriptions of their prey were conducted during the international projects ICANE and CURA. According to Cowies (1974, 1975), prey size selection by copepods depended on food abundance (Parker et al., 1974) and not the ingestion rates of Monotoma. Dagg et al. (1980) measured rates of ingestion and secretion of Calanus chilensis, Eucalanus terrius, and Centropages hamacheri, assessing the particle species that are a important copepod in the coastal waters. As these large species ingested 5–15% of primary production, the authors suggested that smaller zooplankton must consume most primary production. Boyd et al. (1980) studied prey selectivity by Eucalanus, Cylades, and Centropages. They found that Cylades sp. is a non-selective phytophage, while Centropges sp. and Eucalanus sp. were omnivorous feeders. Furthermore, Eucalanus sp. did not feed at the surface at night, but only during the day on a dense detritus. Nitrogen regeneration during a red tide was measured by MacDonald (1978), who estimated that mesozooplankton recycled 1–25% of the nitrogen needed to support phytoplankton production. Espinoza and Bertrand (2005) have recently emphasized that in carbon unit, anchovies feed primarily on euphausiids (66%) and copepods (28%), not diatoms as has traditionally been thought (Pauly et al., 1989).

4.8 Modelling

The first ecological models of the HCS were built by Dugdale and Mackas (1971) and Walsh and Dugdale (1973), who simulated nitrate uptake and flow through the Peruvian upwelling system. Energy budgets for the pelagic system were established by Sorkin and Milhees (1979), using data obtained during the cruises of the Institute of Oceanology in 1974. Walsh (1981) established a carbon budget to understanding changes in the carbon flow through the coastal upwelling system after the crash of the anchovy fisheries in the early 70s. Jaure et al. (1991) presented mass balance models (COMPAT B) for modeling fish stock interactions in the Peruvian upwelling ecosystem, which included also a zooplankton component. Jaure-Telchmann (1998) investigated explored trophic structure with steady-state, mass-balance models (COMPAT B). The mean transfer efficiency from herbivores to top predators was 4–6%. Comparison of the models for the warm sardine regime versus the cold anchovy regime suggested that anchovy abundance varies with the lower components of the ecotone (zooplankton and, to some extent, phytoplankton and detritus), while sardine abundance is out of phase. Jaure-Telchmann (1998) concluded that productivity differences between the two species, with sardines relying on their better swimming capability (Bakun and Breart, 2003) to find suitable forage during periods of decreased productivity. However, more recent studies emphasize that the major reason for alternative anchovy and sardine abundance is due to is climatic and prey selection mediated (with sardines feeding on phytoplankton and small-sized zooplankton and anchovies on larger copepods and euphausiids), and not related to swimming capability (Bertrand et al., 2004; Gerlotto et al., 2006; van der Lingen et al., 2006; Espinoza and Bertrand, 2008).

Carr (2003) used a numerical model to quantify carbon flow through the upwelling ecosystem from 1986 through 1998 at 9.5° off the coast of Peru. The numerical experiments illustrate ecosystem responses to the evolvin conditions associated with EN and EN events.

Ecosystem modelling in the Peruvian upwelling system is only beginning. There is a strong need for theoretical overview, and empirical data is needed as model input. Due to the lack of data, e.g. on the microbial loop, marcooctastaeans and main trophic links, e.g. between anchovies and euphausiids, older models neglect important ecosystem components. Recent trophic models built using the Ecos with Ecosim (Ecos) software focus mainly on commercially important fish and invertebrate stocks. These models do include more recent stomach content data for anchovy (Tan et al., 2006; Taylor et al., 2006; Woff et al., 2006), yet phytoplankton-zooplankton interactions are not well described and the microbial loop has not yet been integrated. Recent physical-biogeochemical simulations (Echevin et al., 2004) do not consider phytoplankton-zooplankton interactions again showing the need for new data and modelling directly specifically towards the plankton.

5. Knowledge gaps and perspectives

Many topics in zooplankton biology and ecology have been examined off Peru, but a synthetic view of zooplankton dynamics in this part of the HCS and its relation to other components of the system has not yet emerged. There are many important issues still poorly understood, such as the interactions of gelatinous and crustacean plankton, adaptations to life in the OML, microzooplankton dynamics and processes related to the microbial loop. Most urgently, we need concepts, data, and models which may help to link climatic processes to the productivity of the pelagic ecosystem off Peru.

5.1. Taxonomy, life cycles, and cryptic taxa

Taxonomy of zooplankton off Peru is still in its infancy. There is a strong need to combine morphological and genetic studies and compare species with their synonyms in other oceans. Furthermore, little to nothing is known of the ecology of most species. Often, developmental stages of holoplankton are not described. Basic knowledge of the life cycles is lacking, such as generation times and growth rates, reproductive biology, starvation potential, and life cycle strategies such as dormancy and resting eggs.

Euphausiids may form a large part of the zooplankton biomass, however, due to difficulties in sampling, their biomass may be significantly underestimated. Similarly, gelatinous plankton is often very abundant, but requires dedicated sampling techniques to quantitatively assess its importance. There is little knowledge on bentho-pelagic coupling and the role of metazooplankton, especially
in the nearshore zone, which is important for artisanal fisheries. This is one of the main focuses of the ongoing CENSOR project.

5.2. Microzooplankton and the microbial loop

The microzooplankton comprises organisms <200 μm (UNESCO, 1958; Smith, 1977; Leez, 2000), and are typically dominated by protozoa (rotifers, foraminifera, radiolarian, diatoms, and flagellates) and copepod eggs and nauplii. Protozoan communities are often myctroplankton or of unknown trophic status. They are generally not caught by zooplankton nets, but may be quantified in bacteria and phytoplankton studies, which may lead to a considerable overlap between bacteria-, phyto-, and zooplankton studies regarding these groups. Microzooplankton can be intense grazers on bacteria and phytoplankton with extremely high production/biomass ratios (Karlbo, 1987; Agis et al., 2007; McManus et al., 2007), however, little is known about its role off Peru, although it is certainly important, especially during EN, as shown by studies in the adjacent southern HCS (Escalante et al., 2004).

The few studies available are all based on single cruises, usually with few stations. Yuransueva and Kopylov (1985a,b) determined the species composition and biomass of planktonic protozoa and their rates of reproduction and production off Peru. In incubation experiments the average FJR ratio was 1.26 day⁻¹, indicating biomass man was more than double each day. Uronichthys marina underwent 8–11 divisions/day. Vinogradov et al. (1980) found similar results and pointed out the importance of microzooplankton production. Heterotrophic microzooplankton was also studied by Sorokin (1978) and Klokowskii et al. (1975), who determined respiration rates of microzooplankton in the equatorial and Peruvian upwelling systems. Sorokin and Kogebuch (1979) studied the role of heterotrophic microzooplankton in the flux of organic matter to the benthos near Punta San Juan, Peru. A drogue study showed that the planktonic community in freshly upwelled water was dominated by microheterotrophs bacteria and protozoans, where bacteria (49 mg C m⁻³) exceeded by two orders of magnitude the biomass of phytoplankton. Total oxygen used by microheterotrophs exceeded by three times that produced by primary production, indicating that the heterotrophic respiration was dependent on organic matter pre-existing in the upwelling waters. Timidmidae and their relation to EN were studied by Gómez (1997). The pelagic ecosystem of the equatorial upwelling, including bacteria, several size fractions of phytoplankton, micro- and mesozooplankton, was analysed by Vinogradov et al. (1977).

Clearly, the studies mentioned above are not nearly sufficient to give even a superficial picture of the processes involving microzooplankton and the microbial loop in the waters off Peru. This shows the urgent need for further studies as to improve our understanding of its highly productive ecosystem.

5.3. Perspectives and suggestions for data acquisition

As it now exists, the Peruvian zooplankton time series is most valuable, and must continue with a consistent methodology and strategy (Table 2). Such time series are essential to study relationships between climate and ecosystems. However, bloom data alone are often not sufficient to understand regime shifts and their consequences for higher trophic levels. More information is needed on taxonomic composition or at least on size spectra. For estimates of trophic transfer a common unit for biomass (dry mass, carbon content) is essential.

For the short term, the addition of modern optical and acoustical zooplankton sensors to standard large-scale surveys will vastly improve our description of the spatial distribution of zooplankton. The new CNOS cruises (Table 2) provide a regular monitoring of primary and secondary production and mesozooplankton grazing. These cruises also provide excellent opportunities for process studies (e.g., microbial loop, microzooplankton grazing, the effects of red tides and bloom blooms on zooplankton population dynamics, physical and trophic processes in fronts and upwelling filaments, etc.).

On the longer-term, new strategies for data acquisition in real time may yield new perspectives on the dynamics of the Peruvian upwelling ecosystem. To better understand the links between climate and fish, all components of the pelagic system, including zooplankton, have to be considered, preferably by synchronous interdisciplinary efforts. Still, little is known about many dynamic processes that characterize upwelling systems, such as the evolution of biological communities within upwelled cells. The scales of events controlling the biological-physical interaction is not clear yet. To construct models which effectively encompass the size of the system actually in operation requires a spectral analysis of the environmental events from the order of days to months, and eventually to years. A powerful device to obtain such information would be an array of autonomous sensors (current meters, CTD, Fluoroscope probe, acoustical optical plankton counters) anchored at appropriate locations along the shelf (Dickie and Valdivia, 1981). Process studies could then be embodied in such a mooring array.

The use of autonomous profiling floats (Roemmich et al., 2004), autonomous underwater vehicles (AUVs, Curini et al., 1993; Griffis et al., 2000; Samson et al., 2001; Yu et al., 2002) and enduring autonomous gliders (Sherman et al., 2001; Rudnick et al., 2004) together with satellite imagery may be an additional possibility to generate long-term high-resolution data on important physical, biogeochemical, and biological variables.

5.4. Models

Little attention has been given to the stochastic nature of upwelling systems (Menzel et al., 1980), that are influenced by random events that make them shift unpredictably between multiple states (e.g. upwelling and relaxation, red tides versus bloom blooms, etc.). Considering this stochastic nature, early statistical descriptions of meteorological, oceanographic, and fisheries data have concluded that predicting the states of the Peruvian upwelling ecosystem is longer than someone could ever reach (Roble-Carbone, 1989). This rather pessimistic view was largely true in the 1970s, considering the unexplained collapse of the anchovy fisheries and ignorance of ENSO and multi-decadal cycles.

Recently, considerable progress has been made in forecasting ENSO (e.g. Peinland and Matsuoka, 2001; Chen et al., 2004; Cass et al., 2006) and in understanding the intrinsic relationship between ENSO and multi-decadal cycles (Tsayana and Hanawa, 2005; Ye and Hsieh, 2006). Individual-based Lagrangian models can integrate physical, biogeochemical and biological data (Leising and Frank, 2000; Woods et al., 2005; Croquette and Eldin, 2006). However, only recently this approach has been applied to model zooplankton advection in coastal upwelling regions (Burch et al., 2002; Carr et al., 2006). Ecosystem modelling should focus on predicting how future cyclic (e.g. ENSO and multi-decadal variation) and non-cyclic changes (e.g. global warming and ocean acidification) will affect upwelling ecosystems.

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* All citation included in this manuscript are compiled in the final list of references.
5.2 Manuscript

ENSO effects on the zooplankton community structure off central Peru, 2005-2007

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Key Words: Community structure, El Niño, copepods, mesozooplankton, temporal patterns, cross-shelf distribution, Humboldt Current System, Peru

Abstract

Factors affecting zooplankton distributions in the Humboldt Current System were investigated using data obtained along a transect perpendicular to the coast off Callao Central Peru (12°S), bimonthly from February 2005 to December 2007. The survey period corresponded to normal conditions in 2005, El Niño 2006, transition between El Niño 2006 to La Niña 2007 and La Niña 2007 at the Peruvian coastal upwelling. There was a pronounced temporal variability in zooplankton composition and distribution of the species in the area. Acartia tonsa was the single dominant species during all periods and on all stations. Although, its abundance was significantly
reduced during a moderate El Niño (EN) event from June to December 2006 (avg. = 250 ind. m\(^{-3}\), 30% of total zoopl.), and increased during a strong La Niña event, from June to December 2007 (avg. = 874 ind. m\(^{-3}\), 44 % of total zoopl.). Other species, such as *Oithona* sp. increased in abundance during the moderate EN event (avg. = 32 ind. m\(^{-3}\) during EN, avg. = 0.07 ind. m\(^{-3}\) during LN). Only few species displayed positive correlation with distance to coast. Copepods were the most abundant and species-rich group, with 179 species from 58 families. The three species *Acartia tonsa* (average = 674 ind. m\(^{-3}\), maximum = 4530 ind. m\(^{-3}\)), *Paracalanus parvus* (avg. = 266 ind. m\(^{-3}\), max. = 3710 ind. m\(^{-3}\)), and *Centropages brachiatus* (avg. = 166 ind. m\(^{-3}\), max. = 1470 ind. m\(^{-3}\)) were dominating and accounted together for 79 % of all organisms caught. Eggs and larvae of the anchovy *Engraulis ringens* (7% of total abundance, avg. = 6.9 ind. m\(^{-3}\), max. = 104.3 ind. m\(^{-3}\)) were also frequent and abundant, together with several meroplankton taxa, such as polychaete, cirripedian, and decapod larvae. Gelatinous predators, such as chaetognaths and hydromedusae, were present at low abundances; with less than 0.1 ind. m\(^{-3}\). Our study suggests that zooplankton off Callao exhibits strong intrannual variability due to changes in the oceanographic conditions related with seasonal and ENSO fluctuations.

Key words: Community structure, copepods, zooplankton, seasonal variation, ENSO, Humboldt Current system.
Introduction

The shelf off Central Peru (12° S) is largely affected by strong upwelling during most of the year. The upwelling is usually persistent over seven months in spring, summer and winter (Zuta and Guillen, 1970, Zuta et al, 1978, Calienes and Guillen, 1981). Previous studies suggest that offshore advection due to active upwelling is an important factor that determines the spatial distribution of copepods (Boyd and Smith., 1983), and highly productive plankton assemblage. Although, the specific composition and biomass of the zooplankton are affect for many factors as biological and physical processes (Santander, 1981, Ayón et al., 2008). As result, temporal variations in zooplankton can occur at a given location in an upwelling region can occur as a result of both biological and physical processes (Smith et al. 1981).

In such environments, particularly in upwelling ecosystems, the wide range of temperature, salinity and oxygen variations also contributes to the stability of the pelagic ecosystem. Physically, variations may occur as result of nearshore - offshore and alongshore advection, which generally has a dominant time scale of several days (Smith et al. 1981). The primary source of interannual of physical variability in the tropical Pacific Ocean is the El Niño Southern Oscillation (ENSO, Strutton and Chavez, 2000).

The highly productive coastal upwelling zone off Central Peru sustains a strong fishery based on pelagic fishes (Alheit and Niquen, 2004). This high fisheries production makes necessary high secondary production to provide large amounts of
carbon to these fish populations (Ayón et al 2008, Escribano et al., 2007, Pauly et al., 2002). Additionally, interannual changes of zooplankton assemblages often reflect an integrated response of the ecosystem to hydro-climatic forcing (Beaugrand and Ibanez, 2004). Although the large fluctuations in abundance of anchovy and sardine are well documented for Peruvian coast (Alheit and Niquen, 2004; Bakun and Broad, 2003; Chavez et al. 2003; Csirke et al., 1996; Swartzman et al., 2008), there are few studies on zooplankton dynamics and seasonal and inter-annual variability. These studies describe only spatial patterns, short time analysis or trends in zooplankton biovolumes (Ayón et al., 2004, Ayón et al., 2008). However, biovolume data alone are not sufficient to understand regime shifts and their consequences for higher trophic levels (Ayón et al., 2008).

In this work, we investigate the relationship between temporal and spatial distribution of zooplankton and changes in environmental conditions over almost three years. The two main objectives of this study were: 1) to quantify the abundance and composition of the zooplankton and its cross-shelf distribution off Central Peru, and 2) to identify possible changes in the zooplankton community structure and their relation to ENSO.

Methods

We had four fixed stations across the continental shelf off Callao (Central Peru, 12° S, 77°W) along a transect perpendicular to the coastline (Fig. 1), at depths of 50m (St 1), 94 m (St 2), 118 m (St3), 146 m (St 4). The stations were located at at 3 nautical miles (St 1, 50 m deep), 8 nautical miles (St 2, 94 m deep), 13 nautical miles (St 3, 118 m deep), and 20 nautical miles (St 4, 146 m deep). We sampled
Results

zooplankton bimonthly from February 2005 to December 2007 using a 300 μm mesh Bongo net. We equipped the net with a calibrated Hydro-Bios flowmeter. We used 4% formalin solution to preserve the samples immediately after collection. The sampling involved three knots during daytime with oblique tows from the surface to 100 m deep or, in the case of shallow stations, to 10 m above the bottom. We did a total of seventy one tows were conducted in total.

We took water samples using Niskin bottles to measure oxygen and chlorophyll a from all stations at six depths (0, 10, 25, 50, 75, and 100 m). We also used a Seabird CTD to obtain vertical profiles of temperature, salinity and additional oxygen. We assessed the state of large-scale ENSO cycle, using the the monthly NOAA reports on SST anomaly data from the Niño 1+2 region, the closest region to the Peruvian coast among the regions considered by NOAA (www.cpc.ncep.noaa.gov /products /expert_assessment /ENSO_DD_ archive .shtml.). Furthermore, we used the Multivariate ENSO Index (MEI) in the analysis (Wolter and Timlin, 1988, data source: www.cpc.ncep. noaa.gov/ENSO/enso.current .htm/indiceces).

In the laboratory, we measured zooplankton biomass of each sample by the determination of displacement volume (Beers, 1976) and wet weight (Postel et al., 2000). We identified all copepod species to the lowest taxonomic level possible and counted the abundance under a stereomicroscope. We also identified invertebrate larvae according to the available literature. Zooplankton samples were diluted to a suitable volume and while stirring small aliquots were poured into each of two beakers. This procedure was repeated two to five times until the samples were split in
Results

halves (Hustman Marine Laboratory - HML beaker technique, Van Guelpen et al. 1982).

Data Analysis

We examined species composition using all identifiable taxa across 71 samples. Shannon diversity (H’) and Pielou's evenness (J) were calculated for each sample (Shannon and Weaber, 1949, Pielou, 1966), using all data. Differences between seasons, ENSO phases and stations were examined for the following zooplankton parameters, using a non-parametric Kruskal-Wallis ANOVA: zooplankton abundance, biovolume, wet weight, Shannon diversity, and equitability. Mann-Whitney test: ENSO extreme periods EN and LN and between onshore and offshore. Non-parametric Spearman rank correlation was used to explore the relationship between environmental parameters (MEI index, hydrological parameters for several depths, Oxygen Minimum Zone depth, and distance to the coast) and zooplankton parameters (Shannon diversity, equitability, and abundance of the most abundant species). These analyses were performed at α = 0.05 with STATISTICA 6.1 (StatSoft Inc.).

We used only the most frequent taxa (that occurred in at least 25% of the samples) to explore and analyze multivariate patterns in community structure. Prior to analysis, we standardized all data were standardized (divided by the total per sample) and made a 4th root-transformed transformation to reduce the contribution from numerically dominant species (Field et al., 1982). We calculated similarity between samples and taxa were calculated using the Bray-Curtis Index.
We examine similarities in zooplankton between samples doing a cluster analysis, non-metric multidimensional scaling (MDS) ordination and Analysis of Similarity (ANOSIM) (Clarke and Warwick, 2001). The dendrogram was cut to produce ecologically interpretable clusters. To verify our interpretation of the dendrogram, the result of the clustering was superimposed on an MDS plot generated from the same similarity matrix (Clarke, 1993, Clarke and Warwick, 2001). A low (< 0.2) MDS Stress coefficient indicates that the multivariate similarity pattern is represented by the plot without much distortion (Clarke and Warwick, 2001). For ANOSIM and MDS plots, analyses were repeated, but using seasons, ENSO phases and stations as a priori factors. The existence of significant effects of these a priori factors on zooplankton community structure were then tested by ANOSIM at \( \alpha = 0.05 \) (Clarke and Warwick, 2001). We used the PRIMER 6.1.6 software (PRIMER-E Ltd., Plymouth, U.K.) for multivariate analyses.

Results

Hydrography

Environmental conditions indicated a highly variable hydrography during the sampling period (Figure 2). Sea Surface Temperature (SST) ranged from 13°C to 21°C (Figure 3). A strong variability in the depth of the OMZ was observed at the offshore St. 4, where it varied from 10 to 50m depth, whereas a much lower oscillation was observed at the onshore station (St. 1)(Figures 2, 4). SST was clearly influenced by season and ENSO phases (Figure 2, 4). Temperature maxima were observed during February 2006 and February 2007, coinciding with the austral summer, and the minima occurred during the austral winter (August) and spring (Oct/Nov). Strong interannual variability in SST and salinity was observed, more
likely linked to ENSO. ENSO-Neutral (i.e. close-to-average) conditions were present from February 2005 to April 2006. Thereafter, a moderate El Niño (EN) arrived at the coastal waters, as seen in the data from June 2006 to February 2007, followed by a short transition period (February and April 2007) and a strong La Niña (LN) period (June to December 2007).

During the moderate 2006/07 EN event, SST, surface salinity and oxygen concentrations were clearly above seasonal average, while OMZ depth increased drastically. These conditions indicated the arrival of high-saline, well-oxygenated and warm Subtropical surface waters (SSW) waters in the region (Figure 2, 4).

During the strong 2007 LN, SST dropped drastically, and was generally below 15°C. Surface salinity also dropped considerably, as compared to the ENSO-Neutral period. Although OMZ depth increased drastically, sea surface oxygen concentration during LN was within average. These conditions indicated a strong upwelling of deep sub-Antarctic waters (SAW) under the influence of moderately oxygenated, unusually cold and low-saline waters that occupied all the shelf area under investigation.

While there was no consistent horizontal gradient for most of the study period, there was an increase in SST towards offshore during February, July and November 2005 (ENSO-neutral conditions) and during June, August, October, and December 2006 (moderate EN).

Abundance, biomass, diversity and equitability

Total abundance, wet biomass, diversity and equitability of zooplankton varied strongly over in time (Table 2). Kruskal-Wallis ANOVA showed that there
was a significant effect of the factor ENSO on the variables total abundance (p = 0.014), volume (p = 0.024), wet biomass (p = 0.011), diversity (p = 0.0003), and evenness (p = 0.0008). When comparing only the ENSO extreme periods EN and LN with Mann-Whitney tests, significant differences were found for all these parameters, with significantly higher total abundance (p = 0.032), volume (p = 0.038), and wet biomass (p = 0.032), during LN, and significantly higher diversity (p = 0.006) and equitability (p = 0.002) during EN. Diversity and equitability also changed significantly between months and seasons. It was lower during the months of autumn in 2005 and 2006 and higher during the months of austral winter in 2005 and 2006. After June 2006, there was clear seasonal pattern, but showed strong monthly variation (Fig. 5). Regarding spatial variation was no consistent spatial gradient in any of these zooplankton community parameters. We did not observed significant effects among Stations.

Community structure

The most abundant group was the copepods, which presented the highest number of species with 179 species from 58 families. The three most abundant species were *Acartia tonsa* (average = 674 ind. m$^{-3}$, maximum = 4530 ind. m$^{-3}$), *Paracalanus parvus* (avg. = 266 ind. m$^{-3}$, max. = 3710 ind. m$^{-3}$), and *Centropages brachiatu* (avg. = 166 ind. m$^{-3}$, max. = 1470 ind. m$^{-3}$) representing 79% of all organisms sampled (Table 1). Eggs and larvae of the anchovy *Engraulis ringens* were also abundant (7% of total abundance, avg. = 6.9 ind. m$^{-3}$, max. = 104.3 ind. m$^{-3}$) along with several meroplankton taxa, such as polychaete, cirripedian, and decapod larvae. Gelatinous predators, such as chaetognaths and hydromedusae, had low abundances or were absent, with less than 0.1 ind. m$^{-3}$ overall average abundance.
There was a pronounced temporal and spatial variability in zooplankton composition. Although *Acartia tonsa* was the single dominating species during all periods and stations, its abundance decreased significantly reduced during the moderate El Niño (EN) event from June to October 2006 (avg. = 250 ind. m\(^{-3}\), 30% of total zooplankton). During the strong La Niña event the abundance of *A. tonsa* increased (avg. = 874 ind. m\(^{-3}\), 44% of total zoopl.) (Mann-Whitney test p = 0.01) (Fig. 6). Another, less abundant species, such as *Oithona* sp., increased in abundance during the moderate EN event (avg. = 32 ind. m\(^{-3}\) during EN, avg. = 0.07 ind. m\(^{-3}\) during LN). The abundances of *Eucalanus inermis* and zoea of *Pleuroncodes monodon* were significantly higher offshore than onshore (Mann-Whitney test, p = 0.007 and 0.025, respectively). In contrast, eggs and larvae of the Peruvian anchovy *Engraulis ringens* were significantly more abundant nearshore than offshore (Mann-Whitney test p = 0.0002). Other species such as the copepods *C. brachiatus*, *P. parvus*, and zoeae of the decapod *P. monodon* varied significantly with seasons. These taxa showed a significant effect of the factor “Season” on their abundance. (Kruskal-Wallis ANOVA p = 0.03, 0.0002, and 0.006 respectively). *C. brachiatus* was more abundant and frequent in winter (average: 297.9 ind. m\(^{-3}\)), and less abundant and frequent in spring (average: 74.6 ind. m\(^{-3}\)) (Fig 6). *P. parvus* increased its abundance in winter (average 653 ind m\(^{-3}\)) and decreased in summer (average 46.5 ind m\(^{-3}\)). The abundance of Zoeae of *P. Monodon* increased in winter (average: 27.1 ind. m\(^{-3}\)) and decreased in spring (average 1.43 ind m\(^{-3}\)).

**Zooplankton assemblages**

Our Spearman Rank Correlation analysis showed that the MEI index was the only environmental variable that explained the changes in abundance of *A. tonsa*, the
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dominant species \( r = -0.33, p < 0.005 \) (Table 1). The negative correlation between these variables confirms that \( A. \) tonsa was negatively affected by EN. Species that were more abundant over the OMZ, such as the copepods \( P. \) parvus, \( C. \) brachiatus, and \( E. \) inermis correlated positively with OMZ depth (Table 1). Conversely, the larvae of the polychaete \( Magelona \) sp. showed a negative correlation to OMZ depth. Finally, many taxa, such as the larvae and eggs of the Peruvian anchovy \( Engraulis \) ringens, cirripedian nauplii and brachiopod larvae, porcellanid zoeae and the copepod \( Hemicyclops \) thalassius showed significant negative correlations between their abundances and the distance to the coast, confirming the importance of nearshore waters for this copepod species and for the development of larvae of anchovy and benthic invertebrates.

Multivariate analysis with MDS and ANOSIM showed that community structure could be well explained by \textit{a priori} defined spatio-temporal factors. ANOSIM showed there were significant effects of the factors “Station”, “Season”, “Year” and “ENSO” on community structure (ANOSIM, \( p = 0.1, 0.2, 0.1 \) and 0.1\%). The effects of these four factors can also be visualized on the MDS plots, by the separation of samples according to these factors (Figure 7). Pairwise comparisons with ANOSIM showed significant differences in community structure between winter and the other seasons (\( p = 0.002 \)). Pairwise comparisons for the factors “Year” and “ENSO phase” showed significant (\( p = 0.001 \)) differences in community structure between 2006 and 2007, and between EN and LN.

When examining the abundance of \( Acartia tonsa, Centropages brachiatus \) and \( Eucalanus inermis \) with MDS, species showed patterns associated to particular
variables (Fig 8). *A. tonsa* showed differences in abundance during ENSO phases, high abundances were found mostly during LN and Neutral phases (Fig. 8a). *C. brachiatus* showed differences between seasons, the highest abundance occurred in spring and winter. *E. inermis* displayed the strongest spatial variability, with highest abundance at offshore stations 3 and 4 (Fig. 8c)

**Discussion**

Our study shows that considerable seasonal and interannual changes occurred in the composition of the zooplankton community and their environmental conditions off Central Peru. These changes occurred mainly between ENSO phases and seasons. The oceanographic characteristics of this area were similar to the rest of coastal upwelling areas in the Humboldt Current System. Strong intra-annual variability was observed, which was superimposed by ENSO events (Thiel, et al., 2007). Comparisons of the results of the present study with time-series data from northern Peru (4°S, Arones et al., 2009) and northern Chile (22°S, Escribano and Hidalgo, 2000) indicate that the weak 2002/2003 El Niño was less intense than the moderate 2006/2007 El Niño, in terms of changes in hydrography and community structure.

A strong decrease in salinity and increase in temperature were detected during previous two EN events, during April 1997 and April 2002. These changes may be explained by local effects such as river discharge, rainfall off northern Peru and by large-scale ENSO-related anomalies (Escribano et al., 2004, Gutierrez et al., 2005, Arónes et al., 2009). Oceanographic changes resulting from EN conditions in 2006 in the study area were first detected in August 2006 (Criales-Hernandez, 2008) and LN
conditions in May 2007. Our data show that the thermal structure of this area did not display any substantial disturbance across the ENSO cycle, as compared to the extreme positive anomalies (SST up to 29°C, Aronés et al., 2009) observed during the record-strength 1997/98 EN. Positive anomalies 16 to 19.8 °C were noted between June 2006 and February 2007, indicating a moderate EN. Negative anomalies of 13 to 15 °C were detected between June and December 2007, indicating a strong LN.

The oxygen concentration at 10 m depth and the vertical gradient in the OMZ displayed significant changes between ENSO phases. The average depth of the upper boundary of the OMZ (20 m) at our stations off Callao is similar to previous estimates for this area during Normal or Cold conditions (Zuta and Guillen, 1970, Criales-Hernandez et al., 2008, Gutierrez et al, 2008). However, during EN conditions, the OMZ deepened down to 50 m depth (Criales-Hernandez et al., 2008, Gutierrez et al., 2008). The observed increase in OMZ depth is probably related to a approach of SSW towards nearshore. SSW are usually located far offshore in oceanic areas during winter and project towards the coast during summer and during EN conditions (Morón, 2006). In addition, the seasonal variability in OMZ depth may be explained by factors such as wind mixing, non-linear interaction between winds, coastal upwelling and relaxation, and characteristics of the water masses (Bohle-Carbonell, 1989, Graco et al., 2001, Sanchez and Delgado, 1996, Graco et al., 2007, Gutierrez et al., 2008).

The main trends in zooplankton abundance, biomass and diversity can be related to the anomalies in SST and the high variability in the oxygen concentration. Strong variability in zooplankton density and biomass was found between ENSO
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phases. During the 2006 EN event, zooplankton abundance decreased and diversity increased. An opposite pattern was observed during the 2007 LN event. Dramatic changes in zooplankton abundance and community structure had been reported previously during the strong 82/83 and 97/98 EN events, with abrupt declines in primary production and subsequent reduction of zooplankton (Santander and Carrasco, 1985, Carrasco and Santander, 1987, Hidalgo and Escribano, 2001, Carr, 2003, Ayón et al., 2008, Aronés et al., 2009). Data off northern Peru display similar patterns (Gutierrez et al., 2005, Aronés et al., 2009). Zooplankton abundance declined and diversity increased during EN 97/98 and the EN 2002/2003 these processes may also be associated with pelagic productivity (Arones et al., 2009). Feeding efficiency of small pelagic fishes is strongly affected by changes in zooplankton abundance in upwelling areas (Cury et al., 2000)

Many zooplankton taxa did not display any consistent nearshore-offshore gradient in abundance, possibly due to their highly aggregated distribution. Aggregation of zooplankton is usually associated with high concentrations of Chl-a in upwelling areas (Escribano, 1998, Hidalgo and Escribano, 2001, Behrenfeld et al., 2001, Pennington et al., 2006, Kang et al., 2008). If we consider that copepods are the main group in upwelled waters (Peterson, 1998, Hutchings et al., 2006), they may have developed a mechanism that allow them to maintain a bulk of zooplankton abundance inside or near the upwelling zones (Barber and Smith, 1981, Peterson, 1998). However, some species, such as *Eucalanus inermis* have consistently displayed higher abundance offshore than nearshore. This pattern can be due to the well known vertical distribution and migration behavior of this species, that is generally located between the low-oxygen waters below the oxycline. (Criales-Hernandez et al., 2008, Hidalgo et al., 2005). *Acartia tonsa* presents an ontogenetic
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migration pattern, with adults constricted to well-oxygenated upper layers and nauplii developing inside the OMZ (Ciales-Hernandez et al., 2008). This species uses the advection flow to nearshore to maintain maximum densities in the coastal areas (Smith et al., 1981). Both mechanisms could help to minimize offshore transport by spending time below the offshore moving layers (Peterson, 1998, Ciales-Hernandez et al., 2008).

Two distinct communities were observed in this study. The nearshore community was characterized the copepods *Acartia tonsa*, *Paracalanus parvus*, *Centropages brachiatus* and by meroplankton. Larvae and eggs of *Engraulis ringes* and porcellanid and brachyuran zoeae, cirripedia nauplii and larvae, and brachiopod larvae were often sampled in this zone. The offshore community was characterized by large holoplanktonic organisms such as the zoeae of *Pleuroncodes monodon*, euphausids and large copepods, such as *Eucalanus* spp. and *Calanus* sp.. Large, actively swimming organisms such as zoeae of *Pleuroncodes monodon*, euphuasiids and *E. inermis* are more independent and developed active swimming strategies and use current shear to keep their populations in place (Peterson, 1998, Antezana, 2002, Hidalgo et al., 2005, Ciales-Hernandez et al., 2008).

In the present study, most samples were dominated by the copepods *Acartia tonsa*, *Paracalanus parvus* and *Centropages brachiatus*. These species are typically associated the nearshore continental shelf in the upwelling system (Santander, 1981, Ayón et al., 2008). Abundance of *A. tonsa* was high during Neutral and LN conditions, while during EN 2006 *A. tonsa* significantly decreased in abundance, and small species, such as *Oithona* sp. and cyclopoids increased. Similar patterns of the abundance and diversity have been found during EN events (Carrasco and Santander,
Species composition of zooplankton has been shown to be shifting from large sized species, mostly herbivorous copepods that are typical in upwelling systems (Santander, 1981, Kleppel, 1993) towards small-sized species, mostly carnivores, during warm conditions (Gonzales et al., 2002, Escribano et al., 2004, Criales-Hernandez et al., 2008).

The upwelling off Peru is generally governed by seasonal variation. Peaks of abundance in some species were controlled by seasonal changes. Paracalanus parvus and Centropages brachiatus were most abundant during wintertime. This peak in abundance was attributed to the particular life cycles of these copepods in the upwelling zone (Santander, 1981, Escribano et al., 2007). Changes in OMZ depth could be determining the distribution of several zooplankton species. Our results showed a strong correlation between OMZ and abundance of the main taxa. When the OMZ was deeper (50 m deep), abundance of certain species increased, e.g. Centropages brachiatus, Paracalanus parvus, Eucalanus inermis, and Pleuroncodes monodon zoeae. Previous studies showed that Paracalanus parvus and Centropages brachiatus were restricted to the well-oxygenated upper layers (Escribano et al, 2007, Criales-Hernandez et al., 2008). The increase of OMZ depth probably has contributed to the extension of the habitat of these taxa. Other taxa, as such as Eucalanus inermis may live inside the OMZ, migrating temporarily towards its upper limit (Hidalgo et al. 2005).

In conclusion, seasonal variability, superimposed by ENSO, are the key factors that govern zooplankton standing stock and community structure. Bulk
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zooplankton biomass was aggregated in upwelling areas without any significant cross-shore gradient, but species composition did display a consistent gradient, with characteristic, well-defined nearshore and offshore communities. Abundance of *A. tonsa*, the dominant species in this study, was significantly correlated to the multiple El Niño index only, indicating that this species may be a sensible indicator for ENSO and for possible future changes in climate regime.

References

* All citation included in this manuscript are compiled in the final list of references.
Results

List of figures legends and table headers

Table 1. Average, minimum and maximum abundance, Relative abundance (%) and frequency of occurrence of the most abundant taxa across the continental shelf off Central Peru, and Spearman rank correlation matrix between environmental variables and abundance of the major taxa. n.s. not significant at p<0.05. DC: Distance from the coast, OMZ: Depth of the Oxygen Minimum Zone, MEI: Multiple El Niño Index)

Table 2. Results of the Kruskal-Wallis ANOVA used to test temporal effects on zooplankton abundance (ind. m⁻³), biovolume (ml m⁻³), wet biomass (g m⁻³) and diversity indexes during time series across the continental shelf off Central Peru. n.s. not significant at α = 0.05.

Figure 1. Study area across the continental shelf off Central Peru. Isobaths are indicated in meters. Dots and numbers indicate sampling stations.

Figure 2. Temporal variation of water temperature, salinity, and oxygen concentration at 10 m depth and Depth of the Oxygen Minimum Zone (depth of the 1 ml l⁻¹ oxycline) off Callao, Central Peru, from February 2005 to December 2007.

Figure 3. Temporal and vertical distribution of temperature (°C), at the four sampling stations on the continental shelf off Central Peru.

Figure 4. Temporal and vertical distribution of Oxygen (ml l⁻¹), at the four sampling stations on the continental shelf off Central Peru.

Figure 5. Time series of total zooplankton density, total species richness (S), Shannon diversity (H’), and Evenness (J’). H’ and J’ were calculated using densities of all
zoo plankton taxa. Samples were obtained at four stations at the continental shelf off Callao, Central Peru, from February 2005 to December 2007.

Figure 6. Times series of abundance (ind m$^{-3}$) of the main taxa. Samples were obtained at four stations at the continental shelf off Callao, Central Peru, from February 2005 to December 2007.

Figure 7. Multi-dimensional scaling (MDS) plot generated from the Bray-Curtis similarity between samples, calculated based on fourth-root transformed abundance data of the 63 most frequent taxa. Samples were obtained from daytime oblique bongo net tows at four stations off Central Peru. Symbol types denote Seasons (top left), ENSO phases (top right), Years (bottom left), or Stations (bottom right).

Figure 8. Multi-dimensional scaling (MDS) plot generated from the Bray-Curtis similarity between samples, calculated based on fourth-root transformed abundance data of the 61 most frequent taxa. Samples were obtained from daytime oblique bongo net tows at four stations off Central Peru. Circle diameters represent the abundances of three selected copepod species: (a) Acartia tonsa, (b) Centropages brachiat us, and (c) Eucalanus inermis.
Table 1.

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<th>Frequency (%)</th>
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### Table 2.

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</table>
Figure 1.
Figure 2.
Figure 3.
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Figure 4.
Figure 5.
Figure 6.
Figure 7.
Results

a) ENSO Phases and Abundance of *Acartia tonsa*

b) Seasons and Abundance of *Centropages brachiatu*s
Results

c)

Figure 8.
5.3 Scientific contribution

Zooplankton vertical distribution and migration off Central Peru in relation to the oxygen minimum layer

M. I. Criales-Hernández · R. Schwamborn · M. Graco · P. Ayón · H.-J. Hörche · M. Wolff

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Abstract Vertical distribution and diel vertical migration of a zooplankton community were studied at two stations off Central Peru in April 2006. Zooplankton was collected at five depth strata by vertical hauls with Hydros-Bios multi-net (300-µm mesh, 0.25-m² mouth size). The zooplankton community was distributed in relation to a strong, shallow oxycline (1 ml l⁻¹ oxygen isopleths generally above 36 m). The highest total abundance was always in the upper, well-oxygenated layer. The most important species were: Acartia tonsa (72.86%), Centropages krabbe (7.5%), and Paracalanus parvus (3.1%); Acartia tonsa was the dominant species at all times. Larvae of the polychaete Magelena sp. (7.5%) and larvae of the brachiopod Diesiella lamarckii (3.5%) were numerically dominant in April and small copepods e.g. Oscura venusta (3.8%) were numerically dominant during August. Five distinct patterns of vertical distribution and migration in relation to the oxygen minimum layer were distinguished in this study: (1) Ontogenetic vertical migration through the oxycline (Acartia tonsa adults, nauplii, and copepodids), (2) permanent limitation to layers above the oxycline (e.g. Olkeplura sp., most invertebrate larvae), (3) distribution mostly below the oxycline with occasional migration into the layers just above the oxycline (Eucalanus infranitens), (4) Diel Vertical Migration (Centropages krabbe), and (5) reverse Diel Vertical Migration (larvae of the polychaete Magelena sp.).

Keywords Vertical distribution · Zooplankton community · Central Peruvian Coast

Introduction

The waters off Central Peru are productive regions that support economically important fisheries (Carrasco and Lozano 1989; Chavez et al. 2005; Alheit and Niqun 2004). Another characteristic of this region is a well-developed oxygen minimum layer (Wyrtki 1967; Jakobs 1980; Mackas et al. 1981), which occurs nearly continuously in most of the Humboldt Current System (Zuta and Guillén 1970; Heinrich 1973; Calienes and Guillén 1981; Pizarro et al. 2002).

Previous works in the Humboldt Current System have suggested that some zooplankton populations display specific patterns of vertical stratification related to changes in environmental conditions in those regions. Judzis (1980) found a discrete vertical distribution of zooplankton over the shelf and slope off Central Peru. Oxygen appeared to be the most important environmental factor determining zooplankton distribution. Again Smith et al. (1981a) and Mackas et al. (1981), found that the thermocline and oxycline appeared to divide the upper 30 m into fairly distinct...
copepod and non-copepod faunal zones. Antezana (2002) described the vertical migration patterns of *Euphausia superba*. Larvae, juveniles and adults of this species were found in the upper 50 m layers during night hours, migrating to deeper layers near sunrise. The majority of copepods are found in the upper 40 m both during day and night, probably due to anoxic water below (Boyd et al. 1981; Sancoto 1981). This behavior is similar to other species in the eastern South Pacific where adult populations are mostly above 50 m in both oceanic (Loughnurth 1967; Flint 1975; Saltzman and Wistener 1997) and coastal waters (Flint et al. 1991). Recently, detailed studies on the vertical distribution of selected copepod species have been conducted in the Humboldt Current System off northern Chile, with emphasis on diet vertical migration performed by the deep-dwelling *Eucalanus immobilis* (Hidalgo et al. 2005; Escribano 2006).

The shelf waters off Callao (Central Peru) were chosen for this study because of their intensive upwelling. Furthermore, an extremely shallow oxygen minimum layer is generally found during upwelling conditions, potentially restricting the available vertical amplitude of migrant species. In spite of its fundamental importance in fisheries and biogeochemical processes, new data on vertical distribution of zooplankton from this area are still lacking. Previous studies in this area were conducted several decades ago (Smith et al. 1981b; Boyd et al. 1981; Semenova et al. 1982). Smith et al. (1981b) studied the vertical migrations of three groups of copepods (*Oncosoma*; *Calanoidae*, small Calanoids) with a 5 m resolution at 9°S. The oxygen minimum layer established a distinct lower boundary for the distribution of many organisms. During daytime, all three groups accumulated above the oxycline, while at night, small calanoids were always more abundant in the upper layers than *Oncosoma*. Restriction to the upper 20 m maintains zooplankton within currents, which may vary to a great extent in this complex upwelling system (Brink et al. 1980) and have strong influence in the onshore-offshore dimension (Smith et al. 1981b). Boyd et al. (1981) observed that *E. immobilis*, Calanus sp. and Centropages huxleyi, show different patterns of diet vertical migration inshore and offshore at 9°S. Semenova et al. (1982), described the vertical and horizontal distribution patterns of 37 species at 26 stations along the transect between 7° and 15°S. Only two species have been found to be able to penetrate and even stay in the oxygen minimum layer.

A better knowledge about the vertical movement and distribution of the whole population is required to evaluate their role in the active vertical transport of energy and matter in this intense upwelling region. Although there is a plethora of studies describing vertical distribution and migration in marine zooplankton (see recent reviews in Hays 2003; Pearsore 2003), only a few studies were conducted explicitly considering and testing the fluctuations in cline depths (Hary et al. 1983; Trenorow 1998; McManus et al. 2005), or testing the effect of specific abiotic variables on migrating organisms (Cohen and Forward 2002; Renz and Hitchc 2006). Previous studies on vertical distribution and migration of zooplankton conducted off Peru have not yet explicitly tested the hypotheses related to specific abiotic variables and fluctuations in cline depths.

The present study aims at characterizing and analyzing the vertical distribution and migration patterns of zooplankton in the Cold Coastal Waters (CCW), which are typical of the highly productive upwelling ecosystems of the Humboldt Current System. The aims of the present study are to characterize and analyse the vertical distribution and migration pattern of zooplankton, and particularly to analyse the effect of cline depths, specifically the depth of the oxygen minimum layer, on zooplankton in the Callao shelf waters.

### Materials and methods

#### Sampling

Zooplankton vertical distribution and migration were studied at a nearshore (station 2) and an offshore station (station 5) off Central Peru (12°02'03" 77°17'32"W and 12°02'45" 77°39'11"W, respectively). It is an open shore area (Fig. 1), wherein a widening of the shelf is observed (Carraico and Lozano 1989). The stations are located in an upwelling zone with elevated levels of primary production during most of the year (Zuza and Guilen 1970). Station 2 is located on the nearshore shelf at 95 m depth, while station 5 is located farther offshore above the shelfbreak, with a column depth of 176 m. In April and August 2006, zooplankton samples were collected over 24-h periods at both stations. Vertically stratified tow was taken with a multi-net (Mid model, 50 × 50 cm mouth size, Hydro-Bios, 50 × 50 cm mouth size, Hydro-Bios, 50 × 50 cm mouth size, Hydro-Bios).
Kiel) equipped with five 300-μm-mesh nets approximately every 3 h. Each of the five nets was equipped with a calibrated Hydro-Bios flowmeter, to allow for individual estimates of filtered volume for each sample. Depth strata sampled by each net were: (1) maximum depth of 50 m, (2) 30-50 m, (3) 20-30 m, (4) 10-20 m, and (5) 10 m to surface. This sampling strategy was chosen to ensure a consistent sampling of the three main strata (oxygen minimum layer, oxycline, and upper layer) of the water column. The first net was deployed for sampling the deepest, hypoxic stratum inside the oxygen minimum layer; the last uppermost net was always sampling the well-oxygenated upper layer, while the intermediate nets were intended for sampling the oxycline and one of both layers, depending on the oxycline depth. Maximum depth sampled with the first net varied from 100 to 75 m, depending on local conditions. Samples were preserved in 4% formaldehyde buffered with borax in seawater solution.

Immediately after each haul, environmental data were obtained with a CTD (Seabird model SBE 19) equipped with sensors for depth, temperature, salinity, chlorophyll a fluorescence (Haeedt, Kiel), and an optical oxygen sensor (Andersson model 3830). Additionally, water samples for chlorophyll a measurements were obtained at discrete depths (0, 10, 25, 50, 75, 94 m at station 2 and 100 m at station 5) using a reticulated system equipped with 5-L Niskin bottles. For each depth, samples of 200 ml were immediately filtered on GF/F filters and refrigerated until the analysis. Later, the filters were extracted in 90% acetone and measured in the laboratory (Holm-Hansen et al. 1965) with a previously calibrated desk fluorometer (Turner Designs 10-AU).

Generally, whole zooplankton samples were analysed. When the density exceeded 200 individuals per species, the samples were split using the Hustman Marine Laboratory beaker technique (Van Gessel, Louis et al. 1983). All copepods were identified to the lowest taxonomic level possible and counted under a stereomicroscope. Invertebrate larvae were identified with the available literature (Gurney 1942; Barnes and Hobson 1974; Alhormoz and Wehrmann 1997; Pohle et al. 1999; Thuesen and Fernández 1999).

Data analysis

Zooplankton abundance was calculated in terms of density (ind. m⁻³) based on flowmeter readings. The most abundant and frequent taxa were chosen for analyses of vertical distribution and correlation to abiotic variables. To assess the vertical distribution center for each taxon and stage at a given time, the weighted mean depth was calculated for each multinet haul (Roe et al. 1984; Pillar et al. 1989). To characterize the vertical distribution in relation to the oxygen minimum layer, the percentage of the abundance in the top oxygenated layer in relation to the total abundance per haul (P_oxy) was calculated for each taxonomic group. The top oxygenated layer was defined as the Multinet strata sampled above the 1 ml⁻¹ oxygen isopleth. Weighted mean depth and P_oxy were only calculated for taxa and stages that displayed total vertically integrated densities in a given multinet haul of at least 0.3 ind. m⁻³.

By comparing changes in weighted mean depth and P_oxy, we were able to distinguish and ascertain which organisms potentially exhibit migration in relation to daytime and oxycline dynamics. Specifically, we tested our data for diel vertical migration (significant differences in WMD between day and night), and diel migration through the oxycline (significant differences in P_oxy between day and night), and migration following the oscillations of the oxycline (significant correlation of weighted mean depth and oxycline depths). To verify whether diel vertical migration occurred, weighted mean depth and P_oxy were tested for differences between day and night for the most abundant taxa using non-parametric Mann-Whitney tests. To check whether diel vertical migration of organisms was due to daily fluctuations ofcline depths, thermos- and oxycline depths (depths of the 15°C isotherm and 1 ml⁻¹ oxygen isopleth) were also tested for differences between day and night using non-parametric Mann-Whitney tests. For taxa, where different life history stages occurred (e.g. copepodids and adults of copepods), weighted mean depth and P_oxy were compared between stages to test for ontogenetic vertical migration with non-parametric Wilcoxon tests for paired samples. Spearman rank correlation analysis was used to test for significant correlations between environmental variables (depth, temperature, salinity, oxygen, and laboratory-derived chlorophyll a) and abundance by stratum and time, for the main taxa and stages, using one average value per sample and depth stratum (n = up to 120). Spearman correlations were also calculated between weighted mean depth, P_oxy and the depths of the 15°C isotherm and 1 ml⁻¹ oxygen isopleth, for the main taxa and stages, using one value per multinet haul (n = up to 24). Statistical tests were performed using Statistica 6.1.

Results

Hydrographical conditions

During April, the water column at both stations showed the presence of CCW, with an extremely shallow and oscillating thermocline (15°C isotherm) located at 10-20 m depth at the nearshore station 2 (Figs. 2, 3). The thermocline was deeper offshore, being 20-40 m at station 5. Surface waters displayed temperatures between 16 and 17°C in April. Deeper waters (ca. 75 m) showed temperatures around 14°C. The vertical distribution and variability of the thermocline was coincident with the variability of the sharp, shallow oxycline.

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Fig. 2 Examples of vertical CTD profiles of salinity, temperature, oxygen concentration, and chlorophyll a fluorescence obtained during the predominance of cold coastal waters (Station 2 in April, a above) and subtropical surface waters (Station 2 in August, b below).

(Fig. 3). The depth of the oxygen isopleth of 1 ml L\(^{-1}\) (here defined as oxycline depth \(Z_{oxy}\)), and the 0.5 ml L\(^{-1}\) oxygen isopleth often referred to as the upper boundary of the oxygen minimum layer varied less and generally were less than 10 m apart from each other, showing a steep gradient in oxygen concentrations (Fig. 2). The oxycline at station 2 in April was extremely shallow, with a \(Z_{oxy}\) of 10-20 m (average 15 ± 4 m), while \(Z_{oxy}\) was clearly deeper at station 5, varying between 14 and 36 m (average 21 ± 9 m). Salinity values ranged from 34.8 to 35.1, indicating the presence of CCW in April. Chlorophyll a fluorescence generally showed a consistent pattern with low values below the thermocline, a clear peak associated to the base of the thermocline, and intermediate high values in the upper layer (Fig. 2).

In August, a different situation was observed at both stations. Warmer waters (>17°C) dominated most of the water column with a significant deepening of the 15°C isotherm down to more than 60 m (Figs. 2, 3). A much more oxygenated water column characterized this period with a deeper oxycline, particularly at station 5, where \(Z_{oxy}\) was mostly below 50 m (Fig. 3). Salinity was higher than in April, with values between 35.1 and 35.3, indicating the presence of subtropical surface waters (SSW) on the shelf. The thermocline and oxycline showed a strong vertical variability over 24 h, particularly at station 2 (Fig. 3).

Thermocline and oxycline depths (\(Z_{oxy}\) and \(Z_{thrm}\)) displayed considerable oscillations within 24 h, especially at station 2 in August and at station 5 in April, when the amplitude of oscillations in \(Z_{oxy}\) and \(Z_{thrm}\) were approximately 20 m (Fig. 3). Wavelength of these oscillations was approximately 12 h during these two 24-h series, with two peaks per 24 h. At station 5 in April, thermocline and oxyclines
Results

The analysis of the vertical distribution showed that in April, the bulk zooplankton was accumulated in the upper layers. At station 2, in April, 91% of all organisms were collected in the upper 20 m depth, and 89% of all organisms were collected in the upper 30 m depth at station 5. Conversely, in August, zooplankton was distributed over all strata of the water column sampled (Fig. 4).

In April, weighted mean depth of the whole community varied from 6 to 25 m. The percentage of the whole community found in the oxygenated upper layer \( P_{\text{oxy}} \) varied from 68 to 88%. In August, weighted mean depth of the whole community was clearly deeper than in April, varying from 40 to 77 m, while \( P_{\text{oxy}} \) was similar to April (67%). Thus, in both periods, most of the zooplankton was generally found in the oxygenated layer. Weighted mean depth and \( P_{\text{oxy}} \) were also used to compare the day and night hauls. The differences between day and night in weighted mean depth were significant for station 5 in April \( (P = 0.02, \alpha = 0.05) \) and at station 2 in August \( (P = 0.04, \alpha = 0.05) \), showing that the whole community was located near the surface at night and was located significantly deeper during the day on both occasions. Conversely, there were no significant differences in \( P_{\text{oxy}} \) between day and night for the whole community, neither for any 24-h series nor for all series pooled together.

In April, Acartia tonsa dominated all multinet hauls at both stations, with 72.9% of the total abundance inshore and 61.1% offshore (Table 1). In August, A. tonsa was still the most important species at the inshore station 2, with 42.7% of all organisms, but at the offshore station 5, A. tonsa was virtually absent from the samples, and a completely different zooplankton community was found associated with the unusual Subtropical Waters. Therefore, the vertical distribution and migration of zooplankton at station 5 in August will not be analysed and discussed in detail. Accordingly, this study focuses on the zooplankton communities associated with CCW found in April at both stations and at station 2 in August.

Considering these three 24-h series together, Centropages brachiatas (7.5%), E. inermis (4.7%) and Paracalanus parvus (3.1%) were also important among the catches (Table 1). Oscura venusta was numerically dominant only in the 24 h series performed in August at station 2 (3.9% of the total at this series). In the meroplankton, larvae of Magedona sp. (Polychaeta) were numerically dominant prominent in April, contributing 7.5% to the whole zooplankton at station 2 and 2.5% at station 5 (Table 1). Larvae

displayed a major elevation during the night and only a lesser peak around noon; thus, \( Z_{\text{oxy}} \) and \( Z_{\text{sum}} \) were generally slightly deeper during the day. However, comparisons of \( Z_{\text{oxy}} \) and \( Z_{\text{sum}} \) at different times with Mann-Whitney U tests did not yield any significant differences between day and night, whether tested for all 24-h series pooled together or tested separately.

Community structure

Highest vertically integrated abundance of the bulk zooplankton was found in April, with an average of 25,090 ± 14,090 ind. m\(^{-2}\) at station 2 and 24,654 ± 12,867 ind. m\(^{-2}\) at station 5. In August, zooplankton abundance was only 9,331 ± 2,613 ind. m\(^{-2}\) at station 2. The vertically integrated bulk zooplankton abundance did not show any differences between day and night during any of the three 24-h series (Fig. 4).
Results

Fig. 4  Depth integrated abundance of bulk zooplankton per stratum sampled off Central Peru in 2006. The shaded area indicates night samples

of Discinocera lamellosa (Brachiopoda) were also numerically dominant in April, contributing 3.5% of the whole zooplankton at station 2. Larvae of both species were virtually absent in August. These conditions permitted the entrance of other mesoplanktonic organisms such as eggs of Engraulis ringens (0.8%, up to 350 ind. m⁻³) and zoone of Pleuromesodes monodon (6.4%, up to 585-4 ind. m⁻³).

The Shannon Weaver (II) species diversity of all three 24-h series ranged from low (0.5) to moderate (2.6), with an average of 1.9. Average evenness was 0.6, with a minimum of 0.2 at 0-10 m depth and maximum of 0.8 at 30-50 m depth during April.

Vertical distribution and ontogenetic migration

Most taxa, including adults of the dominant A. tosa, appear mainly in the oxygenated layers throughout the study period. Ninety-two percent of all A. tosa adults were found at 0-30 m depth. When comparing the average vertical distribution of distinct life history stages of the most abundant copepod species, significant differences were found for A. tosa only (Fig. 8). Average weighted mean depth of A. tosa adults (14 ± 7.5 m) was significantly shallower than weighted mean depth of nauplii (25 ± 12 m) and copepodids (33 ± 14 m) of this species. Copepodids were found with weighted mean depth down to 63 m, and nauplii down to 52 m, while adults generally displayed weighted mean depths above 20 m, and never reached below 30 m. This difference in weighted mean depth was significant for all three 24-h series pooled (P = 0.0001, valid n = 19 for copepodids, and P = 0.005, valid n = 18 for nauplii) and for both 24-h series in April. Copepodids of A. tosa were generally found deeper than nauplii of this species, although average weighted mean depths of nauplii and copepodids were not significantly different when tested for all three 24-h series pooled together. However, P_max of nauplii was significantly higher than P_max of the copepodids of this species (P = 0.036 valid n = 18), indicating that copepodids of A. tosa were generally found in less-oxygenated waters than nauplii.

For E. tuermsis, another species where adults, copepodids, and nauplii were sufficient enough for testing hypotheses...
Table 1  Average, maximum and minimum values of abundance for the most abundant taxa

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Avg. (ind. m⁻³)</th>
<th>Max (ind. m⁻³)</th>
<th>Min (ind. m⁻³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. tosa adults</td>
<td>279.3</td>
<td>4303.7</td>
<td>0.3</td>
</tr>
<tr>
<td>A. tosa copepodids</td>
<td>2.6</td>
<td>16.7</td>
<td>0.0</td>
</tr>
<tr>
<td>A. tosa nauplii</td>
<td>2.8</td>
<td>25.6</td>
<td>0.1</td>
</tr>
<tr>
<td>Calanus sp</td>
<td>1.0</td>
<td>4.4</td>
<td>0.2</td>
</tr>
<tr>
<td>Calanus copepodids</td>
<td>4.3</td>
<td>12.4</td>
<td>0.2</td>
</tr>
<tr>
<td>Centropages brachiatia</td>
<td>38.1</td>
<td>413.0</td>
<td>0.1</td>
</tr>
<tr>
<td>Eucalanus inermis</td>
<td>24.1</td>
<td>502.7</td>
<td>0.2</td>
</tr>
<tr>
<td>E. nauplii</td>
<td>18.9</td>
<td>326.7</td>
<td>0.1</td>
</tr>
<tr>
<td>Corycaeus obliquus</td>
<td>2.0</td>
<td>7.7</td>
<td>0.3</td>
</tr>
<tr>
<td>Paracalanus parvus</td>
<td>15.3</td>
<td>156.7</td>
<td>0.1</td>
</tr>
<tr>
<td>Henicyclops thalassius</td>
<td>2.4</td>
<td>34.5</td>
<td>0.2</td>
</tr>
<tr>
<td>Oithona sp</td>
<td>2.0</td>
<td>6.7</td>
<td>0.1</td>
</tr>
<tr>
<td>Oconoa ventura</td>
<td>0.6</td>
<td>49.1</td>
<td>0.0</td>
</tr>
<tr>
<td>Dicranaca lamellona larvae</td>
<td>24.4</td>
<td>253.3</td>
<td>0.1</td>
</tr>
<tr>
<td>Lomacra sp. larvae</td>
<td>1.1</td>
<td>4.8</td>
<td>0.1</td>
</tr>
<tr>
<td>Magelona sp. larvae</td>
<td>32.2</td>
<td>323.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Octopus sp.</td>
<td>10.1</td>
<td>250.5</td>
<td>0.1</td>
</tr>
<tr>
<td>Physalis polyphemoides</td>
<td>1.3</td>
<td>1.3</td>
<td>1.3</td>
</tr>
</tbody>
</table>

Related to ontogenetic vertical migration, no significant differences in weighted mean depth were found either between life history stages when tested for all three 24-h series pooled together, or for any 24-h series tested separately.

Diel vertical migration

Among the species and stages analyzed, significant differences in weighted mean depth or Pooled between diurnal and nocturnal hauls were detected for several taxa. Centropages brachiatia and E. inermis were found deeper during the day (diel vertical migration) during one 24-h series. Paracalanus parvus and larvae of Magelona sp. were found deeper during the night (reverse diel vertical migration) in at least one series. For P. parvus, Henicyclops thalassius, Oithona sp. and larvae of Magelona sp. were the only taxa to show significant diurnal variations.

Centropages brachiatia (adults and copepodids) showed significant diel vertical migration at station 2 in August (P = 0.02, n = 8). During this 24-h series, weighted mean depth for Centropages brachiatia was 18 ± 1.6 m at night. During the day, this species migrated to a deeper stratum, to a depth of 34 ± 2.5 m.

E. inermis (adults and copepodids) also showed significant diel vertical migration at station 2 in August (P = 0.02, n = 8). During this 24-h series, weighted mean depth for E. inermis was 32 ± 4.5 m at night. During the day, this species also migrated to a deeper stratum, to a depth of 58 ± 4.1 m.

Paracalanus parvus (adults and copepodids) showed significant reverse diel vertical migration at station 5 in April (P = 0.033, valid n = 7). During this 24-h series, weighted mean depth for P. parvus was 30 ± 4.8 m at night. During the day, this species migrated upwards, with a depth of 22 ± 1.5 m.

Magelona sp. larvae showed significant reverse diel vertical migration at station 2 in April (P = 0.002, valid n = 7), and for all three series pooled together (P = 0.001, valid n = 25). Magelona sp. larvae were found at shallower depths during the day and migrated downwards during the night (Figs. 5, 6, 7, 8). Considering all hauls, weighted mean depth for Magelona sp. larvae was 37 ± 15 m at night, while during the day the depth was 15 ± 4 m.

Comparisons of thermocline and thermocline depths (Z_{thermo} and Z_{hem}) at different times with Mann-Whitney U tests did not yield any significant differences between day and night, whether tested for all three 24-h series pooled together or for each series tested separately. Thus, taxa that performed diel vertical migration did not simply follow the fluctuation in cline depths.

For E. inermis, adults and copepodids did not show a regular diel vertical migration pattern, except for station 2 in August. Additionally, this deep-dwelling species showed significant upward movements or "emersion" events. It did appear in considerable amounts above the level during (P = 0.001) at one third of all multinet hauls. These upward movements were observed during day and night. Upward migration of E. inermis adults and copepodids was generally limited to the levels just above the thermocline.

Neither during these singular movements nor during the migration at station 2 in August were peaks of E. inermis abundance ever seen in the upper two layers, above 20 m of depth (Figs. 5, 6, 7).

Diel vertical migration and environmental parameters

The main species showed significant correlations with at least some environmental parameters (Table 3). Adults of A. tosa showed negative correlations with depth and salinity, according to their consistently higher abundances in shallow layers and lower abundances in high-salinity waters in August. There were no significant correlations with oxygen concentration or temperature for adults of A. tosa. Several other taxa also showed negative correlations with depth (Calanus sp., Centropages brachiatia, Dicranaca lamellona larvae, Octopus sp., and Physalis polyphemoides). No significant correlations with environmental parameters were found for nauplii and copepodids of A. tosa. E. inermis (all stages) and Oithona venusta were the only taxa to display positive correlations with depth.
Fig. 5 24-h variation of the vertical distribution of selected species off Callao, station 2 during April 2009. Dotted lines indicate the approximate position of the oxycline, based on the 1 ml$^{-3}$ oxygen pycnocline.

Fig. 6 24-h variation of the vertical distribution of selected species off Callao at station 3 during April 2009. Dotted lines indicate the approximate position of the oxycline, based on the 1 ml$^{-3}$ oxygen pycnocline.
Results

Fig. 7 24-h variation of the vertical distribution of selected species off Callao at station 2 during August 2000. Dotted lines indicate the approximate position of the oxycline, based on the 1-cm1-1 oxygen pynocline.

According to their consistently higher abundances in deep layers, E. inermis did not show any other significant correlations, while Oncocera venusta showed a positive correlation with salinity related to high salinities in August. Significant correlations were observed with temperature, laboratory-derived chlorophyll a and oxygen concentrations for several taxa. Larvae of the polychaete Magelona sp. showed negative correlations with oxygen, laboratory-derived chlorophyll a, and with temperature. Adults and copepods of Callinus sp., Corycaeus dubius, Paracalanus parvus and Oithona sp. showed positive correlations with salinity, as they were more abundant in August, when high-salinity waters predominated (Table 2, Fig. 2).

The correlations between the depths of thermocline and oxycline and weighted mean depth of the main taxa (Table 4) agreed well with the correlation matrix between abundance and absolute values of temperature an oxygen concentration (Table 3). P. parvus (all stages), which displayed positive correlations between absolute values and abundances, also showed positive correlations between cline depths and their weighted mean depths, confirming the importance of these variables in determining the vertical distribution. Many other taxa (A. tonsa adults, C. brachiatus adults and copepods, Oikopleura sp., Hexamita phalasius adults and copepods, adults of P. polyphemoides, and Magelona sp. larvae) showed positive correlations between weighted mean depth and cline depths, showing the importance of cline depths in determining depth regulation of these organisms. Among these organisms Magelona sp. larvae were the only taxa not to show significant correlation with depths of both clines, responding to Zmean only. This may be due to a clearly deeper thermocline at station 5 in comparison with station 2 in April (Fig. 2). Accordingly, in April, Magelona sp. larvae were deeper at station 5 (weighted mean depth: 39.5 ± 16.8 m) than at station 2 (weighted mean depth: 17.8 ± 6.7), which explains the positive correlation with Zmean. On the other hand, there was no consistent difference in oxycline depth between stations 2 and 5 (Fig. 2), which explains the positive correlation with Zmean. Weighted Mean Depths of deep-dwelling E. inermis (all stages) and copepods and nauplii of A. tonsa did not show any significant correlation with cline depths.

Taxa that displayed correlations of weighted mean depth with cline depths did not show any correlation between the percentage found in the oxygenated layer (Pox) and cline depth. This confirms that organisms that are restricted to the upper oxygenated layers (e.g. Oikopleura sp., Centropages brachiatus, Pseudopolyphemoides) display consistently high Pox values, independent of cline depths. Pox values of nauplii of E. inermis and nauplii and
Fig. 8 Temporal variations of the mean depth of adults and copepods of *Acartia tonsa* and larvae of the polyodonts *Magelona* sp. at two stations off Callao, Peru, during 2006.
Results

Table 2  Mean percentage above the 1 mL⁻¹ oxygen (P<sub>oxy</sub>), weighted mean depth (WMD) and standard deviation for the main taxa off Collac

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Percentage at surface (P&lt;sub&gt;oxy&lt;/sub&gt;)</th>
<th>Weighted mean depth (WMD)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>April Station 2 (%)</td>
<td>April Station 5 (%)</td>
</tr>
<tr>
<td>Acatemia tonsa</td>
<td>92</td>
<td>4.5</td>
</tr>
<tr>
<td>A. tonsa copepods</td>
<td>15</td>
<td>20.0</td>
</tr>
<tr>
<td>A. tonsa naupli</td>
<td>30</td>
<td>0.0</td>
</tr>
<tr>
<td>Calanops sp.</td>
<td>73</td>
<td>27.9</td>
</tr>
<tr>
<td>Calanops copepods</td>
<td>70</td>
<td>42.1</td>
</tr>
<tr>
<td>Centropyge breviceps</td>
<td>89</td>
<td>21.4</td>
</tr>
<tr>
<td>Encaloma isorini</td>
<td>84</td>
<td>44.6</td>
</tr>
<tr>
<td>Encaloma naupli</td>
<td>18</td>
<td>19.9</td>
</tr>
<tr>
<td>Corycaeus dubius</td>
<td>99</td>
<td>39.4</td>
</tr>
<tr>
<td>Paracalanus parvus</td>
<td>75</td>
<td>16.4</td>
</tr>
<tr>
<td>Hemichromis thalassicus</td>
<td>53</td>
<td>26.3</td>
</tr>
<tr>
<td>Oithona sp.</td>
<td>65</td>
<td>13.0</td>
</tr>
<tr>
<td>Oncella vesicaula</td>
<td>31</td>
<td>27.7</td>
</tr>
<tr>
<td>Dinaviculata lamellosa</td>
<td>81</td>
<td>30.7</td>
</tr>
<tr>
<td>larvae</td>
<td>92</td>
<td>20.0</td>
</tr>
<tr>
<td>Megalepion sp. larvae</td>
<td>55</td>
<td>37.8</td>
</tr>
<tr>
<td>Oikopleura sp.</td>
<td>97</td>
<td>1.6</td>
</tr>
<tr>
<td>Plesus polynemoides</td>
<td>97</td>
<td>2.6</td>
</tr>
<tr>
<td>Total zooplankton</td>
<td>88</td>
<td>7.2</td>
</tr>
</tbody>
</table>

Table 3  Spearman rank correlation matrix for the main abiotic parameters and the most abundant taxa. Values are only shown for significant correlations (p < 0.05)

<table>
<thead>
<tr>
<th></th>
<th>Depth</th>
<th>Oxygen (µl⁻¹)</th>
<th>Chlorophyll a (µl⁻¹)</th>
<th>Temp</th>
<th>Salinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acatemia tonsa adults</td>
<td>–0.52</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>–0.2</td>
</tr>
<tr>
<td>A. tonsa copepods</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>A. tonsa naupli</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Calanops sp. adults</td>
<td>NS</td>
<td>NS</td>
<td>0.22</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td>Centropyge breviceps adults</td>
<td>–0.3</td>
<td>0.52</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Encaloma isorini adults</td>
<td>0.23</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Encaloma naupli</td>
<td>0.28</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Corycaeus dubius adults</td>
<td>0.35</td>
<td>0.54</td>
<td>0.41</td>
<td>0.35</td>
<td></td>
</tr>
<tr>
<td>Paracalanus parvus adults</td>
<td>NS</td>
<td>0.31</td>
<td>0.31</td>
<td>0.28</td>
<td></td>
</tr>
<tr>
<td>Hemichromis thalassicus</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>–0.2</td>
</tr>
<tr>
<td>Oithona sp. adults</td>
<td>0.34</td>
<td>NS</td>
<td>0.31</td>
<td>0.39</td>
<td>0.49</td>
</tr>
<tr>
<td>Oncella vesicaula</td>
<td>0.25</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>0.23</td>
</tr>
<tr>
<td>Dinaviculata lamellosa larvae</td>
<td>–0.28</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Megalepion sp. larvae</td>
<td>NS</td>
<td>–0.35</td>
<td>–0.51</td>
<td>–0.29</td>
<td>NS</td>
</tr>
<tr>
<td>Oikopleura sp. adults</td>
<td>–0.34</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>–0.25</td>
</tr>
<tr>
<td>Plesus polynemoides adults</td>
<td>–0.38</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>0.43</td>
</tr>
</tbody>
</table>

copepods of A. tonsa displayed significant positive correlations and cline depths, showing that larger amounts of these deep-dwelling organisms occurred in the oxygenated layers when clines moved downwards, thus indicating that oxygen and temperature clines are not the effective borders for these organisms.
Table 4. Spearman rank correlation matrix for the depth of the oxygen column (Z_oxy, 1 ml l$^{-1}$), the depth of the thermocline (Z_th, 15°C), and the weighted mean depth (WMD) and percentage found in the oxygenated layer (Z_reg) for the most abundant and frequent taxa

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Z_reg</th>
<th>Z_th</th>
</tr>
</thead>
<tbody>
<tr>
<td>WMD A. tonsa adults</td>
<td>0.67</td>
<td>0.81</td>
</tr>
<tr>
<td>WMD A. tonsa copep.</td>
<td>0.76</td>
<td>0.76</td>
</tr>
<tr>
<td>WMD A. tonsa nauplii</td>
<td>0.64</td>
<td>0.64</td>
</tr>
<tr>
<td>WMD E. inermis adults</td>
<td>0.53</td>
<td>0.70</td>
</tr>
<tr>
<td>WMD C. brescians adults &amp; copep.</td>
<td>0.60</td>
<td>0.60</td>
</tr>
<tr>
<td>WMD P. parvus adults &amp; copep.</td>
<td>0.70</td>
<td>0.70</td>
</tr>
<tr>
<td>WMD C. brescians adults &amp; copep.</td>
<td>0.59</td>
<td>0.74</td>
</tr>
<tr>
<td>P_0.9% A. tonsa adults</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P_0.9% A. tonsa copep.</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P_0.9% A. tonsa nauplii</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P_0.9% E. inermis adults</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P_0.9% E. inermis nauplii</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P_0.9% C. brescians adults &amp; copep.</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P_0.9% P. parvus adults &amp; copep.</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P_0.9% Magelas spp. larvae</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P_0.9% Oikopleura sp.</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P_0.9% Luminosa sp.</td>
<td>NS</td>
<td>0.89</td>
</tr>
<tr>
<td>P_0.9% H. thalassiae adults &amp; copep.</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P_0.9% Discosoma lamella larvae</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P_0.9% P. polyphemus</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

NS not significant (P > 0.05), Copep: copepodite

Discussion

Dynamics of water masses and zooplankton community

The hydrographic conditions found in this study reflect two very distinct situations: (1) the predominance of CCW and a shallow oxygen column found in April 2006, associated to upwelling events found during non-El Niño conditions in this region (Morón 2000) and (2) the occurrence near the coast of highly oxygenated SSW in August 2005, which off Central Peru are more often located in oceanic areas.

Conditions found in April 2006 reflect the “typical” situation for neritic waters off Peru and the presence of CCW and upwelling events (Zuta and Guillen 1970) with extremely shallow (<20 m) oxy- and thermoclines, which become deeper towards offshore. The vertical distribution of chlorophyll a near the coast generally presents maximum values in the upper layers (Callejes and Guillen 1981). Previous studies off Callao show the maximum concentrations of chlorophyll a in autumn (up to 9 µg l$^{-1}$), and the minimum values under the influence of SSW (<1 µg l$^{-1}$) (Callejes and Guillen 1981), and also suggest the low abundance of phytoplankton during August in the area (S. Sanchez, personal communication).

The observed small-scale variations in salinity below 20-30 m (Fig. 2) are common feature of CTD profiles in this region. One potential explanation is that the huge temperature gradients in the thermocline and the different response times of conductivity and temperature sensors may be generating these salinity peaks, which are often simply smoothed out of the data.

The conditions observed in August 2006 (austral winter), are very different from the expected maximum wind-driven upwelling events that determine the presence of CCW, characterized by low surface temperatures (14-18°C) and low salinities (34.9-35.0) in nearshore shelf waters (Morón 2006). In fact, the SSW, which in winter is usually located far offshore in oceanic areas, appear to be projected onto the coast. In this region, SSW show large horizontal and vertical fluctuations and approach the coast mainly during summer and also during El Niño conditions (Morón 2006). During winter of 2006 the SSW presence off Callao could be associated with the propagation of Equatorial Kelvin Waves (EKW) and their impact on the local water column conditions as coastally trapped waves (CTW). EKW and resulting CTW are more frequent and stronger during El Niño, but may also occur during non-El Niño periods. The analysis of the large-scale ENSO (El Niño Southern Oscillation) cycle, as given by the Multivariate ENSO Index (MEI: Wolter and Timlin 1998) shows that in 2006, conditions switched from weak La Niña conditions in April (MEI: -0.6) to weak El Niño conditions in August (MEI: 0.75). Thus, the onset of the weak El Niño 2006/2007 could also explain the unusually warm and high-salinity SSW found in August 2006. Furthermore, EKW and CTW have been reported to be appearing in this region with a higher intensity since 2002.

This change in the hydrographic conditions between April and August determine significant changes in the mesozooplankton community. In fact, during April the community was characterized by low to moderate diversity, dominated by Acartia tonsa, which has been considered typical for neritic waters in this region (Santander 1981; Giron 2001; Criasles-Hernandez et al. 2005). In August, environmental conditions were not favourable for A. tonsa, and rather warmwater and offshore shelf taxa such as P. parvus, Oithona spp. and Corycaeus sp. became more abundant in the area. The decrease in A. tonsa abundance nearshore, and the disappearance of this key species in the offshore station in August, is certainly associated with the observed occurrence of SSW, which are found in oceanic areas much farther offshore under normal conditions.
Results

Diel vertical migration and oxygen minimum layer dynamics

On a diurnal time scale, the hydrographic conditions also showed some variability, as shown by the oscillations of thermo- and oxycline depths (Z_{thermo} and Z_{oxy}). This variability could be related to internal waves that may affect the vertical dynamics of zooplankton (Pineda 1999; Johnson and Shanks 2002; Rinke et al. 2007). The apparent semidiurnal frequency of the observed oscillations indicates tidal forcing of these internal waves, although local surface tidal amplitude is less than 1 m.

The observed oscillations in cline depths may be stimulating, or at least enhancing, the "regular" diel vertical migration (descent in the early morning) observed for Centropages brachiatas. C. brachiatas showed a diurnal variation in vertical distribution at station 2 in August and also at a series with considerable oscillations in cline depth. Accordingly, no diel vertical migration of any taxa was detected at station 2 in April when cline oscillations were minimal, thus supporting the assumption that diel vertical migration was related to cline oscillations. The results of the correlation analysis also support this idea, since weighted mean depths of C. brachiatas were significantly correlated with thermo- and oxycline depths. Furthermore, the abundance of C. brachiatas was significantly correlated to oxygen concentration, showing the importance of this factor in determining the distribution of this species. On the other hand, thermo- and oxycline depths (Z_{thermo} and Z_{oxy}) oscillated at a higher frequency (12 h) than diel vertical migration, and there were no significant differences between day and night in cline depths. Thus, taxa that performed diel vertical migration did not simply follow the fluctuation in cline depths.

Two explanations are possible for the observed relation between cline depths and diel vertical migration of C. brachiatas: (1) this species may be stimulated or triggered by cline oscillations, possibly together with other factors (e.g., light, feeding) or (2) for taxa that are not adapted to hypoxia the descent of the oxycline gives room for migration into the upper, well-oxygenated layer. This space may then be constricted in regular intervals by cline oscillations. This constriction hypothesis would also explain the absence of any diel vertical migration of this species at station 2 in April, when the oxycline was most shallow. Conversely, Peterson (1998) found no diel vertical migration for these species. Although the data seem to show quite straightforwardly the existence of diel vertical migration for these taxa, the vertical distribution could be explained by physical processes. For example, changes in vertical distribution may also be generated by advection of different water masses with different distributions of organisms. Unless each organism can be tagged and followed individually for relevant periods of time, this last residual uncertainty will always remain in any field study on zooplankton vertical migration. Many uncertainties still remain, but the results of our study confirm that diel vertical migration is a very flexible behaviour that can be adopted by planktonic organisms depending on environmental conditions, especially on oxygen minimum layer depth.

The vertical distribution of different life history stages of A. tonsa revealed a pattern of ontogenetic vertical migration. Adults were observed at surface and copepods and nauplii were observed occupying mostly the deep anoxic layer. Although it might be questionable whether quantitative abundance data for small-sized stages such as nauplii can be obtained with 300-μm nets, the massive occurrence of A. tonsa nauplii in the nets used below the oxycline is a clear evidence for their existence in these deeper strata. A. tonsa might show aggregations at various depths for reproduction. The existence of such layers seems to be an essential element of spatial structure of the plankton community (Longhurst 1981; Vinogradov 1997). This ontogenetic vertical migration has obvious implications for the retention of A. tonsa populations in this highly advective and stratified environment with strong upwellings (Smith et al. 1981a; Peterson 1998).

Mereplankton and reverse diel vertical migration

In our study, most invertebrate larvae stayed permanently in the oxygenated upper layers, with the notable exception of the larvae of the polycheate Magelona sp., which performed reverse diel vertical migration. For mereplankton larvae, high temperature and food abundance found in the upper layers may be used to maximise growth and reduce the time spent in the plankton (Nell 1992; Gray and Kingsford 2003; Irigoien et al. 2004), rather than engaging in diel vertical migration at the risk of prolonging the planktonic phase.

Reverse diel vertical migration (i.e. ascent at the beginning of daytime) has not yet been reported for this region. This inverse pattern has been observed for the copepods Pseudocalanus sp. off the Northwestern USA, concurrently with a normal vertical migration by nocturnal invertebrate predators (Ohman et al. 1983; Ohman 1990). Ohman et al. (1983) suggested that predator avoidance was the cue for this migratory behaviour. In the Antarctic, adults and juveniles of Enhalessia superba migrate upwards to feed on phytoplankton during the day, and downwards during the night to feed on zooplankton (Hernández-León et al. 2001). The authors hypothesized that krill displayed reverse vertical migration to avoid predation by mesopelagic fishes. The unusual reverse diel vertical migration pattern observed for larvae of Magelona sp. may also be related to the avoidance of vertically
migrating predators, although overall vulnerability to visual predators should be higher when ascending at daytime. Another possible explanation for this reverse diel vertical migration could be associated with its feeding strategy (Keppler et al. 1985; Vinogradov 1997), and to a possible strategy of larval retention and transport, utilizing deep undercurrents (Wing et al. 1998; Mace and Morgan 2006; Yannicelli et al. 2006).

Comparisons with previous studies

Several other authors have suggested the existence of vertical migration in this area (Judkins 1986; Boyd et al. 1981; Macas et al. 1981; Smith et al. 1981a; Glebov 1982; Semenova et al. 1982). The vertical distribution of copepods shows similarities and differences with previous data. Judkins (1980) previously described vertical distribution relative to the oxygen minimum layer in Peru from samples collected at 15°S in shelfbreak, slope, and offshore. Most zooplankton taxa were in concentrations exceeding 1.0 ml⁻¹ throughout the upper 85 m. Similar patterns were also described for zooplanktonic taxonomic group off 9°S by (Macas et al. 1981). Zooplankton did not exceed 30-m depth and zooplankton peak was coincident with the sharp gradient in dissolved oxygen concentration. Saltzman and Wischmer (1997) examined the vertical distribution of copepods in the eastern tropical Pacific, and showed how copepods have modified vertical distribution in regions with pronounced midwater oxygen minimum zones and displayed different environments. Several deep-sea animals have modified metabolic systems adapted to survival in water with low oxygen availability (Childress and Thuesen 1992).

The vertical distribution of several species suggests a possible niche separation of closely related species in the extreme conditions of the oxygen minimum layer (Saltzman and Wischmer 1997). E. inermis had the greatest vertical distribution in eastern equatorial Pacific (Fleminger 1973); but in a study off Chile, E. inermis remained near the base of the oxygen and within the upper zone of the oxygen minimum zone (Hidalgo et al. 2005). In the waters off Peru, Boyd et al. (1981) and Macas et al. (1981) showed that Eucalanus could withstand periods of 12 h in anoxic layers. Judkins (1980), when testing vertical distribution between day and night, found significant differences at shelfbreak and offshore stations for E. inermis only, thus showing the occurrence of diel vertical migration for this species, similar to the results of the present study. During the present study, the population of E. inermis was generally located below the oxycline, a strategy, which allows for rapid incursions into oxygenated layers immediately above the oxygen minimum layer (Figs. 5, 6, 7). This pattern may be related to the avoidance of predators, which are limited to oxygenated layers (e.g., anchovies).

Conclusions

The zooplankton off the coast of Central Peru was characterized by marked temporal and spatial heterogeneity, but governed by clear processes and behavioral traits, which could be related to the dynamics of the oxygen minimum layer as follows: (1) the total bulk holo- and mesozooplankton and most taxa were concentrated in the upper oxygenated waters, above the oxygen minimum layer; (2) abundance decreased from April to August due to the increasing influence of SSW; (3) bulk zooplankton and most taxa displayed a wider vertical distribution in the water column in August, clearly following the deepening of the oxygen minimum layer, and 4) average abundances and weighted mean depths of many taxa were correlated to oxygen concentration and oxycline depth, showing the importance of cline dynamics for this community.

Furthermore, five distinct patterns of vertical distribution and migration in relation to the oxygen minimum layer were distinguished in this study: (1) ontogenetic vertical migration through the oxycline (Acartia tonsa adults, nauplii, and copepodite), (2) permanent limitation to layers above the oxycline (e.g. Oikopleura sp., most invertebrate larvae), (3) distribution mostly below the oxycline with occasional immigration into the layers just above the oxycline (E. inermis), (4) diel vertical migration, (e.g. Centropages fortunatus at one station), and (5) reverse diel vertical migration (e.g. larvae of the polychaete Magelona sp.).

Our results have clear implications for the understanding of the retention mechanisms of key zooplankton taxa in an extremely advective environment (Smith et al. 1981a, b) and for prey-predator relationships in the pelagic realm of the Humboldt Current System. The shelf areas of the Humboldt Current System are extremely productive, but display considerable dynamics on several spatial and temporal scales. This study provides evidence that in spite of the high variability in abundance and distribution of the observed communities, changes in oxycline dynamics have predictable effects on zooplankton vertical distribution in these coastal waters.

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References *

* All citation included in this manuscript are compiled in the final list of references.
5.4 Scientific contribution

ENSO effects on phytoplankton dynamics, grazing rates, selectivity, and egg production of the copepod *Acartia tonsa* off Central Peru

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**Key words:** *Acartia tonsa*, feeding selectivity, grazing impact, egg production rates, spatio-temporal variability, ENSO, Humboldt Current System

**Abstract**

*Grazing rates, selectivity, and egg production rates of Acartia tonsa and their relation to phytoplankton density (abundance and phytoplankton carbon), composition, and primary production were studied at four stations off central Peru during different El Niño Southern Oscillation (ENSO) phases in 2006 and 2007. The phytoplankton
community showed extreme changes in density and composition, with a huge change between different phases. Dinoflagellates, nanoflagellates, and diatoms dominated during 2006, including ENSO-neutral conditions in April 2006 and during the weak El Niño in July and August 2006. Diatoms dominated in 2007, including ENSO-neutral conditions in February and April 2007 and the strong La Niña event that impacted the area from May to August 2007. Several diatom, nanoflagellate and dinoflagellate species were readily ingested. Ingestion rates were correlated with phytoplankton density. A tonsa typically ingested prey according to its concentration, although several species including some highly abundant red tide forming species, such as Akashiwo sanguineum (previously known as Gymnodinium sanguineum) and several other dinoflagellate and diatom species were consistently rejected. Diatoms, nanoflagellates and dinoflagellates were effectively ingested only if cell size was < 120 µm (major axis length). Selectivity significantly increased with cell size until a cell size of 120 µm. Egg production rates of A. tonsa were generally very low (0.6 to 9.2 eggs female⁻¹ day⁻¹, average: 6.1 ± 2.3 eggs female⁻¹ day⁻¹). Based on simultaneously performed egg production and in situ grazing experiments, our results indicate a possible negative relationship between the ingestion of dinoflagellates and A. tonsa egg production. This paper presents a discussion on how phytoplankton composition may affect the grazing selectivity by A. tonsa, specifically the formation of red tides off central Peru.

INTRODUCTION

The central Peruvian coast (12° S to 14°S) is an area directly affected by extremely high variability in oceanographic conditions and productivity. Also, it is one of the
most productive areas within the Humboldt Current System (HCS) (Zuta and Guillen, 1970; Guillén and Calienes, 1981). One of the dominant modes in this ecosystem is due to the El-Niño-Southern-Oscillation (ENSO) cycle. During El Niño (EN) phases, unusually warm waters appear in the coastal areas off Peru while La Niña (LN) causes the opposite effects. During the LN phase the trade winds and upwelling strengthen and cold water masses become more dominant (Chen and Cane 2008).

The Peruvian coastal waters as part of the Humboldt Current System (HCS) support the world’s largest single-species fishery (*Engraulis ringens*) which is of central importance for Peru’s national economy (Nixon and Thomas, 2001, Chavez *et al*., 2003; Hutchings *et al*., 2006). In this highly productive coastal upwelling system, copepods are a major component of mesozooplankton and the dominant grazers of phytoplankton (Gonzales *et al*., 2000; Calbet and Landry, 2004; Criales-Hernández *et al*., 2008; Ayón *et al*., 2008). Therefore their grazing rates should be critical in the transfer of matter and energy in this system (Pauly *et al*., 2002)

It is generally assumed that copepods in upwelling ecosystems feed mostly on diatoms and their ingestion rates are directly proportional to diatom abundance (Vargas and González, 2004 and Cowles, 1979). On the other hand, copepods that have been fed natural phytoplankton with a mixture of cell sizes have displayed complex feeding behaviour (Cowles, 1979; Paffenhöfer and Lewis, 1990; Kleppel 1993; Kleppel *et al*., 1996; Paffenhöfer and Mazzocchi, 2002; Vargas *et al*., 2007). Thus copepods often ingest large phytoplankton cells at a faster rate than small cells (Frost, 1972). On the other hand, some copepods feed selectively on size classes with highest relative abundance (Cowles, 1979; Kleppel, 1993; Broglio *et al*., 2003). Selectivity has also been observed with regard to different phytoplankton taxa
Results

Certain species are completely rejected, eventually due to palatability or toxicity (Broglio et al., 2003). Among these are some red tide forming species such as *Prorocentrum minimum*. Since red tides have increased in frequency recently along the Peruvian coast, they could affect secondary productivity and hence yield and quality of fisheries resources (Sanchez and Delgado, 1996). Rejection of red tide forming species by grazers could be a factor involved in the formation of red tides (Anderson, 1997; Turner et al., 1998; Turner and Borkman, 2005; Campbell et al., 2005).

So far, in the waters off Peru, only few single grazing experiments have been conducted on few offshore stations during oceanographic cruises (Smith, 1978; Cowles, 1979; Boyd et al., 1980, Dagg et al., 1980; Paffenhöfer, 1982; Dagg and Cowles, 1982). These studies concentrated mainly on the feeding response and size selectivity by some offshore copepod species (*Calanus australis, Centropages brachiatas* and *Eucalanus inermis*) (Cowles, 1979 and Dagg et al., 1980). Therefore, these studies could not consider the interannual and seasonal variability in grazing rates and selectivity.

In the coastal upwelling zone off Peru, mesozooplankton is usually dominated by the copepod *Acartia tonsa*, which is concentrated in the upper well oxygenated layers of the nearshore zone (Criales-Hernández et al., 2008). This species is adapted to high food concentrations which it encounters in estuaries and upwelled waters (Paffenhöfer and Stearn, 1988). In this study, we will evaluate the effects of seasonal and ENSO-related interannual variability of phytoplankton composition and on primary
Results

production on grazing rates, feeding selectivity, and egg production rates of *A. tonsa* in Peruvian inshore, bay, and shelf areas.

**MATERIAL AND METHODS**

**Sampling**

Sampling of water and copepods for grazing and egg production experiments was performed at four stations (Fig. 1): 1.) Inside Independencia Bay (“Ind” Station), a shallow, semi-enclosed bay located 263 km south of Lima (Tarazona *et al.*, 1989), 2.) At the Pier (“Pier” Station) of the Peruvian Marine Science Institute (IMARPE) in Callao 3.) At the nearshore shelf (“Station 2”, at 90 m depth) off Callao, 4.) At the offshore shelf (“Station 5”, at 176 m depth) off Callao. Experiments were conducted in April, July, and August 2006, and in February, April, May and August 2007. Monthly NOAA reports were used to assess the phases of the large-scale of the ENSO cycle during the study period, based on satellite-derived SST anomaly data from the Niño 1+2 region, the closest region to the Peruvian coast among the regions considered by NOAA (www.cpc.ncep.noaa.gov/products/expert_assessment/ENSO_DD_archive.shtml.)

Zooplankton was collected with a WP2 net (60 cm diameter, 300 μm mesh size) with a solid cod end towed obliquely between 5 m depth and the surface for 5 minutes. Water for incubation was collected with Niskin bottles at 5 m depth and was then gently filtered through a 100 μm mesh to eliminate all mesozooplankton. To determine the density of *A. tonsa* and other dominant copepods in the upper layer, we used available data from quantitative zooplankton samples collected simultaneously.
Results

These samples were obtained with vertical multinet (Hydro-Bios, Kiel, Germany) hauls between 10m depth and the surface at the shelf off Callao, and with a WP2 net in Independencia Bay. Both nets were equipped with 300μm mesh nets and previously calibrated flowmeters. Environmental data were obtained with a CTD (Seabird model SBE 19) equipped with sensors for depth, temperature, salinity and an optical oxygen sensor (Aanderaa model 3830).

2.2 Primary Production

Primary production was measured using the $^{14}$C method (JGOFS, 2004). Water samples were collected from Niskin bottles from 5 m depth as a proxy for the upper layer productivity to compare with grazing activity. Samples were inoculated with $^{14}$C tracer in light and dark bottles and incubated in situ for 6 hrs that allow the samples to be exposed to the natural temperatures and light levels (both intensity and spectral quality). For in situ incubation one dark bottle and three light bottles were hooked and suspended on an in situ array from noon to sunset. After the incubation, samples were filtered through Gf/f filters (nominal pore size ~0.7μm) to give total primary productivity. Filters were store frozen until the determination of radioactivity sample. Daily primary production was expressed as mgC m$^{-3}$d$^{-1}$.

Grazing experiments

Pre-screened water samples were gently homogenized and distributed in nine transparent of polyethylene flasks of 1L each. Three subsamples (250 mL) were immediately preserved in 2% formalin to determine the initial phytoplankton density and composition ($t_0$ water samples). Six samples were then gently filled into 1l flasks. Copepods were then transferred into three of the six flasks ($t_g$ water sample), while three sample flasks were incubated without copepods to determine phytoplankton
Results

growth in controls (t₀ water samples). Undamaged adults of *A. tonsa* were used for grazing and egg production experiments. Copepod densities in the experiments ranged from 75 to 95 ind. L⁻¹. Grazing experiments were generally conducted *in situ*, except at the Pier station, where they were performed in the laboratory under simulated *in situ* conditions and constant temperature. At the shelf and bay stations, the six flasks were firmly placed into a steel basket that was gently lowered to 5 m depth below a surface buoy that was fastened to the vessel by 20 m of rope to avoid shading. Grazing incubations were performed *in situ* during daytime for approximately 9 hours. After incubation, the content of the flasks was screened through a 150 μm mesh. Water and plankton samples from the flasks (tₑ and T₉) were treated and preserved in the same way as the initial t₀ samples. Phytoplankton was identified and counted using the Utermöhl method (Utermöhl, 1931). Microphytoplankton (> 20μm size along the major axis) was identified to species level if possible and measured, nanoplancton (2 to 20μm) was only counted and measured.

**Egg production experiments**

For each experiment, seventy single females of *A. tonsa* were pipetted into cell wells. 5 mL containing pre-screened (20 μm) water from the same stations as the copepods. Samples were incubated for 24 hours at ambient temperatures. Eggs were not separated from the copepods because egg cannibalism by *A. tonsa* is rare (Kiørboe *et al.*, 1985; Kleppel, 1992; Kleppel, 1996; Burkart and Kleppel, 1998; Kleppel *et al.*, 1998; Kleppel and Hazzard, 2000). Eggs were counted every six hours. After 24 h, females were removed and the eggs were incubated for further 24 hours to determine egg viability.
**Results**

**Data analysis**

Phytoplankton abundance and biomass was calculated in terms of density (cells mL\(^{-1}\)) and carbon biomass (μgC L\(^{-1}\)). Estimates of carbon content were based on measures of cell dimensions to calculate cell volumes by assigning specific shapes to each taxon (Hillebrand *et al.*, 1999 and Sun and Lui, 2003;). Thereafter, cell volumes were converted to carbon units using taxon-specific factors and equations (Edler, 1979; Menden-Deuer and Lessard, 2000).

The equations of Frost (1972) were used to calculate ingestion rates. To verify whether significant ingestion occurred, Mann-Whitney U-tests (Zar, 1996) were used to test for differences between tc controls and incubations with copepods t\(_g\). These tests were performed for the total final cell density per incubation flask (sum of all taxa), for the totals per taxonomic group (diatoms, dinoflagellates, silicoflagellates, phytoflagellates, etc.), and for each species separately.

Mann-Whitney U-tests were only performed for the taxa that were present in at least two out of three of the initial replicates, and displayed average initial densities above 300 cells l\(^{-1}\). Ingestion rates were then calculated for the phytoplankton groups only when significant differences between tc controls and t\(_g\) treatments were detected at p < 0.05, or when the mean density in t\(_g\) treatments was less than 60% of the density in tc controls. Ingestion was calculated assuming exponential phytoplankton growth and constant ingestion rates (Frost, 1972; Kleppel, 1996; Meyer-Harms *et al.*, 1999; Schwamborn *et al.*, 2004). Ingestion rates are thus expressed as cells copepod\(^{-1}\) d\(^{-1}\).
Results

Feeding selectivity was assessed by comparing the composition of *A. tonsa* diets (cells mL$^{-1}$ d$^{-1}$) to the composition of the food offered (cells mL$^{-1}$), using the Chesson electivity Index ($\varepsilon$) (Chesson, 1983, Schwamborn *et al.*, 2004). The values of $\varepsilon$ were calculated for each phytoplankton species and experiment, and may range from -1 to 1, where a value of zero means no selection (i.e. ingestion of a specific taxon in the same proportion as in the food offer), -1 means no ingestion, and positive values mean positive preference for a given taxon.

The relationship of cell size and electivity ($\varepsilon$) was analyzed in two steps: A.) Classification of the phytoplankton taxa into size classes, and calculation of the Portion Ingested (PI), i.e. percentage of taxa that suffered ingestion (ingestion rate > 0) in relation to all taxa in a given size class. Size classes with low (PI of 15% or less) or zero ingestion were excluded from the data set prior to the next step. B.) Analysis of the size-selectivity was used to find a relationship for the taxa that occurred during the experiments, and their size classes, where ingestion occurred. Thus, a Spearman correlation analysis was conducted to test for significant relationships between several indicators of cell size (length along major axis, volume, Equivalent Spherical Diameter ESD, and carbon content) and electivity ($\varepsilon$) for the whole data set, and for each time period (EN, LN, ENSO-neutral), and taxonomic group (nanoflagellates, silicoflagellates, dinoflagellates and diatoms) separately. Also, these data were used to test for significant differences in $\varepsilon$ between time periods (EN vs LN) and taxonomic groups (dinoflagellates vs diatoms), using simple Mann-Whitney U-tests.
Results

Daily fecundity \( F \) (eggs female\(^{-1}\) day\(^{-1}\)) (Bellantoni and Peterson, 1987) was calculated based on the egg production rates \( E \): \( F = E/A \), where \( E \) = number of eggs (maximum number of eggs during 24h in each cell), \( A \) = number of females in each bottle. At the end of the egg production experiments, prosome lengths of females were measured. Estimates of carbon content were based on prosome lengths. Thereafter, average prosome lengths of each experiment were converted to carbon units using length-mass equations (Berggreen et al., 1988). The gross efficiency of egg production, expressed in carbon units, was calculated as the ratio of carbon produced as eggs to that ingested as food (Kleppel, 2000). Egg carbon content was based on average egg diameter (Ayón and Hirche in prep) multiplied by 0.018 (Berggreen et al., 1988).

In order to test if grazing and egg production by \( A. \) tonsa changed with food concentration and composition, Spearman rank correlation analysis was used to test for significant correlations between several variables, e.g. cell density, ingestion rates, and egg production. Spearman matrices were calculated for the total phytoplankton and for the main taxonomic groups (diatoms and dinoflagellates) separately. Statistical analyses were performed with Statistica 6.1 or using the “R” language and environment (R Foundation for Statistical Computing).

RESULTS

Hydrography

The hydrographical conditions during the study period reflect three distinct ENSO phases, which resulted in different conditions during the experiments. (i) A moderate El Niño (EN) event in August 2006, which brought unusually high surface water
temperatures (up to 18.4 °C offshore, 17.1°C in Independencia Bay). (ii) A strong La Niña (LN) event in May and August 2007, characterized by low surface water temperatures (14.6 °C in Independencia Bay and 14.8 at station 2), and (iii) ENSO-neutral conditions in April 2006 and from February to April 2007. During both ENSO-neutral phases, temperatures were close to seasonal averages (Table 1).

The analysis of the large-scale state of the ENSO cycle based on satellite data also shows that ENSO-neutral conditions were present during April 2007 in the Niño 1+2 region. Thereafter, moderate El Niño conditions started after July and lasted until February 2007. Then, a transition period with ENSO-neutral conditions was present from March to April 2007. Finally, conditions shifted toward La Niña in the Niño 1+2 region, being evident since May 2007 and continued into 2008.

**Primary production and phytoplankton density, biomass, and composition**

Primary production rates in this study varied from 18 to 149 mgC m⁻³ d⁻¹ (Fig. 2a). Primary production was very low during EN, not exceeding 29 mgC m⁻³ d⁻¹. During LN, production was more than twice that during EN, but not significantly higher than during ENSO-neutral conditions in early 2006 and early 2007. Furthermore, primary production followed a consistent onshore-offshore gradient with maximum values at station 2 and inside Independencia Bay and low values at station 5. The maximum occurred during ENSO-neutral conditions in early 2007 at station 2 (209 mgC m⁻³ d⁻¹) and the minimum occurred during EN at station 5 (15 mgC m⁻³ d⁻¹).
Results

Total phytoplankton density varied over a wide range, from 2920 to 94200 cells mL\(^{-1}\) (Fig. 2, Table 2). Abundance clearly increased from EN towards LN. The lowest abundances were found during ENSO-neutral conditions in early 2006, with 2920 cells mL\(^{-1}\) at station 2 and 3064 cells mL\(^{-1}\) at station 5. During 2007, phytoplankton cell densities were quite different and maximum values were found at station 2 (75168 and 93200 cell mL\(^{-1}\), respectively) (Fig. 2b). This station showed the largest temporal change, with lowest abundance during ENSO-neutral conditions in early 2006 (2920 cell mL\(^{-1}\)) and highest abundance during LN 2007. At the Pier, total phytoplankton abundance varied from 11222 to 51775 cells mL\(^{-1}\). Moreover, in Independencia Bay, low abundance values were found during both ENSO-neutral phases, ranging from 3224 to 12269 cells mL\(^{-1}\) (Fig. 2b).

The phytoplankton community showed extreme changes in density and composition between different phases (Fig. 2b). Dinoflagellates, nanoflagellates, and diatoms were important during 2006 in terms of abundance, while diatoms clearly dominated during 2007 (Fig. 2b). Of the 139 taxa identified during all experiments, only 36 species were frequent, i.e. occurring at least 5 times. *Skeletonema costatum* and *Thalassionema nitzschioides* are chain-forming diatoms, and occurred in at least five experiments, with high densities in 2007 (Table 3). Both of them were among the dominant species during two experiments conducted during LN, both with maxima at the Pier during May and at station 2 during August 2007, with 43308 and 75616 cells mL\(^{-1}\) for *S. costatum*, and 271 and 1470 cells mL\(^{-1}\) for *T. nitzschioides*, respectively) (Table 3). The red tide forming species *Akashiwo sanguineum*, (previously known as *Gymnodinium sanguineum*) was the most abundant dinoflagellate species in our experiments, with up to 3011 cells mL\(^{-1}\) during ENSO-neutral conditions in early
Results

Phytoplankton carbon (PPC) varied from 279 μgC L⁻¹ during EN at the Pier to 3056 μgC L⁻¹ during LN at station 2 (Table 1). The minimum and maximum PPC correspond to the extremes of the ENSO phase that occurred in this study, EN and LN, respectively. PPC changed more at station 2 (between 849 and 3056) and was more stable at station 5 with changes from 1744 μgC L⁻¹ during ENSO-neutral conditions in early 2006 to 1052 μgC L⁻¹ during ENSO-neutral conditions in early 2007. At the Pier, biomass was generally high, varying from 1022 to 2212 μgC L⁻¹. Conversely, low biomass values were found in Independencia Bay in two of three experiments during EN (July, 409 μgC L⁻¹) and LN (May, 433 μgC L⁻¹). The contribution of diatoms and dinoflagellates to PPC shifted from dinoflagellate-dominated communities during 2006 towards diatom-dominated communities in 2007. Dinoflagellates comprised most of the biomass during the experiments at station 5 and in Independencia Bay during EN. Furthermore, dinoflagellates were important at station 2 during ENSO-neutral conditions in early 2006 and in Independencia Bay during EN (July) (Fig. 3a). The only exception to the dinoflagellate dominance during 2006 was found at the Pier during EN, when the very low PPC consisted mainly of nanoflagellates. During ENSO-neutral conditions in early 2007 and the subsequent LN, diatoms were the dominating group in all study areas (Fig. 3a.).
The size range of phytoplankton was from 4.8 to 446 μm (length measured along the major axis) (Fig. 4). Cell densities clearly declined with increasing cell size, following a log-linear pattern. During LN, cell densities increased for most size classes except for the nanoplanlton. Increase in density was highest for the largest sizes classes, as a result of the appearance of large diatoms during LN.

**Abundance of *A. tonsa***

*A. tonsa* was often the single dominant copepod species at the surface with up to 60% of the total zooplankton abundance. Maximum densities (9228 ind m\(^{-3}\)) were observed during ENSO-neutral conditions in early 2007 at station 5 (Fig 5). With the onset of EN, its abundance showed a drastic decline (0.12 and 220 ind m\(^{-3}\) at stations 2 and 5, respectively). Low abundance of *A. tonsa* did not permit to set up grazing experiments at stations 2 and 5 during EN, nor at station 5 during LN.

**Grazing rates**

In all grazing experiments, we found significant ingestion for many phytoplankton taxa, and there was no negative grazing for any taxonomic group. Furthermore, mortality of *A. tonsa* during the experiments was always low (1 to 5 %). Ingestion rates ranged widely, from 0.04 to 28.2 μgC copepod\(^{-1}\) day\(^{-1}\) (Fig. 3b) dependent on food concentration and composition (Table 2). Ingestion rates increased with increasing food concentration during the experiments and did not show any saturation at high phytoplankton densities (Fig. 6). The total amount of phytoplankton grazed by *A. tonsa* ranged widely, from 0.001 to 37693 cells copepod\(^{-1}\) h\(^{-1}\) (Fig. 6).
Results

A. tonsa fed predominantly on diatoms, except during EN, when dinoflagellates were more intensively ingested, specifically in Independencia Bay. Nanoflagellates were the most important food source during EN at the Pier. During 2007 (ENSO-Neutral and LN), they were not very abundant but were frequently ingested. In terms of carbon units, they were more important as an additional food source than dinoflagellates (Fig. 3b). During ENSO-neutral conditions in early 2007, A. tonsa ingested 100% of the dominating diatom Skeletonema costatum at the Pier, but during LN only 23% was ingested at station 2 (Table 3). Total ingestion had a synchronous interannual pattern at stations 2, 5 and at the Pier, with higher total ingestion rates during 2007, when diatoms dominated.

Food selection

A tonsa were not ingested 47% of the total phytoplankton taxa that occurred during the experiments, including 44% of diatoms, 54% of dinoflagellates and the heterotrophic flagellate Leucocryptos marina. The dinoflagellates Ceratium tripos, Protoperidinium excentricum and the diatoms Asterionellopsis glacialis, Scripsiella trochoidea, Dytilum brightwelli were present at least 5 times during the experiments and were always rejected (Table 4). Among the rejected taxa, the diatoms Asterionellopsis glacialis (up to 1590 cells mL⁻¹) and Rhizosolenia setigera (up to 439 cells mL⁻¹) were the most abundant species (Table 4). The red tide species Akashiwo sanguineum, the most abundant dinoflagellate, was consistently rejected in 5 experiments, and only ingested at negligible rates (0.7 cells copepod⁻¹ h⁻¹) with positive selectivity (ε = 0.7) during EN (Table 3). Prorocentrum micans, another red tide species, was ingested only in one out of six experiments where it occurred, and then with low selectivity (ε = 0.3) (Table 3).
Phytoplankton cell size covered a wide range (Fig. 7). Classification of the phytoplankton taxa into size classes and calculation of the Portion Ingested (PI, i.e. percentage of taxa that suffered ingestion in relation to all taxa in a given size class) showed that in the size range of 10 to 120 μm (length along major axis) there is no clear pattern of decline or increase of PI with size. However, there is a clear decrease for cells larger than 120 μm, indicating that *A. tonsa* can not effectively handle larger cells (Fig. 7). Therefore, cells larger than 120 μm were not considered in the subsequent analyses of the size-selectivity relationship (Fig. 7).

When considering only taxa that actually were ingested ($\varepsilon > -1$, cell size $< 120 \mu m$), and all taxonomic groups and experiments, we found a significantly positive correlation between selectivity and all size-related variables (length, ESD, volume, and carbon content), indicating a preference for larger cells (Fig. 7). Furthermore, we found significant differences in $\varepsilon$ between ENSO phases, with higher selectivity during EN than during LN, and between taxonomic groups, with higher selectivity for dinoflagellates than for diatoms (Fig. 8).

Selectivity patterns were related to changes in food concentration when only taxa ingested ($\varepsilon > -1$) were considered (Fig. 6). The selectivity for the chain-forming diatoms *Skeletonema costatum* and *Thalassionema nitzschioides* changed between different ENSO phases, following the trend in relative importance. Both species were negatively selected or totally rejected during 2006, but were positively selected during 2007, ($\varepsilon = 0.3$ and 0.2 and $\varepsilon = 0.3$ and 0.6 respectively), when their abundance increased. *Pleurosigma sp.* (a pennate diatom) occurred in six experiments and was
ingested 4 times, including the high food density during LN, with neutral ($\varepsilon = 0.2$) to positive ($\varepsilon = 0.6$) selectivity (Table 3). Dinoflagellates were an important part of the diet of A. tonsa mostly during 2006, when this group was more abundant. Ceratium furca occurred in eight experiments and was selected only during ENSO-neutral conditions in early 2006 at all stations. Nanoflagellates occurred in all experiments and were positively selected 6 times ($\varepsilon = 0.2$ to $\varepsilon = 0.63$) (Table 3). The remaining non–ingested taxa were found at low abundance, mostly below 10 cells mL$^{-1}$. The data suggest strongly that A. tonsa is highly selective during EN, when food is less abundant, and when dinoflagellates dominated, and closer to non-selective feeding when food is highly abundant, i.e. during LN.

**Egg production rate**

Egg production of A tonsa varied remarkably between experiments and did not show any consistent spatial, seasonal, or interannual pattern. Egg production rates during our experiments varied between 0.6 and 9.2 eggs female$^{-1}$ day$^{-1}$ (Fig. 9), and were lowest during LN and highest during EN at the Pier, opposite to the abundance of A. tonsa. Egg production rates did not show significant correlations with total food concentration (phytoplankton biomass or abundance) nor total ingestion rates. The only significant correlation was found with dinoflagellate ingestion, where we found a negative correlation with egg production rates (Fig. 10).

Since ingestion rates increased drastically from 2006 to 2007, the gross efficiency dropped from 30 to 16 % during 2006 to only 2 to 6% during 2007. Egg viability varied over a wide range from 0.4 % to 100%, and was lowest during LN at station 2.
and highest during ENSO-neutral conditions in early 2007 at the Pier, without any clear seasonal or interannual pattern (Table 1).

DISCUSSION

Oceanographic conditions and phytoplankton dynamics

It is well known that ENSO has a strong impact on primary production and plankton community composition in Eastern Pacific upwelling ecosystems (Fiedler et al., 1992; Escribano, 2004; Pennington et al., 2006). Primary production and phytoplankton abundance has been reported to drastically decrease in the East Pacific as a consequence of strong EN events (Chavez et al., 2003, Escribano et al., 2004, Iriarte et al., 2000). Increased SST and sea-level anomalies are a clear indication of EN, as Cold Coastal Water (CCW) is replaced by Subtropical Surface Waters (SSW, Moron, 2002). SST and sea-level data from satellite observations showed three different ENSO phases during the 2006 and 2007, supporting the findings of the present study (www.cpc.ncep.noaa.gov/ products/expert_assessment/ ENSO_DD_ archive .shtml). Although according to the MEI index the 2006 EN event was only moderate, the consequences of this event for the plankton were drastic: primary production and PPC decreased at offshore and nearshore stations and inside Independencia Bay, and nanoplanckton became the most abundant phytoplankton group at stations 2 and 5 and on the Pier in Callao. Similarly, Iriarte et al., (2000) observed changes in phytoplankton size distribution and a shift from chain-forming diatoms to nanoplanckton in coastal and oceanic areas off Antofagasta, northern Chile.
In May and August 2007, low surface temperatures were (< 15.6) at all stations and strengthened winds across the central Equatorial Pacific (www.cpc.ncep.noaa.gov/products/expert_assessment/ENSO_DD_archive.shtml) indicate a strong LN event. The increased winds may have triggered high primary productivity rates leading to a large increase of phytoplankton biomass, which consisted mainly of diatoms inshore and dinoflagellates offshore. A similar phytoplankton bloom has been reported during LN conditions in late 1998 off northern Chile and in the eastern tropical Pacific, which was related to increased wind strength, upwelling and an unusually shallow thermocline (Ryan et al., 2002; Escribano et al., 2004; Pennington, 2006).

Despite similar hydrographic conditions, the composition of the phytoplankton community changed drastically between ENSO-neutral phases in 2006 and 2007. While during ENSO-neutral conditions in 2006 dinoflagellates dominated in biomass and in the diet of A. tonsa, diatoms were clearly dominating in abundance, biomass, and contribution to A. tonsa diet during ENSO-neutral conditions in early 2007. It is not yet clear, which environmental clues are responsible for the shift from dinoflagellate to diatom-dominated regimes. One possible explanation is that the active upwelling and intermediate conditions in between the extremes winter-summer and EN-LN were more favourable for phytoplankton productivity and the formation of diatom blooms nearshore in early 2007 than in early 2006. It could be possible in 2007 that nutrients were not advected offshore, hence the blooms started nearshore (Echevin et al., 2004; Echevin et al., 2008). During ENSO-neutral conditions in early 2006, the primary production values were in the range for the area (Zuta and Guillen, 1970), however chlorophyll $a$ was in the low range (0.14 to 1.61, Echevin et al.,
Our observations show clearly that oceanographic conditions at the Central Peruvian coast can be highly variable and confirm earlier studies, that the ENSO state strongly affects phytoplankton composition and the magnitude of primary production in the ecosystem (Iriarte et al., 2000; Escribano et al., 2004; Pennington et al., 2006).

**Acartia tonsa abundance and grazing**

ENSO also affected the composition of the zooplankton community and the abundance of *A. tonsa*. During ENSO-neutral conditions in early 2006, the zooplankton community reflected the typical situation for neritic waters of the HCS characterized by low to moderate diversity; *A. tonsa* was the dominant herbivorous copepod species in the upper 10 m accompanied by *Paracalanus parvus* and *Centropages brachiatu*s (Smith, 1978; Santander, 1981; Hidalgo and Escribano, 2001; Criales-Hernandez et al., 2008). During EN, *A. tonsa* decreased drastically off Central Peru and was replaced by other small copepods such as *Paracalanus parvus*, *Oithona spp.* and *Corycaeus sp.* (Criales-Hernandez et al., 2008). A similar reduction of zooplankton biomass off Peru was also observed during EN 1982-83 by Barber and Chavez (1983) and Carrasco and Santander (1987). Phytoplankton composition and feeding behaviour may explain why *A. tonsa* virtually disappeared during EN and during LN at station 5, when small cells dominated. Under these nanoplanckton-dominated conditions, *A. tonsa* may not be able to feed efficiently, as evidenced by the increase in electivity with cell size observed in our study. Similarly, trophic processes may explain the persistence of the *A. tonsa* population in Independencia Bay during EN, where diatoms persisted through this EN event, probably due to the resuspension of nutrients in this shallow bay.
In our study, *A. tonsa* did not reduce its clearance rate with increasing food abundance. Ingestion rate was directly related to food concentration following a log-linear function without any evidence of asymptotic satiation. Similar relationships were found in other studies performed under natural food conditions and higher food levels (Turner and Tester, 1989). Comparison of ingestion rates of *A. tonsa* during different ENSO phases shows that it had low ingestion rates when phytoplankton abundance was low, such as during EN, and displayed ingestion rates that were by several orders of magnitude higher when phytoplankton concentration increased during the transition from EN to LN. Clearly, this species is not adapted to environments with low food concentrations as often found offshore, but is extremely successful in nearshore eutrophic environments such as estuaries and coastal upwelling areas with high chlorophyll *a* concentrations (Paffenhöfer and Stearn, 1988; Escribano and Hidalgo, 2000).

In Northern Chile, Hidalgo and Escribano (2001) did not find such a clear negative impact of EN on the zooplankton community. Instead, the dominant copepod *Calanus chilensis* increased in abundance. Furthermore, Hidalgo and Escribano (2001) did not find differences in phytoplankton availability between EN and neutral periods, and suggested that these copepods always found enough food. Time series data from 1991 to 1998 showed little changes in the population size of *Calanus chilensis* during EN and LN, suggesting that other factors than temperature may regulate interannual differences in population size in this region (Escribano and Hidalgo, 2000).
Diet composition and food selection

Zooplankton can exhibit a different functional response for each resource when that resource is the only nutrition available (Gentleman et al., 2003). According to studies with *A. tonsa* and other calanoids, several feeding strategies have evolved to optimize the nutritional gain obtained from the food environment (Kleppel, 1993). Changing from diatoms to dinoflagellates is an example of how copepods can respond to variations in food composition.

The diet composition of *A. tonsa* off Peru followed closely the composition of the phytoplankton community, as found in earlier studies (Ambler, 1986; Gifford and Dagg, 1988; Kiørboe et al., 1996; Gentleman et al., 2003). Accordingly, during ENSO-neutral conditions in early 2006, *A. tonsa* fed mainly on dinoflagellates, thereafter, during EN, it consumed dinoflagellates and nanoflagellates, however in very low amounts. During 2007, when diatoms dominated the system, *A. tonsa* fed intensively on diatoms and to a minor degree on nanoflagellates and dinoflagellates. Our finding that diatoms were more important for *A. tonsa* during LN, is in line with the concept that upwelling systems could be switching from microbial food webs during EN phases and more linear, diatom-based food webs during ENSO-neutral and LN phases (Gonzales et al., 2000; Escribano et al., 2004; Cuevas and Morales, 2006; Bötjer and Morales, 2007). In the present study, the shift from a dinoflagellate- to a diatom-dominated regime occurred in February 2007, several months before the LN event became tangible in the physical data. The possible anticipation of the 2007 LN event by plankton communities off Central Peru may hint at a response of plankton...
populations to subtle climatic signals, which could serve as a future indicator of
cclimate change (Taylor et al., 2002; Ayón et al., 2008)

*A. tonsa* shows a size-selective feeding behaviour for phytoplankton between 0.5 μm
to 120μm cell size, but does not consume effectively larger cells. Pagano et al.,
(2003) found that largest sizes ingested by *A. tonsa* are 72.1μm. Size selection is a
behaviour that offers a good compromise between reducing handling times and
optimizing food quality and quantity (Frost, 1972; Meyer-Harms et al., 1999; Meyer
et al., 2002). During upwelling periods, phytoplankton is generally dominated by
large cells (> 20 μm), but also smaller cells (< 20 μm) can be a significant part of the
system during both upwelling and relaxation periods (Peterson, 1988; Slaughter et al.,
2006; Gonzalez et al., 2007; Böttjer and Moreno, 2007). In the present study we
found ingestion of nanoflagellates but low electivity on this group. Ingestion of small
phytoplankton provides the food source for *A. tonsa* when food is scarce. Low
selectivity of small phytoplankton may be a strategy to overcome the potential
deficiency of exclusive diatom diets (Kleppel et al., 1991). Cowles (1979)
demonstrated that copepods off Peru fed size-selectively when food is abundant, and
non-selectively when food is scarce. In contrast, we found that *A.tonsa* was size-
selective in both cases. Previous studies have shown that selection of specific modal
size ranges within the spectrum of available natural particles occurs in *A. tonsa*
(Pagano et al., 2003; Libourel and Roman, 1987).

*A. tonsa* displayed a strong negative selection towards certain taxa. From a total of
139 phytoplankton taxa, 66 were not ingested during any experiment, including the
red-tide forming species of *Akashivo sanguineum* and *Prorocentrum micans*. These species may be of low nutritional quality for *A. tonsa*. Accordingly, Dam and Colin (2005) found that *Prorocentrum minimum* is nutritionally insufficient for *A. tonsa*. In their experiments, *A. tonsa* ingested *P. minimum* cells, but egg production was relatively low. Studies by Libourel and Roman (1987), and Roman *et al.*, (2006) with *A. tonsa* found similar results with other dinoflagellates.

It is noteworthy that *A. tonsa* consistently rejected the bloom-forming phytoplankton species *Asterionellopsis glacialis* and *Rhizosolenia setigera*, which formed blooms during ENSO-neutral conditions in early 2006 and early 2007, respectively. As these species have a major axis length of 105μm and 196μm, respectively, *A. tonsa* is probably unable to feed on these taxa. In coastal upwelling areas, these blooms are common during the whole year (Smith, 1978; Gárate and Martínez, 1997; Escribano and Castro, 2004; Martínez-Lopez *et al.*, 2008). We hypothesize that the rejection for specific taxa may be an important factor in the initial formation of phytoplankton blooms. However, more studies are necessary to explain the role of zooplankton in the formation of red tides and other phytoplankton blooms.

**Egg production**

Egg production rates found in this study are low compared to other performed with this species (Dagg, 1977; Kiørboe *et al.*, 1985, Ambler, 1986). On the other hand, they are consistent with results from Kleppel and Hazzard (2000) obtained for *A. tonsa* in Florida Bay. We expected to see differences in egg production rates and food abundance during the study period due to different ingestion rates and feeding selectivity. We did not find any clear relationship between egg production rates and
Results

gross environmental parameters such as total phytoplankton abundance. Based on simultaneously performed egg production and in situ grazing experiments, our results indicate a possible negative relationship between the ingestion of dinoflagellates and *A. tonsa* egg production. However, only few egg production experiments were performed simultaneously with grazing experiments. The possible negative influence of dinoflagellate ingestion on egg production could be attributed to food quality and toxins which may affect egg production rates. Lincoln *et al.*, (2001) found that some nutrients in toxic or non-toxic phytoplankton could be producing low egg production rates.

While the ingestion rate of *A. tonsa* depended on food concentration, egg production was food independent through ENSO phases, egg production did not show a clear relationship to ingestion rates. In addition, we found that gross efficiency was uncoupled from egg production. Similar results were found by Kleppel, (1992), Kleppel and Hazzard (2000). Possibly, the increase in ingestion rates (mainly of diatoms) during LN was not converted to enhanced secondary productivity and thus not passed to upper trophic levels.

The gross efficiency range of egg production by *A. tonsa* for the entire study was between 0.04 to 30 %. These values are low to the gross efficiency of 43% given by Kiørboe *et al* (1985) for this species under near optimal laboratory conditions. Still, the processes leading to an uncoupling of feeding and egg production are to be investigated, and may be related to the biochemical composition of the food or to environmental stressors, such as the shallow oxygen minimum zone.
Conclusions

The extremely high variability of the oceanographic conditions off Central Peru is a factor that strongly affects on primary production and phytoplankton composition. These changes greatly modify the availability of food for the grazers in the area and could be controlling the abundance of *A. tonsa*.

The trophic impact of *A. tonsa* on the primary production during this study was also widely variable. The percentage of the primary production daily consumed by *A. tonsa* was low during 2006 (7% approximately) and increased in 2007 up to 47% and 89% respectively. This large difference was caused by the asynchronous variability of primary production, *A. tonsa* abundance and ingestion rates. High trophic impact values during LN show that this species is well adapted to highly productive (diatom-rich) environments, where it may reach huge densities, thus causing an important impact on primary production and the phytoplankton composition.

*Acartia tonsa* plays an important role in the pelagic food web off Peru, especially nearshore and during non-EN periods. However, the population dynamics and ecology of copepods of the highly productive HCS are still widely unknown. More efforts are necessary to better understand the relationship between phytoplankton blooms, primary production and zooplankton dynamics in upwelling systems.
ACKNOWLEDGEMENTS

This paper forms part of the Ph.D. thesis of the first author at Bremen University. Financial support was granted in the frame of the EU-project CENSOR (Climate Variability and El Niño Southern Oscillation: Implications for Natural Resources and Management, contract 511071) and is CENSOR publication no. 153. The first author was partially supported by short-term scholarships from the German Academic Exchange Service (Deutscher Akademischer Austausch Dienst, DAAD). The authors are deeply indebted to crews of the R/V Olaya, to the participants of the cruises who helped in sample collection and to the Area de Evaluacion Secundaria Laboratory and Area de Producción Primaria of IMARPE for logistic support; help in egg production experiments, and in counting and identifying phytoplankton, and unconditional friendship in Lima and AWI. Thanks to Gordon Swartzman and Aldo Pacheco for improving the original text with important comments and suggestions on earlier versions of the manuscript.

References

* All citation included in this manuscript are compiled in the final list of references.
List of figure legends and tables headers

Table 1. Hydrographic conditions, primary production at 5m depth, egg production rates (.egg female\(^{-1}\) day\(^{-1}\)), viability of eggs (Percentage of Naupliii as egg fecundity per female) and Gross Efficiency (Percentage of carbon produced as eggs to that ingested as food) by *Acartia tonsa* in 2006 and 2007. “Ind”: Independencia Bay, St2 and St5: stations 2 and 5 on the continental shelf off Callao, “Pier”: at the Pier of the Instituto del Mar de Perú (IMARPE) in Callao.

Table 2. *Acartia tonsa*. Ingestion rates in relation to food concentration of the main phytoplankton groups in terms of density (cell mL\(^{-1}\)) and biomass (μgC L\(^{-1}\)) during experiments conducted in 2006 and 2007.

Table 3. Taxonomic composition (cell ml\(^{-1}\)) of the most abundant and frequent phytoplankton taxa and *Acartia tonsa* ingestion rates and electivity (\(\varepsilon\)) during experiments. a) Diatoms b)Dinoflagellates, silicoflagellates and nanoflagellates.

Table 4. Phytoplankton density (cell mL\(^{-1}\)) and cell size (major axis legth, μm) of the rejected taxa by *Acartia tonsa* during the experiments off central Peru.

Fig. 1. Map of the study area indicating the stations where experiments were conducted off Callao and inside Independencia Bay.
Results

Fig. 2. Primary production at 5 m depth (a) and phytoplankton concentration by groups (b) at experimental stations off Callao and Independencia Bay in 2006 and 2007. The shaded area indicates experiments performed during El Niño and La Niña. *Stars* indicate no available data.

Fig. 3. Changes in phytoplankton biomass (μgC L⁻¹) and composition (a) and *A. tonsa* ingestion rates (μgC copepod⁻¹ day⁻¹) (b) during the experiments performed off central Peru. The shaded area indicates experiments performed during El Niño and La Niña. *Stars* indicate no data.

Fig. 4. Specific phytoplankton concentration for all sizes found during the experiments. Squares represent species that occurred during El Niño in 2006, filled black squares represent species that occurred during the La Niña in 2007, and grey filled triangles represent species that occurred during ENSO-Neutral 2006, 2007. Each data point represents average size (major axis length, μm) and average concentration for one phytoplankton species during one experiment.

Fig. 5. Abundance of *Acartia tonsa* (ind m⁻³) at experimental stations off central Peru from 2006 to 2007, obtained with 300μm-mesh plankton nets. These data were obtained from vertical multinet (Hydro-Bios, Kiel, Germany) hauls between 10m depth to surface.
Results

at stations 2 and 5 off Callao, and at surface with a WP2 net at Independencia Bay. The shaded area indicates experiments performed during El Niño and La Niña conditions.

Fig. 6. *Acartia tonsa*. Ingestion rate (cells copep.\(^{-1}\) day\(^{-1}\)) (a) and Selectivity (ε) (b) in relation to phytoplankton cell density throughout the experiments performed during 2006 to 2007. Each data point represents one phytoplankton species during one experiment.

Fig. 7. Relationship between Selectivity (ε) of *Acartia tonsa* and cell size (major axis length, μm). Selectivity was calculated for each phytoplankton species and experiment, where a value of zero means no selection, -1 means no ingestion, and positive values mean positive preference for a given taxon. Each data point in the central graph indicates one value for one taxon during one single experiment. The upper graph gives the percentage of ingested taxa (Selectivity > -1) in each size class.

Fig. 8. Relationship between Selectivity (ε) of *Acartia tonsa* off central Peru, Size along major axis, Taxonomic group, and ENSO phases. Each data point in the graphs on the left side indicates one value for one taxon during one single experiment. Selectivity was calculated for each phytoplankton species and experiment, where a value of zero means no selection, -1 means no ingestion, and positive values mean positive preference for a given taxon. Lines in the left graphs indicate locally weighted scatterplot smoothing
Results

(LOWESS) for each data set, using span = 0.5. Data with Selectivity = -1 or Size > 120μm were excluded from the data set prior plots and analyses.

Fig. 9. *Acartia tonsa* egg production rates during experiments conducted in 2006 and 2007. The shaded area indicates experiments performed during El Niño and La Niña conditions. *Stars* indicate no data.

Fig. 10. *Acartia tonsa* egg production rates as a function of density of diatoms (black squares) and dinoflagellates (white squares) during experiments throughout 2006 and 2007.
### Results

**Table 1**

<table>
<thead>
<tr>
<th>Date/ Station</th>
<th>ENSO Phase</th>
<th>SST (°C)</th>
<th>Oxygen at 5m depth (mL L⁻¹)</th>
<th>Salinity</th>
<th>Chl-a (µg L⁻¹)</th>
<th>Primary Production at 5m depth (mg m⁻³ d⁻¹)</th>
<th>Egg Production rate (µgC female⁻¹ d⁻¹)</th>
<th>Egg viability (%)</th>
<th>Gross Efficiency (%)</th>
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<td>16.6</td>
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**Table 2.**

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<th>Abr-06 Ind</th>
<th>Jul-06 Ind</th>
<th>Aug-06 Pier</th>
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<th>May-07 Pier</th>
<th>Aug-07 St2</th>
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<td>87789.2</td>
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<td>170.6</td>
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## Results

Table 3.

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<th>Abr-06 St2</th>
<th>Abr-06 St5</th>
<th>Abr-06 Ind</th>
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<th>Aug-06 Pier</th>
<th>Feb-07 Pier</th>
<th>Abr-07 Sts5</th>
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<td><strong>Guinardia delicatula</strong> 89.7 µgC</td>
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### Results

**b) Dinoflagellates and other taxa**

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<th>Taxa</th>
<th>Avg Carbon content (pgC)</th>
<th>Avg Size (μm)</th>
<th>Abr-06 St2</th>
<th>Abr-06 St5</th>
<th>Abr-06 Ind</th>
<th>Jul-06 Ind</th>
<th>Aug-06 Pier</th>
<th>Feb-07 Pier</th>
<th>Abr-07 St5</th>
<th>May-07 Pier</th>
<th>Food concentration (cells mL⁻¹)</th>
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<tr>
<td>Akashiwo sanguinolentum</td>
<td>621.7 pgC</td>
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<td>Diplodecta asymmetrica</td>
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<td>Moruloides gymnastica</td>
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</table>

**Table 4**
Fig. 1
Results

Fig. 2
Results

a) Phytoplankton biomass (μgC L^{-1})

- Neutral
- EN
- Neutral
- LN

b) Ingestion (μgC copep{d^{-1}})

- Neutral
- EN
- Neutral
- LN

Station Date: 2, 5, Apr, Ind, Jul, Aug, Pier, Feb, 5 Apr, Pier, May, Ind, 2 Aug

Year: 2006, 2007
Fig. 3

Phytoplankton density (cells mL⁻¹)

Size (μm)

EN  LN  Neutral

Fig. 4.
Results

Fig. 5
Results

Fig. 6

Ingestion (cells copep.⁻¹ h⁻¹)

Electivity (ε)

Phytoplankton density (cells mL⁻¹)
Fig. 7
Fig. 8.
Results

**Fig. 9.**

**Fig. 10.**
Chapter 6. Synoptic Discussion

The results of this research show that the zooplankton community off Central Peru is strongly influenced by environmental conditions. The most visible changes were associated with intrannual (seasonal) and interannual (ENSO) variability. ENSO modulates the large scale circulation patterns and hence influences the productivity of the upwelling ecosystem. A fundamental physical factor that influences zooplankton distribution is the spatial variability of the depth of the Oxygen Minimum Zone (OMZ). Its oscillations between 20m and 50m depth determine which group of zooplankton is either confined or able to disperse in the upper oxygenated layer during different times of the year. However, some taxa (e.g. Eucalanus inermis) are capable of vertical migration into the OMZ, which serves as refuge against predation, during ontogenic development and adult stages (e.g. Acartia tonsa). Productivity was highest in the nearshore waters, where zooplankton aggregate around phytoplanktonic blooms. Drastic changes in phytoplankton composition caused a decline in the abundance of the dominant copepod A. tonsa during the 2006 EN event. The following discussion focuses on zooplankton community structure, its vertical distribution, grazing and egg production of the dominant species (A. tonsa) during different ENSO phases, under the impact of changes in rates of primary production and environmental conditions.
6.1 Review and knowledge gaps

The extensive review of published and grey literature provided perspectives for the future and identified areas where more research efforts is needed. Considerable effort has been made to understand the relationship between climate, environmental factors, and productivity. However, more data on the dynamics of the system and integrative information is still needed. The results of the review showed that the relation between oceanographic processes and the dynamics of key species is still not fully understood. There is a large gap in the knowledge of the life history and ecology of many zooplankton species and their relation to other components of the system. Knowledge of dispersal and retention mechanisms of fish and invertebrate larvae in these highly advective areas was shown to be very limited. Studies of vertical distribution and zooplankton grazing in Peruvian waters are still at an incipient stage; however the results of earlier research provides the basis for understanding some adaptations of zooplankton to the spatial variability of the OMZ.

6.2 Oceanographic conditions and phytoplankton dynamics

General oceanographic conditions and phytoplankton dynamics off Callao have the characteristics of a coastal upwelling. Among these characteristics are the predominance of predominantly cold upwelled coastal waters, a strong and shallow thermocline and oxycline, and a high Cholorophyll-\(a\) concentration and primary productivity, mainly concentrated in the nearshore. Temperature values in this study showed a wide range, due the interaction and mixing of distinct water masses during the year (Zuta and Guillen, 1970; Graco et al., 2007; Echevin et al., 2008). These
patterns have been observed in other locations along the Humboldt Current System (HCS), e.g. off Paita (northern Peru, Aronés et al., 2009), off Pisco (Central Peru, Tarazona et al., 1989), and off Bahia de Mejillones (northern Chile, Escribano et al., 2002).

Seasonal variation in hydrography is associated with changes in the intensity of trade winds, which strengthens in the austral winter and diminishes in summer (Bakun and Nelson, 1981). Trapped coastal waves from the equator can propagate warm water masses along the coast as far south as 40°S during summer and EN events (Ulloa et al., 2001; Bonhomme et al., 2007; Echevin et al., 2008). The hydrographic conditions found in this study reflect this seasonality. SST was higher and the depth of the 15°C isotherm became much deeper during summer and autumn (February to May). In winter and spring the 15 °C isotherm rose and SST fell sharply in the upper layers. The depth of the oxygenated zone is also highly variable between seasons. It is often extremely shallow (< 20m) during winter and becomes deeper (> 50m) towards summer (Chapter 5.2, 5.3).

Upwelling in the HCS can be greatly modified by intrannual and interannual variability in the wind field and the distribution of water masses, mainly due to ENSO (Arntz and Fahrbach, 1996; Morón, 2000). The observed variations in temperature and depth of the OMZ clearly showed the occurrence of three different ENSO phases. ENSO-neutral conditions prevailed detected from February 2005 to April 2006, and also from February to May 2007, while moderate EN conditions were recorded from June 2006 to January 2007. Strong La Niña event occurred from were evident from February to December 2007. Satellite data of sea surface temperature (SST) and sea
level corroborate these findings (www.cpc.ncep.noaa.gov/products/expert_assessment/ENSO_DD_archive.shtml). Data from our own monitoring stations revealed that oxygenation increased during EN conditions in comparison with LN conditions (Chapters 5.2 and 5.3). The increased depth of the OMZ during EN was caused by the intrusion of SSW towards the coast. During LN, the upper limit of the OMZ rose (<20 m) due to the poor oxygen content, and there was high rates of biological activity induced by active upwelling (Bohle-Carbonell, 1989; Sanchez and Delgado, 1996; Graco et al., 2001; Graco et al., 2007; Gutierrez et al., 2008).

The variability in hydrographic conditions between different ENSO phases caused drastic changes in phytoplankton community structure and abundance. Neutral and La Niña conditions were characterized by high phytoplankton abundance, and the dominance of diatoms, especially nearshore. By contrast, during EN conditions, phytoplankton biomass decreased and the community was dominated by nanoflagellates and dinoflagellates near and offshore (Chapter 5.4). Phytoplankton during Neutral conditions is dominated by diatoms due to the high availability of macronutrients such as nitrate, phosphate, and silicate in surface waters (Rojas de Mendiola, 1981). Extensive phytoplankton blooms occur, especially nearshore stations, while offshore waters tend to be dominated mostly by nanoflagellates and dinoflagellates (Gonzales, et al., 2000, Chapter 5.4). These changes are associated with regimes characterized by reduced availability of iron, high nitrate concentrations and lower than expected chlorophyll (Brunald et al., 2006). Thus, the seasonal patterns of phytoplankton biomass and potential productivity at different locations are governed by the circulation of the water masses (Car and kearns, 2003). However, is still not clear yet which environmental drivers are responsible for the shift from
Synoptic discussion

dinoflagellate to diatom-dominated regimes (see discussion in Chapter 5.4). The decrease of diatoms during EN could be linked to the intrusion of Subtropical Surface Waters (SSW), inhibiting the advection of nutrients from upwelled waters (Echevin et al., 2004; Echevin et al., 2008). Overall, the major peak of phytoplankton production (i.e. diatoms blooms) was observed nearshore, specially during the transition from EN to LN (Chapter 5.4).

6.3 Horizontal distribution of zooplankton

The planktonic ecosystem of the HCS shows marked seasonal and interannual changes in the distribution of water masses and zooplankton species. The neritic and coastal zooplankton is dominated by common upwelling species that are typical for Cold Coastal Waters (CCW). Species distribution is influenced by processes of advection, Ekman transport and the intensity of upwelling (Escribano and Morales, 2004; Thiel et al., 2007). At the continental shelf off Callao, many species were distributed along the nearshore-offshore gradient (Chapter 5.2, 5.3). The nearshore community was composed mainly of *Acartia tonsa*, *Centropages brachiautus*, *Paracalanus parvus*, and meroplanktonic invertebrate larvae. Euphausiids, *Pleuroncodes monodon* zoeae and large copepods such as *Eucalanus inermis* were principal components of the offshore community (Chapter 5.2). Similar results were obtained from another upwelling area off Peru between 14°S to 16°S (Santander, 1981).

The temporal variation of zooplankton abundance occurs on daily, intrannual (seasonal) and interannually (ENSO) timescales. Our data confirmed the strong effect
of changes in the intensity of upwelling and the impact of the intrusion of warm waters masses during the 2006 EN on community structure and the abundance of the dominant species. For example, the dominant copepod *Acartia tonsa* decreased drastically in abundance during the 2006 EN and was replaced by other small copepods such as *Paracalanus parvus*, *Oithona spp.* and *Corycaeus sp.* (Chapter 5.2, 5.3, 5.4). In addition, zooplankton species of subtartic water masses are occasionally recorded, mainly during the 2007 La Niña event (Escribano, 2004). Zooplankton have been shown to be a potential indicator of climate change and could be used in long-term monitoring in upwelling areas (Hays, 2005; Chapter 5.1).

6.4 Vertical distribution of zooplankton

The present study revealed several adaptations of zooplankton to a shallow oxygen minimum layer (Rogers, 2000). In our study, the bulk of the zooplankton was always in the upper, well-oxygenated upper layer 20 m layer (Chapter 5.3). Specific vertical distribution and diel vertical migration patterns were detected for selected taxa, and were related to hydrographic parameters and life history strategies (Chapter 5.3). A conceptual models was developed (Fig. 6.1) summarizing the five main vertical distribution patterns found in the coastal upwelling off Callao. One of the main results from our data was the high variability of OMZ depth. The present study showed that this plays a significant role in the vertical distribution of zooplankton.. This calls into question the view of Thiel et al. (2007) that the OMZ cannot be a factor constraining the vertical distribution of zooplankton, because several species may use OMZ as their habitat, either, temporarily or permanently. The results of the present study showed that the OMZ is a natural border in upwelling areas. Although
the bulk of zooplankton is found in the oxygenated layer, some specific species have developed strategies that enable them to live in the OMZ. These strategies could have a number of advantages: i) in helping to maintain the species population in the upwelled waters, i.e. through diel vertical migration (Peterson et al., 1979), ii) by enhancing larval dispersal or larval survival, as in the cases of *Magelona sp.* and brachyuran zoeae (Chapter 6.2), iii) by enabling species to use the upper boundary of the OMZ as a refuge against predators that are confined to the oxygenated layers (Chapter 5.3).

**Figure 6.1** Schematic diagram showing five vertical distribution and migration patterns in relation to the oxygen minimum layer observed off central Peru in 2006, from left to right: 1. Always above (e.g. *Oikopleura* sp.), 2. Ontogenetic vertical migration (*Acartia tonsa* adults, nauplii, and copepodites), 3. Always below (e.g. *Eucalanus inermis*), 4. Daily Vertical Migration (DVM, e.g. *Paracanus parvus* at station 5), and 5.) Inverse Daily Vertical Migration (IDVM, larvae of the polychaete *Magelona* sp.). The shaded area indicates the deep hypoxic layers.
6.5 *A. tonsa* feeding strategy

Zooplankton can exhibit different functional responses for each resource when a given resource is the only food available (Gentleman et al., 2003) and the community structure of the phytoplankton determines the food spectrum (Escribano et al., 2004). In this study the dominant copepod *Acartia tonsa* was used to evaluate the trophodynamic link between phytoplankton and zooplankton in this ecosystem. The composition of *A. tonsa*’s diet closed mirrored the composition of the phytoplankton off Peru (Chapter 5.4). These results were similar to those of earlier studies (Ambler, 1986; Gifford and Dagg, 1988; Kiørboe et al., 1996; Gentleman et al., 2003). During ENSO-neutral conditions in early 2006, *A. tonsa* fed mainly on dinoflagellates. During EN, it consumed dinoflagellates and nanoflagellates, however in very low amounts. During 2007, when diatoms dominated the system, *A. tonsa* fed intensively on diatoms and to a minor degree on nanoflagellates and dinoflagellates (Figure 6.2, Chapter 5.4). *A. tonsa* shows a size-selective feeding behaviour for phytoplankton between 0.5 μm and 120μm cell size, with strong positive electivity for larger cells within this size range, but does not effectively consume cells larger than 120μm. In addition, *A. tonsa* showed strong negative preference selection towards certain taxa. These taxa are red-tide forming species of *Akashaio sanguineum* and *Prorocentrum micans* and bloom-forming phytoplankton species *Asterionellopsis glacialis* and *Rhizosolenia setigera*. These results revealed that *A. tonsa* could be playing a role in controlling the abundance of the dominant autotrophic components, chain-forming diatoms, during Normal and La Niña conditions and of red-tides, during El Niño conditions (Chapter 5.4).
Large differences in primary production, *A. tonsa* abundance and ingestion rates produced an asynchronous variability in daily consumption rates, that were extremely low during 2006 (only approx. 2% of total phytoplankton population growth, mainly due to low *A. tonsa* abundances) and increased in 2007 (to between 4% to 6.7% of total phytoplankton population growth). High trophic impact values during LN show that this species is well adapted to highly productive (diatom-rich) environments, where it may reach huge densities, thus causing an important impact on primary production and phytoplankton composition (Chapter 5.4). Such variability may have important consequences for the trophic structure in the coastal upwelling system (Escribano, et al., 2004; Vargas and Gonzales, 2004).

**Figure 6.2** Conceptual model of the trophic interactions between *Acartia tonsa* adults and the dominant phytoplankton taxa in the coastal upwelling area off central Peru during moderate El Niño (August 2006) and strong La Niña (August 2007) conditions. Mean standing stocks (μg C l⁻¹) are shown for each taxonomic group. Dinofl.: Dinoflagellates; Nanofl.: Nanoflagellates. Numbers on arrows represent mean ingestion rates (μg C ind⁻¹ d⁻¹). Input data were derived by using data from the present study (Chapter 5.4).
6.6 Outlook

This thesis revealed new aspects in the food web dynamics of the coastal upwelling off central Peru during different ENSO phases. New knowledge was generated about the dynamics of zooplankton in this part of the HCS and its relation to phytoplankton was gained. Yet, many new questions emerged, for example regarding the physiological processes leading to the low trophic efficiency of *A. tonsa* and possibly deleterious effects of the ingestion of certain algal species that may have caused low egg production rates. In addition, many other aspects of the zooplankton ecology in Peruvian waters need further investigation, such as the role of euphausiids, carnivorous zooplankton, microzooplankton, and processes related to the microbial loop.

Taxonomy of zooplankton in this area is still an area for work. It will be necessary to combine morphological and genetic studies and to compare species with synonyms in other parts of the world ocean. The horizontal, vertical, and temporal distribution of *Acartia tonsa* and its feeding strategy are now well identified for this system. Its egg production was found to be at the low edge of the range for this species, in comparison to other areas. The most urgent priority is to know more about the autecology of the most important species in these highly productive areas. Little to nothing is known about the development stages and larval ecology of holo- and meroplankton. Basic knowledge of their life cycles is lacking, for example about generation times and growth rates, reproductive biology, starvation potential, and life cycle strategies such as dormancy and resting eggs.
The present study reveals new aspects of the food web dynamics of the coastal upwelling off central Peru in different ENSO phases. One main contribution of this work consists in new concepts and data on the interactions between the phyto- and zooplankton dynamics in this region of the HCS.
Acknowledgements

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I could not have accomplished this thesis without the help, advice, support, and love that I received from many people. When I left my homeland, Colombia four years ago, I carried with me a lot of questions and wishes. I have come a long way with innumerable learning experiences during my life and career, today I feel like another person. This is to say THANKS A LOT to all involved in this experience. I apologize if I forgot to mention someone.

The most important persons behind this achievement are my mother, Alicia, my father, Bernardo, and my husband, Jorge. They walked with me through every step of my studies. They supported me and gave me the words to continue several times when I felt the difficulties were stronger than me. They shared the battles with me and
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Appendix

List of conference contributions


production of dominant copepods in the Humboldt Current System off Central Peru. 4th International Zooplankton Production Symposium, May 28 – June 1, 2007, Hiroshima, Japan. Poster


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