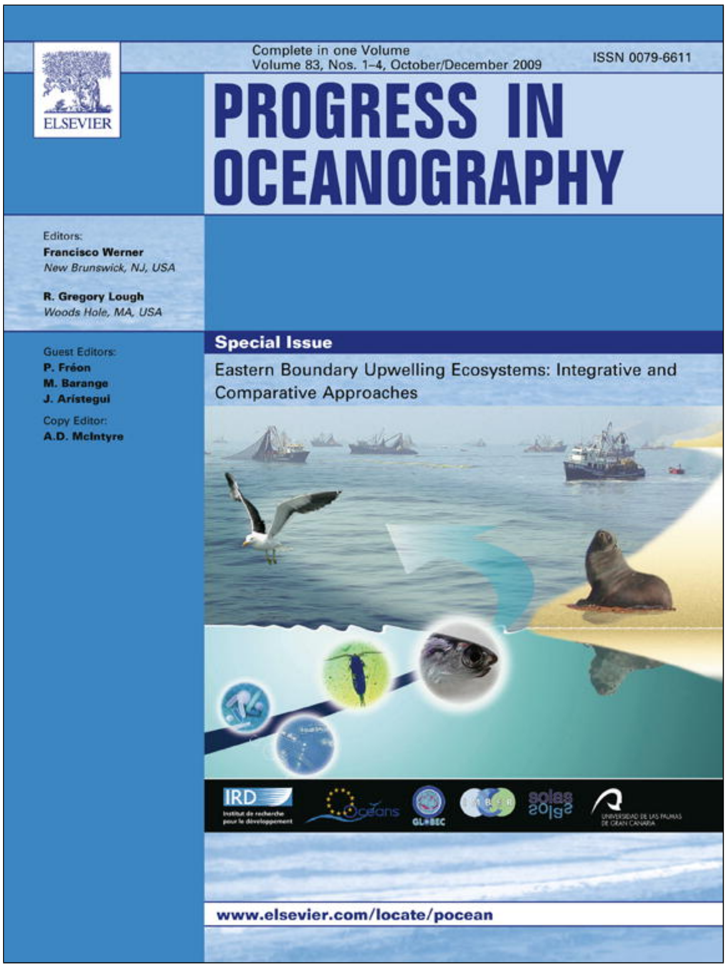
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Preface

Eastern Boundary Upwelling Ecosystems: Integrative and comparative approaches

1. Introduction

Eastern Boundary Upwelling Ecosystems (EBUEs) are some of the most productive marine ecosystems of the world (Fig. 1); the four main EBUEs, the Canary, California, Humboldt and Benguela Currents provide one fifth of the marine fish global catch (Table 1), and contribute significantly to securing food and livelihood strategies in many developing countries. EBUEs are narrow strips of the ocean that extend latitudinally over several thousands of kilometres and longitudinally to beyond the continental shelves (whose widths range from 20 to 200 km). For this reason their limit is often arbitrarily set to the 200 nautical miles (370 km) offshore limit of the national EEZs, over water depths in excess of 1000 m. They are located on the western margin of the continents (eastern parts of the oceans), on each side of the Equator. In these regions, intense trade winds combined with the earth's rotation generate coastal upwelling, bringing cold, nutrient-rich water from the deep ocean (of the order of 200–300 m) to the surface. The arrival of this water to the sunlight-exposed surface layer fuels primary production, which supports a highly productive food web. It also contributes very significantly to gas exchanges between the ocean and the atmosphere, particularly CO_2. The dependency of EBUEs on environmental drivers makes them particularly sensitive to anthropogenic climate change. Understanding how climate change will affect these regions is crucial, both in terms of the biogeochemical balance of the planet, and regarding the social and economic consequences of potential changes in global fish production.

Between the 2nd and 6th of June 2008 over 350 scientists from 40 countries and five continents attended an International symposium on Eastern Boundary Upwelling Ecosystems (EBUEs), held in Las Palmas, Gran Canaria (Spain). The symposium was the first international effort to present the state-of-the-art in our understanding of EBUEs, with particular emphasis on integrating our knowledge from climate processes all the way to fisheries practices, and comparing the dynamics of EBUEs across the world. The ultimate goal was to identify climate change impacts on EBUEs and pave the way for adequate adaptations strategies aimed at reducing vulnerability of people and places. The event was organised and supported by the Institute of Research for Development (IRD), the European network of excellence for Ocean Ecosystems Analysis (EUR-OCEANS), The University of Las Palmas de Gran Canaria (ULPGC), and the international research programmes Global Ocean Ecosystem Dynamics (GLOBEC), Integrated Marine Biogeochemistry and Ecosystem Research (IMBER) and Surface Oceans and Lower Atmosphere (SOLAS). Financial support was further provided by the southern African BENEFIT programme, the German Society for Technical Cooperation (GTZ), the Scientific Committee on Oceanic Research (SCOR), the Spanish Ministry of Education and Science (MEC) and the Autonomous Government of the Canary Islands (GAC). These grants allowed us to fund 26 scientists and students from developing countries and to partly support 20 keynote speakers. This special issue of Progress in Oceanography presents a collection of research papers resulting from the symposium.

The conference followed a number of international meetings that have focused on EBUEs in the recent past, including:

- The 1978 the Food and Agriculture Organization (FAO), the International Council for the Exploration of the Sea (ICES) and the Intergovernmental Oceanographic Commission (IOC) symposium "The Canary Current: studies of an upwelling system", also held in Las Palmas, Spain (Hempel, 1982).
- A series of symposia held in Cape Town, South Africa, under the auspices of the Benguela Ecology Programme (BEP): the International Symposium on "Population and Community Ecology in the Benguela Upwelling Region and Comparable Frontal systems" in 1986 (Payne et al., 1987), the "Benguela Trophic Functioning Symposium" in 1991 (Payne et al., 1992) and the "Benguela Dynamics Symposium" in 1996 (Pillar et al., 1998).
- The California and Humboldt Currents systems received the attention of the 2000 symposium "Dynamics of Pacific Coastal Upwelling Ecosystems" held in Corvallis, USA (http://www.piscoweb.org/outreach/events/symposium2000).
- More recently, IRD, the Instituto del Mar del Perú (IMARPE) and FAO organised the 2006 "International conference on the Humboldt Current system" in Lima, Peru (Bertrand et al., 2008a).

However, none of these symposia explicitly covered the four main EBUEs, namely the California, Humboldt, Canary and Benguela Current ecosystems. The accumulation of knowledge on the dynamics of EBUEs in the last decades, particularly fuelled by recent technological, methodological and conceptual advances on the functioning of these systems, led us to believe that an integrated and comparative symposium was both possible and timely. Such a symposium would consider most aspects of the dynamics, structure and functioning of the four major eastern boundary upwelling. These aspects include climate and ocean dynamics, climate change, physics of the ocean and atmosphere, biogeochemistry, ecosystem production, ecology, food web structure and dynamics, trophic interactions, and fisheries assessment and management. Furthermore, the comparative emphasis of this symposium allowed a better understanding of the key processes responsible of the productivity and dynamics of the four main EBUEs.

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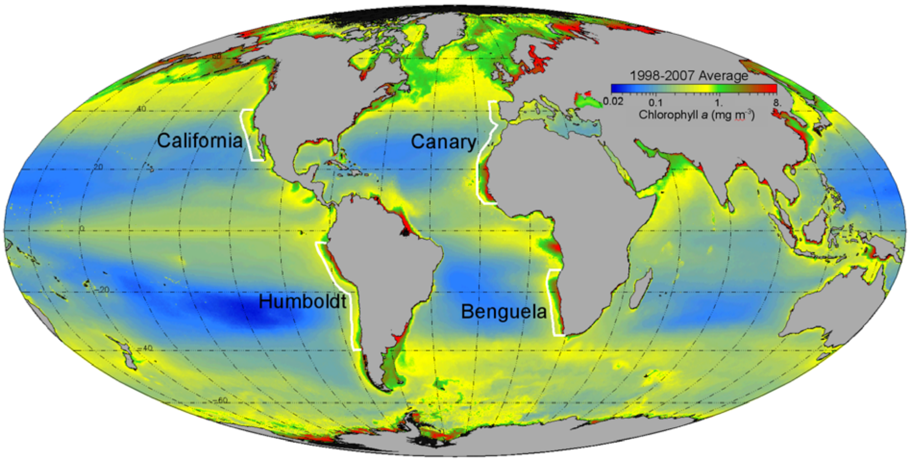

Fig. 1. Chlorophyll-a concentration from SeaWiFS for the 1998–2007 period and EBUEs location arbitrarily delimited by the 200 nautical miles offshore limit and latitudinal extensions including seasonal upwelling zones (courtesy of H. Demarcq, IRD, France).

Table 1
Estimated average yearly catches (metric tons) by commercial fisheries from different countries operating in the EBUEs during the 2004–2007 period (total catches for these years were 19.7, 18.5, 15.2 and 15.5 million tons respectively). Source: FAO FishStat

Country	Benguela	California	Canary	Humboldt	Total
Peru				8159,500	8159,500
Chile				3598,488	3598,488
Morocco			842,123		842,123
South Africa	737,250				737,250
Mexico		658,659		684	659,343
United States of America		554,246		519	554,765
Namibia	501,161				501,161
Senegal			306,239		306,239
Mauritania			213,589		213,589
China	283	3450	1400	195,106	200,238
Portugal	1268		181,642		182,909
Russian federation		597	174,254		174,851
Lithuania			114,233	6186	120,419
Spain	6913	5299	101,861	3017	117,090
Netherlands			82,894	7862	90,756
Ukraine			69,078		69,078
Angola	52,518				52,518
Latvia			51,039		51,039
Panama		29,784	4526	6724	41,034
Japan	3311	7711	3652	26,201	40,875
Republic of Korea	2877	4451	9800	11,477	28,605
Gambia			23,866		23,866
Ireland			16,656		16,656
Taiwan, Province of China	2552	7577	1861	452	12,441
Venezuela, Republic of Bolivia		5899		5334	11,233
Germany			7731		7731
France			6834		6834
Liberia			5660		5660
United Kingdom	166		5270		5437
Italy			5351		5351
Greece			2448		2448
Total	1,308,300	1277,672	2,232,005	12,021,549	16,839,525

The following filters were used:
Areas: Atlantic Northeast (ANE), Atlantic Eastern Central (AEC), Atlantic Southeast (ASE), Pacific Northeast (PNE), Pacific Eastern Central (PEC), Pacific Southeast (PSE).
Fishing countries: (possibly in all above areas by default, except when restricted to area indicated into brackets): Angola (estimated as 1/3 catches in the ASE), Chile, China, France (AEC), Gambia, Germany (AEC), Greece (AEC), Ireland (AEC), Italy (AEC), Japan (AEC, ASE, PNE, PEC, PSE), Korea (AEC, ASE, PNE, PEC, PSE), Latvia (AEC), Liberia (AEC, PSE), Lithuania (AEC, PSE), Mauritania, Mexico, Morocco, Namibia, Netherlands (AEC, PSE), Panama (AEC, PEC, PSE), Peru, Portugal, Russia Federation (AEC, PEC, PNE), Senegal, South Africa, Spain (estimated as 1/5 of catches in the ANE, except for California pilchard and North Pacific hake (100%)), AEC, ASE, PEC, PSE), Taiwan, Province of China, Ukraine (AEC), UK (AEC, ASE), USA (estimated as 1/5 of catches in the PNE, PEC, PSE), Venezuela.
Species: See Table 2.

In order to achieve the objective of addressing integrative and comparative aspects, the sessions were not geographically organised, encouraging comparative investigations and multi-disciplinary integration. The vision behind this structure was the recognition that collaboration and cooperation between countries and disciplines is essential if we want to successfully face the challenges presented by climate change, overexploitation of marine resources and economic globalisation.

In this introductory paper we provide a brief presentation of the 42 papers published in this volume. The volume starts with four reviews (one for each EBUE) followed by an additional overarching comparative overview of EBUEs, and is then organised along the major sessions of the symposium. A final section deals with future research directions.

2. Ecosystem reviews

The reviews of the four EBUEs present some similarities and discrepancies in organisation and focus. In all of them, the authors felt it necessary to split the ecosystems into 3–5 regions based on criteria such as the coastline orientation, physical oceanography traits and seasonality, biogeography, external input, location of exploited fish stocks, etc. In the Benguela EBUE, Hutchings et al. (2009) identified four regions: the Angolan subtropical zone, the northern Benguela, the Lüderitz (intense) upwelling area, and finally the southern Benguela and Agulhas Bank region. In the California EBUE, Checkley and Barth (2009) defined three subdivisions: northern, central and southern California. In the Canary EBUE, Arístegui et al. (2009) split the ecosystem in five sub-regions (Galician, Portuguese, Gulf of Cadiz, Moroccan and Mauritanian-Senegalese), whereas in the Humboldt EBUE, Montecino and Lange (2009) identified three subsystems: northern-central Peru, southern Peru and central Chile (upwelling shadow), and finally central-southern Chile. The latitudinal extensions and subregional splitting of the four EBUEs in these reviews are not identical to those used in the comparative overview (Chavez and Messié, 2009) or indeed to other contributions to the volume. These discrepancies reflect how difficult it is to define clear limits between regions depending on the criteria used.

The Benguela ecosystem is unusual as it is latitudinally bounded by two stratified subtropical or warm temperate boundary regions on either side of the major wind-driven upwelling region (19–34°S), which itself is subdivided at 26°S by the powerful Lüderitz upwelling cell. Widespread oxygen-depleted waters and sulphur eruptions result from local and remote forcing, restricting the habitat available for different species. The existence of costal jets and mesoscale structures, influenced by the retroflexion of the Agulhas Current, impact biological processes in diverse ways, forcing many species to cross boundary areas during their life-history cycles. Several fish stocks have experienced collapses in the Benguela region in the 1960s and 1970s, with different recovery trajectories in the north and the south, the former being currently in a significantly depleted state. The role global climate change will have in the Benguela in terms of shifting boundaries and weakening or intensifying gradients is being explored (Hutchings et al., 2009).

The California ecosystem seems characterized by the importance of offshore, windstress curl-driven upwelling that results in a spatially large, productive habitat (Checkley and Barth, 2009). This ecosystem, as well as the other Pacific Ocean EBUE, the Humboldt ecosystem (Montecino and Lange, 2009), is particularly impacted by basin-scale events such as coastal-trapped Kelvin and Rossby waves, El Niño events and processes connected with the Pacific Decadal Oscillation (PDO). As in other ecosystems, high surface production results in deep and bottom waters depleted of oxygen, arguably even more extended than in the Benguela ecosystem. The presence of oxygen-depleted waters near the seabed allowed the preservation of fish scales in anoxic sediments. Paleontological studies were pioneered in California, showing interdecadal cycles of variability in the abundance of small pelagic fish, subsequently confirmed by similar studies in other EBUEs. In the California ecosystem, fishing has depleted demersal stocks more than pelagic stocks, and marine mammals, including whales, are recovering.

The Canary Current ecosystem is the only one with an offshore archipelago that benefits from the export of coastal upwelled waters rich in organic and plankton matter, though strong filaments. This ecosystem is also characterized by substantial freshwater input in its polewardmost region (Arístegui et al., 2009). This last property is shared with the California ecosystem, but here with the additional complexity provided by the presence of "rías" (long narrow inlets shaped by the incomplete immersion of river valleys). These features, plus the variability in coastline configuration, shelf width, coastal upwelling, nutrient fertilisation, productivity, and retentive versus dispersive physical mechanisms, among other factors, justify the subdivision of this ecosystem into five sub-regions to explain their differences in enrichment processes, productivity, fish distribution and abundances. The Canary ecosystem has warmed the fastest of all the EBUEs, which is the likely cause of the observed slight decrease in productivity over the last decades (Arístegui et al., 2009), in contrast with the positive trend in productivity in other EBUEs (Chavez and Messié, 2009; Demarcq, 2009). However, these overall trends are not directly reflected in the fishing trends of the Canary Current ecosystem, and the relative contribution of natural versus human-induced variability in the populations of at least small pelagic fish continues to be difficult to disentangle.

The Humboldt ecosystem is the EBUE with the strongest interannual (ENSO) and interdecadal variability that affects its biological and abiotic components, ecosystem processes, and fisheries yield, in addition to the variability occurring at seasonal scales (Montecino and Lange, 2009). Its subsurface oxygen minimum zone is shallower, more oxygen-depleted and more extended than in the other EBUEs (Chavez and Messié, 2009). Despite these apparently detrimental effects, and the fact that this ecosystem does not have the highest levels of primary production, it provides the highest contribution to fish production (Table 1), mainly due to a single species: the Humboldt anchovy (anchoveta) *Engraulis ringens*. Sediment studies from the Chilean continental margin encompassing the last 20,000 years of deposition reveal changes in subsurface conditions in the HCS during deglaciation, interpreted to include: a major reorganisation of the oxygen minimum zone (OMZ); a deglacial increase in denitrification decoupled from local marine productivity; and higher deglacial and Holocene paleoproductivities compared to the Last Glacial Maximum at and south of 35°S, while this scheme is reversed for north-central Chile (Montecino and Lange, 2009).

3. Comparative approaches between EBUEs and between EBUEs and non-EBUEs

Three papers focused specifically on the comparison between four ecosystems: Chavez and Messié's (2009) overarching review on the functioning of EBUEs; Fréon et al.'s (2009) biodiversity analysis and Blanchette et al.'s (2009) rocky intertidal communities study. However, the scope of the symposium was such that most papers in this volume compared at least two EBUEs and/or EBUEs with non-EBUEs such as the Kurushio system (e.g. Barange et al., 2009; Espinoza et al., 2009; Brochier et al., 2009; Chaigneau et al., 2009; Demarcq, 2009; Messié et al., 2009; Tapia et al., 2009; Thomas, 2009), as will be discussed later on.

Chavez and Messié (2009) identified common characteristics and processes in the four EBUEs, from physical forcing to top predators' response, and underlined some of their differences. The geographical setting and scale of EBUEs are important in determining the characteristics of each system. Trade winds play a significant role in modulating the intensity of upwelling processes and the depth of the thermocline. So does latitudinal location: there are clear North–South patterns in the doming of the thermocline near the equator and deepening in the subtropical gyres; weather-driven mixing patterns in high latitudes and river discharges close to equator are also observed. Consequently, each EBUE has 3–4 well-defined latitudinally distributed biomes. The southern part of the Benguela ecosystem is strongly influenced by the powerful Agulhas Current that connects two ocean basins; the Canary ecosystem is characterized by its complex topography and circulation, a strong seasonality at the poleward and equatorward ends and the influence of the Mediterranean on the connectivity between the Iberian Peninsula and Northwest Africa; the Humboldt ecosystem is notable by its extraordinary anchovy production concentrated on its northern sub-region and whose productivity is still not fully understood (Chavez and Messié, 2009).

Fréon et al. (2009) studied and compared species diversity of the four major EBUEs with the aim of better understanding their functioning. They defined Functional Groups (FGs) of organisms, which span from plankton to top predators, and used a semi-quantitative approach focusing on dominant species. The analysis was completed by the study of trophic flows through the small pelagic fish FG. The data were interpreted, based on latitudinal, zonal and depth gradients of diversity. Surprisingly, this analysis did 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 trophic levels (TLs). Instead, similar low levels of richness were observed in many FGs of intermediate TL, allowing several energy transfer pathways. The differences in richness and evenness among EBUEs were minor and did not explain the higher secondary and tertiary productivity of the Humboldt ecosystem compared to other EBUEs.

Blanchette et al. (2009) investigated the biological and trophic structure rocky intertidal communities of the Benguela, California and Humboldt EBUEs, plus the New Zealand region for comparison. They concluded that California was taxonomically the richest, and Humboldt the poorest region, consistent with their assertion that strongly seasonal, predictive environments are relatively low in diversity. The functional and trophic structures were otherwise remarkably similar across the four regions, with no evidence of wasp-waist structure. Macrophytes were slightly dominant over filter-feeders in terms of space occupancy in all regions except the Benguela, and the densities of herbivorous grazers were greatest in California and Benguela and far outnumbered carnivore densities in all regions. Despite similarities, the overall structure of the communities from these regions differed significantly, supporting the hypothesis that the biological and ecological consequences of similar physical forcing mechanisms are likely to be context-dependent.

4. Physics of the ocean and climate change influences on ocean–atmosphere exchanges

Recent advances in modelling and observational techniques – of the spatial and temporal variability of EBUEs. Higher definition studies of wind forcing have revealed complex patterns that interact with coastal topography in ways that are being coupled to increasingly realistic ocean models. Remote sensing techniques at relatively high spatial resolution provide gradually longer and more reliable time-series to allow comparative studies between EBUEs on multi-scaled patterns of variability (see Section 11). Chaigneau et al. (2009) investigated eddy activity in the four major EBUEs, using 15 years of satellite altimetry data. Based on the analysis of more than 4000 long-lived eddy trajectories they showed that cyclonic and anticyclonic eddies are generated along continents, and propagate westward with velocities increasing toward the equator. The strongest seasonal variability in eddy generation and associated eddy activity was observed in the California Current, whereas the strongest interannual variability was found in the Benguela Current. All the EBUEs showed contrasted long-term trends in eddy activity, suggesting that eddy activity might be sensitive to global change.

Indeed, climate variability is an important component of the variability in the interaction between the surface ocean and the lower atmosphere in coastal upwelling systems, by influencing a large suite of variables such as gas solubility and fluxes. From a biological point of view, EBUEs represent carbon sinks, because in the long-term the high CO_2 fixation by phytoplankton exceeds plankton community respiration. Nevertheless, in spite of their high productivity, which may be up to two orders-of-magnitude higher than in other coastal or open ocean regions, EBUEs may behave as sources for CO_2 because cold upwelled water releases CO_2 when warmed at the surface. González Dávila et al. (2009) studied the seasonal and interannual variability of the fugacity of surface CO_2 (fCO_2) along a latitudinal section crossing the Benguela EBUE, over 3 years. The section intersected a complex region of offshore filaments in the northern area and coastal upwelled water in the southern area. Climatological seasonal cycles of sea surface temperature (SST) and fCO_2 presented a bi-modal seasonal cycle, related to upwelling activity, between September and March. During the 3 years of study temperature increased in the southern Benguela region, by 0.47 °C yr^{-1} whereas the fCO_2 in seawater decreased 2.5 atm yr^{-1} in the northern Namibia cell, and 0.4 atm yr^{-1} in the southern Benguela area, the surface waters acting as a sink of CO_2 south of 20°S. These observations suggest higher biological activity in the southern Benguela as a result of increases in upwelling intensity and intrusions of lower inorganic carbon content seawater from the Agulhas bank.

The production of nitrogen dioxide, methane (a greenhouse gas) and other volatile gases have been recently considered significant in EBUEs, potentially triggering further acidification of the ocean. For instance, certain phytoplankton groups are known to contribute to increased fluxes of dimethylsulphide (DMS), a trace gas involved in the global biogeochemical cycling of sulphur, which influences climate by inducing aerosol and cloud formation following oxidation in the atmosphere. Franklin et al. (2009) measured DMS, its precursor dimethylsulphoniopropionate (DMSP), and DMSP-lyase activity (DLA; the rate of enzymatic cleavage of DMSP to DMS), with a coupled analysis of microplankton composition, in the Mauritanian region of the Canary Current EBUE. They investigated how the dynamic physical and biological conditions of the Mauritanian upwelling affect DMS and related parameters. They concluded that upwelling waters are prone to produce more DMS than offshore oligotrophic waters, due to enhanced productivity, and discussed the role of upwelling regions in a global warming context given the predicted increases in upwelling activity and productivity and their consequences for DMS production.

Extended OMZs are typical in eastern tropical oceans, close to EBUEs (Fig. 2). Climate models and recent observational studies predict an expansion of OMZs with global warming, which might have tremendous effects on coastal upwelling regions, provided that upwelled water originates in OMZs. Glessmer et al. (2009) used an eddy-resolving general circulation model to investigate the connection between the OMZ and the coastal upwelling in the Mauritanian region of the Canary Current EBUE. From their model output they inferred that the connection is very weak, and that only about 1% of the upwelling waters originate in the OMZ. They suggested that if their findings apply for other EBUEs situated above OMZs, the direct link between denitrification and nitrogen fixation postulated by other authors would be weaker than assumed. Nevertheless, they also recognized that their model did not account for the strength of diapycnal mixing in the area which would need to be better constrained in order to obtain robust estimates of the leakage of OMZ waters into upwelling regions.

5. Primary production, nutrient cycles, and processes in the sediments

Continental margins associated with EBUEs play a major role in global productivity and biogeochemical cycles, accounting for about 10% of oceanic new production, despite representing less than 1% of

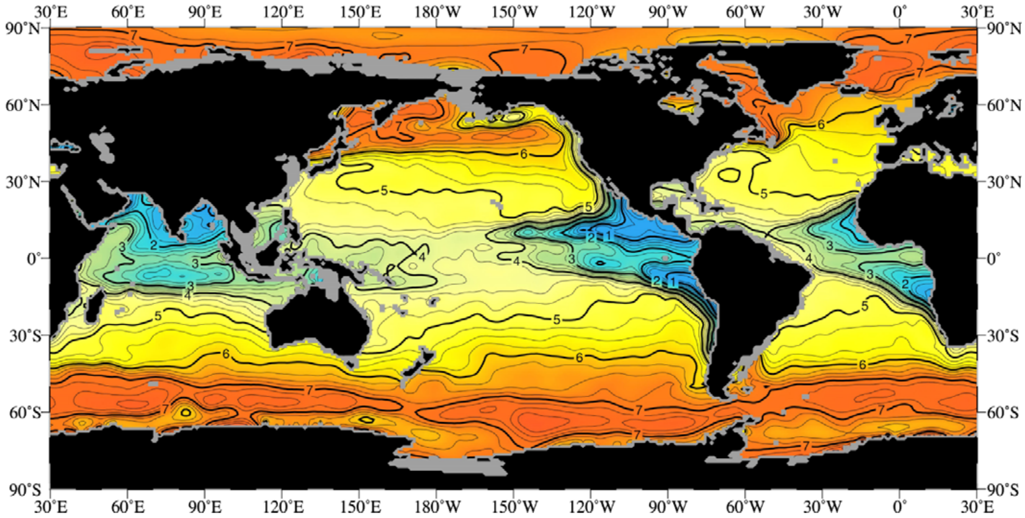

Fig. 2. Oxygen concentration in the global ocean at 100 m depth (Garcia et al., 2006).

the world ocean by area. The potential new production (i.e. the amount of nitrate available for phytoplankton primary production) was estimated by Messié et al. (2009) for the four major EBUEs by combining surface winds measured from space and *in situ* nitrate concentration at 60 m derived from seasonal climatology. They found that the Humboldt, Canary and Benguela EBUEs have similar levels of nitrate supply and hence of potential new production, while the California EBUE has about 60% of the other three.

Upwelling ecosystems however, are not only based on new production. Fernández et al. (2009) reported that primary production in the permanent upwelling system off Peru not only is fuelled by upwelled "new" nitrate but it is also supported by nitrogen regenerated in the upper few meters of the water column either in the form of nitrate (through nitrification in the near-surface layer) or ammonium. Their measurements of nitrogen uptake show a stronger utilisation of ammonium compared to nitrate at all stations, questioning the preferential role of new production in EBUEs, compared to regenerated production.

The processes in the sediments and at the sediment–water interface are clearly identified as critical components in the study of coastal upwelling biogeochemistry. However, the role of benthic processes at the boundary layer is poorly known, due to their complexity and temporal–spatial variability. Brüchert et al. (2009) reported a good example of this complexity by looking at the hydrogen sulphide transport from the sediments in the inner Namibian shelf. The area affected coincides with hatching grounds of commercially important pelagic fish, whose recruitment may be severely affected by recurring toxic sulphide episodes. Their observations showed that fluxes of hydrogen sulphide and methane to the water column, and methane and sulphide concentrations in the bottom waters were decoupled, likely due to the activity of sulphide-oxidizing bacteria. They concluded that although the causal mechanism for the episodic fluctuations in methane and dissolved sulphide concentrations remains unclear, their data suggest that alternating advective and diffusive transports of methane and hydrogen sulphide in bottom waters may be part of the causal mechanism.

6. Dynamics, food web structure and diversity of plankton communities

The structure of the pelagic food web and the interactions between its components has a decisive role in determining the dynamics and productivity of ecosystems. Experimental studies conducted over recent years have helped developed novel and more realistic ecological principles on the structure and dynamics of upwelling food webs, and on the interactions of its components. In particular, the smallest (<100 μm) planktonic size fractions are now recognized as playing a key role in the trophic dynamics of EBUEs. Baltar et al. (2009) studied the temporal and spatial variability of pico-plankton and nano-plankton autotrophic and heterotrophic communities along an inshore-offshore zonal gradient extending across the NW African coastal transition zone. They observed that although seasonality affects the background variability both in pico- and nano-plankton communities, the strong mesoscale variability modulates the patterns of distribution, abundances and changes in community structure, altering the autotrophic to heterotrophic ratio, and concomitantly modifying the carbon pathways within the food web.

Gasol et al. (2009) studied the zonal (shelf-ocean), latitudinal, and depth (epipelagic–mesopelagic) variability of microbial assemblages in the NW Africa–Canary Current Coastal Transition Zone (CTZ). It emerged that prokaryotes in the mesopelagic zone in this area are less abundant than in the epipelagic but have comparable levels of activity. The relationship between prokaryotes and heterotrophic nano-flagellates, their main predators, remains constant throughout the water column, implying that deep ocean bacterial communities are very active. Higher mesopelagic activity was observed closer to the shelf and in regions affected by upwelling features.

It is known that zooplankton strongly reacts to climatic fluctuations in ecosystem-specific ways (Perry et al., 2004). The trend in zooplankton biomass is positive in the Benguela, but negative in the Humboldt and California Current systems (SCOR WG125, 2008). Furthermore, there is evidence of strong poleward displacement of zoogeographic boundaries when temperature and stratification anomalies are positive (Mackas et al., 2006, 2007; Valdes et al., 2007) as also presented in the symposium (contributions not included in this volume). Zooplankton faunal assemblages largely depend on the source of the upwelled waters, which affect their lipid composition, which in turn influence fish growth (Mackas et al., 2007). Hugget et al. (2009) analyzed the variability of mesozooplankton on a range of space and time scales. Their study was based on a biannual sampling off the west and southwest coasts of South Africa since 1988, using the same methodological approach. They reported that copepod biomass, daily production and size composition varied with latitude, season and year, but that there were no consistent trends in interannual variability over the study period. In a comparative exercise, they observed that copepod biomass was of the same magnitude in the four EBUEs, whereas the annual production estimates were surprisingly an order of magnitude greater than those made four decades ago, with highest values for the southern Benguela.

The interaction between phytoplankton growth and (micro- and meso-) zooplankton grazing was studied by Landry et al. (2009) through a set of *in situ* experiments, across a range of environmental conditions in the coastal upwelling ecosystem off Point Conception, California. Following the paths of quasi-Lagrangian drifters they showed that experimentally-derived estimates of phytoplankton community growth, microzooplankton grazing and mesozooplankton grazing can explain a large fraction of the variability observed in the net changes of ambient chlorophyll-α over time scales of 3–5 days. They concluded that the agreement between net ambient observations and experimentally predicted changes is an important point of validation for using field data to develop and constrain coupled physical-biological models of upwelling system dynamics.

Large zooplankton can play a key role in enhancing the downward export flux of primary production in upwelling ecosystems. González et al. (2009) analyzed the composition of drifting sediment traps deployed below 50 m depth along the Humboldt EBUE off Chile, between 1997 and 2006. They observed that when the proportion of sinking carbon was low compared to primary production (PP), a significant amount of the sedimented organic matter was composed of diatoms, regardless of PP rates. In contrast, when the fraction of sinking carbon was high relative to PP, most of the collected organic matter was composed of euphausiid faecal strings. Their results support the role of euphausiids as key species in the Humboldt EBUE, exerting a top–down control over phytoplankton communities and modulating the flux of organic carbon to the continental shelf.

Antezana (2009) elaborated on the special role of euphausiids in EBUEs ecology by identifying species-specific patterns of diel vertical migration into the OMZ in the Humboldt Current. While similar vertical patterns have been observed in the Benguela, this contribution observed species-specific differences in the extent, residence time, timing and duration of the ascent and descent into the OMZ. It was concluded that the euphausiid community structure is based on habitat partitioning to avoid co-occurrence of competing species.

Due to the colder temperatures and productive conditions of coastal upwellings compared with offshore ambient waters, EBUEs also may act as a refuge for species inhabiting higher latitudes. This is the case for the pelagic hyperiid amphipod *Themisto gaudichaudi*, which has a circum-Antarctic epipelagic distribution pattern and plays an important role in Antarctic food webs as an effective link from zooplankton secondary production to higher trophic levels, including seabirds and marine mammals. Auel and Ekau (2009) reported on the presence and distribution of *T. gaudichaudi* at the northernmost limit of its range in the Benguela upwelling system in relation to upwelling intensity and hydrographic conditions, based on time-series data from 2002 to 2008. They combined field data on life-history traits and respiration rates in relation to water temperature to elucidate the environmental and physiological factors limiting the distribution range of this species.

7. Small pelagic fishes and the functioning of EBUEs

EBUEs are characterized by a high abundance (Table 2) of a reduced number of small pelagic fish species that support large fisheries and a number of top predator populations. Because they are situated in the middle of the trophic food web, pelagic fish often play a central role in regulating the functioning of upwelling ecosystems, which are often described as wasp-waist ecosystems (but see Fréon et al., 2009). Small pelagic fish are able to forage on a variety of prey from several trophic levels. Their biomass can reach several million tons, but it varies considerably at different timescales, as does their distribution. Presentations at the symposium confirmed that these fish are more zooplanktivorous than phytoplanktivorous, and that their prey comes from a wider range

Table 2

Estimated average yearly catches (metric tons) by commercial fisheries operating in EBUEs (see list in Table 1) during the 2004–2007 period, according to the International Standard Statistical Classification of Aquatic Animals and Plants (ISSCAAP) group of species. Source: FAO FishStat.

ISSCAAP groups	Benguela	California	Canary	Humboldt	Total
Herrings, sardines, anchovies	546,680	479,089	1,292,066	9,210,458	11,528,293
Miscellaneous pelagic fishes	337,973	36,227	476,616	1,687,610	2,538,425
Squids, cuttlefishes, octopuses	12,621	117,490	104,003	710,364	944,477
Cods, hakes, haddocks	292,455	236,320	34,365	144,113	707,252
Marine fishes not identified	34,098	86,378	169,087	46,725	336,288
Tunas, bonitos, billfishes	7448	72,189	35,248	21,203	136,089
Miscellaneous demersal fishes	52,282	15,718	37,758	18,090	123,848
Shrimps, prawns	2058	51,265	20,014	15,089	88,426
Salmons, trouts, smelts		73,824	3	0	73,827
Clams, cockles, arkshells	7	9295	7691	46,198	63,191
Sharks, rays, chimaeras	8795	18,007	21,027	7782	55,610
Flounders, halibuts, soles	6153	21,973	20,400	367	48,892
Sea-urchins and other echinoderms		7804	103	40,849	48,755
Crabs, sea-spiders	3675	22,232	1219	7652	34,777
Scallops, pectens		13,602	75	18,654	32,331
Abalones, winkles, conchs	202	3967	10,341	16,247	30,757
King crabs, squat-lobsters		2123		11,404	13,527
Mussels		1485	40	11,125	12,649
Lobsters, spiny-rock lobsters	3824	2146	1235	106	7310
Oysters	20	5697	107	7	5831
Miscellaneous marine molluscs	0	455	73	4259	4788
Miscellaneous marine crustaceans	0	324	245	2082	2652
Others[a]	10	61	293	1167	1531
Total	1308,300	1277,672	2232,005	12,021,549	16,839,525

ISSCAAP groups exclude all Patagonian species and: Alaska pollock, Atlantic cod and Pacific cod in the Cods-hakes-haddocks group; rock sole and Yellowfin sole in Flounders-halibuts-soles; Falkland sprat, Pacific anchoveta and Pacific thread herring in Herrings-sardines-anchovies. In order remove from the Tables 1 and 2 fish caught far offshore, the following ratios were applied to some groups: Tunas-bonitos-billfishes/5; Sharks, rays, chimaeras/2; Miscellaneous pelagic fish/1.5. The filters for areas and fishing countries were the same as in Table 1.

[a] Sea-squirts and other tunicates, shads, Miscellaneous aquatic invertebrates, Miscellaneous diadromous fishes.

of organisms than previously suspected. As planktivorous, short-lived species, small pelagic fish react strongly and quickly to changes in upwelling intensity and location, as much for the fate of their food as for that of their eggs and larvae. Reproductive products can be transported offshore with lethal consequences, unless retention adaptive strategies are in place to limit losses. Nonetheless, the reasons for their large fluctuations in abundance are still debated.

Because small pelagic fish respond directly to environmental variability, exploitation patterns and species interactions, understanding their ecology, behaviour and dynamics is central to the study of EBUEs. In addition to papers presented in other sessions (Chavez and Messié, 2009; Heymans et al., 2009; Neira et al., 2009) and to numerous presentations and poster focussing on habitat in relation to environmental constraints, three papers in this volume originated from this session.

Espinoza et al. (2009) described the diet and carbon content of sardine *Sardinops sagax* in the northern Humboldt Current ecosystem off Peru. The results were compared with the diet of anchoveta *Engraulis ringens* off Peru and with the diets of sardines from the southern Benguela and the northern Canary upwelling systems. The diet of sardine off Peru was based primarily on zooplankton (mainly copepods and a few euphausiids), similar to that observed for anchoveta. Nonetheless, sardine fed on smaller zooplankton than do anchoveta and the phytoplankton fraction (<2% of sardine dietary carbon) was dominated by dinoflagellates, whereas diatoms were the dominant phytoplankton consumed by anchoveta. Hence, trophic competition between sardine and anchovy in Peru is minimized by their partitioning of the zooplankton food resource based on prey size. Sardine in Peru forage on larger prey and obtain a substantial portion of their dietary carbon from euphausiids compared to sardine from the northern Canary and southern Benguela Current systems.

Barange et al. (2009) compared the relationships between stock biomass, distribution area and mean density of sardine and anchovy populations off California, Peru, southern Benguela and Japan in order to elucidate whether their ecological responses to habitat availability and use would support the possibility of them developing synchronic, alternating biomass fluctuations. Results indicated that as populations of both species grow in size, both the area they occupy and their packing densities increase, generally consistent with MacCall's (1990) basin model. The relationship between distribution area and stock biomass is allometric, which implies that there is a limit to the stock expansion to new areas. Patterns of space occupation appeared to differ between sardine and anchovy in some regions. Barange et al. (2009) offered possible reasons, and suggested that, in contrast to anchovy, habitat availability may not be a pre-requisite for sardine growth in some areas. They concluded that both species cannot be considered to ecologically replace each other.

Brochier et al. (2009) used an individual-based model to investigate and compare the evolutionary advantages of a natal homing reproductive strategy in three upwelling regions: Peru, Chile and Morocco. The spatial and seasonal spawning patterns that emerged after applying environmental constraints were investigated and compared to observed spawning patterns of sardine and anchovy. The selective environmental constraints were: (1) lethal temperature; (2) retention over the continental shelf; and (3) avoidance of dispersive structures. Temperature was found to be a critical constraint only off Chile. The shelf retention constraint led to selection of a particular spawning season during the period of minimum upwelling in all three regions, and to spatial patterns that matched observed anchovy spawning off Chile and sardine spawning off Morocco. Avoidance of dispersive structures, led to the emergence of a spawning season during the period of maximum upwelling off Chile and Morocco. The most accurate representation of observed spawning patterns off Peru was achieved through a combination of shelf retention and non-dispersion constraints.

8. Near shore and estuarine processes related to EBUEs

Near shore areas (including gulfs, open lagoons and 'rías') and estuaries located in EBUEs influence and modify the upwelling process, thus affecting the dynamics of eastern boundary ecosystems over a wide range of temporal and spatial scales. This occurs through direct water mass exchanges between these nearshore coastal areas and the continental shelf or indirectly through migration of marine species. The productivity, total biomass and biodiversity are usually high in these areas which often host nurseries for species living on the continental shelf, as well as colonies of marine birds and mammals. During periods of low upwelling intensity, they can be used as refuge areas. Unlike offshore ecosystems, the biophysical interaction in the coastal environment acquires a strong spatially-explicit component due to the persistent topographic features of the coastline. Consequently, research in these areas focused on the spatial variation in upwelling intensity, to understand and quantify this variation in the physical environment along the coast, and on the consequences for biological systems. Three main pathways of physical–biological coupling were explored in the different presentations: (a) spatio-temporal variation in upwelling intensity and nutrient delivery to shore, including its consequences for the dynamics of harmful algal blooms and benthic macro-algae, (b) upwelling-driven variation in the supply of organic matter for benthic filter-feeders and grazers, and (c) effects of upwelling on larval transport and patterns of recruitment along the shore.

Oliveira et al. (2009) characterized the wind forcing and the spatio-temporal variability of sea surface temperature SST/chlorophyll-α for periods preceding the summer diatom and dinoflagellate blooms in the Lisbon Bay from 2002 to 2005. Bloom detection occurs either during upwelling events or up to 4 days after wind relaxation. However, no direct relationship was found between the blooms and either the intensity or duration of the wind pulses. Chlorophyll patterns in Lisbon Bay were strongly linked to the orientation and branching of the upwelling filament rooted at Cape Roca and the westward progression of the warm-core cyclones shed from the slope off Setúbal Bay. In the summer, the ocean circulation in the embayments located south of Cape Roca was dominated by the upwelling dynamics and played a key role in the development of phytoplankton blooms off central Portugal.

Tapia et al. (2009) presented local, quantitative indices of small-scale thermal variability, whose patterns across sites were largely driven by variations in coastal upwelling intensity at scales of few kilometres. Index calculations were based on daily records of *in situ* SST, gathered at numerous sites along the Oregon–California coast, and along the coast of northern and central Chile. Several univariate metrics were calculated using daily series of temperature anomalies, and combined to produce a multivariate ordination of sites that allowed the comparison of sites across regions. Multivariate indices calculated for 13 central Chile sites explained 52% and 50% of the between-site variance in some macro-algae biomass and growth rate, respectively.

9. Coastal-open ocean fluxes and processes

Coastal upwelling ecosystems exchange water and bio-chemical properties with the adjacent offshore regions, through hydrographically complex Coastal Transition Zone (CTZ) regions. In the past two decades, several multi-disciplinary studies have addressed physical and biological processes in these highly dynamic boundary regions. However, we still do not fully understand the mechanisms and magnitude of shelf-ocean exchanges of energy, nutrients and materials, or the impacts of export fluxes to the oceanic domain. Here we have selected a set of papers highlighting results from recent studies on oceanographic processes in CTZs, covering topics ranging from the influence of mesoscale features in coastal-offshore transport, the extent of organic matter transport to the ocean interior, or the consequences of fish larvae dispersal by upwelling filaments.

Rubio et al. (2009) characterized eddy activity in the southern Benguela upwelling system with absolute sea level data deduced from remote sensing measurements and numerical simulations with a regional model, using a wavelet-based technique for identification and tracking of coherent structures. They showed that the presence of cyclonic eddies along the upwelling front over the southern Benguela slope was recurrent throughout the year. Their results suggest that cyclonic eddies play a significant role in coastal-open ocean exchanges. With lifetimes of several months, these eddies could export significant volumes of nutrient-rich waters far from the coastal upwelling.

Veitch et al. (2009) used a numerical model to simulate the Benguela system in its entirety, successfully reproducing the large-scale offshore regime and the respective seasonal fluctuations. They observed that the offshore gradient of eddy kinetic energy (EKE) is generally strong in the Benguela system and exceptionally so in the southern Benguela due to vigorous mesoscale activity offshore of the shelf-edge, originating from the Agulhas retroflection area. The juxtaposition between the steep offshore EKE gradients in the south and much weaker offshore gradients of EKE in the northern Benguela would have different implications for cross-shelf exchanges, which are discussed in the paper.

In the California Current, Keister et al. (2009) used satellite (SST) images and *in situ* zooplankton data to investigate whether the physical variables that indicate advective mesoscale circulation features (e.g. upwelling filaments) can be used to infer biological distributions. Their results show that biomass and species abundances varied substantially among cruises and locations and hence could not be quantitatively predicted by SST patterns. However, upwelling filaments consistently expanded the entire shelf region in which high zooplankton biomass occurred, 'spreading' the biomass from the continental shelf onto offshore regions of the upwelling system. The authors conclude with a discussion of the sampling strategies needed to capture ecosystem variability caused by these dynamic circulation features.

Rodríguez et al. (2009) reviewed the current knowledge of the complex interactions and effects of upwelling filaments and island-induced eddies on the offshore transport and distribution of neritic larvae across the Canary Current CTZ. Upwelling filaments originated at Cape Juby and Cape Bojador stretching from the African shelf to the open ocean south of the Canary Islands. Eventually, a filament transporting neritic fish larvae is entrained around the recurrent offshore eddy, located in the trough between the archipelago and the African shelf, returning the larvae back to the African shelf. In contrast, larvae may reach the eastern Canary Islands spreading throughout the neritic region of the archipelago helped by the secondary circulation associated with the numerous eddies shed from the islands.

Fisher et al. (2009) investigated the role of the 'giant' Cape Blanc filament off Mauritania with regards to the transport of chlorophyll and organic carbon from the shelf to the open ocean. Within the filament, chlorophyll is transported about 400 km offshore. Modelled particle distributions along a zonal transect showed that particles with low sinking velocities may be advected offshore by up to 600 km in subsurface particle clouds generally located between 400 m and 800 m water depth, forming an Intermediate Nepheloid Layer (INL) at the same depth as the OMZ. Heavier particles were transported from the shelf within the Bottom Layer (BL) even at longer distances, largely following the topography of the slope. The lateral contribution to offshore deep waters in winter–spring was estimated to be about 70% for organic carbon and total mass, whereas the lateral input for both components on an annual basis was estimated to be in the order of 15%. Biogenic opal increases almost fivefold from the upper mesopelagic to the bathypelagic offshore waters, reflecting an additional source for biogenic silica from eutrophic coastal waters.

The same research group (Karakaş et al., 2009) implemented an aggregation model into an existing biogeochemical model to simulate the distribution of particles in the water column and their downward transport in the Mauritanian upwelling region. Data from settling chambers, sediment traps and particle camera measurements were provided for model validation. They concluded that the aggregation–disaggregation model improved the prediction capability of the original biogeochemical model significantly by giving much better estimates of fluxes for both upper and lower trap. However, the results also point to the need for more studies to enhance our knowledge of particle decay and its variability, and the role that stickiness plays in the distribution of vertical fluxes.

10. Impacts of climate variability and change on EBUEs

Climate change has already been identified as the cause of significant changes in the physical, bio-chemical and biological functioning of the oceans, but it is also affecting the magnitude and patterns of natural climate variability (such as seasonal patterns), and the interactions between atmospheric and ocean climate. Four papers were selected dealing specifically with the interannual impacts of climate variability and change on the dynamics of EBUEs. Two of these papers focused on the Humboldt Current and two on the Canary Current.

Bode et al. (2009) observed a continuous decrease in the upwelling intensity of the northern region of the Canary Current over the last 40 years, associated with a warming trend of surface waters. No significant trends were observed in phytoplankton biomass during the same period but zooplankton biomass decreased offshore and increased near the coast. Diatom abundance decreased regionally and the increase in zooplankton biomass was predominantly due to warm-water species. They concluded that plankton dynamics reflected the climatic patterns of variability.

Thiaw et al. (2009) used a wind-based coastal upwelling index and satellite-derived primary production estimates to compute Maximum Sustainable Yield (MSY) and associated fishing effort (E_{MSY}) in white shrimp off Senegal, based on environmental limits. The paper separates patterns in northern and southern Senegal: In the north, upwelling is highly variable from year to year and constitutes the major factor determining shrimp productivity. In the south, where fishing effort has strongly increased over the past 10 years, hydrodynamic processes seem to dominate and determine the levels of primary production and the white shrimp productivity.

Durazo (2009) investigated changes in physical properties (temperature and salinity) in the southern California region for the period 1997–2008. Periods of distinctive variability were observed from near-surface properties, although subsurface anomalies only depicted a trend towards saltier conditions since 2001.

Lavaniegos (2009) investigated zooplankton trends in the same region and over a similar time frame, and observed a drop in zooplankton biomass in response to an intrusion of subarctic water in 2002. Zooplankton biomass recovered subsequently, reinforced by increased upwelling intensity from 2005 onwards. The author concluded that these patterns were controlled by basin-scale rather than regional processes.

11. Remote and *in situ* time-series studies: EBUEs as ocean observatories for global change

The accumulation over the last decades of conventional field data and modern automated *in situ* or remote sensing data allows for the analysis of long-term changes in EBUEs. Paleontological records in the sediments have also extended the period of study to past centuries and millennia. Because EBUEs are strongly connected to the dynamics and chemical composition of the atmosphere, they are good candidates to track global change and its effects. Given the current interest in setting permanent observatories in a Global Ocean Observation System, the symposium assisted in identifying what has been and should be monitored in EBUEs. Remote sensing and *in situ* long time-series were used in many presentations at the symposium and this is reflected in many papers in this volume (the four EBUEs overviews and their comparison; Barange et al., 2009; Blanchette et al., 2009; Bode et al., 2009; Chaigneau et al., 2009; Crawford, 2009; Durazo, 2009; Fischer, 2009; Huggett et al., 2009; Lavaniegos, 2009; Messié et al., 2009), as well as three specific studies, that we will introduce here, that focus exclusively on satellite data.

Demarcq (2009) analyzed satellite-derived time-series of SST, wind and primary production, focussing on the latter. He contrasted the trends in the four EBUEs with global trends. Whereas the global primary biomass offshore displayed on average a decreasing trend from 1998 to 2007, the productivity of most EBUEs increased over the same period, both in the Atlantic basin and in the Eastern Pacific basins. The long-term relationships between SST and chlorophyll-α biomass estimates were not significant within EBUEs, suggesting that SST anomalies cannot be used as indicators of changes in upwelling intensity, especially during the present period of global warming. In contrast, upwelling-favourable equatorward winds show a high coherency with the observed trends in biomass, and suggest that the trend in the trade winds is probably linked to an increase in the intensity of the Hadley cell circulation observed during the last decades.

Thomas et al. (2009) used the same SeaWiFS dataset to perform a detailed comparison of the chlorophyll interannual variability and physical forcing factors (Multivariate El Niño Index, PDO and the North Pacific Gyre Oscillation) over the California and Humboldt ecosystems. Dominant signals were adjacent to the coast in the wind-driven upwelling zone. The maximum anomalies observed in both systems reflect negative signals during the 1997–1998 El Niño, extended to 1999. Thereafter, anomalies primarily appear to be associated with phenological shifts. Both systems' response to forcing has clear latitudinal differences. At higher latitudes, correlations followed expected relationships of increased (decreased) chlorophyll with positive (negative) upwelling and forcing factors. At particular latitudes though, correlations weakened or opposed expectations.

Hirata et al. (2009) developed a new methodology to derive size-specific photosynthetic rates for EBUEs using satellite ocean colour. Their approach linked size class specific photosynthetic rate to the optical absorption of phytoplankton. Comparisons of their approach with a conventional chlorophyll-based photosynthetic algorithm and with *in situ* measurements showed good agreement. Preliminary results from satellite observations for upwelling regions suggested that production in nano-plankton-dominated communities may be larger than for those where microplankton is dominant, due to the greater spatial extent of the former. However, photosynthetic rate per unit volume was shown to be larger for microplankton-dominated communities.

12. Integrated food web studies and fishing policies in upwelling ecosystems

Integrating the complexity of marine food webs, from primary production and its forcing factors to top predators and fisheries, is a challenging task because of scale issues, feedbacks, non-linear processes, difficulties to predict individual behaviour, parameterisation, among others. Nonetheless, EBUEs are good candidates for end-to-end studies because the number of key species and the length of the food web are limited, and the processes are reasonably well understood. Three papers have been selected for this volume under this theme of work. The first (Neira et al., 2009) investigates bottom–up and top–down processes in generating non-linear food web responses; the second (Heymans et al., 2009) elaborates alternative fishing options based on maximising income, manpower or ecosystem health; the third (Crawford, 2009) exemplifies the interactive role of top predators and their prey in shaping the structure of food webs.

Neira et al. (2009) conducted dynamic food web simulations over 150 years to evaluate when and why shifts in ecosystem state may occur in the Humboldt Current, and whether bottom–up forcing (simulated by changing phytoplankton biomass) or fishing (adjusting fishing mortalities) is more likely to induce such irreversible ecosystem changes. Interactions between fishing and decadal scale bottom–up forcing indicated that the latter can dampen the effects of fishing, whereas fishing may decrease the recovery otherwise observed under decadal scale bottom–up forcing. Their results suggested that fishing (particularly at higher and lower trophic levels) was more likely to cause ecological thresholds to be exceeded and to induce regime shifts than decadal scale bottom–up forcing.

Heymans et al. (2009) investigated alternative fishing policy options and trade-offs in the northern Benguela system, to optimize the discounted profit from the fisheries, maximize jobs and protect ecosystem structure. Two different discount rates were applied: a rate similar to that used by private businesses in Namibia and a lower rate to take explicit account of future generations. The results show that the discount rate was most important when optimising profits, as fishing effort and discounted profit is significantly increased when discount rate is low. When optimising for jobs, fisheries soon become non-profitable, although no significant difference was found between discount rates. Ecosystem longevity was only improved with a reduction in effort by all fleets.

Although not strictly an end-to-end paper, Crawford (2009) was included in this section because it linked ecosystem-driven changes in the distribution and productivity of pelagic fish stocks with consequences for the dynamics of top predators. He related patterns in the population dynamics of swift terns *Thalasseus bergii*, and their main prey species, sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* in the southern Benguela ecosystem. It was observed that there were large increases in the numbers of swift terns breeding in the west and south regions of South Africa in the 2000s, coinciding with increased abundance of sardine and anchovy. After 2005, numbers of swift terns breeding in western regions decreased, whereas numbers breeding farther south increased. This followed displacements to the south and east of sardine and anchovy. It was discussed that swift terns show low fidelity to breeding localities, which enables a rapid adjustment of the location of breeding to an altered availability of prey, while species showing high fidelity to colonies, such as the African penguin *Spheniscus demersus* and Cape gannet *Morus capensis*, showed substantial decreases in overall breeding numbers during the same period.

13. Synthesis

The symposium fostered new and relevant advances in the understanding of the structure and functioning of EBUEs under an integrative and comparative perspective. Here we first present a synthesis of the main findings, especially in the context of ongoing environmental change, followed by the identification of gaps that should point toward future directions in research (next section). In contrast to the previous sections, which concentrated only on the papers published in this volume, here we also reflect on other relevant conclusions that were presented and discussed in the symposium.

The analysis of SST from 1960 to 2007 in the transoceanic band 30°N–30°S (Fig. 3) shows that over the last 20 years (1985–2007) this latitudinal band experienced a clear acceleration of the warming trend, which was less dramatic during the recent period (1998–2007) characterized by the strong signature of the 1997–1998 El Niño (Demarcq, 2009). These observations confirm previous studies (e.g. Hansen et al., 2006; IPCC, 2007). Recent decades are characterized by the strongest and longer warming acceleration ever observed, with a global warming rate close to 0.2 °C per decade, a value more than three times higher than the average warming observed from the previous 60 years (1915–1975). Warming of the oceans is leading to an increase in stratification. This has important consequences in upwelling regions because the oxygen content decreases with increasing biological production, promoting suboxic or anoxic environments. This affects not only the vertical distribution of marine organisms, but also the structure and functioning of the whole food web (see below).

However, the interannual and decadal signals are so strong in EBUEs that long-term trends are difficult to identify or quantify (Fig. 4). Nonetheless, weak positive or negative trends in SST are observed in the Pacific and South Atlantic EBUEs and highly positive trends in the Canary upwelling system during the last 23–25 years (Arístegui et al., 2009; Chavez and Messié, 2009; Demarcq, 2009). The Humboldt system, a region most affected by El Niño events, exhibits a positive trend, except for the central Peruvian and Chilean coasts (null trend; Demarcq, 2009). Similarly, weak positive trends are visible in the Benguela system, especially at its northern and southern boundaries (Hutchings et al., 2009). During the 1998–2007 period, the EBUEs of the northern hemisphere were affected by a strong warming, whereas EBUEs from the southern hemisphere show either no clear trend (Peru and southern Benguela) or a weak cooling (northern Chile and northern Benguela). All this indicates that the warming observed during the last decades, although less intense than at the global scale, is probably strengthening in EBUEs (Demarcq, 2009). Nonetheless, interactions between trends at different time scales (in particular interannual, interdecadal and intersecular), and sometimes with opposite directions (e.g. Montecino and Lange, 2009), prevent accurate predictions. Paleontological studies based on depositions in anoxic marine sediments have allowed us to observe biological changes over long past periods. Off Peru, for example, anchovy abundance during the last century was exceptional, coinciding with an increase in deposited organic carbon during the same period, which flux to the sediment was twice as intense as during the last two millennia. This allows us to interpret present observations in a new and more complete context.

Whereas the worldwide estimate of primary biomass displays on average a decreasing trend from 1998 to 2007 (Demarcq, 2009), the productivity of EBUEs increases, except for some sub-regions of the Canary Current where a significant decrease was observed (Arístegui et al., 2009; Demarcq, 2009; Chavez and Messié, 2009; Montecino and Lange, 2009). In NW Spain, where the production of farmed mussels in rías is very important (15% of the world production), the decrease in intensity of winds and/or changes in direction have reduced the water renewal rate. This has been suggested (Álvarez–Salgado et al., 2008; presented at the symposium) to trigger an increase in the frequency of red tides, resulting in bans on mussel sales, with economic repercussions. Interestingly, no significant trend was visible on continental margins outside coastal upwelling areas.

The importance of biogeochemical cycling in upwelling areas in supporting and determining global ocean production cannot be underestimated. Many of the biogeochemical conditions are hypersensitive to change, so that a small change, e.g. in oxygen depletion (resulting from either natural or anthropogenic reasons), can lead to major changes in biogeochemical pathways and ultimately to orders-of-magnitude changes in the fishery yield of these systems. Upwelling ecosystems play a crucial role in the carbon and nitrogen cycling in the ocean, and although EBUEs are generally interpreted as organic carbon sinks, they frequently behave as CO_2 sources. There is concern that production increases in some regions (such as California) may trigger further ocean acidification (Checkley and Barth, 2009). The production of nitrogen dioxide and methane (also a greenhouse gas) also has been recently considered significant in EBUEs. Nano- and pico-plankton play an important role in the formation on greenhouse gases. For instance, bacteria alone can contribute with up to 30% of the carbon dioxide and 50% of the carbon monoxide gas emissions. However, other sources of CO_2 emissions remain to be discovered in order to explain the strong concentrations observed in recent years.

Significant changes in the foraging behaviour of certain species are linked to human activities other than climate modification. For example, it was observed that in South Africa pelicans attack other bird species' chicks, such as Cape gannets, a behavior that has been

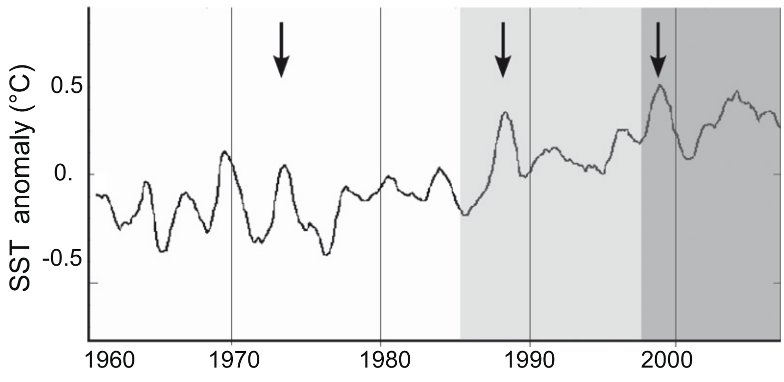

Fig. 3. SST anomalies smoothed data (12-term monthly moving average) and linear trends computed from ICOADS data from 1960 to 2007 for the transoceanic band 30°N–30°S, that is excluding regions subject to strong seasonal variations, and the offshore limit corresponding to the 1,000 m isobath (courtesy of H. Demarcq, IRD, France).

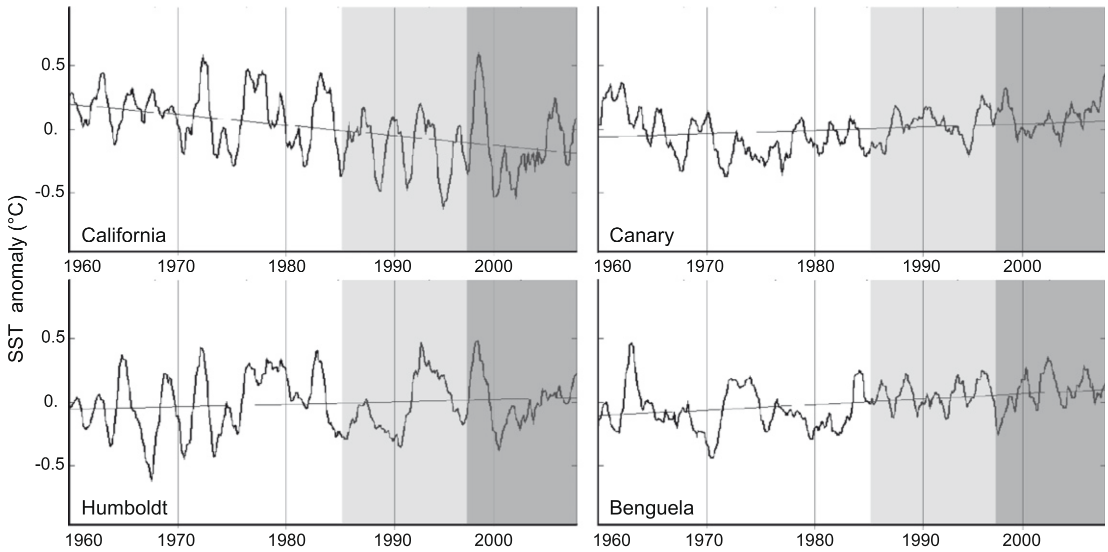

Fig. 4. Same as Fig. 3 for the EBUEs continental margins (California 15°N–45°N; Canary 10°–43°N; Humboldt 40°S–5°S; Benguela 33°–12°S). Major El Niño events are indicated by vertical arrows (courtesy of H. Demarcq, IRD, France).

recently intensified by size increases in pelican populations. This growth appears to be caused by greater availability of agricultural offal to the pelicans, which otherwise were dependent on limited natural food resources (de Ponte Machado, 2007; presented at the symposium). Although adult sea birds survive well feeding off fishing boats discards, this food may not be appropriate for their chicks, causing strong mortality amongst the latter (Grémillet et al., 2008; presented at the symposium). Density-dependent effects on food web functioning are also observed, such as increased cannibalism of adult fish (hake, sardine and anchovy) on their eggs or juveniles.

As already observed in terrestrial and other marine ecosystems, phenological changes have been detected in EBUEs. Changes in the temperature seasonal cycle can provoke a delay of a month or two in the appearance of zooplankton, as observed in California (Mackas et al., 2006; Checkley and Barth, 2009). In other ecosystems, such as the southern Benguela, predators are confronted with unseasonal migrations of their prey. For the last 10 years, a progressive shift of the centre of gravity of anchovy and sardine populations from west to east has been observed (Hutchings et al., 2009). Some of their natural predators, such as the Cape gannet and the African penguin, which live and reproduce at particular islands, experienced the disappearance of their prey from their foraging ground, causing reproduction failures (e.g. Crawford et al., 2008; presented at the symposium). Since the 1970s, after the long-term sardine stock collapse in Namibia, there was a marked shift of gannets from Namibia to South Africa, and recently from western to eastern South Africa (Crawford et al., 2007; presented at the symposium). The bulk of the Cape gannet colony is now at its easternmost breeding locality.

One of the issues raised in the symposium was the need and wish to ensure that ecosystem management takes account of the biological health of stocks and ecosystems, social dynamics of fleet and fishers, as well as other socioeconomic considerations (e.g. employment) in an ecosystem-based context. Vessel Monitoring Systems (VMS) where presented as potential new tools, not just for management (e.g. to monitor effort, study interactions between fleets, monitor protected areas) but also to study interactions between resources, fisheries and top predators (S. Bertrand, IRD, France, pers. com.).

Advances in the understanding of the physical and primary production trends and processes were facilitated by the rapid extension of the number of sensors onboard satellites (from SST sensors to color sensors, altimeters and scatterometers), the new generation of autonomous observing devices (e.g. gliders), and by constant progress in modelling. Numerous presentations demonstrated the benefit of using regional physical models with high spatial resolution, embedded in basin-scale models. This was particularly the case to show the specificity of EBUEs in the export of nutrients, organic matter and plankton toward offshore regions. The role of mesoscale features, such as eddies, filaments and fronts, was highlighted by numerical models, and their ability to reproduce mesoscale features was demonstrated through satellite tracking of drift buoys. Concurrent biological information also contributed to the validation of physical models, through model coupling, allowing a realistic reproduction of the fate of fish early stages after long distance transport. There is the hope that in the near future these tools will be used to build climate change scenarios.

The increase in the size of OMZs worldwide (Fig. 2) is significant in EBUEs. The northern Humboldt and northern Benguela ecosystems are particularly affected by a surface oxygenated layer which can be reduced to few tens of meters or less. Partly due of lack of adequate data, oxygen is not an element that has received much attention so far. However, the vertical range of fish habitat can be limited by the presence of a shallow oxycline. Fish like anchovy appear to benefit from such shallow oxycline conditions while other species like sardine and jack mackerel appear to be disadvantaged (Bertrand et al., 2008b).

14. Gaps and future

Two major overarching gaps were identified, one thematic and one geographic. The human dimension of EBUEs was poorly documented during the symposium and the social sciences were nearly absent despite a plenary session on "resource assessment, management and socioeconomic implications of ecosystem-based management of EBUEs". This gap is not specific to EBUEs, in spite of recent progresses in bridging the gap between "natural" and "social" sciences. In the recent symposium "Coping with global change in marine social-ecological systems" (http://www.peopleandfish.org) held in July 2008 in Rome, Italy, a month after this one, the conveners indicated that "Fisheries stock assessments have yet to fully integrate the environment, climate change, ecology and human behaviour into their models and management recommendations". This is a critical step in the implementation of science-based ecosystem approaches and should be a research priority. The Canary ecosystem, particularly along the NW African coast, is lagging behind the other EBUEs in terms of accumulated knowledge, which hampers management efforts at national and regional scales. Although good progress has been observed in recent years, the differences in the volume and quality of data, and in their management practices, limits comparative approaches across the four main EBUEs. An international effort is called upon to develop research in this region.

There is still a lack of coherent long-term *in situ* observations in many of the EBUEs, particularly in the inner shelf zone, which is currently under-sampled compared to ship-based and modelling-based research. For instance, there is a need for near shore wind measurements to resolve windstress curl variability and velocity drop-off observed near the coast due to coastal morphology. These elements strongly influence the patterns of upwelling circulation, surface temperature, and biogeochemical processes in coastal regions but are not properly quantified by large-scale models or satellite observations. Similarly, despite numerous studies on interactions between species and community-based trophic models, there is a need for detailed data of diet and *in situ* observation of foraging behaviour and plasticity in prey selection. Furthermore, one aspect that has received comparatively little attention in studies of coastal benthic ecosystems is the non-trophic, bottom–up effects produced by variation in nutrients across shores of varying upwelling intensity, which in turn modify turf algae growth and therefore the habitat, settlement and/or foraging activity of benthic species and top predators.

Hypoxia should be a key research area in the future due to the likely increase of anoxic events associated with climate change, and subsequent mortality of fish, shellfish and crustaceans, and was the focus of a special workshop held as part of the EBUEs symposium. Unfortunately the discrete nature of conventional oceanographic sampling (e.g. CTDO cast) overlooks the small-scale variability in oxycline depth and its consequences. In this context a poster presented by Michael Ballon et al. (pers. com.), which won the poster competition, showed that acoustics can be use to determine the oxycline depth at a very high spatial resolution (each 5 m along a survey track). This should allow for a better understanding of the mesoscale spatio-temporal dynamics of oxyclines and the biological processes associated with them.

The understanding of spatio-temporal patterns in the distribution of organisms, from plankton to fish to top predators, could benefit from more descriptive process studies. The role played by euphausiids and mesopelagic fish in the EBUEs is poorly known because of the paucity of biological and ecological observations. Indeed these communities present dramatic biomasses and are important energetic path flows. Furthermore, they play an important role in the OMZ affected regions because some species of euphausiids (Antezana, 2009) and mesopelagic fish can tolerate very low dissolved oxygen concentrations. These communities have a very patchy distribution and are relatively difficult to sample and study using standard nets.

The symposium confirmed that EBUEs play an essential role in the functioning of the oceans, both at the regional scale (from the coast up to a few hundred miles outside the continental shelf) and globally. EBUEs are characterized by dramatic and sudden changes affecting their dynamics at all time and space scales, from their climate forcing all the way to the extreme of the trophic chain (top predators and fishers). EBUEs are open ecosystems where circulation and different fluxes of inorganic and organic matters play an important role. Water mass exchanges, passive transport of organisms and different fluxes of matters and energy (from deep waters to surface; from inshore or estuaries to offshore; from water to atmosphere and vice versa; from water to sediment and vice versa) were quantified thanks to the use of automated observations (*in situ* and remote) and 2D or 3D models. All EBUEs are affected by the climate change but in many aspects they respond differently, due to their differences in location (ocean, latitude) and topography (width of the continental shelf, presence of offshore islands, coast orientation, presence of canyons, etc.).

A number of unresolved issues concerning comparative and integrative aspects of EBUEs were identified during the symposium. Some of the most relevant topics were: (1) How significant are atmospheric teleconnections between basins and what are the connections between upwelling variation and large-scale remote forcing? (2) What is the relative importance of Ekman transport versus mesoscale (filaments, eddies) fluxes from inshore to offshore regions? (3) What limits primary production in EBUEs and why do EBUE's have such dramatic differences in fish production but not in primary production? (4) What role do anoxia-tolerant species, like euphausiids and mesopelagic fish, play in the transfer of energy through EBUE food webs? (5) What is the interaction between food webs structure and biogeochemical cycling? (6) How will EBUE's respond to climate and global change (e.g. will boundary zones shift or will gradients intensify or weaken with global warming)? While these questions are not all new, several of them (for example, 1, 4 and 6) would not have been phrased in the same way in former symposia on EBUEs.

In summary, the symposium presented many scientific advances in different fields of marine science and the willingness of the scientific community to integrate their research further. But as usual, as the scientific advancements improve our knowledge, new questions appear. Despite these unknowns, this symposium represented a big step forward in cementing a multi-disciplinary scientific community focused on the dynamics of upwelling ecosystems, able to exchange ideas and share experiences on how to study and manage these particular and important ecosystems.

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