How fish habitat suitability does shape the 3D spatial organisation of anchovy across scales?

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Functional relationships in marine ecosystems are complex as far as physical and biological parameters are involved. Improving our understanding of ecosystem functioning requires the ability to observe in situ the interactions between physical and biological features. In this context, the Peruvian anchovy (Engraulis ringens) is an interesting case study as this species supports the highest worldwide landings and is known to present very high population, distributional and even biological dynamics at different spatio-temporal scales. A specific behavioural ecology survey was performed in November 2004 to study 3D occupation of space by anchovy in Peru. This study was based on an integrated approach. Indeed, using a series of observation tools (Niskin, CTD probes, zooplankton sampling, stomach content analysis, echo-sounder, multibeam sonar, birds and mammal observations) we assessed interactions between fish and most of the oceanographic and biotic environmental features possibly driving its behaviour. We could link levels of fish organisation (layer, school, shoal, cluster) to different oceanographic and biological features: upwelling plume, plankton patches, water masses fronts, predators and others, varying in space and in time, particularly according to the diel cycle. We adapted the basin model framework to propose a conceptual model of environment impact on fish space occupation. Indeed, the small and medium-scale habitat favourability shaped the fish 3D spatial organisation.

Keywords: fish school behaviour, diel behaviour, predator-prey relationships, pelagic ecosystem functioning, spatial patterns, multibeam sonar.

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Introduction

Inside their range of distribution fish are known to present aggregation patterns at different scales: stock, cluster, and school (Fréon and Misund, 1999). Acoustics allowed fisheries scientists to observe and study these biological constructions for a long time now. In some cases these aggregations could be visually related to “oceanographic events”, and particularly internal waves and fronts, which are easily observed through the acoustic representation of plankton distribution. The purpose of investigating such apparently simple and obvious patterns motivated the elaboration of small scale experiments, for instance repetitive surveys of limited areas. Results were published by several authors and laboratories since the late 60's (e.g. Villanueva et al., 1969). However, the main results consisted in a description of the spatial characteristics of aggregations (e.g. Gohin, 1985), the diel cycles (e.g. Fréon et al., 1996) or in a description of the different levels of aggregation (e.g. Gerlotto, 1993). No or little understanding of the reasons producing such complex arrangement of fish distribution could be obtained, and still little is known about the functional relationships in marine ecosystems leading to such patterns. As a consequence, many questions remain to be examined, e.g.: (i) how the physical environment forces organisms' distribution across scales? (ii) what is the relative importance of social vs. environmental forcing in the formation of fish 3D collective structures? (iii) how does the diel cycle structure and unstructure organisms' distribution and organisation? Such questions have been addressed several times in the 90s, and particularly in Europe through European Projects specifically devoted to it (e.g., EU projects 'TECHO' and 'CLUSTER'). Although great efforts have been made, very few consistent results were obtained, and except some synthesis based on the review of works focusing on specific aspects (e.g. Fréon and Misund, 1999), no true integrated hypothesis could be drawn from these few, unsatisfactory and sometime contradictory results.

Two main reasons can be suggested to explain such lack of consistent results. One is technical. Indeed, improving our understanding of ecosystem functioning requires the ability to observe in situ and simultaneously the interactions between physical and biological features, which is difficult (Bertrand et al., 2003). Acoustics gives extremely detailed information on the fish distribution, from the scale of the individual to the population. But no instrument allowed a satisfactory spatiotemporal recording of physical environmental data. In most of the cases, data are obtained over stations, and are extrapolated to a wide area, volume, or time. Recently automatic sensors have been developed and are able to provide data at a much more precise level and with a wider spatiotemporal coverage. The other reason is more conceptual: the actual 'interactive' role of living organisms in the ecosystem has long been underestimated. Probably under the influence of ‘traditional’ fisheries science approach, which relied mostly on fisheries catch data, fish tended to be considered as a “passive” component authorizing removals and having negligible interaction with the environment. Moreover, the very small scale being ignored, a great part of the dynamic of the ecosystem compartments couldn’t even be suspected. Then, simultaneity of two samplings was often approximated (e.g. a temperature and a trawling) even with hours or miles of distance between them. We need to conduct appropriate integrated observations, avoiding the kind of approximation we evoked.

The Peruvian anchovy (Engraulis ringens) is an interesting case study for such purpose because this species supports the highest worldwide landings and is known to present very high populational, distributional and even biological dynamics at different spatio-temporal scales. The Humboldt Current System where this fish inhabits is highly variable over a wide range of scales, centennial, decadal, inter-annual, intra-annual and smaller. This means that fish have had to evolve adaptive strategies in space and time (Bertrand et al., 2004). For reasons detailed above, until now most of studies focused on large and medium scale patterns (e.g. Bakun and Broad, 2003; Chavez et al., 2003). However, upwelling systems are spatially and temporally very
heterogeneous with a mosaic of nested dynamical physical structures at meso and sub-meso scales such as the frontal zones between coastal rich and oceanic poor water masses, plumes, filaments, eddies, internal waves and other. Oceanographic and trophic conditions can therefore strongly differ from one place to another in a same zone and from one moment to another in a same place (Lavaniegos et al. 2002; Carr and Kearns 2003, Bertrand et al., 2004). This means that anchovy habitat suitability varies according to the place, the scale of observation, the diel period, the oceanographic forcing and others. In such context, the objective of this paper is to attempt a first integrated study to understand better how fish habitat suitability does shape the 3D spatial organisation of anchovy across scales, according to the diel cycle. Indeed, "behaviour is the primary interface between the environment and the organisms […] the behavioural characteristics of pelagic fish intimately reflect the type of ecological niche that they have evolved to exploit" (Pitcher 1995). Thus, fish 3D spatial aggregation patterns could be indicators of ecosystem status in terms of oceanographic conditions and trophic structure.

**Material and Methods**

Experiments were carried out on board the IMARPE R/V “Olaya” (41 m long) along the Peruvian coast in November 2004. Acoustic survey design consisted on two 28 hours long series of square transects, 2 nmi large (1 nmi=1852 m), runs (Fig. 1). Average time of each square run was one hour at a speed of 8 knots. Experiment location was chosen according to anchovy abundance as observed during a first acoustic rake survey and from fishing fleet position (fishing was closed the day before the first experiment).

The first acoustic experiment (Exp. 1) was carried out in front of Pucusana and consisted in 28 runs performed from November 18th at 04:40 h to November 19th at 08:45 h (Fig. 1). The second (Exp. 2) was performed at 20 nmi Northwest from Paracas peninsula and consisted in 28 runs performed from November 21st at 16:45 to November 22nd at 21:45. After each acoustic experiment the oceanographic, planktonic and biologic characteristic of the prospected area were measured across a 24 h sampling period (Fig. 1).

The repeated square sampling strategy we used during acoustic experiments made our data correlated both in space and time. With such strategy we can study the diel variability of a small area but also the small scale spatial variability across the diel cycle. Therefore our data series can be considered as a space-time composite.

**Acoustic data**

Acoustic data were collected with a 38 and 120 kHz Simrad EK500 split-beam, scientific echo-sounder system (Kongsberg Simrad AS, Kongsberg, Norway), calibrated using standard procedures (Foote et al., 1987). The water column was sampled to depths of 100 m for 120 and 38 kHz. Acoustic data processing was done using Echoview (SonarData Pty. Ltd.). Virtual echograms were used to discriminate echoes from anchovy, the pelagic crustacean munida, *Pleuroncodes monodon*, and zooplankton (Fig. 2). Acoustic backscattering strength ($S_v$) was calculated for all anchovy echo-traces and is considered as an indicator of the fish density inside each collective structure (echo-trace).
Figure 1. Survey track (black line) during the whole cruise and zooms on the two square transects experiments (red lines). Trawl (black full circles), CTD (black empty circles), Niskin (black empty squares) and multinet (black capital M) positions are also indicated, blue lines indicates isobaths.

Figure 2. Algorithm used to discriminate echoes from anchovy, munida and zooplankton.
The multibeam sonar (MBS).
The scanning multibeam sonar Reson Seabat 6012 used has 60 beams of 1.5° each one and 22° in
the perpendicular direction. It works at a frequency of 455 kHz with a pulse length of 0.06 ms
and a TVG function adjusted at 20logR. The sonar was mounted on the vessel starboard side on a
vertical mast directed perpendicular to the vessel course in a vertical plan whose axis was 45°.
This technique permitted the scanning of a 90° sector from the vertical line (below the vessel) to
the horizontal one (parallel to sea surface), on the vessel side with a range of 100 m. The third
dimension is obtained through the succession of pulses along the vessel course, as in a
conventional vertical echo sounder, which assumes that the school speed is null when compared
to the speed of the vessel (Gerlotto et al., 1999).

The digital data are recorded for each ping and stored by sequences of about one minute. The data
can be reconstructed into a 3D image of the fish structures using the software SBI Viewer
(Hamitouche-Djabou et al., 1999) that also allows calculating the morphological characteristics
of the school.

Oceanographic data
Sea surface temperature (SST) and dissolved CO2 was continuously recorded using RTD and LI-
and water density between the surface and the bottom were registered by a SEABIRD CTD.
Water samplings from Niskin bottle were collected at the standard depths (0, 10, 25, 50, 75, 100
and 150 m) to estimate dissolved oxygen (DO-modified Winkler method, Carritt and Carpenter

Plankton
Zooplankton samples were taken with a vertically profiling plankton net (Multinet), 300 µm
mesh size at the following vertical strata: 0 - 10 m, 10 - 25 m, 25 – 50 m, 50 – 75 m and 75 - 100
m depth. The samples were fixed in 2% formaldehyde buffered with borax. The zooplankton
volume (mL$^3$) was determined immediately after collection using the displacement method
(Kramer et al., 1972).

Biology
Fish were collected by pelagic trawling. For each trawl, a subsample was collected randomly and
anchovy were measured to the nearest 0.5 cm. Anchovy cardiac and fundulus stomachs section
were extracted onboard and immediately fixed in 5% formalin for later laboratory analysis. In the
laboratory, stomach were opened, contents were extracted and weighted to the nearest 0.001 g.
Stomach fullness was calculated by dividing individual stomach content weight by wet body
weight.

Seabird counts
Seabird densities were estimated using the transect method (Sutherland, 1996) during daylight
hours (06:00 to 18:00 h, local time). One trained and dedicated observer made continuous counts
from the starboard of 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 of the ship. Species names, counts and
behavioural activity (on water, feeding, flying and flight direction) of birds were recorded and the
exact time of each observation noted. These data were then grouped by 0.5 nmi.

Data processing
For each experiment, we sought potential diel rhythm of alimentation using a generalized additive
modelling (GAM) approach (Hastie and Tibshirani, 1990) using cubic spline smoothers in S-Plus
(Insightful Corporation, Seattle, WA, USA).
Space-time series of SST, CO2, acoustic $s_A$ of zooplankton, munida and to a lesser extent anchovy showed a strong diel pattern. We removed this low frequency oscillation to study more in detail small scale variations. For that purpose a spline model was fitted on the data using S-Plus and the diel trend was removed before performing other analyses.

A wavelet approach (Torrence and Compo, 1998) was used to perform a time-space-frequency analysis of the data series, permitting to catch information on the different frequencies of the signal (i.e., the periodic components) as time-space progresses. In complement to wavelet analysis, phase analyses allowed us to characterize the spatiotemporal synchrony between signals (Cazelles and Stone, 2003; Menard et al., submitted). To quantify the statistical significance of the patterns exhibited by wavelet analyses, we performed resampling methods by bootstrap (Efron and Tibshirani, 1993) based on a Markov process that preserves the short temporal correlations of the time series (Cazelles and Stone, 2003). We used the Morlet mother wavelet and the original algorithms used in this study were developed in a MATLAB package (version 6.5, The MathWorks Inc.). They incorporate both cross analyses and statistical procedures (Cazelles et al., submitted).

**Results**

The position of pelagic trawls, CTD, multinet and Niskin sampling stations is indicated Figure 1.

**Oceanographic conditions**

During Exp. 1, temperature ranged from about 17.8°C in surface and 14 °C at 100 m depth; salinity ranged mainly from 34.5 to 35.1; dissolved oxygen (DO) ranged between 6 and 7.5 mL.L$^{-1}$ in surface, and the depth of the oxycline varied of more than 15 m during the experiment; chlorophyll concentration was about 8 μg.L$^{-1}$ in the first meters; finally the ratio between pheopigment and chlorophyll was quite high in the surface waters (about 0.65) indicating a high degradation process (Table 1, Fig. 3). When performing the acoustic runs during Exp. 1 we crossed internal waves (Farmer and Armi, 1999) easily detectable by the presence of surface froth filaments (Fig. 4). These internal waves were associated with typical vertical structures observed with the echosounder (Fig. 4).

During Exp. 2, temperature ranged from about 16.6°C in surface and 14 °C at 100 m depth; salinity ranging mainly from 34.5 to 35.1; DO ranged between 5 and 7.5 mL.L$^{-1}$ in surface to about 2 mL.L$^{-1}$ at 30 m, 1 mL.L$^{-1}$ at 40 m depth and 0.1 mL.L$^{-1}$ at 50 m depth; chlorophyll concentration was very high close to the surface with more than 20 μg.L$^{-1}$; finally the ratio between pheopigment and chlorophyll a was rather low in the surface waters (about 0.32) indicating a very high phytoplankton production (Table 1, Fig. 3).

During both experiments, SST and CO2 presented clear diel variations (not presented here) with SST decreasing during the night and increasing during the day and CO2 presenting an opposite trend (CO2 solubility increase when sea water decrease). When using detrended time series, no more clear relation was observed between CO2 and SST (local increase of CO2 could be related to an increase or decrease of SST).
Seabirds count
In average, 41.3 and 30.6 seabirds per 0.5 nmi, where observed during Exp. 1 and 2, respectively. The biodiversity was higher during Exp. 1 with 11 species when only 7 species were observed during Exp. 2 (Table 1). The proportion of foraging seabirds reached 12.5% during Exp. 1 and 15.1% during Exp. 2.

Figure 3. Vertical profiles of temperature, salinity, dissolved oxygen, chlorophyll a, pheopigment vs. chlorophyll for each experiment. Thick black line indicate mean profile, dotted black line indicate the profile performed just before the 28 hours long acoustic square tracks, grey lines indicate profiles performed after the acoustic tracks.
Figure 4. Synthetic figure describing 2D and 3D features where internal waves were observed.

Figure 5. (a): Fish standard length during Exp. 1 (black solid line) and 2 (black dotted line). (b): Scatter plot (black dots) and cubic spline smoothers fits (black solid lines) of bivariate GAM models based on anchovy fullness during Exp. 1 and 2 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 corresponds to the spline smoother that was fitted on the data, so that a y-value of zero is the mean effect of time on the response.
Organism behaviour and distribution

Zooplankton relative abundance was very different between the two experiments, with more than 3 times more zooplankton during Exp. 1 than Exp. 2, using multitnet or acoustic data (Table 1). Most of zooplankton was distributed above 30 meters whatever the period (Figs. 6, 7 and 8). Acoustic $s_A$ attributed to zooplankton was lower during the day than during the day. This pattern is probably related to a dispersion of organism over a higher vertical range during the day reducing the acoustic capabilities of detection and a vertical migration of part of the organisms. A remarkable feature was the presence of a large patch of zooplankton during the first night of Exp. 2 (see Fig. 9, runs 7 to 11, and Fig. 11).

Munida (see Fig. 4) was observed only during Exp. 1. Its vertical distribution was very close to the one of anchovy during the night (Figs. 6 and 8). During the day, it was distributed slightly deeper, at the depth of the oxycline (following the vertical oscillation of the oxycline, see Fig. 6, particularly when internal waves were present, see Fig. 4).

Anchovy vertical distribution was very stable whatever the time and the place. Its vertical distribution was globally limited by the 2 mL.L\(^{-1}\) isoline (Fig. 8). The density ($S_v$) of anchovy echo-traces (Fig. 9) increased from dawn to midday then decreased until dusk and remained quite stable at law level during the night. So in terms of aggregative pattern, fish concentrated in dense schools at dawn. The school density increased until midday. In the afternoon fish school cohesion decreased, and finally fish dispersed in loose shoals and scattered fish at night (Figs. 6 - 7). When the nocturnal patch of zooplankton was present (mainly during Exp. 2), a cluster of anchovy was concentrated inside (Fig. 11). Where internal waves were present anchovy 3D spatial organisation changed dramatically. Fish formed dense 'filaments' or 'swarms' inside the internal waves as observed from multibeam sonar observations (Fig. 4). Actually it was not possible to extract any 3D images of anchovy collective structure using the MBS at night (as no more dense coherent schools where observed) except for anchovy aggregations inside the internal waves.

Space-time series and wavelet analyses

Space-time series (Figs. 6, 7, 8, 10 and 11) illustrate the very different patterns of distribution and abundance for organisms and dissolved CO2 according to the diel cycle. During both experiments we could observe nocturnal zooplankton patches. In particular, one patch could be sampled during 8 square runs, the first night of Exp. 1. Each time the patch was related with the presence of a cluster of anchovy shoals and a pick in the dissolved CO2. During the day, anchovy and zooplankton spatial distribution was more erratic with a high variability from one place to the other. On the contrary, the daily distribution of munida was apparently related to oceanographic features (munida was distributed deeper at the level of the oxycline) and presented a clear pattern similar to the one of CO2 (Fig. 10). During the night munida dispersed close to the surface and present a more monotonous distribution.

Wavelet, cross wavelet and phase analyses confirm these first results. Analyses performed between anchovy and zooplankton (Fig. 12) show a very clear patter, especially during Exp. 2 (Fig. 12c). During the afternoon and the night, anchovy and zooplankton presented a same 'time-space' period (about 32 unities) corresponding to a square run, with the half period corresponding to the plankton patch size (about 4 nmi). More interestingly, these oscillations were perfectly in phase, indicating a very high spatial correlation between anchovy and zooplankton. At dawn, the periodicity disappeared for both anchovy and zooplankton and erratic small scale periodicity appeared. These species stayed out of phase without any clear spatial pattern until the afternoon when a periodic oscillation and a coherent phasing reappeared. The rather good phase coherency observed between 10h to 14h during Exp. 1 should not be considered as it does not correspond to any significant cross wavelet (Fig. 12a).
Figure 6. Acoustic square transects during Exp. 1. Only one run over two is represented.
Wavelet analyses performed with anchovy and munida (Fig. 12b) did not reveal any strong spatial associations between these species across the diel cycle. These species were significantly in phase only at the end of the day and the beginning of the night, i.e. when anchovy schools were dispersing, munida migrating upward, and internal waves concentrating all organisms. Finally, munida and zooplankton distribution could not be related from wavelet analyses (Figure not presented here).
Discussion

The landscape

The general 'oceanscape' (Steele, 1989) was different between the two experiments. Exp. 1 was performed in an area exploited by fishers the days before the experiments. This area was characterized by an intense biological activity with a high level of degraded chlorophyll, a very shallow oxycline, a high abundance of zooplankton, of munida, anchovy and seabirds. This area corresponded to matured upwelling waters. Exp. 2 was performed in an area that was not exploited by fishers. This area corresponded to the core of an active upwelling zone with low SST, very high chlorophyll concentration and medium zooplankton, anchovy and seabirds abundance.

Fish behaviour: small scale organisation vs. sub-meso scale organisation

In both areas we observed the classic pattern of dispersion at night and aggregation in schools at daytime (Azzali et al. 1985, Fréon et al. 1996, Fréon & Misund 1999, Cardinale et al. 2003), with a decrease in school density during the afternoon and a complete disorganisation at dusk (Fig. 9). The lower school density during the afternoon can be linked to the beginning of the feeding period (Fig. 5b) as zooplankton availability increases (Fig. 8). Indeed, small low cohesive schools are supposed to be well adapted for zooplankton feeding (Robinson et al., 1995; Nøttestad, et al., 1996; Mackinson et al., 1999). Interestingly despite the absence of small scale (10s meters), clear collective structures (schools) during the night, clear sub-meso scale (100s of meters to kms) structures appeared. On the contrary, during the day, fish presented a high level of small scale organisation (dense schools) especially in the morning but no more spatial organisation at higher scale (in the range of scale compatible with our experiments). Such results can be interpreted when taking into account behavioural constraints and habitat suitability.

Diel cycle and anchovy 3D spatial organisation

During the night, most of gregarious pelagic fish are not able to form dense oriented schools (see Bertrand et al., submitted, for an exception) as fish small scale self-organisation is inhibited by low light intensity (Fréon and Misund, 1999). Environmental constraints become preponderant and fish space occupation is structured by the oceanographic and associated planktonic features. This pattern was observed for each experiment but was particularly clear during the first night of Exp. 2, with anchovy distributed inside a patch of plankton (Figs. 7 and 11). The plankton patch was probably associated with a sub-meso-scale oceanographic feature common in upwelling areas (e.g., small eddy, plume) that we could not evidence by itself (see Cotté and Simard, 2005, and Croll et al., 2005 for examples of physical forcing on plankton leading to predator concentration). This sub-meso-scale feature was also characterized by a pick in dissolved CO2 concentration (Fig. 11) that we assume to be related to organisms' respiration. Indeed other studies demonstrated that a dense aggregation of organisms can deplete DO concentration (e.g. McFarland and Moss 1967; Dommasnes et al., 1994; Bertrand et al., submitted) so as a
counterpart to increase CO2 concentration. Therefore, a concentration of organisms in specific oceanographic structures probably affected the chemical characteristics of the water inside these structures.

At dawn, the landscape changed radically. Plankton dispersed and migrated vertically below the oxycline, and became less available to acoustics. Anchovy lost its sub-meso-scale structure but aggregated in well shaped schools. Sea birds and sea lions attacked intensively these schools (sea lions were observed 58% of the time of MBS records and attack rate was very high, Gerlotto et al., 2005). Schools were therefore submitted to a strong predatory pressure and predator avoidance was probably the main function of schooling (Pitcher and Parrish, 1993) during this period. Schools were in perpetual reorganisation (Gerlotto et al., 2005) and no more spatial structuring was observed at a scale of 10s of km (Fig. 12). This general pattern was disrupted by the presence of internal waves during Exp. 1. Indeed in the presence of such features, fish 3D organisation changed dramatically (Fig. 4). In that case anchovy spatial organisation appeared entirely driven by the oceanographic features. Fish seemed to 'pour' inside the internal waves, following passively the horizontal and vertical shape and oscillations of these structures. Internal waves are known to concentrate productivity (e.g., Haury et al., 1978; Mann and Lazier, 1996; Pineda, 1999; Francks, 2005). In this case it seems that being inside the internal wave where prey are concentrated prevails on schooling for avoiding predators. Actually seabirds were actively attacking anchovy almost trapped inside the internal waves. Also, these internal wave-related anchovy 'filaments' and 'swarms' were not different according to the diel cycle when all other 3D structures changed drastically.

The presence of high abundance of munida, a competitor of anchovy could affect anchovy habitat suitability and thus anchovy spatial organisation. Using the same set of data Gutierrez et al. (2005) showed that schooling cycle was not different between Exp. 1 where munida was present and Exp. 2 where no munida was observed.

**Toward a synthetic approach on habitat suitability and fish 3D organisation**

Fish habitat suitability relies on various biotic and abiotic parameters. Physical and chemical features determine the overall viable conditions but the abundance and distribution of prey and predators can improve or deteriorate habitat quality. Ecosystems are known to be heterogeneous and hierarchically organised across scales (e.g., Haury et al., 1978; Wu and Loucks, 1995). We will use such framework to develop our synthesis. To provide a synthetic view of our advances, we adapted the basin model framework (MacCall, 1990) in order to take into account the diel variation of anchovy habitat suitability across scales and its effect and the 3D spatial organisation of anchovy (Fig. 13).

At a large scale (100s km), the experiment took place in the core of anchovy distribution (anchovy main range of distribution: 4º-40ºS). During the whole survey track (Fig. 1) we observed anchovy continually when integrating acoustic data by 4 nmi units and factors such as temperature were far from limiting (range of tolerance for anchovy: ~13-25ºC).

At a smaller scale, the two experiments were performed in rich areas (matured upwelling area for Exp. 1, and active upwelling for Exp. 2). These areas corresponded to meso-scale oceanographic features (10s of km). An important feature was the presence of a shallow oxycline limiting the vertical range of anchovy and preventing any fish diel vertical migration (Fig. 8). Plankton was very abundant (Table 1) and unevenly distributed. Where no specific sub-meso-scale features were present, plankton was distributed in a 'classic' scattering layer. At day, part of zooplankton performed a vertical migration and was less available to anchovy. The consequence was a lower habitat suitability for anchovy (shallower basin). Furthermore high predatory pressure by seabirds
and sea lions also affected the habitat suitability. Anchovy was then distributed in schools with strong interactions with predators. The spatial distribution of these schools was erratic (Figs. 10-12). During the night the upward migration of zooplankton associated with the lower predation pressure (no more seabird attack) increased the habitat suitability (deeper basin compared with the day). Where no specific sub-meso-scale features were present, anchovy was distributed in loose shoals and scattered fish. Apparently, the presence of high abundance of munida did not affect the habitat suitability for anchovy.

Sub-meso-scales features (100s m – kms) had a strong impact on habitat suitability and anchovy 3D spatial distribution. Internal waves (Fig. 4) had the same impact on anchovy 3D organisation whatever the diel period. In all case, fish formed dense, apparently 'passive' swarms or filaments. Anchovy habitat suitability was high inside these internal waves because they concentrated prey (during the day, these structures were concentrating prey in surface when part of the planktonic community was below the oxycline). Nevertheless habitat suitability of these internal waves was probably slightly higher (deeper basin) during the night than during the day because of the lower predation pressure. Finally, the other sub-meso-scales features we observed were the shallow plankton patches. In the same way than for internal waves, inside plankton patches, anchovy habitat suitability was high. During the night, anchovy shoals were concentrated inside the patches. Actually anchovy cluster size was directly related to the patch size. This argues in favour of a fish clustering related to the patchiness of the environment rather than to pure social behaviour or population aspects (see Fréon and Misund, 1999, and Fréon et al., 2005). The plankton patches were no more observed during the day. This does not mean that oceanographic feature responsible of patch formation changed but that plankton dispersed and migrated below the oxycline. A last aspect concerning these patches concerns the impact of plankton and fish concentration on the chemical characteristics of the habitat. As already described, inside the patch dissolved CO2 increased and we can assume that DO decreased. Therefore the suitability of these patches may decrease if many fish are concentrated in. In conclusion it appears that fish habitat suitability does shape the 3D spatial organisation of anchovy (and –probably– reverses) across the diel cycle.

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Figure 13. Synthetic representation adapted from the basin model (MacCall, 1990) framework of the diel variation of anchovy habitat suitability across scales and its effect and the 3D spatial organisation of anchovy. The depth of the basin increases with habitat suitability in terms of oceanographic (e.g., temperature, depth of the oxycline, vorticity) and biotic (e.g., predation, prey abundance and spatial organisation) features. Oceanographic features force most of the biological features with for instance the concentration of plankton in a patch. The larger basin corresponds to a zone of tolerance for anchovy. Inside this general zone, habitat suitability increase in areas rich in prey such as upwelling. Inside these areas, sub-meso scale structures (i.e. internal waves, eddies) can concentrate prey, increasing habitat suitability. During the day (upper figure), the depth of the basin is globally shallower than during the night. Indeed, prey are scarcer (part of plankton migrated below the oxycline) and predation by visual apex predators (e.g. seabirds) is higher. Anchovy form schools that are attacked by predators. Specific oceanographic structures such as internal waves can concentrate plankton but also anchovy. In this case, the 3D spatial organisation of anchovy is 'shaped' by the oceanographic structure rather independently of fish self-organisation. During the night (lower figure) the global depth of the basin increases as prey become more available and predation is reduced. Fish are no more able to construct polarised collective structures (schools) but are concentrated in prey patches. If internal waves are present, fish concentrate inside as during the day. Encapsulated figures below the basin figures show typical examples of fish collective structure in each case as observed with the MBS (3D plots and plot showing a sea lion attacking anchovy schools) or with the echo-sounder.
References


Haury, L. R., J. A. McGowan, and P. H. Wiebe. 1978. Patterns and processes in the time-space scales of plankton distributions, Pages 277-327 Spatial pattern in plankton communities. Plenum, New York, USA.


Table 1. 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 Exp. 1 and 2.

<table>
<thead>
<tr>
<th>Wind speed (knot)</th>
<th>SST (°C)</th>
<th>Salinity</th>
<th>xCO2 (ppmv)</th>
<th>DO (mL.L$^{-1}$)</th>
<th>Chlo-a (µg.L$^{-1}$)</th>
<th>Pheo/Chloa</th>
<th>Zoopl. Mean density (nº.m$^{-3}$)</th>
<th>Zoopl. $s_A$ (m$^2$.mn$^{-2}$)</th>
<th>Munida $s_A$ (m$^2$.mn$^{-2}$)</th>
<th>Anch. $s_A$ (m$^2$.mn$^{-2}$)</th>
<th>Stomach fullness %</th>
<th>Nº of seabirds species</th>
<th>Seabirds (no*0.5 nmi$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exp. 1</td>
<td>3.4</td>
<td>17.8</td>
<td>35.11</td>
<td>359.4</td>
<td>6.6</td>
<td>8.0</td>
<td>0.68</td>
<td>121.0</td>
<td>22.4</td>
<td>563.6</td>
<td>695.1</td>
<td>0.40</td>
<td>11</td>
</tr>
<tr>
<td>Exp. 2</td>
<td>6.1</td>
<td>16.6</td>
<td>35.06</td>
<td>655.3</td>
<td>6.2</td>
<td>21.2</td>
<td>0.32</td>
<td>35.5</td>
<td>7.2</td>
<td>0.0</td>
<td>407.9</td>
<td>0.27</td>
<td>7</td>
</tr>
</tbody>
</table>

Figure 8. Time series of average vertical profiles by acoustic run for anchovy (red line), munida (orange line) and zooplankton (red line) during Exp. 1 (a) and Exp. 2 (b). Data are in log_{10} (s_A+1) except for zooplankton in Exp. 2 where data are in 5*log_{10} (s_A+1). The black continuous and dotted lines indicate the mean depth of the 2 mL.L$^{-1}$ and 1 mL.L$^{-1}$ dissolved oxygen isoline, respectively. It has to be noted that the vertical distribution of the oxycline is variable (see Figure 2) so the values indicated here do not represent the reality at any time.
Figure 10. Detrended time series for anchovy (blue line), zooplankton (red line), munida (orange line) and CO2 (black dots) during Exp. 1. Green diamonds in the upper figure indicate the position of internal waves. Left y-axis correspond to the detrended data for anchovy and munida; right y-axis correspond to the detrended data for zooplankton and CO2.
Figure 11. Detrended time series for anchovy (blue line), zooplankton (red line) and CO2 (black dots) during Exp. 2. Left y-axis corresponds to the detrended data for anchovy; right y-axis corresponds to the detrended data for zooplankton and CO2.
Figure 12. Wavelet analysis of the data of (a) anchovy and zooplankton during Exp. 1; (b) anchovy and
munida during Exp. 1; and (c) anchovy and plankton during Exp. 2. For each case, the upper plots give:
on the left the local wavelet power spectrum of anchovy, zooplankton or munida $s_k$. 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 anchovy series as a function of
period. The Cross wavelet plot gives the wavelet cross spectrum between anchovy and zooplankton or
munida series. The wavelet cross spectrum identifies both 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.