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Ecological niches and areas of overlap of the squat lobster ‘munida’ (*Pleuroncodes monodon*) and anchoveta (*Engraulis ringens*) off Peru

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ABSTRACT

The world's largest mono-specific fishery, the Peruvian anchovy or anchoveta (*Engraulis ringens*) fishery, has been the subject of many studies since the 1960s. Details of its relationship with other species have mainly focused on alternations with sardine, *Sardinops sagax*, and little effort has so far been paid to interactions with other species sharing the same ecosystem. This is the case for *Pleuroncodes monodon*, the crustacean squat lobster or ‘munida’, which has become highly abundant along the Peruvian coast since the mid-1990s. Munida is now an important prey for seabirds, mammals and coastal predatory fish. Knowledge of patterns of distribution and ecological niche of munida is scarce however off Peru. Here we describe and compare spatial patterns of distribution of anchoveta and munida and their ecological niches based on data from 26 acoustic surveys performed along the Peruvian coast between 1998 and 2006. The results indicate that munida and anchoveta share ecological niches but that munida is restricted to the coldest part of the productive cold coastal waters whereas anchoveta do not present any temperature preference over a large range (14–23 °C). The recent increase in munida abundance off Peru is concomitant with colder conditions; with their onset munida extended its range from central Chile northwards. Off Peru the very shallow oxycline keeps munida from its usual bottom habitat and has forced it to adopt pelagic behaviour.

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1. Introduction

The world's largest mono-specific fishery, the Peruvian anchovy or anchoveta (*Engraulis ringens*) fishery, has been the subject of many ecological studies since the 1960s (e.g., Ryther, 1969; Valdivia, 1978; Csirke, 1980; Walsh, 1981; Pauly and Tsukayama, 1987; Pauly et al., 1989; Alheit and Ñiquen, 2004; Bertrand et al., 2004a, 2005; Gutiérrez et al., 2007; Bertrand et al., 2008a,b; Espinoza and Bertrand, 2008; Swartzman et al., 2008). The strategies of fishers relative to the anchoveta's spatial distribution have also been documented (Boerema et al., 1965; Bertrand et al., 2004b, 2005, 2007). Studies detailing the relationship of anchoveta to other species focused on its alternation with sardine, *Sardinops sagax*, (e.g., Schwartzlose et al., 1999; Chavez et al., 2003; Massé and Gerlotto, 2003; Alheit and Ñiquen, 2004; Bertrand et al., 2004a; Gutiérrez et al., 2007; Swartzman et al., 2008) with some attention paid to its relationships with plankton (Alheit and Ñiquen,

2004; Ayón et al., 2008; Espinoza and Bertrand, 2008) and birds and mammals (e.g. Jahncke et al., 1997, 1998). Little effort has been yet allocated to study the relationships and interactions of anchoveta with other species. Here we consider the case of the crustacean squat lobster or ‘munida’, *Pleuroncodes monodon*, which inhabits the Humboldt Current System (HCS) from Chiloe Island (43°S) in Chile to 7°S off Peru (Haig, 1955). Large numbers of munida have occasionally been reported off southern Peru during the last 70 years. Earliest reports indicate that munida was an important prey item of the diet of apex predators such as tunas during the 1930s and 1940s (Del Solar, 1942 in Schweigger, 1964). Munida has become abundant along the Peruvian coast since the mid-1990s, and particularly after the El Niño in 1997–1998 with acoustic estimates ranging between 0.6 and 3.4 million tons from 1998 to 2005. Even before this surge in abundance Elliott and Paredes (1996) observed munida in stomachs of hake (*Merluccius gayi peruanus*), sharks, mackerel (*Scomber japonicus*), jack mackerel (*Trachurus murphyi*), cachema (*Cynoscion analis*), catfish (*Galeichthys peruvianus*) and anchoveta. Munida also constituted 75% of the diet of sea-lions and was important for sea birds in the zone of the Paracas Peninsula, 14°S (Arias-Schreiber, 1996; Jahncke et al., 1997). Like anchoveta, munida is therefore an

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important prey for apex predators. *Munida* is also a predator of plankton (Gallardo et al., 1980; Longhurst et al., 1967). Despite its potential key ecological role as suggested by Schweigger (1964) more than 40 years ago, knowledge of *munida*'s biology and ecology is still poor off Peru. Most references come from Chile where *munida* has a different behaviour. Indeed, *munida*'s early life stages are pelagic off both Peru and Chile but both juveniles and adults are benthic-demersal off Chile (e.g. Gallardo et al., 1992). Off Peru, the life cycle is all pelagic. *Pleuroncodes planipes*, a closely related squat lobster, is similarly holopelagic in the California Current (Longhurst et al., 1967; Longhurst, 1968; Robinson et al., 2004).

Here we describe and compare spatial patterns of distribution of anchoveta and *munida* based on 26 acoustic surveys performed along the Peruvian coast between 1998 and 2006. In addition we describe their respective ecological niches with distance to the coast, sea surface temperature, salinity, dissolved oxygen, nutrients and chlorophyll.

2. Material and methods

2.1. Acoustic data

Acoustic data were collected from 26 surveys performed between 1998 and 2006 by the Peruvian Marine Research Institute (IMARPE) on several vessels, most commonly the R/V Olaya (41 m) but also the R/V SNP2 (21 m) and the RV Humboldt (76 m). At least three acoustic surveys were run each year. Survey design was composed of parallel transects averaging 100 nautical miles (182.5 km) long with an inter-transect distance of 14–16 nautical miles (26–30 km). The acoustic elementary sampling distance units (ESDU) were defined as 1 nmi. The entire observable vertical range of anchoveta and *munida* distributions was covered during most surveys (Fig. 1) even though the surveys performed in winter and spring were often limited to the central and northern part of Peru (5–14°S). Extensive midwater trawling accompanied the acoustic surveys in order to provide biological samples and for species identification. The acoustic surveys used Simrad (Kongsberg Simrad AS, Kongsberg, Norway) scientific echosounders EK500 (RVs Olaya and SNP-2) and EK60 (RV Humboldt) operating at 38 and 120 kHz. The water column was typically insonified till 500 and 150 m at 38 and 120 kHz, respectively. The echosounders were calibrated at least once before each survey with standard procedures (Simmonds and MacLennan, 2005). The acoustic nautical area scattering coefficient (s_A) was recorded for each geo-referenced ESDU. Echo identification was performed by using fishing trawl results and a two-frequencies algorithm on backscattered acoustic volume echograms (S_v) for the surveys performed from 2004 to 2006 using Echoview software (Sonar Data, Tasmania, Australia).

2.2. Environmental data

The measurements of sea surface temperature, salinity and dissolved oxygen (SST, SSS and SSO, respectively) were carried out along the survey transects. Temperature was measured using Furuno MD-500 sensors onboard R/V Olaya and Furuno T-2000 onboard R/V Humboldt. Surface water samples were collected every 2 h for dissolved oxygen (DO) and salinity measurements. Salinity was estimated using a Kahlsico RS 10 sensor until June 1998 then a Portasal 8410A sensor. The concentration of dissolved oxygen was measured using the method of Winkler modified by Carritt and Carpenter (1966). Temperature, salinity and DO data were interpolated by kriging using Surfer software (Golden Software, Colorado, USA). Temperature, salinity and DO values were then averaged for

each ESDU. Finally, distance to the coast was determined for each ESDU.

For the survey performed in January–February 2000, data on nitrates, nitrites, silicates and phosphates and chlorophyll were intensively collected. A total of 220 surface water samples obtained from Niskin bottle were frozen onboard and analysed later in laboratory using the method from Strickland and Parsons (1968). Chlorophyll-*a* was fixed in Whatman filters and analysed using the method from Holm-Hansen et al. (1965).

2.3. Spatial analyses

To study the changes in the geographical distributions of *munida* and anchoveta, for each survey we estimated both the position of the population's centre of gravity (CG) and the related inertia. In 2D, the CG, which represents the mean location of the population, is a vector with two coordinates. The inertia, whose units are surface units (typically nmi^2), quantifies the spatial dispersion of the population around its CG. When sampling is regular, the following equations are used to calculate the centre of gravity (CG) and the inertia (I):

$$CG = \begin{cases} CG_x = \frac{\sum_{i=1}^n x_i z_i}{\sum_{i=1}^n z_i} \\ CG_y = \frac{\sum_{i=1}^n y_i z_i}{\sum_{i=1}^n z_i} \end{cases} \quad I = \frac{\sum_{i=1}^n [(x_i - CG_x)^2 + (y_i - CG_y)^2] z_i}{\sum_{i=1}^n z_i}$$

with, (x_i, y_i) the location of sample i for $i = 1$ in n with n the total number of samples and z_i the value of the sample at this point. All calculations were performed in orthodromic distances. ESDU from inter-transects were not considered in these calculation.

2.4. Ecological niches

For each of the 131,927 geo-referenced ESDU we examined the following indices for anchoveta and *munida*: distance to the coast (DC); SST; SSS; SSO; and the acoustic backscattered energy (s_A), an indice of abundance. As the relationships between *munida* or anchoveta abundance and the environmental parameters were likely to be nonlinear and multivariate, we used a generalized additive model (GAM; Hastie and Tibshirani, 1990) implemented with S-Plus (Insightful Corporation, Seattle, WA, USA). Cubic spline smoothers were used to estimate these nonparametric functions. The response variable, the acoustic energy (s_A) of anchoveta and *munida*, was log-transformed in order to reduce skewness. Models were obtained for each of the 26 surveys and for the entire data set.

To further characterize the ecological niches of *munida* and anchoveta we included the nutrients (nitrates, nitrites, silicates and phosphates) and chlorophyll as explanatory variables in the GAM model for the survey performed in January–February 2000.

Finally we constructed a GAM model by relating log transformed s_A of anchoveta and *munida* to search for relationships between these species at the 1 nmi scale.

3. Results

3.1. Spatiotemporal analyses

Temporal variations of the number of ESDU containing anchoveta, *munida* and both organisms were similar (Figs. 1 and 2), indicating expansion and contraction of the ranges of these species were also similar. The small difference between the numbers of ESDU with *munida* alone and with *munida* and anchoveta illustrates that *munida* mostly occurs within anchoveta range, as it was particularly clear in spring 1999, summer 2002, winter 2003

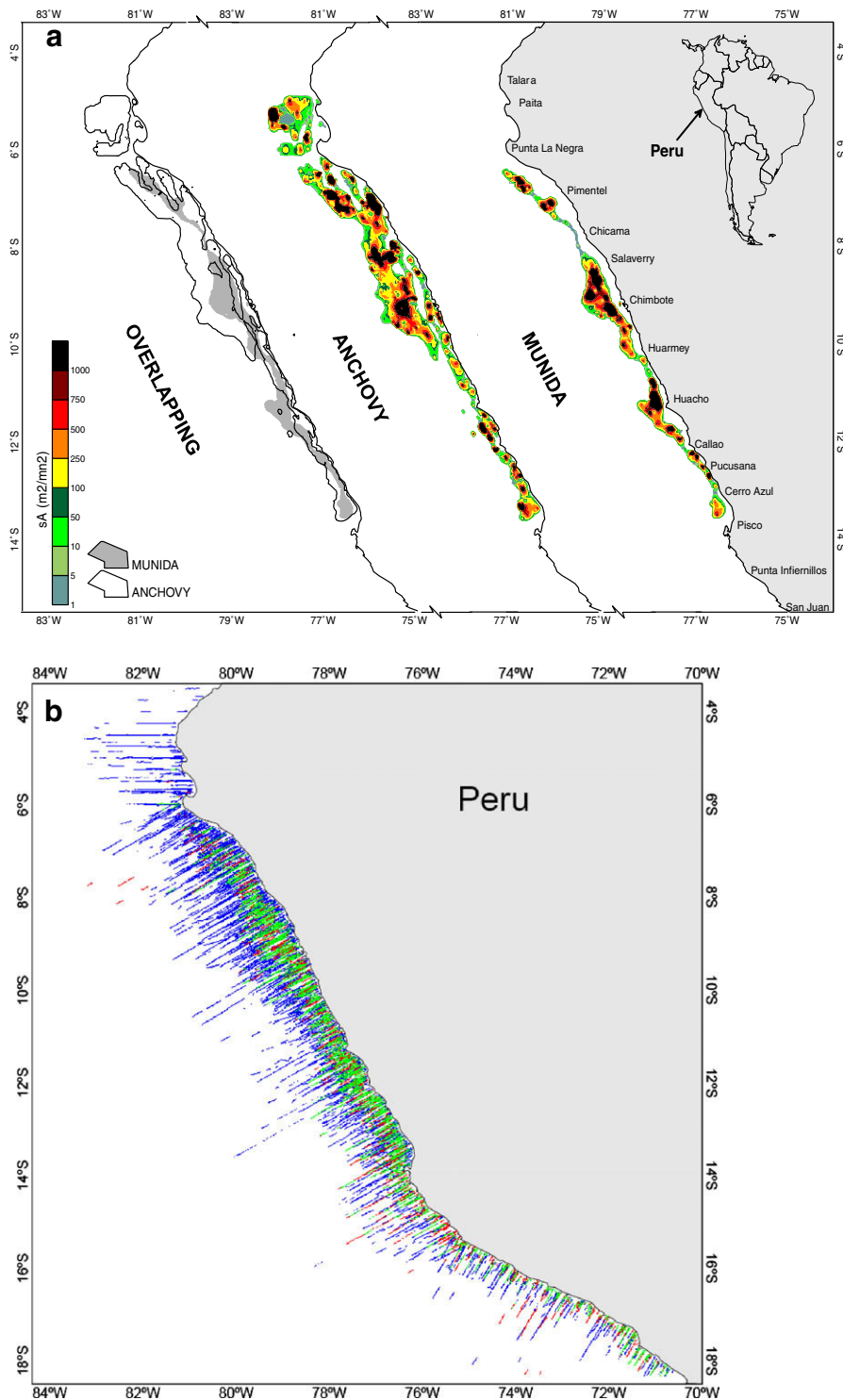


Fig. 1. (a) Study area and example of distribution and relative abundance of munida (*Pleuroncodes monodon*), anchoveta (*Engraulis ringens*) and their horizontal overlapping during Spring 2005 and (b) spatial distribution of all acoustic sampling units (ESDU) from 1998 to 2006 with anchoveta (blue), munida (red) and overlapping of both species (green).

and winter 2006 (Fig. 2). Seasonal patterns however are not clear. Greater area occupancy was observed during summer (February–March) but changes in survey design may have biased the results.

Similar dynamics were observed when considering the population centres of gravity and their inertia (Fig. 3). Changes in centre of gravity and inertia for anchoveta and munida populations were similar. Both species extended their ranges toward the north at the beginning of the time series (Fig. 3a). Then mean latitude

was between 8–11°S, and 9–12°S for anchoveta and munida, respectively, with a slightly more southerly distribution in summer compared to winter. This pattern was also observed for longitude (Fig. 3b), due to the orientation of the Peruvian coast, at a given latitude a higher longitude indicates a more offshore distribution. Anchoveta were thus distributed at lower latitudes and further offshore than munida. Variations in inertia were similar for anchoveta and munida (Fig. 3c).

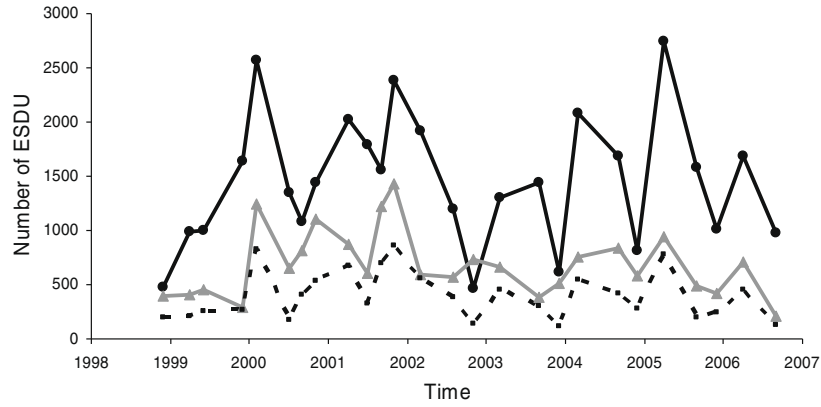


Fig. 2. Time series of the number of acoustic elementary sampling units (ESDU) with presence of anchoveta (black solid line), munida (grey solid line) and both species (black dotted line) during acoustic surveys (1998–2006).

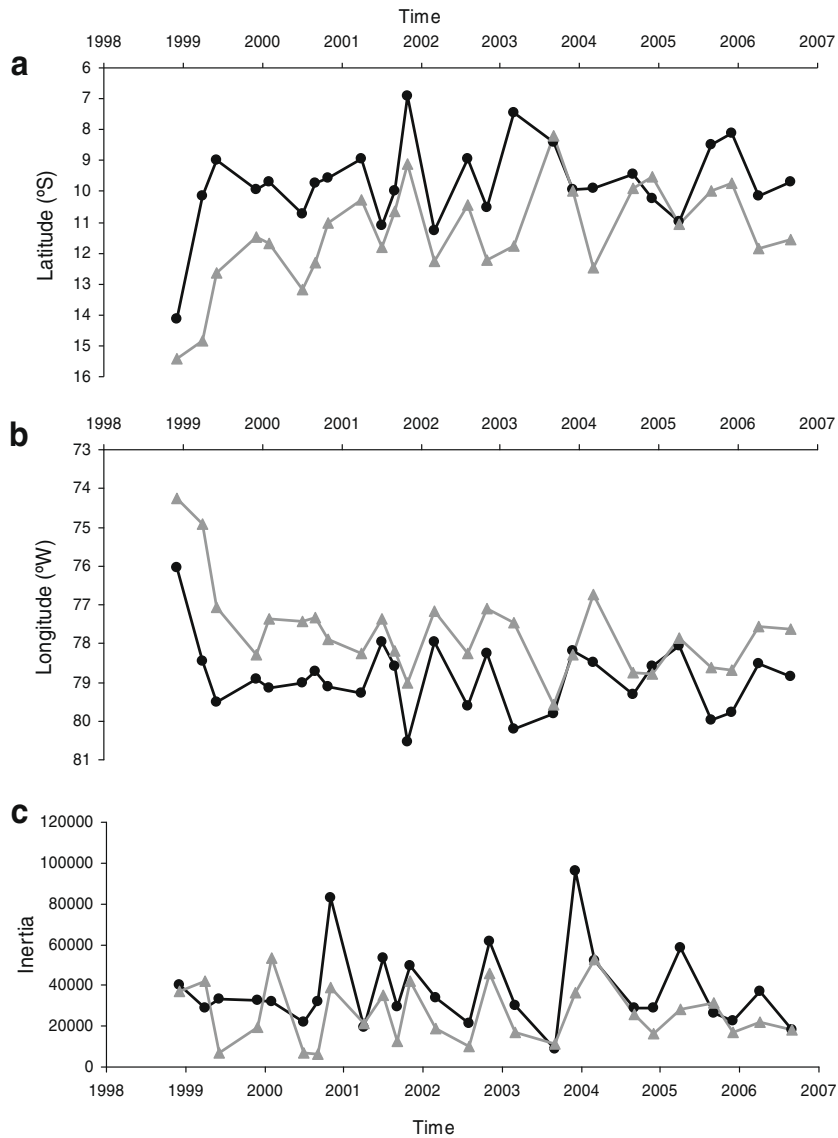


Fig. 3. Time series of the latitudinal (a) and longitudinal (b) location of the centre of gravity and associated inertia of the distribution (c) for anchoveta (black solid line) and munida (grey solid line) during 1998–2006.

3.2. Ecological niches

The abundance relationships between munida and anchoveta at the scale of the ESDU were positive and highly significant

($p < 0.0001$; Fig. 4). Non-linear relationships between munida and anchoveta local abundances and the distance to the coast (DC) and oceanographic parameters (SST, SSS and SSO) for the entire data set are presented Fig. 5. Each plot shows the smoother (spline)

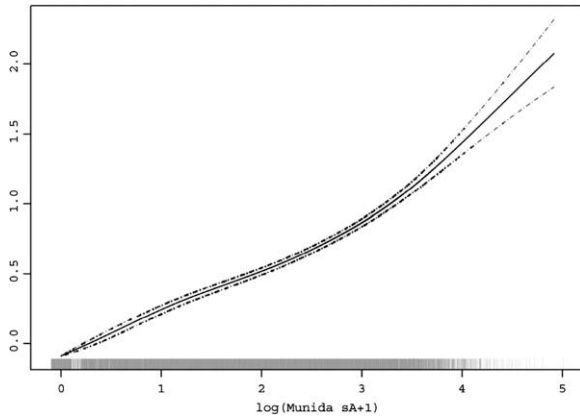


Fig. 4. GAM model based on anchoveta log transformed acoustic abundance (s_A) according to munida log transformed acoustic abundance (s_{A+1}). The black dotted lines show the 95% confidence limits of the GAM model. y -Axis is in relative scale, it corresponds to the spline smoother that was fitted on the data, so that a y -value of zero is the mean effect of the variables on the response. Grey tick marks on the x -axis show the location of data points.

that was fitted to the abundance data for munida (left y -axis) and anchoveta (right y -axis). The y -axes are in relative scale, so that a y -value of zero is the mean effect of the explanatory variable on the munida or anchoveta abundance response. Positive and negative y -values indicate positive and negative responses, respectively. The range of the y -axis indicates the relative importance of each predictor. The 95% confidence limits on the estimated rela-

tionship are indicated by dotted lines. These lines tend to diverge near the extremes of the range for continuous predictors as a consequence of fewer observations (Agenbag et al., 2003). Tick marks on the x -axis show the location of data points. The main trends of GAM results performed separately for each survey were not significantly different from the models constructed with the entire data set and are not presented.

Results (Fig. 5) illustrate similar patterns in the relations of munida and anchoveta with the distance to the coast (DC), sea surface salinity (SSS) and sea surface oxygen (SSO) but a very different pattern for sea surface temperature. Both species were distributed close to the coast, but munida even closer than anchoveta, in the first 40 km (Figs. 3b and Fig. 5a). Relationships with sea surface oxygen presented a first maximum for low values of dissolved oxygen ($<4 \text{ mL L}^{-1}$), a minimum for oxygen concentration between 4 and 6 mL L^{-1} to then increase for high SSO concentrations (Fig. 5b). This bi-modal pattern is an illustration of the non-conservative character of oxygen concentration; oxygen can be either high or low in upwelling areas depending on the relative dominance of photosynthesis and respiration-degradation. Relationships with salinity (Fig. 5c) were very strong and clear for both species with dome-shaped relationships peaking between 34.7 and 35.1 which upwelled cold coastal waters (CCW): 34.80–35.05 (see Morón, 2000; Bertrand et al., 2004a; Swartzman et al., 2008). The curve for munida is contained inside the one for anchoveta illustrating an even more exclusive relationship for munida with the CCW. Finally the relationships with SST (Fig. 5d) showed that anchoveta is broadly distributed over a large range of temperature (14 – $23 \text{ }^\circ\text{C}$) while munida is restricted to colder water ($<18 \text{ }^\circ\text{C}$).

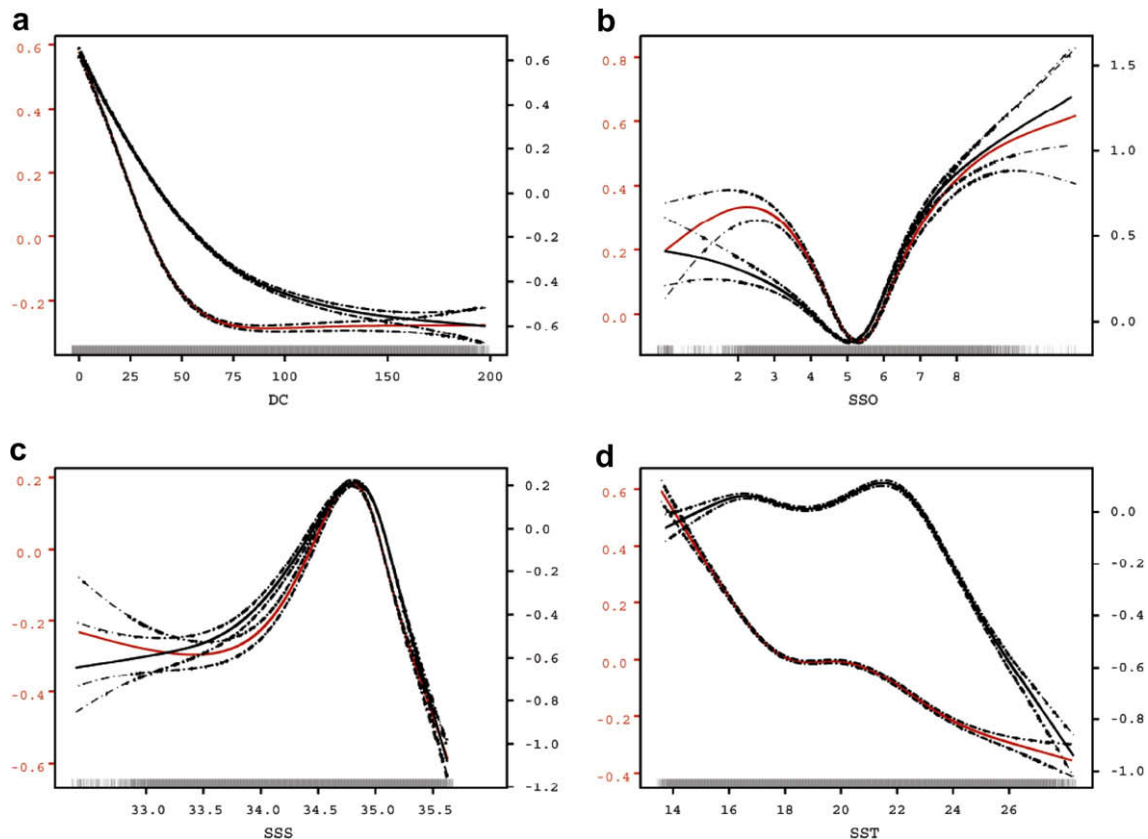


Fig. 5. GAM models based on anchoveta (black lines and right y -axes) and munida (red lines and left y -axes) log transformed acoustic abundance (s_A) according to (a) the distance from the coast (DC), (b) sea surface oxygen (SSO in mLL^{-1}), (c) sea surface salinity (SSS) and sea surface temperature (SST in $^\circ\text{C}$) for the complete set of 131,927 ESDU. The black dotted lines show the 95% confidence limits of GAM models. y -Axes are in relative scale, they correspond to the spline smoother that was fitted on the data, so that a y -value of zero is the mean effect of the variables on the response. Grey tick marks on the x -axis show the location of data points.

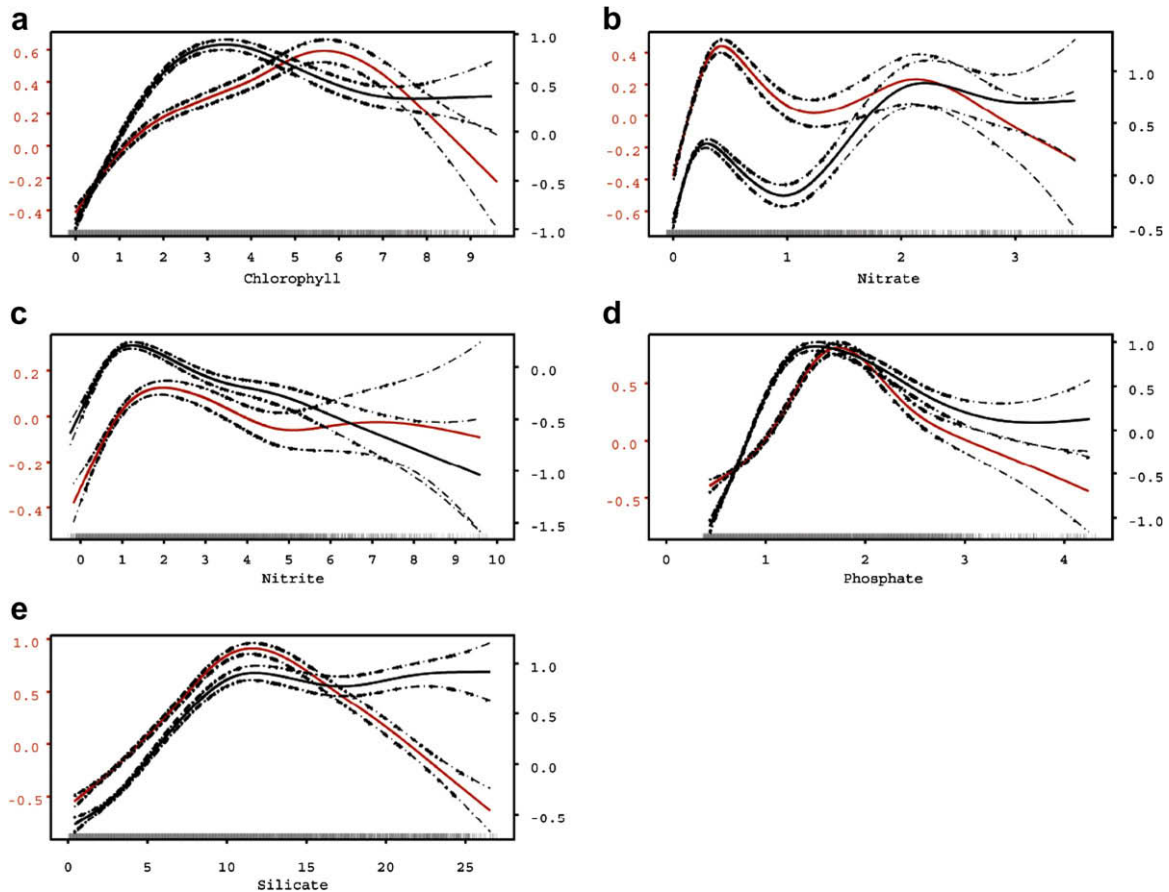


Fig. 6. GAM models based on anchoveta (black lines and right y-axes) and munida (red lines and left y-axes) log transformed acoustic abundance (s_A) according to (a) chlorophyll (in $\mu\text{g L}^{-1}$), (b) nitrate (in $\mu\text{g-at L}^{-1}$), (c) nitrite (in $\mu\text{g-at L}^{-1}$), (d) phosphate (in $\mu\text{g-at L}^{-1}$), and (e) silicate (in $\mu\text{g-at L}^{-1}$) for the survey performed in February–March 2000. The black dotted lines show the 95% confidence limits of GAM models. y-Axes are in relative scale, they correspond to the spline smoother that was fitted on the data, so that a y-value of zero is the mean effect of the variables on the response. Grey tick marks on the x-axis show the location of data points.

Results of GAM models for nutrients and chlorophyll are presented in Fig. 6. Both munida and anchoveta were (i) most abundant in areas with rather low nitrite concentration ($0.5\text{--}3\ \mu\text{g-at L}^{-1}$), (ii) bi-modally distributed relative to nitrate concentration ($0.2\text{--}0.8$ and $1.8\text{--}2.8\ \mu\text{g-at L}^{-1}$), and (iii) unimodally distributed relative to phosphate with higher munida and anchoveta biomass for medium phosphate concentration ($0.8\text{--}2.3\ \mu\text{g-at L}^{-1}$). The relationship with silicate was dome-shaped for munida (max: $5\text{--}20\ \mu\text{g-at L}^{-1}$) but there was no decline in preference for anchoveta from about $10\ \mu\text{g-at L}^{-1}$. With chlorophyll, munida was more abundant in areas with higher phytoplankton biomass ($4\text{--}8\ \mu\text{g L}^{-1}$) than anchoveta ($1\text{--}5\ \mu\text{g L}^{-1}$).

4. Discussion

4.1. Ecological niches

Munida and anchoveta share similar ecological niches and patterns of spatial distribution. Spatial overlapping was strong (Fig. 2). Munida range was smaller but contained within that of anchoveta (Figs. 1 and 2). The centre of gravity of both species shifted toward the north at the beginning of the study period and has remained rather stable since 2000. Relationships with environmental parameters show that both species inhabit cold coastal waters (CCW). Such an association has been described for anchoveta (e.g. Bertrand et al., 2004a; Swartzman et al., 2008) and for pelagic *P. planipes* in the California Current (Robinson et al., 2004), but not for munida.

However, while munida and anchoveta share similar habitats, there are clear differences. Anchoveta do not prefer specific temperatures over a large range ($14\text{--}23\ ^\circ\text{C}$), in accordance with Bertrand et al., 2004a who showed that absolute temperature was not a key parameter determining anchoveta distribution. Munida on the other hand are distributed in the coldest waters available, and in the more coastal part of the anchoveta distribution. Munida therefore mainly occurs in newly upwelled waters. Such waters are highly productive and munida it probably forages on diatoms and zooplankton. Indeed, in the California Current, pelagic *P. planipes* is capable of filter-feeds on diatoms blooms and forage on zooplankton (Longhurst et al., 1967).

The pelagic habitat of munida off Peru differs considerably from its habitat in the central part of Chile where eggs and larvae are pelagic but adults are benthic (Roa et al., 1995, 1997; Bahamonde et al., 1979; Roa and Bahamonde 1993; Roa and Tapia, 1998). Ecological differences are accompanied by biological differences with, for instance, smaller munida in north Chile and Peru than in the central Chile (Guzmán et al., 2002). Another difference relates to the size of the population. Munida is much more abundant off Peru than off Chile. Off Peru biomass estimated acoustically by IMARPE reached several millions of tons over 8 years (maximum: 3.4 millions of tons in winter 2000), compared to the virgin biomass estimated to about 210000 tons off Chile where munida is commonly exploited (Roa et al., 1997). These abundance differences are so large that the presence of a single species vs. two species was debated. Recent genetic analyses confirm that a single species, *Pleuroncodes monodon*, occurs off both Chile and Peru (Pilar Haye and

Elie Poulin, University of Chile, unpublished data). If it is the same species, why are its behaviour and productivity so different? We propose a hypothesis based on dissolved oxygen concentration. Bathymetric distribution of *munida* ranges between 30 and 400 m off Chile (Haig, 1955; Bustos and Retamal, 1985) but varies according to the latitude. Off northern Chile, adult *munida* was observed in shallower waters, between 20 and 40 m (Gutiérrez and Zúñiga, 1977), sometimes with a pelagic behaviour (Jorge Castillo, Instituto de Fomento Pesquero, Chile, personal communication). Off Peru, the vertical distribution is restricted to the first 30–40 m and *munida* is always pelagic. It seems that there is a gradient in the vertical distribution and behaviour of the *munida*, from bathy-benthonic in central Chile to epi-pelagic in Peru. We propose that this pattern is related to the trend in oxycline depth. *Munida* is characteristic of areas with moderately low dissolved oxygen concentration (Wolf Arntz, personal communication). Helly and Levin (2004) showed that the depth of the 0.5 mL L⁻¹ upper layer diminishes from about 500 m off central Chile (30–40°S), 100 m off northern Chile (20°S) and <100 m off Peru. In Central Chile oxygen concentration is high enough at bottom depth for *munida*. Further north, the oxygen minimum zone (OMZ) is shallower and the near-absence of oxygen near the bottom prohibits *munida*'s presence. In Peru where the oxycline is very shallow, and the OMZ starts well above the bottom, *munida* cannot develop any benthonic phase and its life cycle is holopelagic illustrating *munida*'s plasticity (see Espinoza and Bertrand, 2008, for details on anchoveta's plasticity).

4.2. Habitat overlap and interactions

The similarity in their ecological niches and the strong spatial overlap between anchoveta and *munida* may have potential consequences. On one hand, because both species are prey for apex predators (fish, sea birds and mammals), each species might lessen predation pressure on the other. Conversely, anchoveta and *munida* forage on plankton and may compete for food. Anchoveta feed primarily on large zooplankton and to a lesser extent on large phytoplankton, particularly diatoms (Espinoza and Bertrand, 2008). The diet of *munida* has not been studied off Peru. In Chile *munida* forage on amphipods, zoeas, crustacean eggs, diatoms, foraminifers, bacteria, organic wastes and fish scales (Gallardo et al., 1980). In the California Current, pelagic *P. planipes* feeds on protists, zooplankton (mainly copepods, euphausiids and chaetognaths) and large diatoms; the diatom fraction being higher when diatoms are abundant (Longhurst et al., 1967). It is therefore likely that, off Peru, pelagic *munida* forage on both phytoplankton and zooplankton and compete for food with anchoveta. In addition competition for food, anchoveta can eat *munida* eggs, larvae and juveniles, and *munida* may also forage on anchoveta eggs or larvae. There are therefore potential negative competition and predation between these species. If these interactions occur, they do not seem to have had any strong effect at population scale. Indeed both *munida* and anchoveta have shown an increase in their population since the beginning-mid 1990s (see Gutiérrez et al., 2007 for anchoveta). This period is characterised by (i) colder conditions related to stronger upwelling (Francisco Chavez, MBARI, personal communication), (ii) dominance of cold coastal waters along the Peruvian coast (Swartzman et al., 2008), (iii) an increase in primary production (Francisco Chavez, MBARI, personal communication) and (iv) an increase in zooplankton production (Ayón et al., 2008). The recent increase in the *munida* and anchoveta populations associated with cold and productive conditions apparently reflects a bottom-up control (Ayón et al., 2008) and has also been accompanied by a spatial extension of populations to the north.

Any effect of competition for prey could have been dampened by the increased productivity during the last few years. If this productivity declines, competitive interactions between anchoveta

and *munida* may reduce one or both of these populations. Also, their foraging likely impacts other species as well. There is therefore an urgent need for more studies on the huge population of *munida* off Peru.

4.3. *Munida*, the species who came in from the cold

In summary, *munida* and anchoveta share similar ecological niches and overlap spatially but *munida* is more restricted to the coldest part of the productive cold coastal waters. The recent increase in *munida* abundance off Peru was concomitant with a change to colder conditions in the HCS (Francisco Chavez, MBARI, personal communication) characterised by rich upwelling waters, the CCW (Swartzman et al., 2008). *Munida* took advantage of these cold conditions to extend its range north from central Chile to the Peruvian coast (where it probably also occurred in the 1940s; Del Solar, 1942 in Schweigger, 1964). Off Peru the very shallow oxycline keeps *munida* above its bottom habitat and forced it to become holopelagic off Peru. When the present decadal cold ('La Vieja', see Chavez et al., 2003) conditions end, we may expect that *munida* population will decrease or even disappear from the Peruvian coast, with its range again contracting southwards into Chilean waters.

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