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Schooling behaviour and environmental forcing in relation to anchoveta distribution: An analysis across multiple spatial scales

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ABSTRACT

The Peruvian anchovy or anchoveta (Engraulis ringens) supports the highest worldwide fishery landings and varies in space and time over many scales. Here we present the first comprehensive sub-mesocale study of anchoveta distribution in relation to the environment. During November 2004, we conducted a behavioural ecology survey off central Peru and used a series of observational and sampling tools including SST and CO₂ sensors, Niskin bottles, CTD probes, zooplankton sampling, stomach content analvsis, echo-sounder, multibeam sonar, and bird observations. The sub-mesoscale survey areas were chosen from mesoscale acoustic surveys. A routine coast-wide (~2000 km) acoustic survey performed just after the sub-mesoscale surveys, provided information at an even larger population scale. The availability of nearly concurrent sub-mesoscale, mesoscale and coast-wide information on anchoveta distribution allowed for a unique multi-scale synthesis. At the sub-mesoscale (100s m to km) physical processes (internal waves and frontogenesis) concentrated plankton into patches and determined anchoveta spatial distribution. At the mesoscale (10s km) location relative to the zone of active upwelling (and age of the upwelled water) and the depth of the oxycline had strong impacts on the anchoveta. Finally, over 100s km the size of the productive area, as defined by the upwelled cold coastal waters, was the determining factor. We propose a conceptual view of the relative importance of social behaviour and environmental (biotic and abiotic) processes on the spatial distribution of anchoveta. Our ecological space has two yaxis; one based on self-organization (social behaviour), and the other based on the environmental processes. At scales from the individual (10s cm), to the nucleus (m), social behaviour (e.g. the need to school) drives spatial organization. At scales larger than the school, environmental forces are the main driver of fish distribution. The conceptual ecosystem models presented in this paper may provide the final links needed to develop accurate forecasts of the spatial distribution of anchoveta over multiple scales.

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1. Introduction

Peruvian anchovy or anchoveta (*Engraulis ringens*) is a critical element of the Humboldt Current ecosystem, supporting the largest fishery in the world. Anchoveta is commonly referred to as an *r* species because of its fast growth and time to maturity (\sim 1 year), short life span (\sim 4 years), fast response to environmental variability (Valdivia, 1978; Bertrand et al., 2004a; Gutiérrez et al., 2007), and plasticity in terms of the prey it consumes and foraging behav-

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iour (Espinoza and Bertrand, 2008). Anchoveta is both an important predator of planktonic organisms (Pauly et al., 1989; Espinoza and Bertrand, 2008), a prey for apex predators (Arntz and Fahrbach, 1996; Jancke and Goya, 1998; Arias-Schereiber, 2003) and also shares the productive coastal habitat with the sardine, *Sardinops sagax* and more recently the crustacean squat lobster or 'munida', *Pleuroncodes monodon*, which has been very abundant in the Humboldt Current system (HCS) since the mid 1990s (Gutiérrez et al., 2008).

Anchoveta populations can vary rapidly in both space and time. The variability depends on a number of factors that structure its habitat (e.g. Clark, 1977; Bertrand et al., 2004a, 2008; Swartzman et al., 2008). Gregarious or schooling fish such as the anchoveta are sensitive to processes occurring at spatial scales that impact

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Fig. 1. Survey track (thick line) during the mesoscale ('rake survey') cruise and zooms on the two sub-mesoscale surveys (SMSS1 and SMSS2). Trawl (full circles), CTD (black empty circles), Niskin (black empty squares) and multinet (capital M) positions are also indicated, thin black lines indicates isobaths.

the individual (dm), nuclei (ms), schools (ms to 10s m), clusters of schools (km), clusters of clusters (10s km), and populations (100s km) (Gerlotto and Paramo, 2003; Fréon et al., 2005). For example, Bertrand et al. (2008) described the impact of a coastally trapped Kelvin waves (Clarke, 1983) on the spatial distribution of anchoveta and fishers. The Kelvin waves initiate a bottom-up cascade (Frontier, 1987; Russel et al., 1992) that propagates through the ecosystem from physics to anchoveta and fishers. Physical processes modify the three-dimensional distribution of physical (i.e. temperature), chemical (i.e. oxygen) and biological (i.e. plankton) parameters, the so-called oceanic landscape; then, mobile predators such as anchoveta and fishers respond to these spatial perturbations. At smaller scales, schools are known to self-organize, driven by elementary behavioural rules at the individual level: attraction, repulsion, and cohesion, and produce elaborate collective structures (Soria, 1997; Camazine et al., 2001; Couzin and Krause, 2003). Social rules are critical in school internal structure (Gerlotto and Paramo, 2003; Gerlotto et al., 2004) and can interact with environmental forcing of the oceanic landscape to determine school shape (morphology) so that they are either small dense schools, loose shoals or layers (e.g. Gerlotto et al., 2004; Bertrand et al., 2006). Therefore, school types have been considered good indicators of environmental conditions (Petitgas and Levenez, 1996; Reid, 2000; Petitgas et al, 2003; Bertrand et al., 2006).

While the most notable and dramatic changes in anchoveta are associated with large multi-decadal basin-scale changes in the environment (e.g. Chavez et al., 2003) there are many other scales of variability that are just now emerging. For example a new centennial-scale fluctuation has been elucidated from sediment cores (e.g. Sifeddine et al., 2008; Valdés et al., 2008). Further, upwelling ecosystems are highly heterogeneous with oceanographic and trophic conditions differing strongly on short time and space scales (Lavaniegos et al., 2002; Carr and Kearns, 2003; Bertrand et al., 2004a; Gutiérrez et al., 2007; Chaigneau et al., 2008; Espinoza and Bertrand, 2008; Swartzman et al., 2008). This heterogeneity is the result of mesoscale (10s km) and sub-mesoscale (100s m to km) activity that generates sharp fronts between coastal rich and oceanic poor waters (Chaigneau and Pizarro, 2005a), filaments (Thomas, 1999), eddies (Hormazabal et al., 2004; Chaigneau and Pizarro, 2005b). Internal waves are also emerging as important drivers of the oceanic landscape at these scales (Haury et al., 1978; Pineda, 1999). Studies have already shown that mesoscale activity influences the spatial distribution of fish (e.g. Rogachev et al., 1996; Seki et al., 2002; Fossheim et al., 2005). It is also very likely that sub-mesoscale physics may also influence anchoveta and its interaction with other species (prey, competitors and predators), but there is a paucity of *in situ* observations at this smaller scale.

Here we present the first comprehensive sub-mesocale study of anchoveta distribution in relation to the environment. The environment includes temperature, salinity, dissolved CO₂, dissolved O₂, the vertical and horizontal distribution and abundance of other species (predator, prey and competitors); at the temporal scale we resolve the diel cycle. Sub-mesoscale surveys (SMSSs) (~28 h – 2 nmi) were performed in November 2004 to relate environmental forcing and fish behaviour and distribution in central Peru. SST and

Table 1

Number of samples by sub-mesoscale survey (SMSS) for each parameter.

Parameter	Number of samples		
	SMSS1	SMSS2	
Acoustics (anchoveta, munida and zooplankton)	948 ESDUs (0.25 nmi long each)	956 ESDUs (0.25 nmi long each)	
Plankton multinet sampling	10 profiles; 436,861 items identified	10 profiles; 154,364 items identified	
CTD	14 profiles (2 before and 12 after the acoustic track)	11 profiles (1 before, 10 after the acoustic track)	
Sea surface salinity, pCO_2	1568 records (one value each minute except during sensor calibration)	1298 records (one value each minute except during sensor calibration)	
Niskin bottles samples	6 profiles (DO, chlorophyll <i>a</i> , and phaeopigment)	5 profiles (DO, chlorophyll <i>a</i> , and phaeopigment)	
Pelagic trawls	11 trawls, 8 with anchovy catch, 1582 anchoveta sampled for	9 trawls, all with anchovy catch, 1525 anchoveta sampled for	
	biometry and 114 for stomach content analysis	biometry and 128 for stomach content analysis	
Sea bird counting	Along the transects (daylight hours), 9004 seabirds observed over 239 ESDUs	Along the transects (daylight hours), 5878 seabirds observed over 202 ESDUs	
Multibeam sonar	6 h of opportunistic recording (when fish was present)	6 h of opportunistic recording (when fish was present)	

CO₂ sensors, Niskin bottles, CTD probes, zooplankton sampling, stomach content analysis, echo-sounder, multibeam sonar, bird observations were used to assess interactions between fish behaviour and distribution and the environmental parameters (both oceanographic and biotic). Areas particularly suitable for SMSSs (rake survey were identified from mesoscale acoustic surveys). A routine coast-wide (~2000 km) acoustic survey performed by IMA-RPE (Instituto del Mar del Perú, www.imarpe.gob.pe) just after the SMSS's, provided information at an even larger population scale.

The availability of nearly concurrent sub-mesoscale, mesoscale and coast-wide information on anchoveta distribution allowed for a unique multi-scale synthesis. A modified basin model framework (BMF) from MacCall (1990), where fish distribute in a theoretical basin (here basin does not refer to ocean basins but to the area over which the fish are distributed) where 'depth' depends on the growth rate per capita in the area, was constructed. MacCall (1990) postulated that fish first colonize favourable areas then move to less favourable areas as they become more abundant (density-dependence). Swartzman et al. (2008) on the other hand showed that anchoveta are restricted to upwelled cold coastal waters (CCW) independent of anchoveta abundance, as suggested by the habitat-based model proposed by Bertrand et al. (2004a). The size of the favoured habitat (CCW) is then an important factor regulating anchoveta populations. Physical (CCW) and chemical (oxygen) parameters define the size of the favoured habitat (quantity) but abundance and distribution of predators and prey determine habitat quality (basin depth). In our 'habitat-based BMF' anchoveta concentration increases in the favoured habitat when quality increases ('deeper basin') rather than expand spatially to less favourable habitats. Basin depth (for the population) increases with habitat quality, determined by multiple biotic and abiotic parameters at our three scales: large/population, meso and submeso. We propose conceptual models that explain the spatial distribution of anchoveta at multiple scales as well as the relative influence of social behaviour and the environment.

2. Materials and methods

2.1. Survey design

Two acoustic sub-mesoscale surveys (SMSSs) were carried out on board the IMARPE R/V "Olaya" (41 m long) off the Peruvian coast in November 2004, wherein the ship steamed around two, 2 nautical mile side square boxes (Fig. 1) repeatedly. The average time to run a single square was 1 h at 8 knots. The location of the SMSSs was chosen from anchoveta abundance estimated during a preliminary acoustic rake survey along the coast designed to identify favourable areas (see Fig. 1) at the beginning of the cruise and from the locations of the fishing fleet. The position of the boxes was geographically fixed, i.e. we did not implement a lagrangian tracking system. However, no substantial change in communities was observed during each SMSS and anchovy, the target species was always present. We consider each SMSS as independent.

Acoustic sub-mesoscale survey 1 (SMSS1) was carried out off Pucusana (12°34′S) and consisted of 28 repeated squares (to encompass an entire diel cycle) from November 18th at 04:40 to November 19th at 08:45 (Fig. 1). Acoustic sub-mesoscale survey 2 (SMSS2) was performed 20 nautical miles northwest of Paracas peninsula (13°40′S) and consisted in 28 repeated squares from November 21st at 16:45 to November 22nd at 21:24. After each survey the oceanographic, planktonic and biological features of the area were sampled using CTDs and nets during a 28 h sampling period (Fig. 1). The sampling strategy was designed to capture submesoscale variability over a diel cycle.

2.2. Acoustic observations

Vertical acoustic cross section data were collected in with a 38 and 120 kHz Simrad EK500 split-beam, scientific echo-sounder

Table 2

Mean surface conditions (except for the zooplankton mean density which was integrated over 100 m depth and s_{A} , which was integrated over 50 m depth) during small-scale surveys 1 and 2.

Parameter	SMSS1	SMSS2
Wind speed (m s^{-1})	1.75	3.14
SST (°C)	17.8	16.6
Salinity	35.11	35.06
xCO ₂ (ppmv)	359.4	655.3
$DO(mLL^{-1})$	6.6	6.2
Chlo- a (µg L ⁻¹)	8	21.2
Pheo/Chlo-a	0.68	0.32
Main zooplanktonic	81.5% of copepods,	76.8% of copepods,
taxa (% in number)	10.4% of cladoceras,	11.7% of
	and 3.7% of	ichtyoplankton
	ichtyoplankton	(clupeids), 4.4% of
	(clupeids)	polychaetes, and
		3.6%
		of cladoceras
Zooplankton mean density $(number m^{-3})$	121	35.5
Zooplankton s _A (m ² nmi ⁻²)	22.4	7.2
Munida s_A (m ² nmi ⁻²)	563.6	0
Anchoveta s _A (m ² nmi ⁻²)	695.1	407.9
Stomach fullness (%)	0.4	0.27
Number of seabirds species	11	7
Seabirds (number nmi ⁻¹)	73.3	58.2
% of foraging seabirds	12.5	15.1



Fig. 2. Vertical profiles from Niskin bottles for temperature, salinity, dissolved oxygen and chlorophyll *a* and the ratio between phaeopigment and chlorophyll *a*. Thick black lines indicate mean profile, dotted black lines indicate the profile performed just before the 28 h acoustic square tracks, grey lines indicate profiles performed after the acoustic tracks.

system (Kongsberg Simrad AS, Kongsberg, Norway), calibrated as in Foote et al. (1987). Data processing was done using Echoview (SonarData Pty. Ltd.) and Movies+ (Weill et al., 1993). Dual frequency analyses were used to discriminate anchoveta, from munida and zooplankton. Species identification was verified with pelagic trawl and plankton net samples. The acoustic nautical area scattering coefficient (s_A or NASC), an indicator of fish biomass, and the acoustic volume backscattering strength (S_v), an indicator of the fish density inside each collective structure (each acoustic echo-trace), were calculated for all echo-traces. Acoustic symbols and units used here follow MacLennan et al. (2002). Acoustic data were recorded by elementary distance sampling unit (ESDU) of 0.25 nmi.

Fish schools were observed in 3D with a scanning multibeam sonar (Reson Seabat 6012). The sonar was mounted on the vessel starboard side, perpendicular to the vessel course, permitting the scanning of a 90° sector from vertical down (below the vessel) to horizontal starboard (parallel to sea surface), with a range of 100 m. Each ping covered this 90° sector, divided into 60 beams of 1.5° (between beams) by 15° (perpendicular) each. The sonar operated at 455 kHz (20 kHz bandwidth) with a ping duration of 0.06 ms. The data was constructed as a 3D image (Gerlotto et al., 1999) with SBI Viewer software (Hamitouche-Djabou et al., 1999).

2.3. Oceanographic data

Sea surface temperature (SST) and the partial pressure of CO_2 were continuously recorded using a resistance temperature detector and a nondispersive infrared gas analyzer (LI-COR model 6262), which determines the partial pressure of CO_2 in the atmosphere and surface seawater (Friederich et al., 2008).

Surface-to-bottom temperature and salinity profiles were obtained with a SEABIRD CTD. Water samples were collected in Niskin bottles at 0, 10, 25, 50, 75, 100, and 150 m and analyzed for dissolved oxygen (DO-modified Winkler method, Carritt and Carpenter, 1966), chlorophyll *a*, and phaeopigment (concentration method of Holm-Hansen et al., 1965).

2.4. Plankton sampling

Zooplankton were collected with a vertically profiling plankton net (multinet) with a 300 μ m mesh size in the following depth strata: 0–10 m, 10–25 m, 25–50 m, 50–75 m, and 75–100 m depths. Zooplankton settled volume (mL³) was determined immediately after collection using the displacement method (Kramer et al., 1972). Samples were fixed in 2% formaldehyde buffered with borax, then examined in laboratory using a stereoscopic microscope to identify and count zooplankton items.

2.5. Fish sampling

Fish were collected by pelagic trawl 'Engel 124/1800' (12 mm codend mesh). For each trawl, a subsample of the catch was collected randomly and anchoveta size was measured to the nearest 0.5 cm. Anchoveta cardiac and fundulus stomachs were extracted onboard and immediately fixed in 5% formalin for later laboratory analysis where stomachs contents were extracted and weighted to the nearest 0.001 g. Stomach fullness index was calculated by dividing fish stomach content weight by body wet weight.

2.6. Seabird counts

Seabird densities were estimated using transects as in Sutherland (1996) during daylight hours (06:00 to 18:00, local time). One trained observer made continuous counts from the ship bridge (10 m above sea level) using binoculars out to 300 m in a 90° arc from the tip of the bow to the starboard. Species identification, counts and behaviour (on water, active feeding, flying, and flight direction) were recorded and the time noted.



Fig. 3. Vertical features of the water column where internal solitary waves were observed during the day (a, b), the night (c), and surface photograph of a convergence line (d). *Note:* (b) Come from another similar experiment performed in April 2006.



Fig. 4. Examples of acoustic square transects performed during SMSS1 during the day (a), at night (b) and during SMSS2 during the day (c), at night (d). The classical patterns of distribution for anchoveta (*Engraulis ringens*), the squat lobster 'munida' (*Pleuroncodes monodon*) and zooplankton are highlighted.



Fig. 5. (a) Fish standard length during SMSS1 (black solid line) and SMSS2 (black dotted line). (b) Scatter plot (black dots) and cubic spline fits (black solid lines) of bivariate GAM models based on anchoveta fullness during SMSS1 and SMSS2 according to the time. The black dotted lines show the 95% confidence limits of GAM models. Left *y*-axis shows the stomach fullness in percentage. The right *y*-axis are in relative scale, they correspond to the cubic spline that was fit to the data, so that a *y*-value of zero is the mean effect of time on the response.

2.7. Data processing

SST, CO_2 , the acoustic s_A of zooplankton and to a lesser extent munida and anchoveta abundance showed strong diel variability. This diel pattern was related to diurnal warming of SST that in turn impacts CO_2 solubility and to plankton diurnal vertical migration with a daytime dispersion over a large volume that reduces acoustic detection. We removed the diel pattern using a non-parametric spline model in order to study higher frequency variations. We used a wavelet approach (Torrence and Compo, 1998) to search for spatiotemporal synchrony between organisms. There are few wavelet applications in marine ecology (Ménard et al., 2007) following the pioneering work by David and Chapron (1990); however this method is appropriate to analyse biological time series, which are often noisy, nonlinear and non-stationary (Cazelles and Stone, 2003); all features that may interfere with correlation or spectral analyses. Wavelet analysis was applied to the acoustic data time series with the diel cycle removed to investigate



Fig. 6. Time series for anchoveta (blue line), zooplankton (red line), munida (orange line) acoustic abundance and CO₂ (black dots) during SMSS1 where the diel cycle has been removed. Left *y*-axis corresponds to the anchoveta and munida; right *y*-axis corresponds to zooplankton and CO₂.



Fig. 7. Time series for anchoveta (blue line), zooplankton (red line) acoustic abundance and CO₂ (black dots) during SMSS2 where the diel cycle has been removed. Left *y*-axis corresponds to anchoveta; right *y*-axis corresponds to zooplankton and CO₂.

other periodic components. Complementary phase analyses characterised spatiotemporal synchrony between signals (Cazelles and Stone, 2003; Ménard et al., 2007). To quantify wavelet statistical significance, we resampled with a Markov bootstrapping (Efron and Tibshirani, 1993) that preserves the short temporal correlations (Cazelles and Stone, 2003). We used the Morlet mother wavelet and original algorithms that were developed in a MATLAB package (version 6.5, The MathWorks Inc.); these incorporate both cross analyses and statistical significance procedures (Cazelles et al., 2007).

Finally, to determine the diel cycle of anchoveta foraging we analysed, for each SMSS, variations in anchoveta stomach fullness over time. As the relationships are likely to be nonlinear, a generalized additive modelling (GAM) approach was used (Hastie and Tibshirani, 1990) using S-Plus (Insightful Corporation, Seattle, WA, USA). Cubic spline smoothers were used to estimate the nonparametric functions.

3. Results

The acoustic track and the positions of pelagic trawls, CTD, multinet, and Niskin sampling stations are indicated in Fig. 1; the total number of samples for each parameter is listed in Table 1.

3.1. Oceanographic conditions

During sub-mesoscale survey 1 (SMSS1), vertical profiles indicated that temperature ranged from about 17.8 °C at 0 m to 14 °C at 100 m. Salinity ranged from 34.9 to 35.3 but mainly between 34.95 and 35.1, values characteristic of upwelled cold coastal waters (Morón, 2000). Dissolved oxygen concentration (DO) ranged between 6 and 7.5 mL L^{-1} at 0 m; the depth of the oxycline (where oxygen changes rapidly from the surface values to close to zero) varied from 15 to 25 m. Chlorophyll concentration was about $8 \ \mu g \ L^{-1}$ at $0 \ m$ and very low at $50 \ m$. Finally, the ratio between phaeopigment and chlorophyll was high for surface water (about 0.65), indicating a very active degradation process (Table 2 and Fig. 2). During SMSS1, we crossed convergence lines which were visible as "scum" (accumulations of foam and degraded particulate material) lines (Fig. 3d). These lines, commonly observed off Peru, tend to occur over solitary internal waves (Farmer and Armi, 1999), and during the surveys were associated with two vertical structures observed with the echo-sounder: (i) a deepening of the mixed layer illustrated by

the 'v shape' of the munida and plankton layer (Fig. 3a-c), or (ii) in some cases anchoveta were observed inside these structures forming schools during the day (Fig. 3a and b) and layers during the night (Fig. 3c).

During sub-mesoscale survey 2 (SMSS2) temperature ranged from about 16.6 °C at 0 m to 14 °C at 100 m. Salinity ranged from 34.96 to 35.30. Dissolved oxygen concentration decreased from 5–7.5 mL L⁻¹ at 0 m to 2 mL L⁻¹ at 25–30 m, to 1 mL L⁻¹ at 30– 45 m and finally to 0.1 mL L⁻¹ at 50 m. Chlorophyll concentration was higher (20 μ g L⁻¹) within several meters of the surface and very low at 50 m. Finally, the ratio between phaeopigment and chlorophyll *a* was rather low in the surface waters (about 0.32), indicating very high phytoplankton production and less active degradation processes (Table 2 and Fig. 2).

3.2. Zooplankton, munida, and anchoveta

Fig. 4 shows examples of acoustic square transects performed during SMSSs, illustrating the classic diel patterns of distribution for anchoveta (schools during the day, dispersed at night), munida (layers in the oxycline during the day, dispersed at night) and zooplankton (surface diel vertical migration with nighttime maxima near the surface, and daytime maxima at depth).

The zooplankton community was dominated by copepods; its abundance was three times higher during SMSS1 than SMSS2, regardless to the sampling method, multinet or acoustics (Table 2). The acoustic s_A of zooplankton was lower by day than by night in both areas. This pattern is due to the dispersion of zooplankton over a broader depth range during daily vertical migration (Fig. 4). Dense patches of zooplankton occurred during the first night of SMSS2.

Munida were observed only during SMSS1, scattered close to the surface during night (Fig. 4). During day, munida formed denser layers in the oxycline, and are physically "moved" vertically by the passage of internal waves (Figs. 3 and 4).

During SMSS1 and SMSS2 8 and 9 positive (with anchoveta catch) trawls were performed just after acoustic sampling. Fish size distribution was not significantly different between SMSSs ($\chi^2 = 17.16$, d.f. = 17, p = 0.44) and was strongly dominated by one year class of anchovy with a mode of 15 cm (Fig. 5a). Stomach fullness varied according to the time of the day and was significant in both surveys (GAM, p < 0.0001). The mean stomach fullness was higher during SMSS1 than SMSS2 (Table 2; *t*-test[1,240] = 3.54, p = 0.0005), but in both cases was highest between midday and



Fig. 8. Wavelet analysis for (a) anchoveta and zooplankton acoustic abundance during SMSS1; (b) anchoveta and munida acoustic abundance during SMSS1; and (c) anchoveta and plankton acoustic abundance during SMSS2. For each case, the upper plots give: on the left the local wavelet power spectrum of anchoveta, zooplankton or munida *s*_A. The local wavelet power spectrum gives a measure of the variance distribution of the space-time series according to time and for each period; on the right: global wavelet power spectrum of the anchoveta series as a function of period. The cross wavelet plot gives the wavelet cross spectrum between anchoveta and zooplankton or munida series. The wavelet cross spectrum identifies period bands and time intervals within which the two series co-vary. The black solid lines show the cone of influence, i.e. the region where edge effects are present. The black dashed lines show the 5% significance level computed based on 50 bootstrapped series. The lower plot gives the oscillating components computed with the wavelet transform.

18:00–21:00 (Fig. 5b). High stomach fullness was also observed during the night for some (\sim 15%) anchovies. The beginning of the

feeding period was not determined for SMSS1, as trawls performed between 08:00 and 14:50 did not catch fish. Anchoveta was always



Fig. 8 (continued)

above the 2 mL L⁻¹ oxygen isoline and the primary diel difference was that they were in schools during the day and scattered at night. The density (S_v) inside anchoveta echo-traces increased from dawn to midday then decreased until dusk and remained stable at a low level during night (ANOVA: F[3,34467] = 105.5, p < 0.00001 for SMSS1; F[3,30783] = 390.3, p < 0.00001 for SMSS2). Anchoveta reformed into schools at dawn (Fig. 4).

3.3. Seabirds

Eleven species of seabirds were observed during SMSS1 (mean density: 73.3 individuals/nmi⁻¹). The most abundant were Franklin's gull (*Larus pipixcan*), the Peruvian booby (*Sula variegata*), the Inca tern (*Larosterna inca*), and the Peruvian pelican (*Pelecanus tha-gus*), listed in decreasing order. Bird abundance was less during SMSS2 with 58.2 individuals/nmi⁻¹ with seven species being observed. Listed in decreasing order, the dominant species were the Peruvian booby, the Inca tern, the Guanay cormorant (*Leucocarbo bougainvillii*), and Franklin's gull. The proportion of actively feeding seabirds was 12.5% during SMSS1 and 15.1% during SMSS2. Among these species the Guanay and the Peruvian booby are major predators for anchovy. Others are mainly zooplanktivorous species.

3.4. Space-time series and wavelet analyses

During the SMSSs, SST, and CO_2 presented clear diel variations (not presented) with SST decreasing during the night (magnitude of change: 2.5 °C). CO_2 exhibited the opposite trend, as its solubility increased with decreasing SST. After removing the diel cycle, no relation remained between SST and CO_2 . Variation in the SST time series (with the diel cycle removed) could not be related to any other parameter and was eliminated from the analysis. The other space–time series (Figs. 6 and 7) illustrates the varying and dramatically different dynamics between day and night. We observed nocturnal zooplankton patches, in particular during SMSS2, when one patch was sampled repeatedly during 8, 1 h squares during the first night. A cluster of anchoveta and a peak in dissolved CO_2 was always associated with this zooplankton patch (Fig. 7). Such associations were less clear during SMSS1, probably because zooplankton patches were looser or absent in the sampled area. Outside zooplankton patches, anchoveta were also observed but were less abundant and scattered. During the day, both anchoveta schools and zooplankton patches were evenly distributed. Conversely, munida were concentrated in dense layers during daytime, at the depth of the oxycline. Munida local abundance presented a pattern of variation similar to the one of CO_2 (Fig. 6). During night munida was dispersed close to the surface and presented a more homogeneous distribution.

Wavelets, cross wavelets, and phase analyses were applied to reveal possible spatiotemporal synchrony between the organism distributions. Anchoveta and zooplankton acoustic abundances show a clear pattern of synchrony, especially during SMSS2 (Fig. 8a and c). During the afternoon and the night, anchoveta and zooplankton were present in the same 'time-space' period (about 32 ESDU, corresponding to a complete square, i.e. 8 nmi), with the half period indicating the plankton patch size, about 4 nmi. More interestingly, acoustic abundances of these two organisms oscillated perfectly in phase, indicating spatial correlation between anchoveta and zooplankton. At dawn, the spatial periodicity suddenly disappeared, as well as the association between anchoveta and zooplankton (i.e. the zooplankton patch and anchoveta cluster), and irregular small-scale periodicity appeared. Zooplankton and anchoveta stayed out of phase without any clear spatial association until the afternoon, when periodic oscillation and coherent phasing reappeared allowing interactions. During SMSS1 (Fig. 8a), cross wavelet and phase analysis between anchoveta and zooplankton local abundances also showed significant correlation during night (19:00-20:30 and 23:00-02:30), though the signal was weaker than in SMSS2. Note that the phase coherency observed between 10:00 and 14:00 during SMSS1 (Fig. 8a) and between 10:00 and 12:00 during SMSS2 (Fig. 8c) was insignificant, as it did not correspond to any significant cross wavelet (Fig. 8a and c).

Wavelet analyses performed with anchoveta and munida abundance data (Fig. 8b) did not reveal consistent spatial associations between these species. Anchoveta and munida acoustic abundances were in phase only at the end of the day and beginning of the night, i.e. when anchoveta schools were dispersing downwards and munida migrating upwards. Finally, munida and zooplankton distributions were not spatiotemporally associated in wavelet analyses (figure not presented).

3.5. The oceanic landscape

At the anchoveta population scale (100s of km), routine acoustic surveys were conducted in the core of anchoveta distribution by IMARPE just after the SMSSs (November 28–December 21, 2004). Anchoveta were distributed all along the Peruvian coast and the region where SMSSs took place corresponded to a particularly rich area, in an important upwelling cell (www.imarpe.gob.pe).

At a mesoscale (10s of km) the landscape was different between surveys (Table 2) even though both SMSSs' took place in cold coastal waters (see Morón, 2000; Bertrand et al., 2004a; Swartzman et al., 2008). SMSS1 was performed in older upwelled waters characterized by a high proportion of degraded chlorophyll, a very shallow oxycline, and high abundances of zooplankton, munida, anchoveta, and seabirds. The types of seabirds were mostly coastal species (Fraklin's gull and Inca tern) foraging mainly on zooplankton, including munida. SMSS2 was performed in active upwelling waters characterized by lower SST, very high chlorophyll concentration, and medium abundances of zooplankton and anchoveta. Seabirds were less abundant than in SMSS1, but dominated by the Peruvian booby, which forages on anchoveta. During both SMSSs, the main patterns in organisms' distribution over time followed the conventional pelagic diel scheme. Zooplankton performed diel vertical migration and were, during the day, mainly distributed below the oxycline (15–30 m). Munida (Fig. 4) were scattered in the same shallow laver as anchoveta during the night. but migrated deeper than the fish during the day, forming concentrated layers (Fig. 4) at the depth of the oxycline (15-30 m). Anchoveta vertical distribution was restricted to the first 30 m, above the oxycline. Zooplankton apparently finds a daytime refuge from anchoveta within the oxycline.

4. Discussion

4.1. Relative contribution of environment and behaviour in anchoveta schooling dynamics

In both SMSS1 and SMSS2 we observed the classic pattern of fish dispersion at night and aggregation in schools during day (Azzali et al., 1985; Fréon et al., 1996; Fréon and Misund, 1999; Cardinale et al., 2003), with a decrease in school internal density during afternoon and disintegration at dusk. The reduced school internal density during the afternoon appears associated with the beginning of the feeding period (Fig. 5b) as most of zooplankton migrates upwards (30-50 m to 5-20 m) and its availability increases. Indeed, less cohesive fish schools are assumed to be well adapted for feeding on zooplankton as each fish has to catch individual prey (Robinson et al., 1995; Nøttestad et al., 1996; Mackinson et al., 1999). During the night, despite the absence of smallscale (m to 10s of m) fish schools, clear sub-mesoscale (100s of m to km) fish clusters appeared. During the day, fish occurred in dense schools, especially in the morning, but not in larger-scale spatial structures such as clusters (at least on scales observable

in our SMSSs). These observations are interpreted below via behavioural constraints and habitat suitability.

During the night, most gregarious pelagic fish do not form dense schools because small-scale collective organisation is generally inhibited by low light intensity [see Fréon and Misund (1999) for a synthesis and Bertrand et al. (2006) for an exception]. At night, environmental features controlled fish distribution. This was particularly clear during the first night of SMSS2, when anchoveta formed a cluster inside a patch of zooplankton (Figs. 7 and 8c). Stomach fullness analyses indicated that the main foraging period was the afternoon and first part of the night (Fig. 5b). Anchoveta were then primarily in the zooplankton patch for foraging, but remained well into the night. Espinoza and Bertrand (2008) showed that even if anchoveta mainly feed during day, they will also feed at other times as long as prey are available. The zooplankton patch probably developed in response to a sub-mesoscale oceanographic feature (e.g. eddy, plume) that we could not identify (see Cotté and Simard, 2005; Croll et al., 2005; Fossheim et al., 2005, for examples of physical forcing on plankton leading to predator concentration or recruitment success). This patch was also characterized by a peak in dissolved CO₂ concentration (Fig. 7) that we relate to respiration by organisms. Indeed, a dense aggregation of organisms has been shown to deplete DO concentration (e.g. McFarland and Moss 1967; Dommasnes et al., 1994); the inverse, increased CO₂ as a result of respiration follows. We think this might be the first observation of this kind.

After dawn, zooplankton migrated down below the oxycline, while anchoveta aggregated in schools. Gerlotto et al. (2006), working with multibeam sonar data obtained after SMSS2 observed that sea birds and sea lions attacked these schools intensively. Indeed sea lions were observed with the multibeam 58% of the time and the attack rate was very high. Schools were in constant reorganization (Gerlotto et al., 2006) and no more spatial structures were evidenced at a scale of 100 s of m to km (Figs. 6 and 7).

4.2. Habitat-based BMF and 3D fish distribution

In an attempt to synthesize the information we adapted the basin model framework (BMF, MacCall, 1990, see also Fréon et al., 2005). As described in Section 1, under our 'habitat-based BMF', the theoretical basin increases in 'depth' with habitat suitability (i.e. not a literal depth but an index of habitat suitability) as determined by physical (e.g. temperature, depth of the oxycline), and biotic (e.g. predation, prey abundance, and spatial distribution) features, independent of density-dependent effects. As the diel cycle is a key factor in anchoveta patterns of aggregation, we constructed a diurnal and a nocturnal representation of the adapted BMF; each BMF being characterized by three different spatial scales: large (100s of km), meso (10s of km) and sub-meso (100s of m to km) (Fig. 9).

The larger basin (100s km) is defined by anchoveta tolerance limits and corresponds to the zone of possible population distribution defined by overall abiotic conditions. The SMSSs took place near the centre of anchoveta species distribution. During the whole cruise survey track (Fig. 1) temperature was not limiting (range of tolerance for anchoveta: \sim 13–25 °C, Bertrand et al., 2004a; Gutiérrez et al., 2008).

At a mesoscale (10s km), the SMSS1 was performed in aged upwelled waters and SMSS2 in freshly upwelled waters. In both SMSS1 and 2, productivity was high and a shallow oxycline (Fig. 2) limited the depth of anchoveta and prevented diel vertical migration. Zooplankton was abundant (Table 2) and patchily distributed. During the day, part of the zooplankton escaped the anchoveta by migrating into and below the oxycline. The consequence was lower habitat suitability for anchoveta ('shallower' basin, Fig. 9). Predation by seabirds and sea lions also reduced



Fig. 9. Synthetic representation of the diel variation of the quality of anchoveta habitat across scales and its consequences on the 3D spatial distribution of anchoveta, adapted from the 'habitat-based basin model framework' of MacCall (1990). The depth of the basin increases with habitat quality in terms of oceanographic (e.g. temperature, depth of the oxycline) and biotic (e.g. predation, prey abundance, and spatial organization) features. The larger basin corresponds to the zone of anchoveta distribution. Inside this general zone, habitat quality increases in areas rich in prey surrounding an upwelling zone for example. Inside the rich areas, sub-mesoscale structures (i.e. internal solitary waves, eddies) can concentrate prey, further increasing habitat quality. During the day (upper figure), the depth of the basin is shallower than during the night since prey are less accessible (some of the plankton have migrated below the oxycline) and predation by visual apex predators (e.g. seabirds) is higher. Anchoveta form schools that are attacked by predators (see Gerlotto et al., 2006). During the night (lower figure) the depth of the basin increases as prey become more available and predation is reduced. Fish are no longer able to construct polarised collective structures (schools) but are concentrated in prey patches or internal waves, when present. Encapsulated figures above the basin figures show anchoveta distribution of anchoveta off Peru (left) and a zoom in to an upwelling area (right). Encapsulated figures below the basin figures show typical examples of fish collective structure in each case as observed with the multibeam sonar (3D plots and plot showing a sea lion attacking anchoveta schools) or with the echo-sounder.

anchoveta habitat suitability during day. During the day anchoveta was in highly concentrated schools that were irregularly distributed (Figs. 6–8), a response to predators (Gerlotto et al., 2006). During night the vertical upward migration of zooplankton and reduced predation on anchoveta (no seabird attacks) created a 'deeper' (i.e. more suitable) BMF basin (Fig. 9). At night, anchoveta were distributed as loose shoals and scattered fish. It is during the night that the tight coupling between organisms (anchoveta and zooplankton), and their chemical signature (i.e. respiration) develops (Figs. 6 and 7); during the day these relationships dissipate. At sub-mesoscale (100s m to km) physical processes (internal waves and frontogenesis) concentrated plankton into patches and impacted anchoveta habitat suitability and spatial distribution. Inside the zooplankton patches, conditions were favourable for anchovy so the 'depth' of the BMF basins was high (Fig. 9). During the night, anchoveta cluster size corresponded to zooplankton patch size, suggesting that the size of fish clusters depends on the environment rather than on the total abundance of the fish population. On first order apex predators, fishers included, tend to search for fish clusters, rather than individuals or schools, to for-

age (Bertrand et al., 2004b; Fréon and Misund, 1999). Surface zooplankton patches were not observed during the day because zooplankton migrated below the oxycline and were less affected by the physical processes. Solitary internal waves (Fig. 3) modified the habitat by deepening the mixed layer and concentrating particulate matter (Haury et al., 1978; Mann and Lazier, 1996; Pineda, 1999; Francks, 2005). Anchoveta habitat suitability was increased by internal waves for at least two reasons. First, solitary internal waves create convergences that concentrate prey above the oxycline, which was particularly important during the day when most zooplankton would otherwise be distributed below the oxycline. Secondly, they increased the available habitat by deepening the oxycline allowing anchoveta to form larger and more elongated (vertically) schools (Fig. 3b).

4.3. Synthesis

We linked levels of fish aggregation (schools, clusters, layers), on a diel basis, to different oceanographic and biological features such as upwelling, zooplankton patches, solitary internal waves, and predators. Based on the observations reported here and published literature we propose a conceptual view of the relative importance of social behaviour and environmental (biotic and abiotic) processes on the spatial distribution of anchoveta. Our ecological space has two y-axis; one based on self-organization (social behaviour), and the other based on the environment processes. The importance of the axis to the patterns of fish aggregation depends on spatial scale (Fig. 10). At scales from the individual (10s cm), to the nucleus (m), which are very high density patches inside fish schools that are small enough to allow quasi-instantaneous communication on predator presence, change of direction (Gerlotto and Paramo, 2003), to the school (10s m), social behaviour (e.g. the need to school) drives spatial organization (Fig. 10). At this scale, individual based models, in which individual action is governed by the actions of the individual's immediate neighbours, produce realistic schools (Huth and Wissel, 1994; Couzin and Krause, 2003; Grimm et al., 2005), indicating that inter-individual interactions are crucial. At the school scale or below, social interactions with neighbours (which produce collective structures, e.g. schools, through self organization) are the first priority for an individual. For gregarious fish, the school is "an essential life unit in which fish feed, breed, rest, and flee" (Aoki, 1980).

School size, shape, and location depends (i) on the local habitat characteristics, in particular the presence of prey and their distribution (e.g. Nøttestad et al., 1996; Mackinson et al., 1999; Bertrand et al., 2006), physical forces, like the presence of strong vertical gradients in oxygen (or other "fronts"), or the presence of predators (e.g. Axelsen et al., 2001; Nøttestad et al. 2004; Gerlotto et al., 2006), and (ii) on behaviour related to physiological needs, for instance reproduction in the presence of predators (e.g. Axelsen et al., 2000). At scales larger than the school, environmental forces (from physics to organisms, see Bertrand et al., 2008) are the main driver of fish distribution (Fig. 10). Cluster size depends on submesoscale physical features (e.g. upwelling plumes, eddies) that shape the distribution of zooplankton patches (given that there is motivation for feeding). If the size of the fish cluster depends directly on the physical structures, the number and the internal density of clusters may be more related to intrinsic populational aspects such as total abundance. The size and distribution of larger aggregative units, such as the cluster of clusters, or fish stocks are determined by mesoscale (~100 km) physical features increasing and concentrating productivity such as upwelling cells (high abundance of anchovy in the upwelling cell in our case). Finally, the level of the fish population depends on large scale basin-wide conditions favourable or unfavourable to anchoveta (Chavez et al., 2003) that manifest themselves locally in the physical area occupied by the upwelled cold coastal waters (Swartzman et al., 2008).

Recent advances in space-based real time sensors, high performance computing, robust ecosystem theory, and very high-resolution coupled physical-biological models (e.g. ROMS, Penven et al., 2005) now permit relating the different scales of fish population dynamics over a broad range of scales and make possible operational forecasts of fish availability. Accurate and timely forecasts can provide the information needed to maintain long-term sustainability of fish stocks and protect the ecosystem of which the fish are an integral part, while maximizing social and economic benefits and preventing wasteful overinvestment of economic resources. This new power has been won by hard earned advances in technology and science. Previously, forecasting of how environmental variability and fishing pressure affected fish stocks and their ecosystem was impossible because we lacked efficient, high-resolution ocean observing systems to provide the data for assimilation into operational physical-biological models and final-



Fig. 10. A conceptual model describing the relative importance of factors regulating aggregation of gregarious fish as a function of scale. There are two *y*-axis one based on self-organization, the other on environmental forcing. The importance of these on fish distribution depends on the spatial scale. At smaller scales, self organization mechanisms are likely to be dominant; at larger-scales adaptation and response to the environment are more important.

ly the ecosystem theory to relate physical forcing all the way from phytoplankton to fish. The conceptual ecosystem models presented in this paper may provide the final links.

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