



Functional group biodiversity in Eastern Boundary Upwelling Ecosystems questions the wasp-waist trophic structure

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ARTICLE INFO

Article history:

Received 22 July 2008

Received in revised form 9 April 2009

Accepted 16 July 2009

Available online 30 July 2009

ABSTRACT

The species diversity of the four major Eastern Boundary Upwelling Ecosystems (EBUEs) is studied and compared with the aim of better understanding their functioning. Functional groups (FGs) of organisms were defined according to their taxonomy, body size and trophic level (TL), and span from plankton to top predators. Four large sub-divisions are defined in each system: two latitudinal sub-divisions (north and south) and two zonal sub-divisions (inshore and offshore), resulting in four sub-ecosystems per EBUE. A semi-quantitative approach is used in which only the dominant species (contributing 90% of overall biomass) are considered. EBUEs are compared in regard to their species composition, dominant species richness and evenness within FGs. The data are interpreted, focusing on latitudinal, zonal and depth gradients of diversity. Trophic flows (inflow and outflow) through the small pelagic fish FG are derived from different Ecopath models. This analysis of the four ecosystems and their sub-divisions does not provide support for the expected wasp-waist food web structure and functioning, with a single or several species of small pelagic fish primarily channelling the energy flow from lower to higher TL. Instead, similar low levels of richness were observed in many FGs of intermediate TL, allowing several energy transfer pathways. The gamma diversity is high due to the geographical distance between EBUEs and the presence or absence of rivers, but not to differences in their latitudinal position. The beta diversity is also high, due to the same factors plus the variation in shelf width and the contrast between inshore and offshore sub-divisions. The differences in richness and evenness among EBUEs are minor and do not explain the higher secondary and tertiary productivity of the Humboldt ecosystem.

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1. Introduction

Eastern ocean boundary ecosystems can be classified into three zones according to Mackas et al. (2005): (1) mid and low latitude upwelling; (2) equatorial and (3) high latitude with poleward surface flow and downwelling. In this paper we focus on the first

group which comprises the Benguela, California, Canary, and the Humboldt Current Ecosystems (Fig. 1). These four ecosystems are characterized by local wind-driven upwelling, strong alongshore advection, a poleward undercurrent, very low to moderate precipitation and high productivity of plankton and fish, especially pelagic fish. These systems are highly dynamic and display strong variability at all spatial and temporal scales. They are also characterized by seaward extension of the boundary current and biological system beyond the continental shelf and remote physical forcing by larger-scale teleconnections.

Despite these similarities, the four EBUEs differ in their latitudinal range, shelf width and other physical features such as wind

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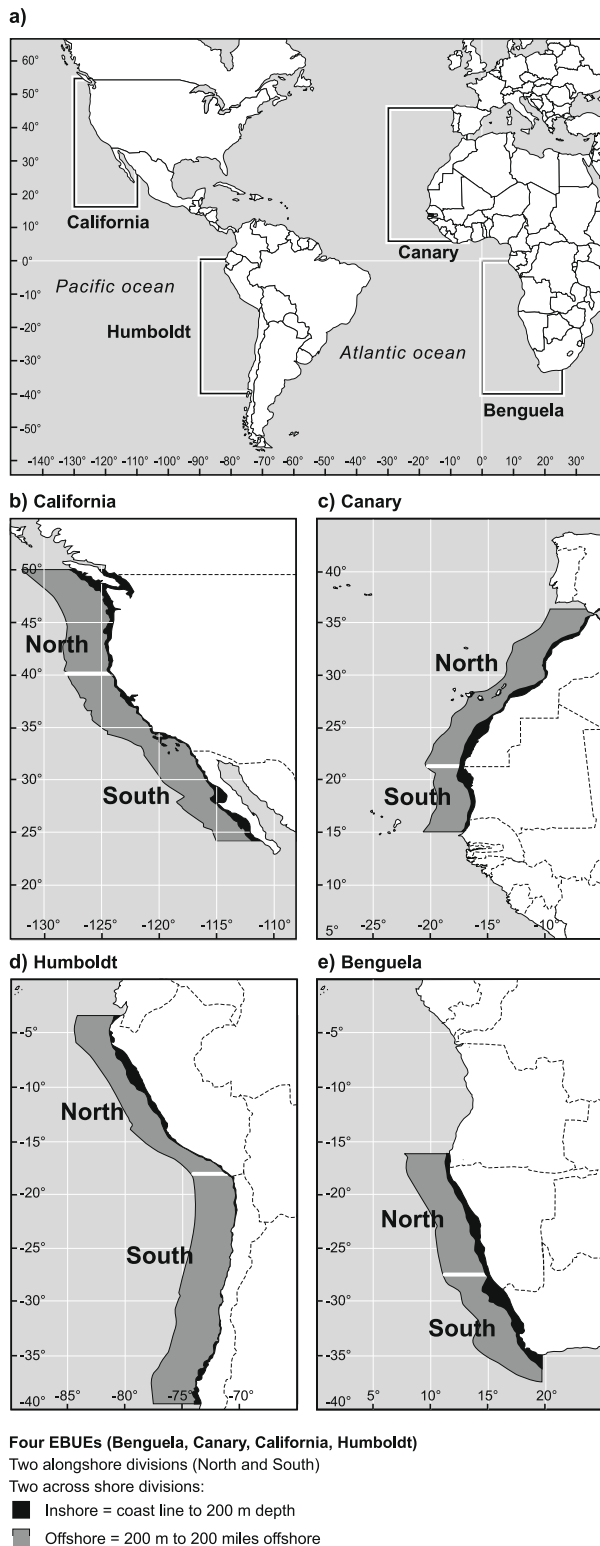


Fig. 1. Location of the four Eastern Boundary Upwelling Ecosystems (a) and their latitudinal (north, south) and zonal (inshore in black, offshore in dark grey) sub-divisions as detailed in Table 1 (b).

stress, stratification, freshwater input and ecological features (Table 1S in [Supplementary information](#)). One challenging question about EBUEs is the reason for the higher fish production of the Northern Humboldt ecosystem ([Bakun, 1996](#)). Since this ecosystem does not seem to benefit from a higher primary production than the three others based on satellite observations (e.g. [Carr and](#)

[Kearns, 2003](#); but note that sea colour provides estimates of the biomass, not the production), we tested the hypothesis of a different functioning linked to particular food web architecture. Although there is growing consensus among terrestrial ecologists that there is a positive but weak relationship between the diversity, stability and productivity of an ecosystem (review in [Kindt, 2002](#)), controversy continues with respect to a general appreciation of the role of diversity in enhancing either ecosystem stability or productivity in open marine ecosystems ([Worm et al., 2006](#); [Longhurst, 2007](#)). Species richness acts as a buffer of the physical and biological environment, resulting in a higher stability, as stated by [Yachi and Loreau \(1999\)](#) in their “insurance hypothesis”. A positive relationship between diversity and productivity was hypothesised by Darwin for plant communities ([McNaughton, 1994](#)). Nonetheless, it seems that there is a saturating effect and above a threshold of diversity the additional gain in productivity is limited ([Tilman et al., 1996](#)). Interestingly, the “minimal biodiversity” depends both on the number of FGs and on the biodiversity within FGs ([Tilman et al., 1997](#); [Hector et al., 1999](#); [Loreau et al., 2001](#)). [Kindt \(2002\)](#) summarizes his review saying that “conditions for positive relationship between diversity, stability and productivity include diversity and trade-offs in traits of species (or individuals), diversity in environmental characteristics, and disturbance that maintains turnover of species and spatio-temporal variation”.

Understanding the functioning of EBUEs as a whole is essential to manage properly these highly productive systems (one third to one fifth of the world fish catch over the last five decades) within the framework of ecosystem-based management. Furthermore, ongoing climate change is known to interact with intensive exploitation which decreases the resilience of natural ecosystems ([Hsieh et al., 2006](#)). Reduction in marine diversity at ecosystem levels may lead to a reduction in the resilience and an increase in the response of populations and ecosystems to future climate variability and change ([Planque et al., in press](#)).

Few previous studies have dealt with biodiversity patterns either within or among EBUEs, as far as we know this is the first one comparing the four EBUEs using many FGs. [Sakko \(1998\)](#) studied the biodiversity of many FGs in the Northern Benguela ecosystem and concluded that the highly fluctuating and productive environment of this ecosystem tends to favour the persistence of a few abundant generalist species. Species diversity in this ecosystem is often lower than in comparable habitats in the Southern Benguela. In Northern California, [Hoof and Peterson \(2006\)](#) found a negative relationship between copepod biodiversity and copepod biomass at different temporal scales: seasonal, interannual (El Niño events) and interdecadal (Pacific Decadal Oscillation). They linked this relationship to basin scale variations in wind direction that result in the transport and delivery of different source waters to the ecosystem. [Blanchette et al. \(this issue\)](#) compared the trophic structure and diversity in rocky intertidal communities from locations in three EBUEs (Benguela, California and Humboldt). They found a remarkable consistency in the trophic structure across these systems, with the higher trophic levels containing increasingly lower taxonomic diversity. In contrast, differences in the richness of these ecosystems were observed, with California the most and Humboldt the least taxonomically rich, and appeared inversely correlated with temporal variability in SST. [Ottens and Nederbragt \(1992\)](#) studied diversity and evenness in different areas of the North Atlantic, Indian Ocean and adjacent seas, including upwelling areas such as south of India, southwest of Sumatra and the Arabian Sea. They found that upwelling conditions and spring blooms are characterized by relatively low diversity and evenness values.

The comparative approach is relevant when one works at the scale of ecosystems ([Bakun, 1996](#)) and this work addresses the question of the trophic functioning of EBUEs through the compar-

ative study of species diversity and trophic flows (inflow and out-flow) through the small pelagic fish FG. The data are interpreted, focusing on gradients in diversity, differences in the topography and the food web architectures of the four EBUEs.

2. Materials and methods

Four large sub-divisions were defined in each system: two latitudinal sub-divisions (north and south) and two zonal sub-divisions (inshore and offshore), resulting in four sub-ecosystems per EBUE, for a total of sixteen sub-ecosystems (Fig. 1). In contrast to the work of Mackas et al. (2005), the latitudinal limits that are used here exclude the transition zones at the latitudinal boundaries of the EBUEs (Table 1) in order to concentrate on species characteristic of EBUEs. The boundary between northern and southern sub-ecosystems was based on geographical or biogeography patterns and oceanographic characteristics to the extent practicable, although sometimes conflicting information made this choice difficult (e.g. the Canary ecosystem). The inshore sub-divisions were bounded longitudinally by the coastline and the 200 m isobath which characterises the shelf break, whereas the offshore sub-divisions span from this 200 m isobath to 200 nautical miles from the coastline. The 200 miles limit, although partly arbitrary, allows the inclusion of water masses influenced by upwelling (Demarcq, this issue; Chavez and Messie, this issue). The vertical extension of the offshore sub-ecosystem was set to 1000 m in order to exclude the bathypelagic zone. As the limit of the southern Benguela extends beyond the tip of Africa on the eastern part of the Agulhas Bank, special limits had to be set to mimic a southern extension of the coast line (Table 1).

Species were pooled into sixteen major functional groups (FGs) defined according to their taxonomy, body size and trophic levels (TLs). They span from plankton to top predators (Table 2). Benthic organisms were ignored, and FGs considered to be of low relative biomass were excluded in order to focus on the comparison of major species and contrast, when necessary, the different EBUEs. This occurred for four FGs and 22 sub-divisions (Table 2S). The decision to exclude the diatom FG from all offshore sub-divisions was based on a sharp drop in their abundance offshore in the Northern Canary and the Northern Benguela, except during short, local blooms. Although we lacked information on the offshore distribution of this FG in some ecosystems, we assumed that they reflected the situation in the Northern Canary and Northern Benguela systems. Small pelagic fish (SPF) and pinnipeds are usually abundant only in inshore sub-divisions, except when the continental shelf is narrow (e.g., California, Southern Humboldt). In contrast, meso-pelagic fish are usually found in low abundance on the continental shelf, especially when the shelf is wide (see Section 3).

In order to overcome the common difficulty of getting an exhaustive list of species and the corresponding biomasses, a semi-quantitative approach was used. Instead of analyzing the full species diversity, the study was limited to the few dominant species considered to comprise at least 90% of the biomass of a FG

Table 2

Index of dominant species richness (overall R and mean R for the 16 sub-divisions) according to functional groups (FG). The third column is the mean trophic level (TL) of the FG, the fourth column the logarithm of the median length at maturity (Lm). TL and Lm values are weighted by the relative abundance index.

FG	Overall R	Mean R	TL	Log ₁₀ (Lm)
Diatoms	36	11.8	1.0	-2.3
Dinoflagellates	24	8.4	1.0	-2.1
Copepods	28	3.8	2.5	-0.6
Euphausiids	26	2.3	2.7	0.2
Small pelagic fish	12	3.1	3.0	1.2
Chaetognaths	13	2.8	3.2	0.3
Meso-pelagic fish	18	1.1	3.2	0.7
Planktivorous vertebrates ^a	17	4.9	3.4	3.2
Medium-sized pelagic fish	9	2.4	3.6	1.3
Cephalopods	19	3.0	3.8	1.4
Demersal fish	67	8.5	3.8	1.5
Seabirds	67	10.3	3.9	1.7
Dolphins & toothwhales	19	5.5	4.2	2.6
Sharks & rays ^b	43	9.3	4.3	2.3
Large pelagic fish	25	3.6	4.3	1.8
Pinnipeds	11	1.8	4.5	2.3
Total	434	11.8	-	-

^a Baleen whales, planktivorous sharks and rays.

^b Excluding planktivorous species.

of a given sub-ecosystem. An index of the relative biomass of a species within a FG (IRB_{FG_i}) was defined as:

$$\text{IRB}_{\text{FG}_i} = B_i / \sum_{i=1}^n B_i \quad (1)$$

where B_i is the estimated biomass of species i and $\sum_{i=1}^n B_i$ an estimate of the combined biomass of the n species in that FG. Three classes of the index of relative biomass were recognized: *Low* $\leq 20\%$; *Medium* $\leq 60\%$; *High* $> 60\%$, of which one was associated with each species considered. No temporal dynamics were considered in this study. Seasonal variability in the abundance of migratory species, particularly at the latitudinal and zonal boundaries of the ecosystems, was accounted for by considering the mean time of residence of a species when estimating its average biomass in any sub-division of the ecosystem. Although we acknowledge the influence of interannual changes in biodiversity, especially in the California and Humboldt ecosystems under ENSO influence, our intention was only to depict and compare average conditions in EBUEs over the last few decades (at least two, according to available information). Each input row of our dataset (not shown) contains the following information: FG, family, genus, species (including the option of using spp. or sp. when necessary), number of significant species (1 by default, ≥ 1 when spp. or sp. was used), ecosystem, latitudinal sub-division, zonal sub-division, relative biomass index (IRB_{FG_i}), median length of mature individuals (Lm), TL and bibliographic reference(s). In practice, spp. or sp. were used only for 37 genera in 85 entries, mainly for phytoplankton. The data came from stock assessments, scientific surveys, food

Table 1

Boundaries of the 16 sub-ecosystems and their latitudinal and zonal boundaries.

Ecosystem	North	South	Inshore	Offshore
Canary	21–36°N (range 15°)	15–21°N (range 6°)	Coast-line to 200 m isobath	200 m isobath to 200 miles offshore
Benguela	17–28°S (range 11°)	28–37°S (range 9°)	As above, from 17°S to 35°S, then the 20°E meridian	As above, from 17°S to 35°S, then 200 miles offshore of the 20°E meridian
California	40–50°N (range 10°)	25–40°N (range 15°)	Same as Canary	Same as Canary
Humboldt	4–18°S (range 14°)	18–40°S (range 22°)	Same as Canary	Same as Canary

web models, commercial catch data (relevant Bibliography in Supplementary information) and knowledge of the authors. The data for the chaetognath sizes come from Pierrrot Bults (<http://nlbif.eti.uva.nl/bis/chaetognatha.php>). When TL and Lm were not available from the literature, we used FishBase data (<http://fishbase.org/>).

Cross-tabulations and statistical analyses were performed for inter-EBUEs comparisons regarding their species composition, dominant species richness (number of species) and evenness (how equally abundant are each of the species), using the R language (R, 2007) and the ADE4 package (Dray et al., 2007). The species composition was studied in two steps. First a factor analysis (FA) was performed on a contingency table with the 434 species names in rows and the 16 sub-ecosystems in columns. The value in each cell was the central value of the class of biomass (*Low* = 13; *Medium* = 40; *High* = 80). Second, cluster analyses of sub-ecosystems were performed on the main factor scores of the FA.

The same two steps were used for the study of dominant species richness. This multivariate analysis was preceded by an ANOVA on the total species richness per sub-ecosystem. Due to limited degrees of freedom, three of the following four factors were used at a time: ecosystem, ocean (Atlantic or Pacific), latitudinal sub-division (poleward or equatorward) and zonal sub-division (inshore or offshore). Furthermore, dominant species richness was plotted in relation to the mean TL to study the structure of the trophic web.

Evenness is conventionally measured by different indices based on the frequency distribution of the number of individuals of each species (Legendre and Legendre, 1998). Since we did not have access to numerical abundance, the three classes of biomass were used as proxies. First, a principal component analysis (PCA) was performed on these three classes of biomass for each set of FGxsub-ecosystem, followed by a between-class analysis, focussing on the between-FG variability. Second, major patterns of biomass distribution within FGs were defined (Table 3S, Supplementary information) and then used to perform a multiple correspondence analysis followed by a cluster analysis. The clustering was based on Euclidean distances and made use of the Ward method (Ward, 1963).

Conventionally, three scales of diversity are identified: (1) alpha diversity or within-habitat diversity, which refers to a group of organisms interacting and competing for the same resources or sharing the same environment and is usually expressed by the richness in that ecosystem; (2) beta diversity or between-habitat diversity, which refers to the response of organisms to spatial heterogeneity and can be expressed in a number of ways (review in Koleff et al., 2003), the simplest and most commonly used being the ratio between the number of species in a composite sample (combining a number of alpha samples) and the mean number of species in the alpha samples; (3) gamma diversity or geographical diversity, which refers to diversity of a larger geographical unit and can be represented by the total richness for all ecosystems of the studied area (Whittaker, 1972; Perlman and Adelson, 1997).

Although this concept is mainly applied to terrestrial ecology and at smaller scales than in marine ecology, we consider here that richness within sub-ecosystems corresponds to alpha diversity, the ratio of the number of species in a given ecosystem (S_c) to the mean number of species by sub-ecosystems \bar{S} corresponds to beta diversity, and the total number of species in all EBUEs to gamma diversity.

Trophic flows (inflow and outflow) through the small pelagic fish FG are derived from different Ecopath models of EBUEs (Jarre-Teichmann et al., 1998; Shannon et al., 2003; Neira et al., this issue; C. Mullon, A. Jarre, C. Moloney, S. Neira and J. Tam, unpublished data). Although these models do not identify precisely the same FGs as ours, all of them identify small pelagic fish species (individually or as single FG). Flows are expressed in $t\ km^{-2}$ of “biomass equivalent to PP” (BEPP) which was computed as follows. Let us denote F_{ij} the flow from FG i to FG j , Y_i the BEPP of FG i , X_{ij} the BEPP of flows from FG i to FG j . The ratio of flows, in %, can be expressed as:

$$R_{ij} = 100 \cdot F_{ij} / \sum_k F_{kj} \quad (2)$$

If i is a PP component, put $X_{ij} = F_{ij}$, and $Y_i = \sum_j X_{ij}$, else put $X_{ij} = Y_i R_{ij}$, $Y_i = \sum_k X_{ki}$. When there are loops in the network, this procedure is iterated until stable.

When several Ecopath components were defined for any of our FGs, we simply summed the corresponding BEEPs.

3. Results

3.1. Species composition

The beta diversity index varies from 1.75 (Benguela) to values close to 2.10 (Humboldt and Canary) (Table 3). The cross-tabulation of species and sub-ecosystems shows that out of the 434 dominant species, 179 were only present in one sub-ecosystem. These species are mainly from the demersal fish (48), seabirds (27), diatoms (27, including species identified at the genus level only) and to a lesser extent copepods (14). The sub-ecosystems with the highest number of unique dominant species are the inshore sub-division of Northern Canary (23 species; 25% of the total number of species in this sub-ecosystem) and the Northern Humboldt (19; 26%). The sub-ecosystem with the lowest number of dominant species not found in abundance elsewhere is the offshore sub-division of the Northern Benguela (2; 3%). By contrast, a few dominant species are found in most sub-ecosystems. For instance 18 species are present in at least 9 sub-ecosystems, (at least three ecosystems), including species in the FGs of dolphins & toothed whales (5), planktivorous vertebrates (4) and sharks & rays (3) The most ubiquitous species is the seabird *Puffinus griseus*, recorded in 15

Table 3
Indices of alpha, beta and gamma biodiversity in Eastern boundary upwelling ecosystems. Alpha and gamma indices are simply richness values in individual sub-ecosystems and in all systems pooled together, respectively, whereas beta diversity is the a ratio of richness: (S_c/\bar{S} , see text).

	Benguela				California				Canary				Humboldt			
Indice Biod.	Ben-N. I.	Ben-N. O.	Ben-S. I.	Ben-S. O.	Cal-N. I.	Cal-N. O.	Cal-S. I.	Cal-S. O.	Can-N. I.	Can-N. O.	Can-S. I.	Can-S. O.	Hum-N. I.	Hum-N. O.	Hum-S. I.	Hum-S. O.
Alpha Diversity	74	70	75	69	78	79	102	82	89	67	91	69	74	66	75	70
S_c	126				161				166				149			
\bar{S}_c	72.0				85.3				79.0				71.3			
Beta Diversity	1.75				1.89				2.10				2.09			
Gamma D. (Richness)	434															

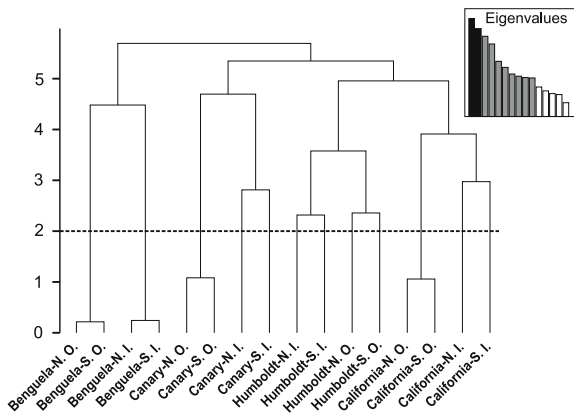


Fig. 2. Cluster analysis of the sub-ecosystems, according to species composition, performed on the ten first factors of the FA. The eigenvalues of the FA are shown in the top right corner.

sub-ecosystems. When looking at EBUEs as a whole, 22 dominant species are present in all of them and 34 in three of them. These species belong to the same FGs as for species widespread across sub-ecosystems.

When considering genus only, 63 genera out of 254 are dominant in only one sub-ecosystem and most of them belong to the same four FGs identified for the species (demersal fish, seabirds, diatoms and copepods) as well as the FG of meso-pelagic fish. Genera displaying high ubiquity are also found roughly in the same FGs as for species.

The factor analysis on the species composition resulted in a slow decline of the eigenvalues (Fig. 2). The first 10 factors were retained in the cluster analyses. The dendrogram of sub-ecosystems shows different levels of clustering corresponding to different factors. The first two clusters (Fig. 2; cut at height 5.5) are according to ecosystems: the four Benguela sub-ecosystems in one and the 12 remaining sub-ecosystems in the other, but this clustering level is weak. A second and somewhat stronger (longer branches in the tree diagram) clustering can be obtained by a cut at the height of 4.0 resulting in five clusters, regrouping each the four sub-divisions of each EBUE, except for the Canary EBUE for which inshore and offshore sub-divisions are separated. A third level of clustering, with the same intermediate strength as the previous one, results from a cut at the height of 3.0 and in which all EBUEs shown are split in two groups according to their zonal sub-divisions. The last and strongest clustering level (longest branches) results from a cut at the height of 2.0. Here some of the previous levels of clustering, according to zonal divisions, are retained (offshore sub-divisions of Canary, California and Benguela, plus the inshore sub-division of Benguela) while all the other sub-ecosystems stand alone.

3.2. Species richness

The gamma diversity index is 434 and the alpha diversity index varies from 66 to 102, with the offshore sub-ecosystems nearly always displaying lower values than the inshore sub-ecosystems (Table 3). The dominant species richness varies more according to FG than to sub-ecosystems (mean coefficients of variation 72% and 50%, respectively). FGs with higher richness are seabirds, sharks and rays, dinoflagellates and demersal fish, whereas the lowest richness is found in pinnipeds and small and medium pelagic fish (Table 2). The factor analysis on the species richness resulted in a sharp decline of the eigenvalues (Fig. 3). The first five factors were conservatively retained in the cluster analyses. The dendrogram of sub-ecosystems shows a strong clustering in two groups (Fig. 3) according to the zonal sub-divisions of all ecosys-

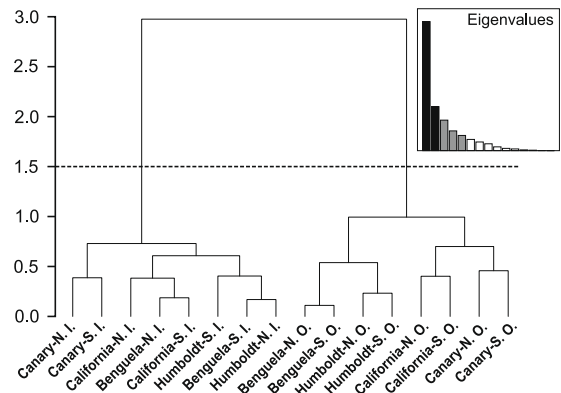


Fig. 3. Cluster analysis of sub-ecosystems, according to richness, performed on the five first factors of the FA. The eigenvalues of the FA are shown in the top right corner.

tems. The dendrogram of FGs shows a strong clustering in two groups: diatoms, pinnipeds and small pelagic fish in one and all other FGs in the other (Fig. 15). Indeed, indices of richness of these three FGs are positively correlated (Table 6S).

Tests performed to control the homogeneity of variance (Hartley F-max, Cochran C, Bartlett Chi-squared and Levene tests) for the ANOVAs on dominant species richness according to sub-ecosystems, did not show violation of this assumption except for some FGs when using the Levene test. Even quite major violations of assumption of the homogeneity of variance are not that critical according to Lindman (1974) except under the most severe violations. Some correlations were found between mean and variance for a few FGs, but when these were removed from the analysis, the results were unchanged. There were no major outlier points and the residual analysis showed neither strong trends nor strong dissymmetrical distributions. Nonetheless, in order to be conservative, only factors with $P < 0.01$ were retained. Only one out of four factors was consistently significant regardless of the combinations: zonal sub-division (31–36% of the variance, $P < 0.01^{**}$). The ecosystem, latitudinal and ocean effects were never significant.

Due to the clear difference among sub-ecosystems according to zonal sub-divisions, plots of dominant species richness according to FGs were produced separately for the eight inshore and the eight offshore sub-ecosystems (Fig. 4; Table 2S). For the two plots, the same mean TL was used to sort, in increasing order, the FGs, despite some minor differences in ordering when inshore and offshore TLs were computed separately. The inshore plot shows high richness for FGs with low (phytoplankton) and high TLs, with the exception of the FGs with highest TLs (dolphins & toothed whales, large pelagic fish, pinnipeds). A large number of FGs of intermediate TLs, spanning from 2.5 to 3.8, (zooplankton, small, medium and meso-pelagic fish, planktivorous vertebrates and cephalopods) tend to display low values of richness. The offshore plot displays a similar general pattern, although the diatoms FG is not included and the dolphins & toothed whales species are more numerous.

3.3. Evenness

The PCA on the three classes of biomass followed by the between-class analysis mainly shows some strong associations between FGs and classes of biomass (Fig. 2S, Supplementary information). Not surprisingly, the FGs with low richness (e.g. cephalopods, SPF, pinnipeds and euphausiids) are associated with class *High* and those with high richness (e.g. birds, sharks & rays) with class *Low*. The class *Medium* is associated mainly with cope-

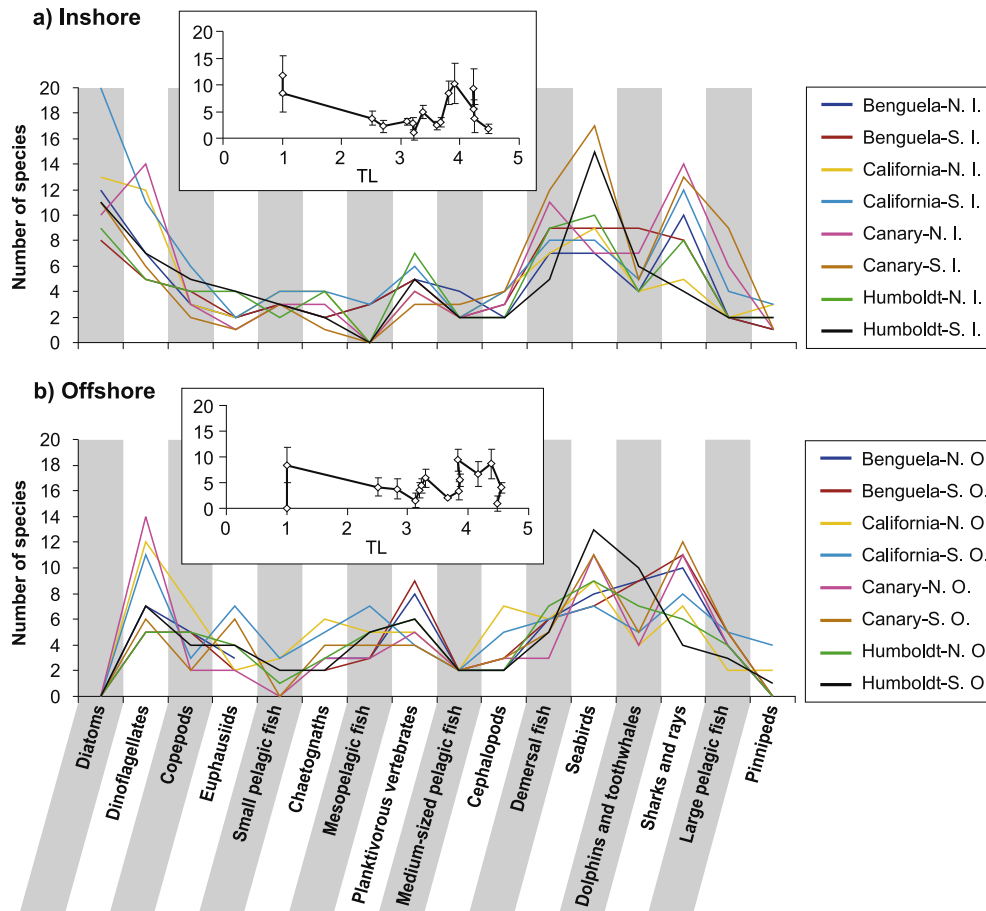


Fig. 4. Richness according to FG. Note that the same ordering was used for inshore and offshore FGs according to their overall mean TL (see Table 2). The inset shows ordering and spacing of FGs according to their TL values inshore and offshore, although the lines joining FGs are consistent with the main graphs.

Pods. Less trivial are the results on the multiple correspondence analysis on the eight typologies of evenness per sub-ecosystem and FG we defined, including absence of the FG (Table 3S, Supplementary information). The eigenvalues display a slow decrease (Fig. 3S, Supplementary information), suggesting a complex structure. The cluster analysis performed on the first four factors shows a clear clustering, where the five groups are made of: (1) one cluster with both Benguela inshore sub-ecosystems and all Humboldt sub-ecosystems except the Northern offshore; (2) the other Humboldt and Benguela sub-divisions; (3) the two Canary offshore sub-divisions; (4) the two Canary inshore sub-divisions; and (5) the four California sub-ecosystems.

3.4. Trophic flows

Table 4 displays the BEPP proportions of input and output flows flowing through small pelagic fish species for the northern and southern sub-ecosystems of Humboldt and Benguela, at different time periods. Inflow values vary from <0.5% to 25% and outflow values from <0.5% to 78%, with only four values out of 13 over passing 50%.

4. Discussion

4.1. Methodological considerations

As we used a semi-quantitative approach and limited our species inventory to 90% of the cumulated biomass, we could not make use of the common indices of diversity (e.g. Shannon's index,

Table 4

Proportions of input and output flows, computed from "biomass equivalent to primary production", flowing through small pelagic fish species for the northern and southern sub-ecosystems of Humboldt and Benguela, at different time periods, suggesting the existence of alternative energy transfer pathways at mid trophic levels.

Sub-ecosystem	Inflow (%)	Outflow (%)
Northern Humboldt 1995–1996	25	78
Northern Humboldt 1997–1998	20	66
Southern Humboldt 1950	3	62
Southern Humboldt 1992	5	8
Southern Humboldt 2005	10	34
Northern Benguela 1900	6	22
Northern Benguela 1960	3	14
Northern Benguela 1980	<0.5	<0.5
Northern Benguela 1995	<0.5	1
Southern Benguela 1900	3	49
Southern Benguela 1980	3	26
Southern Benguela 1990	2	16
Southern Benguela 2000	21	59

Pielou's evenness). Estimations based on extrapolating or modeling a species-accumulation or species-area curve (review in Chao, 2005) also could not be used because our data sources and methodologies differ according to ecosystems, FGs and time. The same applies to ABC or k-dominance curves (Warwick, 1986). Instead, we used simple indicators of species diversity, separating richness from evenness, as recommended by many authors (e.g. Magurran, 1998). We assumed that these indicators captured the differences in real richness and evenness among ecosystems, and similarly that their main differences and similarities in species composition

were reflected by the first 90% of cumulated biomass. Using this threshold is not conceptually different from some conventional approaches that use all available information, since the real species composition of an ecosystem is never perfectly known, especially in marine ecosystems. Therefore there is a hidden biomass threshold in all diversity studies (Marchant, 1999), which is highly variable according to the FGs. Here at least we use the same threshold for all of them. Another advantage of this approach is that excluding rare species limits the number of zero values and eases statistical analysis. As neither short (interannual) nor long term (interdecadal) temporal dynamics are explicitly considered in this study, our data represent an average situation, not necessarily observed during the last decades. But at least this bias is consistent for all EBUEs.

We had to convert the three classes of the qualitative index of relative biomass into quantitative data in order to perform the factorial analysis on the species composition, which could appear as contradictory. In order to test this potential flaw, we compared the clustering of sub-ecosystems according to species relative biomass using the same analysis as performed on presence/absence data and we found similar results (not shown). This similarity indicates that, as expected, the clustering is more dependent on presence/absence of the dominant species than on their relative abundance.

The decision regarding the location of the ecosystems and sub-ecosystem borders often resulted from a trade-off between several conflicting sets of information regarding topography, oceanography and biogeography and practical consideration such as easier access to information by country. For instance, the limit between the northern and southern Humboldt has been set to 18°S at the location of an abrupt change of the coast orientation, which generates differences in oceanographic processes (e.g. retention) and also corresponds to the border between Peru and Chile. Nonetheless, according to Camus (2001), Southern Peru and Northern Chile belong to the same biogeographical province. Measures of species diversity are dependent on the spatial and temporal scales. For example, the size of each sampling unit, the spatial configuration or relative proximity of sampling units across the landscape or seascape, and the spatial extent of the area from which samples are drawn affect inferences about species richness and composition (e.g. Mac Nally et al., 2004).

Finally, as in all food web studies, the number and delimitation of FGs is partly subjective. Despite our effort to cover the whole food web, important planktonic FGs are missing (e.g. microbial realm, gelatinous species) due to lack of information for some EBUEs, which prevented us from plotting graphs of richness in relation to TL classes. No benthic FG was considered, assuming that these species are not critical for biodiversity comparisons among EBUEs. However, this assumption is somewhat arbitrary and could be further evaluated. Furthermore, some FGs are more heterogeneous than others, with the number of families varying from 1 (euphausiids) to 29 (demersal fish).

4.2. Gradients of diversity

There are three widely recognized global patterns in ecology, i.e., gradients in species diversity on the latitudinal and zonal directions, plus the gradient with altitude or depth. Species richness increases from the poles to the tropics. Although the reasons of this gradient are still debated (Clarke and Gaston, 2006), Hillebrand (2004) demonstrated that it occurs in marine, terrestrial, and freshwater ecosystems, in both hemispheres. In our dataset, this gradient is not significant in the ANOVA analysis. This lack of significance is interpreted by the relatively low range of latitudes of the EBUEs, but most of all by our purposeful exclusion of the transition zones at the latitudinal boundaries of the EBUEs (Table

1). Stevens (1989) suggested that the latitudinal gradient of diversity is mainly due to seasonal variations in climate because organisms living at high latitudes tend to be generalists. The latitudinal variability of temperature is special in EBUEs, since most of it results from combined effects of solar seasonal heating and latitudinal variations in upwelling-favourable wind intensity. This in turn results in an increase in seasonal variation both poleward and equatorward, particularly in the northern hemisphere (Hervé Demarcq, IRD, pers. com.). This peculiarity explains the anomaly in the “Rapoport’s rule” reported by Stevens (1989) and partly invalidates the dispute of this rule made by Roy et al. (1998) and by Clarke and Gaston (2006), because both works ignored EBUEs. As they are defined, the four EBUEs are relatively homogenous in their dominant species richness, but differ in their species composition (high gamma diversity).

The zonal pattern is specific to marine ecology and structured by the identification of the “coral triangle”, centred on Indonesia. From this triangle the diversity shows a decreasing zonal gradient, strong to the East and a weaker to the West (Briggs, 2000). This gradient is mainly structured by tropical species from coral reef ecosystems and is not apparent in our data, since the Benguela and the Humboldt are the EBUE with the lowest richness (Table 2S).

The depth dependence of diversity is commonly described in marine ecosystems, including for pelagic fish species for which diversity decreases steeply with increasing depth (Smith and Brown, 2002). Within EBUEs, the major sub-division in richness is observed across-shelf (658 entries inshore versus 572 offshore) and is likely due to the lower diversity of habitats in the offshore sub-ecosystems and to their lower productivity (species–energy hypotheses reviewed in Clarke and Gaston, 2006). This contrast is mainly due to demersal species (68 inshore versus 44 offshore) and small pelagic fish (25 versus 9). Despite such moderate contrast in overall richness indices across-shelf, the pattern of richness according to FGs is strongly structured by this sub-division (Fig. 3), indicating a high degree of similarity among the four EBUEs, particularly in the inshore sub-ecosystems (Fig. 4; Table 5S). Furthermore, the beta diversity is high, due to differences in the species composition across and along shore, as detailed below.

4.3. Species composition

The analysis of the species composition indicates that 41% of the dominant species are only dominant in one of the 16 sub-ecosystems, showing a low degree of dispersion, not to say endemism (keeping in mind that these species could be rare but present in other sub-ecosystems, within the 10% of the biomass not represented in our dataset). At the opposite extreme, only 4% of the dominant species are shared among at least nine sub-ecosystems. Not surprisingly, when one considers the sub-ecosystems of a given EBUE, many species are shared within the two alongshore and/or the two zonal sub-divisions, although not always with the same index of relative abundance. Notable exceptions to this rule are the diatoms, which we considered as absent from all offshore sub-ecosystems, and the large pelagic fish, for which none of the dominant species was present at the same time offshore and inshore. Nonetheless, when these two FGs are removed from the multivariate analysis of species composition, a very similar cluster tree is obtained (not shown), the only major difference being that the two inshore Humboldt sub-ecosystems now clustered. This indicates that the zonal contrast is a robust pattern.

Only 5% of the dominant species are dominant in all four EBUEs and an additional 3% are found in three of the four. This is due to the large distance among EBUEs that allowed colonisation almost exclusively by the large mobile species such as some sharks, rays, dolphins, whales and birds. Although less frequently, smaller spe-

cies display ubiquity. This is the case of planktonic species that are passively transported, such as the copepod *Paracalanus parvus*, or migratory medium pelagic species like *Scomber japonicus*, both species being found in the four EBUEs. Nonetheless, molecular methods are revealing an ever-increasing number of cryptic species (e.g. Goetze 2003; Hyde et al., 2008) which may serve eventually to dampen similarities among systems at the species level. Particular small pelagic individual fish species are found only in three EBUEs at the most, e.g., *Sardinops sagax* which is absent from the Canary current, where its ecological niche is occupied by the European sardine *Sardina pilchardus* and by two species of *Sardinella*.

The more endemic, or at least sub-ecosystem-specific species (and genera) are mainly found in the southern-inshore Canary and northern-inshore Humboldt sub-ecosystems, which are both characterized by strong variations in temperature at the seasonal and interannual scales, respectively (Chavez and Messie, this issue). This observation is consistent with the individualisation of these two sub-ecosystems in the higher level of clustering. The other single sub-ecosystems (in addition to the “sister sub-ecosystems” of the previous ones, that is northern-inshore Canary and southern-inshore Humboldt) are the two inshore California sub-divisions and the two offshore Humboldt sub-divisions. In California, the presence of rivers in the north allows the presence of different anadromous species like salmonids. This ecosystem also hosts up to 70 species of the genus *Sebastes* (Hyde and Vetter, 2007), although many are at low, or poorly estimated, levels of abundance. Shelf width varies even more in the Humboldt and explains the split between its two offshore divisions. Many coastal species are found offshore of the southern Humboldt where the continental shelf is often narrower than 10 nm. This is for instance the case for *Centropages brachiatus*, *S. sagax*, *Engraulis ringens* and pinnipeds. Other explanations could be found by studying the phylogeny of the different species in relation with continental drift, but this study is beyond the scope of this work.

4.4. Wasp-waist food-web?

Conventional hypotheses on speciation (review in Pimm, 1991) suggest that it is driven first by the complexity of habitat or diversity of resources (number of niches) and then by predation and competition (Shurin and Allen, 2001). Natural ecosystems are usually not in equilibrium and moderate habitat disturbance results in higher biodiversity (Van der Maarel, 1993; Reice, 1994). However, species diversity in EBUEs is low compared to other ecosystems despite their unstable environment at different scales (Sakko, 1998; Ottens and Nederbragt, 1992; Blanchette et al., this issue). It is thought that environmental instability in EBUEs is so high that it prevents the fine-tuning of genotypes to local conditions and favours generalist feeders as a result of variability in single prey abundance (McNaughton and Wolf, 1970; Barnes and Hughes, 1988; Sakko, 1998). Species diversity is expected to be higher when the number of predators is high because they prevent prey species from monopolizing some important and limiting resource (Fryer, 1965), among other processes (Shurin and Allen, 2001). In addition, Paine (1966) suggests that the number of predators decreases when the ecosystem is unstable, which is the case for EBUEs, especially for those in the Pacific Ocean, exposed to El Niño and La Niña events. Nonetheless, our results do not indicate systematically lower predator diversity in the Humboldt and California ecosystems (Fig. 4).

EBUE food webs are supposedly (Bakun, 1996) characterized by a wasp-waist architecture (*sensu* Rice, 1995), although it has been quantified only in South Africa (including its Indian Ocean coast; Cury et al., 2000) as far as we know. In this architecture, “there is often a crucial intermediate TL, occupied by small, plankton-

feeding pelagic fishes, that is typically dominated by only one, or at most several, species [...] For example, the fish biomass of temperate coastal upwelling systems tends to be dominated by one species of sardine and one species of anchovy, and most often only one of the two is dominant at any particular time” (Bakun, 1996). Furthermore, according to Rice (1995) “the presence of this species as the primary channel for energy flow from lower to higher TLs makes it impossible, in theory and practice, to relate dynamics of any single upper level predator to any lower prey”. Here we question these two characteristics of the wasp-waist architecture. First the number of dominant small pelagic fish species in the inshore sub-divisions of the four EBUEs varies from two (Humboldt) to four (California), with high or high-medium evenness (Table 4S, Supplementary information). It can be argued that at a given time (regime) only one species of sardine or anchovy dominates, as observed in the California Current during the historical period (MacCall, 1996), but paleontological records suggest that this has not always been the case (Baumgartner et al., 1992; Gutiérrez et al., 2008; Valdés et al., 2008). In the Northern Humboldt ecosystem, anchovy were as abundant as sardine during the last “sardine regime” (Gutiérrez et al., 2007). In the southern part of the Southern Humboldt, the catches of common sardine (*Strangomera bentincki*) were similar to those of anchovy during the decades 1960–1990s, reflecting a similar level of abundance at least during the 1990s when abundance estimates were available (Cubillos et al., 2002). In the Benguela and Canary ecosystems two or three small pelagic fish species were abundant at the same time according to acoustic surveys. These species are *S. sagax*, *Engraulis encrasicolus* and *Etrumeus whiteheadi* in the Benguela (Pecquerie et al., 2004; van der Lingen et al., 2006) and *S. pilchardus*, *E. encrasicolus*, *Sardinella aurita* and/or *S. maderensis* in the Canary ecosystem (Berraho et al., 2005).

Another and more important reason to dispute the wasp-waist architecture in EBUEs is that other FGs with trophic levels spanning from 2.5 to 3.8, that is just below or above that of SPF species, display levels of richness similar to SPF (Fig. 4; Table 2S) and some of them are abundant. The later is true at least for copepods, euphausiids, meso-pelagic fish and medium-sized pelagic fish (potential explanations for changes in the richness of FGs from the lowest to highest TL are provided in the Supplementary information). As result, SPF are not always “the primary channel for energy flow from lower to higher TLs” and several energy transfer pathways can take place. Trophic models available for the four EBUEs (Shannon et al., 2003; Hinke et al. 2004; Sidi and Guénette, 2004; Neira et al., this issue; Tam et al., 2008; Field et al. 2006; Brand et al. 2007) also show that food webs of EBUEs are networked at all TLs. Despite some limitations of these models (poor estimates of primary production, overestimation of phytoplankton consumption by SPF compared to zooplankton, lack of data for many functional groups, debatable number and definition of FGs, difficulties in estimation of diet and its variability, etc.) we assumed that Table 4 provides realistic orders of magnitude of the trophic flows. These results clearly show that SPF species seldom channel most of the trophic flow, especially the inflow.

5. Conclusions

Despite its limitations, our semi-quantitative approach to analyzing diversity within different functional groups yielded results in agreement with the major theories and observations of diversity gradients. The biggest departure from existing theories is the lack of support for a wasp-waisted architecture and functioning of the food-web, which concurs with the observation of Taylor et al. (2008) in the Northern Humboldt and Blanchette et al. (this issue) on rocky intertidal communities of EBUEs. The four EBUEs and

their sub-divisions display similar low levels of richness of several FGs of intermediate TL, particularly in their inshore sub-divisions, and rarely does a single species channel most the energy flow from lower to higher TLs. Although these traits require further research, these general results are likely to be due to the challenges associated with living in unstable pelagic environments. We did not find evidence for different food web architecture (richness or evenness of FGs) of the Humboldt ecosystem linked to its high fish production. Recent studies suggest that the high fish production in the Humboldt ecosystem could be related to the early life history dynamics of its fish (Brochier et al., this issue) and to the access to highly energetic food (Espinoza et al., this issue).

Acknowledgements

This is a contribution of the EUR-OCEANS network of excellence, EC Contract No. 511106 and of the ECO-UP program (UR097) of IRD. We would not have been able to complete the project without help from the following persons: Bill Peterson, Dave Mackas, Moira Galbraith, Mark Ohman, Bertha Lavaniegos, Ismael Gárate and Aida Martínez Campos for the California Current; Ruben Escribano, Elisa Goya, Patricia Ayón, Miguel Romero and Carmen Morales for the Humboldt system; Deon Louw for the Northern Namibia system, and Jenny Huggett for the Southern Benguela system; Alain Fonteneau and Francis Marsac who provided us information on tunas; Rainer Froese who compiled TL and Lm data from FishBase and Dave Checkley who made useful editorial corrections.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.pocean.2009.07.034.

References

- Bakun, A., 1996. Patterns in the ocean: ocean processes and marine population dynamics. University of California Sea Grant, San Diego, California, USA, in cooperation with Centro de Investigaciones Biológicas de Noroeste, La Paz, Baja California Sur, Mexico.
- Barnes, R.S.K., Hughes, R.N., 1988. An Introduction to Marine Biology, second ed. Blackwell Scientific Publications, London.
- Baumgartner, T.R., Soutar, A., Ferreira-Bartrina, V., 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. California Cooperative Oceanic Fisheries Investigations Reports 33, 24–40.
- Berraho, A., Ettahiri, O., Letourneur, Y., Orbi, A., Yahyaoui, A., 2005. Importance des paramètres hydrologiques dans la distribution des oeufs et des larves des petits pélagiques du sud de l'Atlantique marocain. Cybium 29 (1), 21–31.
- Blanchette, C., Wieters, E., Broitman, B., this issue. Trophic structure in rocky intertidal communities across the California, Humboldt and Benguela upwelling ecosystems.
- Brand, E.J., Kaplan, I.C., Harvey, C.J., Levin, P.S., Fulton, E.A., Hermann, A.J., Field, J.C., 2007. A spatially explicit ecosystem model of the California Current's food web and oceanography. NOAA Technical Memorandum NMFS-NWFSC-84, 145 p.
- Briggs, J.C., 2000. Centrifugal speciation and centre of origin. Journal of Biogeography 27 (5), 1183–1188.
- Brochier, T., Colas, F., Lett, C., Echevin, V., Cubillos, L.A., Tam, J., Chlaida, M., Mullon, C., Fréon, P., this issue. Small pelagic fish reproductive strategies in upwelling systems: a natal homing evolutionary model to study environmental constraints.
- Camus, P., 2001. Biogeografía marina de Chile continental. Revista Chilena de Historia Natural 74, 587–617.
- Carr, M.-E., Kearns, E.J., 2003. Production regimes in four Eastern boundary current systems. Deep-Sea Research II 50, 3199–3221.
- Chao, A., 2005. Species richness estimation. In: Balakrishnan, N., Read, C.B., Vidakovic, B. (Eds.), Encyclopedia of Statistical Sciences. Wiley, New York, pp. 7909–7916.
- Chavez, F., Messie, M.A., this issue. Comparative analysis of eastern boundary upwelling ecosystems.
- Clarke, A., Gaston, K.J., 2006. Climate, energy and diversity. Proceeding of the Royal Society B 273, 2257–2266.
- Cubillos, L.A., Bucarey, D.A., Canales, M., 2002. Monthly abundance estimation for common sardine *Strangomera bentincki* and anchovy *Engraulis ringens* in the central-southern area off Chile (34–40°S). Fisheries Research 57, 117–130.
- Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñones, R.A., Shannon, L.J., Verheye, H.M., 2000. Small pelagic in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. ICES Journal of Marine Science 57, 603–618.
- Demarcq, H., this issue. Trends in primary production, sea surface temperature and winds in upwelling systems (1998–2007). Progress in Oceanography.
- Dray, S., Dufour, A.B., Chessel, D., 2007. The ade4 package – II: two-table and K-table methods. R News 7 (2), 47–54.
- Espinoza, P., Bertrand, A., van der Lingen, C.D., Garrido, S., Rojas de Mendiola, B., this issue. Diet of sardine (*Sardinops sagax*) in the northern Humboldt Current system and comparison with the diets of clupeoids in this and other eastern boundary upwelling systems. Progress in Oceanography.
- Field, J.C., Francis, R.C., Aydin, K., 2006. Top-down modeling and bottom-up dynamics: linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. Progress in Oceanography 68, 238–270.
- Fryer, G., 1965. Predation and its effects on migration and speciation in African fishes: a comment. Proceedings of the Zoological Society of London 144, 3001–3010.
- Goetze, E., 2003. Cryptic speciation on the high seas; global phylogenetics of the copepod family Eucalanidae. Proceedings of the Royal Society of London Series B – Biological Sciences 270 (1531), 2321–2331.
- Gutiérrez, M., Swartzman, G., Bertrand, A., Bertrand, S., 2007. Anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) spatial dynamics and aggregation patterns in the Humboldt Current ecosystem, Peru, from 1983–2003. Fisheries Oceanography 16, 155–168.
- Gutiérrez, D. et al., 2008. Rapid reorganization in ocean biogeochemistry off Peru towards the end of the Little Ice Age. Biogeosciences Discussion 5, 3919–3943.
- Hector, A. et al., 1999. Plant diversity and productivity experiments in European grasslands. Science 286, 1123–1127.
- Hillebrand, H., 2004. On the generality of the latitudinal diversity gradient. American Naturalist 163, 192–211.
- Hinke, J.T., Kaplan, I.C., Aydin, K., Watters, G.M., Olson, R.J., Kitchell J.F., 2004. Visualizing the food-web effects of fishing for tunas in the Pacific Ocean. Ecology and Society 9 (1), 10. <http://www.ecologyandsociety.org/vol9/iss1/art10/>.
- Hoof, R.C., Peterson, W.T., 2006. Copepod biodiversity as an indicator of changes in ocean and climate conditions of the northern California current ecosystem. Limnology Oceanography 51 (6), 2607–2620.
- Hsieh, C.H., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M., Sugihara, G., 2006. Fishing elevates variability in the abundance of exploited species. Nature 443, 859–862.
- Hyde, J.R., Vetter, R.D., 2007. The origin, evolution, and diversification of rockfishes of the genus *Sebastes* (Cuvier). Molecular Phylogenetics and Evolution 44, 490–811.
- Hyde, J.R., Kimbrell, C.A., Budrick, J.E., Lynn, E.A., Vetter, R.D., 2008. Cryptic speciation in the vermilion rockfish (*Sebastes miniatus*) and the role of bathymetry in the speciation process. Molecular Ecology 17, 1122–1136.
- Jarre-Teichmann, A., Shannon, L.J., Moloney, C.L., Wickens, P.A., 1998. Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems. South African Journal of Marine Science 19, 391–414.
- Kindt, R., 2002. Methodology for tree species diversification planning for African agroecosystems. Thesis Ghent University, Belgium, 332 p.
- Koleff, P., Gaston, K.J., Lennon, J.J., 2003. Measuring beta diversity for presence-absence data. Journal of Animal Ecology 72, 367–382.
- Legendre, P., Legendre, L., 1998. Numerical Ecology, second ed. Elsevier Science, Amsterdam, 853 p.
- Lindman, H.R., 1974. Analysis of Variance in Complex Experimental Designs. W.H. Freeman & Co., San Francisco.
- Longhurst, A., 2007. Doubt and certainty in fishery science. Are we really headed for a global collapse of stocks? Fisheries Research 86, 1–5.
- Loreau, M., Naem, S., Inchausti, P., Bengtsson, J., Grime, J.-P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808.
- Mac Nally, R., Fleishman, E., Bulluck, L.P., Betrus, C.J., 2004. Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. Journal of Biogeography 31, 917–929.
- MacCall, A.D., 1996. Patterns of low-frequency variability in fish populations of the California Current. California Cooperative Oceanic Fisheries Investigations Reports 37, 100–110.
- Mackas, D.L., Strub, P.T., Thomas, A., Montecino, V., 2005. Eastern ocean boundaries pan-regional overview. In: Robinson, A.R., Brink, K. (Eds.), The Sea, vol. 14. Harvard University Press, Cambridge, MA, pp. 21–59 (chapter 2).
- Magurran, A.E., 1998. Measuring richness and evenness. Trends in Ecology & Evolution 13 (4), 165–166.
- Marchant, R., 1999. How important are rare species in aquatic community ecology and bioassessment? A comment on the conclusions of Cao et al. Limnology Oceanography 44, 1840–1841.
- McNaughton, S.J., 1994. Biodiversity and function of grazing ecosystems, in Biodiversity and ecosystem function. In: Schulze, E.-D., Mooney, H.A. (Eds.). Springer Verlag, Berlin, pp. 361–405.
- McNaughton, S.J., Wolf, L.L., 1970. Dominance and the niche in ecological systems. Science 167, 131–139.
- Neira, S., Arancibia, H., Shannon, L.J., this issue. Interaction strength and keystones in upwelling food webs: comparing the southern Benguela and the southern Humboldt.

- Ottens, J.J., Nederbragt, A.J., 1992. Planktic foraminiferal diversity as indicator of ocean environments. *Marine Micropaleontology* 19, 13–28.
- Paine, R.T., 1966. Food web complexity and species diversity. *American Naturalist* 100, 65–75.
- Pecquerie, L., Drapeau, L., Freon, P., Coetzee, J.C., Leslie, R.W., Griffiths, M.H., 2004. Distribution patterns of key fish species of the southern Benguela ecosystem: an approach combining fishery-dependent and fishery-independent data. *African Journal of Marine Science* 26, 115–139.
- Perlman, D.L., Adelson, G., 1997. *Biodiversity. Exploring Values and Priorities in Conservation*. Blackwell Science, Oxford, UK.
- Pimm, 1991. *The Balance of Nature?* University of Chicago Press, Chicago.
- Planque, B., Fromentin, J.-M., Cury, P., Drinkwater, K., Perry, R.I., in press. How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems*. doi:10.1016/j.jmarsys.2008.12.018.
- R Development Core Team, 2007. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <<http://www.R-project.org>>.
- Reice, S.R., 1994. Nonequilibrium determinants of biological community structure. *American Scientist* 82, 424–435.
- Rice, J., 1995. Food web theory, marine food webs, and what climate change may do to northern marine fish populations. *Canadian Special Publication of Fisheries and Aquatic Sciences* 121, 561–568.
- Roy, K., Jablonski, D., Valentine, J.W., Rosenberg, G., 1998. Marine latitudinal diversity gradients: tests of causal hypotheses. *Proceedings of the National Academy of Science of USA* 95, 3600–3702.
- Sakko, A.L., 1998. The influence of the Benguela upwelling system on Namibia's marine biodiversity. *Biodiversity and Conservation* 4, 419–433.
- Shannon, L.J., Moloney, C.L., Jarre, A., Field, J.G., 2003. Trophic flows in the southern Benguela during the 1980s and 1990s. *Journal of Marine Systems* 39, 83–116.
- Shurin, J.B., Allen, E.G., 2001. Effects of competition, predation, dispersal on local and regional species richness. *American Naturalist* 158, 624–637.
- Sidi, M.T., Guénette, S., 2004. Modèle trophique de la ZEE mauritanienne: comparaison de deux périodes (1987 et 1998). In: *West African Marine Ecosystems: Models and Fisheries Impacts*. In: Palomares, M.L.D., Pauly, D. (Eds.), *Fisheries Centre Research Reports*, vol. 12 (7). Fisheries Centre, UBC, Vancouver, pp. 12–38.
- Smith, K.F., Brown, J.H., 2002. Patterns of diversity, depth range and body size among pelagic fishes along a gradient of depth. *Global Ecology and Biogeography* 11 (4), 313–322.
- Stevens, G.C., 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* 133, 240–256.
- Tam, J., Taylor, M.H., Blaskovic, V., Espinoza, P., Ballón, R.M., Díaz, E., Wosnitza-Mendo, C., Argüelles, J., Purca, S., Ayón, P., Quiquiza, L., Gutiérrez, D., Goya, E., Ochoa, N., Wolff, M., 2008. Trophic modeling of the Northern Humboldt current ecosystem, Part I: comparing trophic linkages under La Niña and El Niño conditions. *Progress in Oceanography* 79 (2–4), 352–365.
- Taylor, M.H., Tam, J., Blaskovic, V., Espinoza, P., Ballón, R.M., Claudia Wosnitza-Mendo, C., Argüelles, J., Purca, Díaz, E., Ochoa, N., Ayón, P., Goya, E., Gutiérrez, D., Quiquiza, L., Wolff, W., 2008. Trophic modeling of the Northern Humboldt Current Ecosystem, Part II: elucidating ecosystem dynamics from 1995 to 2004 with a focus on the impact of ENSO. *Progress in Oceanography* 79 (2–4), 366–378.
- Tilman, D., Wedin, D., Knops, J., 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379, 718–720.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition of ecosystem processes. *Science* 277, 1300–1302.
- Valdés, J., Ortlieb, L., Gutiérrez, D., Marinovic, L., Vargas, G., Sifeddine, A., 2008. 250 years of sardine and anchovy scale deposition record in Mejillones Bay, Northern Chile. *Progress in Oceanography* 79, 198–207.
- van der Lingen, C.D., Shannon, L.J., Cury, P., Kreiner, A., Moloney, C.L., Roux, J.-P., vaz Velho, F., 2006. Resource and ecosystem variability, including regime shifts, in the Benguela current system. In: Shannon, V., Hempel, G., Malanotte-Rizzoli, P., Moloney, C., Woods, J. (Eds.), *Benguela: Predicting a Large Marine Ecosystem*. Elsevier, Amsterdam, pp. 147–184.
- Van der Maarel, E., 1993. Some remarks on disturbance and its relation to diversity and stability. *Journal of Vegetation Science* 4, 733–736.
- Ward, J.H., 1963. Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* 58, 236.
- Warwick, R.M., 1986. A new method for detecting pollution effects on marine macrobenthic communities. *Marine Biology* 92, 557–562.
- Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon* 21, 213–251.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314 (5800), 787–790.
- Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment : the insurance hypothesis. *Proceedings of the National Academy of Sciences, USA* 96, 1463–1468.