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**Ecosystem scenarios shape fishermen spatial behavior.  
The case of the Peruvian anchovy fishery in the  
Northern Humboldt Current system**

Rocio de Abril Joo Arakawa, Arnaud Bertrand, Marilu Bouchon, Alexis Chaigneau, Hervé Demarcq, Jorge Tam, Monique Simier, Dimitri Gutierrez, Mariano Gutierrez, Marceliano Segura, et al.

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1 2 Title: Ecosystem scenarios shape fishermen spatial behavior. The case of the Peruvian anchovy  
2 3 fishery in the Northern Humboldt Current system.

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## 164 Abstract

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365 A major goal in marine ecology is the understanding of the interactions between the dynamics of  
466 the different ecosystem components, from physics to top predators. While fishermen are among  
567 the main top predators at sea, almost none of the existing studies on ecology from physics to top  
768 predators contemplate fishermen as part of the system. The present work focuses on the coastal  
969 processes in the Northern Humboldt Current System, which encompasses both an intense climatic  
1070 variability and the largest monospecific fishery of the world. From concomitant satellite, acoustic  
1271 survey and Vessel Monitoring System data (~90000 fishing trips) for a ten-year period (2000-2009),  
1472 we quantify the associations between the dynamics of the spatial behavior of fishermen,  
1573 environmental conditions and anchovy (*Engraulis ringens*) biomass and spatial distribution. Using  
1774 multivariate statistical analyses we show that environmental and anchovy conditions do  
1975 significantly shape fishermen spatial behavior and present evidences that environmental  
2076 fluctuations smoothed out along trophic levels. We propose a retrospective analysis of the study  
2277 period in the light of the ecosystem scenarios evidenced and we finally discuss the potential use of  
2478 fishermen spatial behavior as ecosystem indicator.

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## 1. Introduction

Marine ecosystems are highly structured in space (Margalef, 1979) and pelagic ecosystems, where habitats are made of constantly moving water masses, are also highly dynamic in time (Levin, 1992; Fréon and Misund, 1999). Because those natural systems tend to be out of balance (Pimm, 1991), it is fundamental to consider their spatio-temporal variability to understand the relative contributions of bottom-up and top-down controls in their functioning (Matson and

101 Hunter, 1992; Gripenberg and Roslin, 2007; Polishchuk *et al.*, 2013). Also, in general, since each  
 102 organism tends to feed on smaller organisms, the high-frequency environmental variations tend to  
 103 smooth out along trophic levels (Mann and Lazier, 2006).

104  
 105 Observation limitations to examine such processes have been largely overcome in the last  
 106 decades thanks to new technologies and ecosystem models. There are now, in several  
 107 ecosystems, spatially explicit data on abiotic factors, prey and predator distribution and abundance  
 108 at high time resolution (Costa, 1993; Decker and O'Dor, 2003; Boyd *et al.*, 2004; Rutz and Hays,  
 109 2009; Bograd *et al.*, 2010). Recent works studied the linkages between environmental conditions,  
 110 prey distribution and predators' behavior in time and space. The predators studied included sea  
 111 mammals (Croll *et al.*, 2005; Stevick *et al.*, 2008; Cotté and Guinet, 2011; Hazen *et al.*, 2011;  
 112 Santora *et al.*, 2012; Thompson *et al.*, 2012), seabirds (Embling *et al.*, 2012; Santora *et al.*, 2012;  
 113 Thompson *et al.*, 2012) and fish (Thompson *et al.*, 2012; Embling *et al.*, 2013).

114  
 115 Those studies identified critical processes and key areas that can be directly useful in  
 116 conservation, marine spatial planning, or in the management of human activities in marine  
 117 ecosystems. Nevertheless, while fishing represents world catches of ~89.8 million of tonnes per  
 118 year (between 2006 and 2011; FAO, 2012) and competes directly with natural predators, none of  
 119 those studies on spatial ecology from physics to top predators contemplated fishermen as part of  
 120 the system. Admittedly, fishermen are peculiar top predators because they rely on technology and  
 121 are driven by a distinct currency than that of natural predators. Nonetheless, in pelagic ecosystems  
 122 water masses and fish schools are constantly moving (Swartzman *et al.*, 2008; Peraltila and  
 123 Bertrand, 2014). Thus, fishermen do face the same uncertainty on prey localization as natural  
 124 predators do and their spatial behavior reflects their need for solving the same challenge. In that  
 125 sense, it has been shown that fishermen in the Peruvian anchovy fishery deploy similar spatial  
 126 foraging strategies to those of other animal predators (Bertrand *et al.*, 2007).

127  
 128 The Northern Humboldt Current System (NHCS) off Peru provides a great opportunity for  
 129 studying the association between the dynamics of ecosystem components in a bottom-up-  
 130 controlled exploited ecosystem (Ayón *et al.*, 2008; Bertrand *et al.*, 2008a). The NHCS is  
 131 characterized by an intense variability from secular to intra-seasonal timescales. Variations of the  
 132 Eastern Pacific intertropical convergence zone or the Pacific decadal oscillation can impact the  
 133 NHCS at inter-decadal and secular scales (Chavez *et al.*, 2003; Gutierrez *et al.*, 2009; Salvatecci  
 134 *et al.*, 2012). At inter-annual scales, El Niño Southern Oscillation – characterized by relatively  
 135 warm/cold El Niño / La Niña events – has a strong effect on the eastern south Pacific region (Colas  
 136 *et al.*, 2008; Takahashi *et al.*, 2011; Dewitte *et al.*, 2012; among others). At seasonal and intra-  
 137 seasonal scales, the NHCS is mostly modulated by wave dynamics of equatorial origin and local  
 138 wind forcing (Penven *et al.*, 2005; Echevin *et al.*, 2011, 2014; Dewitte *et al.*, 2012; Chaigneau *et*

139 *al.*, 2013; Pietri *et al.*, 2014). The resulting environmental scenarios directly determine the extent of  
140 the tridimensional anchovy habitat (Bertrand *et al.*, 2004a, 2011), which in turn conditions fish  
141 availability for the main predators in this system, the fishermen (Bertrand *et al.*, 2008a). Besides,  
142 the NHCS produces more fish per unit area than any other region in the world oceans and sustains  
143 the world's largest monospecific fishery (Peruvian anchovy or anchoveta, *Engraulis ringens*). To  
144 cope with the intense climatic variability, the management of the anchovy fishery is adaptive, i.e.  
145 catch limits are re-assessed every ~6 months and opening and closure periods decided on the  
146 basis of daily monitoring of the ecosystem, the fish population and the fishery (Chavez *et al.*,  
147 2008). The Peruvian Marine Research Institute (IMARPE) is in charge of this intense monitoring. It  
148 comprises satellite information on environmental conditions (e.g. sea surface temperature,  
149 chlorophyll-a and sea level anomaly, among others) at daily and weekly resolutions. Fish  
150 population distribution and biomass are monitored through scientific acoustic surveys (two to three  
151 times a year). The fishing activity is supervised through landing statistics, Vessel Monitoring  
152 System (VMS) and on-board observers reports (Bertrand *et al.*, 2008b; Joo *et al.*, 2011). The  
153 amount of available data makes the NHCS a highly appealing ecosystem for an integrated  
154 approach on ecosystem dynamics. In this highly-variable and data-rich ecosystem, Bertrand *et al.*  
155 (2008a) analyzed how large-scale oceanic forcing, via Kelvin waves, affected the coastal  
156 ecosystem (from oceanography to fishermen). They pioneered the incorporation of fishermen as a  
157 top predator for studying ecological dynamics and proposed contrasting scenarios of coastal  
158 oceanography, anchovy distribution and fishing activity, during the passage of coastally trapped  
159 upwelling and downwelling Kelvin waves.

160  
161 The present work focuses more closely on the coastal processes in the NHCS, and on the  
162 spatial response of fishermen to varying environmental and anchovy conditions. In particular, we  
163 explore and quantify the associations between the dynamics of three ecosystem compartments:  
164 environmental conditions (Environment), anchovy biomass and distribution (Anchovy) and  
165 fishermen spatial behavior (Fishermen), for a ten-year period (2000-2009). Data on Environment  
166 and Anchovy were obtained from acoustic surveys performed by IMARPE and satellite  
167 observations. Data on Fishermen were based on VMS data (~90000 fishing trips from 2000 to  
168 2009), processed with a state-space model so that the nature of the behavior in which fishermen  
169 are engaged is known at each position (Joo *et al.*, 2013). The existent evidence of bottom-up  
170 forcing in the NHCS (Ayón *et al.*, 2008; Bertrand *et al.*, 2008a) indicates that strong Environment-  
171 Anchovy and Anchovy-Fishermen associations should be expected. Since Fishermen have shown  
172 similar spatial foraging strategies to those of other predators (Bertrand *et al.*, 2007), we  
173 hypothesize that – as for other predators – their spatial behavior responds to prey and  
174 environmental conditions. Then, significant Environment-Fishermen associations are expected,  
175 though not as strong as for Anchovy and Fishermen (direct prey-predator relationship). The studied  
176 decade does not encompass strong ENSO (El Niño Southern Oscillation) events. Season is thus

177 expected to be the main scale of variability for environmental conditions. We tested for differences  
 178 between two seasonal modes, summer and spring/winter, within each ecological compartment and  
 179 analyzed trends separately for each seasonal mode. We eventually propose ecosystem scenarios  
 180 based on the linkages evidenced between the three compartments and discuss the potential use of  
 181 fishermen spatial behavior as ecosystem indicator.

## 183 2. Materials and Methods

184  
 185 We focused on several time-periods from 2000 to 2009 such that concomitant data on the  
 186 environment, fisheries acoustic and VMS were available. In total, 16 time-periods were  
 187 available, 6 in austral summer and 10 in austral winter/spring (Table 1). Since only one value  
 188 per time-period was obtained for each Anchovy descriptor, one representative value per time-  
 189 period was computed for each Environment and Fishermen descriptor. This measure allowed  
 190 for multivariate analyses involving the three compartments.

### 192 2.1. Environmental data

193  
 194 For each time-period, we produced a description of the environment as detailed in Table 2.  
 195 We used sea surface temperature (SST) from the AVHRR sensor of NOAA satellites from 2000 to  
 196 2009. The chlorophyll-a (CHL) satellite data from 2000 to 2007 were obtained from the SeaWiFS  
 197 sensor and from 2008 to 2009 from the MODIS sensor. In order to correct the MODIS CHL data  
 198 from significant departures from the better calibrated SeaWiFS sensor, the seasonal and spatial  
 199 differences were previously computed during the common period between both sensors (2003-  
 200 2007) and then applied to the 2008-2009 MODIS data. All satellite data, initially at a spatial  
 201 resolution of 4 km and a weekly time resolution, were averaged the entire time period and the  
 202 whole study area (from 3°S to 16°S and from the shore up to the 2500 m isobath) to obtain one  
 203 representative value per time-period (Table 1).

204  
 205 To account for the vertical distribution of the oxygen minimum zone (OMZ), a critical  
 206 parameter of the NHCS (Bertrand *et al.*, 2011), we computed the depth of the oxycline (OXY), i.e.  
 207 the depth at which the dissolved oxygen equals 2 mL L<sup>-1</sup>. All measurements were made from  
 208 Niskin bottles and CTD data sampled during IMARPE scientific surveys. For each time-period, the  
 209 mean oxycline depth was computed as a weighted average of monthly values, taking into account  
 210 the number of observations per month. Those observations correspond to a latitudinal range  
 211 between 7°S and 16°S. A sharp change in oxygen concentration and oxygen minimum zone  
 212 intensity occurs at ca. 7°S (Fuenzalida *et al.*, 2009; Bertrand *et al.*, 2010). North of 7°S the intensity  
 213 of the OMZ is highly variable and depends on the dynamics of Tropical/Equatorial water masses.

214 The range 7°S - 16°S provides a more robust proxy of oxygen condition where most of the  
 215 anchovy is distributed (i.e. not in Tropical/Equatorial water masses).

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## 217 2.2. Anchovy data

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Since 1983, IMARPE has been conducting on average two acoustic surveys per year to monitor fish population distribution and biomass. These surveys consist of parallel cross-shore transects of ~100 nm long, with a ~15 nm inter-transect spacing. Simrad (Kongsberg Maritime AS, Norway) scientific echosounders working at several frequencies are used to estimate biomasses (see Gutiérrez *et al.*, 2007; Castillo *et al.*, 2009; Simmonds *et al.*, 2009). An extensive midwater-trawl sampling completes the acoustic surveys for species identification. The nautical-area-backscattering coefficient (NASC, in  $\text{m}^2 \text{mn}^{-2}$ ), an index of fish biomass (Simmonds and MacLennan, 2005), is recorded at each georeferenced elementary distance sampling unit (EDSU) of 1 nm. From each acoustic survey, we extracted five descriptors of the spatial distribution of anchovy (Table 2): (i) the mean anchovy NASC, used as an index of fish biomass ( $s_A$ ); (ii) an index of local biomass ( $s_{A+}$ ), i.e. the mean anchovy NASC for the set of ESDUs with non-zero fish biomass; (iii) an index of spatial occupation (ISO), i.e. the percentage of ESDU with anchovy; and (iv) the center of gravity and the inertia of the distance to the coast of anchovy NASC (DC and I, respectively).

## 234 2.3. Fishermen spatial behavior

The pelagic fishery in the NHCS is mono-specific, since anchovy represents 95% of the total catches (Fréon *et al.*, 2008). The anchovy fishing trips, which exclusively aim at fishing anchovy, constitute the world's largest mono-specific fishery (average annual catch of 6.8 millions of tonnes between 2000 and 2011; FAO, 2013). The fishing activity in the NHCS is monitored by IMARPE through landing statistics, VMS and on-board observers' data. Since 2000, VMS records precise geographical positions once an hour for the entire industrial fleet. Only fishing trips from the industrial fleet along the north-center (3°S-16°S) Peruvian coast were considered for the analysis (the southern region was excluded because of its lesser contribution to the catches and a different management policy). We report in Table 1 the number of fishing trips documented for each time-period.

Pre-processing of VMS data was performed as described in Bertrand *et al.* (2005, 2007) and Joo *et al.* (2011). We identified positions at sea or at port based on their distance to the nearest port and their speed. We considered each series of consecutive positions at sea as a trip. To select fishing trips only, we excluded trips with a minimum speed greater than 3 knots (indicating the impossibility of fishing activity). To exclude the few trips targeting other pelagic species (e.g.



252 jack mackerel), trips from vessels with fishing authorization for multiple species and lasting more  
 253 than 5 days were not considered (anchovy fishing trips typically last ~24 hours).

254  
 255 Eventually, for each fishing trip, the following global indicators were computed: the duration  
 256 (Dur), the total distance traveled (Dist) and the maximum distance from the coast (Max.DC).  
 257 Additionally, we used two metrics,  $k$  and  $\sigma$ , that characterize the geometry of the fishermen  
 258 movements (Bertrand *et al.*, in review). They are derived from the fit of a Generalized Pareto  
 259 random walk model to the move-length distribution displayed by fishing trip trajectories. This  
 260 random walk model involves two parameters of interest: a shape parameter  $k$  which characterizes  
 261 the movement diffusion (finite and light tails with normal diffusion patterns for  $k < 0$ , and  $k$  between 0  
 262 and 0.5, respectively, and heavy tails with super diffusion patterns for  $k > 0.5$ ), and a scale  
 263 parameter  $\sigma$  (where  $\sigma > 0$ ) which relates to the average length of the moves used to  
 264 search for fish. Super diffusion is characterized by the mixing of rare, long and relatively straight  
 265 movements with movement bouts composed of short moves and high turning rates (Dubkov *et al.*,  
 266 2008). Metrics  $k$  and  $\sigma$  were computed for each vessel from the fishing trips performed within  
 267 each time-period.

268  
 269 Another source of information regarding fishing activities comes from the program of on-  
 270 board observers 'Bitácoras de Pesca' deployed by IMARPE. For ~1% of the fishing trips, on-board  
 271 observers record the location and time of three main activities occurring during the trips: fishing,  
 272 searching and cruising. In order to infer the activities for the remaining 99% of the fishing trips, a  
 273 supervised hidden semi-Markov model was trained and validated using the on-board observer  
 274 dataset (Joo *et al.*, 2013). This model reached a mean accuracy of 80% in the determination of the  
 275 correct activities from the VMS data. From the reconstructed sequence of fishing activities, we  
 276 computed four additional features: the proportion of time spent searching (Searching), fishing  
 277 (Fishing) and cruising (Cruising), and the time spent from the beginning of the trip until the first  
 278 fishing set (Bef.Fishing).

279  
 280 For the multivariate analyses, we computed a median per time-period over all fishing  
 281 vessels for each descriptor.

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## 284 2.4. Statistical analyses

285

286 A synoptic sketch of the statistical analyses between the ecosystem compartments is  
 287 reported in Figure 1. After pre-processing the data, univariate statistics were computed for each  
 288 variable to test for differences between seasonal modes and characterize overall tendencies and  
 289 potentially remarkable time-periods. The Wilcoxon rank sum test (Wilcoxon, 1945) was performed

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290 for testing for mean differences between summer and winter/spring periods. This test is one of the  
 291 best non-parametric alternatives to the t-test when its assumptions are not met (at least 95% of  
 292 statistical power compared to the t-test when assumptions are met; Siegel, 1956). Trends were  
 293 computed using least trimmed squares robust regression (Rousseeuw, 1984). It is based on the  
 294 subset of  $h$  observations (out of  $n$ ) whose least squares fit possesses the smallest sum of squared  
 295 residuals. The parameter  $h$  is computed as  $n/2 + (p+1)/2$  (Rousseeuw, 1984), where  $p$  is the number  
 296 of explanatory variables (equal to 1 in our case).

297  
 298 For multivariate analyses, all variables were standardized (Z-scores). Since we first aimed  
 299 at characterizing each compartment and then associations between them, we first carried out a  
 300 Principal Component Analysis (PCA; Pearson, 1901; Husson *et al.*, 2010) for each compartment at  
 301 the scale of the time-periods. These PCAs identify the main modes of variability. For quantifying  
 302 the linear association between the first principal component of Environment, Anchovy and  
 303 Fishermen, we computed Kendall's Tau rank correlation coefficients (Kendall, 1938; Siegel, 1956)  
 304 between each pair of first components. Kendall's Tau was preferred as correlation coefficient since  
 305 it allows computing asymptotically distribution-free confidence intervals (Hollander and Wolfe,  
 306 1999).

307  
 308 In addition to Kendall's tau, the overall association between each pair of compartments  
 309 (Environment and Anchovy, Anchovy and Fishermen, and Environment and Fishermen) was  
 310 analyzed through RV coefficients (Escoufier, 1973). The RV coefficient is a multivariate  
 311 generalization of the squared Pearson correlation coefficient. RV values range between 0 and 1,  
 312 where 0 means no association and 1 means perfect association. Confidence intervals were  
 313 computed using a bootstrap procedure (Claude, 2008) at a 90% confidence level. The significance  
 314 of the RV coefficient was estimated by means of a permutation test (Heo and Gabriel, 1998).

315  
 316 We also performed a multiple coinertia analysis (Chessel and Hanafi, 1996) between the  
 317 three PCAs. This is a multivariate method for coupling  $k$  tables ( $k > 2$ ) sharing the same rows  
 318 (individuals or variables). The tables must be previously analyzed by separate inertia analyses (for  
 319 instance, PCAs). With the multiple coinertia analysis, we aim at resorting a synoptic understanding  
 320 of the three compartments by: (i) calculating a synthetic table representing the common structure  
 321 of the PCAs, and (ii) projecting individuals (i.e. time-periods) and variables from the three  
 322 ecosystem compartments in a common space. Tables are weighted equally for the multiple  
 323 coinertia analysis. Finally, we performed a hierarchical clustering on the scores of the time-periods  
 324 in the synthetic table with a view to discriminating groups of time-periods.

325  
 326 Statistical analyses were performed with R software (R Core Team, 2013). Robustbase  
 327 package (Rousseeuw *et al.*, 2012) was used for least trimmed regression, FactoMineR package

328 (Husson *et al.*, 2013) was used for PCA and ade4 (Dray *et al.*, 2007) for multiple coinertia  
 329 analyses, and the stats package (R Core Team, 2013) for the hierarchical clustering analysis.

### 331 **3. Results**

#### 333 *3.1. Univariate analyses*

334  
 335 Series of environmental conditions are shown in Figure 2a-c. SST and CHL values were  
 336 greater in summer than in winter/spring periods ( $p < 0.001$  for both variables) and exhibited  
 337 increasing trends ( $p < 0.01$  for both variables) on winter/spring periods. The differences in SST and  
 338 CHL between seasons were larger at the first half of the series than at the second half. For OXY no  
 339 significant differences between seasons were observed and no trend was observed either. Still, the  
 340 October - December 2003 time-period (denoted 2003/10-12 hereafter) was characterized by a  
 341 remarkably deep oxycline.

342  
 343 Fish distribution also varied in time (Fig. 2d-h). The  $s_A$  and  $s_{A+}$  indexes differed significantly  
 344 among seasonal modes ( $p < 0.01$ ) and an increasing trend ( $p < 0.01$ ) was observed for  $s_{A+}$  in  
 345 winter/spring periods. Two periods presenting the greatest  $s_A$  (and  $s_{A+}$ ) values lied out of the  
 346 general trend: 2008/02-04 and 2002/02-03. The former period, 2008/02-04, along with 2003/10-12,  
 347 were also characterized by the lowest ISO. Finally, 2000/06-07, 2000/10-11 and 2001/10-11 had  
 348 the greatest DC and I features.

349  
 350 Since hundreds of fishing trips were comprised in each time-period (Table 1), we analyzed  
 351 the temporal evolution of both the median values and the distribution of each Fishermen variable.  
 352 In order to facilitate visualization, the values associated with the greatest occurrences are shown in  
 353 Figure 3. The complete range of values is available in Figure A.1 in Appendix A.

354  
 355 Only Cruising showed significant differences between seasonal modes ( $p < 0.01$ ). Therefore,  
 356 for Fishermen variables robust trends were computed for the whole series without discriminating  
 357 between seasonal modes. Negative trends were observed for Dur, Dist, Bef.Fishing, Cruising and  
 358 sigma ( $p < 0.0001$ ). By contrast, Searching, Fishing and k reported increasing trends ( $p < 0.0001$ ).  
 359 2001/10-11, 2003/10-12 and to a lesser extent 2002/10-11 presented the greatest values for Dur,  
 360 Dist, Max.DC, Bef.Fishing and Cruising, and 2001/10-11 and 2003/10-12 presented the greatest  
 361 variability for Dur, Dist, Max.DC, Bef.Fishing (cf. distributions in Fig. 3a,b,c,d). Conversely, in  
 362 2002/02-03, Dist, Max.DC, Bef.Fishing and Cruising were low and Fishing was high.

#### 364 *3.2 Multivariate Analyses*

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366 Significant correlations between variables and principal components are shown in Table 3.

367 We also present the scores of each time-period for the first principal components (Fig. 4).

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### 369 3.2.1. Environmental conditions

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In the Environment PCA, the first principal component, which accounted for 75% of the variance, was positively correlated with CHL and SST, and negatively with OXY (Table 3 and Fig. A.2 in Appendix A). These relations mainly refer to the seasonal cycles. During summer, waters are warmer (greater SST values), and due to a reduced cloud cover, more light penetrates into the water column, what positively impacts the productivity at sea (higher CHL; Echevin *et al.*, 2008). The thermocline and oxycline are also shallower during summer (lower OXY; Gutiérrez *et al.*, 2011). The opposite phenomenon occurs during winter. The reported scores reflected the seasonality: all summer periods had greater scores than winter and spring periods (Fig. 4;  $p < 0.001$  for differences in scores between seasonal modes). Nonetheless, the intensity of the seasonality (difference summer – winter/spring) was reduced during the second half of the series. This was accounted for by fitting a linear regression to the scores and computing the sums of squared residuals for the first and second half of the series. Large differences were found (10.9 vs. 1.2, for first and second half, respectively; Table B). The second principal component represented 21% of the variance and was significantly correlated with OXY (Table 3). This component did not reflect a significant seasonality. Although the temporal variability of the oxycline depth is partly related to the seasonal cycle, specific large scale forcing events such as downwelling Kelvin waves can deepen the oxycline (Gutiérrez *et al.*, 2008). Within the studied period, 2003/10-12 and 2007/02-04 had the lowest scores (deepest oxycline depth) for this component (Fig. 4).

### 390 3.2.2. Anchovy distribution

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The first principal component, accounting for 60% of the variance, was positively correlated with  $s_A$  and  $s_{A+}$ , and negatively correlated with DC and I (Table 3 and Figure A.3 in Appendix A). This axis can be interpreted as an index of fish biomass and proximity to the coast. Scores reflected, although with less intensity, the seasonality observed in the first axis of the Environment PCA (Fig. 4;  $p < 0.01$ ). A significant increasing trend over time was observed for this first component ( $p < 0.01$ ) through a linear regression. The second component, explaining 23% of the variance, was significantly correlated to ISO (Table 3). It can be seen as fish evenness, and it should be interpreted considering the scenarios in terms of  $s_A$ ,  $s_{A+}$  and DC: high evenness is favorable to fishermen activity if the global biomass is high, since there is lot of anchovy everywhere. On the opposite, if the biomass is low, a high evenness means highly dispersed anchovy (low  $s_{A+}$ ), which are difficult to catch (Bertrand *et al.*, 2004b). The latter scenario corresponds to 2003/10-12, which had by far the lowest score (Fig. 4).

404

## 405 3.2.3. Fishermen spatial behavior

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408 Due to the relatively large number of variables for a small number of individuals, we

409 discarded from the multivariate analyses the variables presenting very strong correlations ( $r > 0.9$ ;

410 i.e. Dist., Bef.Fishing and Dur, all of them strongly correlated with Cruising). We also discarded

411 Searching since the proportions of the time spent Cruising, Fishing and Searching sum to one (no

412 variable should be expressed as a linear combination of others). Overall, we used Max.DC,

413 Fishing, Cruising,  $k$  and  $\sigma$ . The other variables were still used as supplementary variables and

414 projected in the PCA space (Fig. A.4 in Appendix A). The first principal component, explaining 71%

415 of the variance (Table 3), refers to fishermen activity budget, which indicates the investment in

416 energy and time necessary for their activities (Altmann, 1974; Defler, 1995). High values on this

417 activity budget axis correspond to 'cheap foraging' (more time is allocated to searching and fishing

418 than to cruising), while low values indicate 'expensive foraging' (more time is dedicated to cruising,

419 longer distances are traveled, more time is spent before the first fishing set, farther distances from

420 the coast are traveled). Scores showed an increasing linear trend (towards 'cheap foraging') with

421 time ( $p < 0.0001$ ; Fig. 4). Those scores are coherent with the overall increasing 'efficiency' shown by

422 the fishermen through the years (i.e., increasing trend in daily catches and decreasing trend in the

423 number of fishing days until the quota was filled, until the individual vessel quota system was

424 established; IMARPE, 2013). The second principal component (not shown) accounted for 23% of

425 the variance (Table 3). It had significant correlations with only two variables ( $k$  and Max.DC) and

426

## 427 3.2.4. Environment vs. Anchovy vs. Fishermen

428

429 Regarding the association between the first principal components only, the activity budget

430 component of Fishermen PCA was strongly correlated with the fish biomass and proximity

431 component of Anchovy PCA ( $0.65 \pm 0.20$ ;  $p < 0.001$ ). The latter was also correlated with the432 seasonal cycle component of Environment PCA ( $0.68 \pm 0.18$ ;  $p < 0.0001$ ). Likewise, the seasonal433 cycle was positively correlated with activity budget ( $0.60 \pm 0.25$ ;  $p < 0.001$ ). However, none of these

434 correlations is statistically greater than the others, since their confidence intervals overlap. The

435 three RV coefficients were also strong, i.e. Environment and Anchovy ( $0.61$ ;  $p < 0.001$ ), Anchovy436 and Fishermen ( $0.63$ ;  $p < 0.001$ ) and Environment and Fishermen ( $0.56$ ;  $p < 0.01$ ). Their 90%437 confidence intervals overlapped:  $\langle 0.28, 0.65 \rangle$ ,  $\langle 0.37, 0.63 \rangle$  and  $\langle 0.29, 0.59 \rangle$ , for Environment and

438 Anchovy, Anchovy and Fishermen, and Environment and Fishermen, respectively. Nevertheless,

439 those significant associations provide a powerful way to quantify the strength of the relationships

440 between the ecosystem compartments.

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442 A multiple coinertia analysis was applied to Environment, Anchovy and Fishermen PCAs  
 443 (Fig. 5; Table 4). The multiple coinertia space was composed of two axes, accounting for 73% and  
 444 17% of the variance each. The interpretation of the graphical projection of the variables on the  
 445 coinertia space (Fig. 5; left panel) is analogous to that on a PCA space (see Fig. A.2, A.3, A.4 in  
 446 Appendix A). High SST and CHL values were strongly related to high  $s_A$  (local biomass), high  
 447 Fishing, low Cruising, low DC and I (distance from the coast of anchovy and its inertia). To a lesser  
 448 extent, high SST and CHL were also related to high  $s_A$  and low Max.DC (distance to the coast of  
 449 fishermen). Deep oxycline (OXY) was partly associated with low  $s_A$  and ISO (anchovy spatial  
 450 occupation), and high Max.DC. Low ISO was also associated with high k (diffusivity of fishermen  
 451 movements).

452  
 453 Regarding the time-periods, a hierarchical clustering analysis was performed. Based on the  
 454 computed dendrogram (Fig. A.5 in Appendix A) and the explained variance (i.e. the percentage of  
 455 total variance represented by the between-cluster variance; Husson *et al.* 2010; Table A.2 in  
 456 Appendix A), the 4-cluster structure, which accounted for 80% of the explained variance, was  
 457 retained. The time-periods that correspond to each cluster are represented by distinct colors in  
 458 Figure 5 (right panel). Because of the great variability within each cluster, we characterized only  
 459 one time-period per cluster. We chose the ones that stood out in the preceding analyses: 2008/02-  
 460 04, 2002/02-03, 2003/10-12 (the only period in its cluster) and 2001/10-11. 2002/02-03 was  
 461 characterized by a superficial OXY, very large ISO and  $s_A$  values, and to a lesser extent, high SST,  
 462 CHL,  $s_A$  and Fishing values. 2008/02-04 was characterized by the greatest SST, CHL,  $s_A$  and  
 463 Fishing, and low DC, I, Cruising and Max.DC values. 2003/10-12, on the contrary, corresponded to  
 464 the deepest OXY, the lowest ISO, low  $s_A$ , the highest Cruising, high Max.DC and k. 2001/10-11  
 465 corresponded to the lowest SST, the highest I, a very high ISO, the highest Max.DC and low  
 466 Fishing.

## 4. Discussion

### 4.1 *Environment, Anchovy, Fishermen and the bottom-up transfer*

473 In this study, we explored and quantified the associations between the dynamics of three  
 474 ecosystem compartments (Environment, Anchovy and Fishermen) and showed that ecosystem  
 475 scenarios – abiotic and biotic conditions – do shape fishing spatial behavior. Most of the existent  
 476 literature in fisheries deduces fish abundance and distribution from catchability indicators, making  
 477 the implicit assumption that fishing effort reflects fish conditions. Only a few works have studied the  
 478 actual relationships between the patterns of fisheries and their target species (e.g., Hancock *et al.*,  
 479 1995; Bertrand *et al.*, 2004b, 2005, 2008b). Here, we used a richer dataset in terms of the amounts

480 of data - 16 concomitant fishing seasons and scientific acoustic surveys – and in the nature of the  
481 variables used. To cope with the uncertainties and complexities related to data from different  
482 sources, sampling methods and scales, the analyses were kept as simple as possible: the scale of  
483 analysis was constrained by the lowest resolution of the available data and exploratory methods  
484 were used.

485  
486 A major drawback related to our dataset – as mentioned above – is that we did not have  
487 both summer and winter/spring periods for all years. Moreover, winter/spring periods did not  
488 always comprise the same months (e.g., 06-07 and 10-11). Therefore, the trends fitted should only  
489 be used for interpreting the variations experienced during the studied time-periods; not as  
490 increasing SST and CHL trends for the whole 2000-2009 decade. When compared with complete  
491 monthly 2000-2009 series, no linear trend in winter was found for SST nor CHL. However, we did  
492 find a reduction in the intensity of the seasonality in the second half of the decade, observed in Fig.  
493 2a-b and Fig. 4.

494  
495 Regarding the associations between ecosystem compartments, the three pairwise  
496 associations were statistically significant. Concerning point estimates, Environment-Anchovy and  
497 Anchovy-Fishermen links were the strongest compared with the least direct one (Environment-  
498 Fishermen) whatever the metric considered (RV and Kendall's tau). We cannot conclude on the  
499 superiority of the direct links since the confidence intervals overlapped. The computation of  
500 confidence intervals was strongly penalized by the low number of observations (Hollander and  
501 Wolfer, 1999). Gathering data from more time-periods could contribute to reduce confidence  
502 intervals and improve correlation estimates.

503  
504 Nevertheless, our findings are consistent with a bottom-up transfer that was already  
505 evidenced by Bertrand *et al.* (2008a) when analyzing the effect of upwelling and downwelling  
506 Kelvin waves on several descriptors of the Peruvian coastal oceanography, anchovy distribution  
507 and fishing fleet behavior. They characterized contrasting ecological scenarios that corresponded  
508 to strong El Niño events (warm scenarios) and to average upwelling periods (cold scenarios).

509  
510 Unlike Bertrand *et al.* (2008a), we focus on the coastal processes of the NHCS, and our  
511 studied period, 2000-2009, does not encompass strong El Niño events, but only 'weak' events  
512 (2002-03, 2004-05 and 2009-10). These events correspond to 'El Niño Modoki' or 'Central Pacific  
513 El Niño' that are distinct from the extraordinary warm events such as the ones from 1982-83 and  
514 1997-98 (Takahashi *et al.*, 2011). When Central Pacific El Niño occurs, the conditions off Peru can  
515 even be slightly cooler than average (Dewitte *et al.*, 2012), far from the archetypal El Niño effects  
516 on the Peruvian ecosystem (Barber and Chavez, 1983; Alheit and Ñiquen, 2004; Bertrand *et al.*,  
517 2004a, Ñiquen and Bouchon, 2004). The studied period therefore lies within the dominant

518 ecosystem state corresponding to an average 'upwelling dominant scenario' without extreme El  
519 Niño events (Bertrand *et al.*, 2008a). Indeed, 'El Niño Modoki' did not show to impact on fishermen  
520 behavior. In this context, the seasonal scale becomes the scale of greatest environmental  
521 variability.

522  
523 An important contribution of our work concerns the Fishermen compartment. Based on  
524 statistics computed from an unprecedented rich dataset (spatially-explicit data from ~90000 fishing  
525 trips), we showed that Fishermen spatial behavior could be seen as a function of anchovy biomass  
526 and distribution, and environmental conditions. Fishermen-Anchovy association (RV=0.63)  
527 suggested that, despite the available technology and all the economic drivers involved in fishermen  
528 behavior, uncertainty on prey location is a major driver of their spatial behavior. This finding  
529 supports the evidence that fishermen deploy spatial foraging strategies comparable to that of other  
530 animal predators (Bertrand *et al.*, 2007). Fishermen-Environment association was not at all  
531 despicable (RV=0.56), showing that fishermen behavior is sensitive to changes in environmental  
532 conditions, most likely through transfer via Anchovy (RV=0.61 for Environment-Anchovy). The  
533 association between Environment and Fishermen is regarded as an indirect link, since Fishermen  
534 are not directly shaped by the Environment: SST, CHL and OXY only affect Fishermen through  
535 their effects on anchovy biomass and distribution. Moreover, in the NHCS off Peru, there are no  
536 extreme weather conditions that could affect fishermen tactics and strategies directly.

537  
538 Looking closely at the trends of the first principal components (Fig. 4), the strong  
539 seasonality observed for Environment (seasonal cycle component) is less pronounced for Anchovy  
540 (fish biomass and proximity) and almost unnoticeable for Fishermen (activity budget). Conversely,  
541 the marked increasing trend observed for Fishermen, seemed to be occluded for Anchovy and then  
542 for Environment by the seasonal variability. These results are regarded as empirical evidence of  
543 high-frequency environmental variations being smoothed out through trophic levels (Mann and  
544 Lazier, 2006; Di Lorenzo and Ohman, 2013). Future studies based on the analysis of longer time  
545 series, with more regularly-sampled time-periods (with at least one winter and one spring/summer  
546 period per year), could provide a definitive statistical demonstration of this result.

547  
548 How environmental fluctuations influence population dynamics and animal behavior are  
549 questions that have been examined in several studies. McManus and Woodson (2012) showed  
550 that the more organism size and motility increase, the weaker are the relations between organism  
551 behavior and physical processes. Other studies (e.g. Miramontes and Rohani, 1998; Petchey,  
552 2000; Greenman and Benton, 2003) showed transfer of environmental variability in *ex situ* and  
553 theoretical populations. Rouyer *et al.* (2012) showed, using empirical data, that mortality of larger  
554 fish lead to more prevalent short-term fluctuations in fish populations. However, to our knowledge,  
555 no work had shown empirical evidences of smoothed out transfer through several ecosystem



556 compartments, from the environment to top predators. Here we provide – for the first time –  
 557 empirical evidence of (1) bottom-up and smoothed out transfer of the high-frequency  
 558 environmental fluctuations through the main compartments of an ecosystem (i.e. seasonal effect  
 559 through Environment-Anchovy-Fishermen); and (2) magnification of low-frequency fluctuations by  
 560 trophic transfer (i.e. magnified temporal trends through Fishermen-Anchovy-Environment).  
 561 Furthermore, after the first half of the time-series, the scores of the first component of Environment  
 562 and, to a lesser extent, Anchovy and then Fishermen, showed a weaker variability though  
 563 continued showing a positive trend (Fig. 4). For each compartment, the variability – computed as  
 564 the sum of squared residuals from a fitted linear regression – was greater during the first half of the  
 565 studied series than after (Table A.3 in Appendix A). Moreover, variability values decreased when  
 566 rising into the ecological levels.

#### 568 4.2 Fishermen response to ecosystem scenarios

569  
 570 Based on the statistical analyses, we identified four ecosystem scenarios (Fig. 6). Each  
 571 scenario involved a distinct cluster in the coinertia space (Fig. 5, right panel). The first two  
 572 scenarios corresponded to favorable ecosystem conditions and are associated with the time-  
 573 periods 2002/02-03 and 2008/02-04 while the third and fourth are less favorable and can be  
 574 illustrated by the time-periods 2003/10-12 and 2001/10-11. Here, we analyze and discuss those  
 575 scenarios taking into account that changes in biomass of organisms and in environmental  
 576 conditions are not always simultaneous. Whereas unfavorable environmental conditions can trigger  
 577 mortality and translate into low biomass almost instantaneously, favorable environmental  
 578 conditions will affect recruitment, producing increased population biomass with delay. By contrast,  
 579 patterns of geographic distribution or organism movements may adjust rapidly to physical forcing  
 580 (Bertrand *et al.*, 2008a).

##### 582 4.2.1 The favorable scenarios

583  
 584 Scenarios I and II (Fig. 6, upper panels), illustrated by the time-periods 2002/02-03 and  
 585 2008/02-04, were characterized by relatively high SST (relatively to the range of temperatures  
 586 encompassed in our dataset), high primary production and a shallow oxycline. Under both  
 587 scenarios, anchovy was abundant and close to the coast. High SST and CHL values characterized  
 588 productive summertime conditions (Echevin *et al.*, 2008; Gutiérrez *et al.*, 2011) with cold coastal  
 589 waters close to the coast that favored locally-concentrated anchovy biomass (Gutiérrez *et al.*,  
 590 2007; Swartzman *et al.*, 2008). Evidence of negative relation between anchovy acoustic biomass  
 591 and oxycline depth was also shown by Bertrand *et al.* (2011). They suggested that anchovy is  
 592 capable of surviving in areas where the oxygen minimum zone is very shallow, where they escape  
 593 from predation by larger fish that need more oxygen, and forage on prey concentrated over a thin

594 surface layer. The two scenarios described above represent favorable conditions for fishermen  
 595 because fish is easily catchable. Overall, fishermen had an efficient activity budget: more time was  
 596 spent fishing rather than cruising and vessels did not need to go far from the coast. Nevertheless,  
 597 in 2008/02-04 (Fig. 6, right-upper panel), local biomass was higher, and highly concentrated near  
 598 the coast. Compared to 2002/02-03, this scenario was even more favorable for fishermen not only  
 599 in terms of activity budget but also in terms of movement geometry. Strong patchiness of anchovy  
 600 led to more diffusive spatial behavior of fishermen (Bertrand *et al.*, 2005, 2007). Since anchovy  
 601 patches were very close to the coast, fishermen did not need to go far to fish, so the average  
 602 length of the moves was very small. Because fish was very close and highly patchy, only a small  
 603 proportion of time was spent cruising; most of the time they were searching and fishing (Fig. 3).  
 604 That translated into movements composed of a large proportion of small moves (searching  
 605 behavior within fish aggregation) and a small proportion of large moves (straight transit between  
 606 port and anchovy aggregation), creating a super diffusive, Lévy-like movement (Codling *et al.*,  
 607 2008).

608  
 609 Conversely, in 2002/02-03 (Fig. 6, left-upper panel) anchovy was spread over more space  
 610 and exhibited a lower local biomass than in 2008/02-04. That meant that, in spite of the overall  
 611 availability of anchovy, it was not very patchy so it pushed fishermen to visit more patches to fill the  
 612 vessel hold. Thus, the relationship rare-large-moves vs. numerous-small-moves was not observed;  
 613 instead moves were about the same length, producing a normally diffusive movement.  
 614 Nonetheless, fish was close to the coast, so the average length of the moves was small.

#### 615 616 4.2.2 The unfavorable scenarios

617  
 618 Scenarios III and IV (Fig. 6, lower panels), illustrated by the time-periods 2003/10-12 and  
 619 2001/10-11, were characterized by relatively low SST (relatively to the range of temperatures  
 620 encompassed by our dataset), low primary production and deep oxycline. In both scenarios,  
 621 anchovy was scarce. Low SST and CHL characterized winter conditions (Echevin *et al.*, 2008;  
 622 Gutiérrez *et al.*, 2011), associated to low local biomass (Gutiérrez *et al.*, 2007).

623  
 624 2003/10-12 was the only member of its cluster, indicating it was an extreme scenario  
 625 among the ones analyzed in this work. In 2003/10-12, the extent of cold coastal upwelling waters  
 626 was very limited, and so was anchovy habitat (Bertrand *et al.*, 2004a; Swartzman *et al.*, 2008),  
 627 explaining the lowest ISO of the series. Although anchovy was not too far from the coast, it was  
 628 very scarce (the lowest  $s_A$  value of the series), concentrated in very few spots and most likely deep  
 629 (since oxycline was remarkably deep). This corresponded to an adverse scenario for fishermen.  
 630 For starters, fishermen went far from the coast and made fishing trips that lasted longer (Fig. 3)  
 631 due to the scarceness of anchovy and the difficulty to find them. They spent most of the time

632 cruising, and low time searching and fishing. Since the scarce anchovy was concentrated (low  
 633 ISO), this led to super diffusive movements (less diffusive than in Scenario II). Fishermen made  
 634 few large moves – 'large' compared to the 'small' ones – looking for a zone they presumed to be of  
 635 high prey density, and many small moves within these zones trying to find attractive densities of  
 636 prey to fish. Since fishermen went far from the coast looking for fish, the average length of moves  
 637 (large and small altogether) was higher than in Scenario II.

638  
 639 In 2001/10-11, the extent of cold coastal upwelling waters was high, and so was the area  
 640 occupied by anchovy (Bertrand *et al.*, 2004a; Swartzman *et al.*, 2008). Anchovy distribution was  
 641 even but extended very far from the coast in the form of sparse aggregations. This was a difficult  
 642 scenario for fishermen too, mostly expressed through the high variability in their behavior (the  
 643 highest variability in most Fishermen variables; Fig. 3 and Fig. A.1 in Appendix A). In general,  
 644 fishermen went farther from the coast looking for prey. Because scarce anchovy was distributed in  
 645 many ESDUs, close and far from the coast, fishermen seemed to use normally diffusive  
 646 movements, moving constantly between aggregations of dispersed anchovy. That spatial behavior  
 647 produces inefficient activity budgets, since most of the time at sea was spent cruising between  
 648 aggregations and going far from the coast, rather than fishing/searching. Moreover and as a  
 649 consequence, the average length of the moves was larger.

650  
 651 It should be stressed that both unfavorable scenarios presented the greatest variability in  
 652 fishermen spatial behavior among all the studied periods (greater in 2001/10-11 than in 2003/10-  
 653 12; Fig. 3 and Fig. A.6 in Appendix A). It may evidence that in scenarios of high accessibility to  
 654 prey, fishermen act more homogeneously, as it is easy for everyone to find fish and to catch it. But  
 655 when conditions are difficult, each fisherman manages risks differently, and personal strategies  
 656 count more. This type of behavior is likely to be enhanced in El Niño/La Niña conditions, for which  
 657 a similar scenario-based analysis would be appealing.

#### 658 659 660 *4.3 Fishermen behavior and ecosystem approach to fisheries*

661  
 662 This work provides a better understanding of how changes in environment and prey  
 663 conditions shape fishermen behavior. We call it spatio-temporal or spatial behavior because it is  
 664 characterized by spatial and temporal descriptors of fishing trips (e.g. distance traveled, maximum  
 665 distance to the coast, duration of the fishing trip, time spent cruising, fishing, etc.).

666  
 667 As stated by Boyd *et al.* (2004), we intuitively think in terms of space and time dimensions  
 668 partly because these are the easiest to measure but there are many other dimensions that  
 669 characterize an animal's – or in this case human's – state. Some other variables may explain an

670 important part of the behavioral variability, such as the vessel holding capacity, the personality of  
 671 the captain, oil and fish meal prices, technology improvements, government management  
 672 measures for specific seasons, company strategies and tactics (i.e. how many vessels to deploy  
 673 each day and in which zones, at which factories to land the fish), the degree of competition or  
 674 cooperation between fishing vessels. Taking into account these other variables would improve our  
 675 understanding of fishermen behavior, which is under the joint influence of economics, politics,  
 676 oceanographic and biological conditions (Wilen, 2004). A remaining challenge is the  
 677 characterization of the collective behavior, since we always consider all fishing trips as  
 678 independent from the others (the same approach is usually taken in animal behavior; Boyd *et al.*,  
 679 2004). Despite we did not consider all these potential factors, we have shown that prey availability  
 680 and environmental conditions already play a great and significant role in shaping fishermen  
 681 behavior, at least at the scale of average characteristics of fishing trips during two or three months  
 682 periods.

683  
 684 In synthesis, this study showed how ecosystem scenarios shape fishermen spatial  
 685 behavior. We also provided empirical evidences of bottom-up and smoothed out transfer of the  
 686 high-frequency environmental fluctuations and magnification of low-frequency fluctuations along  
 687 the ecosystem compartments. Top predators are increasingly seen as integrators of the state of the  
 688 ecosystem they inhabit (Boyd *et al.*, 2006). In the need for information to support the ecosystem  
 689 approach to fisheries (EAF; Browman and Stergiou, 2004; Garcia and Cochrane, 2005; Jennings,  
 690 2005), top predators could be used as indicators of the ecosystem they inhabit. Because  
 691 ecosystems are spatially heterogeneous, and spatial patterns and processes are important to  
 692 ecosystem structure and function (Babcock *et al.*, 2005), indicators on top predators should be  
 693 spatially explicit for accounting for the spatial variations in the ecosystem. Here we have used  
 694 spatially explicit descriptors on fishermen behavior. In the bottom-up dynamics we described, the  
 695 first Fishermen component (i.e. activity budget) was significantly associated with the first  
 696 components of Anchovy and Environment, and the ecological implications of these associations in  
 697 several ecosystem scenarios were described previously. Therefore, fishermen PCA scores could  
 698 be considered for use as ecosystem indicators of ecosystem scenarios. Interestingly, two specific  
 699 fishermen movement characteristic features, namely Max.DC and k, might provide complementary  
 700 characterization of the main variations on the other ecosystem compartments. However, to test for  
 701 the robustness of such indicators it is necessary to rely on larger time series. Besides, strong El  
 702 Niño events should be encompassed to cope with scales of variability in the NHCS that have not  
 703 been included in the studied period. Larger time series would also allow detecting reference points  
 704 for the statistical discrimination between ecosystem scenarios.

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706 The pertinence of ecosystem indicators have been commonly examined through  
 707 multivariate methods (e.g. Link *et al.*, 2002 and 2010) or through the discussion on their pertinence  
 708 for effective management (Jennings, 2005). The use of a model – for instance, simplified food-web  
 709 models (Plitzko *et al.*, 2012) could be a complementary approach to check the sensibility of data-  
 710 constructed indicators. Those models would require several assumptions on relationships between  
 711 the considered ecosystem compartments and other predator-prey relationships that have not been  
 712 accounted for in this study. The interactions between fishermen; other top-predators competing for  
 713 the same prey (e.g. seabirds and mammals; Bertrand *et al.*, 2012) and ecosystem scenarios  
 714 (Pikitch *et al.*, 2004; Hooker *et al.*, 2011) should also be understood for implementing conservation  
 715 plans and EAF management. For that reason, spatio-temporal data on top predators, including  
 716 fishermen, are key for fisheries ecology and sustainable management of the fisheries (Hinz *et al.*,  
 717 2013).

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 961 **Appendices**

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 963 Appendix A. Supplementary figures and tables for the analyses.

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 967 **Figure captions.**

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 969 Figure 1. Synoptic sketch of the statistical analyses.

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971 Figure 2. Univariate series of Environment and Anchovy variables: sea surface temperature or SST  
 972 (a), chlorophyll-a or CHL (b), oxycline depth or OXY (c), global biomass or  $s_A$  (d), local biomass or  
 973  $s_A^+$  (e), index of spatial occupation or ISO (f), center of gravity of distance from the coast or DC (g),  
 974 inertia of DC or I (h). Blue points correspond to winter/spring time-periods, and red points  
 975 correspond to summer periods. Blue dashed lines indicate the significant winter/spring trends.  
 976 Here, the time-periods at the x axes are plotted at regular steps, but the trends were actually fitted  
 977 considering the real intervals between time-periods. Standard deviations of Environment variables  
 978 are shown in Appendix A, Table A.1.

979  
 980 Figure 3. Marginal distributions and median by time-period for each Fishermen variable: fishing trip  
 981 duration (a), distance traveled (b), maximum distance from the coast (c), absolute time from the  
 982 beginning of the trip until the first fishing set (d), proportion of trip duration spent searching (e),  
 983 proportion of trip duration spent fishing (f), proportion of trip duration spent cruising (g), shape  
 984 parameter from random walk modeling (h), scale parameter from random walk modeling (i). In  
 985 each subplot, the colors relate to the marginal distribution of the corresponding variable at each  
 986 time-period (i.e. column). Therefore, colors represent values between 0 and 1. Each colorbar is  
 987 bounded by the minimum and the maximum value of the marginal distributions comprised in the  
 988 subplot. Blue solid lines indicate significant trends ( $p < 0.01$ ) over the whole studied period. Here,  
 989 the time-periods at the x axes are plotted at regular steps, but the trends were actually fitted  
 990 considering the real intervals between time-periods. Complete ranges of values are shown in  
 991 Appendix A; here, the values associated with the highest marginal distributions are shown.

992  
 993 Figure 4. Time series of PCA scores for each ecosystem compartment. Percentage of explained  
 994 variance are in parentheses at the top of each subplot. Red points correspond to summer time-  
 995 periods and blue points to winter and spring periods. At the right side of each subplot, a label is  
 996 given to each principal component. (+) and (-) symbols indicate favorable and unfavorable  
 997 conditions for Fishermen, respectively. \*Oxycline depth follows the seasonal cycling. But some  
 998 specific events such as downwelling Kelvin wave could deepen the oxycline. \*\*This component is  
 999 only useful when comparing similar scenarios in terms of  $s_A$ ,  $s_A^+$  and DC.

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 1001  
 1002 Figure 5. Multiple coinertia analysis between Environment, Anchovy and Fishermen compartments.  
 1003 Left panel: projection of variables in the coinertia space. The definition of each variable is given in  
 1004 Table 2. Fishermen variables are in black, Anchovy in blue and Environment in red. Right panel:  
 1005 projection of time-periods in the coinertia space. Each period has three associated points,  
 1006 corresponding to the position of the period described by each compartment. The position of the  
 1007 label of each period corresponds to its location according to the synthetic table. Roman numerals  
 1008 and colors indicate the different clusters of time-periods.

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1010 Figure 6. Idealized 3D representation of the ecological conditions in scenarios I (2002/02-03), II  
1011 (2008/02-04), III (2003/10-12) and IV (2001/10-11).

1012 The sun or clouds and their size represent the amount of SST which for this study. Tones of blue-  
1013 green color represent the amount of chlorophyll-a. Spots in dark yellow and red represent anchovy  
1014 aggregations; the level of local aggregation is proportional to the darkness of the red color. Local  
1015 aggregation is also represented by the amount of fish in the school. Arrows represent fishermen  
1016 movements; each color is associated to a fishing trip. At the right, a table indicates the level of  
1017 each variable for the given scenario. Levels can take values of: --, -, + and ++ and are associated  
1018 to the values taken by each variable in Figures 2 and 3.

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Table 1: Number of fishing trips corresponding to each time-period.

Time-period	Fishing trips
2000/06 – 07	5839
2000/10 – 11	5750
2001/03 – 04	7012
2001/07 – 08	865
2001/10 – 11	1612
2002/02 – 03	1368
2002/10 – 11	6409
2003/10 – 12	6262
2004/11 – 12	8983
2005/11 – 12	15252
2006/02 – 04	2990
2006/11 – 12	8593
2007/02 – 04	2395
2008/02 – 04	4611
2008/11 – 12	8604
2009/02 – 04	3151

Table 2: Description of Environment, Anchovy and Fishermen variables.

Ecosystem compartment	Variable acronym	Description	Data type	Scale of data
Environment	SST	Averaged sea surface temperature from 3°S to 16°S and from the shore up to the 2500 m isobath (in °C)	AHRRR	Monthly data
	CHL	Averaged Chlorophyll-a from 3°S to 16°S and up to the 2500 m isobath (in mg.m <sup>-3</sup> )	SEAWIFS and MODIS	Monthly data
	OXY	Average of oxycline depth from 7°S to 16°S (in m)	CTD and NISKIN	Scientific survey
Anchovy	$s_A$	Index of global fish acoustic biomass equal to $\log((\sum_{i=1}^n \text{NASCI}_i/n) + 1)$ (in m <sup>2</sup> .nm <sup>-2</sup> )	Output from acoustic surveys (Bertrand et al., 2004)	Acoustic survey
	$s_{A+}$	Index of local fish biomass equal to $\log((\sum_{i=1}^n \text{NASCI}_i/n) + 1)$ , $\forall \text{NASCI} > 0$ (in m <sup>2</sup> .nm <sup>-2</sup> )	Output from acoustic surveys (Gutierrez et al., 2007)	Acoustic survey
	ISO	Index of spatial occupation. Percentage of ESDU where anchovy is present ( $\text{NASCI} > 0$ )	Output from acoustic surveys (Gutierrez et al., 2007)	Acoustic survey
Anchovy	DC	Center of gravity of the distance to the coast of the acoustically observed anchovy (in km)	Output from acoustic surveys (Gutierrez et al., 2007)	Acoustic survey
	I	$\text{DC} = \sum_{i=1}^n (\text{dc}_i \log(\text{NASCI}_i + 1)) / \sum_{i=1}^n \log(\text{NASCI}_i + 1)$	Output from acoustic surveys	Acoustic survey
	I	Inertia of DC (in km)	Output from acoustic surveys	Acoustic survey
Fishermen	Dur	$\text{I} = \sum_{i=1}^n (\text{dc}_i - \text{DC})^2 \log(\text{NASCI}_i + 1) / \sum_{i=1}^n \log(\text{NASCI}_i + 1)$	Output from acoustic surveys	Acoustic survey
	Dist	Fishing trip duration (in hours)	Computed from VMS data	Fishing trip
	Max.DC	Distance traveled during a fishing trip (in nm)	Computed from VMS data	Fishing trip
	Searching	Maximum distance to the coast during a fishing trip (in nm)	Computed from VMS data	Fishing trip
	Fishing	Proportion of fishing trip duration spent searching	Model output from VMS and observers data (Joo et al., 2013)	Fishing trip
	Cruising	Proportion of fishing trip duration spent fishing	Model output from VMS and observers data (Joo et al., 2013)	Fishing trip
	Bef.Fishing	Proportion of fishing trip duration spent cruising	Model output from VMS and observers data (Joo et al., 2013)	Fishing trip
	k	Absolute time from the beginning of the trip until the first fishing set (in hours)	Model output from VMS and observers data (Joo et al., 2013)	Fishing trip
	sigma	Shape parameter from random walk modeling	Model output from VMS data (Bertrand et al. in review)	Vessel moves by season
		Scale parameter from random walk modeling	Model output from VMS data (Bertrand et al. in review)	Vessel moves by season

Notes:  $\text{NASCI}_i$ : nautical-area-backscatter coefficient at  $i^{\text{th}}$  georeferenced elementary distance sampling unit (ESDU).  $\text{dc}_i$ : distance to the coast at the  $i^{\text{th}}$  ESDU.



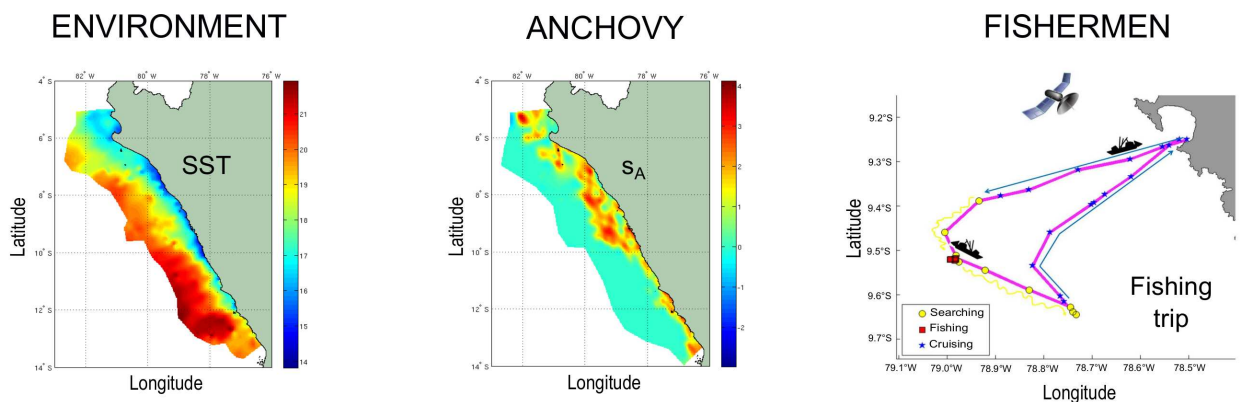
Table 3: Significant correlations between variables and their principal components ( $p < 0.05$ ). The percentage of explained variance of each component at each compartment is showed in italic.

Ecosystem Compartment	Variables	Components	
		1	2
Environment	CHL	0.93	–
	SST	0.94	–
	OXY	–0.71	–0.70
	<i>Explained variance</i>	75%	21%
Anchovy	$s_{A+}$	0.88	–
	$s_A$	0.84	–
	DC	–0.87	–
	I	–0.87	–
	ISO	–	0.94
	<i>Explained variance</i>	60%	23%
Fishermen	Fishing	0.92	–
	k	0.70	–0.69
	Searching	0.67	–
	Dur	–0.70	–
	Max.DC	–0.78	–0.59
	Bef.Fishing	–0.81	–
	Dist	–0.83	–
	sigma	–0.86	–
	Cruising	–0.93	–
	<i>Explained variance</i>	71%	23%

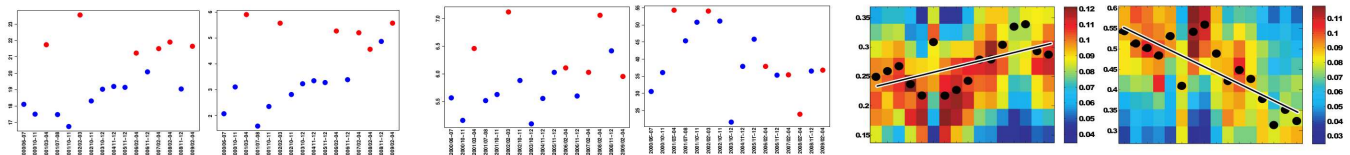
Table 4: Correlations between variables and the multiple coinertia axes.

Variables	Axis 1 (73%)	Axis 2 (17%)
SST	0.89	0.03
CHL	0.84	0.01
OXY	-0.55	-0.64
$s_A^+$	0.86	0.02
$s_A$	0.80	0.37
ISO	-0.13	0.74
DC	-0.81	0.15
I	-0.81	0.12
Fishing	0.88	0.10
k	0.64	-0.62
Max.DC	-0.77	-0.35
sigma	-0.82	0.49
Cruising	-0.86	-0.05

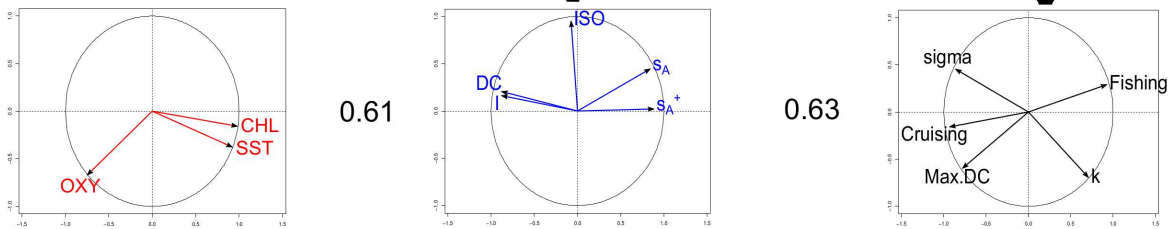
Figure 1



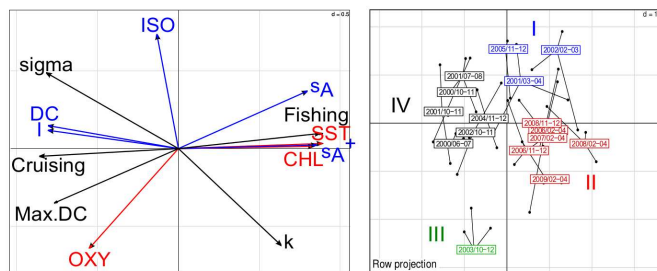
UNIVARIATE ANALYSIS



PCA



MULTIPLE COINERTIA + CLUSTER ANALYSIS



SCENARIOS

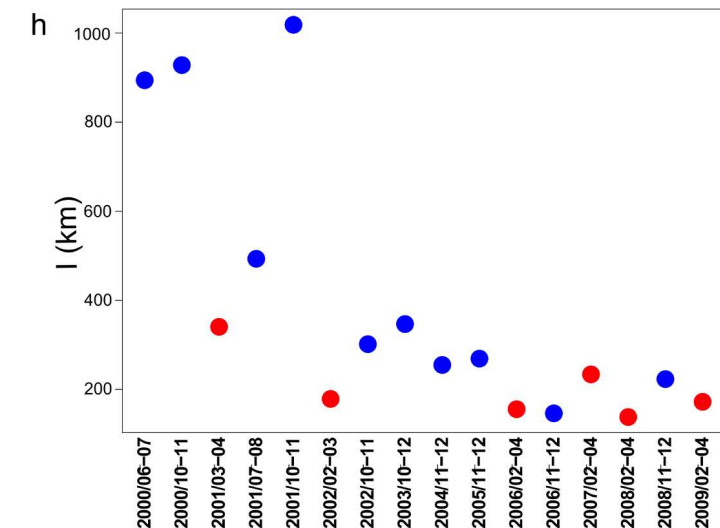
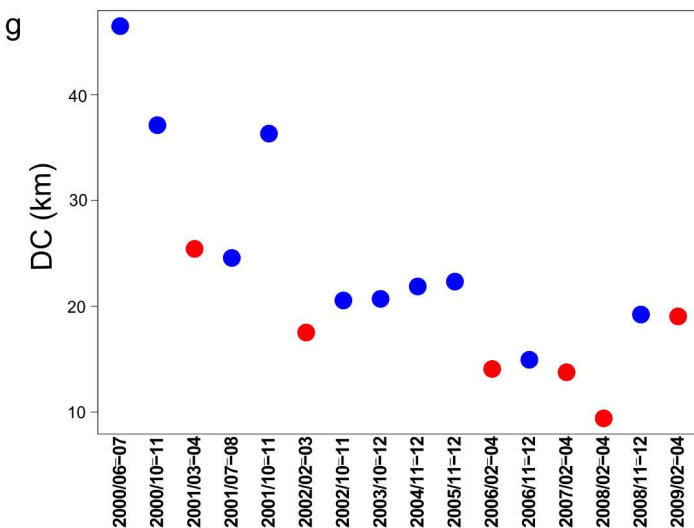
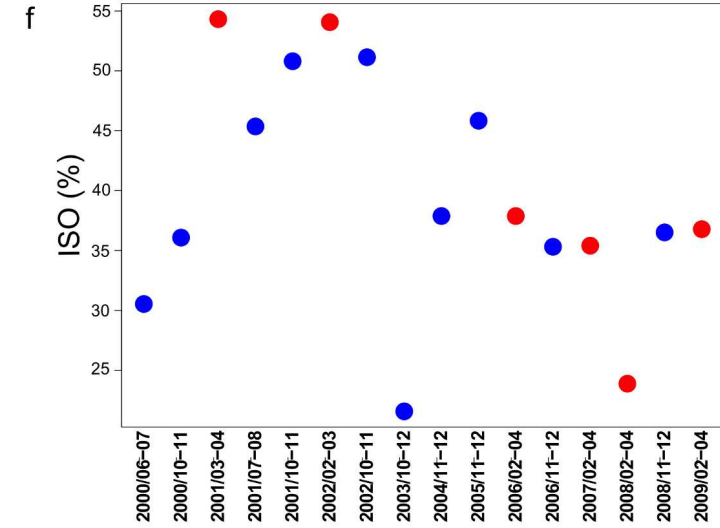
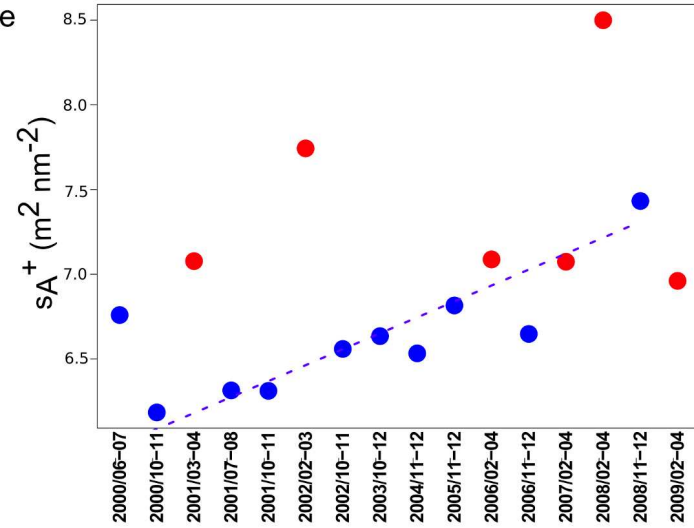
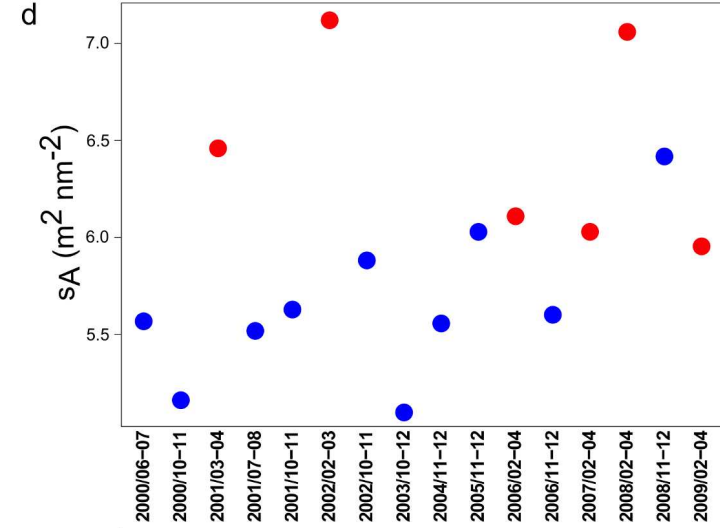
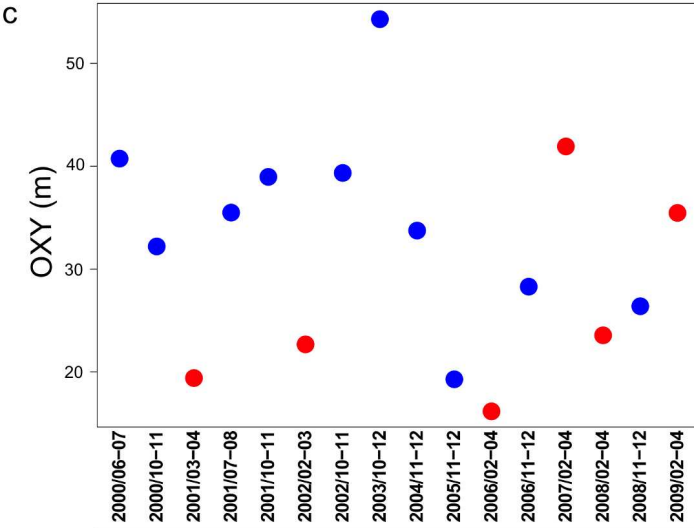
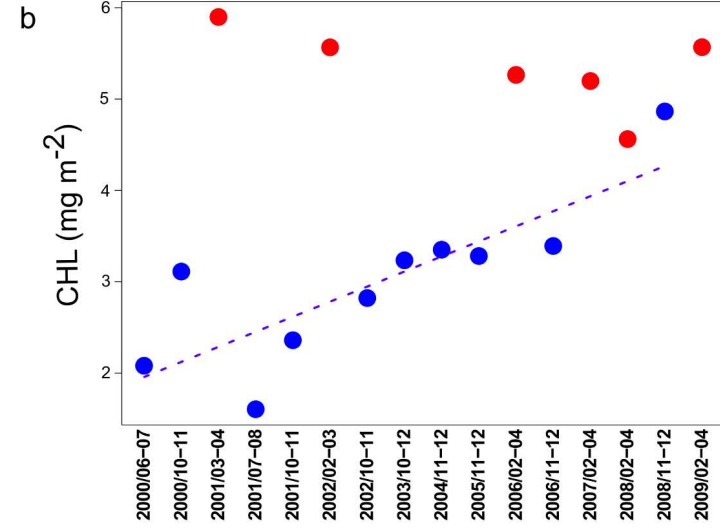
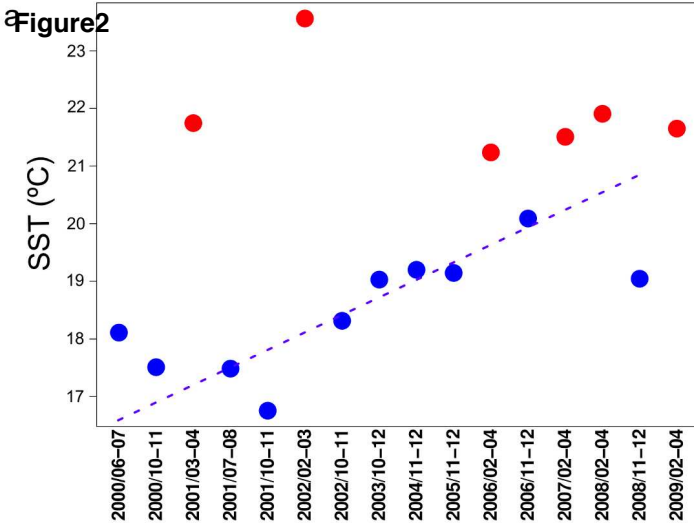


Figure3

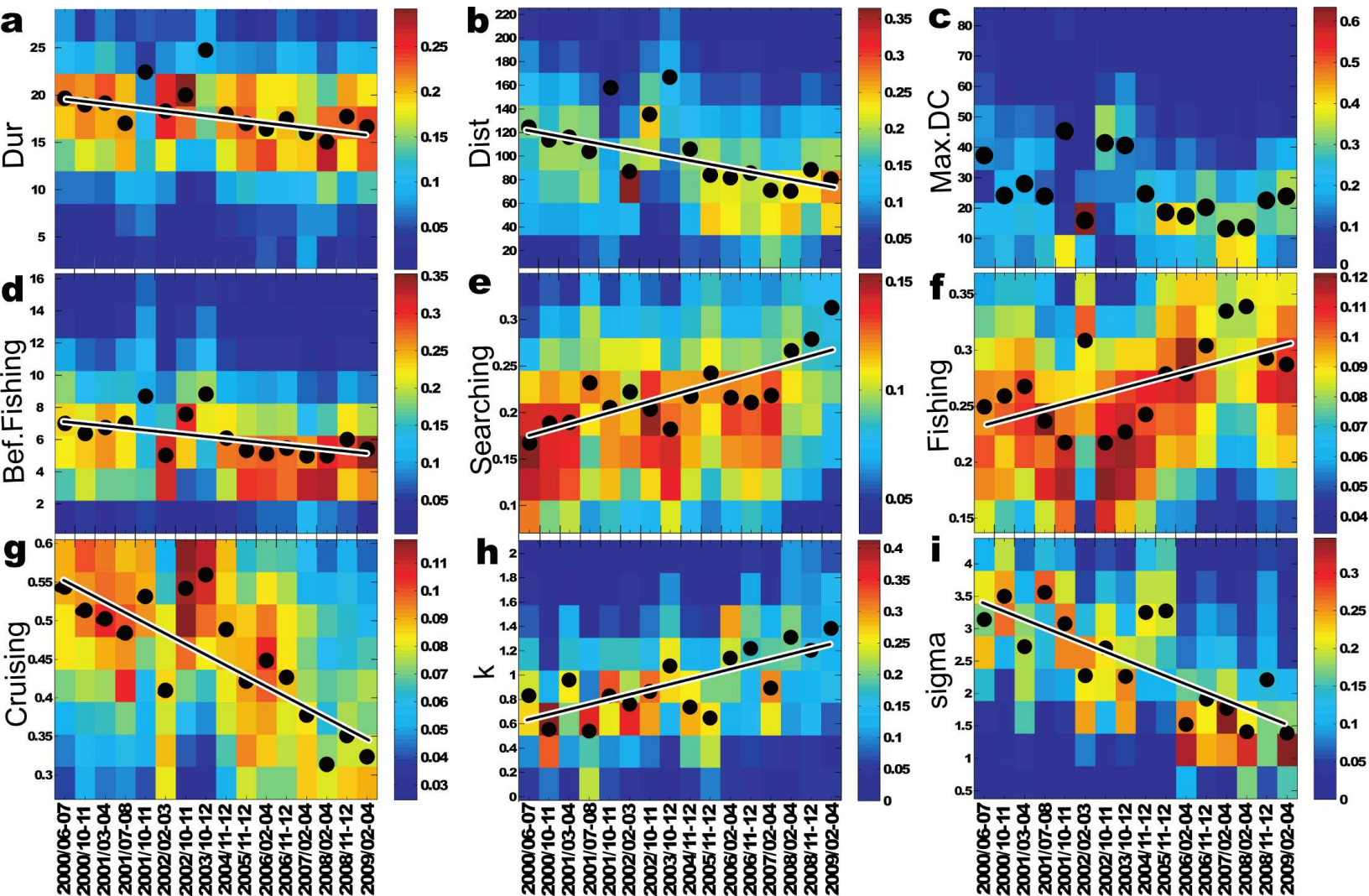


Figure4

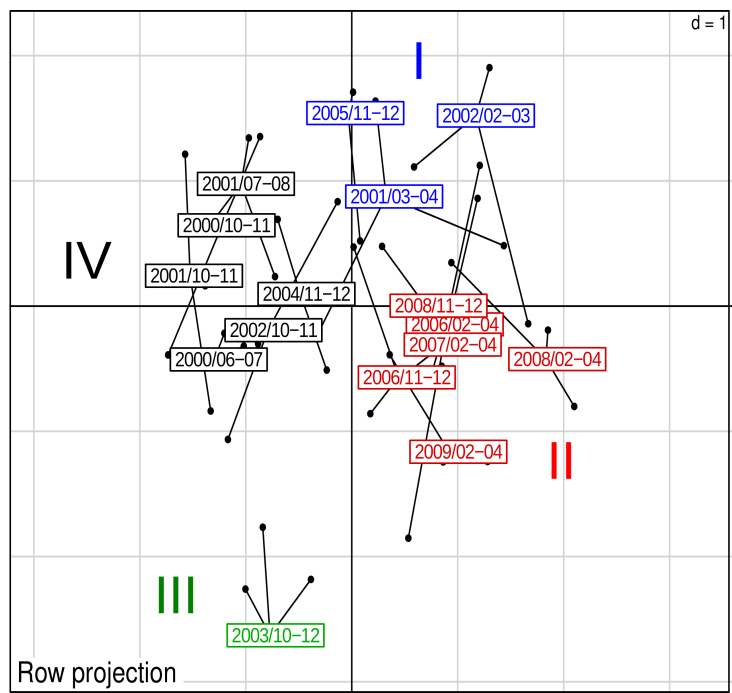
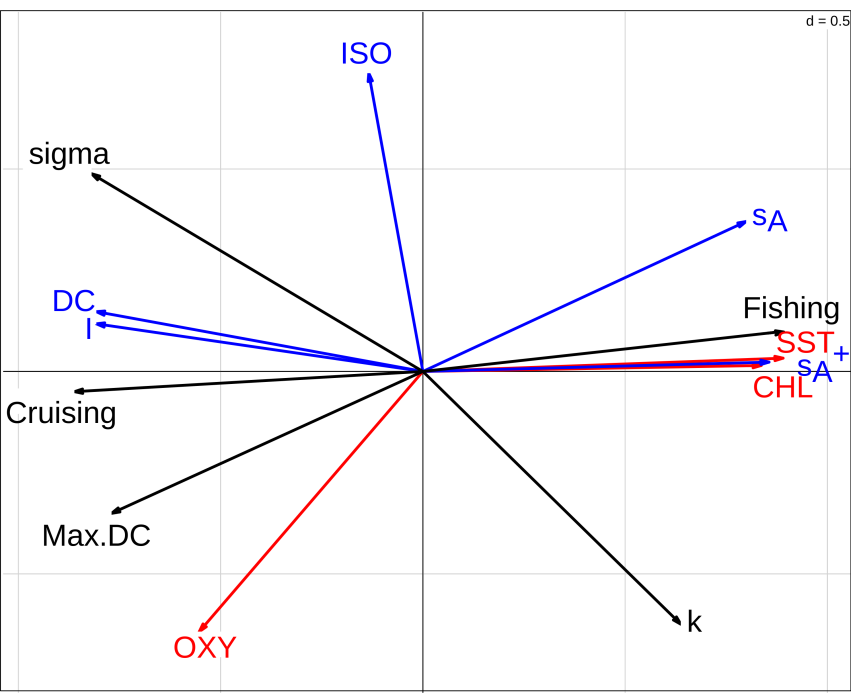
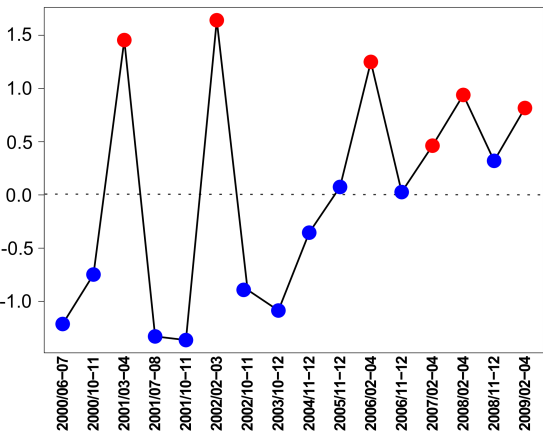


Figure5

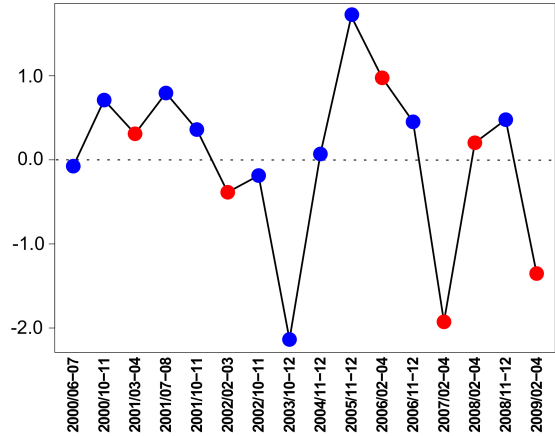
ENVIRONMENT: PC1 (75%)

+ (Summer)



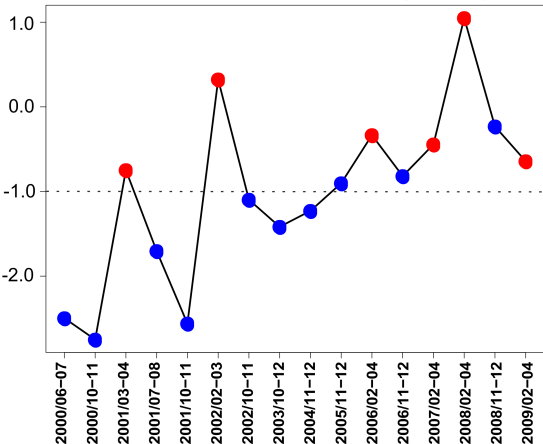
ENVIRONMENT: PC2 (21%)

+ (Superficial)



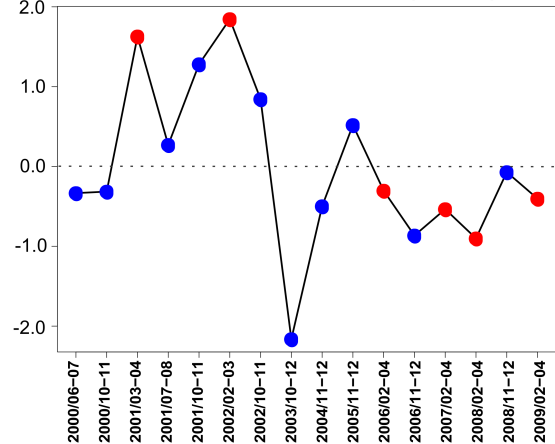
ANCHOVY: PC1 (60%)

+ (Abundant in large and coastal aggregations)



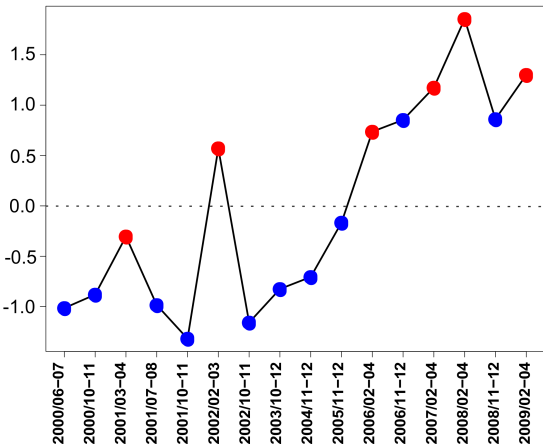
ANCHOVY: PC2 (23%)

+ (strong evenness: present over a large range)

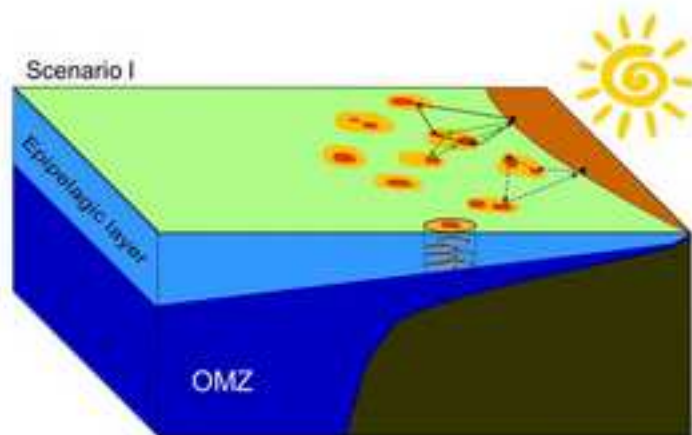


FISHERMEN: PC1 (71%)

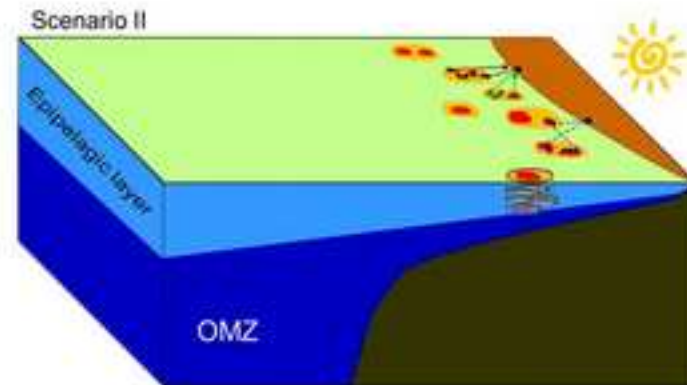
+ (Cheap foraging)



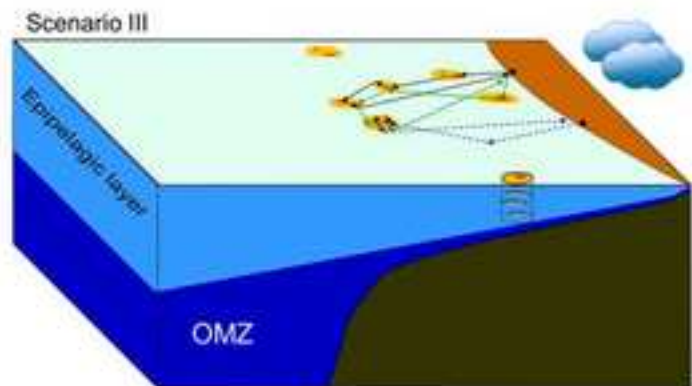
**Figure6**  
[Click here to download high resolution image](#)



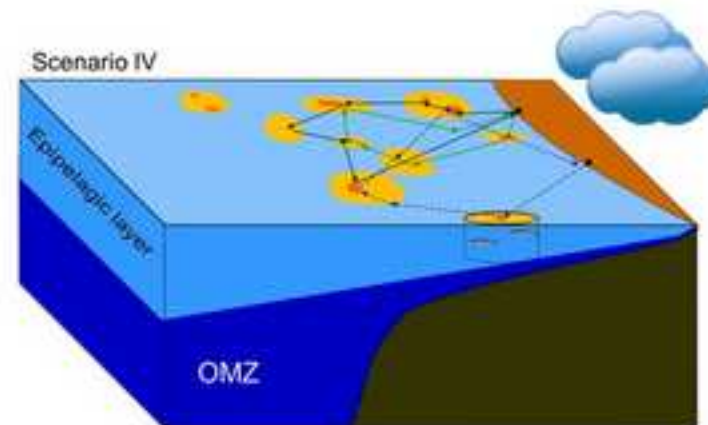
Variable	Level
SST	++
CHL	++
OXY	-
$\beta_A$	++
$\beta_A^*$	+
ISO	++
DC	-
$l$	-
Max.DC	-
Fishing	+
Cruising	-
$k$	-
sigma	-



Variable	Level
SST	+
CHL	++
OXY	-
$\beta_A$	++
$\beta_A^*$	++
ISO	-
DC	-
$l$	-
Max.DC	-
Fishing	++
Cruising	-
$k$	+
sigma	-



Variable	Level
SST	-
CHL	-
OXY	++
$\beta_A$	-
$\beta_A^*$	-
ISO	-
DC	-
$l$	-
Max.DC	++
Fishing	-
Cruising	++
$k$	+
sigma	-



Variable	Level
SST	-
CHL	-
OXY	+
$\beta_A$	-
$\beta_A^*$	-
ISO	++
DC	+
$l$	++
Max.DC	++
Fishing	-
Cruising	++
$k$	-
sigma	+



**Supplementary Material**

[Click here to download e-component: AppA.pdf](#)