



## Zooplankton and forage fish species off Peru: Large-scale bottom-up forcing and local-scale depletion

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### ABSTRACT

The Humboldt Current System, like all upwelling systems, has dramatic quantities of plankton-feeding fish, which suggested that their population dynamics may 'drive' or 'control' ecosystem dynamics. With this in mind we analysed the relationship between forage fish populations and their main prey, zooplankton populations. Our study combined a zooplankton sampling program (1961–2005) with simultaneous acoustic observations on fish from 40 pelagic surveys (1983–2005) conducted by the Peruvian Marine Research Institute (IMARPE) and landing statistics for anchoveta (*Engraulis ringens*) and sardine (*Sardinops sagax*) along the Peruvian coast from 1961 to 2005. The multi-year trend of anchoveta population abundance varied consistently with zooplankton biovolume trend, suggesting bottom-up control on anchovy at the population scale (since oceanographic conditions and phytoplankton production support the changes in zooplankton abundance). For a finer-scale analysis (km) we statistically modelled zooplankton biovolume as a function of geographical (latitude and distance from the 200-m isobath), environmental (sea surface temperature), temporal (year, month and time-of-day) and biological (acoustic anchovy and sardine biomass within 5 km of each zooplankton sample) covariates over all survey using both classification and regression trees (CART) and generalized additive models (GAM). CART showed local anchoveta density to have the strongest effect on zooplankton biovolume, with significantly reduced levels of biovolume for higher neighbourhood anchoveta biomass. Additionally, zooplankton biovolume was higher offshore than on the shelf. GAM results corroborated the CART findings, also showing a clear diel effect on zooplankton biovolume, probably due to diel migration or daytime net avoidance. Apparently, the observed multi-year population scale bottom-up control is not inconsistent with local depletion of zooplankton when anchoveta are locally abundant, since the latter effect was observed over a wide range of overall anchoveta abundance.

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### 1. Introduction

Understanding ecosystem functioning requires identifying the main determinants of species abundance and distribution. Predator–prey relationships are one of these major driving functional processes in marine ecosystem dynamics. The Peruvian coastal upwelling ecosystem is characterized by the presence of two highly abundant, but also highly variable, forage fish species; the Peruvian anchovy or anchoveta (*Engraulis ringens*) and sardine (*Sardinops sagax*). The large fluctuations in abundance of anchoveta and sardine have been the subject of a large number of studies (Csirke et al., 1996; Bakun and Broad, 2003; Chavez et al., 2003; Alheit and Niquen, 2004; Bertrand et al., 2004b; Gutiérrez et al., 2007; Swartzman et al., 2008). These studies show that,

at the population and multi-year scale, anchoveta population dynamics appears to depend on the overall productivity of the ecosystem and that they are more abundant when upwelling is enhanced and phytoplankton and zooplankton are abundant. Such bottom-up forcing is a long-term process that can only be observed in smooth trends from long time series (multi-decadal). Indeed the small time scale variability (e.g. seasonal) and the large measurement variance intrinsic to the data that we used (e.g. net plankton sampling, acoustic estimates, landings and associate changes in CPUE) blur these patterns in shorter time series. Such apparent evidence of bottom-up forcing detected at decadal time scales seems confirmed by studies at a centennial scale by Sifedine et al. (2008) and Valdés et al. (2008) who used laminated sediment cores to show that a large shift in productivity occurred by ~1815. Prior to 1815, during the little ice age, the northern Humboldt Current region was marked by low ecosystem productivity and low anchoveta scale deposition rate. Afterwards, an increase of wind-driven upwelling resulted in higher productivity

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and increased anchoveta scale deposit. These productive conditions (plankton and fish) intensified during the 20th century. While bottom-up control seems to occur at the population scale, little is known about the potential depletion effect that these vast quantities of pelagic fish may have at a smaller spatiotemporal scale (local scale, 10–100 kms – weeks) on lower trophic levels, particularly on zooplankton, which comprises the bulk of their diet (van der Lingen et al., 2006, in press; Espinoza and Bertrand, 2008). While predator–prey relationships clearly occur at a local scale, an important question is whether fish foraging impacts locally zooplankton biomass and/or if potential local depletion effects are spatially pervasive enough to be detected at the population scale, through, for instance, a top-down control of zooplankton by forage fish as proposed by the wasp-waist hypothesis (Cury et al., 2000, 2003).

To check for bottom-up control on anchoveta we used a long time series available for zooplankton biovolume, i.e. 1961–2005 (extended from Ayón et al., 2004) and commercial pelagic fish landings for the corresponding period. These data allowed us to look at changes in population abundance on large spatial and temporal scales. Concomitantly we examined local-scale questions of distribution and trophic interactions from scientific surveys data over the shorter, but still substantial, time period over which these are available (1983–2005). On this scale we studied the potential depletion effect of pelagic fish on zooplankton. To this end we examined the relative effect on zooplankton biovolume of SST, latitude, bottom depth, diel period, time (year–month) and the abundance of anchoveta and sardine within a neighbourhood of the zooplankton. This small-scale analysis used long term (1983–2005) and fairly high-resolution (1–2 nautical miles) acoustic data from surveys transecting almost the entire Peruvian coastal marine ecosystem, accompanied by an intensive zooplankton sampling program. This time period encompassed large fluctuations in sardine and anchoveta population abundance: the decline of the sardine population and the increase of the anchoveta up to a ‘full anchovy era’ (Gutiérrez et al., 2007) since the end of the 1990s. These data allowed us to look at changes in population abundance at a fine spatial scale over a large spatial region and long time period, permitting examination of local-scale questions of distribution and trophic interactions.

## 2. Data and methods

### 2.1. Landing data

Yearly landing data for anchoveta and sardine in Peru between 1961 and 2005 are from the official statistics of the Instituto del Mar del Peru ([www.imarpe.gob.pe](http://www.imarpe.gob.pe)).

### 2.2. Acoustic survey data

Acoustic data were collected from 1983 to 2005 by the Instituto del Mar del Perú (IMARPE) on a variety of vessels, most commonly the R/V Humboldt (76 m long), the R/V Olaya (41 m long) and the R/V SNP-1 (36 m long). Surveys consisted of parallel transects averaging 90 nautical miles (167 km) with an inter-transect distance between 14 and 16 nautical miles (26–30 km) depending on the cruise.

The entire observable range of anchoveta distribution was covered (transects shown in Fig. 1 are typical of almost all surveys). Extensive midwater trawl sampling accompanied the acoustic surveys for species identification. The seasonal and temporal distributions of scientific acoustic surveys are: spring (1983, 1996–2005), summer (1990–96, 1999–2005), autumn (1985, 2 surveys in 1998), and winter (1984, 1987–89, 1991, 1998–2003 with 2 winter

surveys in 1999, 2000 and 2001). The acoustic surveys deployed Simrad (Kongsberg Simrad AS, Kongsberg, Norway) scientific echosounders EK, EKS, EK400, EY500, EK500 and EK60 (2001–2003 in one vessel). Calibration of the echosounders was done before all surveys. Calibration up until 1992 was done using hydrophones and after 1992 sphere calibration followed a standard procedure (Foote et al., 1987). The acoustic nautical area scattering coefficient ( $s_A$  or NASC; see MacLennan et al., 2002 for acoustic definitions), an indicator of fish biomass, was recorded for each geo-referenced elementary sampling distance unit (ESDU) of 1 n. mi. (1994–2003) or 2 n. mi. (1983–1993). Acoustic echo identification was performed using fishing trawl results and echotrace characteristics (see Gutiérrez et al., 2007 for more information on the acoustic protocol). Biomass estimation based on both the trawls and acoustic backscatter for each species was carried out by IMARPE for each survey. Surface temperature and salinity were measured and averaged per ESDU for almost all surveys (exceptions are missing samples in summer of 1990 for both temperature and salinity and additionally summer 1994 and spring 2000 for salinity).

### 2.3. Zooplankton data

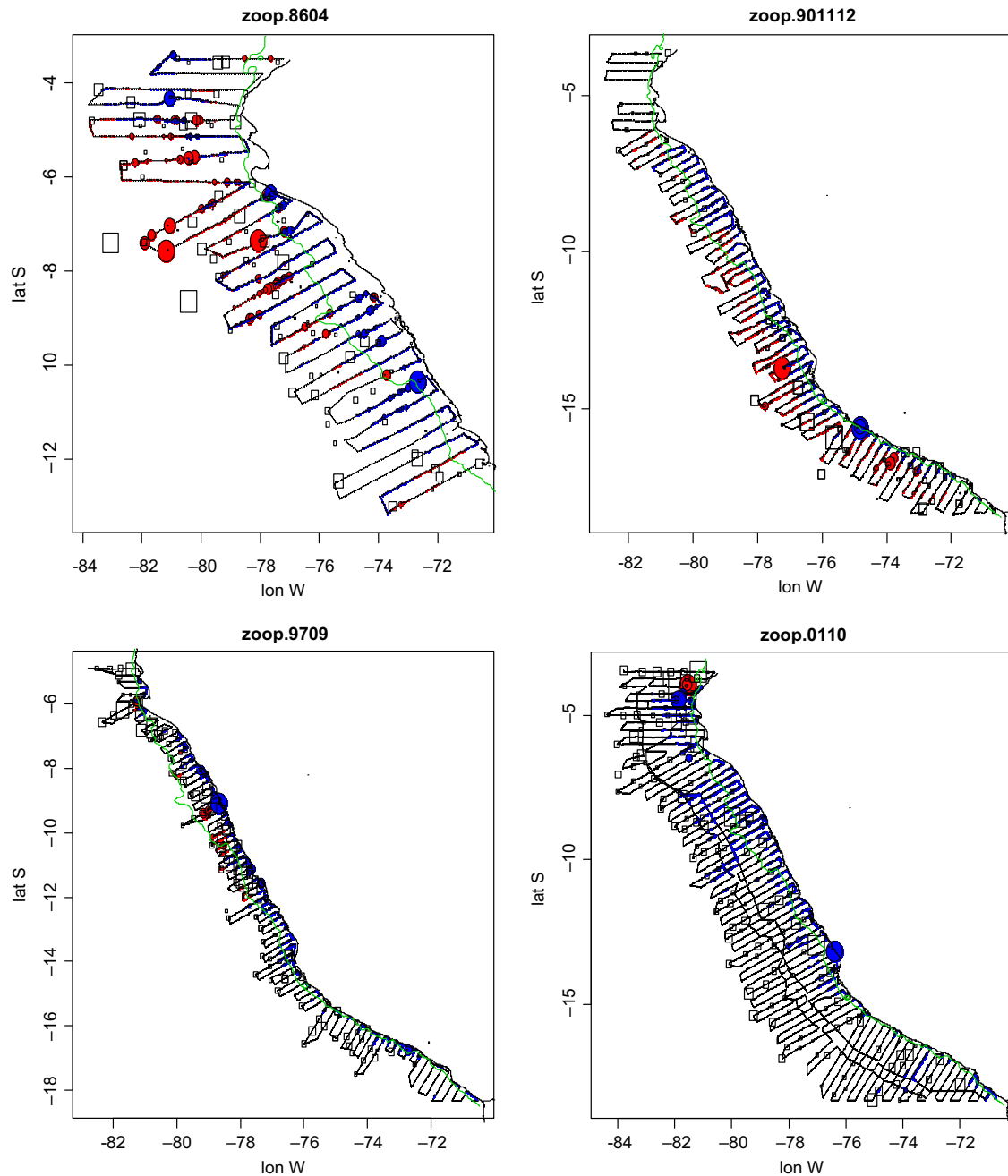
Zooplankton samples were taken with Hensen nets of 0.33 m<sup>2</sup> mouth area with a 300  $\mu$ m mesh, in vertical hauls between 0 and 50 m. Samples were fixed with 2% formaldehyde buffered with borax. Zooplankton biovolume (mL/sample) was determined at the time of collection using the displacement method (Kramer et al., 1972). Ichthyoplankton and large coelenterates were removed before determining the biovolume. This sampling protocol has been followed consistently for the entire period covered by this study (1961–2005). The hour of sampling was available for most of the data since 1971, for all data since 1983, but for few zooplankton surveys before 1971.

### 2.4. Zooplankton and forage fish dynamics, population scale

To examine the large-scale relationship between zooplankton biovolume and pelagic fish abundance we used time series on anchoveta and sardine landings and on zooplankton biovolume from 1961 to 2005. Changes in zooplankton biovolume over time were averaged by month (Fig. 2a) and smoothed by fitting a non-parametric spline model to the data in order to reduce the variance and look at rather low frequency patterns (Fig. 2b). Euphausiids, which are an essential part of anchoveta diets (Espinoza and Bertrand, 2008) are not sampled efficiently by Hensen net tows, and this introduced a bias into the data used to estimate fish prey abundance. To reduce this bias we compared the time series using the complete set of zooplankton data with a subset composed of the night-time data (19 h–05 h, local time since 1971). Clearly, euphausiids and other large zooplankton are better sampled at night because of a reduced net avoidance and a shallower distribution (for organisms performing diel migration). The nocturnal data are probably more representative of the anchovy prey community than the entire data set.

### 2.5. Environmental and fish effects on zooplankton, local scale

To examine the potential effect of anchoveta foraging on zooplankton communities we computed, for each zooplankton net haul, total sardine and anchoveta  $s_A$  within 5 km. This threshold was chosen as representative of an ‘accessible’ neighbourhood for fish to zooplankton prey. Since the shape of predator–prey relationships is known to depend on the spatial scale of observation (e.g., Rose and Leggett, 1990; Swartzman et al., 2002; Bertrand et al., 2004a), the analysis was later checked for range of robustness by using neighbourhood ranges between 3 and 30 km. Because results



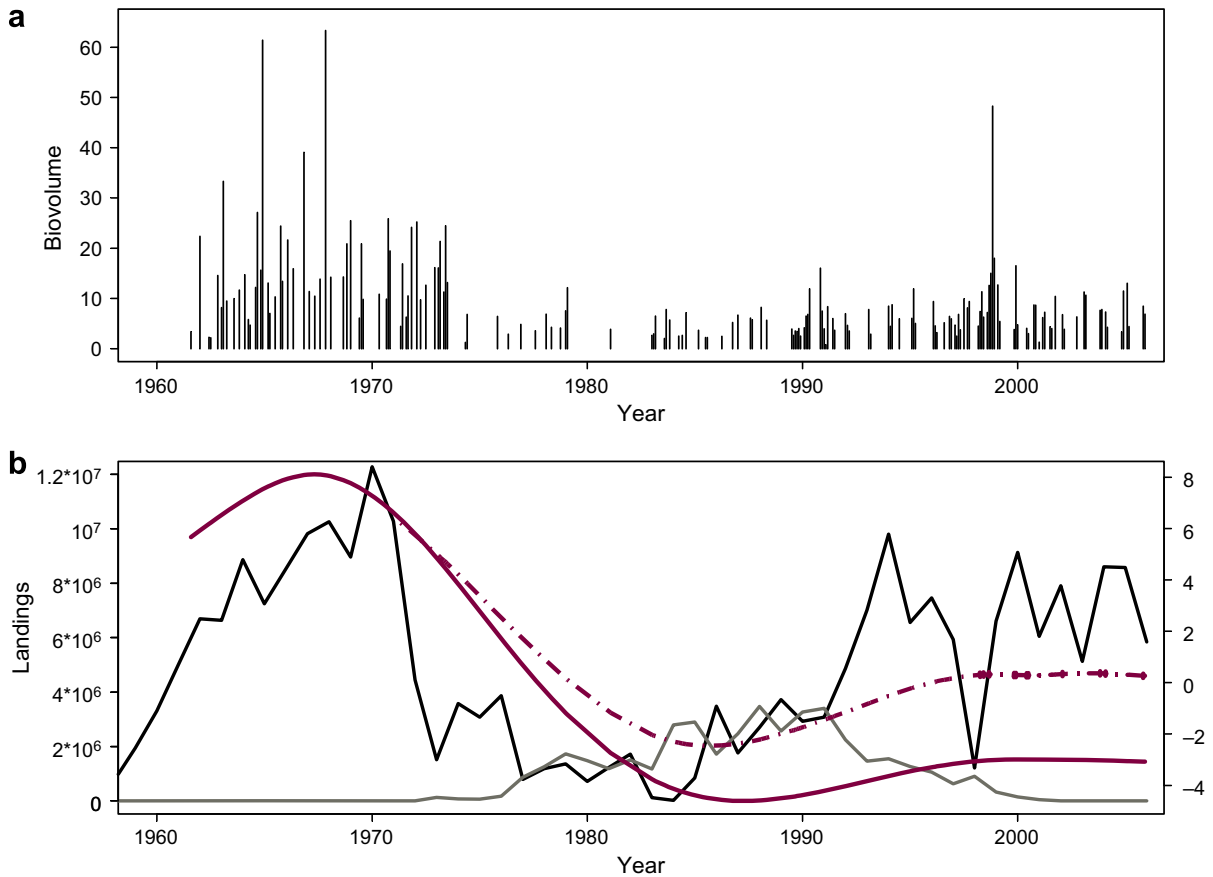
**Fig. 1.** Graphs of the survey transects along the Peruvian coast in (a) 1986 during a 'warm' period; (b) 1990, later in the 'warm' period; (c) 1997, during the El Niño; and (d) 2001 during a 'cold' period. The sardine and anchovy  $s_A$  per ESDU are shown with red and blue filled circles respectively proportional in area to  $s_A$  (for that survey). Zooplankton biovolume at zooplankton sampling locations are depicted by squares proportional in area to the biovolume. The 200-m isobath is shown with a green line.

were not significantly different over this range (i.e. they were robust) we only present results for the 5 km neighbourhood.

Since the shelf break location varies markedly along the Peruvian coastline (Fig. 1), we computed the distance in km of each sample location from the 200-m isobath (distance to the closest point at the same latitude). Negative values can be considered to be on-shelf and positive values off-shelf or on the continental slope. Thus, this variable separates the shelf from the abyssal area. Additional covariates associated with each sample location were sea surface temperature (SST), latitude (degrees S), and time of the day, also represented by a categorical day–night variable, and year and month of the sample.

We used classification and regression trees (CART, Brieman et al., 1984) to distinguish the relative importance of environmen-

tal and fish (anchoveta and sardine) effects on local zooplankton abundance. We modelled the logarithm of zooplankton biovolume using a regression tree with year, month, latitude, anchoveta and (separately) sardine in the 5 km neighbourhood, distance in km from the 200 m isobath, sea surface temperature (SST) and a day–night categorical covariate. In CART the dependent variable is modelled as a function of covariates. CART divides the data set through a sequence (tree) of binary splits on the values of one of the covariates at a time such that the overall variance in the dependent variable is minimized at each split. The CART tree is usually pruned to fewer nodes for clarity of explanation. For pruning the tree and validating the robustness of the CART results we used the recursive partitioning method (*rpart*; De'ath and Fabricius, 2000). This method divides the data set into a number of sub-



**Fig. 2.** Time series of (a) zooplankton biovolume (mL/sample) averaged by month; (b) commercial landings for anchovy (black solid line) and sardine (grey solid line), and smoothed trend of biovolume for all zooplankton samples (red continuous line) and night-time samples (red dotted line), the right y-axis is relative and corresponds to the spline smoother that was fitted on the data such that a y-value of zero is the mean effect of the variable (time) on the response (biovolume). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

groups (we used 10 groups following De'ath and Fabricius, 2000) and then repeats the CART analysis sequentially, removing one subgroup each time. This replication gives a measure of robustness in the node splits in CART. Using a graph of the relative performance (i.e., the total model variance plus the number of nodes multiplied by a weighting factor, against the weighting factor) we chose a weighting factor such that the relative performance did not improve markedly with the addition of more nodes. To further examine the overall relationship between mean biovolume and the local covariates used in the CART model we used a Generalized Additive Model (GAM, Hastie and Tibshirani, 1990) regression. We chose the Poisson distribution, which is often used for counts of animals, because the 'link function' for the Poisson distribution requires a logarithmic transformation of the dependent variable, making it similar to the log transformation used in the CART model. The independent variables in the GAM regression were the same as those used for the CART model except instead of day–night we used actual time of day.

### 3. Results

#### 3.1. Zooplankton and forage fish dynamics, population scale

Time series on pelagic fish landings and zooplankton biovolumes are presented in Fig. 2. Anchoveta and sardine landings according to time (Fig. 2b) have already been presented by several authors (e.g. Chavez et al., 2003; Alheit and Niquen, 2004). Anchovy landings were high during two periods: the 1960s and early

1970s, and the period since the mid-1990s. Sardine captures were highest from the mid 1970s to the mid-1990s. Zooplankton biovolume (Fig. 2a and b) was very high until the early 1970s, then drastically decreased. Biovolume remained low until later in the 1980s and then increased, but without reaching the levels observed during the 1960s. Zooplankton biovolume and anchoveta landings are globally in phase (out of phase with sardine), in particular when considering nocturnal biovolume (Fig. 2b).

#### 3.2. Local effects: CART models

Based on the recursive partitioning method in CART we chose a penalty value  $cp = 0.0059$ , which resulted in nine nodes, these being the number of nodes having minimum relative error (total error with a penalty for additional nodes). Neither sardine local abundance ( $s_A$ ) nor latitude (both included in the CART model) had a major effect on zooplankton biovolume (Table 1), while anchoveta abundance had the strongest effect (i.e. it was the first split in the CART; Table 1). The lowest overall biovolume occurred with high levels of anchoveta ( $s_A > 543 \text{ m}^2 \text{ nmi}^{-2}$ ), particularly on the shelf during winter and summer months. This is an indication of local depletion of zooplankton by anchoveta. Since 1992.5 (mid-1992), the biovolume of zooplankton was lower on the shelf than farther offshore (for anchoveta  $s_A < 543 \text{ m}^2 \text{ nmi}^{-2}$ ). Interestingly, the night-time samples offshore had medium (not low) levels of zooplankton associated with higher levels of anchoveta (Table 1). The low on-shelf zooplankton biovolume associated with high anchoveta abundance may reflect the targeting of zooplankton

**Table 1**  
 CART results for logarithm of zooplankton biovolume with year, month, latitude, distance from the 200 m isobath (dist200; in km), sea surface temperature, anchovy and sardine  $s_A$  within 5 km of the zooplankton samples, and whether the sample was taken during the daytime or at night. Numbers of observations at each node are in parentheses. Number of splits from the top of the CART tree is shown with bold symbols.

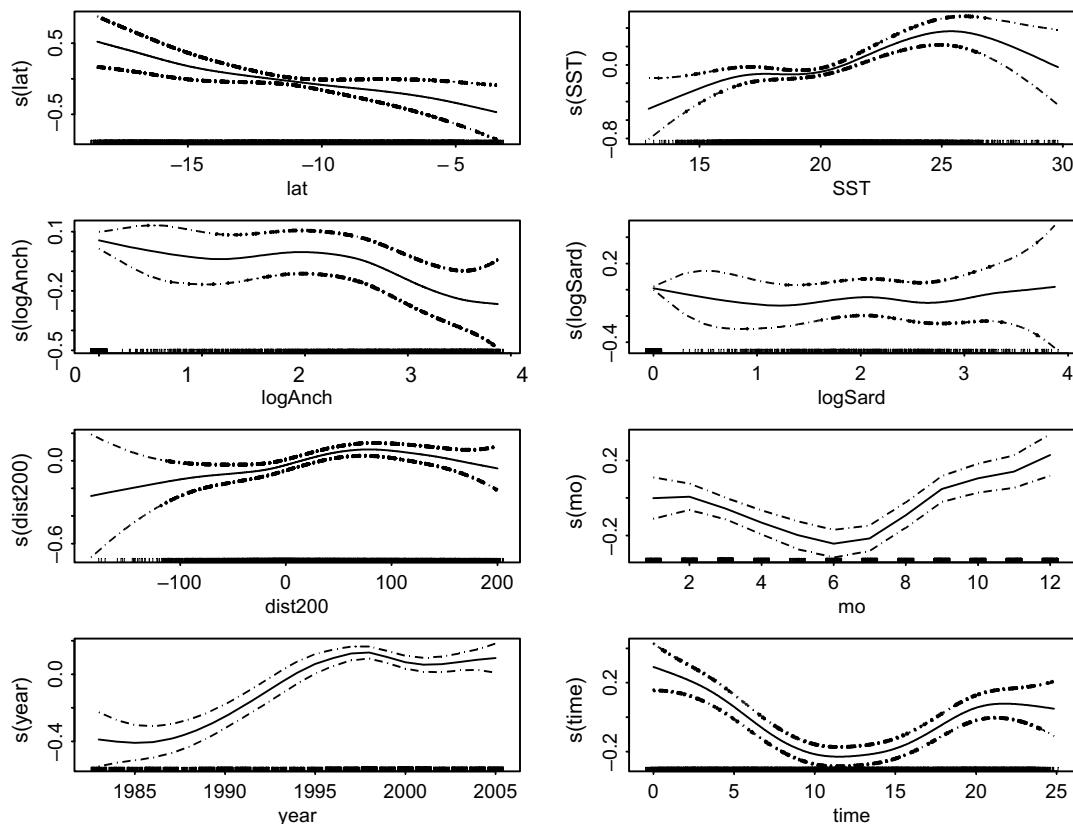
Anchovy $s_A$ (m <sup>2</sup> nmi <sup>-2</sup> )	Year	Dist200	Month	SST	Day-night	Log (vol)
≥ 543			spring, autumn			1.38 (364) <b>2</b>
" "		< -26.9 (shelf)	summer, winter			0.04 (307) <b>3</b>
" "		≥ -26.9 (shelf-break, offshore)	" "		Day	0.53 (269) <b>4</b>
" "		" "	" "		Night	1.27 (277) <b>4</b>
< 543	before 1992.5					1.27 (1281) <b>2</b>
" "	since 1992.5	< 13.15 (shelf, shelf-break)	June, July, January, March, November	< 21.2		0.94 (400) <b>5</b>
" "	" "	≥ 13.15 (offshore)	" "	" "		1.51 (542) <b>5</b>
" "	" "	" "	" "	≥ 21.2		1.85 (649) <b>4</b>
" "	" "	" "	February, April–May, August–September, December			1.95 (1827) <b>3</b>

found near shore by the high abundance anchoveta aggregations. In the off-shelf region the zooplankton abundances near high anchoveta aggregations were greater than on-shelf. There was a notable day–night difference.

3.3. Local effects: GAM models

GAM results (Fig. 3) illustrated the ‘classic’ overall day–night effect as a significant time-of-day change in zooplankton biovolume. The observation in CART of higher biovolume in the spring and autumn near high anchoveta  $s_A$  and in selected months under lower anchoveta  $s_A$  and different environmental conditions (Table 1) is different than the GAM model which shows a more ‘classic’ winter low, spring and summer high effect on biovolume. These results are not necessary contradictory, since the CART seasonal pattern also depends on local anchoveta abundance, while the GAM pattern does not. The CART observation that off-shelf biovolume was

often higher than shelf biovolume was shown in the GAM relationship of the mean biovolume to distance from the 200 m isobath, with peak biovolume occurring at around 150 km offshore of the 200 m isobath, but with not much change between 50 and 200 km offshore of that isobath. The year effect showed an increase in biovolume between the end of the 1980s and 1998, a small dip in 1998–2000 and a further stabilization thereafter. The latitude effect showed a general increase in biovolume north to south. The sea surface temperature effect had two peaks, with a slight dip at about 20 °C. The second peak was significantly higher, which agrees with the CART result, which suggested a temperature effect, with a split around 21° and higher biovolume above this split. Finally, although both neighbourhood (within 5 km) anchoveta and sardine acoustic biomass ( $s_A$ ) effects on zooplankton biovolume were significant in the GAM, the anchoveta effect was stronger ( $p < 10^{-7}$  for anchoveta and  $p = 6.0 \times 10^{-4}$  for sardine based on  $\chi^2$ -values for non-parametric effects). The anchoveta effect sug-



**Fig. 3.** GAM smooths for the effects on zooplankton biovolume of survey year and month and local variables time of day, sea surface temperature, distance from the 200-m isobath (km), and the logarithm (base 10) acoustic biomass ( $s_A$ ) of anchovy and sardine within 5 km of the net haul.



gested a decline in local zooplankton biovolume with increasing fish biomass (Fig. 3). The small significance level appears to depend on an extremely large sample size including zooplankton samples for all acoustic surveys (15133 samples).

## 4. Discussion

### 4.1. Population abundance: bottom-up control

Our results show that the multi-year trend of both zooplankton biovolume and anchoveta landings are globally in phase (Fig. 2), which provides further evidence for bottom-up control by zooplankton on the anchoveta population, as previously suggested by Alheit and Niquen, 2004. In particular, they indicated that the decrease of the anchoveta population in the early 1970s was caused partially by a decrease of its food source, but they stated that there was no clear indication whether the early phase of the anchoveta recovery during the 1980s was based on an increase of zooplankton. The time series on zooplankton data they relied on was not long enough to show the increasing trend in zooplankton biovolume from the 1980s to nowadays. This was presented by Ayón et al. (2004) and for a somewhat longer time period here (Fig. 2), although absolute values of recent zooplankton biovolume are far below the ones observed during the 1960s. It is difficult to understand these differences (Ayón et al., 2004). Obviously patterns and processes are not simple and ecosystem functioning cannot be reduced to 'simple' trophic controls even if the bottom-up forcing seems dominant. Taylor et al., 2008 also concluded there was bottom-up control for anchoveta using a modelling approach. Others (Alheit and Niquen, 2004; Bertrand et al., 2004b; Swartzman et al., 2008) suggested how water masses, and their intrinsic characteristics in terms of hydrology, and primary and secondary production, drive the abundance and distribution of forage fish species. For instance, the latest anchoveta 'dominance' period we are experiencing since 1992, but particularly since the 1997–1998 El Niño event (Gutiérrez et al., 2007), corresponds to overall colder conditions (Francisco Chavez pers. com.) along the Peruvian coast that led to an extension of cold coastal upwelling waters (Swartzman et al., 2008), high levels of primary production (Francisco Chavez pers. com. and Fig. 5 in Alheit and Niquen, 2004) and high zooplankton abundance (Fig. 2). The typical bottom-up control in the northern HCS does not support the wasp-waist control hypothesis (Cury et al., 2000, 2003), which considers forage fish species to be the driving force in upwelling ecosystems for both higher and lower trophic levels.

### 4.2. Distribution patterns: local depletion effect

Predation effects of fish on zooplankton are difficult to observe, because predation is a local phenomenon requiring simultaneity in space and time of both predator and prey and the scale of sampling can hardly replicate this simultaneity. On the other hand, the pervasive abundance of anchoveta in some regions may provide an opportunity for observing reduction of zooplankton in regions of high predation. The main uncertainty in such relationships is separating the effect of predation from the effect of production, since some samples may show low abundance due to poor growing conditions rather than higher predation. Our study relies on a large sample which provides an opportunity to find an effect of predation if it exists, and to distinguish it from the noise commonly found in such labile ecosystems due to variability in local conditions, recent history, sampling variability and the mixing of many sizes and species of zooplankton into a single sample number; the biovolume.

Our results strongly suggest local reduction in zooplankton biovolume by anchoveta predation in neighbourhoods where ancho-

veta abundance is high. This is supported by several pieces of evidence. The CART analysis suggested that when anchoveta abundance within 5 km of the zooplankton samples was high ( $s_A$  above  $543 \text{ m}^2 \text{ nmi}^{-2}$ ) average zooplankton abundance was significantly lower than zooplankton abundance in areas having lower density of anchoveta in the region. The anchoveta effect was the most important effect found by CART, as shown by the highest level split in the data being on anchoveta abundance (Table 1). This suggests that anchoveta abundance has more influence on local zooplankton biovolume than any other covariate, including year, latitude, SST, distance onshore or offshore of the shelf break (200 m isobath), sardine abundance, time of day and month. Furthermore, sensitivity analysis on the distance from samples (currently 5 km) to define the region of influence of anchoveta showed the anchoveta abundance to be the most important factor for distances between 3 km and 30 km suggesting a highly robust effect. These results are also seen in the GAM analysis, which differs from CART in design by considering effects due to smooths of covariates, rather than thresholds and in not explicitly including multivariate interactions. In GAM, zooplankton biovolume decreased with increasing anchoveta abundance over a range of anchoveta  $s_A$  from 0 to  $4000 \text{ m}^2 \text{ nmi}^{-2}$  (up to 3.6 in  $\log_{10}$  scale), with a stronger effect for high value of  $s_A$  ( $\log_{10}$  value between 2.5 and 3.0; Fig. 3), close to the threshold observed from the CART analysis ( $\log_{10}(543) = 2.73$ ).

We think the apparent depression of zooplankton near high anchoveta densities is highly unlikely to be due to lower production, since anchoveta is more prevalent in highly productive upwelling and mixed waters than in less productive oceanic or equatorial waters (Alheit and Niquen, 2004; Bertrand et al., 2004b; Gutiérrez et al., 2007; Swartzman et al., 2008). Anchoveta is a plankton predator, depending much more on zooplankton than on phytoplankton. Zooplankton, particularly euphausiids and large copepods, accounts for about 98% of its diet in carbon (Espinoza and Bertrand, 2008). It is therefore not surprising to see a local effect of anchoveta foraging when large fish aggregations are concerned. It is important to note that the results we obtained were limited by the lack of reliability of euphausiid abundance (67.5% of anchoveta diet in carbon) from Hensen net sampling. We probably mainly detected an anchoveta effect on copepods (23.6% of anchoveta diet in carbon), which are better sampled by these nets. Ongoing estimation of euphausiid abundance from historical acoustic data may soon provide better data on euphausiids (Michael Ballón, pers. com.). The depletion effect we observed is only local (i.e. up to 30 km) and does not constitute large-scale or long-term control on plankton population. Finally, sardine, which forages at a lower trophic level than anchoveta (Konchina, 1991; van der Lingen, 2002, 2006, in press), has no evident impact on zooplankton biovolume. The 300  $\mu\text{m}$  mesh net used for plankton sampling allows a rather good representation of the prey community of anchoveta (except for euphausiids) which forage efficiently at sizes higher than 200–250  $\mu\text{m}$ , particularly from 580  $\mu\text{m}$  (van der Lingen et al., 2006) but not for sardine which is able to forage directly on net-phytoplankton (20–200  $\mu\text{m}$ ). Studying potential local sardine impact on its prey community would therefore require sampling based on a finer mesh.

Apart from the anchoveta's impact on zooplankton biovolume we observed other covariate effects. We observed a significant and clear diel effect (Table 1, Fig. 3), with higher zooplankton biovolumes during the night. This classic result is likely mainly due to both reduced gear selectivity during the daytime and to diel migration of zooplankton where some zooplankton migrate below the top 50 m of the water column during the daytime. Zooplankton biovolume was higher from the shelf break to 100 km offshore, which corresponds to rather warm temperatures (Table 1; Fig. 3). Such results may be related to the offshore transport of the matur-

ing production, leading that part of the zooplankton community to be distributed away from the coast where the predation is limited as anchoveta has a rather coastal distribution (Bertrand et al., 2004b; Gutiérrez et al., 2007; Swartzman et al., 2008), but also where diel migration can allow zooplankton some daytime protection from anchoveta predation (Bertrand et al., this issue; Escribano et al., in press; Espinoza and Bertrand, 2008). The month effect on zooplankton biovolume was also very clear with higher biovolume in summer than in winter (Fig. 3), which is consistent with enhanced primary production in austral summer (Francisco Chavez, com. pers.).

Other studies illustrated similar direct effects of predation on the distribution and abundance of organisms in the ocean. For instance, Swartzman et al. (2002) and Winter and Swartzman (2006) evidenced an inverse relationship between the local abundance of juvenile pollock (*Theragra chalcogramma*) and zooplankton near the Pribilof Islands, Alaska. Hunt et al., 2002 provided direct evidence of heavy predation of murre (*Uria aalge*) on juvenile pollock upwelled onto a shelf in the Pribilof Canyon, Alaska. Bertrand et al., 2004a found that in the southern part of the HCS, the biomass of the mesopelagic community was lower in areas where high abundance of jack mackerel (*Trachurus murphyi*), their main predator, was observed.

In summary, at the local scale there is clear evidence for a depletion effect on zooplankton biovolume by high neighbourhood densities (spatial range: 3–30 km) of anchoveta. At the population level anchoveta biomass and zooplankton biovolume appeared to co-vary on a multi-year basis. The increase in zooplankton and anchoveta biomass since the 1990s corresponds to a colder period with enhanced primary production in the HCS (Francisco Chavez com. pers.). Thus, although zooplankton likely exerts a bottom-up control on the anchoveta population, when locally abundant anchoveta can induce local depletion (independent of the total anchoveta population level) of zooplankton abundance.

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