

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



Doctoral Thesis

By

Maria Isabel Criales-Hernández



Submitted to Faculty 2 (Biology & Chemistry),

Bremen University

**in partial fulfilment of the requirements for the degree
of *Doctor rerum naturalium* (Doctor of Natural Sciences)**



April 2009, Bremen

Advisory Committee:

First Reviewer: *Prof. Dr. Matthias Wolff* (Charles Darwin Foundation, Galapagos, Ecuador and Bremen University), Bremen, Germany.

Second Reviewer: *Dr. Ralf Schwamborn* Zoology Dept., Federal University of Pernambuco, Recife, Brazil.

First Examiner: *Dr. Claudio Richter* Professor. Benthic-Pelagic Processes. Alfred Wegener Polar and Marine Research Institute (AWI), Bremerhaven, Germany.

Second Examiner: *Prof. Dr. Ulrich Saint-Paul*. Center for Tropical Marine Ecology (ZMT), Bremen, Germany.

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 of 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

Die Ökosysteme im Küstenauftrieb des Humboldtstrom-Systems zeichnen sich durch hohe biologische Produktivität aus. Diese Produktivität beginnt in den unteren trophischen Stufen durch die Düngung der Oberflächenschichten durch Nährstoffe, die durch windgetriebene Prozesse aus tieferen Schichten nach oben transportiert werden. Phytoplankton wird vor allem von Zooplankton konsumiert, welches seinerseits Beute für kleine pelagische Fische ist. Diese Organismen sind erheblichen jahreszeitlichen und interannuellen (El Niño Südliche Oszillation - ENSO) Veränderungen der ozeanographischen Bedingungen unterworfen. Diese Arbeit beschreibt und quantifiziert die räumlich-zeitliche Variabilität der Biomasse, Zusammensetzung und Größenverteilung von Phyto- und Zooplankton in einer Bucht (Bahia de Independencia) und vor offenen Küsten (Kontinentalschelf vor Callao) Zentralperus. Der Schwerpunkt lag auf der Untersuchung der Mechanismen, die das Zooplankton in Bezug auf die Sauerstoff-Minimum-Zone (SMZ) entwickelt hat. Zudem untersuchte ich anhand der dominanten Copoden-Art *Acartia tonsa* die Prozesse und Faktoren, die das Ernährungsverhalten (*Grazing*) und die Eiproduktion des Zooplanktons bestimmen, und wie diese Prozesse mit dem ENSO-Zyklus in Verbindung stehen.

Die Phytoplanktongemeinschaft zeigte extreme Veränderungen in Dichte und Zusammensetzung zwischen verschiedenen ENSO-Phasen. 2006 dominierten Dinoflagellaten, Nanoflagellaten und Diatomeen, auch während der ENSO-neutralen Bedingungen im April 2006 und während des mäßig starken El Niño im Juli und August 2006. 2007 dominierten Diatomeen, auch unter ENSO-neutralen Bedingungen im Februar und April 2007 und während des starken La Niña-Ereignisses, das von Mai

bis August 2007 auf das Gebiet einwirkte. Maximale Biomassen und Abundanzen an Zooplankton wurden während normaler und kalter Bedingungen vor allem in Küstennähe und in der aeroben Oberflächenschicht oberhalb von 20 m Tiefe gefunden, abgesehen von wenigen Arten, die Vertikalwanderungen in die SMZ hinein zeigten. Während warmer Bedingungen war aufgrund der Ausweitung der SMZ das gesamte Zooplankton über die oberen 50 m verteilt. Der Copepode *Acartia tonsa* war im Allgemeinen die dominante Art, aber ihre Population war während des EN 2006 stark reduziert. Nahrungsaufnahmeraten und Selektivität wurden also durch das im Gebiet verfügbare Phytoplankton reguliert. Der Fraßdruck (trophic impact) von *A. tonsa* auf die Primärproduktion während dieser Studie war stark variabel. Diese große Variabilität wurde durch die asynchrone Veränderlichkeit von Primärproduktion, Abundanz von *A. tonsa* sowie Nahrungsaufnahme-Raten verursacht. Die Ergebnisse dieser Arbeit zeigen, dass die Zooplanktongemeinschaft vor Zentralperu stark durch die physikalischen Bedingungen beeinflusst wird. Die offensichtlichsten Veränderungen waren mit den jahreszeitlichen und interannuellen (El Niño Südliche Oszillation - ENSO) Zyklen verbunden. Ein fundamentaler physikalischer Faktor, der die Verteilung des Zooplanktons bestimmt, ist die räumliche Variabilität in der Tiefe der SMZ.

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 mínima de oxígeno. 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 especie 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 más 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).

Contents

Summary	i
Zusammenfassung	iii
Resumen	v
Contents	vii
List of figures	ix
List of Abbreviations	xi
Chapter 1. Background and scope of thesis	1
Chapter 2. General introduction	6
2.1 The Humboldt Current System off Peru	7
2.2 El Niño Southern Oscillation (ENSO)	9
2.3 Zooplankton distribution in upwelling systems	11
Chapter 3. Study areas	13
3.1 Continental shelf off Callao	13
3.2 Independencia Bay	13
Chapter 4. Synopsis of main methods employed	16
4.1 Sampling and Experiments	16
<i>Bimonthly sampling</i>	16
<i>Seasonal intensive sampling (winter and autumn)</i>	17
<i>Grazing experiments</i>	18
4.2 Data analysis	19
<i>Temporal and spatial dynamics in community structure</i>	19
<i>Vertical distribution and migration in relation to the OMZ</i>	19
<i>ENSO effect on primary production, grazing rates, electivity and egg production of <i>A. tonsa</i></i>	20
Chapter 5. Scientific contribution	21
5.1 Ayón P., Criales-Hernandez, M.I., Hirche, H.J., Schwamborn 2008. Zooplankto research off Peru: A review. Progr. Ocenogr. 79:238-25	21
5.2 Criales-Hernandez, M.I., Schwamborn, R., Graco, M., Gutierrez, D., Ayón, P., Hirche, H.J., Wolff, M. ENSO effects on the zooplankton community structure off central Peru, 2005-2007. Manuscript	35
5.3 Criales-Hernandez, M.I., Schwamborn, R., Graco, M., Ayón, P., Hirche, H.J., Wolff, M. 2008. Zooplankton vertical distribution and migration off Central Peru	66

in relation to the oxygen minimum zone. Helg. Mar. Res. 62:85-100

5.4 Criales-Hernandez, M.I., Schwamborn, R., Sanchez, S., Graco, M., Ayón, P., **81**

Hirche, H.J., Wolff, M. 2009. ENSO effects on phytoplankton dynamics, grazing rates, selectivity and egg production of the copepod *Acartia tonsa* off Central peru. Accepted Journal Plankton Research.

Chapter 6. Synoptic discussion **124**

6.1 Review and Knowledge gaps **125**

6.2 Oceanographic conditions and phytoplankton dynamics **125**

6.3 Horizontal distribution of zooplankton **128**

6.4 Vertical distribution of zooplankton **129**

6.5 *A. tonsa* feeding strategy **131**

6.6 Outlook **133**

Acknowledgements **135**

Appendix **138**

References **141**

List of figures

Figure 1.1(a) Overview of the surface current in the eastern South Pacific that influence the main flow of Humboldt Current System (HCS) (b), schematic distribution of characteristic surface water masses (c). The approximate locations for main upwelling areas for nutrient-rich waters are indicated (“X”). According to Murphy (1937), Gunther (1936), Wyrki(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), 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, SSTW: 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

Figure 1.2 Schematic diagram of ENSO (El Niño Southern Oscillation). (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>) .

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).

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).

Figure 4.1 Photos from oblique tows with Bongo net during typical sampling procedure off Callao (photos taken by Maria Isabel Criales)

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

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).

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: 1. Ontogenetic vertical migration (*Acartia tonsa* adults, nauplii, and copepodites), 2. Always above (e.g. *Oikopleura* sp.), 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

Figure 6.2 Conceptual scheme 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 (May 2007) conditions. Mean standing stocks ($\mu\text{gC l}^{-1}$) are shown for each taxonomic group. Dinofl.: Dinoflagellates; Nanofl.: Nanoflagellates. Numbers on arrows represent mean ingestion rates ($\mu\text{gC copep d}^{-1}$). Input data were derived by using data from the present study (Chapter 5.4).

List of abbreviations

Abbreviation	Description
ANOSIM	Analysis of Similarity
CCW	Cold Coastal Water
CENSOR	Climate Variability and El Niño Southern Oscillation: Implications for Natural Coastal Resources and Management
Chl- <i>a</i>	Chlorophyll <i>a</i>
CTW	Coastal Trapped Waves
CUEA	Coastal Upwelling Ecosystem Analysis
DVM	Daily Vertical Migration
EKW	Equatorial Kelvin Waves
EN	El Niño
ENSO	El Niño Southern Oscillation
ESD	Equivalent spherical diameter
ESW	Equatorial Surface Water
ESW	Equatorial Surface Water
EUC	Equatorial Undercurrent or Cromwell Current
EwE	Ecopath with Ecosim
ε	Chesson electivity Index
H'	Shannon diversity
HCS	Humboldt Current System
ICANE	Investigacion Cooperativa de la Anchoveta y su ecosistema
IDVM	Inverse Daily Vertical Migration
IMARPE	Instituto del Mar del Peru
J	Pielou's evenness
LN	La Niña
MDS	Multidimensional scaling
MEI	Multivariate ENSO index
OML	Oxygen Minimum Layer
OMZ	Oxygen Minimum Zone
PaC	Panama Current
PCC	Peru Coastal Current
PCCC	Peru-Chile Counter-Current
PCUC	Peru Coastal Undercurrent
PDO	Pacific Decadal Oscillation
PI	Portion Ingested
POC	Peru Oceanic Current
P _{oxy}	Percentage at the top oxygenated layer in relation to the total abundance per haul
PPC	Phytoplankton carbon
PUC	Poleward Undercurrent
SAW	Sub-Antarctic waters
SST	Sea surface temperature
SSW	Subtropical Surface Water
t_0	Initial phytoplankton density and composition
t_c	Phytoplankton density and composition without copepods
t_g	Phytoplankton density and composition with copepods
TSW	Tropical Surface Water.
WMD	Weighted mean depth
Z _{oxy}	Oxycline depth at 1ml L ⁻¹
Z _{therm}	Thermocline depth at 15°C

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 of 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-Jürgen 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

supervision of P. Ayón. Finally, I analyzed and evaluated the results. Then, I wrote the manuscript with scientific and editorial help of Dr. R. Schwamborn. The final version of the manuscript took account of the comments and recommendations of all the coauthors.

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 (Caliènes et al. 1985; Chavez et al., 1989; Nixon and Thomas, 2001; Pennington 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 Fahrback, 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 $2.04 \text{ g C m}^{-2} \text{ day}^{-1}$ in the HCS as a whole and between 4 and $6.5 \text{ g C m}^{-2} \text{ day}^{-1}$ 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 of 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 (Wyrтки 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.

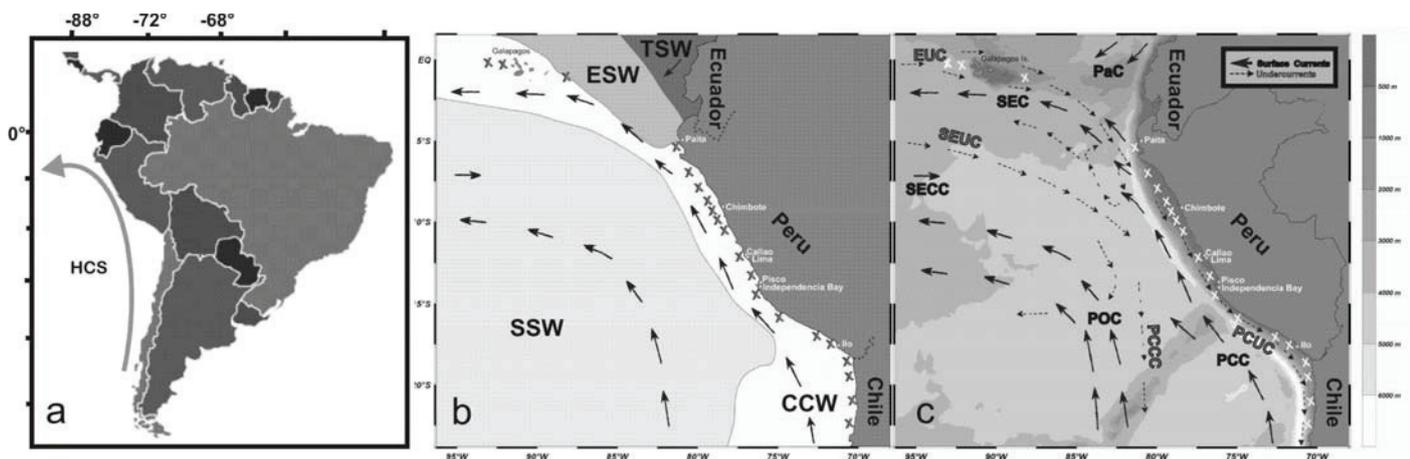


Figure 1.1 (a) Location of the Humboldt Current System;(b), schematic distribution of characteristic surface water masses, figure adapted from Ayón et al 2008 (c). overview of the surface and under currents in the eastern South Pacific that comprise the main flows of the HCS, Ayón et al 2008 The approximate locations for main upwelling areas for nutrient-rich waters are indicated (“X”). Adapted from Murphy (1937), Gunther (1936), Wyrтки(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),

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 Fahrback, 1991; Arntz et

al., 2006). In consequence, a dramatic impoverishment occurs in the entire HCS of marine biological communities (Arntz and Fahrback, 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).

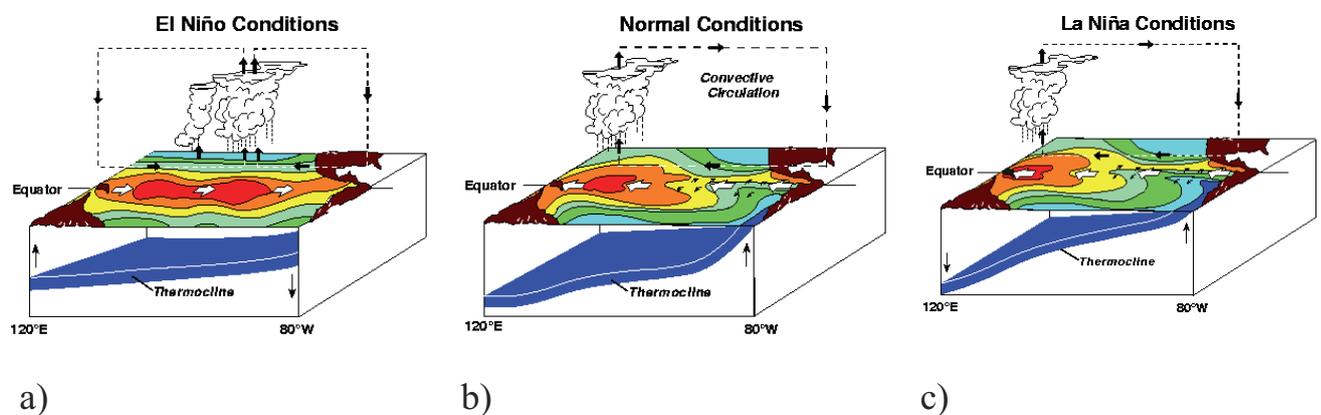


Figure 1.2 Schematic diagram showing of the ENSO (El Niño Southern Oscillation) cycle. (a) Warm conditions El Niño, (b) Normal and (c) La Niña in the Pacific Ocean. The underlying blue layer denotes the relative depth of the thermocline. Decreased trade winds during El Niño allow the basin-wide slope 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>).

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; Escibano, et al., 2004; Chapter 5.1). During EN conditions, the usually dominant copepods (*Acartia tonsa*, *Paracalanus parvus*, and *Centropages brachiatus*) 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 ($14^{\circ}06'$ - $14^{\circ}20'S$; $76^{\circ}00'$ - $76^{\circ}18'W$) 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 Independence 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).

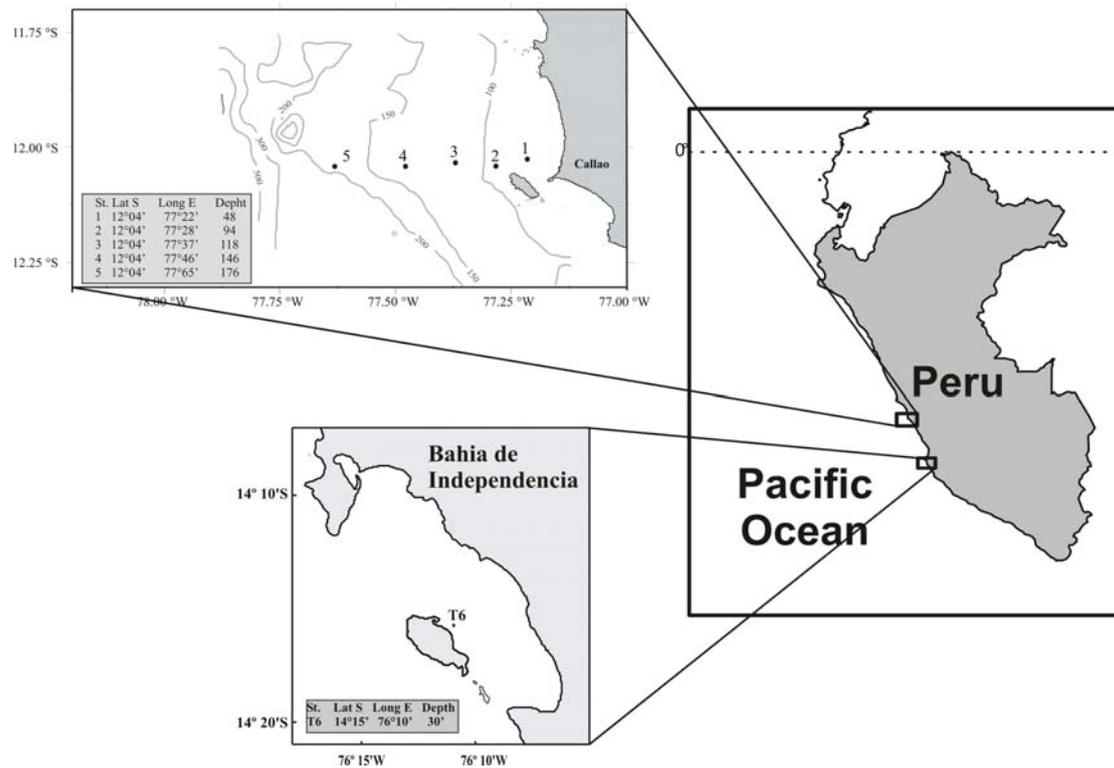


Figure 3.3 Map of the continental shelf off Callao and Independence Bay. Experimental and sampling stations from 2006 and 2007 are indicated. Bi-monthly sampling occurred at four stations off Callao (1, 2, 3 and 4), seasonal intensive sampling at two stations off Callao (2 and 5), and grazing experiments at three stations off Callao (at the IMARPE pier, not pictured, and stations 2 and 5) and one stations in Independence 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- μ m-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 Criales)

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 electivity Index (ϵ) to asses 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.

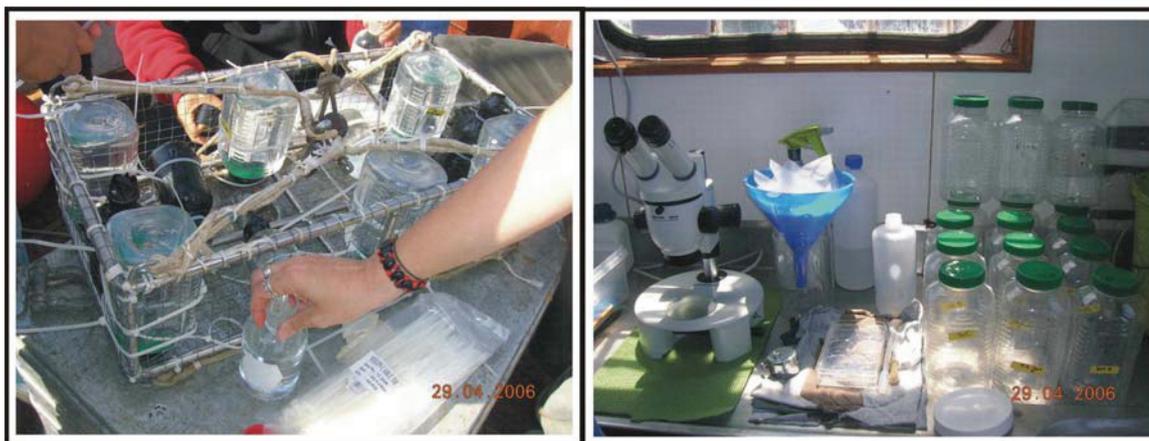


Figure 4.3 Photos from primary production and grazing experiments. Steel basket used for *in situ* incubations, left, general set-up for grazing experiments onboard (photos taken by Maria Isabel Criaes).

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 (ϵ). 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 ϵ 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

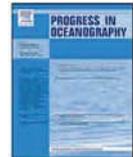
Progress in Oceanography 79 (2008) 238–255



Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean



Zooplankton research off Peru: A review

Patricia Ayón^{a,*}, Maria I. Criales-Hernandez^a, Ralf Schwamborn^{b,c}, Hans-Jürgen Hirche^c

^a Instituto del Mar del Perú, Apartado 22 Callao, Peru

^b Department of Zoology, Universidade Federal de Pernambuco, Recife, Brazil

^c Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany

ARTICLE INFO

Article history:

Accepted 14 October 2008

Available online 21 October 2008

Keywords:

Zooplankton

Review

ENSO

Time series

Humboldt Current

Peru

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 meroplankton 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 brachiatus*; (2) a continental slope group characterized by siphonophores, bivalves, foraminifera and radiolaria; (3) and 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.

© 2008 Elsevier Ltd. All rights reserved.

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 sunlit 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 planktivorous 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 meroplankton, macro-, meso-, and microzooplankton, but left the extensive literature on Peruvian ichthyoplankton for a separate review. We build on the short review by Guzmán and Carrasco (1996) of IMARPE ichthyo- and zooplankton studies. Montecino et al. (2006) and Pennington et al. (2006) pro-

vided 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), Tarazona and Arntz (2001) and Tarazona 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-Álamo and Färber-Lorda (2006), 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 basis for comparison with other upwelling regions, by (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 (IREMAR) with the financial and technical support of FAO, which in 1964 changed its name to Instituto del Mar de Perú (IMARPE). IMARPE's

* Corresponding author. Tel.: +51 14202000x263; fax: +51 14296069.
E-mail address: payon@imarpe.gob.pe (P. Ayón).

initial mission was to compile scientific information about Peru's fish stocks to provide a scientific base for management decisions. With time, events 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's on the anchoveta fishery and Peru's continued dependence on this single-species fishery (Dickie and Valdivia, 1981).

Early zooplankton work concentrated on taxonomy and horizontal distribution (Vásquez, 1967; Alvarado, 1972; Gómez, 1972), especially of euphausiids (Santander, 1967; Santander and Sandoval de Castillo, 1969) and appendicularians (Fenaux, 1968). Additional work followed in the 70s 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 (Ancieta, 1981). Interest in the biological production in Peruvian coastal waters was high due to the prosperous anchovy-meal 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 Brun" Cruise off Peru in 1966 (e.g. Ryther et al., 1966; Ryther, 1967; Barber and Chavez, 1991). Under CUEA, interdisciplinary multiship studies were conducted off Peru during the JOINT-II expedition from March to October 1976 and March to May, 1977. Results were presented in a series of meetings (Barcelona, 1970; Investigaciones Pesqueras 35, 1, 1975; Marseille, 1973; Tethys 6, 1974; Kiel, 1975; Upwelling Ecosystems, 1978) and on the IDOE (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 intensive upwelling. The majority of the results are published in the journal *Oceanology*.

In 1975, the Peruvian-German Program PROCOPA (Programa Cooperativo Peruano-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 Paíta and San José ("Fixed Coastal Stations Program", Table 2). Sampling at these stations is ongoing.

The bi-country project ICANE (Investigación Cooperativa de la Anchoveta 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 of the anchovy population, with the goal of predicting events in this system on time scales relevant to fishery management (Dickie and Valdivia, 1981). Results were published in *Boletín Instituto del Mar del Perú-Callao*, Vol. extraor-

Table 2
Summary of the main types of regular zooplankton surveys off Peru.

Program	Method	Comment
Hensen Net Program	Hensen net (330 µm mesh, 60 cm diameter), towed vertically from 50 m to the surface. Determination of Zooplankton settlement volume → Additional oblique bongo hauls (330 µm mesh, 60 cm diameter) from 200 m to surface	Several times per year since 1964. Hundreds of stations located over the whole marine area off Peru
Fixed Coastal Stations Program	WP2 net (330 µm mesh, 50 cm diameter), horizontal subsurface tows → Since 2004, oblique bongo net samples have been regularly taken at the Fixed Coastal Stations (330 µm mesh, 60 cm diameter for the Callao transect, 330 µm mesh and 22 cm diameter for Paíta and San José transects) from 200 m to the surface or from the bottom to the surface	Bimonthly since 1994. Stations located on three transects perpendicular to the coast off Paíta, San José, and Callao
Intensive Cruises Program (CRIOS)	Experiments for secondary production and grazing, Multinet (330 µm mesh), WP2 net (330 µm mesh) oblique bongo net sampling, laser optical plankton counter	Twice a year since 2005. Stations located on three transects off Callao and inside Bahía de Independencia. Started in the context of the CENSOR project

dinario (1981). These interdisciplinary programs improved Peruvian field work and data analysis and also established collaborations between Peruvian and foreign scientists.

During the 80s, most of the zooplankton papers published by IMARPE scientists (Table 3) focused on taxonomy (e.g. Santander et al., 1981a,b; Carrasco, 1989), species distributions, water mass indicator species (e.g. Véliz, 1981, 1985; Carrasco de Luyo, 1981; Dextre, 1983; Santander and Carrasco, 1985; Sandoval de Castillo, 1987), effects of El Niño on zooplankton biomass (Santander and Carrasco, 1985), and zooplankton biovolumes (1964–1985; Carrasco and Lozano, 1989). Non-IMARPE researchers published studies (Table 3) on community structure (e.g. Boyd and Smith, 1983; Timonin and Flint, 1986; Vinogradov et al., 1980), diel vertical migration (e.g. Judkins, 1980; Mackas et al., 1981; Smith et al., 1981b) and trophic ecology (e.g. Dagg et al., 1980; Boyd et al., 1980; Herman, 1984).

From the 90s to the present (2007), IMARPE zooplankton scientists have published papers on interaction between zooplankton and the environment (particularly El Niño; Aronés and Ayón, 2002; Castillo et al., 2005), species composition and abundance (Abanto, 2001), diel vertical migration (Escudero, 2003), and zooplankton time series relative to fish stock (Alheit and Niquen, 2004) or hydrographic variability (Gutiérrez et al., 2005; Ayón et al., 2004; Aronés et al., in press; Ayón et al., 2008). This work was supported by the European Community VECEP Program (1993–1999), which supported several fisheries surveys, and World Bank loans to purchase laboratory equipment (1999). In 1998 the research vessel "José Olaya Balandra" was donated by the Japanese government including sampling gear and laboratory equipment. CICESE (Mexico) provided funds from 2004 to 2005 for the analysis of zooplankton time series. In 2005, the multi-country project CENSOR was launched in Peru, funded by the European Union ("Climate variability and El Niño Southern Oscillation: Implications for natural coastal resources and management"; Argentina, Chile, Peru, France, Germany, Spain). CENSOR's zooplankton component focuses on trophodynamic impacts on the time series variability, especially in coastal areas.

Table 1
Water masses found in surface waters off Peru.

Water masses	Salinity	Temperature (°C)
Tropical Surface Water (TSW)	<33.8 ^a	>25 ^b
Equatorial Surface Water (ESW)	33.8–34.8 ^b	>20 ^b
Subtropical Surface Water (SSW)	35.1–35.7 ^a	18–27 ^b
Cold Coastal Water (CCW)	34.8–35.1 ^a	14–18 ^c

^a Zuta and Guillén (1970).

^b Gutiérrez et al. (2005).

^c Morón (2000).

Table 3

Overview over selected publications on specific topics related to the zooplankton in marine waters off Peru.

Topics	Main references
Biogeography, distribution, and ecology of specific taxa	Siphonophores (Bigelow, 1911; Véliz, 1985; Sears, 1953) Ostracods (Castillo, 2004; Castillo et al., 2005, 2007) Copepods (Alvarado, 1972; Gómez, 1972, 1982; Geyrikh, 1973; Santander et al., 1981b; Ayón et al., 1999; Abanto, 2001; Aronés, 2002; Aronés and Ayón, 2002) Amphipods (Carrasco de Luyo, 1981; Santander et al., 1981b; Carrasco, 1989; Aronés, 1997) Euphausiids (Santander, 1967; Santander and Sandoval de Castillo, 1969; Alvarado, 1972; Antezana, 1978; Santander et al., 1981a,b; Antezana, 2002a) Holoplanktonic molluscs (Quesquén and Guzmán, 1999; Quesquén, 2005) Chaetognaths (Bieri (1957, 1959); Alvarado, 1972; Santander et al., 1981a,b; Dextre, 1983; Sandoval de Castillo, 1987) Appendicularians (Fenaux, 1968) Zooplankton guides (Santander, 1981; Santander et al., 1981a,b) Horizontal distribution and biogeography (Vásquez, 1967; Beers et al., 1971; Vinogradov, 1977; Guillén, 1978; Santander et al., 1981a,b; Dextre, 1983; Timonin and Flint, 1986; Vasil'ev, 1991; Ayón et al., 1996; Ayón and Girón, 1996; Aronés and Ayón, 2001; Aronés et al., 2001; Quesquén, 2004; Aronés, 2004; Gutiérrez et al., 2005)
Vertical distribution	Judkins (1980), Sameoto (1981), Mackas et al. (1981), Smith et al. (1981a,b), Glebov (1982), Semenova et al. (1982) and Antezana (2002b) (for <i>Euphausia mucronata</i>); Escudero (2003) and Ciales-Hernández et al. (2008)
Development of plankton communities	Mikheyev (1977a,b), Smith (1978), Vinogradov and Shushkina (1978), Vinogradov et al. (1980) and Boyd and Smith (1983)
Time series	Zooplankton volumes off Peru since 1964 (Carrasco and Lozano, 1989; Ayón et al., 2004) Hydrography and mesozooplankton abundance and diversity off Paita 1994–2004 (Aronés et al., in press)
El Niño	Dextre (1983), Santander and Carrasco (1985), Carrasco and Santander (1987), Aronés (1997), Gómez (1997), Ayón et al. (1999), Aronés and Ayón (2002) and Castillo et al. (2005)
Trophic ecology	Grazing and excretion (Cowles, 1978, 1979; Dagg et al., 1980; Boyd et al., 1980; Paffenhöfer, 1982; Arashkevich et al., 1982; Herman, 1984) Zooplankton productivity (Shushkina and Kislyakov, 1977) Functional characteristics of planktonic communities (Shushkina et al., 1978) Microzooplankton production (Sorokin, 1978; Tumantseva and Kopylov, 1985a)

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 PIO vol. 69). 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 (Penven et al., 2005). The flow of the PCC is strongest in austral winter, when equatorward winds are maximal (Bakun and Nelson, 1991; Echevin et al., 2004a,b; Croquette 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 EN. 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-Álamo and Färber-Lorda, 2006). Plumes of upwelled water may extend several hundred km offshore at the

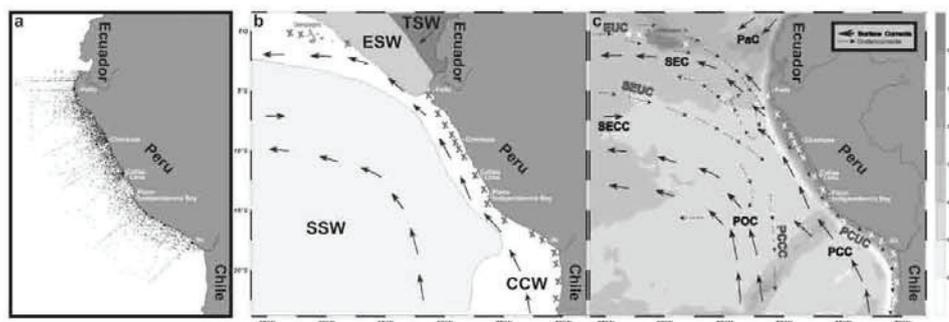


Fig. 1. Study area along the Peruvian coast showing zooplankton sampling stations covered since 1964 (Ayón et al., 2004, modified) (a), schematic distribution of characteristic surface water masses (b), and bathymetry with main currents (c). The approximate locations for main upwelling areas for nutrient-rich waters are indicated (“X”). According to Gunther (1936), Wyrki (1963, 1967), Zuta and Guillén (1970), Tsuchiya (1981), Huyer et al. (1991), Strub et al. (1998), Schneider et al. (2003), Penven et al. (2005) and Croquette and Eldin (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: ELUC, 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.

surface, leading to large-scale offshore blooms, but in general offshore oceanic waters are warmer and contain less nutrients than nearshore upwelled waters. The upwelled and offshore PCC waters interact on several time scales, e.g. the alternation of upwelling and relaxation episodes, seasonal variability upwelling strength, and most drastically by EN. During EN, warm and low-salinity Equatorial Surface Water (ESW) and Tropical Surface Water (TSW) spread southward, and offshore PCC water reaches closer to the coast (Zuta and Guillen, 1970; Fiedler and Talley, 2006). Replacement of nutrient-rich upwelled water by warmer and more oligotrophic offshore water masses leads to drastic changes in pelagic ecosystems.

Sea surface temperatures (SST) increase towards the equator. In northern Peru, equatorward of 14°S, summer SSTs reach 26 °C, while to the south minimum summer SSTs are 17–18 °C (Zuta and Guillen, 1970). In central and southern Peru, in winter, SST varies from 13 to 17 °C, and the 19 °C isotherm is found north of 10°S. Stronger than seasonal SST changes, however, ENSO generates a huge interannual variability (Fig. 4). Spatial SST differences are caused by basin scale latitudinal and local (shelf width, water depth) components. The Peruvian shelf is <200 m deep and widest (65 nm) between 7°S and 10°S, and narrowest (3–5 nm) equatorward 7°S and poleward of 15°S (Zuta and Guillen, 1970).

4. Research topics

4.1. Sampling and survey development

IMARPE has always focused on fisheries. Zooplankton samples were a by-product of ichthyoplankton sampling, which was conducted on all surveys, be it 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 coelenterates and ichthyoplankton, the zooplankton settlement volume is measured (Carrasco and Lozano, 1989; Ayón et al., 2004). The stations are located on a predefined meander-shaped cruise track covering the whole coastal area of Peru, although the cruise track was sometimes modified. Zooplankton samples were only taken at stations where echograms indicated fish were present and fish trawling should also be conducted. Since 1996, additional zooplankton sampling has been conducted where distance between trawl positions was >20 nm.
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 1994 with a WP2 net (Working Party 2; UNESCO, 1968; 330 µm mesh, 50 cm diameter). Additionally, since 2004, oblique bongo net tows (60 cm diameter, 300 µm mesh size; Table 2) have been included.

During a limited project in 1996/1997, vertically stratified samples with a closing net (200 µm mesh, 85 cm mouth diameter) were taken, usually from 100–50–25–10–0 m on two fixed stations near Callao (12°12.0'S, 077°18.0'W, Escudero, 2003) 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 recently been used during the Intensive Cruises Program (CRIOS) 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. Bigelow (1911) and later Sears (1953) worked on siphonophores collected by the US Steamer Albatross in 1904/1905. Santander et al. (1981a,b) catalogued 3 siphonophore, 31 copepod, 35 amphipod, 6 euphausiid, and 6 chaetognath species. Abanto (2001) presented a list of 152 copepod species from 54 genera collected on 15 cruises between 3°30'S and 14°S and 1980–1989. The zooplankton species in Table 4 were identified from the Fixed Coastal Stations Program since 1994, and since 1997 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 chilensis* (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 pteropods). In 1987, Carrasco and Santander found that during normal conditions between 6°S and 12°S, copepods were 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 Girón, 1996, 1997; Ayón and Aronés, 1997a,b; Ayón et al., 1996; Ayón and Girón, 2004). Off Paita and San José, ca. 98% 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 1976 and 1977. She concluded that food quality and concentration were regulating the zooplankton composition, being low primary production associated to the dominance of euryphagous or carnivorous species, with less herbivorous species. Santander (1981), defined three major zooplankton groups: (1) continental shelf (dominated by *A. tonsa* and *C. brachiatus*); (2) continental slope (siphonophores, bivalves, foraminifera, and radiolaria), (3) oceanic group (*Mecynocera clausi*, *Pleuromamma gracilis*, *Scolecithrix danae*, *Lucicutia flavicornis*, *Euchaeta marina*, *Euchirella bella*, *Oithona plumifera*, *Calocalanus pavo*, *Temora stylifera*, *T. discaudata*, *Nannocalanus minor*, *Eucalanus subtenuis*, *Acrocalanus* sp., *Corycaeus* sp., *Oithona* sp., *Oncaea* sp., *Sapphirina* sp., *Corycella* sp., *Copilia* sp.). Sameoto (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 4

List of species identified in Peruvian zooplankton samples (Ayón et al., 2008, status of 2006). References: (1) IMARPE, unpublished; (2) Sears (1953); (3) Véziz (1985); (4) Santander et al. (1981a,b); (5) Quesquén (2005); (6) Castillo (2004); (7) Abanto (2001); (8) Gómez (1982); (9) Carrasco and Santander (1987); (10) Carrasco (1989); (11) Aronés (1997); (12) Santander (1967); (13) Dextre (1983); (14) Sund (1964); (15) Sandoval de Castillo (1987); (16) Fenaux (1968).

Cnidaria	<i>Dyphyes dispar</i> 3	<i>Porroecia pseudoparthenoda</i> 6
<i>Solmundella bitentaculata</i> 1	<i>Eudoxoides mitra</i> 1	<i>Procerroecia decipiens</i> 6
<i>Aegimura grimaldii</i> 1	<i>Eudoxoides spiralis</i> 3	Copepoda
<i>Aequorea coerulescens</i> 1	<i>Lensia campanella</i> 1	<i>Acartia danae</i> 7, 8
<i>Aequorea macrodactyla</i> 1	<i>Lensia conoidea</i> 1	<i>Acartia erytraea</i> 7
<i>Bougainvillia superciliosa</i> 1	<i>Lensia cassack</i> 1	<i>Acartia negligens</i> 7
<i>Bougainvillia fulva</i> 1	<i>Lensia fowleri</i> 1	<i>Acartia liljeborgii</i> 1
<i>Heterotara anonyma</i> 1	<i>Lensia hotspur</i> 1	<i>Acartia tonsa</i> 7, 8
<i>Obelia</i> sp. 1	<i>Muggiaea atlantica</i> 4	<i>Aetideus armatus</i> 7
<i>Phialidium uchidai</i> 1	<i>Muggiaea kochii</i> 3	<i>Aetideus giesbrechti</i> 7
<i>Cladonema</i> sp. 1	<i>Hippodius hippopus</i> 1	<i>Euaitideus bradyi</i> 7, 8
<i>Euphysa tentaculata</i> 1	<i>Physophora hydrostatica</i> 1	<i>Euchirella bella</i> 7, 8
<i>Sarsia edmia</i> 1	<i>Rosacea plicata</i> 1	<i>Euchirella messinensis</i> 1
<i>Sarsia</i> sp. 1	Ctenophora	<i>Haliotilus acutifrons</i> 7
<i>Cunina octonaria</i> 1	<i>Bolinopsis infundibulum</i> 1	<i>Haliotilus ornatus</i> 7
<i>Cunina frugifera</i> 1	<i>Velamem</i> sp. 1	<i>Haliotilus oxycephalus</i> 7
<i>Cunina peregrina</i> 1	<i>Pleurobrachia pileus</i> 1	<i>Haliotilus</i> sp. 7
<i>Cunina globosa</i> 1	<i>Hormiphora plumosa</i> 1	<i>Calanus australis</i> 7, 8
<i>Cunina tenella</i> 1	<i>Beroe cucumis</i> 1	<i>Calanus chilensis</i> 8
<i>Cunina duplicata</i> 1	Annelida	<i>Calanus darwinii</i> 1
<i>Solmissus incisus</i> 1	<i>Pelagobia longicirrata</i> 1	<i>Calanus tenuicornis</i> 7
<i>Cytaeis tetrastyla</i> 1	<i>Tomopteris</i> sp. 1	<i>Canthocalanus pauper</i> 1
<i>Geryonia proboscidalis</i> 1	Mollusca	<i>Nannocalanus minor</i> 7
<i>Liriope tetraphylla</i> 1	<i>Protantata souloyeti</i> 5	<i>Neocalanus robustior</i> 7
<i>Halicreas minimum</i> 1	<i>Oxygyrus keraudreni</i> 5	<i>Undimula darwinii</i> 7
<i>Hydractinia</i> sp. 1	<i>Atlanta turriculata</i> 5	<i>Undimula</i> sp. 7
<i>Euchelota menoni</i> 1	<i>Atlanta helicinoidea</i> 1	<i>Candacia bipinnata</i> 7
<i>Taricodon coerulens</i> 1	<i>Atlanta leseuri</i> 5	<i>Candacia catula</i> 7, 9
<i>Amphinema</i> sp. 1	<i>Atlanta peroni</i> 5	<i>Candacia curta</i> 7, 8
<i>Leuckartiara octona</i> 1	<i>Atlanta gaudichaudi</i> 5	<i>Candacia simplex</i> 1
<i>Leuckartiara zacae</i> 1	<i>Atlanta inclinata</i> 5	<i>Candacia pachydactyla</i> 7
<i>Stomatoca pterophylla</i> 1	<i>Carinaria lamarecki</i> 5	<i>Paracandacia truncata</i> 7
<i>Stomatoca atra</i> 1	<i>Cardiopoda placenta</i> 1	<i>Centropages brachiatus</i> 7, 8
<i>Halitholus intermedia</i> 1	<i>Pterotrachea hippocampus</i> 5	<i>Centropages elongatus</i> 7
<i>Porpita porpita</i> 1	<i>Pterotrachea coronata</i> 5	<i>Centropages furcatus</i> 7
<i>Vellela vellela</i> 1	<i>Frioloida desmaresti</i> 5	<i>Centropages gracilis</i> 7
<i>Pochella polynema</i> 1	<i>Limacina bulinoides</i> 5	<i>Clausocalanus arcuicornis</i> 7, 9
<i>Aglaura hemistoma</i> 1	<i>Limacina inflata</i> 5	<i>Clausocalanus</i> sp. 7
<i>Rhopalonema funerarum</i> 1	<i>Limacina trochiformis</i> 5	<i>Clausocalanus jobei</i> 1
<i>Rhopalonema velatum</i> 1	<i>Cavolinia inflexa</i> 5	<i>Clausocalanus furcatus</i> 1
<i>Sminthea eurygaster</i> 1	<i>Cavolinia longirostris</i> 5	<i>Chytemnestra rostrata</i> 7, 8
<i>Amphogona apicata</i> 1	<i>Cavolinia uncinata</i> 5	<i>Chytemnestra scutellata</i> 7
<i>Pantachogon</i> sp. 1	<i>Diacria quadridentata</i> 5	<i>Corycaeus auroniensis</i> 1
<i>Pegantia laevis</i> 1	<i>Clio pyramidata</i> 5	<i>Corycaeus dubius</i> 8
<i>Pegantia mortagon</i> 1	<i>Creseis acicula</i> 5	<i>Corycaeus catus</i> 7
<i>Pegantia clara</i> 1	<i>Creseis virgula</i> 5	<i>Corycaeus crassiusculus</i> 7
<i>Pegantia triloba</i> 1	<i>Hyalocylis striata</i> 5	<i>Corycaeus flaccus</i> 7
<i>Solmaris</i> sp. 1	<i>Cymbulia sibogae</i> 5	<i>Corycaeus furcifer</i> 7
<i>Chromatonema crythronon</i> 1	<i>Desmopteris papillo</i> 5	<i>Corycaeus gibbulus</i> 10
<i>Ectopleura dumortieri</i> 1	<i>Peracis apacfulva</i> 1	<i>Corycaeus lautus</i> 1
<i>Ectopleura sacculifera</i> 1	<i>Peracis reticulata</i> 1	<i>Corycaeus limbatus</i> 7
<i>Atoilla wyvillei</i> 1	<i>Glaucus</i> sp. 1	<i>Corycaeus longistylis</i> 1
<i>Nausithoe punctata</i> 1	<i>Phyllirhoe bucephala</i> 1	<i>Corycaeus robustus</i> 7
<i>Nausithoe rubra</i> 1	<i>Cephalopyge trematoidea</i> 1	<i>Corycaeus speciosus</i> 7
<i>Pelagia noctiluca</i> 1	Branchiopoda	<i>Corycaeus</i> spp. 7
<i>Chrysaora plocamia</i> 1	<i>Penilia avirostris</i> 1	<i>Farranula gibbula</i> 7
<i>Periphylla periphylla</i> 1	<i>Pleopis polyphemoides</i> 1	<i>Microsetella gracilis</i> 7
<i>Stomolophora meteagris</i> 1	<i>Evadne espinifera</i> 1	<i>Microsetella rosea</i> 7
<i>Phacelophora camtschatic</i> 1	<i>Evadne nordmanni</i> 1	<i>Eucalanus inermis</i> 7, 8
<i>Abyla peruana</i> 2	<i>Pseudoevadne tergestina</i> 1	<i>Eucalanus elongatus</i> 1
<i>Ceratocymba leuckarti</i> 1	Ostracoda	<i>Paraeucalanus attenuatus</i> 7
<i>Abylopsis tetragona</i> 3	<i>Archiconchoecia striata</i> 6	<i>Rhincalanus cornutus</i> 7
<i>Abylopsis eschscholtzi</i> 3	<i>Halocypris inflata</i> 6	<i>Rhincalanus nasutus</i> 7, 8
<i>Bassia bassensis</i> 1	<i>Euconchoecia aculeata</i> 6	<i>Subeucalanus crassus</i> 7
<i>Enneagonium hyalinum</i> 1	<i>Euconchoecia chierchiae</i> 1	<i>Subeucalanus micronatus</i> 7
<i>Nanomia cara</i> 1	<i>Conchoecetta giesbrechti</i> 6	<i>Subeucalanus subcrassus</i> 7
<i>Agalma elegans</i> 3	<i>Conchoecia aff magna</i> 6	<i>Euchaeta acuta</i> 7, 10
<i>Athoribia rosacea</i> 1	<i>Disconchoecia tamensis</i> 6	<i>Euchaeta indica</i> 7
<i>Suculeolaria biloba</i> 1	<i>Metaconchoecia inflata</i> 6	<i>Euchaeta longicornis</i> 7
<i>Suculeolaria chumi</i> 1	<i>Metaconchoecia kyrtophora</i> 6	<i>Euchaeta media</i> 1
<i>Suculeolaria quadrivalvis</i> 1	<i>Metaconchoecia teretivalvata</i> 6	<i>Euchaeta plana</i> 7
<i>Suculeolaria turgida</i> 1	<i>Orthoconchoecia agassizi</i> 6	<i>Euchaeta rimana</i> 7
<i>Chelophyes appendiculata</i> 1	<i>Orthoconchoecia striola</i> 6	<i>Euchaeta</i> sp. 7
<i>Chelophyes contorta</i> 1	<i>Porroecia parthenoda</i> 6	<i>Euterpina acutifrons</i> 10; 7
<i>Dyphyes bojani</i> 1	<i>Porroecia porroecia pacifica</i> 6	<i>Heterorhabdus lobatus</i> 1

Table 4 (continued)

<i>Heterorhabdus papilliger</i> 7	<i>Temora discaudata</i> 7	<i>Pagurus</i> sp. 1
<i>Lucicutia flavicornis</i> 7, 8	<i>Temora stylifera</i> 1	<i>Blefaripoda</i> sp. 1
<i>Lucicutia gaussae</i> 7	<i>Tharybis</i> sp. 7	<i>Lepidopa</i> sp. 1
<i>Mecynocera clausii</i> 7, 8	Amphipoda	<i>Emerita analoga</i> 1
<i>Pleuromamma borealis</i> 7, 8	<i>Anapronoe</i> sp. 1	<i>Cancer setosus</i> 1
<i>Pleuromamma abdominalis</i> 1	<i>Dairella</i> sp. 1	<i>Platyanthus</i> sp. 1
<i>Pleuromamma gracilis</i> 8	<i>Hyperoides sibaginis</i> 10, 11	<i>Libinia</i> sp. 1
<i>Pleuromamma piseki</i> 7	<i>Phronimopsis spinifera</i> 10, 11	Euphausiacea
<i>Pleuromamma xiphias</i> 7	<i>Hyperia medusarum</i> 10	<i>Euphausia diomedae</i> 1
<i>Oithona</i> sp. 7	<i>Hyperietta vosseleri</i> 11	<i>Euphausia mucronata</i> 12
<i>Oithona atlantica</i> 1	<i>Hyperietta luzoni</i> 11	<i>Euphausia tenera</i> 12
<i>Oithona fallax</i> 7	<i>Hyperietta stephensi</i> 11	<i>Euphausia eximia</i> 12
<i>Oithona nana</i> 1	<i>Hyperoides longipes</i> 11	<i>Euphausia distinguenda</i> 12
<i>Oithona plumifera</i> 7, 8	<i>Hyperoche</i> sp. 1	<i>Euphausia lamelligera</i> 12
<i>Oithona setigera</i> 7, 8	<i>Lestrignonus bengalensis</i> 11	<i>Euphausia mutica</i> 1
<i>Oithona similis</i> 10	<i>Lestrignonus macrophthalmus</i> 11	<i>Nyctiphanes simplex</i> 12
<i>Paraoithona parvula</i> 7	<i>Lestrignonus shoemakeri</i> 11	<i>Nematoscelis tenella</i> 1
<i>Paraoithona</i> sp. 7	<i>Lestrignonus schizogenetis</i> 11	<i>Nematoscelis gracilis</i> 1
<i>Lubbockia squillimana</i> 7	<i>Themistella fusca</i> 11	<i>Nematoscelis flexipes</i> 1
<i>Oncaea conifera</i> 7, 8	<i>Lanceola</i> sp. 1	<i>Stylocheiron affine</i> 1
<i>Oncaea venusta</i> 7	<i>Anapronoe</i> sp. 1	<i>Stylocheiron carinatum</i> 1
<i>Pachysoma dentatum</i> 7	<i>Brachyscelus crusculum</i> 10, 11	<i>Stylocheiron elongatum</i> 1
<i>Acrocalanus gracilis</i> 7	<i>Lycæa</i> spp. 11	<i>Nematobrachium flexipes</i> 1
<i>Acrocalanus monachus</i> 9	<i>Pseudolycaea</i> sp. 1	Mysida
<i>Acrocalanus armatus</i> 9	<i>Thamneus</i> sp. 1	<i>Heteromysis</i> sp. 1
<i>Acrocalanus</i> sp. 7	<i>Tryphana malmi</i> 11	<i>Archaeomysis</i> sp. 1
<i>Calocalanus pavo</i> 7	<i>Lycæopsis themistoides</i> 10, 11	<i>Mysidopsis</i> 1
<i>Calocalanus plumulosus</i> 7	<i>Oxycephalus piscator</i> 10, 11	<i>Siriella</i> sp. 1
<i>Paracalanus parvus</i> 7, 8	<i>Oxycephalus armatus</i> 10	<i>Gybberrithrops</i> sp. 1
<i>Oithona plumifera</i> 7, 8	<i>Oxycephalus clausi</i> 1	<i>Metamysidopsis pacifica</i> 1
<i>Oithona setigera</i> 7, 8	<i>Simorhynchus antenarius</i> 10	Chaetognatha
<i>Parvocalanus</i> sp. 7	<i>Calamorrhynchus</i> sp. 1	<i>Khronitta pacifica</i> 1
<i>Phaenna spinifera</i> 7	<i>Cranocephalus</i> sp. 1	<i>Khronitta subtilis</i> 13
<i>Calanopia</i> sp. 1	<i>Rhabdosoma armatum</i> 1	<i>Pterosagitta draco</i> 13
<i>Labidocera acuta</i> 7	<i>Streetsia</i> sp. 1	<i>Sagitta bedoti</i> 14
<i>Labidocera acutifrons</i> 7	<i>Turbogella</i> sp. 1	<i>Sagitta decipiens</i> 15
<i>Labidocera</i> sp. 7	<i>Glossoccephalus</i> sp. 1	<i>Sagitta enflata</i> 13
<i>Labidocera pavo</i> 1	<i>Leptocotis spinifera</i> 11	<i>Sagitta ferox</i> 14
<i>Pontella</i> sp. 1	<i>Rhabdosoma minor</i> 11	<i>Sagitta hexaptera</i> 15
<i>Pontellina plumata</i> 7, 8	<i>Paraphronima gracilis</i> 11	<i>Sagitta minima</i> 13
<i>Pontellopsis armata</i> 7	<i>Thyropus diaphanus</i> 11	<i>Sagitta maxima</i> 1
<i>Pontellopsis perpicans</i> 1	<i>Euscelus robustus</i> 11	<i>Sagitta neglecta</i> 14
<i>Pontellopsis regalis</i> 1	<i>Schizoscelus ornatus</i> 11	<i>Sagitta pacifica</i> 1
<i>Pseudodiaptomus</i> sp. 7	<i>Phronima sedentaria</i> 10	<i>Sagitta peruviana</i> 14
<i>Copilia mirabilis</i> 7	<i>Phronimella elongata</i> 10, 11	<i>Sagitta pulchra</i> 14
<i>Copilia quadrata</i> 1	<i>Phronima dunbari</i> 11	<i>Sagitta regularis</i> 13
<i>Sapphirina angusta</i> 1	<i>Phronima colleti</i> 1	Thalassia
<i>Sapphirina auronitens</i> 7	<i>Phronima bowmani</i> 11	<i>Cyclosalpa bakeri</i> 1
<i>Sapphirina darwini</i> 7	<i>Phrosina semilunata</i> 11	<i>Helicosalpa komaii</i> 1
<i>Sapphirina gastrica</i> 7	<i>Anchylomera</i> sp. 1	<i>Iasis zonaria</i> 1
<i>Sapphirina gemma</i> 7	<i>Primno macropa</i> 11	<i>Pegæa confederata</i> 1
<i>Sapphirina intestinata</i> 7	<i>Amphithyrus sculpturatus</i> 11	<i>Ritteriella picteti</i> 1
<i>Sapphirina iris</i> 1	<i>Hemityphis tenuimanus</i> 11	<i>Salpa fusiformis</i> 1
<i>Sapphirina metalina</i> 7	<i>Platyscelus</i> sp. 1	<i>Thalia democratica</i> 1
<i>Sapphirina nigromaculata</i> 7	<i>Tetrathyrus forcipatus</i> 11	<i>Thetys vagina</i> 1
<i>Sapphirina opalina</i> 7	<i>Parapronoe parva</i> 10	<i>Weelia cylindrica</i> 1
<i>Sapphirina ovalanceolata</i> 7	<i>Sympronoe</i> sp. 1	<i>Doliolum gegenbauri</i> 1
<i>Sapphirina</i> spp. 7	<i>Eupronoe maculata</i> 11	<i>Doliolum denticulum</i> 1
<i>Sapphirina stellata</i> 7	<i>Scina</i> sp. 1	<i>Doliolum nationalis</i> 1
<i>Amaliothrix</i> sp. 7	<i>Vibilia armata</i> 11	Appendicularia
<i>Scaphocalanus echinatus</i> 7	<i>Vibilia chuni</i> 11	<i>Oikopleura dioica</i> 16
<i>Scaphocalanus</i> sp. 7	Decapoda	<i>Oikopleura fusiformis</i> 16
<i>Scolecithricella abyssalis</i> 7	<i>Solenocera</i> sp. 1	<i>Oikopleura albicans</i> 16
<i>Scolecithricella aupoecten</i> 7	<i>Penaeus stylirostris</i> 1	<i>Oikopleura cophocerca</i> 16
<i>Scolecithricella bradyi</i> 7, 8	<i>P. vannamei</i> 1	<i>Oikopleura intermedia</i> 16
<i>Scolecithricella dentata</i> 7	<i>P. californicus</i> 1	<i>Oikopleura longicauda</i> 16
<i>Scolecithricella minor</i> 7	<i>P. occidentalis</i> 1	<i>Oikopleura rufescens</i> 16
<i>Scolecithricella</i> spp. 7	<i>Sergestes</i> sp. 1	<i>Stegosoma magnum</i> 16
<i>Scolecithricella danae</i> 7	<i>Lucifer</i> sp. 1	Cephalochordata
<i>Scolecithricella spinipedata</i> 7	<i>Callinassa</i> sp. 1	<i>Branchiostoma elongatum</i> 1
<i>Scottocalanus</i> sp. 7	<i>Callichirus</i> sp. 1	
<i>Temeropsis mayumbaensis</i> 7	<i>Pleuroncodes monodon</i> 1	

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) (Santander, 1981; Carrasco and Lozano, 1989; Ayón et al., 2004). The high biovolumes in the north may be due to the influence of the ESW, which have 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 neritic herbivores like *Calanus australis* and *Eucalanus inermis* may grow in mass (Geynrikh, 1973). Off northern and central Peru, euphausiids were less but the remaining mesozooplankton were more abundant (Gunther, 1936).

EN 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 during EN shows 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 meroplanktonic larvae and ichthyoplankton in the coastal waters during EN.

Specific attention on the regional and seasonal distribution of certain taxonomic groups was drawn by Véliz (1981), who identified ten species of siphonophores between 5°47' and 9°13' up to 260 km offshore, and by Castillo (2004) and Castillo et al. (2007) who studied the distribution of 15 ostracod species. During the 1998 EN ostracod species shifted south and their distributions showed positive or negative correlations with salinity and distance to shore.

Some species can be used as water masses indicators (Gómez, 1972; Geynrikh, 1973; Aronés, 2002; Castillo, 2004). Sandoval de Castillo (1987) used chaetognaths as water mass indicators, with *Sagitta bedoti*, *S. neglecta*, *S. peruviana*, and *S. pulchra* associated in ESW, and *S. ferox*, *S. regularis* and *Khronittia pacifica* in SSW. Carrasco and Santander (1987) showed that the copepods *Centropages furcatus*, *Acrocalanus gracilis*, and *A. monachus* were typical in ESW, while CCW species were *Clausocalanus arcuicornis*, *Acartia tonsa*, *Oithona plumifera*, *Paracalanus parvus*, *Centropages brachiatus*, and *Eucalanus inermis*. A recent study conducted off northern Peru (Gutiérrez et al., 2005) recognized several copepod species as indicators of SSW: *Acartia danae*, *Calocalanus pavo*, *Ishnocalanus plumulosus*, *Mecynocera clausii*, and *Oncaea conifera*. Abanto (2001) related the distribution of 152 copepod species to hydrographic data between 3°30'S and 14°S between 1980 and 1989. Examples are presented in Fig. 5. Thus, *Acartia tonsa*, *Calanus australis*, *Clausocalanus* sp., *Paracalanus parvus* are apparently eurythermal and euryhaline and not water mass specific, while *Subeucalanus crassus*, *Sapphirina darwinii*, *Pleuromamma abdominalis* were restricted to SSW, and *C. brachiatus*, *E. inermis*, *Euaetideus bradyi* could be used as indicator species for CCW. During EN, *Centropages furcatus* shifts south and replaced the CCW species *C. brachiatus* and *Eucalanus inermis* (Abanto, 2001). The shift between *C. brachiatus* (non-EN) and *C. furcatus* (EN) was also noticed by Gutiérrez et al. (2005), who related hydrographic parameters to changes in microphytoplankton, mesozooplankton (volume, abundance, and species richness), ichthyoplankton 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 the 0.5 ml L⁻¹ (Escribano et al., 2000) or 1 ml 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 (Wyrski, 1966; Judkins, 1980; Escribano 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). Judkins (1980) pumped samples down to 85 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 ml 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 inermis*, which other studies have shown can with stand 12 h of anoxia (Judkins, 1980; Boyd et al., 1980), and *Euphausia mucronata* (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 (Escribano 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 mucronata* 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 (Oncaeidae, Oithonidae, 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 Oncaeidae. These daily excursions seemed sufficient to expose Oncaeidae 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 inermis*, *Calanus australis*, and *Centropages brachiatus* 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 in 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 ml L⁻¹, but concentrations <0.2 ml L⁻¹ have drastic effects on most taxa. They also found that *Eucalanus inermis*, *Euaetideus bradyi*, *Rhincalanus nasutus*, amphipods, and ostracods occur mainly between 50 and 100 m, where the oxygen content was <0.5 ml L⁻¹. Using a closing net off Callao during three 48 h-periods, Escudero (2003) distinguished four types of migration, with species: (1) spending day at depth and coming to the surface between dusk and midnight; (2) not-migrating; (3) migrating several times each 24 h; and (4) reverse migrating, swimming up in the day and down at night, as in *Lucicutia flavicornis*. Environmental conditions modified the migrations, as O₂ concentrations <0.5 ml 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 along-shore 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; Croquette et al., 2005; Aronés 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 90s when no seasonal trend was evident. Aronés et al. (in press) analysed the seasonality of zooplankton abundance off Paíta (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 Paíta was at minimum during winter, and thus displayed a positive correlation with temperature (Aronés 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 Mendo, 1987; Cury and Roy, 1989). Similar con-

cepts have also been called the “optimal environmental window” (Cury and Roy, 1989; Sugimoto and Tadokoro, 1998) 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 (Aronés et al., in press), although the dominating mechanisms and processes are not yet clear. Cury 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 et al., 1970; 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 (Franks, 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; Franks, 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) advective losses, (2) shrinking habitat due to the rise of the oxycline, or (3) match-mismatch during the succession of upwelling → phytoplankton bloom → zooplankton grazing → zooplankton population growth in developing upwelling lenses and filaments. The theoretical implications and possible mechanisms of prey-predator match-mismatch have been reviewed elsewhere (e.g. Durant et al., 2007). Very strong upwelling may also produce adverse physical-chemical conditions in recently upwelled water (steep temperature gradients, low oxygen, high ammonia concentrations, etc.). This “intermediate upwelling” hypothesis may also be relevant to interannual variability. Accordingly, minimum zooplankton abundance from 1970 to 1976 coincided with long periods with strong La Niña (LN) conditions (Fig. 3), when upwelling intensity was maximal.

The large interannual variability in biomass and species composition off Peru was first shown by Santander (1981). Long-term observations are so far only available as zooplankton volumes (1964–2002; Ayón et al., 2004). The relatively large meshed (300 μ m) net used to collect these samples does not quantitatively collect smaller zooplankton that likely dominate the nearshore region. Ongoing research is testing capture efficiencies for smaller mesozooplankton (comparing 300 and 200 μ m net catches under different conditions), to determine if biases are stable for given taxa. If so, historical zooplankton collections can be reanalyzed. Carrasco and Lozano (1989) presented abundance data from 1964 to 1987 for the northern, central and southern Peruvian coast and recognized a decline. During the 1983 EN copepod abundance between 6°S and 12°S decreased to 1/6 of values for 1977–1981. Nearer the equator (3–6°S), copepod abundance was higher due to advection of larger equatorial species. Ayón et al. (2004) extended this series to 2002 (Fig. 3). The long-term trend of annual mean zooplankton volume, from 1964 to 2001, displayed three different periods: maximum values from 1964 to 1973, a collapse after 1973, low values from 1974 to 1989 (although the recovery seems to start in 1985), and an intermediate level of biovolumes from 1990 to 2002 (Ayón et al., 2004).

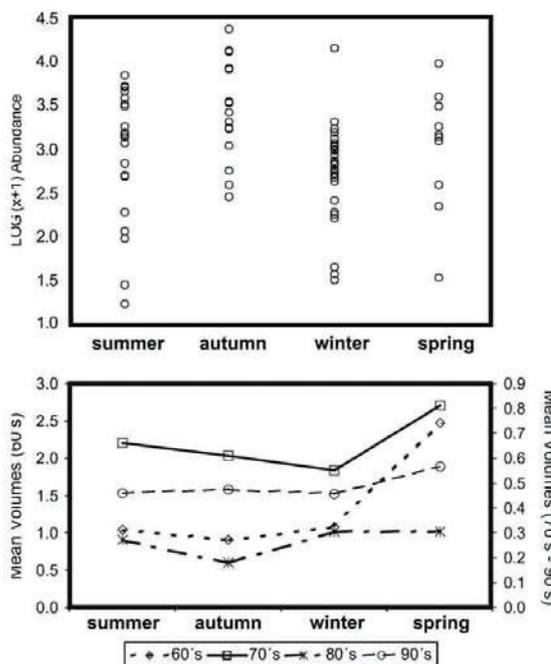


Fig. 2. Seasonality of zooplankton abundance and biovolumes off Peru. Above: seasonal variation of log total zooplankton abundance off Paíta, northern Peru, from August 1994 to December 2004 (modified from Aronés et al., in press). Below: mean seasonal zooplankton volumes off Peru for four decades, since 1964. Note that the scale of the ordinate in the 1960s differs from that of the 1970s and 1990s (Ayón et al., 2004).

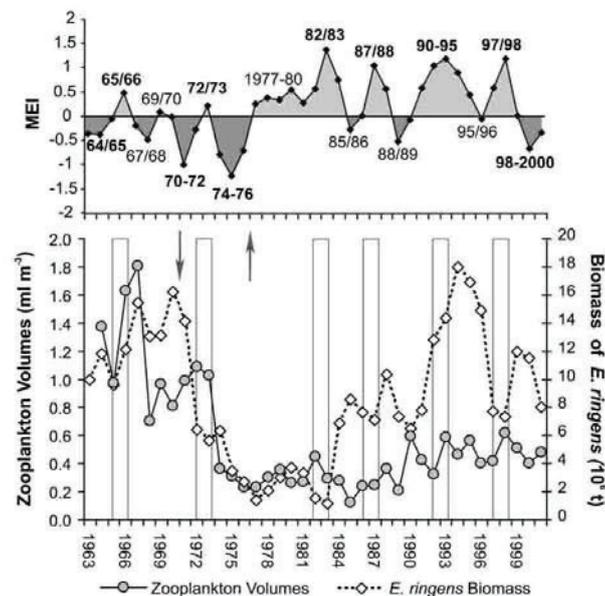


Fig. 3. Mean annual tropical Pacific Multivariate ENSO Index (MEI), zooplankton volumes, and biomass of Peruvian anchoveta (*Engraulis ringens*) from 1963 to 2001. Above: the MEI time series shown is the annual average calculated from the original bimonthly MEI series (Wolter and Timlin, 1998). The variables used to calculate the MEI are: sea-level pressure (P), zonal (U) and meridional (V) components of the surface wind, sea surface temperature (S), surface air temperature (A), and total cloudiness fraction of the sky (C). Original data are 2-degree-cells from the tropical Pacific (30°N–30°S) taken from the COADS data base (<http://www.icoads.noaa.gov>). El Niño periods are highlighted above; La Niña periods are shown below zero. Source: <http://www.cdc.noaa.gov>. Below: average zooplankton volumes from more than 10,000 samples taken from the Peruvian coast to 300 nautical miles offshore. Values of 1979 and 1988 were interpolated with a 5-year moving average [according to Ayón et al. (2004), modified]. Strong El Niño events are shown as vertical bars. Arrows indicate global sea surface temperature regime shifts in 1970–1971 and 1976–1977 (Yasunaka and Hanawa, 2005).

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 60s, 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 1976–1977 (transition from the strong 74–76 LN to EN 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. 3). 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 climatic 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 1999 or 2000 apparently affected pelagic ecosystems in the north-eastern (Greene, 2002; Mackas et al., 2004; Litzow, 2006), north-western (Rebstock and Kang, 2003; Tadokoro et al., 2005), and south-eastern Pacific (Aronés 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., 2003; Litzow, 2006; Gutiérrez et al., 2007). An analysis of spatial distribution of anchovies and sardines off Peru also showed a dramatic shift after the 1997–1999 ENSO (Gutiérrez et al., 2007). Although sardines were already declining and anchovies had been increasing in biomass before 1999, Gutiérrez et al. (2007) concluded that “since 1999, 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 euphausiid abundance, which at least off northern Peru, showed an abrupt increase after 1999 (Aronés 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

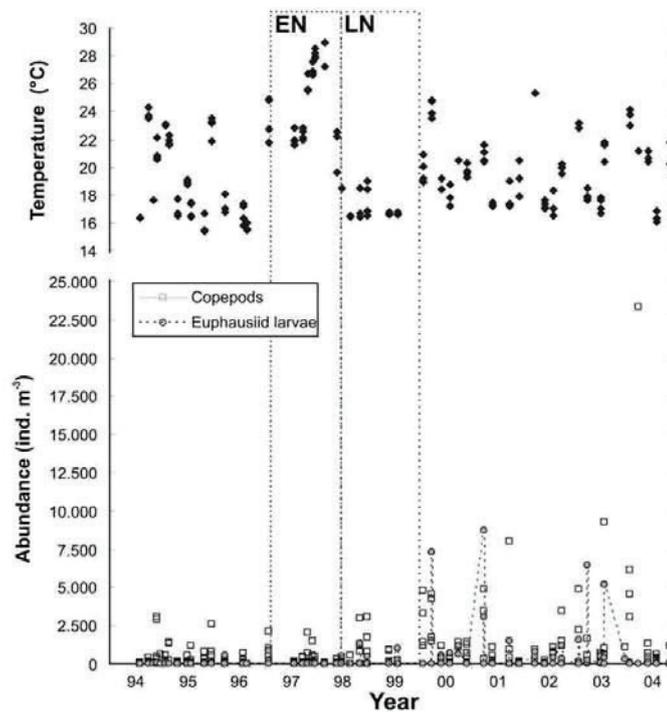


Fig. 4. Temporal variation of surface water temperature and subsurface abundance of copepods and euphausiid larvae off Paíta, northern Peru, from August 1994 to December 2004. EN, El Niño 1997/1998; LN, La Niña 1998/1999. Source: Aronés et al. (in press).

the effect of the diel cycle, other environmental factors, and biological interactions on biovolume. The CART results showed a strong negative impact of anchovy but not sardine biomass on zooplankton. Additionally, zooplankton biovolume was higher offshore than on the shelf and was higher when SST was above 21.2 °C for some years and months. GAM results corroborated the CART.

4.5. Pelagic macrocrustaceans (Euphausiacea and Decapoda)

Two pelagic macrocrustaceans are characteristic of the Peruvian Humboldt Current System (HCS): *Euphausia mucronata* (or 'krill'; Escribano et al., 2000; Antezana, 2006), and the galatheid crab *Pleuroncodes monodon* ('red crab', 'squat lobster', 'langostino colorado', or 'munida'). These species can be very abundant (Antezana, 2002a,b; Bertrand et al., 2005) and thus likely interact with the even larger biomass of *Engraulis ringens* (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 (Mejía 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 (Luciferidae, Sergestidae, Penaeidae, and Caridea; Criales and McGowan, 1994; Schwaborn et al., 1999; Schwaborn et al., 2001; Martins et al., 2005; Koetker and Freire, 2006) and occur off Peru (Fernández-Álamo and Färber-Lorda, 2006, Table 4), there is little information on these groups. Hendricks and Estrada-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 euphausiid research focused on taxonomy (Santander, 1967; Santander and Sandoval de Castillo, 1969; Ponomareva,

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 furcilia and calytopis larvae (Aronés et al., in press). Antezana (1978, 2002a,b) studied the distribution of *Euphausia mucronata* 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 HCS.

The distribution of red crab extends from Chiloe Island (43°S) off Chile to 7°S off Peru (Haig, 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. Haig, 1955; Palma, 1976; Gutiérrez and Zúñiga, 1977; Bustos et al., 1982; Gallardo et al., 1993, 1994; Palma, 1994; Rivera and Santander, 2005). The biology of red crab in Peruvian waters is not well known (Segura and Castillo, 1996; Chimpén, 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

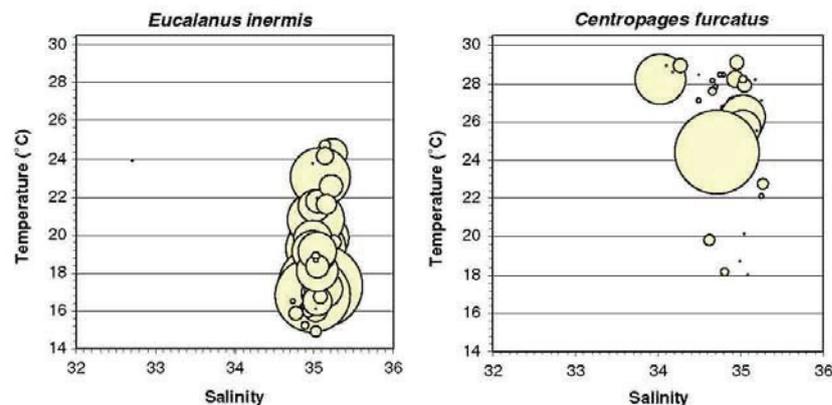


Fig. 5. Temperature–salinity diagrams of waters sampled at surface off Callao and San José, Peru, from 1994 to 2004, with superimposed abundances of the copepods *Eucalanus inermis* and *Centropages furcatus*. Samples were taken off Callao, San José from 1994 to 2004 with WP-2 hauls. From Abanto, 2001).

1940s. According to Gutiérrez et al. (2008), *P. monodon* became highly abundant along the Peruvian coast after the 1997–1998 EN. Biomass ranged between 0.6 and 3.4×10^6 t from 1998 to 2005 (acoustic estimates in Gutiérrez et al., 2008) in upwelled nearshore waters where red crab are preyed on by seabirds, mammals, and fish (anchovy preys on red crab zoeae). 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. Meroplankton

Meroplanktonic larvae of benthic invertebrates (e.g. Decapoda, Cirripedia, Mollusca, Polychaeta) constitute an important fraction of the zooplankton, especially nearshore (Ciraless-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 (1975), follow an r-strategy and produce huge numbers of larvae, few few of whom return to shore.

The meroplanktonic larvae of many commercially important benthic organisms remain largely undescribed. The distribution of pelecypod larvae has been described for two cruises 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 “scallop outbursts” 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 meroplankton 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 huge densities nearshore, specifically in Independencia Bay (M. Wolff, personal communication). Yamashiro et al. (1990) evaluated larval stocks in Independencia Bay. The meroplankton was comprised of brachyuran zoeae, brachiopod, gastropod, and polychaete larvae, together with young pteropods and euphausiid larvae. Tidal fluctuations in larval abundance were also observed. Macro-invertebrate settlement in this bay during the 1997–1998 EN has been described by Ramos et al. (1999) by determining recruitment to artificial substrates. *Argopecten purpuratus* only settled during EN, together with warm water turritiform gastropods. In contrast, the bivalve *Hiattella solida*, the turbellarian *Notoplana* sp., and the gastropod *Caecum chilense* settled mainly during the preceding cold period. A third group, comprised by the brachiopod *Discinisca lamellosa*, the echinoderm *Ophiactis kroyeri*, and mytilid bivalves, settled only at the very onset of EN (March 1997). 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 *Pteria sterna* 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. Costlow and Fagetti, 1967; Quintana, 1983; Dittel and Epifanio, 1984; Quintana and Saelzer, 1986; Báez and Martín, 1992; Báez, 1997; Wehrmann and Báez, 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 25% of the daily primary production.

During the cruises of the Institute of Oceanology in 1974, attempts were made to describe plankton community dynamics (Vinogradov and Shushkina, 1978; Flint and Timonin, 1985) and to estimate zooplankton production (Shushkina and Kislyakov, 1977). Drits (1985) measured the ingestion rate of *Calanus australis* under natural conditions and studied the content of the gut and faecal pellets. Mikheyev (1977a) described 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 (Mikheyev, 1977b). Flint and Timonin (1985) assessed 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 ^{14}C -labelled phytoplankton and applying a mathematical simulation of a trophic model (Shushkina and Kislyakov, 1977). According to Petipa 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 CUEA. According to Cowles (1978, 1979), prey size selection by copepods depended food abundance. Smith et al. (1981a,b) measured ingestion rates of *Acartia tonsa*. Dagg et al. (1980) measured rates of ingestion and excretion of *Calanus chilensis*, *Eucalanus inermis*, and *Centropages brachiatus*, assessing the particle spectrum with a Coulter Counter. As these large species ingested <5% of primary production, the authors suggested that smaller zooplankton must consume most primary production. Boyd et al. (1980) studied prey selectivity by *Eucalanus*, *Calanus*, and *Centropages*. They found that *Calanus* sp. is a non-selective phytophage, while *Centropages* sp. and *Eucalanus* sp. were omnivorous feeders. Furthermore, *Eucalanus* sp. did not feed at the surface at night, but only during the day on OMZ detritus. Nitrogen regeneration during a red tide was measured by Smith (1978), who estimated that mesozooplankton recycled 1–25% of the nitrogen needed to support phytoplankton production. Espinoza and Bertrand (2008) have recently emphasized that in carbon units, 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 MacIsaac (1971) and Walsh and Dugdale (1971), who simulated nitrate uptake and flow through the Peruvian upwelling system. Energy budgets for the pelagic system were established by Sorokin and Mikheev (1979), using data obtained during the cruises of the Institute of Oceanology in 1974. Walsh (1981) established a carbon budget to understand changes in the carbon flow through the coastal upwelling system after the crash of the anchovy fisheries in the early 70s. Jarre et al. (1991) presented mass balance models (ECOPATH II) for modeling fish stock interactions in the Peruvian upwelling ecosystem, which included also a zooplankton component. Jarre-Teichmann (1998) investigated explored trophic structure with steady-state, mass-balance models (ECOPATH II). 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 ecosys-

tem (zooplankton and, to some extent, phytoplankton and detritus), while sardine abundance is out of phase. Jarre-Teichmann (1998) concluded that mobility differences between the two species, with sardines relying on their better swimming capability (Bakun and Broad, 2003) to find suitable forage during periods of decreased productivity at lower trophic levels. However, more recent studies emphasize that the major reason for alternation 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 1996 through 1998 at 9.5° off the coast of Peru. The numerical experiments illustrate ecosystem responses to the evolving conditions associated with EN and LN 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, macrocrustaceans and main trophic links, e.g. between anchovies and euphausiids, older models neglect important ecosystem components. Recent trophic models built using the Ecopath with Ecosim (EwE) software focus mainly on commercially important fish and invertebrate stocks. These models do include more recent stomach content data for anchovy (Tam et al., 2006; Taylor et al., 2006; Wolff 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., 2004b) also do not consider phytoplankton–zooplankton interactions, again showing the need for new data and modelling directed 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 holo- and meroplankton 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 benthic–pelagic coupling and the role of meroplankton, 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, 1968; Smith, 1977; Lenz, 2000), and are typically dominated by protozoa (rotifers, foraminiferans, radiolarians, ciliates, and flagellates) and copepod eggs and nauplii. Protozoan communities are often mixotrophic or of unknown trophic status. They are generally not caught by zooplankton nets, but may be quantified in bacterio- and phytoplankton studies, which may lead to a considerable overlap between bacterio-, phyto-, and zooplankton studies regarding these groups. Microzooplankton can be intense grazers on bacteria and phytoplankton with extremely high production/biomass ratios (Kjørboe, 1997; 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 (Escribano et al., 2004).

The few studies available are all based on single cruises, usually with few stations. Tumentseva 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 P/B ratio was 1.26 day^{-1} , indicating biomass was more than doubling each day. *Urotricha marina* underwent 8–11 divisions/day. Vinogradov et al. (1980) found similar results and pointed out the importance of microzooplankton production. Heterotrophic microplankton was also studied by Sorokin (1978) and Klekowski et al. (1975), who determined respiration rates of microzooplankton in the equatorial and Peruvian upwelling systems. Sorokin and Kogelschatz (1979) studied the role of heterotrophic microplankton 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 microheterotrophic 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. Tintinnids 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 analyzed 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, biovolume 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 CRIOS 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 diatom blooms on zooplankton population dynamics, physical and trophic processes in fronts and upwelling filaments, etc.).

On the long-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 scale 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 at the very least 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, ctdo, fluorescence probe, acoustical and optical plankton counters) anchored at appropriate locations along the shelf (Dickie and Valdivia, 1981). Process studies could then be embedded in such a mooring array.

The use of autonomous profiling floats (Roemmich et al., 2004), autonomous underwater vehicles (AUVs, Curtin et al., 1993; Griffiths 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 (Menshutkin 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 diatom 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 “longer than some months ahead may be beyond reach” (Bohle-Carbonell, 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. Penland and Matrosova, 2001; Chen et al., 2004; Cash et al., 2006) and in understanding the intrinsic relationship between ENSO and multi-decadal cycles (Yasunaka and Hanawa, 2005; Ye and Hsieh, 2006). Individual-based Lagrangian models can integrate physical, biogeochemical and biological data (Leising and Franks, 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 (Batchelder et al., 2002; Carr et al., 2008). 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.

Acknowledgements

We would like to thank the Area de Evaluación Producción Secundaria team at IMARPE for their invaluable cooperation in building up the necessary references for this work. Thanks to Mark Taylor, Francisco Chavez, David Mackas, and two anonymous reviewers for improving the original text with important

comments and suggestions. This work is a contribution of the Zooplankton Study Group at IMARPE, and was conducted in the frame of the EU-project CENSOR (Climate variability and El Niño Southern Oscillation: impact for natural resources and management, contract 511071). It is CENSOR publication no. 87. This paper forms part of the Ph.D. Thesis of the second author at Bremen University.

References ♦

♦ 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

M.I. Criales-Hernández¹, R. Schwamborn², M. Graco¹, D. Gutierrez¹, P. Ayón¹, H.-J. Hirche³ and M. Wolff⁴

1: Instituto del Mar del Perú, Lima, Peru

2: Zoology Dept., Federal University of Pernambuco, Recife, Brazil

3: Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany

4: Charles Darwin Foundation, Galapagos, Ecuador

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 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

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_hm/indexes).

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

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 Weaver, 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 $\alpha = 0.05$ 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 brachiatus* (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

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 *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

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 (Aronés 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

migration pattern, with adults constricted to well-oxygenated upper layers and nauplii developing inside the OMZ (Criales-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, Criales-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*, euphausiids 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, Criales-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,

1987, Escribano et al., 2004, Arónes et al., 2009). 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 *Pleuromcodes 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

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.

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 Nino 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 $\alpha = 0.05$.

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 ($^{\circ}C$), 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

zooplankton 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 brachiatus*, and (c) *Eucalanus inermis*.

Table 1.

Taxa	Density (ind m ⁻³)		Abundance (%)	Frequency (%)	Spearman Correlation			
	Average	Max			DC	OMZ	MEI	
	<i>Acartia tonsa</i>	673.8	4537.2	0.47	49	89	n.s.	n.s.
<i>Centropages brachiatus</i>	166.1	1467.9	0.04	12	87	0.33	0.33	n.s.
<i>Eucalanus inermis</i>	24.2	222.5	0.02	2	86	0.53	0.36	n.s.
<i>Engrulis ringens</i>	104.3	1370.4	0.08	7	80	-0.38	n.s.	n.s.
<i>Paracalanus parvus</i>	266.3	3712.5	0.02	18	80	n.s.	0.24	n.s.
<i>Pleuromcodes monodon</i> zoeae	13.7	197.7	0.01	1	86	0.31	0.29	n.s.
<i>Oncaea venusta</i>	7.4	93.2	0.01	<1	82	n.s.	0.34	n.s.
Cirripedia larvae (nauplii and cypri)	29.6	499.6	0.01	2	79	-0.48	n.s.	n.s.
<i>Emerita analoga</i> zoeae	1.4	11.4	0.01	<1	80	n.s.	n.s.	0.3
<i>Hemycyclops thalassius</i>	18.9	618.0	0.00	1	76	-0.33	n.s.	n.s.
<i>Pleopis polyphemoides</i>	14.9	202.5	0.01	<1	65	n.s.	n.s.	n.s.
Lophadorinchiidae larvae	2.9	95.3	0.01	<1	66	n.s.	n.s.	n.s.
Porcelanids zoeae	0.7	9.7	0.01	<1	63	-0.37	n.s.	n.s.
<i>Magelona</i> sp. Larvae	21.4	422.1	0.01	1	66	n.s.	-0.3	n.s.
Brachyuran zoeae	1.3	43.3	0.00	<1	61	-0.48	n.s.	-0.3

Table 2.

Source of variation	Independent Variable	d.f.	p	Max	Min
Season	Density (ind m ⁻³)	3	n.s		
	Bio volume (ml m ⁻³)	3	n.s		
	Biomass (g m ⁻³)	3	n.s		
	Evennes	3	0.04	Winter	Autumn
	Diversity	3	0.0257	Winter	Autumn
ENSO	Density (ind m ⁻³)	2	0.0147	LN	EN
	Bio volume (ml m ⁻³)	2	0.0242	EN	LN
	Biomass (g m ⁻³)	2	0.0115	EN	LN
	Evennes	2	0.0008	ENSO Neutral	ENSO Neutral
	Diversity	2	0.0003	ENSO Neutral	ENSO Neutral

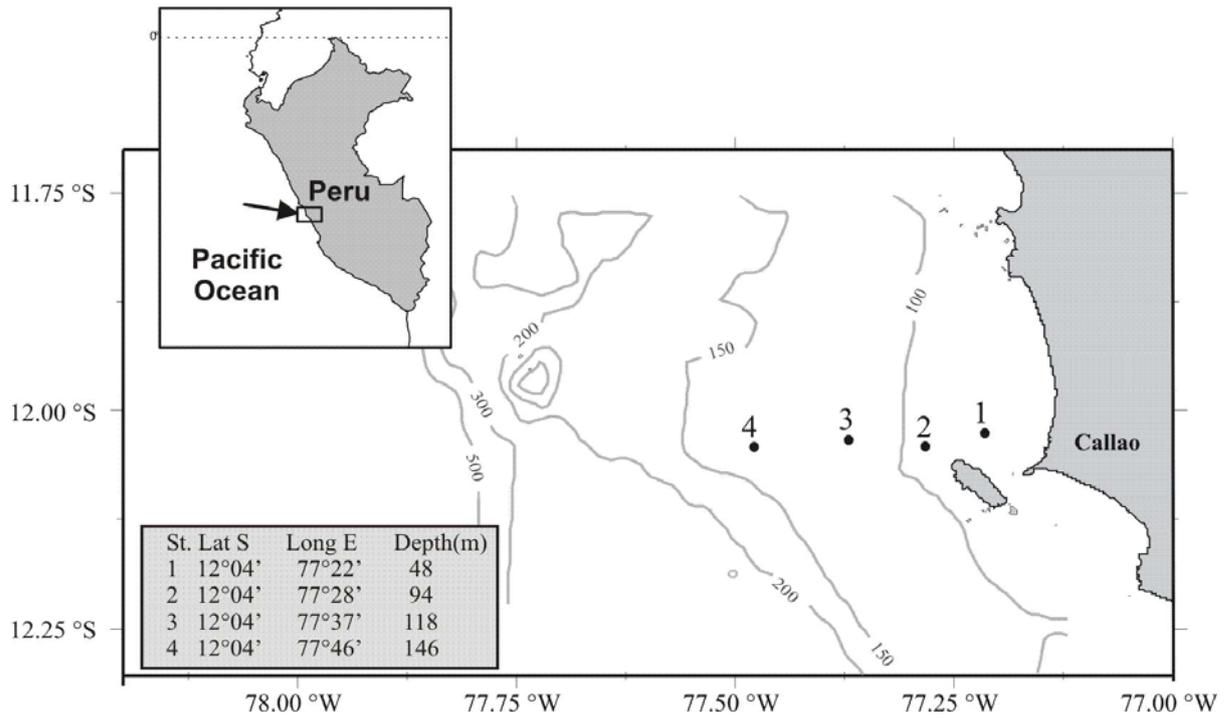


Figure 1.

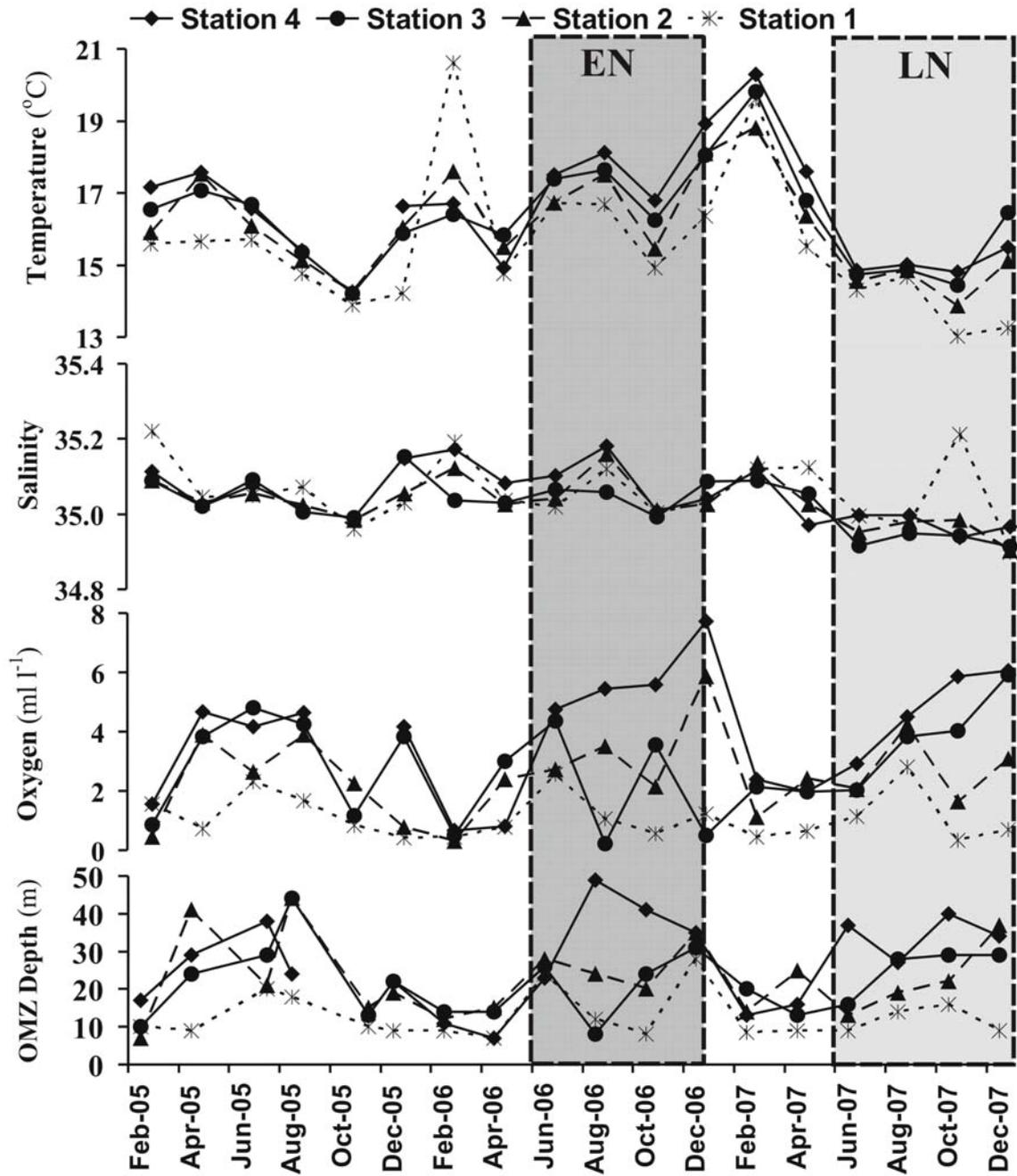


Figure 2.

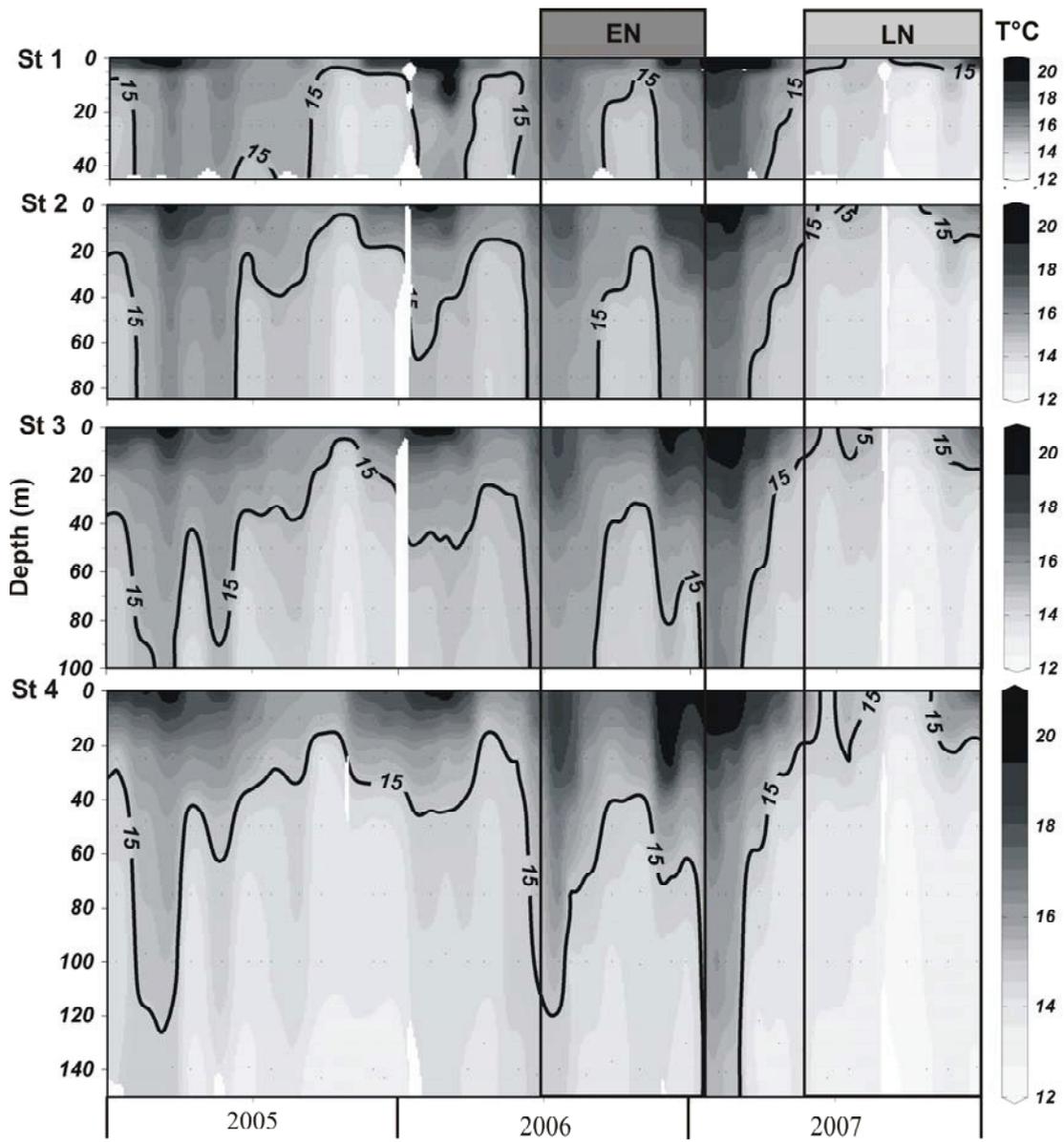


Figure 3.

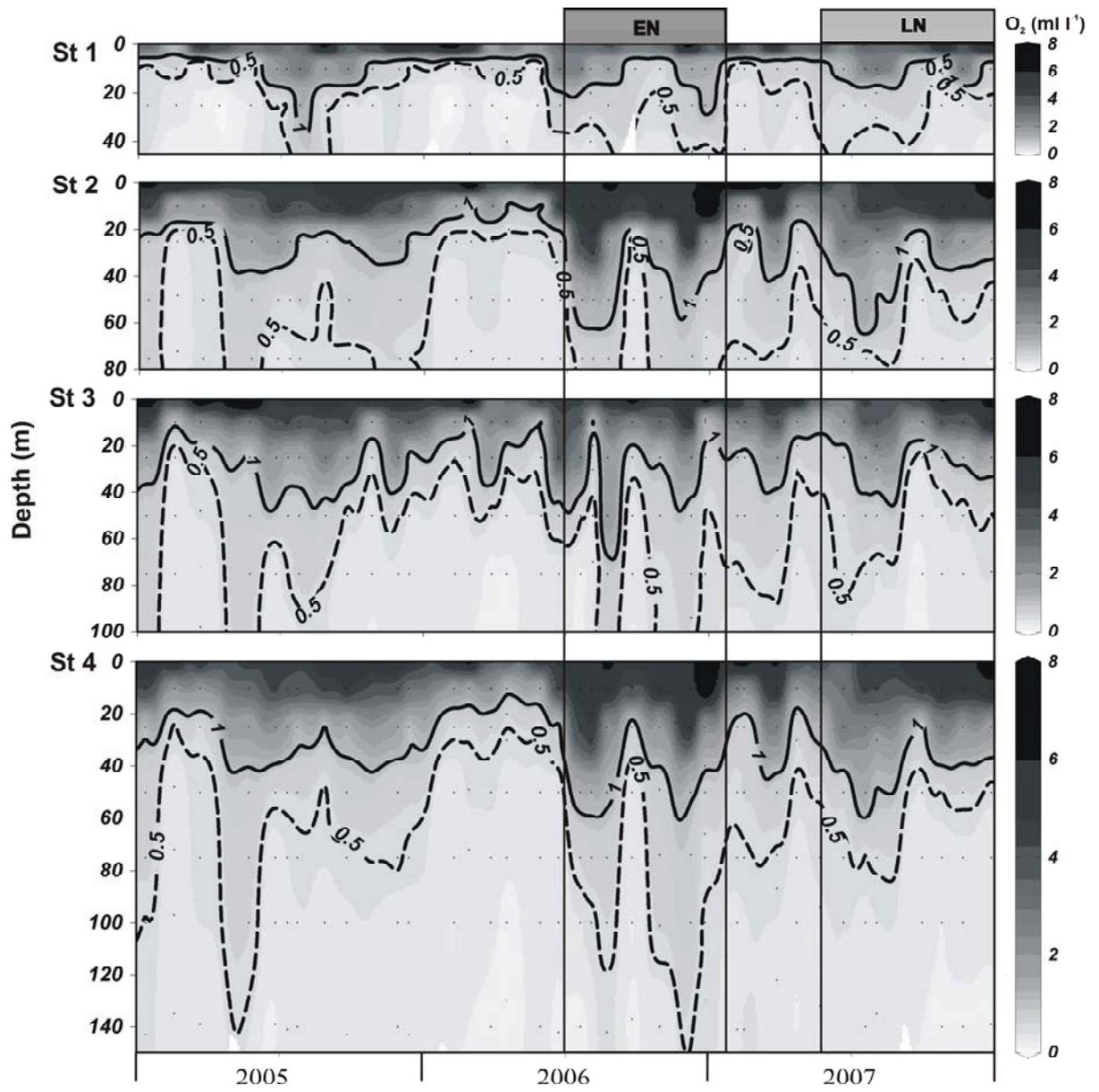


Figure 4.

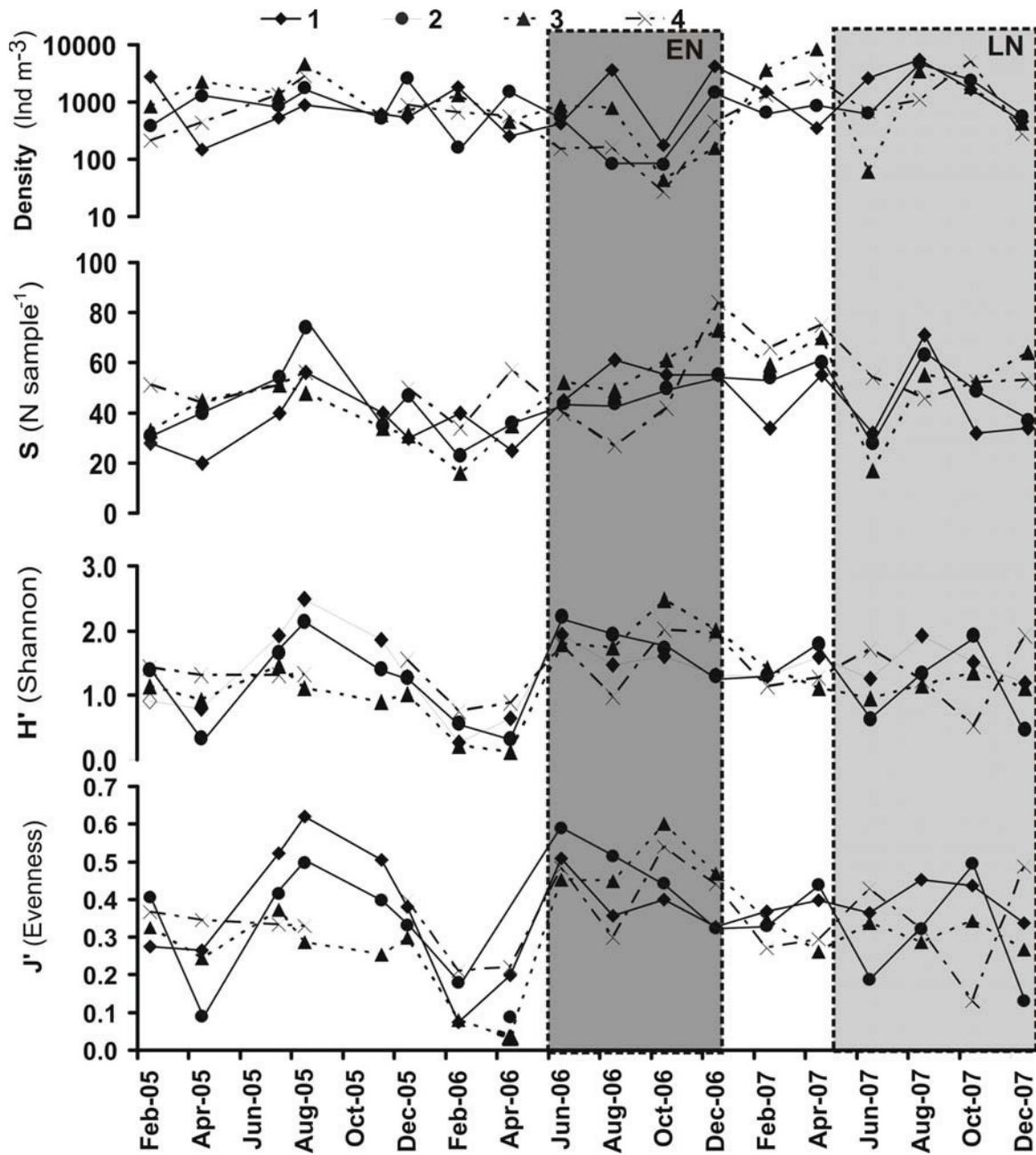


Figure 5.

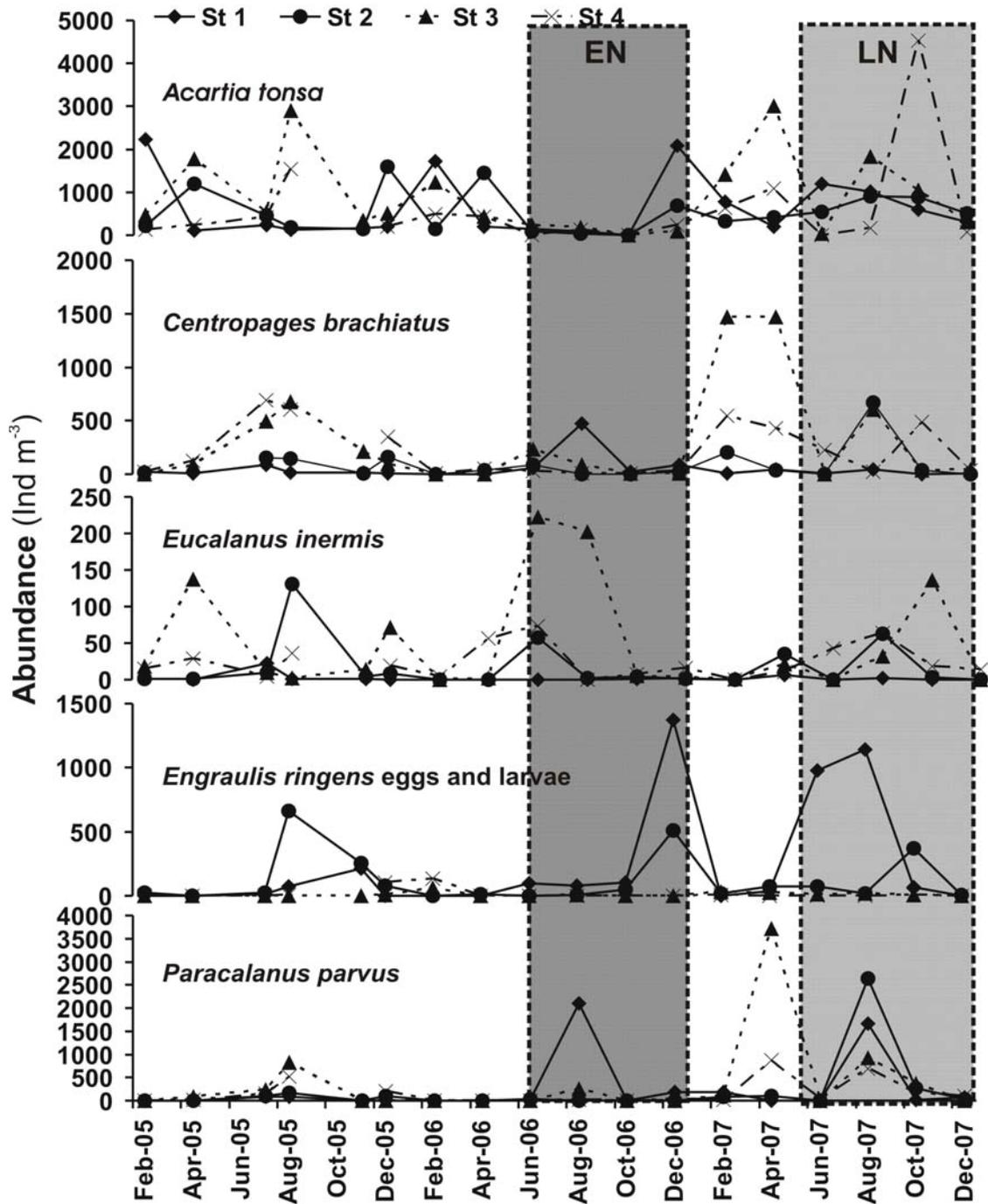


Figure 6.

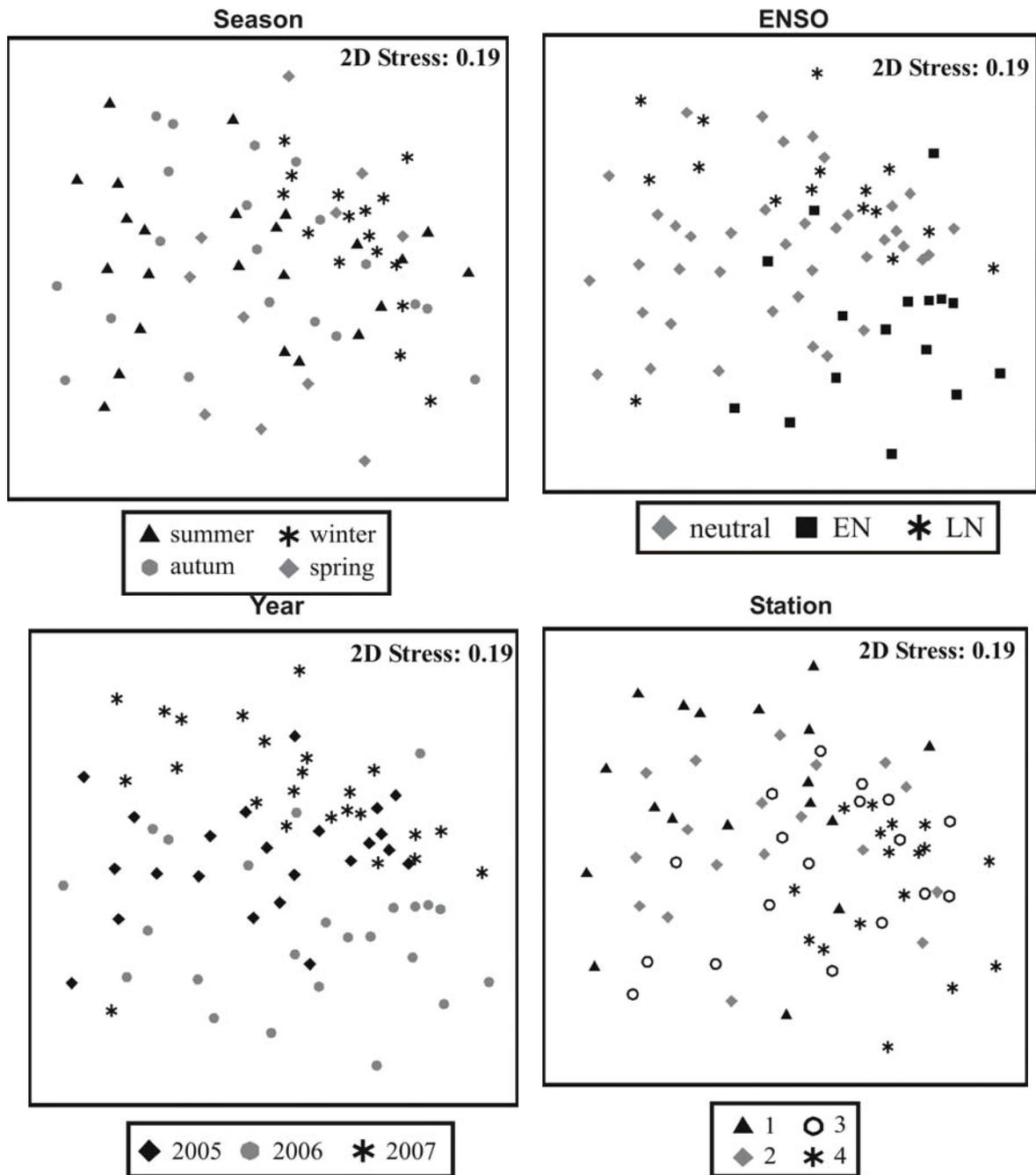
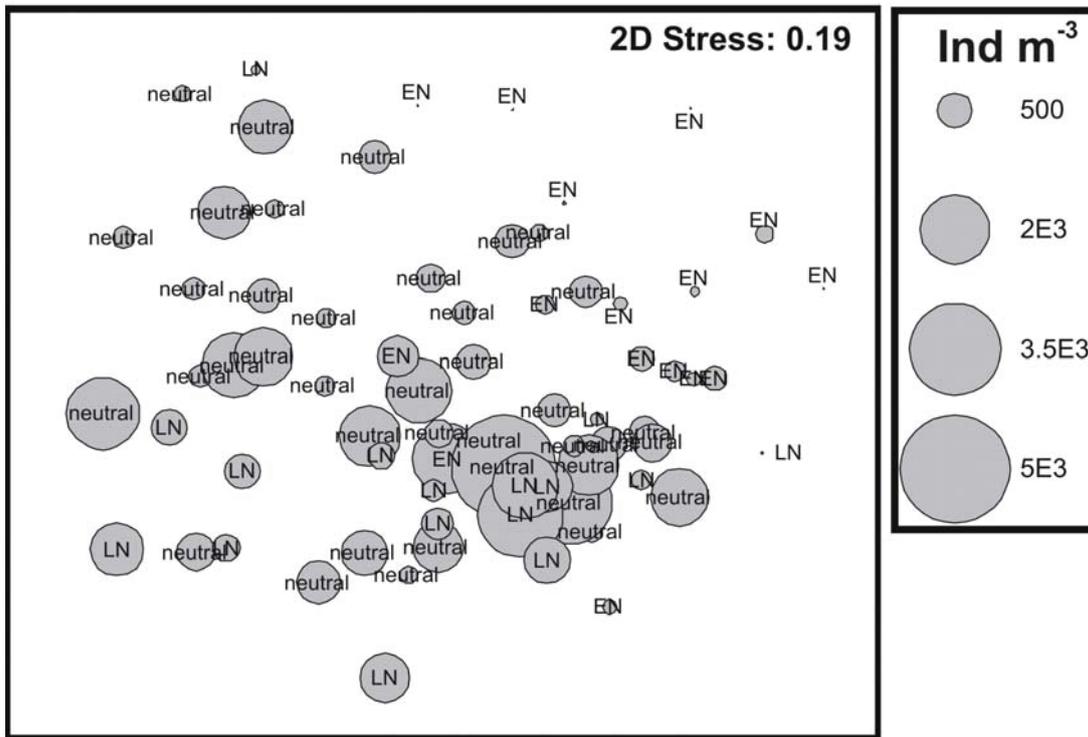


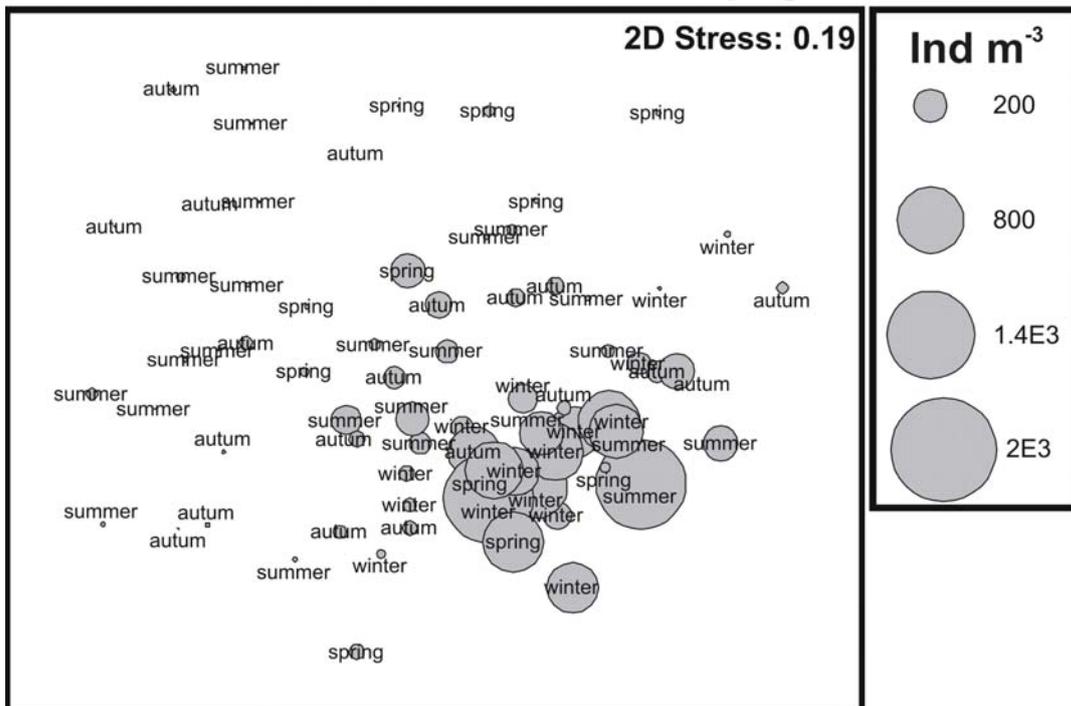
Figure 7.

ENSO Phases and Abundance of *Acartia tonsa*



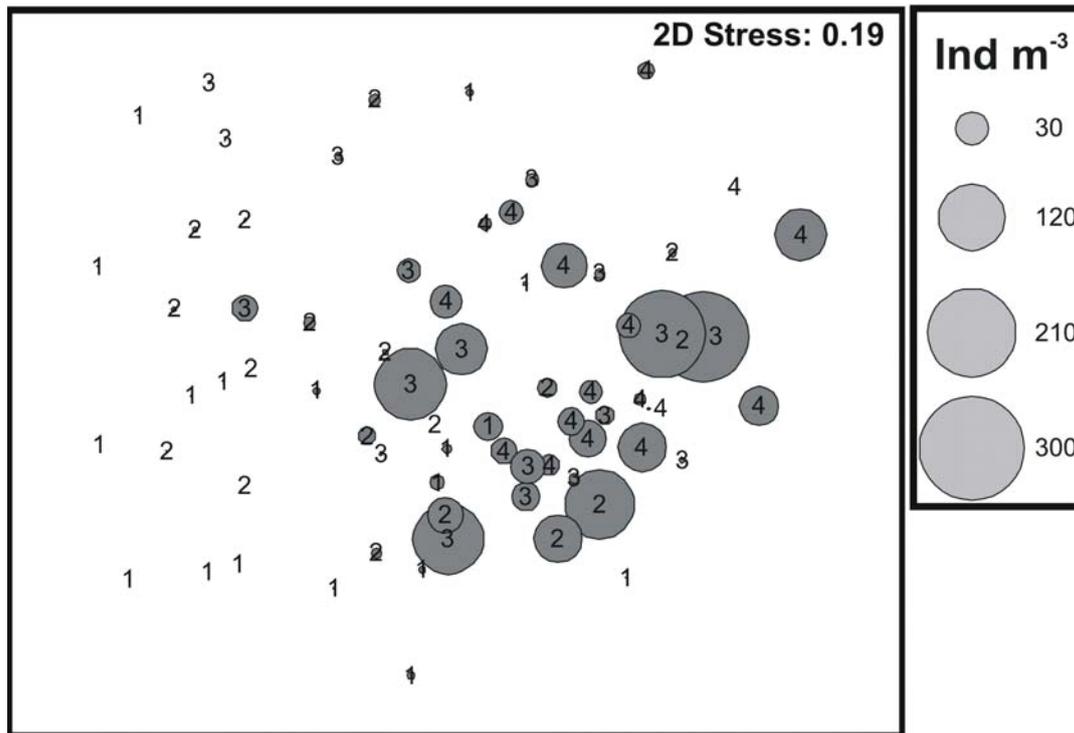
a)

Seasons and Abundance of *Centropages brachiatus*



b)

Stations and Abundance of *Eucalanus inermis*



c)

Figure 8.

5.3 Scientific contribution

Helgol Mar Res (2008) 62 (Suppl 1):S85–S100
DOI 10.1007/s10152-007-0094-3

ORIGINAL ARTICLE

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. Hirche · M. Wolff

Received: 31 May 2007 / Revised: 10 September 2007 / Accepted: 1 October 2007 / Published online: 23 November 2007
© Springer-Verlag and AWI 2007

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 Hydro-Bios multi-net (300- μm mesh, 0.25- m^2 mouth size). The zooplankton community was distributed in relation to a strong, shallow oxycline (1 ml l^{-1} oxygen isopleth 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 brachiatus* (7.5%), and *Paracalanus parvus* (3.1%); *Acartia tonsa* was the dominant species at all times. Larvae of the polychaete *Magelona* sp. (7.5%) and larvae of the brachiopod *Discinisca lamellosa* (3.5%) were numerically dominant in April and small copepods e.g. *Oncaea venusta* (3.88%) 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. *Oikopleura* sp., most invertebrate larvae), (3) distribution mostly below the oxycline with occasional migration into the layers just above the oxycline (*Eucalanus inermis*), (4) Diel Vertical Migration (*Centropages brachiatus*), and (5) reverse Diel Vertical Migration (larvae of the polychaete *Magelona* 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. 2003; Alheit and Niquen 2004). Another characteristic of this region is a well-developed oxygen minimum layer (Wyrki 1967; Judkins 1980; Mackas et al. 1981), which occurs nearly continuously in most of the Humboldt Current System (Zuta and Guillen 1970; Heinrich 1973; Calienes and Guillen 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 these regions. Judkins (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

Communicated by S. Thatje.

Communicated by: Sven Thatje. Special Issue: Climate variability and El Niño Southern Oscillation: implications for natural coastal resources and management. S. Thatje (ed.)

M. I. Criales-Hernández (✉) · M. Graco · P. Ayón
Instituto del Mar del Perú, Lima, Peru
e-mail: micriales@imarpe.gob.pe

R. Schwamborn · H.-J. Hirche
Alfred Wegener Institute for Polar and Marine Research,
Bremerhaven, Germany

R. Schwamborn
Zoology Department,
Universidade Federal de Pernambuco, Recife, Brazil

M. Wolff
Center for Tropical Marine Ecology, Bremen, Germany

 Springer

copepod and non-copepod faunal zones. Antezana (2002) described the vertical migration patterns of *Euphasia mucronata*. 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; Sameoto 1981). This behaviour is similar to other species in the eastern South Pacific where adult populations are mostly above 50 m in both oceanic (Longhurst 1967; Flint 1975; Saltzman and Wishner 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 diel vertical migration performed by the deep-dwelling *Eucalanus inermis* (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 (Oncaeidae, Oithonidae, small Calanoida) 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 Oncaeidae. 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. inermis*, *Calanus* sp. and *Centropages brachiatus*, show different patterns of diel 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; Pearre 2003), only a few studies were

conducted explicitly considering and testing the fluctuations in cline depths (Haury et al. 1983; Trevorrow 1998; McManus et al. 2005), or testing the effect of specific abiotic variables on migrating organisms (Cohen and Forward 2002; Renz and Hirche 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 patterns 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°02.03S 77°17.32W and 12°02.4S 77°39.1W, respectively). It is an open shore area (Fig. 1), wherein a widening of the shelf is observed (Carrasco and Lozano 1989). The stations are located in an upwelling zone with elevated levels of primary production during most of the year (Zuta and Guillen 1970). Station 2 is located on the nearshore shelf at 93-m depth, while station 5 is located further 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 tows were taken with a multi-net (Midi model, 50 × 50 cm mouth size, Hydro-Bios,

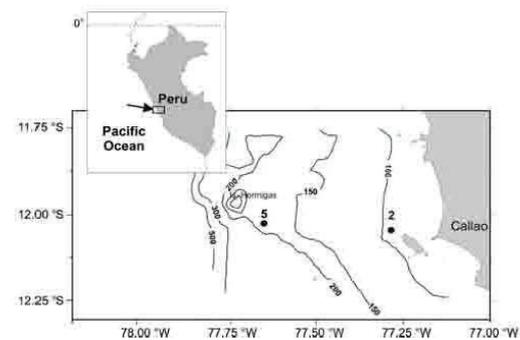


Fig. 1 Map of the study area off Central Peru showing both sampling stations

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) 50–30 m, (3) 30–20 m, (4) 20–10 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 (Haardt, Kiel), and an optical oxygen sensor (Aanderaa 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 rosette 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 Guelpen Louis et al. 1982). 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; Banse and Hobson 1974; Alborno and Wehrmann 1997; Pohle et al. 1999; Thuessen and Fernandez 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 l^{-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^{-2} .

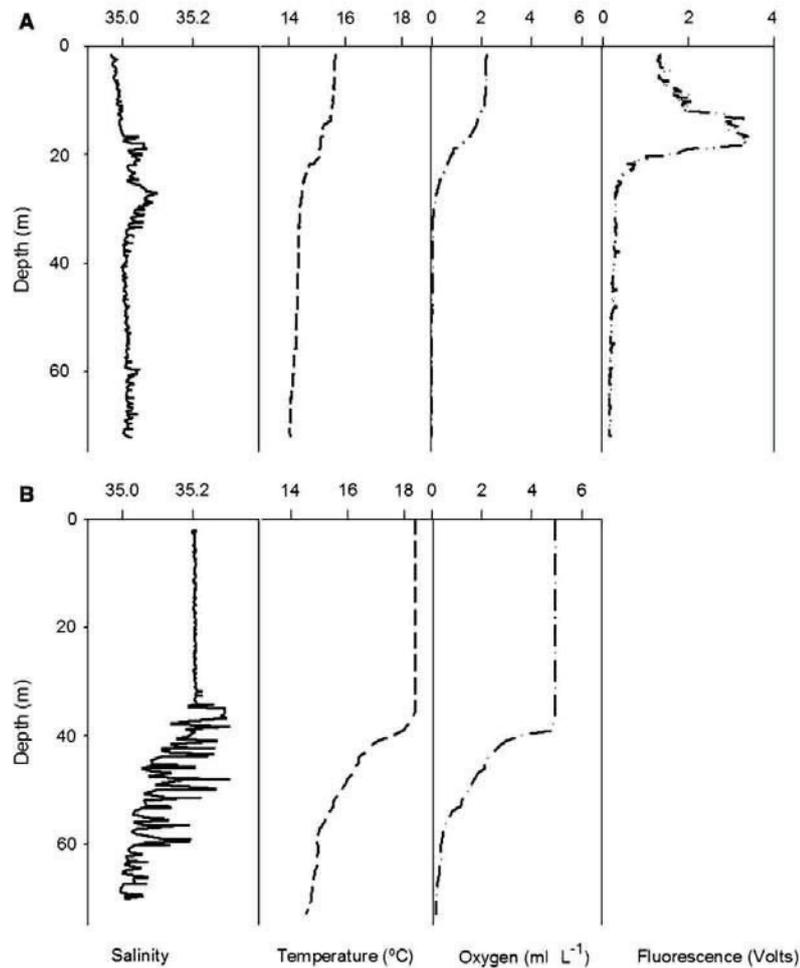
By comparing changes in weighted mean depth and P_{oxy} , we were able to distinguish and ascertain which organisms potentially exhibit migration in relation to daytime and oxycline dynamics. Specifically, we tested our data for diel vertical migration (significant differences in WMD between day and 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 were due to daily fluctuations of cline depths, thermo- and oxycline depths (depths of the 15°C isotherm and 1 ml l^{-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 ($n = \text{up to } 120$). Spearman correlations were also calculated between weighted mean depth, P_{oxy} , and the depths of the 15°C isotherm and 1 ml l^{-1} oxygen isopleth, for the main taxa and stages, using one value per multinet haul ($n = \text{up to } 24$). 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

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 $15 \pm 4 \text{ m}$), while Z_{oxy} was clearly deeper at station 5, varying between 14 and 36 m (average $21 \pm 9 \text{ m}$). 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 ($>17^\circ\text{C}$) 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).

Thermo- and oxycline depths (Z_{oxy} and Z_{therm}) 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_{therm} 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, thermo- and oxyclines

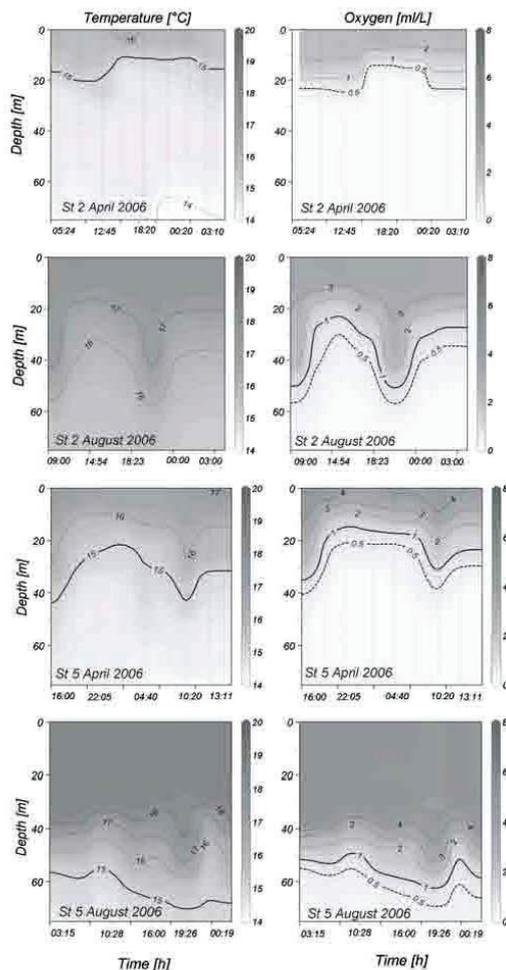


Fig. 3 24-h variation of the vertical distribution of temperature and oxygen concentration at stations 2 and 5 off Central Peru in April and August 2006

displayed a major elevation during the night and only a lesser peak around noon; thus, Z_{oxy} and Z_{therm} were generally slightly deeper during the day. However, comparisons of Z_{oxy} and Z_{therm} 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 $25,090 \pm$

$14,090 \text{ ind. m}^{-2}$ at station 2 and $24,654 \pm 12,867 \text{ ind. m}^{-2}$ at station 5. In August, zooplankton abundance was only $9,331 \pm 2,613 \text{ ind. m}^{-2}$ 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).

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_{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_{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_{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 ($P = 0.02$, $n = 8$) and at station 2 in August ($P = 0.04$, $n = 8$), 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_{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 brachiatus* (7.5%), *E. inermis* (4.7%) and *Paracalanus parvus* (3.1%) were also important among the catches (Table 1). *Oncaea 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 *Magelona* 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

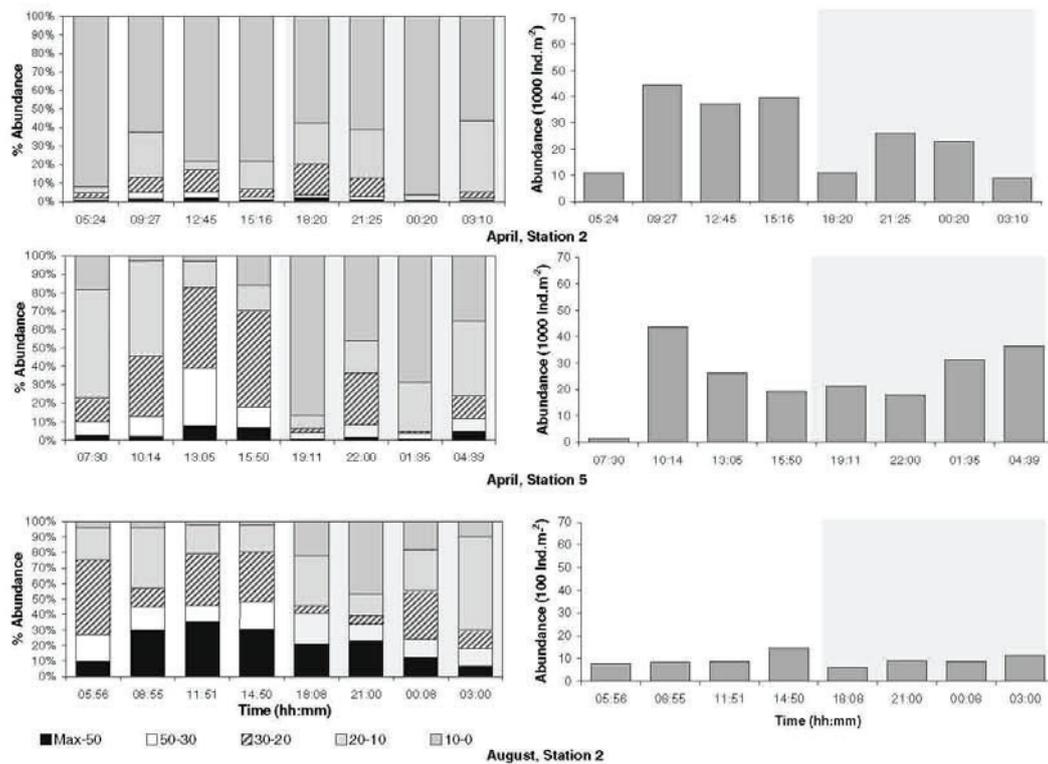


Fig. 4 Depth-integrated abundance of bulk zooplankton per stratum sampled off Central Peru in 2006. The shaded area indicates night samples

of *Discinisca 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 meroplanktonic organisms such as eggs of *Engraulis ringens* (3.8%, up to 350 ind. m⁻³) and zoeae of *Pleuroncodes monodon* (6.4%, up to 585.4 ind. m⁻³).

The Shannon Weaver (H') 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. tonsa* appear mainly in the oxygenated layers throughout the study period. Ninety-two percent of all *A. tonsa* 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. tonsa* only (Fig. 8). Average weighted mean depth of *A. tonsa* 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. tonsa* 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_{oxy} of nauplii was significantly higher than P_{oxy} of the copepodids of this species ($P = 0.036$ valid $n = 18$), indicating that copepodids of *A. tonsa* were generally found in less-oxygenated waters than nauplii.

For *E. inermis*, 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

	Avg. (ind. m ⁻³)	Max (ind. m ⁻³)	Min (ind. m ⁻³)
<i>Acartia tonsa</i> adults	279.3	4393.7	0.3
<i>A. tonsa</i> copepodids	2.6	16.7	0.0
<i>A. tonsa</i> nauplii	2.8	25.6	0.1
<i>Calanus</i> sp.	1.0	4.4	0.2
<i>Calanus</i> copepodids	4.3	12.4	0.2
<i>Centropages brachiatus</i>	38.1	413.0	0.1
<i>Eucalanus inermis</i>	24.1	502.7	0.2
<i>E. nauplii</i>	18.9	326.7	0.1
<i>Coryceus dubius</i>	2.0	7.7	0.3
<i>Paracalanus parvus</i>	15.3	167.6	0.1
<i>Hemicyclops thalassius</i>	2.4	34.5	0.2
<i>Oithona</i> sp.	2.0	6.7	0.1
<i>Oncaea venusta</i>	6.6	49.1	0.0
<i>Disciniscia lamellosa</i> larvae	24.4	253.3	0.1
<i>Limacina</i> sp. larvae	1.1	4.8	0.1
<i>Magelona</i> sp. larvae	32.2	323.1	0.1
<i>Oikopleura</i> sp.	10.1	250.5	0.1
<i>Pleopis polyphemoides</i>	1.3	1.3	1.3

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 analysed, significant differences in weighted mean depth or P_{oxy} between diurnal and nocturnal hauls were detected for several taxa. *Centropages brachiatus* 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_{oxy} , *Hemicyclops thalassius*, *Oithona* sp. and larvae of *Magelona* sp. were the only taxa to show significant diurnal variations.

Centropages brachiatus (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 brachiatus* 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 ($P = 0.02$, valid $n = 7$), and for all three series pooled together ($P = 0.001$, valid $n = 23$). *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 thermo- and oxycline depths (Z_{oxy} and Z_{therm}) 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 singular upward movements or “emersion” events. It did appear in considerable amounts above the oxycline ($P_{oxy} > 50\%$) 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 layer 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. tonsa* 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. tonsa*. Several other taxa also showed negative correlations with depth (*Calanus* sp., *Centropages brachiatus*, *Disciniscia lamellosa* larvae, *Oikopleura* sp., and *Pleopis polyphemoides*). No significant correlations with environmental parameters were found for nauplii and copepodids of *A. tonsa*. *E. inermis* (all stages) and *Oncaea 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 2006. *Dotted lines* indicate the approximate position of the oxycline, based on the 1-ml^{-1} oxygen pycnocline

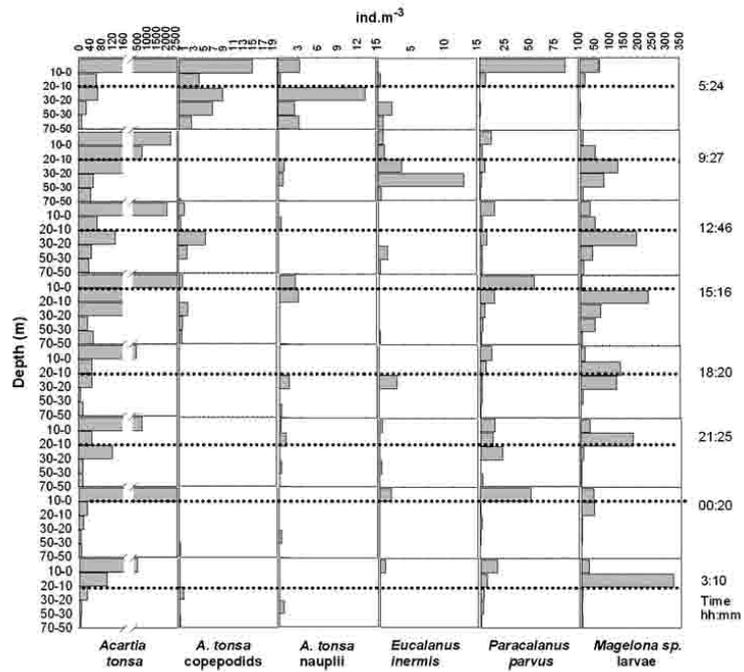


Fig. 6 24-h variation of the vertical distribution of selected species off Callao at station 5 during April 2006. *Dotted lines* indicate the approximate position of the oxycline, based on the 1-ml^{-1} oxygen pycnocline

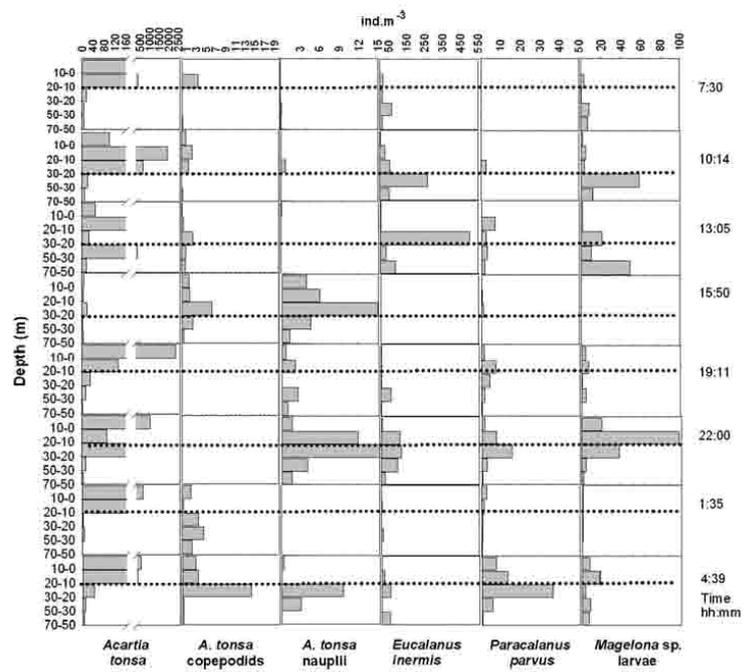
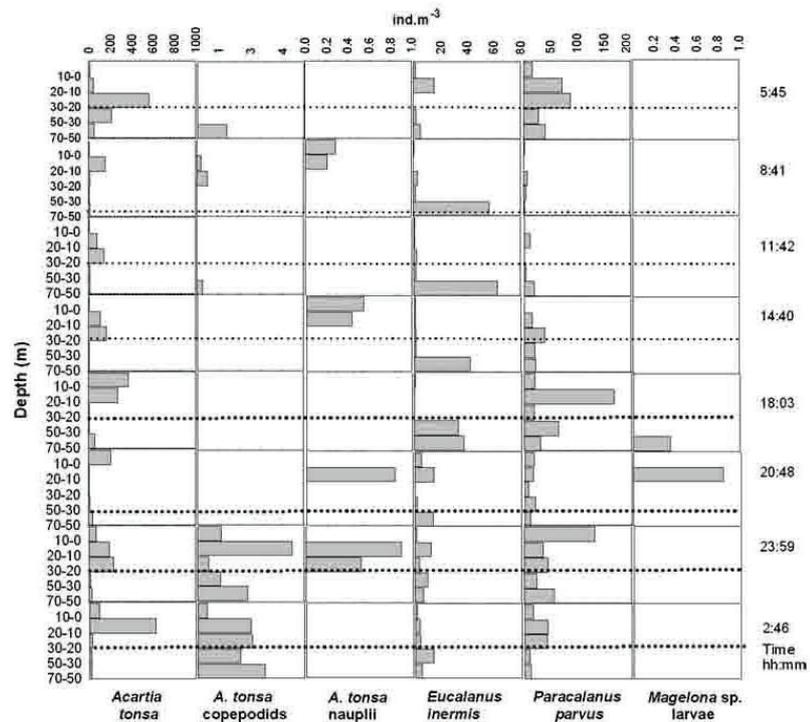


Fig. 7 24-h variation of the vertical distribution of selected species off Callao at station 2 during August 2006. Dotted lines indicate the approximate position of the oxycline, based on the 1-ml l^{-1} oxygen pycnocline



according to their consistently higher abundances in deep layers. *E. inermis* did not show any other significant correlations, while *Oncaea 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 copepodids of *Calanus* sp., *Coryceus 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 thermo- and oxyclines and weighted mean depth of the main taxa (Table 4) agreed well with the correlation matrix between abundance and absolute values of temperature and 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 copepodids, *Oikopleura* sp., *Hemicyclops thalassius* adults and copepodids, 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 Z_{therm} 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 Z_{therm} . 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 Z_{therm} . Weighted Mean Depths of deep-dwelling *E. inermis* (all stages) and copepodids and nauplii of *A. tonsa* did not show any significant correlations 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 (P_{oxy}) and cline depth. This confirms that organisms that are restricted to the upper oxygenated layers (e.g. *Oikopleura* sp., *Centropages brachiatus*, *Pleopis polyphemoides*) display consistently high P_{oxy} values, independent of cline depths. P_{oxy} values of nauplii of *E. inermis* and nauplii and

Fig. 8 Temporal variations of the weighed mean depth of adults and copepodids of *Acartia tonsa* and larvae of the polychaete *Magelona* sp. at two stations off Callao, Peru, during 2006

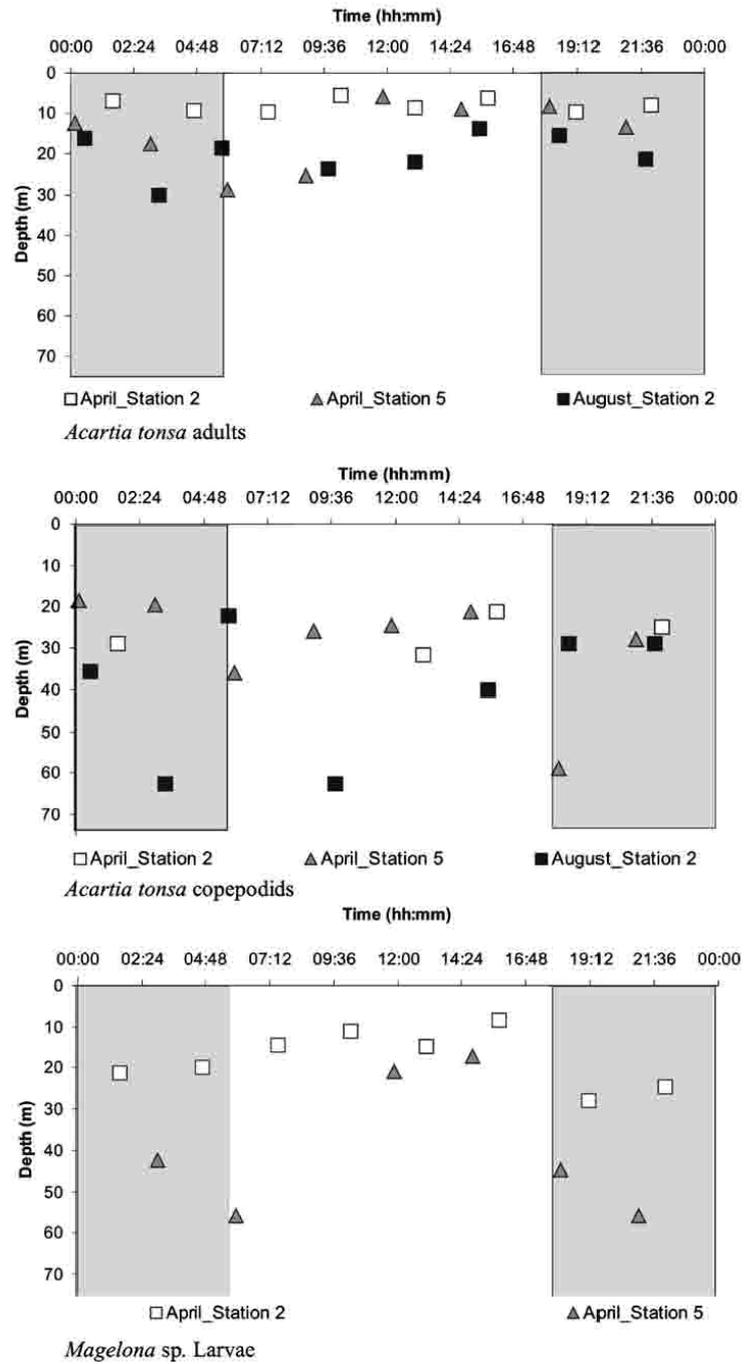


Table 2 Mean percentage above the 1·ml⁻¹ oxycline (P_{oxy}), weighted mean depth (WMD) and standard deviation for the main taxa off Callao

Taxa	Percentage at surface (P_{oxy})						Weighted mean depth (WMD)					
	April Station-2 (%)	St. dev. (%)	April Station-5 (%)	St. dev. (%)	August Station-2 (%)	St. dev. (%)	April Station-2	St. dev.	April Station-5	St. dev.	August Station-2	St. dev.
<i>Acartia tonsa</i>	92	4.5	89	8.9	88	17.4	7.9	1.6	15.0	8.2	20.1	5.3
<i>A. tonsa</i> copepodids	15	20.0	51	37.9	58	28.6	26.7	4.6	29.1	13.3	40.1	16.3
<i>A. tonsa</i> nauplii	30	40.0	100	0.0	81	26.2	27.1	11.1	31.2	10.6	13.1	4.6
<i>Calanus</i> sp			73	27.9								
<i>Calanus</i> copepodids			70	42.1								
<i>Centropages brachiatus</i>	89	21.4	75	22.9	80	28.5						
<i>Eucalanus inermis</i>	34	44.3	32	29.4	36	26.9	7.6	2.5	18.7	9.8	26.3	8.5
<i>Eucalanus</i> nauplii			18	19.9	31	39.8	25.3	16.2	40.8	11.9	45.0	14.2
<i>Coryceus dubius</i>			80	14.4					39.1	14.0	49.6	7.3
<i>Paracalanus parvus</i>	75	16.4	68	16.8	65	26.5	12.8	4.8	26.3	5.5	29.6	6.8
<i>Hemicyclops thalassius</i>	53	26.3	49	44.1	92	10.7	20.0	4.6	20.4	5.3	40.5	14.7
<i>Oithona</i> sp.			65	13.0	69	45.5						
<i>Oncaea venusta</i>			38	27.7	60	37.9					25.2	6.9
<i>Discinisca lamellosa</i> larvae	81	30.7			71	48.1	10.6	2.7				
<i>Limacina</i> sp.	92	20.9	46	44.1	37	26.8	6.2	0.8	21.1	6.4	21.5	13.1
<i>Magelona</i> sp. larvae	55	37.8	50	70.7	70	26.9	17.8	6.7	39.5	16.8		
<i>Oikopleura</i> sp.	97	1.6	90	26.1	89	21.2						
<i>Pleopis polyphemoides</i>	97	2.6					7.1	2.4	11.3	8.4		
Total zooplankton	88	7.2	68	12.2	67	30.8	9.4	2.3	21.9	8.0	56.6	14.1

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

	Depth	Oxygen (ml l ⁻³)	Chlorophyll <i>a</i> (µl l ⁻¹)	Temp.	Salinity
<i>Acartia tonsa</i> adults	-0.52	NS	NS	NS.	-0.2
<i>A. tonsa</i> copepodids	NS	NS	NS	NS	NS
<i>A. tonsa</i> nauplii	NS	NS	NS	NS	NS
<i>Calanus</i> sp. adults	NS	NS	NS	0.22	0.3
<i>Calanus</i> copepodids	-0.39	NS	NS	0.4	0.43
<i>Centropages brachiatus</i> adults	-0.3	0.52	NS	NS	NS
<i>Eucalanus inermis</i> adults and copep.	0.33	NS	NS	NS	NS
<i>Eucalanus inermis</i> nauplii	0.28	NS	NS	NS	NS
<i>Coryceus dubius</i> adults	NS	0.35	0.54	0.41	0.35
<i>Paracalanus parvus</i> adults and copep.	NS	0.3	0.4	0.31	0.28
<i>Hemicyclops thalassius</i> adults	NS	NS	NS	-0.2	NS
<i>Oithona</i> sp. adults	NS	0.34	0.51	0.39	0.49
<i>Oncaea venusta</i> adults	0.25	NS	NS	NS	0.23
<i>Discinisca lamellosa</i> larvae	-0.28	NS	NS	NS	NS
<i>Limacina</i> sp. adults	NS	0.27	NS	NS	NS
<i>Magelona</i> sp. larvae	NS	-0.35	-0.51	-0.29	NS
<i>Oikopleura</i> sp. adults	-0.34	NS	NS	NS	-0.25
<i>Pleopis polyphemoides</i> adults	-0.38	NS	NS	NS.	0.43

copepodids 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 oxycline (Z_{oxy}) (1 ml l^{-1}), the depth of the thermocline (Z_{therm}) (15°C), and the weighted mean depth (WMD) and percentage found in the oxygenated layer (P_{oxy}) for the most abundant and frequent taxa

	Z_{oxy}	Z_{therm}
Z_{oxy}	NS	0.81
WMD <i>A. tonsa</i> adults	0.67	0.82
WMD <i>A. tonsa</i> copep.	NS	NS
WMD <i>A. tonsa</i> nauplii	NS	NS
WMD <i>E. inermis</i> adults	NS	NS
WMD <i>C. brachiatus</i> adults & copep.	0.63	0.80
WMD <i>P. parvus</i> adults & copep.	0.47	0.76
WMD <i>Magelona</i> sp. larvae	NS	0.64
WMD <i>Oikopleura</i> sp.	0.53	0.70
WMD <i>H. thalassius</i> adults & copep.	0.48	0.53
WMD <i>P. polyphemoides</i>	0.59	0.74
P_{oxy} <i>A. tonsa</i> adults	NS	NS
P_{oxy} <i>A. tonsa</i> copep.	0.60	NS
P_{oxy} <i>A. tonsa</i> nauplii	0.60	0.70
P_{oxy} <i>E. inermis</i> adults	NS	NS
P_{oxy} <i>E. inermis</i> nauplii	0.57	NS
P_{oxy} <i>C. brachiatus</i> adults & copep.	NS	NS
P_{oxy} <i>P. parvus</i> adults & copep.	NS	NS
P_{oxy} <i>Magelona</i> sp. larvae	NS	NS
P_{oxy} <i>Oikopleura</i> sp.	NS	NS
P_{oxy} <i>Limacina</i> sp.	NS	0.89
P_{oxy} <i>H. thalassius</i> adults & copep.	NS	NS
P_{oxy} <i>Disciniscia lamellosa</i> larvae	NS	NS
P_{oxy} <i>P. polyphemoides</i>	NS	NS

NS not significant ($P > 0.05$), *Copep.* copepodids

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 oxycline 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 2006, 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 (Caliènes and Guillen 1981). Previous studies off Callao show the maximum concentrations

of chlorophyll *a* in autumn (up to $9 \mu\text{g l}^{-1}$), and the minimum values under the influence of SSW ($<1 \mu\text{g l}^{-1}$) (Caliènes 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 ($14\text{--}18^\circ\text{C}$) 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; Criales-Hernandez et al. 2006). 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.

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_{therm} 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 brachiatus*. *C. brachiatus* 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. brachiatus* were significantly correlated with thermo- and oxycline depths. Furthermore, the abundance of *C. brachiatus* 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_{oxy} and Z_{therm}) 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. brachiatus*: (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 the 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 copepodids 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 undercurrents (Smith et al. 1981a; Peterson 1998).

Meroplankton 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 polychaete *Magelona* sp., which performed reverse diel vertical migration. For meroplanktonic 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 (Neill 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 clue for this migratory behaviour. In the Antarctic, adults and juveniles of *Euphausia 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 (Keppel et al. 1985; Vinogradov 1997), and to a possible strategy of larval retention and transport, utilising 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 1980; Boyd et al. 1981; Mackas 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 l^{-1} throughout the upper 85 m. Similar patterns were also described for zooplanktonic taxonomic group off 9°S by (Mackas 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 Wishner (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 Wishner 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 oxycline and within the upper zone of the oxygen minimum zone (Hidalgo et al. 2005). In the waters off Peru, Boyd et al. (1981) and Mackas et al. (1981) showed that *Eucalanus* could withstand periods of 12 h in anoxic layers. Judkins (1980), when testing vertical distribution between day and nights, 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 avoid-

ance 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 behavioural traits, which could be related to the dynamics of the oxygen minimum layer as follows: (1) the total bulk holo- and meroplankton 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 copepodids), (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 brachiatus* 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.

Acknowledgments This paper forms part of the Ph.D. thesis of the first author, at Bremen University. Financial support was granted by the frame of the EU-project CENSOR (Climate variability and El Niño Southern Oscillation: implications for natural coastal resources and management, contract 511071) and this is CENSOR publication 0106. The first author was partially supported by a short-term scholarship from Deutscher Akademischer Austauschdienst (DAAD). The authors are grateful to crew of the R/V Olaya, to the participants of the cruises who helped in sample collection and to the Area de Evaluación Secundaria Laboratory of IMARPE for logistical support, help in identifying

zooplankton, and unconditional friendship in Lima. The authors also thank Dr. Cathy Lucas, Dr. Luis Giménez, and an anonymous reviewer for improving the original text with important comments and suggestions.

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

M.I. Criales-Hernández^{1*}, R. Schwamborn³, H-J. Hirche², S. Sanchez¹, P. Ayón¹, M. Graco¹ and M. Wolff⁴

* Área de Evaluación Producción Secundaria, Instituto del Mar del Perú, Esquina Gamarra y General Valle S/N Chucuito- Callao, micriales@imarpe.gob.pe, tel: +51 16250800 ext 230, Lima, Peru

1: Instituto del Mar del Perú, Lima, Peru

2: Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany

3: Zoology Department, Universidade Federal de Pernambuco, Recife, Brazil

4: Charles Darwin Foundation, Galapagos, Ecuador

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 $< 120 \mu\text{m}$ (major axis length). Selectivity significantly increased with cell size until a cell size of $120 \mu\text{m}$. 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 Gonzalez, 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

(Kleppel, 1993). Certain species are completely rejected, eventually due to palatability or toxicity (Broglia *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 brachiatus* 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

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.

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 300 μ m 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 $\sim 0.7 \mu\text{m}$) to give total primary productivity. Filters were store frozen until the determination of radioactivity sample. Daily primary production was expressed as $\text{mgC m}^{-3} \text{d}^{-1}$.

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 11 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

growth in controls (t_c 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 (t_c and T_g) were treated and preserved in the same way as the initial t_0 samples. Phytoplankton was identified and counted using the Utermöhl method (Utermöhl, 1931). Microphytoplankton ($> 20\mu m$ size along the major axis) was identified to species level if possible and measured, nanoplankton (2 to $20\mu m$) 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 (Kjørboe *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.

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 t_c 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 t_c 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 t_c 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.

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 (ϵ) (Chesson, 1983, Schwamborn *et al.*, 2004). The values of ϵ 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 (ϵ) 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 (ϵ) 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 ϵ between time periods (EN *vs* LN) and taxonomic groups (dinoflagellates *vs* diatoms), using simple Mann-Whitney U-tests.

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).

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

2006 (overall average: 560 cells mL⁻¹) (Table 3). It occurred in considerable densities in six experiments.

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 nanoplankton. 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 $\mu\text{gC copepod}^{-1} \text{ day}^{-1}$ (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 $^{-1} \text{ h}^{-1}$ (Fig. 6).

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*, *Protoperdinium excentricum* and the diatoms *Asterionellopsis glacialis*, *Scriptsiella 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 ($\epsilon = 0.7$) 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 ($\epsilon = 0.3$) (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 ($\epsilon > -1$, cell size $< 120 \mu\text{m}$), 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 ϵ 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 ($\epsilon > -1$) 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, ($\epsilon = 0.3$ and 0.2 and $\epsilon = 0.3$ 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 ($\epsilon = 0.2$) to positive ($\epsilon = 0.6$) selectivity (Table 3). Dinoflagellates were an important part for 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 ($\epsilon = 0.2$ to $\epsilon = 0.63$) (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 nanoplankton 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 nanoplankton 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.*,

2008). 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 brachiatus* (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 nanoplankton-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 Independecia 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 climate change (Taylor *et al.*, 2002; Ayón *et al.*, 2008)

A. tonsa shows a size-selective feeding behaviour for phytoplankton between 0.5 μm to 120 μm cell size, but does not consume effectively larger cells. Pagano *et al.*, (2003) found that largest sizes ingested by *A. tonsa* are 72.1 μm . 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 *Akaschivo 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 105 μ m and 196 μ m, 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

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 effects 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 Nauplii 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 (ε) 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.

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. *Star* indicate no available data.

Fig. 3. Changes in phytoplankton biomass ($\mu\text{gC L}^{-1}$) and composition (a) and *A. tonsa* ingestion rates ($\mu\text{gC copepod}^{-1} \text{ day}^{-1}$) (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 300 μm -mesh plankton nets. These data were obtained from vertical multinet (Hydro-Bios, Kiel, Germany) hauls between 10m depth to surface

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 (Electivity > -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

(*LOWESS*) for each data set, using span = 0.5. Data with Selectivity = -1 or Size > 120 μ m 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.

Table 1

Date/ Station	ENSO Phase	SST (°C)	Oxygen at 5m depth (mL L ⁻¹)	Salinity	Chl- <i>a</i> (µg L ⁻¹)	Primary Production at 5m depth (mg m ⁻³ d ⁻¹)	Egg Production rate (µgC female ⁻¹ d ⁻¹)	Egg viability (%)	Gross Efficiency (%)
April 2006/ St2	Neutral 2006	15.8	2.6	35.00	0.14	77.66	0.02	25.92	3.11
April 2006/ St5	Neutral 2006	16.6	4.1	35.10	1.61	23.63	0.02	26.39	2.96
April 2006/ Ind	Neutral 2006	15.1	3.2	35.10	0.35	39.59	-	-	-
July 2007/ Ind	EN 2006	17.1	4.7	35.10	2.22	18.08	-	-	-
August 2006/ St5	EN 2006	18.4	5.5	35.00	1.16	29.79	-	-	-
August 2006/ Pier	EN 2006	16.9	2.3	35.00	-	-	0.03	58.43	1.62
February 2007/ Pier	Neutral 2007	18.6	2.5	35.06	-	-	0.05	89.82	0.12
April 2007/ St5	Neutral 2007	18.6	4.7	35.02	12.50	103.57	0.03	6.06	0.62
May 2007/ Pier	LN 2007	15.6	-	35.05	35.02	-	0.00	67.44	0.00
May 2007/ Ind	LN 2007	14.6	3.1	35.00	3.10	148.36	-	-	-
August 2007/ St2	LN 2007	14.8	2.5	35.00	6.48	74.97	0.02	0.38	0.04

Table 2.

	Group	Abr-06 St2	Abr-06 St5	Abr-06 Ind	Jul-06 Ind	Aug-06 Pier	Feb-07 Pier	Abr-07 St5	May-07 Pier	Aug-07 St2
Food offer (cell mL⁻¹)	Diatoms	1851.0	36.0	5796.0	2269.2	1148.6	11537.5	10019.4	45504.6	87789.2
	Dinoflagellates	828.3	2774.6	1629.9	759.8	17.8	1.3	245.3	262.0	1002.5
	Nanoflagellates	241.2	253.9	156.9	195.6	10056.5	739.7	1779.5	6008.5	5026.3
	Total phytoplankton	2920.5	3064.4	7582.8	3224.6	11222.8	12278.5	12044.2	51775.1	93818.0
Food Offer µgC L⁻¹	Diatoms	468.6	4.5	290.7	182.1	89.5	1011.5	736.5	2002.5	2789.6
	Dinoflagellates	377.5	1736.3	1245.9	224.2	49.4	0.3	291.8	122.2	170.6
	Nanoflagellates	3.3	3.5	2.2	2.7	140.4	10.5	24.6	89.9	96.2
	Total phytoplankton	849.5	1744.2	1538.8	409.0	279.3	1022.3	1052.9	2214.6	3056.4
Ingestion rate (cells copepod⁻¹ day⁻¹)	Diatoms	1316.5	523.1	114722.9	45.7	3406.5	37576.8	26433.5	1026662.1	524893.6
	Dinoflagellates	1041.1	149.8	26034.8	45.1	16.6	4.8	35.0	3067.3	8211.3
	Nanoflagellates	0.0	3140.3	0.0	0.0	66927.3	31970.5	24310.2	85886.4	43115.9
	Total phytoplankton	2357.5	3813.2	140757.7	90.8	70350.3	69552.1	50778.7	1115615.8	576220.9
Ingestion rate (µgC Copepod⁻¹ d⁻¹)	Diatoms	0.05	0.07	4.60	0.02	0.16	13.54	1.78	26.49	15.15
	Dinoflagellates	0.40	0.22	20.06	0.03	0.01	0.00	0.03	0.55	0.36
	Nanoflagellates	0.00	0.04	0.00	0.00	0.92	0.44	0.34	1.19	1.44
	Total phytoplankton	0.45	0.33	24.67	0.05	1.09	13.98	2.15	28.22	16.94

Table 3.

a)

Diatoms / Avg Carbon content		Abr-06 St2	Abr-06 St5	Abr-06 Ind	Jul-06 Ind	Aug-06 Pier	Feb-07 Pier	Abr-07 St5	May-07 Pier
<i>Amphiprora sp.</i> 117.3 pgC	Food offer (cell mL ⁻¹)	1.44	0.16	0.53		0.85	1.60	4.48	35.47
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	1.46	0.00	0.00		0.31	1.13	0.00	0.00
	Electivity (ε)	-0.23	-1.00	-1.00		-0.86	0.55	-1.00	-1.00
<i>Chaetoceros sp.</i> 24.4 pgC	Food offer (cell mL ⁻¹)	625.22	4.21			365.34		35.52	86.99
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	509.62	0.00			122.55		0.00	0.00
	Electivity (ε)	-0.10	-1.00			-0.86		-1.00	-1.00
<i>Cyclotella sp.</i> 30.3 pgC	Food offer (cell mL ⁻¹)				2.08		5.65	1.39	26.93
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)				0.00		6.92	0.00	17.96
	Electivity (ε)				-1.00		0.56	-1.00	0.12
<i>Detonula pumila</i> 78.7 pgC	Food offer (cell mL ⁻¹)			0.00	4.27		6.40	11.95	17.07
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)			1.65	0.00		0.00	5.16	9.00
	Electivity (ε)			0.54	-1.00		-1.00	0.54	-0.17
<i>Eucampia zoodiacus</i> 155.2 pgC	Food offer (cell mL ⁻¹)	0.80	1.17	0.21			1.44	172.89	41.75
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	0.52	1.05	0.00			0.00	0.00	24.87
	Electivity (ε)	-0.46	0.81	-1.00			-1.00	-1.00	-0.03
<i>Guinardia delicatula</i> 89.7pgC	Food offer (cell mL ⁻¹)		0.27	18.09		691.54	2749.87	4003.56	234.43
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)		0.00	12.48		0.00	0.00	798.31	126.11
	Electivity (ε)		-1.00	0.13		-1.00	-1.00	0.03	0.00
<i>Hemiaulus sinensis</i> 116.6 pgC	Food offer (cell mL ⁻¹)	0.32		0.75				3.63	23.47
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	0.00		0.00				0.92	13.19
	Electivity (ε)	-1.00		-1.00				0.11	-0.06
	Carbon contain (pgC)	120.22		120.22				114.19	114.19
<i>Lithodesmium undulatum</i> 228.8 pgC	Food offer (cell mL ⁻¹)	0.85	0.00	21.75				0.11	21.33
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	0.00	0.00	0.00				1.12	0.00
	Electivity (ε)	-1.00	-1.00	-1.00				0.89	-1.00
<i>Pennata</i> 46.8 pgC	Food offer (cell mL ⁻¹)	37.28	1.12	2762.31		0.00			264.44
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	12.49	0.00	3221.44		0.00			0.00
	Electivity (ε)	-0.72	-1.00	0.47		-1.00			-1.00
<i>Pleurosigma sp.</i> 109.2 pgC	Food offer (cell mL ⁻¹)			0.85	1156.92		299.02	3.36	34.13
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)			0.84	0.00		371.15	0.00	23.44
	Electivity (ε)			0.46	-1.00		0.52	-1.00	0.11
<i>Skeletonema costatum</i> 34.0 pgC	Food offer (cell mL ⁻¹)	30.77					620.92	791.04	43308.92
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	25.14					0.00	0.00	37694.87
	Electivity (ε)	-0.19					-1.00	-1.00	0.29
<i>Thalassionema nitzschioides</i> 35.2 pgC	Food offer (cell mL ⁻¹)	1.76	0.32	4170.63	3.20	60.80	360.45	44.58	271.40
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	0.00	0.00	1541.18	0.00	0.00	0.00	0.00	277.26
	Electivity (ε)	-1.00	-1.00	-0.14	-1.00	-1.00	-1.00	-1.00	0.31
<i>Thalassiosira angulata</i> 109.5 pgC	Food offer (cell mL ⁻¹)				2.40	28.16	2.45	1.71	304.67
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)				0.00	12.93	0.00	0.00	262.90
	Electivity (ε)				-1.00	-0.82	-1.00	-1.00	0.13
<i>Thalassiosira subtilis</i> 50.0 pgC	Food offer (cell mL ⁻¹)			0.00	0.64		3283.75	405.03	467.99
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)			0.00	0.00		0.00	0.00	1060.77
	Electivity (ε)			-1.00	-1.00		-1.00	-1.00	0.42

b)

Dinoflagellates and other taxa / Avg Carbon content		Abr-06 St2	Abr-06 St5	Abr-06 Ind	Jul-06 Ind	Aug-06 Pier	Feb-07 Pier	Abr-07 St5	May-07 Pier
<i>Akashiwo sanguineum</i> 621.7 pgC	Food offer (cell mL ⁻¹)	345.77	3011.91	1.39	0.00	1.28		2.45	
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	0.00	0.00	0.00	0.00	0.69		0.00	
	Electivity (ε)	-1.00	-1.00	-1.00	-1.00	0.70		-1.00	
<i>Ceratium furca</i> 5909.9 pgC	Food offer (cell mL ⁻¹)	0.64	1.17	1.28	7.09	3.20		0.21	3.60
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	0.00	1.23	0.80	0.00	0.00		0.00	0.00
	Electivity (ε)	0.87	0.60	0.25	-1.00	-1.00		-1.00	-1.00
<i>Ceratium fusus</i> 6166 pgC	Food offer (cell mL ⁻¹)	6.51	1.60	0.43	0.53	1.49		0.75	12.80
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	6.17	0.00	0.00	0.00	0.00		0.00	0.00
	Electivity (ε)	0.30	-1.00	-1.00	-1.00	-1.00		-1.00	-1.00
<i>Diplopelta asymmetrica</i> 413.1 pgC	Food offer (cell mL ⁻¹)	0.16	2.75		1.97		0.32	0.96	3.60
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	0.13	4.46		0.00		0.00	0.67	0.00
	Electivity (ε)		0.80		-1.00		-1.00	0.71	-1.00
<i>Gymnodinium lohmanii</i> 608.1pgC	Food offer (cell mL ⁻¹)	1.67					0.00	1.39	17.07
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	0.00					0.59	0.00	0.00
	Electivity (ε)	-1.00					0.82	-1.00	-1.00
<i>Prorocentrum gracile</i> 768.4 pgC	Food offer (cell mL ⁻¹)	0.83	0.27	2136.39				185.93	45.02
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	0.00	0.00	1081.34				0.00	0.00
	Electivity (ε)	-1.00	-1.00	0.32				-1.00	-1.00
<i>Prorocentrum micans</i> 244.9 pgC	Food offer (cell mL ⁻¹)	509.96	8.85	0.21	769.83			0.43	4.27
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	419.99	0.00	0.00	0.00			0.00	0.00
	Electivity (ε)	0.30	-1.00	-1.00	-1.00			-1.00	-1.00
<i>Protoperidinium mendiolae</i> 13863 pgC	Food offer (cell mL ⁻¹)	0.00	0.11			0.43			8.53
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	0.00	0.00			0.00			8.78
	Electivity (ε)	-1.00	-1.00			-1.00			0.39
<i>Protoperidinium steinii</i> 2426 pgC	Food offer (cell mL ⁻¹)	0.33	0.37		0.96			0.32	
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	0.00	0.00		0.59			0.24	
	Electivity (ε)	-1.00	-1.00		0.74			0.53	
<i>Eutreptiella gymnastica</i> 186.2 pgC	Food offer (cell mL ⁻¹)			0.09		14.19	1.11		36.10
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)			0.00		0.00	0.00		0.00
	Electivity (ε)			-1.00		-1.00	-1.00		-1.00
<i>Monadas</i> 13.8 pgC	Food offer (cell mL ⁻¹)	255.38	282.71	142.46	147.33	9354.90	768.20	1945.24	5824.63
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	0.00	130.85	0.00	0.00	2788.64	1332.11	1012.93	3578.60
	Electivity (ε)	-1.00	0.40	-1.00	-1.00	0.40	0.63	0.60	0.02
<i>Dictyocha fibula</i> 4.92 pgC	Food offer (cell mL ⁻¹)	2.00	1.33	0.67	4.69	7.47	10.99	1.07	17.40
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)	0.00	0.00	0.00	0.00	0.00	14.69	0.00	16.10
	Electivity (ε)	-1.00	-1.00	-1.00	-1.00	-1.00	0.56	-1.00	0.26
<i>Octactis octonaria</i> 2795.4 pgC	Food offer (cell mL ⁻¹)		0.05		0.64	1.07	0.53	1.28	27.84
	Ingestion rate (cell copepod ⁻¹ h ⁻¹)		0.00		0.00	0.00	0.92	0.00	22.43
	Electivity (ε)		-1.00		-1.00	-1.00	0.66	-1.00	-0.05

Table 4

Taxa	Avg Carbon content (pgC)	Avg Size (μm)	Abr-06 St2	Abr-06 St5	Abr-06 Ind	Jul-06 Ind	Aug-06 Pier	Feb-07 Pier	Abr-07 St5	May-07 Pier
			Food concentration (cells mL ⁻¹)							
<i>Asterionellopsis glacialis</i>	313.6	105.20	1586.42	0.00			2.29	28.87	8.33	251.85
<i>Coscinodiscus perforatus</i>	1902	137.20					5.44	8.53	10.67	0.32
<i>Cylindrotheca closterium</i>	47	36.20								4.16
<i>Ditylum brightwellii</i>	4943	120.00	0.11			0.32	8.96	56.80	4.00	
<i>Rhizosolenia setigera</i>	622	196.00	0.00				3.84	431.45	150.67	
<i>Guinardia striata</i>	88.1	30.00	0.16			0.53	7.68			
<i>Thalassiosira anguste-lineata</i>	173.3	36.00				0.00	0.00	21.33	170.00	
<i>Ceratium tripos</i>	10613	225.40	0.21	0.21	0.85		0.32	8.53	8.00	
<i>Dinophysis acuminata</i>	581.7	45.00	0.11				0.75			0.11
<i>Protoperidinium conicum</i>	7839.3	70.40		0.16			0.11			0.32
<i>Protoperidinium excentricum</i>	165.3	46.25					0.21		7.33	0.75
<i>Protoperidinium minutum</i>	2315.1	27.70	0.50	0.00						0.43
<i>Protoperidinium obtusum</i> (ACF)	65194	63.75	0.00	0.11	0.43			2.13		0.21
<i>Scrippsiella trochoidea</i>	2401.4	30.00	0.50	0.00			66.33	8.53	6.33	0.32
<i>Leucocryptos marina</i>	1.33	4.80	0.00	3.26					127.33	0.54

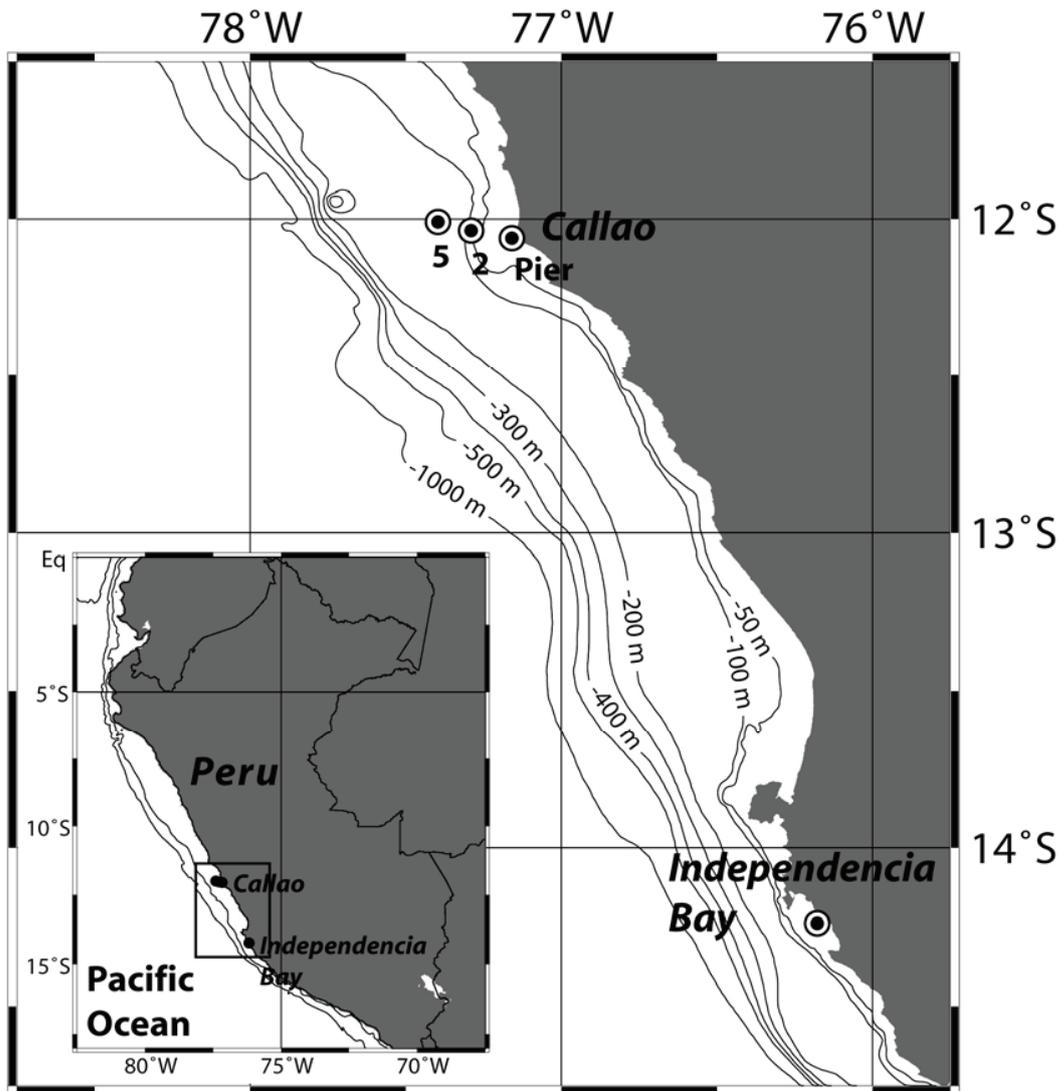


Fig. 1

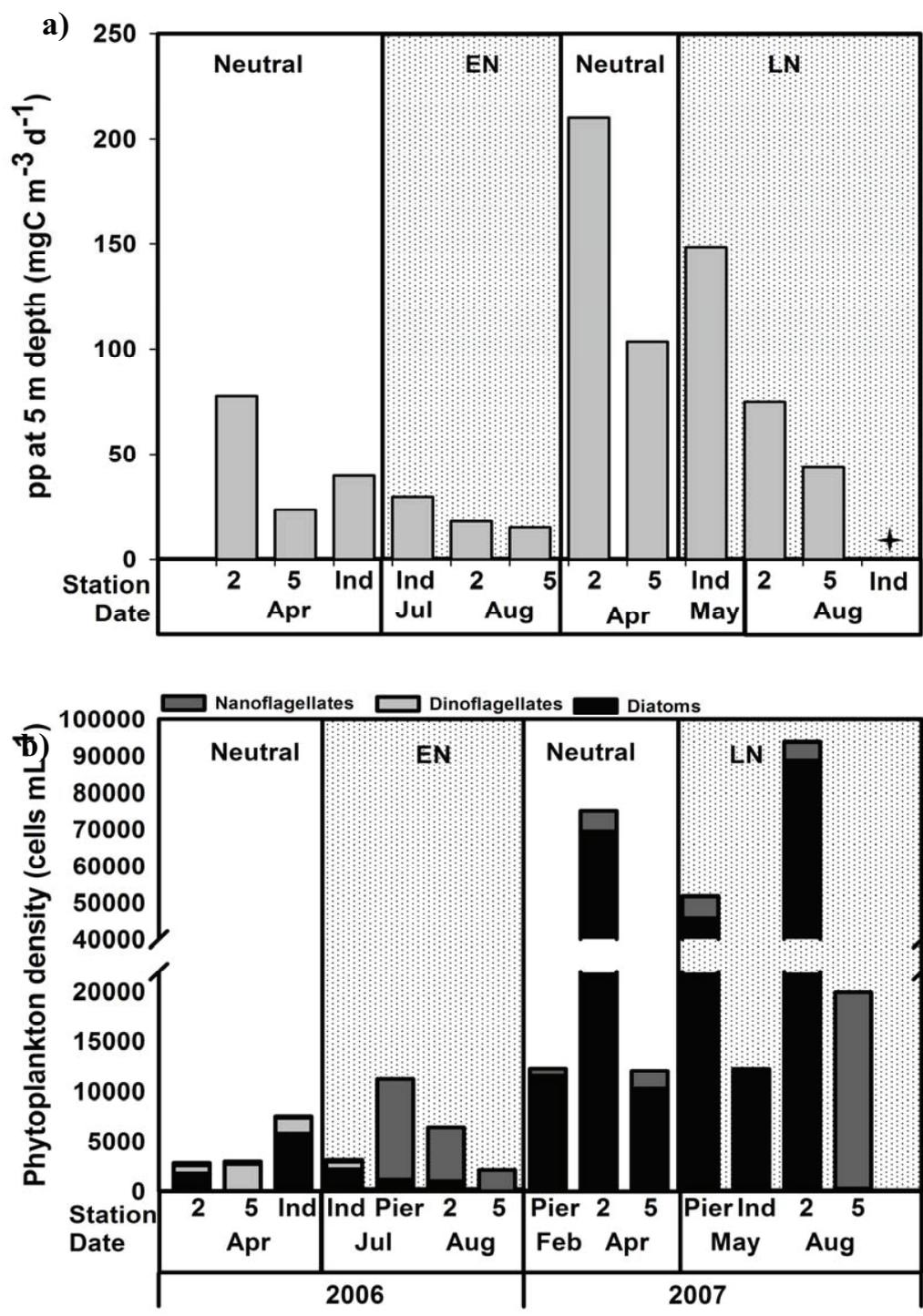


Fig. 2

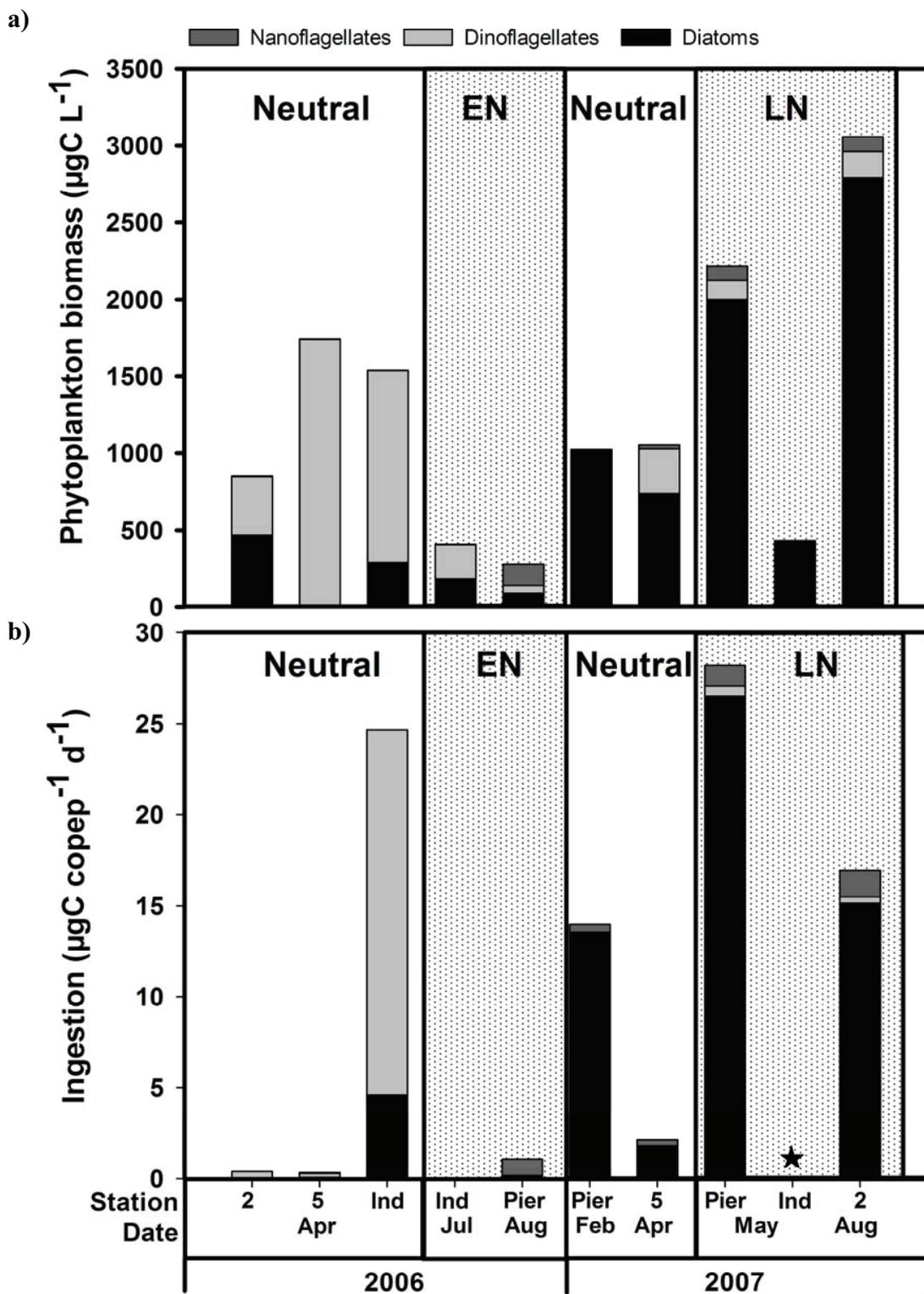


Fig. 3

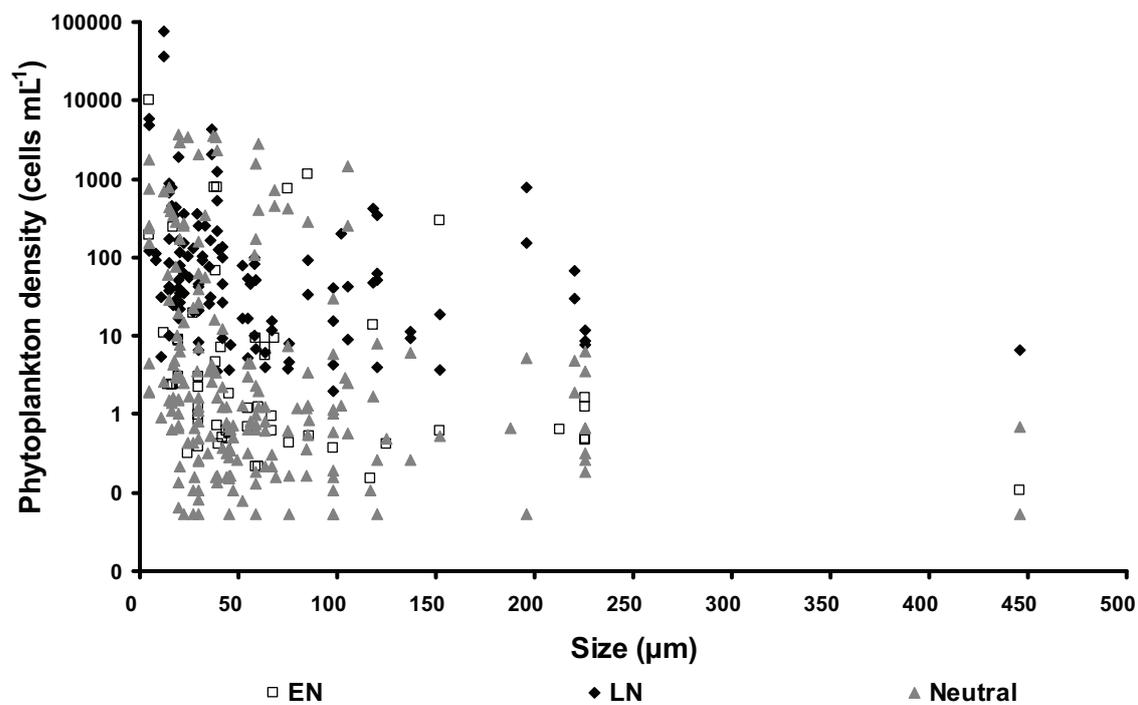


Fig. 4.

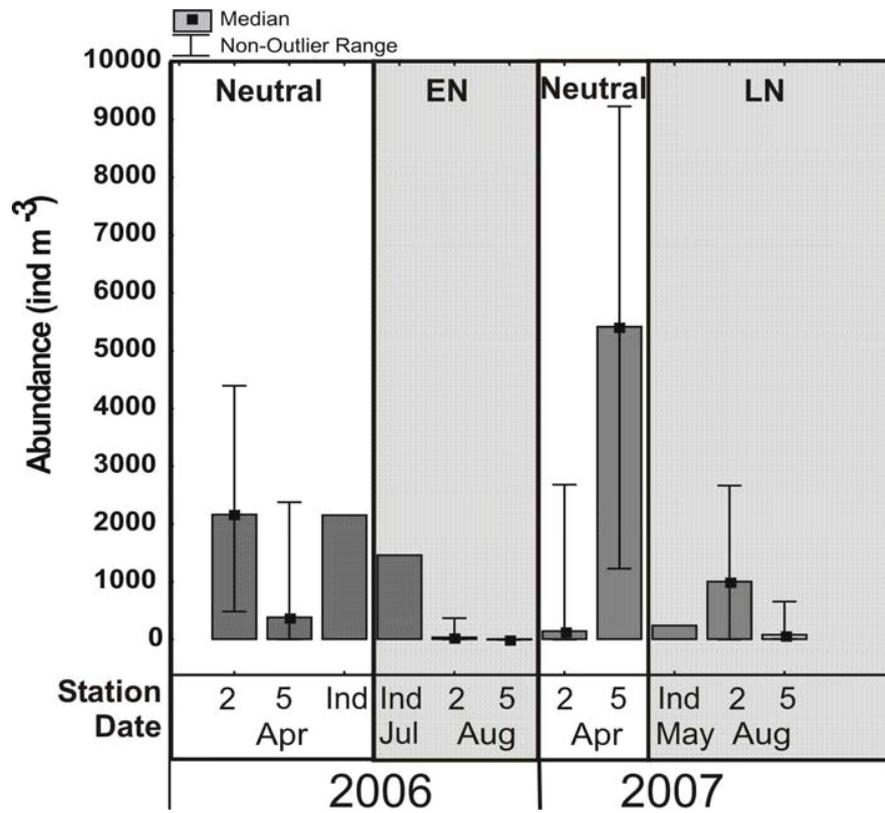


Fig. 5

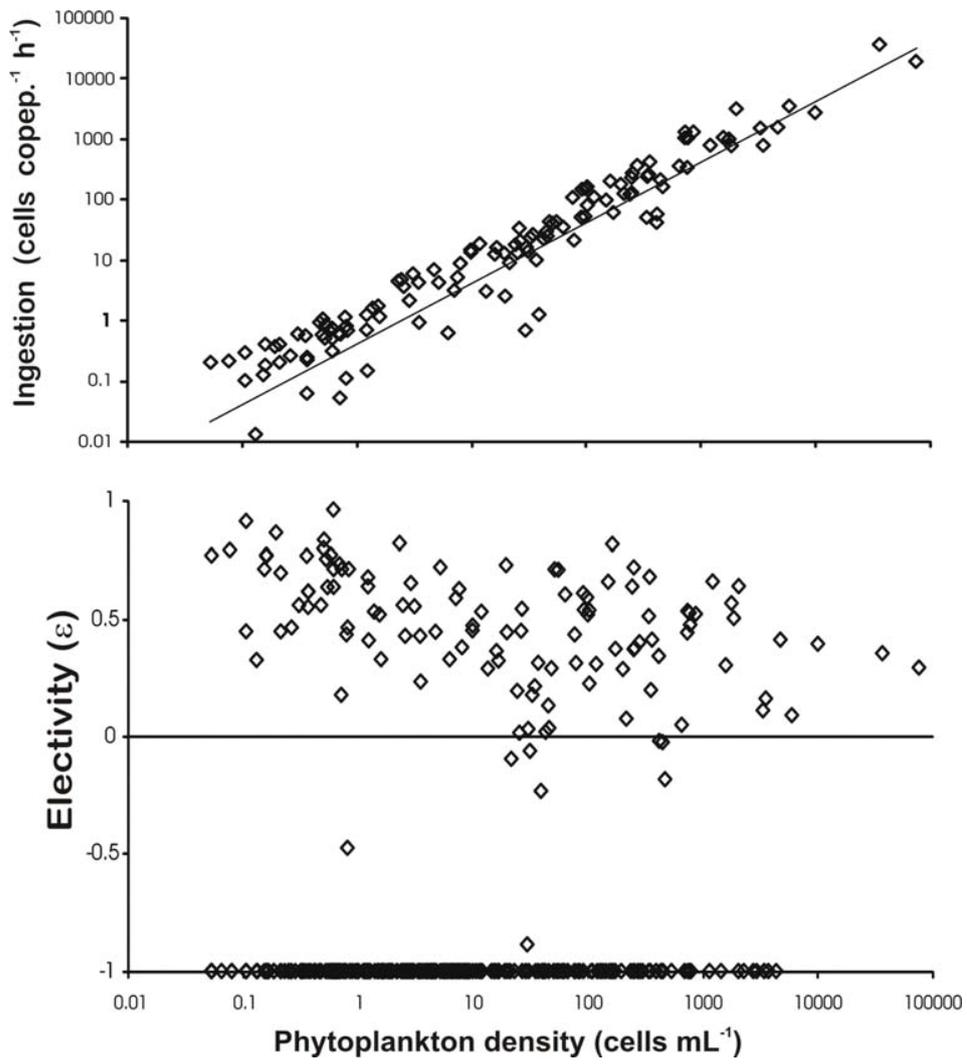


Fig. 6

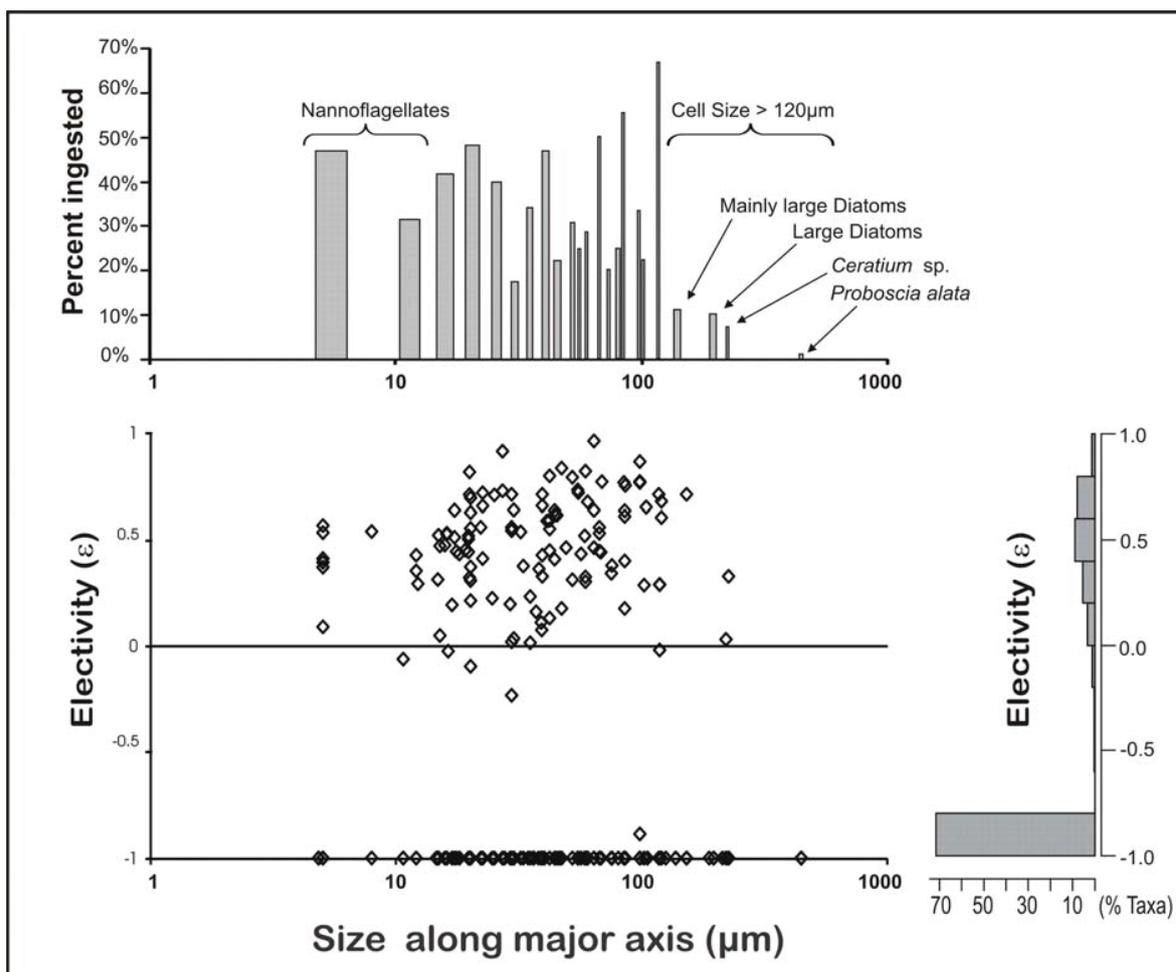


Fig. 7

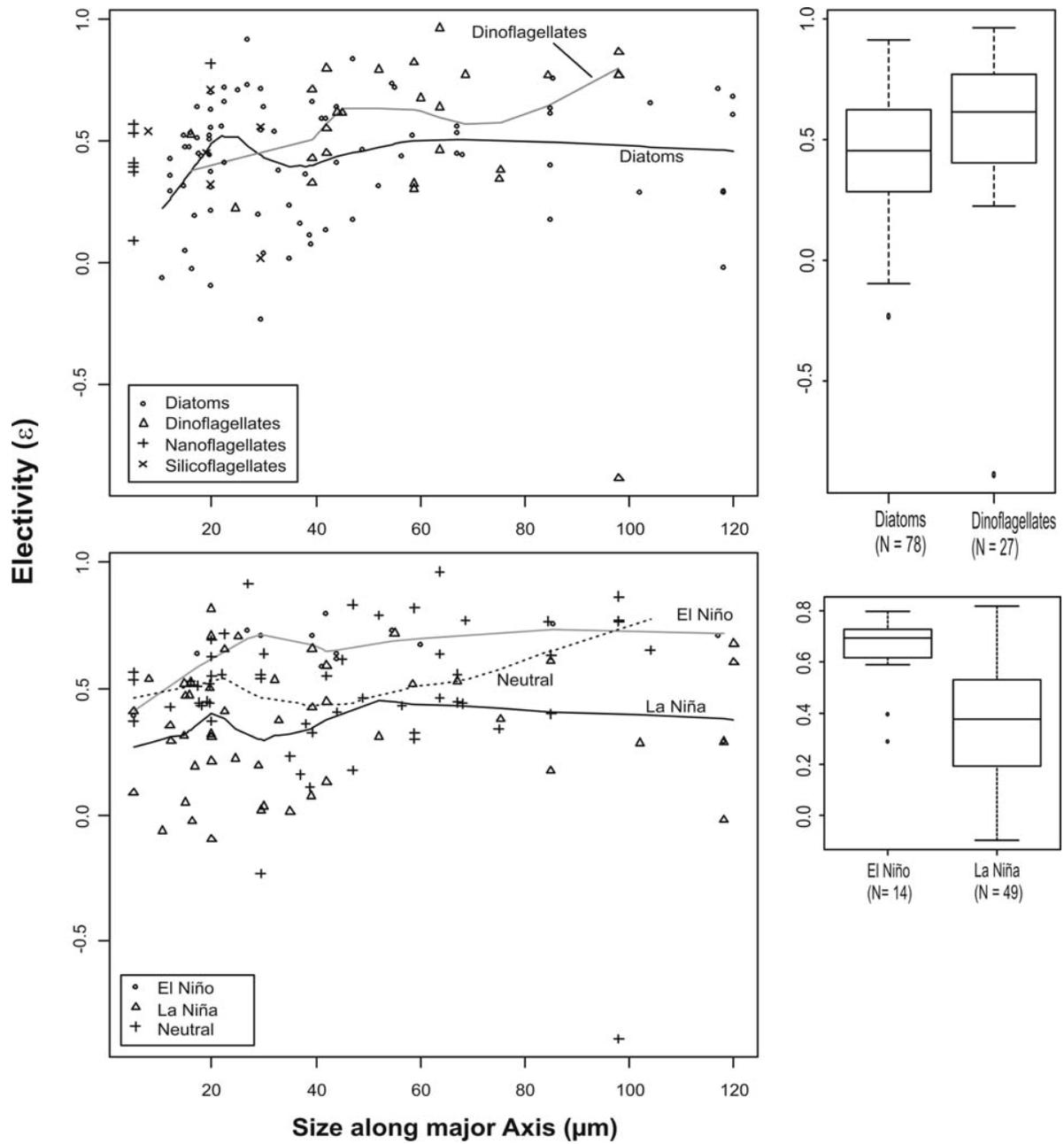


Fig. 8.

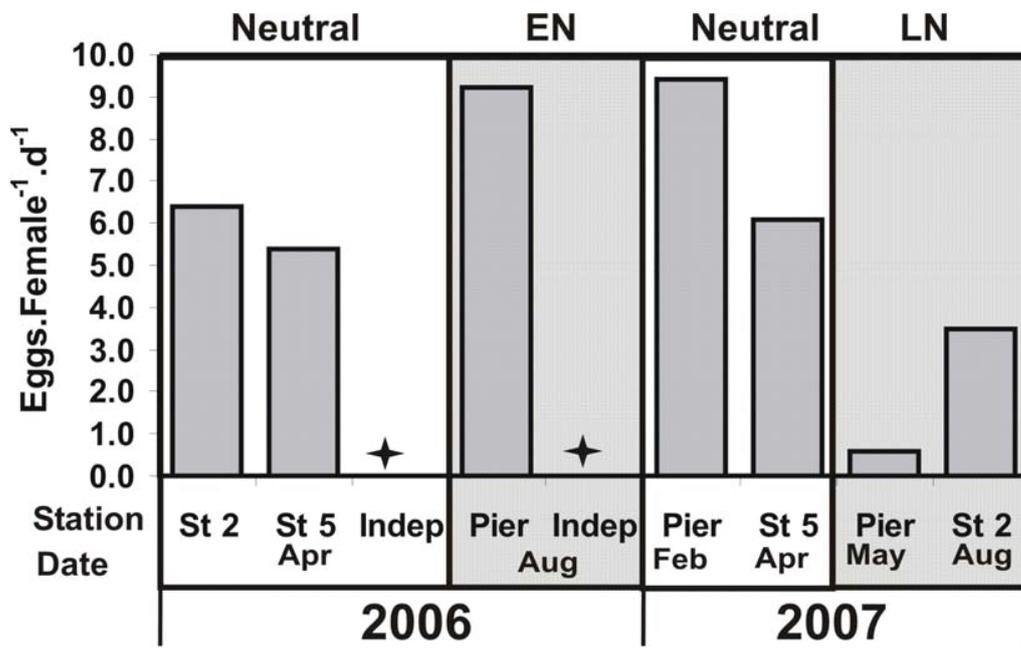


Fig. 9.

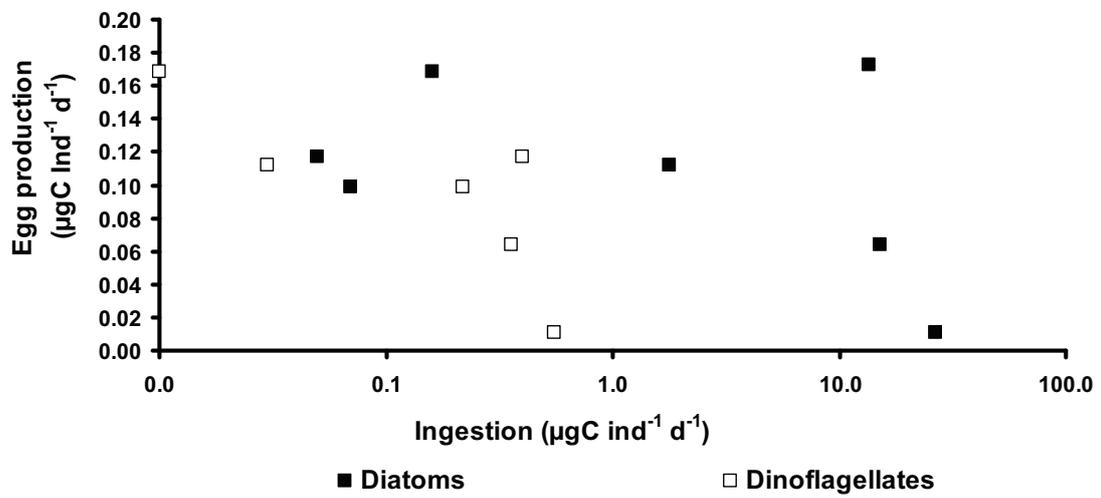


Fig. 10.

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 Chlorophyll-*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](http://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

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, *Pleuoncodes 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 subantarctic 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).

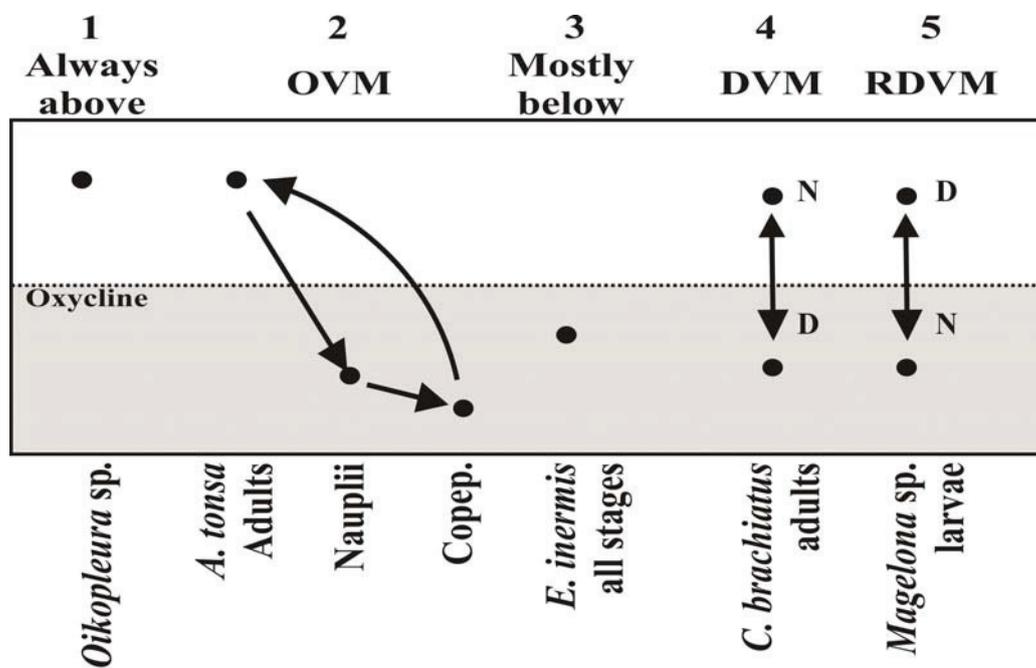


Figure 6.1 Schematic diagram showing five vertical distribution and migration patterns in relation to the oxygen minimum layer observed off central Peru in 2006, from left to right :1. Always above (e.g. *Oikopleura sp.*), 2. Ontogenetic vertical migration (*Acartia tonsa* adults, nauplii, and copepodites), 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 closely 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 120 μm cell size, with strong positive electivity for larger cells within this size range, but does not effectively consume cells larger than 120 μm . In addition, *A. tonsa* showed strong negative preference selection towards certain taxa. These taxa are red-tide forming species of *Akaschivo 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).

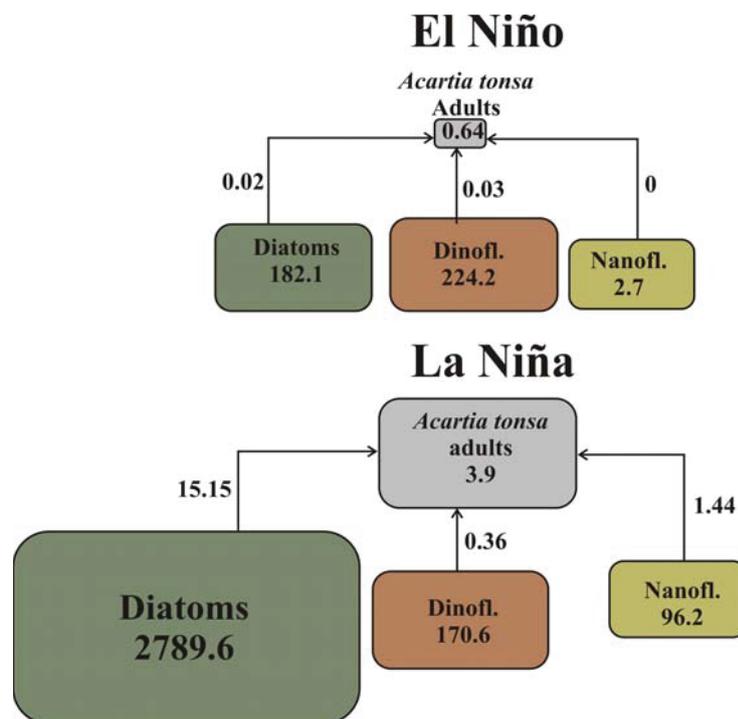


Figure 6.2 Conceptual model of the trophic interactions between *Acartia tonsa* adults and the dominant phytoplankton taxa in the coastal upwelling area off central Peru during moderate El Niño (August 2006) and strong La Niña (August 2007) conditions. Mean standing stocks ($\mu\text{gC l}^{-1}$) are shown for each taxonomic group. Dinofl.: Dinoflagellates; Nanofl.: Nanoflagellates. Numbers on arrows represent mean ingestion rates ($\mu\text{gC ind}^{-1} \text{d}^{-1}$). 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

I would like to express my deepest gratitude to the Instituto del Mar del Peru IMARPE in Lima (Peru). They opened their doors and gave me the opportunity to develop my studies. IMARPE made me feel at home like the other Peruvian citizens. This study was financed by CENSOR (Climate Variability and El Niño Southern Oscillation: Implications for Natural Coastal Resources and Management, www.censor.name) project and DAAD (Deutscher Akademischer Austausch Dienst) in the form of four short-term scholarships.

I also would like to acknowledge Dr. Hans-Jürgen Hirche for his advice and for accepting me as a guest scientist at Alfred Wegener Institute for Polar and Marine Research (AWI). To my major advisor Prof. Dr. Matthias Wolff, thank you for receiving me into your student group, I was honored to have you as my mentor.

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

sometimes believed in my dream more than I did. I thank them for their patience and love.

Thanks to the people at the Area de Evaluación Producción Secundaria was like my second family and home. They taught me to walk and talk like a Peruvian, took care of me when I was sunburned during summers in Lima, showed me the best beaches, assisted in the many times I was sick from the food, stored my things, and some even served as my confidante many times. In addition, they shared and helped on all of the cruises, teaching me how to work with Peruvian zooplankton. They endured my touchy temperament during three years. I especially want to thank those who are now “Mis Patas” Carmela Nakazaki, Jessica Bonichelli, Jasmin Escudero, Elda Luz Pinedo, Katy Arónes, Juanita Fiestas and “Frutica Frutica” Roberto Quezquen. I cannot omit Patricia Ayón who always listened to me, offered solutions to my problems, or offered her opinion. You have a special place in my heart.

I have been blessed with many close friends, Maria Fernanda Vidal, who has been with me since childhood; Tania Peña, Adriana Bermudez, Guerly Avila, Ursula Neira, who I have met a long the way; and finally those in the last few years, “Che” Michelle Graco, Aldo Pacheco “Pilas pues”, Marco Magallanes, and the Cuban team in Bremen (Zaida, Deisy and Yuri). They constitute an important part of my life.

It was a pleasure to work and learn with Dr. Ralf Schwamborn, he gave me unconditional help and feedback. His advice, support, and frequent tutorials throughout this thesis transformed me into a Doctor. I am also grateful to my colleagues at AWI: Kristina Barz, Dirk Mengedoht, Jasmin Renz, Jan Michels,

Andrea Bleayer and friends at Bremen: Ricardo Chero, Keil Friderman, Gabriel Boheme, Sophie Streck who shared their experience and helped me during my days in Germany. DANKE SEHR!!!

I have been graced with excellent people around me along this way. Special thanks to the crews of Bic Olaya and SNP 2, Mr. Godofredo Cañote, Dr. Dimitri Gutierrez, Mrs. Soledad Guzman, Mr. Renato Guevara, colleagues from the Area de Producción Primaria, Bentos, and secretaries at IMARPE for providing facilities during my Cruises and during my time in the Institute. In Bremerhaven my latest friend Kristen Jenkins for helping to improve my English during my last months (Laly Laly La).

There are still many people who supported me in one way or another, many times even without noticing it. I can not mention everybody, so if I forgot someone, I apologize and hope you understand.

Appendix

List of conference contributions

Criales-Hernández, M.I., Ayón, P., Graco, M., Schwamborn, R. Dominguez, N., Hirche, H.-J., Gutierrez, D., Wolff, M., 2006. Changes in the vertical distribution of an onshore zooplankton community over a 24 h period off central peru. CENSOR Midterm Symposium, Concepción, Chile, 04 – 08. September 2006. **Poster**

Criales-Hernández, M.I., Graco, M., Ayón, P., Flores, G., Schwamborn, R., Hirche, H.-J., Wolff, M. 2006. Intra-annual variability of zooplankton community structure as related to oceanographic conditions off central peru. CENSOR Midterm Symposium, Concepción, Chile, 04 – 08. September 2006. **Talk**

Criales-Hernández, M.I., Graco, M., Ayón, P., Flores, G., Schwamborn, R., Hirche, H.-J., Wolff, M. Temporal variability of the mesozooplankton community in the Humboldt upwelling system off central peru.. International Conference on The Humboldt current system: Climate, Ocean dynamics, ecosystem processes, and fisheries. Nov 27-Dec 1, 2006. **Poster**

Schwamborn, R., Nakazaki, C., Ayón, P., Criales-Hernandez, M. I., Menedoht, D., Hirche, H.-J., 2006. Small-scale patchiness of plankton in Peruvian coastal and shelf habitats as detected by using PELSS (Particle and Environmental Parameter Logging and Sampling System). International Conference on The Humboldt current system: Climate, Ocean dynamics, ecosystem processes, and fisheries. Nov 27-Dec 1, 2006. **Poster**

Criales-Hernandez, M.I., Schwamborn, R., Ayón, P., Sanchez, S., Hirche, H.-J., Wolff, M., 2007. Seasonal and spatial changes in abundance, vertical distribution, grazing and egg

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

Criales-Hernandez, M.I., Schwamborn, R., Ayón, P., Graco, M., Hirche, H-J., Wolff, M., 2007 Vertical distribution and migration of nearshore and offshore zooplankton in relation to the oxygen minimum zone off central Peru. 4th International Zooplankton Production Symposium, May 28 – June 1, 2007, Hiroshima, Japan. **Poster**

Criales-Hernandez, M.I. Schwamborn, R., Graco, M., Ayón, P., Hirche H-J., Wolff, M., 2007. Vertical distribution and migration of nearshore and offshore zooplankton in relation to the oxygen minimum zone off central Peru.. Pelagic-benthic processes in the coastal zone and terrestrial impact in the Humboldt Current System workshop AWI Institute in Bremerhaven, Germany, in September, 23 to 24,2007. **Talk**

Graco, M. Flores, G., Gutiérrez, D., Ledesma, J., Domínguez, N., Criales-Hernandez, M.I., Morón, O., 2007. Variabilidad temporal de las condiciones oceanograficas, químicas y la productividad frente a callao (12° c): evidencias de El niño 2006. I congreso ciencias del mar del Peru Lambayeque, 27 – 30 noviembre 2007. **Talk**

Criales-Hernandez, M.I., Ramos, E., Schwamborn, R., Passuni, G., Ayón, P. Graco, M. Hirche, H-J., Wolff. M., 2007. Variabilidad temporal de la comunidad de mesozooplancton en la Bahía Independencia, Ica-Perú. I congreso ciencias del mar del Peru Lambayeque, 27 – 30 noviembre 2007. **Talk**

Criales-Hernandez M. I., Schwamborn R., Sanchez, S. Ayón, P., Hirche, H-J., Wolff, M.
2008. Zooplankton grazing and secondary production off central Peru during recent El Niño and La Niña events (2006 to 2007). 2008 Proceedings of the Eastern Boundary Upwelling Ecosystems Symposium, 6 to 8 June 2008, Las Palmas de Gran Canaria, Spain. **Talk**

Schwamborn R., Criales-Hernandez, M. I., Ayón, P., Swartzman, G., Hirche, H.-J.,
2008. Zooplankton size spectra in Peruvian marine ecosystems – preliminary results and perspectives for the comparison between large upwelling ecosystems. (2008) Proceedings of the Eastern Boundary Upwelling Ecosystems Symposium, 6 to 8 June 2008, Las Palmas de Gran Canaria, Spain. **Talk**

References

- Abanto, M.R., 2001. Composición, distribución y abundancia de copépodos planctónicos marinos en la costa Norte - Centro (03°30' S - 14°00'S) frente al litoral Peruano entre los años 1980 y 1989. Tesis de Licenciatura. Facultad de Ciencias Naturales y Matemáticas Universidad de Lima. Unpublished.
- Agis, M., Granda, A., Dolan, J.R., 2007. A cautionary note: Examples of possible microbial community dynamics in dilution grazing experiments. *Journal of Experimental Marine Biology and Ecology* 341 (2), 176-183.
- Albornoz, L, Wehrtmann, I.S. 1997. Descripción y clave de los primeros estadios larvales de camarones carídeos (Decapoda: Hippolytidae, Alpheidae, Rhynchocinetidae) de aguas costeras de Chile. *Investigaciones Marinas de Valparaíso* 25, 121-133.
- Alheit, J., Niquen, M., 2004. Regime shifts in the Humboldt Current ecosystem. *Progress in Oceanography* 60(2-4), 201-222.
- Alvarado, A., 1972. Variación cuantitativa de copépodos, eufáusidos y quetognatos de la zona norte Peruana (07°01' y 08°56' Latitud Sur) verano-invierno 1967. Tesis de Biólogo, Universidad Nacional de Trujillo. Unpublished.
- Ambler, J.W. 1986. Effect of food quantity and quality on egg production of *Acartia tonsa* Dana from East Lagoon, Galveston, Texas. *Estuarine, Coastal and Shelf Science* 23,183-196.
- Anderson, D.M. 1997. Bloom dynamics of toxic *Alexandrium* species in the northeastern US. *Limnology and Oceanography* 42, 1009-1022.
- Ancieta, F., 1981. The importance of coastal upwelling research for Peru. In: Richards FA (ed). *Coastal Upwelling Coastal and Estuarine Sciences*, 1, 4-5. Washington D.C. American Geophysical Union.
- Antezana-Jeréz, T., 1978. Distribution of euphasiids in the Chile-Peru current with particular reference to the Endemic *Euphasia mucronata* and the oxygen minima layer. PhD. thesis. University of California, San Diego. Unpublished.
- Antezana, T., 2002a. Adaptive behaviour of *Euphausia mucronata* in relation to the oxygen minimum layer of the Humboldt Current. In: Färber Jaime (ed). *Oceanography of the Eastern Pacific II* (pp. 29-40). Mexico. Centro de Investigación Científica y de Educación Superior de Ensenada CICESE.
- Antezana, T., 2002b. Vertical distribution and diel migration of *Euphausia mucronata* in the oxygen minimum layer of the Humboldt Current. In: Färber Jaime (ed). *Oceanography of the Eastern Pacific II* (pp. 13-28) Mexico. Centro de Investigación Científica y de Educación Superior de Ensenada CICESE.

- Antezana, T., 2006. *Euphasia mucronata* a keystone and prey of the Humboldt Current. In Book of extended abstracts, International Conference the Humboldt Current System: Climate, Ocean dynamics, ecosystem processes, and fisheries (pp. 51-53) Lima, Peru, November 27 - December 1, 2006.
- Arashkevich, E.G., Flint, M.B., Pelymskij, A.G., 1982. Qualitative characteristics of feeding of abundant zooplankton species in Peruvian coastal waters. *Okeanologiya* 22(4), 645-651. *In Russian*.
- Arntz, W.E., 1984. El Niño and Peru: positive aspects. *Oceanus* 27, 36-39.
- Arntz, W.E., Fahrbach, E., 1991. El Niño Klimaexperiment der Natur: Physikalische Ursachen und biologische Folgen. Birkhäuser Verlag Basel. Germany. 264p.
- Arntz, W.E., Fahrbach, E., 1996. El Niño Experimento Climático de la Naturaleza. Causas Físicas y Efectos Biológicos. Fondo de Cultura Económica, México. 311 pp.
- Arntz, W.E., Valdivia, E., 1985. Incidencia de fenómeno "El Niño" sobre los mariscos en el litoral Peruano. *Boletín del Instituto del mar del Perú Vol.extraordinario*, 91-101.
- Arntz, W.E., Tarazona, J., Gallardo, V.A., Flores, L.A., Salzwedel, H., 1991. Benthos communities in oxygen deficient shelf and upper slope areas of the Peruvian and Chilean Pacific coast, and changes caused by El Niño. In: Tyson, R.V., Pearson, T.H. (Eds.), *Modern and ancient Continental Shelf Anoxia*. Geological Society Special Publication No. 58, London, pp.131–154.
- Arntz, W.E., Gallardo, V., Gutiérrez, D., Isla, E., Levin, L., Mendo, J., Neira, C., Rowe, G.T., Tarazona, J., Wolff, M., 2006. El Niño and similar perturbation effects on the benthos of the Humboldt, California and Benguela current upwelling ecosystems. *Advances in Geosciences* 6, 243-265.
- Aronés, K.J., 1997. Distribución horizontal de los amphipoda (crustacea) en el mar Peruano durante el fenómeno "El Niño" verano 1983. tesis de Licenciatura. Facultad de Ciencias Biológicas, Universidad Ricardo Palma, Lima. Unpublished.
- Aronés, K.J., 2002. Estudios comparativos de copépodos costeros frente a Paita y San Jose. In: Retuerto F, Talledo M (eds) XI Reunión científica Instituto de Investigación de Ciencias Biológicas "Antonio Raimondi" (ICBAR). 2002, Lima, pp 74. Unpublished.
- Aronés, K.J., 2004. Zooplancton e ictioplancton del mar Peruano durante el verano 2001. Informe del Instituto del Mar del Perú 32(1), 47-56.
- Aronés, K., Ayón, P., 2001 Variabilidad del zooplancton e ictioplancton frente a Paita entre febrero y diciembre del 2000. In: Retuerto F, Talledo M (eds) X Reunión científica Instituto de Investigación de Ciencias Biológicas "Antonio Raimondi" (ICBAR). Editora EISA SRL, Lima, Unpublished.

- Aronés, K., Ayón, P., 2002. Effects of El Niño 1997-1998 on copepods community structure at San Jose Coastal Station (Peru). In: Salinas, S., Urban, H., Arntz, W. (Eds), Workshop impacts of El Niño and Basin scales climate changes on Ecosystems and Living Marine Resources: A comparison between the California and the Humboldt Current systems. Investigaciones Marinas, Chile, pp 104-105.
- Aronés, K., Girón, M., Ayón, P., 2001. Caracterización del zooplancton en cuatro zonas de la costa Norte-centro del Perú durante el 2000. In: Retuerto F, Talledo M (eds) X Reunión científica Instituto de Investigación de Ciencias Biológicas "Antonio Raimondi" (ICBAR). Lima, pp 60. Unpublished.
- Aronés, K., Ayón, P., Hirche, H.J., Schwaborn, R., 2009. Hydrographic structure and zooplankton abundance and diversity off Paita, northern Peru (1994 to 2004) - ENSO effects, trends and changes. Journal Marine Science, 10.1016/j.jmarsys.2009.01.002.
- Ayón, P., 1999. Volumenes de zooplancton e ictioplancton frente a la costa peruana en verano e inicios de otoño 1999. Crucero BIC José Olaya Balandra 9902-03, de Tumbes a Tacna. Informe del Instituto del Mar del Perú 147, 59-70.
- Ayón, 2002. Informe del zooplancton e ictioplancton 0202. Internal Report. IMARPE. Unpublished.
- Ayón, P., Aronés, K., 1997a. Características generales del zooplancton en la costa norte centro durante el Crucero BIC SNP-1 9607-08. Informe del Instituto del Mar del Perú 124, 51-56.
- Ayón, P., Aronés, K., 1997b. Comunidades de zooplancton e ictioplancton frente a la costa norte centro del Perú. Crucero BIC Humboldt 9705-06. Informe del Instituto del Mar del Perú 128, 70-79.
- Ayón, P., Girón, M., 1996. Características del zooplancton e ictioplancton durante el periodo de verano 1995 frente a la costa Peruana crucero de evaluación de recursos pelagicos 9502-04 Bic Snp-1 (13 Febrero-05 abril 1995). Informe del Instituto del Mar del Perú 116, 73-81.
- Ayón, P., Girón, M., 1997. Composición y distribución del zooplancton e ictioplancton frente a la costa peruana durante febrero a abril 1997. Informe del Instituto del Mar del Perú 127, 49-55.
- Ayón, P., Girón, M., 2004. El ictioplancton del mar peruano durante la Primavera austral 2001. Informe del Instituto del Mar del Perú 32(2), 181-187.
- Ayón, P., Aronés, K., Zarate, M., 1999. Variaciones en el comportamiento del copépodo calanoideo *Centropages brachiatus* (Dana, 1849), frente a la costa Peruana durante el evento El Niño 97-98. In: Tresierra, A, Culquichicon, Z., (Eds), VIII Congreso Latinoamericano sobre ciencias del Mar. 1999, Trujillo-Perú, pp 730-731. Unpublished.
- Ayón, P., Purca, S., Guevara-Carrasco, R., 2004. Zooplankton volume trends off Peru between 1964 and 2001. Ices Journal of Marine Science 61, 478-484.

- Ayón, P., Sanchez, S., Girón, M., Villanueva, P., Delgado, E., 1996. Composición y distribución del plancton en el litoral Peruano en el verano de 1996. Crucero de evaluación hidroacústica de recursos pelágicos. BIC SNP-1 9602-04. Informe del Instituto del Mar del Perú 122,69-78.
- Ayón, P., Swartzman, G., Bertrand, A., Gutierrez, M. and Bertrand, S., 2008. Zooplankton and forage fish species off Peru: from local depletion to large scale bottom up control. *Progress in Oceanography* 79,218-214.
- Ayón, P., Criales-Hernandez, M.I., Schwamborn, R., Hirche, H.J., 2008. Zooplankton research off Peru: A review. *Progress in Oceanography* 79(2-4), 208-214.
- Báez, P., 1997. Clave de larvas de crustáceos decápodos recolectadas frente al norte de Chile durante un fenómeno El Niño. *Investigaciones Marinas* 25, 167-176.
- Báez, P., Martín, J.W., 1992. Decapod Crustacea larvae collected off northern Chile during an El Niño event (February-March, 1983). *Contributions in Science, Natural History Museum of Los Angeles County* 432, 1-10.
- Bakun, A., Broad, K., 2003. Environmental 'loopholes' and fish population dynamics: comparative pattern recognition with focus on El Niño effects in the Pacific. *Fisheries Oceanography* 12, 458-473.
- Bakun, A., Nelson, C.S., 1991. The seasonal cycle of wind stress curl in sub-tropical eastern boundary current regions. *Journal of Physical Oceanography* 21, 1815-1834.
- Banse, K., Hobson, K.D., 1974. Principal external diagnostic characters of Families of Benthic errantiate Polychaetes. *Bulletin of the Fisheries Research board of Canada* 11-19.
- Barber, R.T., Chavez, F.P., 1983. Biological consequences of El Niño. *Science* 222, 1203-1210.
- Barber, R.T., Chavez F.P., 1991. Regulation of Primary Productivity Rate in the Equatorial Pacific *Limnology and Oceanography*, Vol. 36, No. 8, What Controls Phytoplankton Production in Nutrient-Rich Areas of the Open Sea? (Dec., 1991), pp. 1803-1815.
- Barber, R.T., Kogelschatz, J.E., 1990. Nutrients and productivity during the 1982/83 El Niño, p. 21- 53. Zn P. Glynn [ed.], *Global ecological consequences of the 1982-1983 El Niño-Southern Oscillation*. Elsevier.
- Barber, R.T., Smith, R., 1981. Coastal Uwelling Ecosystems. In. Longhurst, A. (ed), *Analyses of marine ecosystems*. Academic Press. pp 31-69.
- Batten, D.S., Welch, D.W., 2004. Changes in oceanic zooplankton populations in the north-east Pacific associated with the possible climatic regime shift of 1998/1999. *Deep-Sea Research II*, 51,863-873.

- Beaugrand, G., Ibanez, F., 2004. Monitoring marine plankton ecosystems. II: Long-term changes in North Sea calanoid copepods in relation to hydro-climatic variability. *Marine Ecology Progress Series* 284, 35-47.
- Beers, J.R, Stevenson, M.R, Eppley, R.W., Brooks, E.R., 1971. Plankton populations and upwelling off the coast of Peru, June 1969. *Fishery Bulletin* 69,859-876.
- Behrenfeld, M.T., Randerson, J.T., McClain, C.R., Feldman, G.C, Los, S.O., Tucker, C.J., Falkowski, P.G., Field, C.B., Frouin, R., Esaias, W.E., Kolber, D.D., Pollack, N.H., 2001. Biospheric primary production during an ENSO Transition. *Science*. 291, 2594-2597.
- Bellantoni D.C., Peterson, W.T., 1987. Temporal variability in egg production rates of *Acartia tonsa* Dana in Long Island Sound. *Journal Experimental Marine Biology and Ecology* 107, 199-208.
- Berggreen U, Hansen B, Kiørboe T. 1988. Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: Implications for determination of copepod production. *Marine Biology* 99, 341-352.
- Bertrand, A., Segura, M., Gutiérrez, M., Vásquez, L., 2005. From small-scale habitat loopholes to decadal cycles: a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. *Fish and Fisheries* 5, 296-316.
- Bieri, R., 1957. The Chaetognath fauna off Peru in 1941. *Pacific Science* 11, 255-264.
- Bieri, R., 1959. The distribution of the planktonic Chaetognatha in the Pacific and their relationship to the water masses. *Limnology and Oceanography* 4, 1-27.
- Bigelow, H.B., 1911. The Siphonophorae. Reports on the scientific results of the expedition to the eastern tropical Pacific by the U.S. Fish Commission Steamer "Albatross". *Mem. Mus. Comp. Zool., Harvard Coll.* 38 (2), 173-401.
- Blanco, J.L., Thomas, A.C., Carr, M.E., Strub, P.T., 2001. Seasonal climatology of hydrographic conditions in the upwelling region off northern Chile. *Journal Geophysical Research-Oceans* 106, 11451-11467.
- Bohle-Carbonell, M., 1989. On the variability of the Peruvian upwelling system. In Pauly, D., Muck, P., Mendo, J., Tsukayama, I. (Eds.). *ICLARM Conference Proceedings of The Peruvian Upwelling Ecosystem, 1953–1984*, vol. 18, pp. 14-32.
- Bond, N.A., Overland, J.E., Spillane, M., Stabeno, P., 2003 Recent shifts in the state of the North Pacific. *Geophysical Research Letter* 30(23), 2183.

- Bonhomme, C., Aumont, O., Echevin, V., 2007. Advective transport caused by intraseasonal Rossby waves: a key player of the high chlorophyll variability off the Peru upwelling region. *Journal of Geophysical Research* 112, C09018.
- Boyd, C.M., Smith, S.L., 1983. Plankton, upwelling, and coastally trapped waves off Peru. *Deep Sea Research Part A* 30(7),723-742.
- Boyd, C.M., Smith, S.L., Cowles, T.J., 1980. Grazing patterns of copepods in the upwelling system off Peru. *Limnology and Oceanography* 25, 583-596.
- Boyd CM, Smith, SL, Cowles T.J. 1981. Grazing patterns of copepods in the upwelling system off Peru. *Boletín Instituto del Mar del Peru Volumen Extraordinario*, 144-154.
- Böttjer, D, Morales, C.E., 2007. Nanoplanktonic assemblages in the upwelling area off Concepción (~36°S), central Chile: Abundance, biomass, and grazing potential during the annual cycle. *Progress in Oceanography* 75, 415-434.
- Brink, K.H., Halpern, D., Smith, R.L., 1980. Circulation in the Peruvian upwelling system near 15°S. *Journal Geophysical Research* 85, 4036-4048.
- Brink, K., Halpern, D., Huyer, A., Smith, R., 1980. Near-shore circulation near 15°S the physical environment of the Peruvian upwelling system. Elsevier, Amsterdam.
- Brink, K.H., Halpern, D., Huyers, T.A., Smiths, R.L., 1983. The physical environment of the Peruvian upwelling system. *Progress in Oceanography* 22, 285-305.
- Broglio, E., Jónasdóttir, S.H., Calbet, A., Jakobsen, H.H. Saiz, E., 2003. Effect of heterotrophic versus autotrophic food on feeding and reproduction of the calanoid copepod *Acartia tonsa*, relationship with prey fatty acid composition. *Aquatic Microbiology and Ecology* 31, 267-278.
- Bruland, K., 2006. A review of the chemistries of redox sensitive elements within suboxic zones of oxygen minimum regions. *Gayana (Concepc.)* 70 (Supplement), 6-13.
- Burkart, C.A., Kleppel, G.S., 1998. Egg production of the copepod *Acartia tonsa* in Florida Bay during summer. 1. The role of the food environment and diet. *Estuaries* 21, 328-339.
- Bustos, H., Aracena, O., Mora, S., Palma, W., 1982. Estudio de crecimiento y edad en el recurso langostino colorado (*Pleuroncodes monodon* H. Milne Edwards, 1837). Informe del Instituto Pesquero, Santiago, 120 pp.
- Calbet, A.C., Landry, M.R., 2004. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnology and Oceanography* 49(1), 51-57.

- Calienes R, Guillen, O., 1981. Masas de agua y producción primaria en el Perú. In: Investigación cooperativa de la anchoveta y su ecosistema. Boletín Instituto Mar del Peru. Volumen Extraordinario, 130-144.
- Calienes, R., Guillen, O., Lostaunau, N., 1985. Variabilidad espacio-temporal de clorofila, producción primaria y nutrientes frente a la costa peruana. Boletín del Instituto del Mar del Peru 10, 6-12.
- Camayo, R., Campos, E.J.D., 2006. Application of wavelet transform in the study of coastal trapped waves off the west coast of South America. Geophysical Research Letters 33, L22601.
- Campbell, R.G., Teegarden, J.G., Cembella, A.D., Durbin, E.G., 2005. Zooplankton grazing impacts on *Alexandrium spp.* in the nearshore environment of the Gulf of Maine. Deep Sea Research part II 52, 2817-2833.
- Cane, M.E., 2004. The evolution of El Niño, past and future. Earth Planetary Science. Letters 164,1-10.
- Carr, M.E., 2003. Simulation of carbon pathways in the planktonic ecosystem off Peru during the 1997-1998 El Niño and La Niña. Journal of Geophysical Research 108(10), 1- 15.
- Carr, M-E., Kearns, E.J., 2003. Production regimes in four Eastern Boundary Current systems. Deep Sea Research Part II 50,3199-3221.
- Carrasco de Luyo, S., 1981. Anfípodos y su relación con mareas rojas, p. 45-53 In Memorias del Seminario sobre indicadores biológicos del plancton. Instituto del Mar del Peru., Callao- Peru, 8-11 de Septiembre de 1980. UNESCO. Unpublished
- Carrasco, S., 1989. Anfípodos planctónicos del área comprendida ente Paita y norte de Chimbote. Tesis de Licenciatura, Facultad de biología, Universidad Particular Ricardo Palma. Lima. Unpublished
- Carrasco, S., Lozano, O., 1989. Seasonal and long-term variations of zooplankton volumes in the Peruvian sea, 1964-1987. Instituto del Mar del Perú (IMARPE), Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) and International Center for Living Aquatic Resources Management (ICLARM), Manila, pp. 82-95.
- Carrasco, S., Santander, H., 1987. The El Niño event and its influence on the zooplankton off Peru. Journal of Geophysical Research 92(C13), 14405-14410.
- Castillo, R.F., 2004. Composición específica, distribución y abundancia de ostracodos epipelágicos en el mar Peruano durante los años 1998 y 2001. Tesis de Licenciatura. Facultad de ciencias departamento de Biología, Universidad Nacional Agraria La Molina, Lima. Unpublished.
- Castillo, R.F., Antezana, T., Ayón, P., Mendo, J., 2005. Distribution of ostracods off Peru under the influence of El Niño 1997-98 First Alexander Von Humboldt/ International Conference on the El Niño Fenomenon and It's global impact., Guayaquil, pp 104. Unpublished.

- Castillo, R., Antezana, T., Ayón, P., 2007. The influence of El Niño 1997-98 on pelagic ostracods in the Humboldt Current Ecosystem off Peru. *Hydrobiologia* 585,29-41.
- Chavez, F.P., Barber, R.T., Sanderson, M.P., 1989. The potential Primary Production of the Peruvian Upwelling System, Vol. Instituto del Mar del Peru (IMARPE), Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) and International Center for Living Aquatic Resources Management (ICLARM).
- Chavez, F.P., Ryan, J., Lluch-Cota, S.E., Ñiquen, C.M., 2003. Climate: From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science* 299, 217-221.
- Chen, D., Cane, M.A., 2008. El Niño prediction and predictability. *Journal of Computational Physics* 227, 3625-3640.
- Chesson, J., 1983. The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64, 1297-1304.
- Childress, J.J., Thuessen, E.V., 1992. Metabolic potential of deep-sea animals: regional and global scales. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Chimpén, C., 1999. Nuevas alternativas tecnológicas para recursos pesqueros no explotados. *Revista Focus*, Instituto Tecnológico Pesquero del Perú (ITP) Año 2, 1, 36 p.
- Cohen, J.H., Forward, Jr. R.B., 2002. Spectral sensitivity of vertically migrating marine copepods. *Biological Bulletin* 203, 307-314.
- Costlow, J., Fagetti, E., 1967. The larval development of the crab, *Cyclograpsus cinereus* Dana, under laboratory conditions. *Pacific Science* 21(2), 166-177.
- Cowles, T.J., 1978. Copepod feeding in the Peru upwelling system. PhD Thesis. Department of zoology, Duke University, Durham. Unpublished.
- Cowles, T., 1979. The feeding responses of copepods from the Peru upwelling system: food size selection. *Journal of Marine Research* 37, 601-622.
- Clarke, K.R.; Warwick, R.M., 2001. Changes in marine communities: an approach to statistical analysis and interpretation. 2nd Edition. PRIMER-E Plymouth, UK. 172 pp.
- Criales, M.M., McGowan, M.F., 1994. Horizontal and vertical distribution of penaeidean and caridean larvae and micronektonic shrimps in the Florida Keys. *Bulletin of Marine Science* 54 (3), 843-856.
- Criales-Hernandez, M.I., Graco, M., Ayón, P., Flores, G., Schwamborn, R., Hirche, H-J., Wolff, M., 2006. Temporal variability of the mesozooplankton community in the Humboldt Upwelling System off

- Central Peru International Conference on the Humboldt Current System, 27 Nov-2 Dec, Published by. IMARPE, IRD and FAO, Lima, Peru., 151 pp.
- Criales-Hernández, M.I., Schwamborn, R., Graco, M., Ayón, P., Hirche, H-J., Wolff, M., 2008. Zooplankton vertical distribution and migration off Central Peru in relation to the oxygen minimum layer. *Helgoland Marine Research* 62, 85-100.
- Croquette, M., Eldin, G., 2006. A Lagrangian study of the PCUC source waters. In Book of extended abstracts, International Conference The Humboldt Current System, Climate, Ocean dynamics, ecosystem processes, and fisheries (pp.41) Lima, Perú, November 27 - December 1, 2006. Unpublished.
- Croquette, M., Eldin, G. and Echevin, V., 2004. On the contributions of Ekman transport and pumping to the dynamics of coastal upwelling in the south-east pacific. *Gayana (Concepc.)*. 68(2),136-141.
- Csirke, J, Guevara-Carrasco, R, Cárdenas, G., Niquen, M., Chipollini, A., 1996. Situación de los recursos anchoveta (*Engraulis ringens*) y sardina (*Sardinops sagax*) a principios de 1994 y perspectivas para la pesca en el Perú, con particular referencia a las regiones Norte y Centro de la costa peruana. *Boletín del Instituto del Mar del Perú* 15(1),1-23.
- Cuevas, L.A., Morales, C.E., 2006. Nano-heterotroph grazing on bacteria and cyanobacteria in oxic and suboxic waters in coastal upwelling areas off northern Chile. *Journal of Plankton Research* 28 (4), 385-397.
- Cury, P., Shannon, L., Shin, Y.J., 2001. The functioning of marine ecosystems. Reykjavik Conference on Responsible Fisheries in the Marine Ecosystem. Reykjavik, Iceland, 22 pp.
- Dagg, M., 1977. Some effects of patchy food environments on copepods. *Limnology and Oceanography* 22, 99-107.
- Dagg, M.J., Cowles, T.J., 1982. Grazing by copepods in the Peru upwelling. *Deep Sea Research* 29(1A), 147.
- Dagg, M.J., Cowles, T., Whitley, T., Smith, S., Howe, S., Judkins, D., 1980. Grazing and excretion by zooplankton in the Peru upwelling system during April 1977. *Deep Sea Research* 27, 43-59.
- Dam, H.G., Colin, S.P., 2005. *Prorocentrum minimum* (clone Exuv) is nutritionally insufficient, but not toxic to the copepod *Acartia tonsa*. *Harmful Algae* 4, 575-584.
- Dextre, C., 1983. Distribución horizontal del grupo Chaetognatha y del zooplancton en general en el mar del norte Peruano durante el desarrollo del Fenómeno El Niño en Febrero de 1972. Tesis de Licenciatura, Facultad de Biología, Universidad Nacional Federico Villareal, Lima. Unpublished.
- Dickie, L.M., Valdivia, J.E., 1981. Investigación cooperativa de la Anchoveta y su ecosistema (ICANE) entre Perú y Canadá. Informe sumario. *Boletín del Instituto del Perú*, volumen extraordinario, I-XII.

- Dittel, A., Epifanio, C.E., 1984. Desarrollo larval de *Ozius verreauxii* Saussure (Brachyura: Xanthidae) en el laboratorio. *Revista de Biología Tropical* 32, 171-172.
- Drits, A.V., 1985. Food ingestion rate of *Calanus australis* as a function of food concentration under natural conditions. *Oceanology* 25,116-119.
- Dugdale, R.C., Goering, J.J., 1970. Nutrient limitation and the path of nitrogen in Peru Current production. In: E. Chin (ed), A collection of manuscripts on the biological oceanography of the southeast Pacific Ocean. U.S. Gov. Print. Off., Washington, D.C.
- Dugdale, R.C., MacIsaac, J.J., 1971. A computational model for the uptake of nitrate in the Peru upwelling region. *Investigacion Pesquera* 35(1), 299-308.
- Echevin, V., Puillat, I., Grados, C. Dewitte, B., 2004a. Seasonal and mesoscale variability in the Peru upwelling system from in situ data during the years 2000 to 2004. *Gayana* 68 (2)supl, 167-173.
- Echevin, V., Aumont, O., Tam, J., Pasapera, J., 2004b. The seasonal cycle of surface chlorophyll along the Peruvian coast: comparison between SeaWiFS satellite observations and dynamical/biogeochemical coupled model simulations. *Gayana* 68, 325-326.
- Echevin, V., Aumont, O., Ledesma, J., Flores, G., 2008. The seasonal cycle of surface chlorophyll in the Peruvian upwelling system: A modeling study. *Progress in Oceanography* 79, 167-176.
- Edler, L., 1979. Recommendations on methods for marine biological studies in the Baltic Sea, Phytoplankton and Chlorophyll. *The Baltic Marine Biology Publication* 5, 1-38.
- Enfield, D., 1975. Oceanografía de la región norte del Frente Ecuatorial: aspectos físicos. Instituto Oceanográfico de la Armada del Ecuador – INOCAR. Guayaquil, Ecuador.
- Escribano, R., 1998. Population dynamics of *Calanus chilensis* in the Chilean Eastern Boundary Humboldt Current. *Fisheries Oceanography* 7, 245-251.
- Escribano, R., 2006. Zooplankton interactions with the oxygen minimum zone in the eastern south pacific. *Suplemento Gayana* 70, 19-21.
- Escribano, R., Castro, L., 2004. Plancton y productividad. In Werlinger, C., Alveal, K., Romo, H. (Eds). *Biología Marina y Oceanografía: Conceptos y procesos. Tomo I. Trama Impresores. pp 289-312.*
- Escribano, R., Hidalgo, P., 2000. Influence of El Niño and la Niña on the population dynamics of *Calanus chilensis* in the Humboldt Current ecosystem of northern Chile. *ICES Journal of Marine Science* 57, 1867-1874.

- Escribano, R., Morales, C., 2004. Capítulo 21 Sistemas de Surgencia costera. En: Werlinger, C. (ed). *Biología marina y Oceanografía: conceptos y procesos*. Consejo Nacional del Libro y la lectura – Universidad de Concepcion Trama Impresores S.A. Chile. Pp 475-497.
- Escribano, R., Marin, V.H., Iribarren, C., 2000. Distribution of *Euphausia mucronata* at the upwelling area of Peninsula Mejillones, northern Chile: The influence of the oxygen minimum layer. *Scientia Marina* 64 (1), 69-77.
- Escribano, R., Marín, V.H., Hidalgo, P., Olivares, G., 2002. Physical-biological interactions in the pelagic ecosystem of the nearshore zone of the northern Humboldt Current System. In *The Oceanography and Ecology of the Nearshore and Bays in Chile*, Castilla, J.C., Largier, J.L. (eds). Santiago, Chile: Ediciones Universidad Católica de Chile, 145-175.
- Escribano, R., Hidalgo, P., Gonzalez, H., Giesecke, R., Riquelme-Bugueño, R. Maríquez, K., 2007. Seasonal and inter-annual variation of mesozooplankton in the coastal upwelling zone off central-southern Chile. *Progress in Oceanography* 75(3), 470-485.
- Escribano, R., Daneri, G., Farías, L., Gallardo, V.A., González, H.E., Gutiérrez, D., Lange, C.B., Morales, C.E., Pizarro, O., Ulloa, O., Braun, M., 2004. Biological and chemical consequences of the 1997-1998 El Niño in the Chilean coastal upwelling system: A synthesis *Deep-Sea Research II* 51, 2389-2411.
- Escudero, Y.M., 2003. Migración nictimeral del zooplancton marino en un estación frente al Callao (Perú). Tesis de Licenciatura, Facultad de Ciencias Naturales y Matemática, Univerisidad Federico Villa Real, Lima. Unpublished.
- Espinoza, P., Bertrand, A., 2008. Revising anchovy's (*Engraulis ringens*) trophic niche and ecological role reveals its plasticity provides a new vision of the Humboldt Current system., *Progress in Oceanography* 79, 215-227.
- Fenau, R., 1968. Algunas apendicularias de la costa Peruana. *Boletín Instituto del Mar del Perú*. 1(9),536-552.
- Fernández-Álamo, M.A., Färber-Lorda, J., 2006. Zooplankton and the oceanography of the eastern tropical Pacific: A review. *Progress in Oceanography* 69 (2-4), 318-359.
- Fiedler, P.C., 2002. Environmental change in the eastern tropical Pacific Ocean: review of ENSO and decadal variability. *Marine Ecology Progress Series* 244,265-283.
- Fiedler, P.C., Chavez, F.P. Behringer, D.W., Reilly, S.B., 1992. Physical and biological effects of Los Niños in the eastern tropical Pacific, 1986-1989. *Deep Sea Research* 39(2A), 199-219.
- Flint, M.V., 1975. Trophic structure and vertical distribution of trophic groups of mesoplankton of the Equator (97°W). *Truddiy P.P., Shirshov Inst. Okeanologiya* 102,238-244. *In Russian*.

- Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series*. 8, 37-52.
- Fleminger, A., 1973. Pattern, number, variability, and taxonomic significance of integumental organs (sencilla and glandular pores) in the genus *Eucalamus* (copepoda Calanoida). *Fisheries Bulletin* 71, 965-1010.
- Flint M.V., 1975. Trophic structure and vertical distribution of trophic groups of mesoplankton of the Equator (97°W). *Okeanologiya* 102, 238-244 *In Russian*.
- Flint, MV; Timonin, A., 1985. Trophic structure of mesoplankton in the northern part of Peruvian coastal waters. *Oceanologiya* 25(1),139-145. *In Russian*.
- Flint, MV, Drits, A.V., Pasternak, A.F., 1991. Characteristic features of body composition and metabolism in some interzonals copepods. *Marine Biology* 111, 199-205.
- Franco, M., 2003. Aspectos biológico-pesqueros del camaroncito rojo *Pleuroncodes monodon* (M. Edwards, 1837) en el litoral Peruano. Tesis de Ingeniero Pesquero, Facultad de Ingeniería Pesquera y de Alimentos, Universidad Nacional del Callao, 225 p.
- Frost, B.W., 1972. Effects of size and concentration of food particles on the feeding behaviour of the marine planktonic copepod *Calanus pacificus*. *Limnology and Oceanography* 17, 805-815.
- Gallardo, V., Cañete, I., Enríquez-Brionez, S., Roa, R., Acuña, A., Baltazar, M., 1993. Biología del langostino colorado *Pleuroncodes monodon* H. Milne Edwards, 1837 y especies afines (Crustacea, Decapoda, Anomura, Galatheidae): sinopsis. In: F. Faranda, O. Parra (eds.). Elementos básicos para la gestión de los recursos vivos marinos costeros de la región del Biobío. Programa EULA, Universidad de Concepción, Monografías Científicas 2, 67-113.
- Gallardo, V., Cañete, I., Roa, R., Enríquez-Brionez, S., Baltazar, M., 1994. Recruitment of the squat lobster *Pleuroncodes monodon* on the continental shelf off central Chile. *Journal of Crustaceana Biology* 14(4), 665-669.
- Gárate, L.I., Martínez, L.A., 1997. Primer registro de una marea roja de *Prorocentrum mexicanum* (Prorocentaceae) en aguas del Golfo de California. *Revista de Biología Tropical* 45, 1263-1271.
- Glebov, B.V., 1982. Diurnal variations in the vertical distribution of zooplankton in Coastal Peru waters. *Vestnik Moskovskogo universiteta. Seriya biologiya*. Moscow. 3,6-11. *In Russian*.
- Gentleman, W., Leising, A., Frost, B., Strom, S., Murray, J., 2003. Functional responses for zooplankton feeding on multiple resources of assumption and biological dynamics. *Deep Sea Research Part II* 50, 2847-2875.
- Geynrikh, A.K., 1973. Horizontal distribution of copepods in the Peru Current Region. *Oceanology* 13, 94-103.

- Gifford, D.J., Dagg, M.J., 1988. Feeding of the estuarine copepod *Acartia tonsa* Dana: carnivory vs. herbivory in natural microplankton assemblages. *Bulletin of Marine Science* 43, 458–468.
- Giron, M., 2001. Zooplankton e ictioplankton durante el crucero oceanográfico regional Conjunto 0005-06. *Informes del Instituto del Mar del Perú* 163, 47-57.
- Gómez, O., 1972. Contribución al conocimiento de los copépodos de la costa Peruana. Tesis de Licenciatura, Facultad de Biología, Universidad Nacional Mayor de San Marcos. Lima. Unpublished.
- Gómez, O., 1982. Los copépodos planctónicos del Mar Peruano. *Boletín de Lima* 23,1-16
- Gómez, I.O., 1997. Los tintinidos (Protozoa: Ciliata) del mar Peruano y sus relaciones con el fenómeno El Niño. *Boletín del Instituto del Mar del Perú* 16(2),61-84.
- Gonzalez, H.E., Ortiz, V.C., Sobarzo, M., 2000. The role of faecal material in the particulate organic carbon flux in the northern Humboldt Current, Chile (23°S), before and during the 1997-1998 El Niño. *Journal of Plankton Research* 22, 499-529.
- Gonzalez, H.E., Menschel, E., Aparicio, C., Barria, C., 2007. Spatial and temporal variability of microplankton and detritus, and their export to the shelf sediments in the upwelling area off Concepcion, Chile (~36°S), during 2002-2005. *Progress in Oceanography* 75, 435-451.
- González, H.E., Sobarzo, M., Figueroa, D., Nöthig, E-M., 2000. Composition, biomass and potential grazing impact of the crustacean and pelagic tunicates in the northern Humboldt Current area off Chile: differences between El Niño and non-El Niño years. *Marine Ecology Progress Series* 195,201-220.
- Graco, M., Farías, L., Molina, V., Gutiérrez, D., Nielsen, L.P., 2001. Massive developments of microbial mats following phytoplankton blooms in a naturally eutrophic bay: implications for nitrogen cycling. *Limnology and Oceanography* 46, 821–832.
- Graco, M.I., Ledesma, J., Flores, G., Giron, M., 2007. Nutrientes, oxígeno y procesos biogeoquímicos en el sistema de las surgencias de la corriente de Humboldt frente al Perú. *Revista Peruana de Biología* 14(1), 117-128.
- Gray CA, Kingsford, M.J., 2003. Variability in thermocline depth and strength, and relationships with vertical distributions of fish larvae and mesozooplankton in dynamic waters coastal waters. *Marine Ecology Progress Series* 247, 211-224.
- Greene, K., 2002. Ocean sciences meeting: coastal cool-down. *Science* 295(5561), 1823.
- Guillen, V., 1978. Distribución horizontal de algunos copépodos calonoideas en el Area Peruto Pizaro-Callao (03°40- 11°55 LS) en diciembre de 1976. Tesis. Universidad Nacional San Cristóbal de Huamanga. Ayacucho, Peru. Unpublished

- Guillen, O., Calienes, R., 1981. Upwelling off Chimbote. *Coastal and Estuarine Science* 1, 312-326.
- Gunter, E.R., 1936. A report on oceanographical investigations in the Peru Coastal Current. *Discovery Reports* Vol XIII, 107-276.
- Gurney, R., 1942. The larvae of decapod crustacea. *Ray Soc. Publ.* 129, 1-306.
- Gutiérrez, D., Aronés, K., Chang, F., Quipuzcoa, L., Villanueva, P., 2005. Impacto de la variación oceanográfica estacional e interanual sobre los ensambles de Microfitoplancton, mesozooplancton, ictioplancton y macrozoobentos de dos áreas costeras del norte del Perú entre 1994 a 2002. *Boletín Inst. Mar Perú* 22(1-2), 1-60.
- Gutiérrez, D., Enríquez, E., Purca, S., Quipúzcoa, L., Marquina, R., Flores, G., Graco, M., 2008. Oxygenation episodes on the continental shelf of central Peru: Remote forcing and benthic ecosystem response. *Progress in Oceanography* 79, 177-189.
- Gutiérrez, J., Zúñiga, O., 1977. *Pleuroncodes monodon* H. Milne Edwards, 1837 en la bahía de Mejillones del sur, Chile (Crustacea, Decapoda, Anomura). *Revista de Biología Marina, Valparaíso* 16(2), 161- 169.
- Gutiérrez, M., Bertrand, A., Ramirez, A., Bertrand, S., Gerlotto, F., Moron, O., Peraltilla, S., 2008. Ecological niche, patterns of distribution and overlapping of the squat lobster 'munida' (*Pleuroncodes monodon*) and anchovy (*Engraulis ringens*) off Peru from 1998 - 2006. *Progress in Oceanography* 79, 256-263.
- Guzmán, S., Carrasco, S., 1996. Las investigaciones del ictioplancton y el zooplancton en el IMARPE. Necesidades y perspectivas. *Informe Progresivo del Instituto del Mar del Perú*. Perú 28, 3-18.
- Haig, J., 1955. The crustacean Anomura of Chile. *Report of the Lunds University Chile Expedition 1848-49.* *Lund Univ. Arsskr. (N.F. Avd. 2)* 51(12), 1-60.
- Haurly, LR, Wiebe, P.H., Orr, M.H., Briscoe, M.G., 1983. Tidally generated high-frequency internal wave packets and their effects on plankton in Massachusetts Bay. *Journal of Marine Research* 41, 65-112.
- Hays, G.C., 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologica* 503, 163-170.
- Hays, G.C, Richardson, A.J., Robinson, C., 2005. Climate change and marine plankton. *Trends in Ecology and Evolution* 20(6), 337-344.
- Heinrich, A.K., 1973. Horizontal distribution of copepods in the Peru Current region. *Oceanology* 13, 94-103.
- Hendricks, M.E., Estrada-Navarrete, F.D., 1989. A checklist of the species of pelagic shrimps (Penoidea and Caridea) from the Eastern Pacific, with notes on their geographic and depth distribution. *California Cooperative Oceanic Fisheries Investigation Reports* 30, 104-121.

- Herman, A.W., 1984. Vertical copepod aggregations and interactions with chlorophyll and production on the Peru Shelf. *Continental Shelf Research* 3(2),131-146.
- Herman, A.W., Sameoto, D., 1981. Copepod distributions on the Peru shelf at 9°S during November, 1977. *Boletín Instituto del Mar del Peru Volumen Extraordinario*, 228-233.
- Hernández-León, S., Almeida, C.G., M., Torres, S.M., Portillo-Hahnefeld, I., 2001. Zooplankton biomass and indices of feeding and metabolism in island-generated eddies around Gran Canaria. *Journal of Marine Systems* 30, 51-66.
- Hidalgo, P., Escribano, R., 2001. Succession of pelagic copepod species in coastal waters off northern Chile: the influence of the 1997-98 El Niño. *Hydrobiologia* 454/454, 153-160.
- Hidalgo, P., Escribano, R., Morales, C.E., 2005. Ontogenetic vertical distribution and diel migration of the copepod *Eucalanus inermis* in the oxygen minimum zone off northern Chile (20-21°S). *Journal of Plankton Research* 27, 519-529.
- Hill, A.E., Hickey, B.M., Shillington, F.A., Strub, P.T., Brink, K., Barton, E.D., Thomas, A.C., 1998. Chapter 2. Eastern Ocean Boundaries Coastal segment. In: A.R. Robinson, A.R. Brink, K. (eds), *The Sea*, John Wiley & Sons Inc 11 (29-67).
- Hillebrand, H., Duerselen, C.D., Kirschtel, D., Pollinger, U., Zohary, T., 1999. Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology* 35, 403-424.
- Hooff, R.C., Peterson, W.T., 2006. Copepod biodiversity as an indicator of changes in ocean and climate conditions of the northern California current ecosystem. *Limnology and Oceanography* 51(6), 2607-2620.
- Holm-Hansen, A, Lorenzen, C., Holmes, R., Strickland, J., 1965. Fluorometric determination of Chlorophyll. *Journal du Conseil Permanent International pour l'Exploration de la Mer* 30, 3-15.
- Hutchings, L., Verheye, H., Huggett, J.A., Demarcq, H., Barlow, R.G., da Silva, A., 2006. Variability of plankton with references to fish variability in Benguela Current Large Marine Ecosystem- an overview. In: Shannon, V., Hempel, G., Malonotter-Riyyoli, P., Moloney, C., Woods, J. (eds), *The Benguela: Predicting a Large Marine Ecosystems*. Elsevier, pp 91-124.
- Huyer, A., Knoll, M., Paluszkiwicz, T., Smith, R. L., 1991. The Peru Undercurrent: A study in variability. *Deep-Sea Research* 38 (Suppl. 1), 247-279.
- Iriarte, J.L., Pizarro, G., Troncoso, V.A., Sobarzo, M., 2000. Primary production and biomass of size-fractionated phytoplankton off Antofagasta, Chile (23-24°S) during pre-El Niño and El Niño 1997. *Journal of Marine System* 26(1), 37-51.

- Irigoin, X, Conway, D.V.P., Harris, R.P., 2004. Flexible diel vertical migration behaviour of zooplankton in the Irish Sea. *Marine Ecology Progress Series* 267, 85-97.
- Jarre-Teichmann, A., 1998. The potential role of mass of balance models for the management of upwelling ecosystems. *Ecological Applications*, 8(1) supplement, s93-s103.
- Jarre, A., Muck, P., Pauly D., 1991. Two approaches for modeling fish stock interactions in the Peruvian upwelling ecosystem. *ICES Marine Science Symp.* 193, 171-184.
- JGOFS, 1996. Primary production by 14C. In: protocols for the joint Global Ocean Flux studies (JGOFS) core measurements. Chapter 19. Published by SCOR. pp.155-162.
- Johnson, J., Shanks, A.L., 2002. Time series of the abundance of the post-larvae of the crabs *Cancer magister* and *Cancer spp.* on the southern Oregon coast and their cross-shelf transport. *Estuaries* 25, 1138-1142.
- Judkins, D., 1980. Vertical distribution of zooplankton in relation to the oxygen minimum off Peru. *Deep Sea Research* 27A, 475-487.
- Kang, J.H., Kim, W.S., Chang, K.I., 2008. Latitudinal distribution of mesozooplankton in the off-equatorial northeastern Pacific before and after the 1998/99 La Niña event. *Marine Environmental Research* 65, 218-234.
- Kjørboe, T., 1997. Population regulation and role of mesozooplankton in shaping marine pelagic food webs. *Hydrobiologia* 363, 13-27.
- Kjørboe, T., Saiz, E., Viitasalo, M., 1996. Prey switching behaviour in the planktonic copepod *Acartia tonsa*. *Marine Ecology Progress Series* 143, 65-75.
- Kjørboe, T., Mohlenberg, E., Hamburger, K., 1985. Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration and composition of specific dynamic action. *Marine Ecology Progress Series* 40, 1-10.
- Klekowski, R.R., Kukina, I.V., Tumantseva, N.I., 1975. Metabolic rate in microzooplankton. *Trudy IOAN SSSR* 102. *In Russian*.
- Kleppel, G.S., 1992. Environmental regulation of feeding and egg production by *Acartia tonsa* off southern California. *Marine Biology* 112, 57-65.
- Kleppel, G.S., 1993. On the diets of calanoid copepods. *Marine Ecology Progress Series* 99, 183-195.
- Kleppel, G.S., Hazzard, S.E., 2000. Diet and egg production of the copepod *Acartia tonsa* in Florida Bay. II. Role of the nutritional environment. *Marine Biology* 137, 111-121
- Kleppel, G.S., Burkart, C.A., Carter, K., Tomas, C., 1996. Diets of calanoid copepods on the West Florida continental shelf: Relationships between food concentration, food composition and feeding activity. *Marine Biology* 127, 209-217.

- Kleppel, G.S., Burkard, C.A., Tomas, C., 1998. Egg production of the copepod *Acartia tonsa* in Florida bay during summer. 1. The roles of food environment and diet. *Estuaries* 21, 328-339.
- Kleppel, G.S., Holliday, D.V., Pieper, R.E., 1991. Trophic interactions between copepods and microplankton: a question about the role of diatoms. *Limnology and Oceanography* 36, 172-178.
- Kleppel, G.S., Willbanks, L., Pieper, R.E., 1985. Diel variation in body carotenoid content and feeding activity in marine zooplankton assemblages. *Journal of Plankton Research* 7, 569-580.
- Koettker, A.G., Freire, A.S., 2006. Spatial and temporal distribution of decapod larvae in the subtropical waters of the Arvoredo archipelago, SC, Brazil. *Iheringia - Serie Zoologia* 96 (1), 31-39.
- Konololova, G.V., 1980. Nannoplankton of intensive upwelling in the coastal waters off Peru. *Biol. mor., Akad. Nauk SSSR*, 1980(1), 43-47. *In Russian*.
- Lenz, J., 2000. Introduction. In: Harris, R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M. (Eds.), *ICES Zooplankton Methodology Manual*. Academic Press, San Diego/London, pp. 1-32.
- Libourel, S.E., Roman, M.R., 1987. Effects of food quality on the functional ingestion response of the copepod *Acartia tonsa*. *Marine Ecology Progress Series* 40, 69-77.
- Lincoln, J.A., Turner, J.T., Bates, S.S., Léger, C., Gauthier, D.A., 2001. Feeding, egg production, and egg hatching success of the copepods *Acartia tonsa* and *Temora longicornis* on diets of the toxic diatom *Pseudo-nitzschia multiseries* and the non-toxic diatom *Pseudo-nitzschia pungens*. *Hydrobiologia* 453/454, 107-120.
- Litzow, M.A., 2006. Climate regime shifts and community reorganization in the Gulf of Alaska: how do recent shifts compare with 1976/1977. *ICES J. Mar. Sci.* 63, 1386-1396.
- Longhurst, A.R., 1967. Vertical distribution of zooplankton in relation to the eastern Pacific oxygen minimum. *Deep-Sea Research* 14, 51-63.
- Longhurst, A.R., 1981. *Significance of spatial variability*. Academic Press, London.
- Longhurst, A., 2007. *Ecological geography of the sea*. Chapter 11 Pacific Ocean. 2 ed. Academic Press. USA. pp 409-417.
- Mace, A.J., Morgan, S.G., 2006. Biological and physical coupling in the lee of a small headland: Contrasting transport mechanisms for crab larvae in an upwelling region. *Marine Ecology Progress Series* 324, 185-196.
- Mackas, D.L., Peterson, W.T., Zamon, J.E., 2004. Comparisons of interannual biomass anomalies of zooplankton communities along the continental margins of British Columbia and Oregon. *Deep-Sea Research Part II* 51, 875-896.

- Mackas, D.L., Boyd, C.M., Smith, S., Santander, H., 1981. Vertical distributions of plankton in the upper 35 m of the Peruvian upwelling zone - application of a shipboard electronic plankton counting system. *Boletín Instituto del Mar del Perú Volumen Extraordinario*, 67-71.
- Martins, A.S., Haimovici, M., Palacios, R., 2005. Diet and feeding of the cutlassfish *Trichiurus lepturus* in the Subtropical Convergence Ecosystem of southern Brazil. *Journal of the Marine Biological Association of the United Kingdom* 85(5), 1223-1229.
- Martínez-López, A., Escobedo-Urías, D.C., Ulloa-Pérez, A.E., Aguirre, R. 2008. Dynamics of a *Prorocentrum minimum* bloom along the northern coast of Sinaloa, Mexico. *Continental Shelf Research* 28, 1693-1701.
- McManus, G.B., Costas, B.A., Dam, H.G., Lopes, R.M., Gaeta, S.A., Susini, S.M., Rosetta, C.H., 2007. Microzooplankton grazing of phytoplankton in a tropical upwelling region. *Hydrobiologia* 575 (1), 69-81.
- McManus, M.A., Cheriton, O.M., Drake, P.J., Holliday, D.V., Storlazzi, C.D., Donaghay, P.L., Greenlaw, C.F., 2005. Effects of physical processes on structure and transport of thin zooplankton layers in the coastal ocean. *Marine Ecology Progress Series* 301, 199-215.
- McPhaden, M.J., Zebiak, S.E., Glantz, M.H., 2006. ENSO as an Integrating Concept in Earth Science. *Science* 314,1740-1745.
- Mejia, J., Flores, L.A., Segura, G., 1971. Exploración sobre recursos costeros y recursos demersales. Crucero 7104 B/I SNP-1. Serie de Informes Especiales N° IM-88. Unpublished.
- Mejia, J., Esquerre, M., Castillo, J., 1980. Situación del recurso merluza y sus características biológicas en la primavera de 1978. *Informe del Instituto del Mar del Perú* 58, 1-54
- Menden-Deuer, S., Lessard, E., 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnology and Oceanography* 45(3), 549-579.
- Mendo, J., Yamashiro, C., Rubio, J., Kameya, A., Jurado, E., Maldonado, M., Guzmán, S., 1989. Evaluación de la Población de Concha de Abanico (*Argopecten purpuratus*) en la Bahía Independencia, Pisco, Perú 23 de Setiembre - 9 de Octubre de 1987. *Informe, Instituto del Mar del Perú* 94,1-65.
- Menshutkin, V.V., Tseytlin, V.B., Vinogradov, M.Ye., 1980. Stochastic approach to modeling an upwelling ecosystem. In: *Ecosistemy pelagiali Peruanskogo rayona (Pelagic ecosystems of the Peru area)*, Nauka press, Moscow, pp.257-267.
- Meyer-Harms, B., Irigoien, X., Head, R., Harris, R., 1999. Selective feeding on natural phytoplankton by *Calanus firmanchicuis* before, during and after the 1997 spring bloom in the Norwegian Sea. *Limnology and Oceanography* 44, 154-165.

- Meyer, B., Irigoien, X., Graeye, M., Head, R.N., Harris, R.P., 2002. Feeding rates and selectivity among nauplii, copepodites and adult females of *Calanus finmarchicus* and *Calanus helgolandicus*. *Helgoland Marine Research* 56, 169-176.
- Mikheyev, V.N., 1977a. Age structure of populations of a zoocenosis in the Peruvian coastal upwelling. *Oceanologia* 17, 700-706.
- Mikheyev, V.N., 1977b. Structural characteristics of populations of common copepod species in the Peruvian Upwelling Region. Comparison of sampling devices. *Oceanology* 17(3), 336-339.
- Morales, C.E., Blanco, J.L., Braun, M., Reyes, H., Silva, N., 1996. Chlorophyll-a distribution and associated oceanographic conditions in the upwelling region off northern Chile during the winter and spring 1993. *Deep-Sea Research I* 43, 267-289.
- Morón, O., 2000. Características del ambiente marino frente a la costa peruana. *Boletín del Instituto del Mar del Perú* 19, 179-204. (In Spanish, with English abstract).
- Morón, O., 2006. Monthly sea surface salinity by marsden squares off the Peruvian coast (1960 - 2004). *International Conference on the Humboldt Current System*. IMARPE, IRD and FAO, Lima, Peru, pp 104.
- Mullin, M., 1995. The Californian El Niño of 1992 and the fall of *Calanus*. *California Cooperative Oceanic Fisheries Investigations Reports* 36, 175-178.
- Neill, W.E., 1992. Population variation in the ontogeny of predator-induced vertical migration of copepods. *Nature* 356, 55-57.
- Nixon, S., Thomas, A., 2001. On the size of the Peru upwelling ecosystem. *Deep Sea Research* 48(1A), 2521-2528.
- Ohman, M.D., 1990. The demographic benefits of diel vertical migration by zooplankton. *Ecological Monographs* 60, 257-281.
- Ohman, M.D., Frost, B.W., Cohen, E.H., 1983. Reverse diel vertical migration - an escape from invertebrate predators. *Science* 220, 1404-1407.
- Packard, T.T., Blasco, D., Jones, V., 1979. Special experiments with nitrate reductase and ETS in plankton from the Peru upwelling system. *CUEA Technical report* 54. 84p.
- Pacheco, A., Garate, A., 2005. Bioincrustantes de cultivo de *Argopecten purpuratus* en Bahía Samanco, Perú. *Ecología Aplicada* 4(1-2), 149-152.
- Paffenhöfer, G.A., 1982. Grazing by copepods in the Peru upwelling. *Deep Sea Research* 29(1A), 145-146.

- Paffenhöfer, G.A., Stearns, D.E., 1988. Why is *Acartia tonsa* (Copepoda: Calanoida) restricted to nearshore environments? Marine Ecology Progress Series 42, 33-38.
- Paffenhöfer, G.A., Lewis, K.D., 1990. Perceptive performance and feeding behaviour of calanoid copepods. Journal of Plankton Research 12, 933-946.
- Paffenhöfer G.A., Mazzocchi, M.G., 2002. On some aspects of the behaviour of *Oithona plumifera* (Copepoda: Cyclopoida). Journal of Plankton Research 24, 129-135.
- Pagano, M., Kouassi, E., Saint-Jean, L., Arfi, R., Bouvy, M., 2003. Feeding of *Acartia clausi* and *Pseudodiaptomus hessei* (Copepoda:Calanoida) on natural particles in a tropical lagoon (Ebrié, Côte d'Ivoire). Estuarine Coastal and Shelf Science 56, 433-445.
- Palma, S., 1976. Meroplankton de la región de Valparaíso. Ciencia y Tecnología del Mar 2, 99-116.
- Palma, S., 1994. Distribución y abundancia de larvas de langostino colorado *Pleuromcodes monodon* frente a la costa de Concepción, Chile. Investigaciones Marinas, Valparaíso 22, 13-29.
- Pauly, D., Jarre, A., Luna, S., 1989. On the quantity and types of food ingested by *Peruvian Anchoveta*, 1953-1982. In Pauly, D., Muck, P., Mendo, J., Tsukayama, I. (Eds), The peruvian upwelling ecosystem: Dynamic and interactions. ICLARM Conference Proceedings 18, 109-124 pp.
- Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. Nature 418, 689-695.
- Pearre, S., 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. Biological Reviews 78, 1-79.
- Pennington, J.T., Mahoney, K. L., Kuwahara, V.S., Kolber, D.D., Calienes, R., Chavez, F.P., 2006. Primary production in the eastern tropical Pacific: A review. Progress in Oceanography 69(2-4), 285-317.
- Penven, P., Echevin, V., Pasopera, J., Colas, F., Tam, J., 2005. Average circulation, seasonal cycle, and mesoscale dynamics of the Peru Current System: A modeling approach. Journal of Geophysical Research 110, C10021.
- Perry, R.I., Batchelder, H.P., Mackas, D.L., Chiba, S., Durbin, E., Greve, W., Verheye, H.M., 2004. Identifying global synchronies in marine zooplankton populations: Issues and opportunities. ICES Journal of Marine Science 61, 445-456.
- Peterson, W., 1998. Life cycle strategies of copepods in coastal upwelling zones. Journal of Marine System 15, 313-326.
- Peterson, W.T., Miller, C.B., Myers, A.H., 1979. Zonation and maintenance of copepod population in the Oregon upwelling zone. Deep sea Research 26, 267-494.

- Petipa, T.S., Monakov, A.V., Sorokin, Yu.I., Voloshina, A.V., 1977. Balance of matter and energy in copepods of the tropical upwellings of Pacific Ocean. *Polskie Archiwum Hydrobiologii* 24, 413-430.
- Philander, S.G., 1999. A review of tropical ocean-atmosphere interactions. *Tellus* 51, 71-90.
- Philander, S.G.H., 1999. A review of tropical ocean-atmosphere interactions. *Tellus* 51,71-90.
- Pielou, E. C., 1966. Species diversity and pattern diversity in the study of ecological succession. *Journal of Theoretical Biology* 10, 370-383.
- Pielou, E., 1975. *Ecological diversity*. John Wiley and Sons. 165p.
- Pillar, S.C., Armstrong, D.A., Hutchings, L., 1989. Vertical migration, dispersal and transport of *Euphasia ludens* in the southern Benguella current. *Marine Ecology Progress Series* 53, 179-190.
- Pineda, J., 1999. Circulation and larval distribution in internal tide bore warm fronts. *Limnology and Oceanography*. 44, 1400-1414.
- Pizarro, O., Shaffer, G., Dewitte, B., Ramos, M., 2002. Dynamics of seasonal and interannual variability of the Peru-Chile Undercurrent. *Geophysical Research letters* 29, 10.1029/2002GL014790.
- Pizarro, O., Clarke, A.J., Van Gorder, S., 2001. El Niño sea level and current along the South American coast: comparison of observations with theory. *Journal of Physical Oceanography* 31, 1891-1903.
- Pohle, G., Fransozo, A., Negreiros-Fransozo, M.L., Medina, F.L., 1999. *Larval Decapoda (Brachyura)*. Backhuys, Leiden
- Ponomareva, L.A., 1982. Early stages of larvae nictiphanes simplex (Euphausiacea) in the Peru Current area. *Oceanology* XXII, 98-101.
- Postel, L., Fock, H. and Hagen, W., 2000. Biomass and Abundance. In: R. Harris, P. Wiebe, J. Lenz, H.R. Skjoldal and M. Huntley (Editors), *Ices Zooplankton methodology manual*. Academic Press, Great Britain, pp. 83-174.
- Quesquén, R., 2004. Zooplankton e ictioplancton del mar Peruano durante el invierno 2001. Informe del Instituto del Mar del Perú 32(1), 81-86.
- Quesquén, R., 2005. Moluscos holoplanctonicos heteropoda y pteropoda colectados en noviembre y diciembre de 1996 en el Mar Peruano. Tesis de Licenciatura. Facultad de Ciencias Biológicas, Universidad Ricardo Palma. Lima. Unpublished.
- Quesquén, R., Guzmán, S., 1999. Nuevo registro de *Phylliroe bucephala* (Mollusca, Gastropoda: Nudibranchia) para el mar Peruano. In: Tresierra A, Culquichicon Z (eds) VIII Congreso Latinoamericano sobre Ciencias del Mar. Lima, Trujillo - Perú, 374-375. Unpublished.

- Quintana, R., 1983. Larval development of the edible crab, *Cancer edwardsi* Bell, 1835 under laboratory conditions (Decapoda, Brachyura). Rep. Usa Mar. Biol. Inst. Kochi Univ., 5, 1-19.
- Quintana, R. Saelzer, H., 1986. The complete larval development of the edible crab, *Cancer setosus* Molina and observations on the prezoel and first zoel stages of *C. coronatus* Molina (Decapoda: Brachyura, Cancridae). J. Fac. Sci., Hokkaido Univ., Ser. VI, zool., 24 (4): 267-303.
- Ramos, E., Indacochea, A., Tarazona, J., 1999. Impacto de 'El Niño 1997-1998' sobre el asentamiento larval de algunos invertebrados marinos bentónicos de bahía de independencia, Pisco, Peru. In: Tarazona, J., Castillo, E., (eds.) El Niño 1997-1998 y su impacto sobre los ecosistemas marino y terrestre, Revista Peruana de Biología, Vol Extraordinario, 60-68.
- Rebstock, G.A., Kang, Y.S., 2003. A comparison of three marine ecosystems surrounding the Korean peninsula: responses to climate change. Progress in Oceanography 59, 357-379.
- Reid PC, Beaugrand G., 2002. Interregional biological responses in the North Atlantic to hydrometeorological forcing. In: Sherman K, Skjoldal HR (eds) Changing states of the large marine ecosystems of the North Atlantic. Elsevier Science, Amsterdam, p 27-48.
- Renz, J., Hirche, H-J. 2006. Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. Marine Biology 148, 567-580.
- Rinke, K., Hubner, I., Petzoldt, T., 2007. How internal waves influence the vertical distribution of zooplankton. Freshwater biology 52, 137-144.
- Rivera, J., Santander, E., 2005. Variabilidad estacional de la distribución y abundancia de larvas de langostino colorado en la zona norte de Chile (Decapoda, Anomura, Galatheidae). Investigaciones Marinas 33(1), 3-23.
- Ryan, J.P., Polito, P.S., Strutton, P.G., Chavez, F.P., 2002. Unusual large-scale phytoplankton blooms in the equatorial Pacific. Progress in Oceanography 55(3-4), 263-285.
- Roe, H.S.J., Angel, M.V., Badcock, J., Domanski, P., James, P.T., Pugh, P.R., Thurston, M.H., 1984. The diel migrations, distributions within a mesopelagic community in the North East Atlantic. 1. Introduction, sampling procedures. Progress in Oceanography 13, 189-199.
- Rojas de Mendiola, B.R., 1981. Seasonal phytoplankton distribution along the Peruvian coast. In: Richards, F.A. (Ed.), Coastal Upwelling. American Geophysical Union, Washington, DC, pp. 348-356.
- Roman, M.R., Reaugh, M.L., Zhang, X., 2006. Ingestion of the dinoflagellate, *Pfiesteria piscicida*, by the calanoid copepod, *Acartia tonsa*. Harmful Algae 5, 435-441.

- Rosenberg, R., Arntz, W.E., Chumán de Flores, E., Flores, L.A., Carbajal, G., Finger, I., Tarazona, J., 1983. Benthos biomass and oxygen deficiency in the Peruvian upwelling system. *Journal of Marine Research* 41, 263-279.
- Ryan, J.P., Polito, P.S., Strutton, P.G., Chavez, F.P., 2002. Unusual large-scale phytoplankton blooms in the equatorial Pacific. *Progress in Oceanography* 55, 263-285.
- Saltzman, J., Wishner, K., 1997. Zooplankton ecology in the eastern tropical Pacific oxygen minimum zone above a seamount: 2. vertical distribution of copepods. *Deep-Sea Research I* 44, 931-954.
- Sameoto, D., 1981. Horizontal and vertical distributions of zooplankton numbers and biomass off the coast of Peru. *Boletín Instituto del Mar del Perú Volumen Extraordinario*, 164-170.
- Sánchez, S. Delgado, E., 1996. Mareas Rojas en el área del Callao (12°S) 1980-1995 IMARPE, Callao. Informe Progresivo Instituto del Mar del Perú 44, 19-37. (In Spanish, with English abstract).
- Sandoval de Castillo, O., 1987. Los quetognatos: indicadores zooplanctonicos del fenómeno "El Niño". *Boletín de Lima* 49, 17-23.
- Santander, H., 1967. Los euphausidos en la zona Callao- Chimbote y la composición general del zooplancton en agosto de 1961. Tesis de Licenciatura. Facultad de Biología, Universidad Nacional Mayor de San Marcos, Lima. Unpublished.
- Santander, H., 1981. The zooplankton in an upwelling area off Peru. In: Richards FA (ed) *Coastal Upwelling Coastal and Estuarine Sciences* 1,400-410pp. American Geophysical Union, Washington D.C.
- Santander, H., Carrasco, S. 1985. Cambios en el zooplancton durante El Niño 1982-1983 en el área de Chimbote. In: Aguilar AET (ed) *I Congreso Nacional de Biología Pesquera*, Trujillo, 201-206 pp.
- Santander, H., Flores, R., 1983. Los desoves y distribución larval de cuatro especies pelágicas y sus relaciones con las variaciones del ambiente marino frente al Perú. Sharp, G.D., Csirke, J. (Ed), *Proceedings of the Expert Consultation to examine changes in abundance and species of neritic fish resources*. San Jose, Costa Rica, 18-29 April 1983. *FAO Fisheries Report* 291(3), 835-870pp.
- Santander, H., Sandoval de Castillo, O., 1969. La importancia de los Euphausidos y Chaetognatos y resultados de su distribución en base al Crucero de Febrero del 1967. *Informe del Instituto del Mar del Perú* 49, 1-17.
- Santander, H, Carrasco, S, Luyo, G., 1981a. El zooplancton del área norte del Perú. *Boletín Instituto del Mar del Perú Volumen extraordinario*, 245-253
- Santander, H., Luyo, G., Carrasco, S., Veliz, M., Sandoval, O., 1981b. Catálogo de zooplancton en el mar Peruano, primera parte: Area Pisco- San Juan. *Boletín Instituto del Mar del Perú* 6, 1-75.

- Schneider, W., Fuenzalida, R., Rodríguez-Rubio, E., Garcés-Vargas, J., Bravo, L., 2003. Characteristics and formation of Eastern South Pacific Intermediate Water. *Geophysical Research Letters* 30, 35-1.
- Schwamborn, R., Ekau, W., Silva, A.P., Silva, T.A., Saint-Paul, U., 1999. The contribution of estuarine decapod larvae to marine zooplankton communities in north-east Brazil. *Archive of Fishery and Marine Research* 47 (2-3), 167-182.
- Schwamborn, R., Neumann-Leitão, S., Silva, T. A., Silva, A. P., Ekau, W., Saint-Paul, U., 2001. Distribution and dispersal of decapod crustacean larvae and other zooplankton in the Itamaracá estuarine system, Brazil. *Tropical Oceanography* 29 (1), 1-13.
- Schwamborn, R., Bonecker, S.L.C., Galvao, I.B., Silva, T.A., Neumann-Leitao, S., 2004. Mesozooplankton grazing under conditions of extreme eutrophication in Guanabara Bay, Brazil. *Journal of Plankton Research* 26, 983-992.
- Sears, M., 1953. Notes on the Siphonophores. 2. A revision of the Abylinae. *Bulletin of the Museum of Comparative Zoology* 109(1),4-119.
- Segura, M., Castillo, R., 1996. Distribución y concentración de la “*Munida*” (*Pleuroncodes monodon*) en el verano 1996. *Informe del Instituto del Mar del Perú* 122, 79-85.
- Semenova, TN, Timonin, AG, Flint, MV, 1982. Horizontal and vertical distribution patterns of mass zooplankton species off Peru. *Okeanologica. Moscow* 22 (2), 297-304. *In Russian*.
- Shannon, C. E., Weaver, W., 1949. *The mathematical theory of communication*. Urbana IL: University of Illinois Press.
- Shanks, A.L., Brink, L., 2005. Upwelling, downwelling, and cross-shelf transport of bivalve larvae: Test of a hypothesis. *Marine Ecology Progress Series* 302, 1-12.
- Shushkina, E.A., Kislyakov, Yu.J., 1975. Evaluation of zooplankton production in the Equatorial Pacific. *Trans. Inst. Oceanol. Acad. Sci. USSR* 102, 384–395. *In Russian*.
- Shushkina, E.A., Kislyakov, Yu.J., 1977a. Estimation of the zooplankton production in the equatorial region of the eastern Pacific Ocean and the Peruvian upwelling. *Polskie Archiwum Hydrobiologii* 24(suppl.), 491-502.
- Shushkina, E.A., Kislyakov, Yu.J., 1977b. Estimation of zooplankton productivity in the Equatorial Region of the Eastern Pacific Ocean and the Peruvian Upwelling *Polskie Archiwum Hydrobiologii* 24, 491-502.
- Shushkina, E.A., Vinogradov, M.E., Sorokin, Yu.I., Lebedeva, L.P., Mikheyev, V.N., 1978. Functional characteristics of planktonic communities in the Peruvian upwelling region. *Oceanology* 18, 578-588.

- Siegert, F, Ruecker, G, Hinrichs, A, Hoffmann, A.A., 2001. Increased damage from fires in logged forests during droughts caused by El Niño. *Nature* 414(6862),437-440.
- Slaughter, A.M., Bollens, S.M., Bollens, G.R., 2006. Grazing impact of mesozooplankton in an upwelling region off northern California, 2000-2003. *Deep Sea Res. II.* 53, 3099-3115.
- Smith, D.L., 1977. A guide to marine Coastal plankton and marine invertebrate larvae. Kendall publishing company, United States, 161p.
- Smith, S.L., 1978. Nutrient regeneration by zooplankton during a red tide off Peru, with notes on biomass and species composition of zooplankton. *Marine Biology* 49, 125-132.
- Smith, R.L., 1995. The physical processes of coastal ocean upwelling systems. in: *Upwelling in the Ocean: Modern Processes and Ancient Records*, C.P. Summerhayes, K.-C. Emeis, M.V. Angel, R.L. Smith, Zeitzschel, B. eds., John Wiley and Sons, Chichester, pp. 39-64.
- Smith, S.L., Boyd, C.M., Lane, P.V.Z., 1981b. Short term variation in the vertical distribution of copepods off the coast of northern Peru. *Boletín Instituto del Mar del Perú Volumen extraordinario*, 112-118.
- Smith, S.L., Brink, K.H, Santander, H., Cowles, T.J., Huyer, A., 1981a. The effect of advection on variations in zooplankton at a single location near Cabo Nazca, Perú. In: Richards F.A. (ed) *Coastal and Estuarine Sciences* 1, 400-410.
- Sorokin, Y.I., 1978. Description of primary production and of the heterotrophic microplankton in the Peruvian upwelling region. *Oceanology* 18, 62-71
- Sorokin, Y.I., Kogelschatz, J.E., 1979. Analysis of heterotrophic microplankton in an upwelling area. *Hydrobiologia*, 66, 195-208.
- Sorokin, Y.I., Mikheev, V.N., 1979. On characteristics of the Peruvian upwelling ecosystem. *Hydrobiologia* 62, 165-189.
- Stemann, N.E., 1952. The use of radio-active carbon ¹⁴C for measuring organic production in the sea. *Journal du Conseil Permanent International pour l'Exploration de la Mer* 18(2), 117-140.
- Stevenson, M., Taft, V., 1971. New evidence of the equatorial undercurrent eastern of the Galapagos Island. *Journal of Marine Research* 29(2), 103-115.
- Strub, P.T., Mesias, J.M. Montecino, V., Rutllant, J., Salinas, S., 1998. Coastal circulation off western South America. In: A. R. Robinson and K. H. Brink (ed), *The Sea, 11: The Global Coastal Ocean - Regional Studies and Syntheses*, pp 273-313.
- Strutton, P.G., Chavez, F.P., 2000. Primary productivity in the equatorial Pacific during 1997–1998 El Niño. *Journal of Geophysical Research* 105, 26089-26101.

- Sullivan, S.K, Bustamante, G., 1999. Setting Geographic Priorities for Marine Conservation in Latin America and the Caribbean. Arlington, Virginia, USA: The Nature Conservancy.
- Sun, J., Lui, D., 2003. Geometric models for calculating cell biovolume and surface area for phytoplankton. *Journal of Plankton Research* 25 (11), 1331–1346.
- Swartzman, G., Bertrand, A., Gutiérrez, M., Bertrand, S., Vasquez, L., 2008. The relationship of anchovy and sardine to water masses in the Peruvian Humboldt Current System from 1983–2005. *Progress in Oceanography* 79, 228-237.
- Tadokoro, K., Chiba, S., Ono, T., Midorikawa, T., 2005. Interannual variation in *Neocalanus* biomass in the Oyashio waters of the western North Pacific. *Fisheries Oceanography* 14 (3), 210-222.
- Takahashi, K., 2005. The annual cycle of heat content in the Peru Current region. *Journal of Climate* 18, 4937-4954.
- Tam, J., Taylor, M., Baskovic, V., Espinoza, Ballon, M.,P., Purca, S., Diaz, S., Gutierrez, D., Quipuzcoa, Ayón, P.L. Sánchez, S., Goya, E., Arguelles, J., Wolff, M., Wosnitza-Mendo C., 2006. Trophic flows in the Northern Humboldt Current Ecosystem, Part 1: Comparing 1995-96 and 1997-98. In. Abstracts of International Conference The Humboldt Current System Climate ocean dynamics ecosystem processes, and fisheries. Nov 27 to Dec. 1 2006. Unpublished.
- Tarazona, J., Arntz, W., 2001. The Peruvian Coastal Upwelling System. In: Seeliger, U., Kjerfve, B. (Eds.), “Coastal Marine Ecosystems of Latin America”. *Ecological Studies*. Springer-Verlag vol. 144., pp. 229-244.
- Tarazona J, Paredes C, Romero L., 1989. Mecanismos y procesos que controlan la colonización y recuperación postcatastrófica de recursos bentónicos de importancia económica en dos areas de diferente productividad del sistema de afloramiento peruano. Informe final del proyecto AID No. 936-5542, Universidad Nacional Mayor de San Marcos, Facultad de Ciencias Biológicas, Lima, Perú, 305 pp.
- Tarazona, J., Gutiérrez, D., Pareces, C., Indacochea, A., 2003. Overview and challenges of marine biodiversity research in Peru. *Gayana*.67 (2), 206-231.
- Tarazona, J., Paredes, C., Romero, L., Guzman, S., 1988. La recolonización de las comunidades de Mitílidos en la Costa Central del Perú después de El Niño 1982-83. In: Salzwedel, H., Landa, A. (ed), *Recursos y Dinámica del Ecosistema de Afloramiento Peruano*. Boletín Inst. del Mar del Perú Volumen Extraordinario, 115-120.
- Tarazona, J., Santander, H., Sanchez, S., Carrasco S., Guzmán, S., 1989. Características del Plancton. In: Tarazona, J. Paredes, C., Romero, L. Mecanismos y procesos que controlan la colonización y recuperación

- post-catastrófica de recursos bentónicos de importancia económica en dos áreas de diferente productividad del sistema de afloramiento Peruano. Informe Final Proyecto AID. 936-5542. 69-118 pp. Unpublished.
- Taylor, A.H., Allen, J.I., Clark, P.A., 2002. Extraction of a weak climatic signal by an ecosystem. *Nature* 416,629-632.
- Taylor, M., Tam, J., Baskovic, V., Espinoza, P., Purca, S., Arguelles, J., Ayón, P., Ballon, M., Díaz, E., Goya, E., Gutierrez, D., Quipezcoa, L. Sánchez, S., Wolff, M., Wosnitza-Mendo C., 2006. Trophic flows in the Northern Humboldt Current Ecosystem, Part 2: elucidating mechanisms of ecosystem change over an ENSO cycle by simulating changes in low trophic level dynamics. In. Abstracts of International Conference The Humboldt Current System Climate ocean dynamics ecosystem processes, and fisheries. Nov 27 to Dec. 1 2006. Unpublished.
- Thiel, M., Macaya, C., Acuña, E., Arntz, WE., Bastías, H., Brokordt, K., Camus, P., Castilla, JC., Castro, LR., Cortés, M., Dumont, CP., Escribano, R., Fernandez, M., Gajardo, JA., Gaymer, CF., Gomez, I., González, AE., González, HE., Haye, PA., Illanes, JE., Iriarte, JL., Lancellotti, DA., Luna-Jorquera, G., Luxoro, C., Manriquez, PH., Marín, V., Muñoz, P., Navarrete, SA., Pérez, E., Poulin, E., Sellanes, J., Sepúlveda, HH., Stotz, W., Tala, F., Thomas, A., Vargas, CA., Vasquez, JA., Vega, JMA., 2007. The Humboldt Current system of northern and central Chile oceanographic processes, ecological interactions and socioeconomic feedback. *Oceanography and Marine Biology Annual Review* 45, 195-344.
- Thuesen, E., Fernandez, M.A., 1999. *Polychaeta*. Backhuys, Leiden.
- Timonin, A.G., Voronina, N.M., 1975. Distribution on net plankton along the equator. *Trudy IOAN SSSR* 102, 213-231 *In Russian*.
- Timonin, A.G., Flint, M.B., 1986. Effect of hydrologic conditions on distribution of zooplankton off the coast of Peru. *Oceanology of the Academy of Sciences of the USSR*. 26(3),366-369. *In Russian*.
- Trevorrow, M.V., 1998. Observations of internal solitary waves near the Oregon coast with an inverted echo sounder. *Journal of Geophysical Research Council Oceans* 103, 7671-7680.
- Tsuchiya, M., 1981. The Origin of the Pacific Equatorial 13°C Water. *Journal of Physical Oceanography*, 11, 794-812.
- Tumantseva, N.I., Kopylov, A.I., 1985a. Reproduction and production rates of *Planktic infusoria* in coastal waters of Peru. *Oceanology (Academy of Sciences of the USSR)*. 25(3),390-394. *In Russian*.
- Tumantseva, N.I., Kopylov, A.I., 1985b. Reproductive rate and production of planktonic ciliates in the coastal Peruvian waters. *Okeanologiya* 25(3),503-508.

- Turner, J.T., Tester, P.A., 1989. Zooplankton feeding ecology: nonselective grazing by the copepods *Acartia tonsa* Dana, *Centropages velificatus* De Oliveira, and *Eucalanus pileatus* Giesbrecht in plume of the Mississippi River. *Journal of Experimental Marine Biology and Ecology* 126, 21-43.
- Turner, J.T., Borkman, D.G., 2005. Impact of zooplankton grazing on *Alexandrium blooms* in the offshore Gulf of Maine. *Deep Sea Research Part II* 52, 2801-2816.
- Turner, J.T., Tester, P.A., Hansen, P.J., 1998. Interactions between toxic marine phytoplankton and metazoan and protistan grazers. In: Anderson, D.M., Cembella, A.D., Hallegraeff, G.M. (Eds.), *Physiological Ecology of Harmful Algal Blooms*. Springer, pp. 453-474.
- Ulloa, O., Escribano, R., Hormazabal, S., Quinones, R.A., Gonzalez, R.R., Ramos, M., 2001. Evolution and biological effects of the 1997–1998 El Niño in the upwelling ecosystem off northern Chile. *Geophysical Research Letters* 28 (8), 1591-1594.
- UNESCO, 1968. UNESCO Report. *Monograph on Oceanographic Methodology*, 2, 153-159.
- Utermöhl, von H., 1931. Neue Wege in der quantitativen Erfassung des Planktons. (Mit besondere Berücksichtigung des Ultraplanktons). *Verh. Int. Verein. Theor. Angew. Limnology and Oceanography* 5, 567-595.
- Van Guelpen, L., Douglas, F., Markle, D.J., Duggan, 1982. An evaluation of accuracy, precision, and speed of several zooplankton subsampling techniques. *Journal du Conseil Permanent International pour l'Exploration de la Mer* 40, 226-236.
- Vargas, C. A., González, H.E., 2004. Plankton community structure and carbon cycling in a coastal upwelling system. I Diet of copepods and appendicularians. *Aquatic Microbiology and Ecology* 34(2), 151-164.
- Vargas, C.A., Martínez, R.A., Cuevas, L.A., Pavez, M.A., Cartes, C., Gonzalez, H.E., Escribano, R., Daneri, G., 2007. The relative importance of microbial and classical food webs in a highly productive coastal upwelling area. *Limnology and Oceanography* 52(4), 1495-1510.
- Vasil'ev, V.I., 1991. Characteristics of zooplankton in the oceanic zone off Peru. Kuz'micheva, VI (ed). *Book monograph. In Russian*.
- Vasquez, F., 1967. *Ensayo sobre la relación de los factores abióticos con la distribución del zooplankton en la costa sur del Peru*. Tesis de Licenciatura, Facultad de Biología, Universidad Nacional de Trujillo. Unpublished.
- Velazco, F, Sarmiento, M, 2007. Topografía y naturaleza del fondo marino. WWW Page, http://www.imarpe.gob.pe/informes/info_merluza/topografia.html.

- Vélez, J.A., Watson, W., Sandknop, E.M., Arntz, W., Wolff, M., 2003a. Larval and osteological development of the Mote Sculpin (*Normanichthys rockeri*)(Pisces:Normanichthyidae) from the Independencia Bay, Pisco, Peru. *Journal of Plankton Research* 25(3), 279-290.
- Velez, J., Arntz, W., 2005. Ichthyoplankton in Independencia bay, Pisco, Peru:Temporal and spatial relationships, 29th Annual Larval Fish Conference. Barcelona, Spain, 11-14 July.
- Véliz, M., 1981. Sifonóforos como posibles indicadores biológicos. In. UNESCO, Memorias del seminario sobre indicadores biológicos del plancton. Inst. Mar del Perú. 8-11 de setiembre de 1980. 104-116 pp.
- Véliz, M., 1985. Sifonóforos en el área norte del Peru. In: Aguilar AET (ed) I Congreso nacional de Biología Pesquera, Trujillo, pp 118-121. Unpublished.
- Verano, R., 1974. Foraminiferos del litoral del departamento de Lima. *Revista Peruana de Biología* 1(1),63-80.
- Vidal, J., 1968. Copepodos calanoideos epipelagicos de la expedición Marchile II *Gayana* 15, 13-93
- Vinogradov, M.E., 1997. Some problems of vertical distribution of Meso and Macroplankton in the Ocean. *Advances in Marine Biology* 32, 2-92.
- Vinogradov, M.E., 1977. Pelagic ecosystems studies on the upwellings of the eastern Pacific Ocean: Cruise 17 of the R/V "Akademik Kurchatov". *Polskie Archiwum Hydrobiologii* 24 (suppl), 7-19.
- Vinogradov, M.E., Shushkina, E.A., 1978. Some development patterns of plankton communities in the upwelling areas of the Pacific Ocean. *Marine Biology* 48(4),357-366.
- Vinogradov, M.E., Shushkina, E.A., Kukina, I.N., 1977. Structural and fuctional analysis of pelagic communities in equatorial upwelling. *Polskie Archiwum Hydrobiologi* 24, 503-526
- Vinogradov, M.E., Shushkina, E.A., Lebedeva, L.P., 1980. Functional characteristics of communities in the northern Peru coastal areas. *Peruvian area pelagic Ecosystems. M. Science*, 242-256. In Russian.
- Walsh, J., 1981. A carbon budget for overfishing off Peru. *Nature*. 290,300-304.
- Walsh, J.J., Dugdale, R.C., 1971. A simulation model of the nitrogen flow in the Peruvian upwelling system. *Investigacion Pesquera* 35(1), 309-330.
- Wehrtmann, I.S., Báez, P., 1997. Larvas y estadíos tempranos de desarrollo de crustáceos decápodos de Chile: descripciones publicadas. *Investigaciones Marinas, Valparaíso* 25, 263-276.
- Wing, S.R., Botsford, L.W., Ralston, S.V., Largier, J.L., 1998. Meroplanktonic distribution and circulation in a coastal retention zone of the northern California upwelling system. *Limnology and Oceanography* 43, 1710-1721.

- Wolff, M., Mendo, J., 2000. Management of the Peruvian bay scallop (*Argopecten purpuratus*) metapopulation with regard to environmental change. *Aquatic Conservation: Marine and Freshwater Ecosystems* 10 (2), 117-126.
- Wolff, M., Taylor, M., Mendo, J., 2006. Simulating ecosystem transition from upwelling to El Niño conditions: the case of Independencia Bay, Southern Peru. In Book of extended abstracts, International Conference The Humboldt Current System: Climate, Ocean dynamics, ecosystem processes, and fisheries (pp.62-63) Lima, Peru, November 27 - December 1, 2006. Unpublished.
- Wolter, K., Timlin, M.S., 1998. Measuring the strength of ENSO - how does 1997/98 rank? *Weather* 53, 315-324.
- Wyrtki, K., 1966. Oceanography of the Eastern Equatorial Pacific Ocean, *Mar Biol Ann. Rev.* 4, 33-68.
- Wyrtki, K., 1967. Circulation and water masses in the eastern equatorial Pacific ocean. *International Journal of Oceanology and Limnology* 1, 117-147.
- Wyrtki, K., 1981. An estimate of equatorial upwelling in the Pacific. *Journal of Physical Oceanography* 11, 1205-1214.
- Yamashiro, C., Rubio, J., Jurado, E., Auza, E., Maldonado, M., Ayón, P., Antonietti, E., 1990. Evaluación de la Poblacion de Concha de Abanico en la Bahía Independencia, Pisco, Peru. Informe Instituto del mar del Peru, 981-58.
- Yannicelli, B., Castro, L.R., Valle-Levinson, A., Atkinson, L., Figueroa, D., 2006. Vertical distribution of decapod larvae in the entrance of an equatorward facing bay of central Chile: Implications for transport. *Journal of Plankton Research* 28, 19-37.
- Yasunaka, S., Hanawa, K., 2005. Regime shift in the global sea-surface temperatures: its relation to El Niño–Southern Oscillation events and dominant variation modes. *International Journal of Climatology* 25, 913-930.
- Zuta, S., Guillen, O., 1970. Oceanografía de las aguas costeras del Perú. *Boletín del Instituto del del Perú* 5, 157-324.
- Zuta, S., Rivera, S., Bustamante, A., 1978. Hydrologic aspects of the main upwelling areas off Peru.
- Zar, J.H., 1996. *Biostatistical Analysis*. Simon and Schuster.