Large Marine Ecosystems, Vol. 14 V. Shannon, G. Hempel, P. Malanotte-Rizzoli, C. Moloney and J. Woods (Editors) © 2006 Elsevier B.V./Ltd. All rights reserved.

Modelling, Forecasting and Scenarios in Comparable Upwelling Ecosystems: California, Canary and Humboldt

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ABSTRACT

The three eastern boundary ecosystems comparable to the Benguela ecosystem (BCE) display differences and commonalities. The California (CalCE) and Humboldt Current (HCE) ecosystems are continuous topographically, whereas the Canary Current ecosystem (CanCE) is interrupted by the Gulf of Cadiz and the Canaries archipelago. All have similar regimes of equatorward flow over shelf and slope associated with upwelling and a subsurface poleward flow over the slope, though in the HCE multiple flows and counter-flows appear offshore. All systems exhibit year round upwelling in their centre and seasonal upwelling at their extremes as the trade wind systems that drive them migrate north and south, though the HCE is strongly skewed toward the equator. All systems vary on scales from the event or synoptic scale of a few days, through seasonal, to inter-decadal and long term. Productivity of each system follows the upwelling cycle, though intra-regional variations in nutrient content and forcing cause significant variability within regions. The CanCE is relatively unproductive compared to the CalCE and HCE as a result of differences in large scale circulation between the Pacific and Atlantic. The latter two systems are dominated by El Niño -Southern Oscillation (ENSO) variability on a scale of 4-7 years. Physical modeling with the Princeton Ocean Model and the Regional Oceanic Modeling System has advanced recently to the stage of reproducing realistic mesoscale features and energy levels with climatic wind forcing. Operational forecasting by these models with assimilation of sea surface temperature and other data is successfully implemented in CalCE. On longer time scales, the Lamont-Doherty Earth Observatory model is able to hindcast El Niño variability over the long term up to 2 years in advance. Empirical ecological models in all three systems have attempted prediction of permissible catch level (fractional Maximum Sustainable Yield), recruitment, catches or onset of migration with lack of continued success, partly because discontinuous or inadequate observations hamper model implementation and assessment. Moreover, empirical models tuned to particular environments fail when fundamental regime shifts occur. One of the most successful approaches is that of intensive monitoring of catch and environmental parameters linked to an informal Operational Management Procedure (OMP) to inform fisheries management off Peru. This OMP contributed to preservation of anchovy stock during the 1997-8 El Niño but remains to be formalized or tested under varying conditions. Prediction on time scales of global warming are uncertain because physical climate models still disagree on whether upwelling will intensify or weaken. Possible scenarios on decadal scale based on warming or cooling of waters in the Eastern Boundary Current systems can be proffered, albeit with little confidence at present. Future approaches for all systems, including the BCE, will in the long run likely combine coupled atmospheric/ocean models with biological process models. Judicious application of purely statistical modeling based on inherent time series properties will assist, though such techniques are unable to cope with regime shifts.

INTRODUCTION

The objective of this chapter is to review the variability and change in systems that can be compared to the Benguela system and to show what lessons can be learned from the modelling and forecasting activities in those systems. Eastern ocean boundary ecosystems can be classified into three zones (Mackas et al., in press): 1) mid & low latitude upwelling; 2) equatorial; and 3) high latitude, poleward surface flow and downwelling. The Benguela Current ecosystem (BCE) falls in the first group, which is characterized by local wind-driven upwelling, strong alongshore advection, a poleward undercurrent, high productivity of plankton and pelagic fish, seaward extension of the boundary current and biological system beyond the continental shelf, remote physical forcing by large scale teleconnections, very low to moderate precipitation and coastal freshwater inputs at least in the core area of the system, and highly dynamic systems displaying strong variability at all spatial and temporal scales.

Here we focus on the other three ecosystems that belong to this first category (Figure 9-1): the California Current (CalCE), the Canary Current (CanCE) and the Humboldt Current (HCE) ecosystems. After briefly describing these three systems (part 1), we review efforts to model and forecast them (part 2), and finally we speculate on possible biological scenarios that represent the response of key populations to forecasted changes in the physical environment associated with global change (part 3). In part 1 we describe each system separately using three sub-sections: physical traits, productivity and fish and fisheries. In order to facilitate comparison between the three systems, in part 2 we present first a review of physical modelling and forecasting activities, then a review of ecology. In part 3, global scenarios are presented briefly, and their likely effect on each system is discussed.

Although there is no consistent definition of regime shift, this terminology is frequently used in the present work as it is in the current literature. Here we followed de Young et al. (2004) in considering that a regime shift is an abrupt change from a quantifiable ecosystem state, representing substantial restructuring of the ecosystem persisting for long enough that a new quasi-equilibrium state can be observed.



Figure 9-1. Schematic map of the eastern boundaries of the Pacific and Atlantic showing major current systems (CalCE = California Current Ecosystem; CanCE = Canary Current Ecosystem; HCE = Humboldt Current Ecosystem; BCE = Benguela Current Ecosystem) and their main features. (Longitude scale is compressed).

PART 1. BRIEF DESCRIPTIONS OF CALIFORNIA, CANARY AND HUMBOLDT CURRENT ECOSYSTEMS

California Current Ecosystem (CalCE)

Physical traits

The collection of eastern boundary currents in the CalCE abutting the continental U.S. West Coast (often called the California Current System) has been extensively studied. Since 1950 the California Cooperative Ocean Fisheries Investigation (CalCOFI) has provided a large-scale time series of hydrographic measurements off Central and Southern California. A series of process experiments (Coastal Upwelling Experiment, CUE; Coastal Transition Zone, CTZ; Eastern Boundary Current, EBC; Coastal Ocean Dynamics Experiment, CODE; Coastal Ocean Processes, CoOP; Global Ocean Ecosystem Dynamics, GLOBEC) has been carried out with shipboard hydrographic

and Doppler current surveys, plus moored arrays and Lagrangian drifters to sample both large-scale and mesoscale currents. Satellite measurements of SST (sea-surface temperature) (AVHRR), sea-surface height (altimetry), and color (SeaWIFS) give extensive coverage, but are limited to the surface. Finally, theoretical and computational models have provided useful paradigms for understanding the dynamics of the CCS (Marchesiello et al. 2003). A recent review of observations, laboratory experiments, and model results on the CalCE can be found in Hickey (1998). Recent CalCE observations are reported in special issues of Deep Sea Research II (2000; 47, 761-1176) and Progress in Oceanography (2002; 53, Issue 2-4).

Theoretical and modeling studies of the CalCE have traditionally focused on coastal upwelling and downwelling driven by strong alongshore winds over the narrow continental shelf. The system extends from about 47°N, where the West Wind Drift impinges on the coast to near 21°N at the tip of Baja California. Observations show that energetic near-shore currents respond to local wind forcing and remote influences transmitted along the coastal waveguide. During the upwelling season, strong southward jets develop along the upwelling front separating cool upwelled- from warm oceanic- waters, with significant topographically modulated variability. The persistent alongshore currents are unstable, and some separate from the near-shore region (Barth et al. 2000) to form offshore-flowing currents entraining cold upwelled water in the form of filaments (Brink and Cowles 1991). Upwelling is most intense along the central and northern California coast, and very seasonal to both north and south. At a depth around 300 m, a California Undercurrent flows northward along the slope all year (Collins et al. 2004). During winter a surface northward Davidson Current and downwelling develop nearshore along much of the coast (Strub and James 2002).

The CalCE contains three characteristic water masses: Pacific Subarctic Water (low salinity S and temperature T; high oxygen and nutrients) is advected equatorward with the coastal current; North Pacific Central Water (high S, T, and nutrients; low oxygen) enters from the west with the West-Wind Drift; and Southern Water (high S and T; low oxygen and nutrients) comes from the south with the California Undercurrent. In general, S and T increase equatorward in the CalCE. Salinity also increases with depth in the CalCE, thereby enhancing stratification and baroclinicity; this constitutes a major and dynamically fundamental difference to all other eastern-boundary upwelling regimes. The intrinsic mesoscale variability is only weakly related to local wind stress fluctuations (Kelly et al. 1998). Instability of the coastal jets does not require topographic effects, but capes and ridges may promote locally enhanced upwelling centres and cross-shore transport (Narimousa and Maxworthy 1989; McCreary et al. 1991; Batteen 1997; Marchesiello et al. 2003). Eastern-boundary current systems are also affected by Rossby-wave dynamics, which transport energy westward to the open ocean (McCreary and Kundu 1985; Strub and James 2002).

Productivity

Satellite images often show sharp cross-shelf gradients in sea surface temperature (SST) and colour, barriers to material exchanges, which often develop into filamentary intrusions of cold, nutrient- and pigment-rich water forming a 300 km wide coastal transition zone. The shelf-flushing time of a few days, associated with cross-shelf

transport by the cold filaments and associated mesoscale activity, thus is an important mechanism for shelf-ocean exchange of heat, nutrients, biota and pollutants (Mooers and Robinson 1984; Marchesiello et al. 2004).

New production of phytoplankton in this system, largely caused by upwelling, forms the basis of a simple chain-like ecosystem along the coast characterized by large cell sizes (diatoms), mesozooplankton grazing, high biomass and nutrients. Upwelled nutrients are rapidly taken up by the growing coastal diatom populations, which can be advected over large distances offshore within mesoscale features. The formation of these near-shore phytoplankton blooms and their subsequent offshore advection in filaments is a striking feature of CalCE satellite ocean color images and has been used to demonstrate the tight coupling between biology and physics in the highly turbulent coastal region. A continental-shelf-resident zooplankton community is observed off the northern CalCE, dominated by the copepods Calanus marshallae, Pseudocalanus mimus, and Acartia longiremis, and the euphausiid Thysanoessa spinifera, whereas further to the south, a distinctive zooplankton assemblage has been observed (Mackas, in press; Jiménez-Pérez et al. 2000). The copepod community does not generally control the phytoplankton population. Copepods often utilise coastal embayments, where an additional source of food is available and which act as retention regions for the dominant large copepods (and also fish larvae). Also, vertical migration is observed to be significant within the CalCE (Mackas et al. 1991; Batchelder et al. 2002), possibly providing an additional retention mechanism. In the coastal CalCE ecosystem, the mesozooplankton formed by the copepod community does not control the phytoplankton, because of the slow growing rates of the mesozooplankton. Along the coast, river run-off may affect the near-shore ecosystem, and the embayments provide an additional source of food for zooplankton and larval fish. At the same time, embayments are retention regions for the dominant large copepods and larval fish. Also, vertical migration is observed to be significant within the CalCE (Mackas et al. 1991; Batchelder et al. 2002), possibly providing an additional retention mechanism. Retention is crucial to the survival of zooplankton and larval fish in the CalCE, where particularly intense mesoscale activity leads to rapid offshore dispersal.

Fish and fisheries

Sinclair et al. (1985) analyzed El Niño impacts on larval success in decades of CalCOFI data and suggested that, despite reduced enrichment of coastal waters, El Niño provides a period of limited dispersal of fish eggs and larvae for certain species, which is favorable to later recruitment. Indeed, most of the biomass harvested from the CalCE is pelagic or semi-pelagic, mainly hake, market squid, anchovy, sardine, mackerel, jack mackerel, herring and, in the northern part of the system, salmon (Ware and McFarlane 1989; California Cooperative Oceanic Fisheries Investigations annual reports). These species occur throughout the continental shelf of the CalCE, although most display seasonal migration. Salmonids, demersal fishes, and some benthic invertebrates display narrower alongshore ranges. Several pelagic fish species spawn preferentially (Parrish et al. 1981; Bakun and Parrish 1982) in the Southern California Bight.

The Pacific sardine (*Sardinops sagax*) has displayed dramatic population changes: biomass estimates declined from 3 million tonnes in 1933 to <10,000 tonnes in 1975 then recovered to the present ~1 million tonnes (Smith and Moser 2003). In response to the collapse of the sardine fishery, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) was initiated in 1947 and has since collected ichthyoplankton data (Figure 9-2) and many other oceanic data.

From 1988, use of the Continuous Underway Fish Egg Sampler (Checkley et al. 1997, Checkley et al. 2000) has confirmed that spawning of coastal pelagic species is broadly concentrated in and immediately north of the Southern California Bight. Spawning is frequently associated with the boundaries of eddies and upwelling plumes (Mackas et al., in press) and exhibits considerable interannual variation. Paleontological records of anoxic core sediment from the Santa Barbara basin indicate interdecadal variation in sardine and anchovy abundance prior to any substantial exploitation (Baumgartner et al. 1992).

Catch rates, total biomass, and recruitment of most exploited species have varied 10-100 fold at interannual and decadal time scales (Mantua et al. 1997; Bakun 2004; Chavez 2004; CalCOFI Reports series, http://www.calcofi.org/default.html), which is mainly attributed to variations in natural mortality. Similarly, several unexploited species of marine mammals and seabirds also show variability in population and reproductive success, alongshore migration, and seasonality and spatial zonation of their reproductive activity (e.g., Abraham and Sydeman 2004; Sydeman et al. 2001; Bertram et al. 2001; Veit et al. 1997).

Canary Current Ecosystem (CanCE)

Physical traits

The CanCE, defined broadly by the eastern boundary of the North Atlantic subtropical gyre (Figure 9-1), extends from northern Iberia (43°N) to Guinea (10°N) (Barton 1998). The ecosystem is divided into the Iberian and the Northwest African areas, discontinuous across the Strait of Gibraltar. Reviews by Barton (1989), Mittelstaedt (1991), Barton (1998) and Arístegui et al., (in press) detail the physical oceanography and biogeochemistry of the region. Recent observations in the system are reported in volumes of Progress in Oceanography (2004, 62/2-4) and Deep-Sea Research (2002, 49).

A weak Portugal Current flows southward offshore of Iberia. It and the Azores Current contribute to the Canary Current, which flows along the African coast to Cape Blanc (21°N), where the Canary Current separates to flow westward into the North Equatorial Current (Figure 9-1). Between Capes Blanc and Verde, a permanent cyclonic recirculation feeds water northwards along the coast. Part of this poleward flow continues beyond Cape Blanc as an undercurrent, possibly continuous as far north as Iberia. The north-south migration of the Azores High produces summertime upwelling off Iberia, year-round (more intense in summer) upwelling between 35° and

20°N, and winter upwelling south of Cape Blanc (Wooster et al. 1976). The upwelling is associated with formation of a strong temperature front and associated strong, equatorward jet-like flow near-shore. When wind forcing weakens or disappears, even briefly, this southward flow may be replaced by northward flow as the undercurrent extends to the sea surface, as occurs off Iberia in winter or Senegal in summer. The poleward flow may inject slope water into the open sea by shedding anticyclonic eddies (Peliz et al., 2003a, 2003b). Variability of upwelling occurs on decadal scales, in association with the North Atlantic Oscillation (NAO), but >70% of the variance is related to synoptic scale changes (<30 days) in wind forcing.

Throughout the region, coastal upwelling filaments stretch offshore from capes and promontories to export waters rich in organic matter into the oligotrophic waters of the subtropical gyre (Arístegui et al. in press). Especially notable are the large filaments off Cape Ghir and off Cape Blanc, where the Canary Current separates from the coast.



Figure 9-2. Examples of fish larval abundance 10m⁻² obtained from CalCOFI data; surveys were triennial from 1966 to 1984 (Figure reprinted from *Deep-Sea Research*-II, 50, Smith and Moser, Long-term trends and variability in the larvae of Pacific sardine and associated fish species of the California Current region, pp 2519-2536, copyright 2003, with permission of Elsevier).

Pelegrí et al. (2005) suggest the Cape Ghir filament in autumn represents a separation of the main flow from the coast, similar to that at Cape Blanc, with a cyclonic recirculation extending south of the Canary Islands. This archipelago, unique in the eastern boundary current systems, introduces large mesoscale variability, mainly in the form of downstream vortices (Arístegui et al. 1994).

Productivity

Varieties of North Atlantic Central Water (NACW) dominate the upper layers between Cape Finisterre and Cape Blanc. Eastern North Atlantic Central Water of subtropical (nutrient–poor) and subpolar (nutrient–rich) origin extends from the Canaries northward. High nutrient content South Atlantic Central Water (SACW) is separated from NACW by a front at 21°N (Cape Blanc). Upwelling related productivity is therefore a function of latitude as well as upwelling strength. Off Mauritania (~18°N), high surface nutrient concentrations are probably related to the doming in the cyclonic recirculation (Arístegui et al. in press). Generally, the region exhibits anomalously low productivity and chlorophyll concentrations relative to the observed nutrient concentrations (Minas et al. 1982). Compared to other upwelling regions, the source waters off NW Africa are poorer in nutrients but richer in oxygen as result of the global scale circulation (Codispoti et al. 1982), which may explain differences in productivity and regeneration rates found, for instance, between the NW Africa and the Peru ecosystems (Minas et al. 1982).

Nutrient assimilation and regeneration ratios in the NW African coast are similar to other coastal upwelling regions, although significant regional differences within this system exist, particularly in silicon. Depending on geomorphological changes along the coast and the rate of regeneration, silicon can be either in excess or deficient (Herbland and Voituriez 1974; Minas et al. 1982). The interplay between Canary Islands eddies and upwelling filaments is likely to favour exportation of coastal enriched water to the oligotrophic open ocean. This would explain the strong imbalance between phytoplankton production and community respiration observed in the subtropical gyre (Arístegui et al., in press).

Fish and fisheries

The CanCE can be divided biogeographically into two areas that overlap at Cape Blanc, where the water masses transition between NACW and SACW. Sardine (*Sardina pilchardus*) is the predominant species off the Iberian and Moroccan coasts whereas sardinellas (*Sardinella aurita* and *S. maderensis*) and horse mackerels (*Trachurus spp*) are dominant further south off Mauritania and Senegal.

At present, the CanCE overall produces ~3 million tonnes of marine catches. Small pelagic fish, mainly European sardine, represent ~44% of the catch, followed by medium-size pelagic fish, horse-mackerel and mackerel, (24%), semi-pelagic species like hake and blue whiting (5%) and cephalopods (mainly octopuses) (5%). Industrial exploitation along the West African coast is more recent than in the other upwelling ecosystems (Figure 9-3) and was initiated by European countries. In contrast, exploitation of pinnipeds started many centuries ago and almost led to extinction of the monk seal *Monachus*, which shows no signs of recovery despite increasing



Figure 9-3. Landings of fish (excluding tunas) and shellfish from the Canary Current ecosystem for 1950-2001 and from the Iberian Peninsula for 1973-2001, (Source: FAO and ICES data).

protection of the few hundred individuals surviving in the southern part of the CanCE (CMS 1999). Another characteristic of the CanCE is that there are few marine bird colonies (Cushing 1969) and consequently little competition between fishing activities and bird predation.

Drastic fluctuations of abundance have been observed for sardines, sardinellas and other pelagic- and bottom- fish during the last fifty years. A downward trend shown by long-lived versus short-lived species ratios in the commercial fisheries (Figure 9-4) is caused by the partial replacement of longer-lived bottom fish species by short-lived small pelagics and cephalopods.

Uncontrolled exploitation during the 1960s drastically reduced stocks of sparids and other ground fish but allowed growth of other fish stocks (Caddy 1983; Gulland and Garcia 1984, FAO 1986; Roy and Cury 2003). Increased cephalopod landings after the late 1960s partly reflect increased market demand. However, indirect evidence indicates that heavy fishing pressure removed the cephalopods' predators (Caddy 1983, Caddy and Rodhouse 1998) while discards enhanced the abundance of some scavenger species that constitute cephalopod prey (Balguerias et al. 2000).

In the 1970s, snipefish (Macrorhamphosus scolopax and M. gracilis) abundance increased dramatically in Iberian and Moroccan waters (Brêthes 1979) while triggerfish (Balistes carolinensis) spread geographically from Ghana to Mauritania, colonizing both pelagic and demersal ecosystems (Caverivière 1991; Fréon and Misund 1999). After attaining a peak biomass >1 million tonnes at the end of the 1970s, these populations collapsed in NW African waters (Sætersdal et al. 1999; Belvèze 1984). These events remain largely unexplained.



Figure 9-4. Evolution of the ratio of long lived to short-lived species in the landings from the Canary Current ecosystem from 1950 to 2001.

Since 1969, the southern sardine stock and fishery have grown rapidly and spread further south (Holzlohner 1975; Barkova and Domanevsky 1976), while to the north sardine has come to dominate the small pelagic fish community (Gulland and Garcia 1984). This trend seemed to reverse in the mid-1990s when sardinellas extended north of Cape Barbas, and the sardine stock off Sahara crashed from ~5 to ~1 million tonnes in 1997 off Sahara. Sardines recovered gradually after 1997, whereas other small pelagic species remained abundant in the region (Anonyme 2003). These observed changes seem to be climate-driven. Quero et al. (1998) and Brander et al. (2003) noticed northward shifts of commercial and non-commercial fish distribution from southern Portugal to northern Norway since the late 1980s. As in the case of the triggerfish and the snipefish, the sardine collapse in 1997 does not appear to be linked to fishing pressure.

Fish population abundance in the CanCE has been linked to climatic indices. Longterm changes in winds off Portugal in recent decades, related to NAO, modify Iberian upwelling patterns, and thus the annual catch of sardine (Borges et al. 2003). Roy and Reason (2001) found significant correlation between ENSO, NAO and upwelling intensity in the CanCE, and suggested that global environmental signals affect the fish populations through atmospheric teleconnections. On other hand, sardine abundance fluctuates differently in different zones of the CanCE (Kifani 1998; ICES 2002a, 2002b; Borges et al. 2003; Carrera and Porteiro 2003). Decadal changes of some sardine populations in the CanCE parallel some in other eastern boundary currents, but within any region, different populations may be in or out of phase, which renders difficult any teleconnection hypothesis.

Humboldt Current ecosystem (HCE)

Physical traits

The HCE extends from northern Peru (4°S) to central Chile (40°S). It stands out from other eastern boundary current systems because it extends very near to the equator. It is directly influenced by ENSO and displays the most extended, most superficial and most depleted minimum oxygen layer (MOL). The HCE is characterized by a complex set of flows and counterflows that persist between the coast and 1000 km offshore (Alheit and Bernal 1993). The oceanic sector is dominated by a sluggish, wide, equatorward flow of about 0.04 ms⁻¹ that coincides with the boundary of the anticyclonic gyre of the Southeast Pacific, and is recognized as the Chile-Peru Oceanic Current. Nearer the coast, a southward counter-flow of about 0.06 ms⁻¹, the Peruvian Oceanic Counter-current, has been identified at 79°W off Peru and between 76° and 77°W, 500 km off the Chilean coast. The faster (~0.18 ms⁻¹) Humboldt Current is located somewhat closer to the coast, between 300 and 400 km offshore, with a core at about 200 m depth. Between the Humboldt Current and the coast, three seasonally varying and unstable branches can occasionally be distinguished. The most permanent branch is a counter-flow to the south centered at about 100 m depth off Peru and at 200 m depth off Chile. This Gunther Current or Peru-Chile Undercurrent is oxygen-poor and nutrient-rich. A spectrum of plumes, eddies, filaments and other transient structures has been observed (Montecino et al. in press). A thorough description of coastal ocean circulation off western South America is given in Strub et al. (1998).

In Peru, coastal upwelling reaches a maximum during winter and a minimum during summer. In northern Chile (18°-30°S) it peaks during late spring and off Central Chile (30°-38°S) it peaks during late spring and summer. This temporal progression of coastal upwelling from the north to the south results from the displacement of the subtropical centre of high atmospheric pressure that intensifies and moves southward as summer progresses. Therefore, off Peru, upwelling occurs all year, whereas in central Chile it is restricted to spring and summer.

Productivity

Carr (2002) compared the productivity of the four eastern boundary upwelling systems using different satellite-borne colour sensors data from 1997 to 1999 and found that, despite higher fish productivity in the HCE, its productivity per unit area and its total production (rate x surface area) were lower than in the BCE and CanCE, in contrast with earlier works based on in situ measurements and estimated production areas. The lower values found by Carr (2002) are largely explained by a better estimation of production area for the Humboldt (half the size of the CanCE) and the occurrence of the strong El Niño event of 1997-98 during the study period. A time series of zooplankton volume started in 1961 indicates large interannual variations related to regime shift (Ayon et al. 2004). The species identification for this series promises to shed further light on this topic.

In Chilean coastal waters, much chlorophyll biomass is found within 10-50 km of the coast. The maximum surface chlorophyll occurs in austral summer off both Peru and

Chile despite the above-mentioned out of phase upwelling seasons between these two countries. The dominant zooplankton taxa are copepods (*Calanus chilensis* and *Centropages brachiatus*), euphausiids and the large holozooplankton such as salps, appendicularia (tunicata), siphonophores (cnidaria) and chaetognaths (Montecino et al., in press).

Fish and fisheries

The HCE supports extremely high fish production which is dominated by anchovy, although the usual mix of other pelagic fish stocks characteristic of eastern boundary systems is also present: sardine, horse mackerel and mackerel. Since the beginning of industrial fisheries, catches were mainly dominated by anchovy whereas from 1977 to 1998 sardine catches were substantial (Figure 9-5). Catches of horse mackerel and mackerel are less important. The most important demersal fish in the HCE is hake. The reason why the HCE has the highest fish yield whereas its satellite-based production estimates are lower than in the BCE and CanCE are still unclear. Among various hypotheses, Carr (2002) favoured the differences in trophic structure or spatial and temporal accessibility for different upwelling systems.

The fisheries are sensitive to different scales of variability, especially the interdecadal variability that translates into changes in water mass characteristics (in terms of temperature, plankton structure, etc.) and the El Niño/ La Niña events (Chavez et al., 2003; Alheit and Niquen 2004; Bertrand et al. 2004a). Furthermore, the location and depth of the MOL plays a major role in the distribution and sometimes mortality of fish and ichthyoplankton (Mathiesen 1989; Ulloa et al. 2001; Montecino et al., in press).

PART 2. REVIEW OF MODELLING AND FORECASTING EFFORTS IN THE THREE ECOSYSTEMS

PHYSICS

California Current system

Because near-shore and offshore currents have distinctive spatial scales (1-10 km nearshore and 100-1000 km offshore), they are usually measured and modelled with separate methods, implicitly assuming their interactions are weak. The few realistic regional modelling studies of the CalCE mostly have used simplified dynamics, domains, and forcing, with coarse spatial resolution and/or short integration times. These studies nonetheless have identified the primary mechanisms for seasonal, mesoscale, and sub-mesoscale variability of the CalCE (i.e. wind forcing, Kelvin waves, Rossby-wave propagation, and a large range of instability processes). Batteen's (1997) model results indicate that, consistent with observations, the seasonal cycle in the CalCE is largely a deterministic response to the forcing, with phase and amplitude shifts due to Rossby waves. Strong intrinsic variability emerges from many numerical

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Figure 9-5. Alternating anchovy and sardine regimes in Humboldt Current ecosystem. (a) First principal component of normalized interdecadal SST time series from coastal stations (solid line) and Extended Reconstructed Sea Surface Temperature data (dashed line; Smith and Reynolds 2004; http://lwf.ncdc.noaa.gov/oa/climate/research/sst/sst.html) Montecinos, A., Purca, S. and Pizarro, O. Interannual-to-interdecadal sea surface temperature variability along the western coast of South America, Geophys. Res. Lett., 30 (11), 1570, doi:10.1029/2003GL017345. 2003. Copyright 2003 American Geophysical Union. Reproduced by permission of American Geophysical Union. (b) catches of anchovy and sardine in Peru (Miguel Niquen, IMARPE, Peru, pers. comm.) and Chile (Anuarios Estadísticos de Pesca, Servicio Nacional de Pesca de Chile, SERNAPESCA-Chile).

solutions (Ikeda et al. 1984; Auad et al. 1991; McCreary et al. 1991; Haidvogel et al. 1991; Pares-Sierra et al. 1993; Batteen 1997, Haney et al. 2001), which makes small-scale forecasting imprecise. Quasi-geostrophic models implicate baroclinic instability as the cause of variability of offshore currents; however, they lack the ability to produce sharp fronts and their associated instabilities.

More recently, Marchesiello et al. (2003) used the Regional Oceanic Modeling System (ROMS) to simulate the mean-seasonal equilibrium CalCE with realistic dynamics and domain configuration. The level of eddy kinetic energy in their high resolution solutions is comparable to drifter and altimeter estimates. Since the model lacks transient forcing, they conclude that the dominant mesoscale variability in the CalCE is intrinsic. Eddy generation is mainly by baroclinic instability of upwelling, alongshore currents. There is progressive movement of mean-seasonal currents and eddy energy offshore and downwards into the oceanic interior in an annually repeating cycle. The associated offshore eddy heat fluxes essentially compensate near-shore cooling caused by transport and upwelling. The currents are highly non-uniform along the coast; capes and ridges give rise to mean standing eddies and transient filaments and fronts.

ROMS is being used operationally by the Jet Propulsion Laboratory (http://ourocean.jpl.nasa.gov) for CalCE, with nesting to zoom into the Monterey region. A VAR3D-type assimilation scheme (Li et al., in prep.) allows forcing with satellite as well as local in situ data. A similar approach has also been developed by the Office of Naval Research using the Princeton Ocean Model (POM).

Canary Current system

Analytical studies of the dependence of upwelling on wind forcing in the CanCE provide reasonable possibility of forecasting ocean response to atmospheric perturbation (Arístegui et al., in press). More accurate representation, which includes other factors (topography, boundary conditions, tides, etc.), can be expected from hydrodynamic models, although the capability of models is limited by the accuracy of wind forcings.

There has been limited effort to model the hydrodynamics of the CanCE until very recently. A 2D tidal circulation model of the Atlantic continental shelf of the Iberian Peninsula using a finite element triangular grid of variable size produced output that compared well with coastal tide gauges, and provided a database for forecasting sea levels and currents in this area (Sauvaget et al. 2000).

Johnson and Stevens (2000) modelled the region from Finisterre to the Canary Islands using monthly mean winds from the European Centre for Medium-range Weather Forecasts. They used the regional Modular Ocean Model with a horizontal resolution of 20 km and 36 vertical levels to reproduce many features of the circulation between the Canary Islands, the Azores and the Strait of Gibraltar, including a quasi-continuous slope undercurrent. Bateen et al. (2000) also showed that seasonal wind forcing was

sufficient to produce eddy and filament-like features, especially in the presence of realistic coastline configuration. Neither model included realistic topography, however, and did not reproduce the smaller scale features of the CanCE.

A similar scale hydrodynamics model of the Iberian region, coupled to a biological model including eight state variables from nutrients to zooplankton and detritus (Slagstad and Wassmann 2001), modelled the physics and phytoplankton production satisfactorily, but not the carbon export. More recently, an implementation of the ROMS hydrodynamics model in the same region (Peliz et al. 2003a, 2003b) investigated the poleward flow response to the interactions of two forcing mechanisms: an along-coast density gradient and wind forcing.

On the larger scale, IRD (Institut de Recherche pour le Développement, France) and LPA (Laboratoire de Physique de l'Atmosphère, Senegal) are implementing a similar model for the whole CanCE, with two-level imbedded models allowing for fine scale study of key areas of ecological interest, e.g. retention areas (Marchesiello et al. 2004). The "parent" model has horizontal resolution of 25 km, and is aimed at describing the seasonal oscillation of the Azores and Canary Currents as well as the branches of the Equatorial counter-current. The first level of imbedding, presently implemented only off Senegal at a resolution of 5 km, will allow representation of mesoscale processes such as eddies and filaments. A second level of imbedding is currently implemented with 1 km grid cells in order to describe sub-mesoscale processes and circulation in bays and around capes arising from tidal and localised wind forcings.

Humboldt Current system

Basin scale hydrodynamic models represent the Pacific Ocean variability in temperature, salinity and current, using different codes such as POM, or the Ocean General Circulation modelling System (OPA). Some models are mainly process oriented, others are used for prediction. The latest version (5) of the Lamont-Doherty Earth Observatory (LDEO) ocean–atmosphere coupled model incorporates an assimilated SST field, which directly affects the surface wind field and has a persistent effect on the coupled system (Chen et al. 2004). The model's internal variability generates a self-sustaining oscillation with El Niño-like periods and amplitudes. Using sea level, winds and SST for initialisation, the model satisfactorily forecasted monthly SST for the period 1857 to 2003 at lead times of up to two years (Figure 9-6), including all prominent El Niño events within this period.

Penven et al. (2003) used the ROMS code to model the mean 3d-circulation of the Peruvian upwelling system, its, seasonal cycle and its mesoscale dynamics at intermediate scales.



Figure 9-6. Hindcasts of El Niño and La Niña in the past 148 yr. using the LDEO5 model: (a) time series of SST anomalies averaged in the NINO3.4 region (58 S–58 N, 120–1708 W). The red curve is monthly analysis of ref. 12 and the blue curve is the LDEO5 prediction at 6-month lead; (b) Six of the largest El Niños since 1856. The thick red curves are observed NINO3.4 SST anomalies, and the thin curves of green, blue, magenta and cyan are predictions started respectively 24, 21, 18 and 15 months before the peak of each El Niño (reproduced from Chen et al. 2004).

ECOLOGY

California Current ecosystem

Parrish and MacCall (1978) developed a forecast model for chub mackerel (*Scomber japonicus*) recruitment in the California Current region by incorporating environmental variables in the Ricker stock-recruitment relationship (Figure 9-7). Sea level and an index of transport collected from the late 1920s to the late 1960s were included into the model. Despite high r2 values (0.60 and 0.76) forecasting failed in recent years due to a regime shift.

Conser et al. (2002) found that sardine productivity (fraction of mean sustainable yield) could be expressed as a quadratic function of the 3-year average temperature at



Figure 9-7. Observed and predicted recruitment of Pacific mackerel. (a) Ricker sea level model, (b) Ricker transport model (Reproduced from Parrish and MacCall, 1978 with permission from the "California Department of Fish and Game" and "NOAA Fisheries").

Scripps Pier, La Jolla, California. The Pacific Fishery Management Council adopted a policy to decrease sardine annual allowable catches from 15% to 5% of spawning biomass when average temperature falls below a threshold value. Based on temperatures observed since adoption of this procedure (1983-on), the indicated fraction of spawning biomass has consistently been 15% (Conser et al. 2004). Smith and Moser (2003) pointed out that while extrapolation from observed oscillations may provide useful short term predictions, the inherently unpredictable nature of regime shifts implies that vigilance and a cautious fishery regulation provide the best prospect.

A good example of spatial prediction is provided by MacCall's "basin model" which is based on the concept of density-dependent habitat suitability (MacCall 1990). During periods of low abundance, the population is restricted to the best-suited habitat, but the higher the biomass, the more extended is the population distribution. This model was successfully applied to the distribution of the Californian northern anchovy population Canary Current ecosystem

A few models coupling physical forcing with fishery data at a yearly scale were developed in the region. For instance, one conceptual model off Portugal indicated that upwelling during winter spawning from 1993-1997 caused offshore transport of larvae, impacting negatively on sardine (*Sardina pilchardus*) and horse mackerel

(*Trachurus trachurus*) recruitment and catches the following year (Santos et al. 2001). However, these conclusions, based on few years of data, require further validation before being used for forecasting. As a first step in that direction, Santos et al. (2004) used a simplified 2D model and Lagrangian tracking to simulate the observed distributions of sardine eggs and larvae. Other models, based on linear or non-linear multiple regressions between fish abundance proxies (catches or catches per unit of effort (CPUE)) as a dependent variable and fishing effort and environmental variables, are largely empirical. Despite efforts to combine these models with existing surplus production models to reduce spurious correlations (Fréon et al. 1993), this approach is inherently limited.

Nevertheless, practical applications of this kind of model have been implemented in Sénégal, Morocco and Côte d'Ivoire, where the interannual variations of clupeoid species abundance was related to fishing effort and an upwelling index (Fréon 1988, 1989). The models explained between 72% and 94% of the CPUE variability of the 20-year time series (Figure 9-8). Lack of systematic CPUE data in recent decades has prevented the updating of these models (Do Chi 1994). A similar empirical model describes variations in octopus (*Octopus vulgaris*) recruitment in Senegal according to different upwelling or retention indices computed from wind or satellite data (Demarcq and Faure 2000; Caverivière and Demarcq 2002; Laurans et al. 2002). Here also, the forecasting capability of these models cannot be assessed for lack of updated systematic observations.

Other empirical relationships have been found between, for instance, the time of arrival of adult sardinella on the Petite Côte of Senegal at the beginning of the year and the time of relaxation of upwelling off Mauritania, where they originate. This is suggested by negative correlations between monthly anomalies of CPUE and upwelling indices (Fréon 1986). Similarly, the migration of the emblematic thiof (*Epinephelus aeneus*) along the north coast of Senegal seems related to both the onset of the upwelling in Senegal and its relaxation in Mauritania (Cury and Roy 1988). In neither case was the relationship updated, and so evaluation of its forecasting ability is difficult.

Humboldt Current ecosystem

In Chile, empirical models similar to those developed for West Africa were used to link CPUE of pelagic species to fishing effort and/or environmental variables related to the upwelling intensity or turbulence (Yáñez et al. 2001). A similar model used on anchovy data from 1957 to 1977 considered the Peruvian and Chilean stocks as a single unit (Fréon and Yáñez 1995). Attempts to update this model were unsuccessful due to profound changes in the fisheries and a changed response of the ecosystem to environmental perturbation after the regime shift in the 1970s.

In Northern Chile, operational models were used to predict favourable fishing grounds for small pelagic species (Silva et al. 2000; Nieto et al. 2001) and sailfish (Barbieri et al. 2000). These models couple real-time satellite data to an expert-system that learned



Figure 9-8. Additive exponential model where the upwelling index (mean wind speed, V) influences the *Sardinella* spp stock abundance and catches (Y) in the Senegalese fishery, from 1966 to 1983. Upper graph: theoretical catches according to V values and fishing effort (solid curves) and observed catches (line with annual dots). Lower graph: time series of observed and predicted total catches (Fréon 1986, 1989).

from previous relationships between CPUE distribution and historical satellite data of SST and/or chlorophyll.

In Peru, El Niño events impact the small pelagic fishery to such a large extent that IMARPE (Instituto del Mar del Perú) developed a series of tools to manage this pelagic fishery in real time according to environmental conditions and abundances estimated from acoustic and fishery surveys (www.imarpe.gob.pe). Month-long scientific acoustic surveys by one or two research vessels are normally performed 2 to

4 times a year. These are augmented during El Niños with near-synoptic surveys (<48 hours) of the entire Peruvian continental shelf by up to 40 fishing vessels equipped with commercial echo-sounders. Furthermore, IMARPE observers on the vessels send real-time information on the catch composition (species and body length), SST, and ancillary data to a central office via satellite (Ñiquen et al. 2000; Bertrand et al. 2004b). On the basis of this information and previous experience, IMARPE advises the fishery minister on fisheries management. The advice has often translated into partial or total closure of the fishery with immediate application. Although no official operational management procedure (OMP) is formally documented, this method likely was one key factor in helping prevent collapse of the anchovy stock during the long and severe El Niño of 1997-1998 (Bouchón et al. 2000, Ñiquen et al. 2000; Bertrand et al. 2004a). The challenge in maintaining such OMPs is that not all El Niño events have similar effect, even when their temperature anomalies have the same amplitude (Bertrand et al. 2004a; Niquen and Bouchon 2004).

TELECONNECTIONS BETWEEN ECOSYSTEMS

Regime-like signals appear in many fisheries, which though distant may be linked through environmental teleconnections. These climatic oscillations can potentially induce synchrony among pelagic fish populations living in different ecosystems, as has been observed around the world (Kawasaki 1983; Klyashtorin 1998; Schwartzlose et al. 1999). Nonetheless, most of the observed synchronies are statistically insignificant, given that the series are only a few decades long and largely auto-correlated, and therefore have few degrees of freedom. In the absence of clearly identified processes linking the various ecosystems, one cannot yet firmly conclude that remote synchronies exist (Fréon et al. 2003), nor use them for prediction.

PART 3. DEVELOPMENT OF BIOLOGICAL SCENARIOS BASED ON FORECASTED PHYSICAL SCENARIOS

Recently, a number of authors attempted to predict the reaction of eastern boundary upwelling ecosystems to global climate change (Bakun 1990, Mote and Mantua 2002, Snyder et al. 2003, Diffenbaugh et al. 2004, Bakun and Weeks 2004). Citing evidence from different eastern boundary systems, Bakun (1990) suggested that global greenhouse warming was deepening the continental low pressure centres, thereby enhancing the cross-shore atmospheric pressure gradient to intensify the alongshore sea surface wind stress and coastal upwelling. This was confirmed by Schwing and Mendelssohn (1997) and Snyder et al. (2003) for the California Current system, and Mendelssohn and Schwing (2002) demonstrated common trends in the California and Humboldt Current systems. Different models were applied to test the impact of future warming (Mote and Mantua 2002; Snyder et al. 2003; Diffenbaugh et al 2004; Bakun and Weeks 2004), with very different outcomes. Mote and Mantua (2002) used two "state-of-the-art climate models" and reported that, in each of the upwelling zones they modelled, the seasonal cycle of upwelling remains unchanged throughout the 21st century. In contrast, Snyder et al. (2003), who used a regional climate model to

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estimate changes inn wind-driven upwelling, suggested that substantial changes of upwelling will occur under increased CO_2 concentrations. However, different regions of the California Current system respond differently, resulting in changes in phase and an intensified peak season in the northern limb and a muted peak season in the southern limb (Figure 9)



Figure 9-9. Difference of the monthly average modeled wind-stress curl (N/m2), calculated as: (1980-1999) – (2080-2099) (Snyder, M.A., L.C. Sloan, N.S. Diffenbaugh and J.L. Bell. Future climate change and upwelling in the California Current. *Geophys. Res. Lett.*, 30: 1823-1826, 2003. Copyright 2003 American Geophysical Union. Reproduced by permission of American Geophysical Union).

Summing up, eastern boundary current upwelling systems (or parts of them) might react to global warming with either increased or decreased upwelling intensity. We will describe now how long-term dynamics of key populations in the three ecosystems could react to increased or decreased upwelling intensity, following suggestions of DeAngelis and Cushman (1990), but without using the modelling toolbox they suggested.

California Current ecosystem

A warming trend of about 1°C in SST from 1950 to 1999 has been observed along the Southern California coast (Bograd and Lynn 2003; Roemmich 1992). Increasing stratification and declining zooplankton have been linked with this warming trend (McGowan et al. 2003; Roemmich and McGowan 1995). On the other hand, evidence

has been found that upwelling-favourable winds have increased in recent decades (Schwing and Mendelssohn 1997). This increase in upwelling-favourable winds is consistent with the ideas of Bakun (1990) and also with recent regional climate modeling experiments (Snyder et al. 2003), which suggest that alongshore winds intensify as a response to warmer ocean temperatures. Upper ocean warming and increased upwelling-favourable winds may, at first, appear as two inconsistent scenarios for global warming effects. A recent regional modeling experiment using ROMS, (Di Lorenzo et al. 2005) shows that two opposed processes can explain this apparent inconsistency. On one hand, a cooling of about 0.5°C in SST is driven in their ocean model by the 50 year NCEP wind reanalyses, which contain a positive trend in upwelling favourable winds along the California coast. However a net warming trend of 1°C in SST occurs when the effects of surface heat fluxes are included as forcing functions. Previous analyses of observed surface heat fluxes (Cayan 1992) and ocean model hindcasts of the surface layer heat budget (Miller et al. 1994) confirm that along the California coast the long-term SST signal is indeed dominated by changes in surface heat fluxes. The ocean model simulations show that increased stratification associated with the warming reduces the efficiency of coastal upwelling in lifting subsurface waters to the ocean surface, masking any effects of the increased strength of the upwelling winds.

This scenario is consistent with a reduction of the nutrient supply at the coast, which may in turn explain the observed decline in zooplankton concentration. It is worthwhile noting that, in the simulations, increased static stability arising from upper ocean warming leads to increased mesoscale eddy variance and therefore increased cross-shore transport of material properties. This may provide an additional scenario for declining coastal planktonic communities due to warming trends. As a result, one can expect a decrease in abundance of small pelagic fish due to both dispersion of their larvae and decrease in prey for adults. Nonetheless this scenario remains largely speculative because we are ignorant of how this trend will interact (or not) with natural interdecadal variability of pelagic fish abundance (Baumgartner et al. 1992), whose underlying processes remain unknown. If prediction had to be based only on the long-term autocorrelation in sardine abundance observed in the time series of sediment cores, the recent recovery of the Californian sardine stock should last for a few decades.

Canary Current ecosystem

The northward shifts in distribution of commercial and non-commercial fish species that occurred from southern Portugal to northern Norway from the late 1980s has been related to an increase in water temperature (Quero et al. 1998; Brander et al. 2003). Although one should be extremely cautious in forecasting long-term scenarios, these changes in fish distribution and community could be accentuated by a further warming. Under this scenario, the northward extension of Mediterranean and NW Africa tropical or subtropical species could be exacerbated, whereas a scenario of cooling temperature could lead to a restoration of the previous situation, especially if the exploitation rate remains at a reasonable level for all compartments of the ecosystem.

Prediction related to global changes might be hampered by independent (and poorly understood) decadal fluctuations in the abundance of small pelagic fish species and related changes in the ecosystem, as observed on the Iberian shelf (Borges et al. 2003; Cendrero 2002). Here and in similar upwelling ecosystems, pseudo-cycles of 40 to 60 years have been observed (Klyashtorin 1998; Schwartzlose et al. 1999). Based on empirical relationships between pelagic fish abundance and climatic indices (Klyashtorin 2001) or simply on autocorrelation (Fréon et al. 2005), one can infer that the present decline in sardine abundance should reverse during the next decade. Once more this type of prediction is highly uncertain due to its empirical nature.

On the West African shelf, if there is no major change in the seasonal cycle of alongshore wind stress during the next decades, as supposed by Mote and Mantua (2002), the ecosystem should mainly undergo changes in the exploitation rates of the different compartments of the ecosystem. Nonetheless, population outbursts similar to those previously mentioned, but possibly in other species, are likely to occur unpredictably. Though triggered by largely unknown processes, such events seem favoured by an unbalanced exploitation of resources (Gulland and Garcia 1984; Caddy and Rodhouse 1998; Verity et al. 2002).

Under the scenario of intensified upwelling, one expects enhanced southward migration of the central sardine stock, favouring the Moroccan fishery. The southern sardine stock should also display southward migration and extension of its habitat in Mauritania while sardinellas should retreat. In Senegal, the abundance of sardinella species should increase.

Decadal changes in upwelling strength and SST as observed around the 1970s are likely to occur and are difficult to predict, despite some understanding of their functional link with the major atmospheric patterns, e.g. North Atlantic Oscillation (Arístegui et al., in press). The observation that warm ENSO (El Niño/Southern Oscillation) events in the Pacific lead positive SST anomalies in the southern CanCE by about 3 to 6 months during late winter and early spring (Enfield and Mayer 1997; Roy and Reason 2001) may allow prediction of fish population abundance. In several studies (Fréon and Stéquert 1976; Fréon 1989; Belvèze 1991; Binet 1997; Binet et al., 1998) high pelagic fish abundance and catches were related to enhanced coastal upwelling, therefore recruitment and population growth. Nonetheless, because the origin of this lag is not fully understood, associated predictions remain uncertain.

Humboldt Current ecosystem

As in other eastern boundary currents, the decadal-scale dynamics of the HCE are governed by alternating anchovy and sardine periods (Schwartzlose et al. 1999, Chavez et al. 2003, Alheit and Niquen 2004; Bertrand et al. 2004a), which reflect the entire restructuring of the ecosystem from phytoplankton to the top predators (Jarre-Teichmann 1998, Alheit and Niquen 2004) (Figure 9-5). These regime shifts are associated with lasting warm or cool periods as warm subtropical oceanic waters approach or retreat from the Peru–Chile coast. Although fisheries might give a biased

index of abundance due to the influence of anthropogenic factors, it seems that cool phases parallel anchovy regimes (1950s-early 1970s; 1985 on) while the warm period (early 1970s-1985) clearly favoured sardine recruitment, taking into account a 3-year lag due to the age structure of the catches of this species.

Like an El Niño, the warm periods drastically change trophic relationships in the entire HCE exposing the Peruvian anchovy to a multitude of adverse conditions. Higher temperatures off Peru restrict the anchovy to the cooler upwelling zone at the coast, thereby decreasing their area of distribution and spawning. This concentration of the population favours egg and larval cannibalism and dramatically increases catchability. Increased spatial overlap between anchovies and the warmer water preferred by sardines permits heavy sardine predation on anchovy eggs. The anchovies' diet of phyto- and zooplankton is limited to a narrower coastal zone of restricted upwelling in warm years. Both phytoplankton and zooplankton have lower volumes, the latter likely reflecting a diminution in the large copepods, their main food source. Horse mackerel and mackerel increase predation pressure on anchovies by invading the anchovy habitat in warmer years (Alheit and Niguen 2004). In this ecosystem, where "variability is normality" (M. Espino, personal communication), fish have developed adaptive strategies in space and time (Bertrand et al. 2004a) and trophic relationships are not the only parameters affecting population fluctuation. Thus, to understand the effect of any climatic event on fish, various factors occurring at different spatiotemporal scales (e.g., the inter-decadal regime; the ENSO situation; the population's condition before the event; fishing pressure and other predation; the adaptation of reproductive behaviour; the presence of local efficient upwelling) have to be considered. Such an integrated approach from fine to large spatio-temporal scales helps understanding of variations in fish population (Bertrand et al. 2004a).

If the greenhouse gas build-up leads to increased upwelling, the HCE will support a higher phyto- and zooplankton biomass, the anchovy would be favoured and we could expect more and/or longer anchovy periods (Alheit and Niquen 2004). The size spectrum of copepods would shift towards larger specimens favourable for anchovy feeding. Predation on anchovy eggs, larvae, juveniles and adults would decrease because of less overlap with warm water predators and reduced density-dependent effects. Anchovy catches could increase to higher levels sustainable for longer periods, given application of an appropriate fishing policy. If, in contrast, future greenhouse gas build-up leads to decreased upwelling in the HCE, we could expect more and/or longer sardine periods resulting in reduced anchovy and augmented sardine catches. Nonetheless this kind of prediction, largely based on a bottom-up control, remains uncertain because top-down (Cushing 1971) or wasp-waist (Cury et al. 2001) controls, or selective and behavioural processes resulting in diet switches (Verity et al. 2002), can structure the functioning of pelagic ecosystems. In Peru for instance, recent plankton data question the exclusive scheme of bottom-up control (Ayon et al. 2004).

Bakun and Weeks (2004) recently suggested a different scenario resulting from increased upwelling intensity. The world's strongest eastern boundary upwelling zone, the Lüderitz cell in the Benguela Current ecosystem off Namibia, is characterized by widespread hypoxia and massive eruptions of noxious, radiatively active gases. The rapid offshore transport of the ocean surface layer (plus its organic and inorganic contents) in the Lüderitz cell prevents herbivorous copepods from maintaining substantial populations within and adjacent to the strongly divergent upwelling zone. This allows massive build-up of phytoplankton biomass, much of which sinks unutilised to accumulate as thick deposits of unoxidized organic matter on the sea floor. Generally increased upwelling could lead to extensive sea bed areas of low or zero dissolved oxygen concentrations, which could eventually lead to eruptions of poisonous gases from the sediment with detrimental effects to fish and fisheries. Bakun and Weeks (2004) suggest a hypothetical biological buffering process that might counter such a scenario. Sardines, because of their very fine-meshed gillraker structures, which allow them to filter and consume microscopic phytoplankton directly, could constrain phytoplankton growth by heavy grazing. In such a way, increased upwelling, in contrast to the scenario developed above, might eventually lead to a sardine regime, providing that the stock is not overexploited as is presently the case.

CONCLUSIONS AND FURTHER GENERAL THOUGHTS

The three ecosystems briefly presented here are all upwelling systems physically forced by local winds and influenced by larger scale teleconnections. All are characterised by strong alongshore advection, a poleward undercurrent, generally weak tidal mixing, weak winter convective mixing, zero to moderate precipitation and coastal freshwater input, and, finally, high productivity of plankton and pelagic fish resulting in the dominance of pelagic vs demersal consumers. All these properties are shared with the Benguela ecosystem. Another feature common to the four ecosystems is the strong variability at interannual to decadal time scales. This variability manifests at all levels: hydrodynamics and water properties, primary and secondary production, abundance and species composition, and fisheries (Mackas et al., in press), which renders forecasting a high priority, although a challenge.

These systems also differ in a number of ways which depend on which ocean they are located in, on geographical and topographical characteristics, and on seasonal and shorter term temporal variability related to wind forcing, atmospheric fronts and waves, coastal trapped waves, and stratification (Table 9-1). Major differences are the great width of the Pacific basin, which allows ENSO development, and the related existence of "older", nutrient-rich (therefore low oxygen) sub-pycnocline water in the Pacific. The South Atlantic coastal boundary also ends about 15° further north than the Pacific, so that the BCE is open to both Antarctic and Indian Oceans at its southern limit. The CanCE is characterised by the gap at the Gibraltar Strait and the interruption presented by the Canary Islands off NW Africa. Eddies and filaments are less important and frequent in the HCE than in the three other systems. The abundance of some top predators (pinnipeds, birds) is presently low in the CanCE

Table 1. Comparison of Pacific and Atlantic Eastern Boundaries (summarized from three larger tables from Mackas *et al.* in press; Ecosystem Feature added).

California Current Large Marine Ecosystem		
Latitude range	23-51°N	
	$f = 0.6 \text{ to } 1.1 \text{ x } 10^{-4}$	
Shelf width	Mainly <50 km but up to 100 km in places	
Physical	Strong ENSO.	
Features	Sheltered Southern California Bight.	
	Filaments off capes.	
Wind stress & stratifications	CTW. Aeolian dust near 30N	
	23-32°N all year.	
	>32°N summer.	
	Strong in S,	
	Moderate in N.	
Freshwater	Low in S, high in N (Columbia).	
input		
Ecosystem	Large variation in pelagic stock abundance and long period of collapse of the sardine	
Feature	stock	
	Importance of salmonid stocks (northern part, coastal zone)	

Canary Current Ecosystem		
Latitude range	15-44°N (incl. Iberia 36-44°N)	
Shelf width	f = 0.9 to 1.0 x 10 25-75 km off Iberia, varies off NW Africa between 10 and 120 km.	
Physical Features Wind stress & stratifications	ENSO+NAO effects. Sheltered Gulf of Cadiz/Gibraltar Strait, Canaries archipelago. Filaments off capes. CTW? Ria systems in north. Aeolian dust off Sahara 29-44°N summer, 20-28°N all year, 15-20°N winter.	
Freshwater input	Moderate. Mainly near zero, but significant at >37°N and at 15°N.	
Ecosystem Feature	Dominance of sardine (north) or sardinella (south) compared to anchovy. Frequent burst of secondary species. Partial replacement of longer lived bottom fish species, by short lived small pelagics and cephalopods, in the commercial fisheries. Low abundance of top predators (birds, large sharks and mammals)	

Table 1 continued

Humboldt Current Ecosystem		
Latitude range	$5-45^{\circ}S$ f = -0.1 to -1.0 x 10 ⁻⁴	
Shelf width	Often <25 km but up to 100 km. Bordered by deep trench.	
Physical Features	Strong ENSO. Sheltered Gulf of Guayaquil in north. Few filaments? Strong CTW. Hypoxia and OML. High trophic efficiency & fish production.	
Wind stress & stratifications	5-32°S all year, >32°S summer. Weak in N, Moderate-strong to S.	
Freshwater input	Very low	
Ecosystem Feature	Most extended system. Most extended, most superficial and most depleted MOL. Dominance of anchovy versus sardine. Frequent burst of secondary species. Strong effect of ENSO events on all living organisms	

Benguela Current Ecosystem		
Latitude range	15-37°S	
	$f = -0.4$ to -0.9×10^{-4}	
Shelf width	Mainly narrow off west coast (<25 km) but up to 250 km on zonal Agulhas Bank.	
Physical Features	ENSO + "Benguela Ninos". Wide Agulhas Bank & Agulhas influence. Filaments & rings. Strong CTW. Hypoxia locally. Low fish production.	
Wind stress & stratifications	15-30°S all year, >30°S summer. Strong in S, moderate to N.	
Freshwater input	Low in S, high in N (Congo).	
Ecosystem Feature	Alternation between anchovy dominated and sardine dominated regimes Spawning area of many species located upstream of their nursery area. Observed mortality of fish and shellfish due to H ₂ S and/or low oxygen concentration and/or sulfide emissions.	

compared to the other three and this ecosystem is also characterised by the dominance of sardine and sardinella, whereas anchovies are also important in the other ecosystems. The CanCE and the HCE display more frequent outbursts of secondary or rare species than the two other systems. Because many rivers flow into the northern CalCE, several species of salmon occur in coastal waters of this system. Finally, the biological variability in the two Pacific systems is largely dominated by El Niño/La Niña events, whereas in both Atlantic regions El Niño has weaker influence complemented by NAO in the north. In all regions, coastal trapped waves play a significant if not fully understood role.

The way in which climate changes affect ecosystems, on both land and ocean, is complex and difficult to forecast, although efforts in meta-analysis, process studies and modeling with data assimilation are promising (Drinkwater and Myers 1987; DeAngelis and Cushman 1990; Bakun and Broad 2002). Uncertainty persists in the physical effects of climate change. Model based scenarios of the impact of global warming on the physical components of the earth system still remain coarse and uncertain. The poor resolution of these simulations introduces major uncertainties when trying to resolve regional scales. Further work is needed before global climate change scenarios will be directly applicable to the regional responses of the upwelling and other ecosystems. Furthermore, under any given scenario, additional uncertainty surrounds the biological responses to physical forcing. The effects of anthropogenic forcing, particularly increasing fishing pressure but also habitat invasions, eutrophication and diseases, complicate the issue (Verity et al. 2002). Increased fishing effort, and consequent increased fish mortality, will likely increase the relative abundance of low trophic levels in these ecosystems (Pauly et al. 1998) and might favour or exacerbate regime shifts and possibly population outbursts as observed in the CanCE.

The most promising example of environmental forecasting from a model including data assimilation is provided by Chen et al. (2004) on El Niño/La Niña predictions. There is a clear need to develop similar environmental models coupling atmospheric and oceanographic processes in the other upwelling systems, with data assimilation to make them more realistic. One can expect that this kind of physical prediction will help in forecasting biological responses of the ecosystem based on our understanding of processes.

In the mean time, biological or fishery related predictions can be made simply by using autoregressive properties of time series (e.g. Stergiou et al. 1997) but the resulting forecast is likely to fail whenever a major change (regime shift, modification of the exploitation pattern) occurs (Ulltang 1996). Simple or multiple regression models suffer from the same limitation, aggravated by the poor predictive power of these models due to limited degrees of freedom, the difficulty of selecting the right explanatory variables and the uncertainty in the functional form of variable relationships (Fréon et al. 2005). Furthermore, for purely mathematical reasons, when $r^2<0.65$ the predicting value is limited (Prairie 1996). Nonetheless the positive side of this approach is that it identifies significant variables for inclusion in conventional population dynamics models (e.g. Fréon et al. 1993) or simple regressions. Process-based models, like the Bakun (1998) triad and the optimal environmental window (Cury and Roy 1989), are more satisfactory, assuming that the processes are correctly identified and lasting. Our major challenge, of understanding and forecasting regime shifts, will likely require several decades of research to acquire a basic knowledge of

the nature of the controlling factors and to unravel the complexity and variability in predation that complicate prediction (Bax 1998; Verity et al. 2002). In the near future, a two-level (short- and long-term) management strategy should be investigated for the small pelagic species that are exploited (Fréon et al. 2005). The first level could be a conventional adaptive management approach incorporating new ecosystem-based thresholds or Limit Reference Points as much as possible. The second level of the strategy should address the problem of inter-decadal variations in the abundance of pelagic fish that induce counterproductive investments in the fishing sector. Based on the pseudo periodicity of around 40 to 60 years, as observed in many large stocks, some management action could limit long-term investment in fishing units and related infrastructure, especially once a turning point is passed and therefore uncertainty decreases (Figure 9-10). This suggested approach requires further investigation to quantify the risks and benefits.



Figure 9-10. Schemes of typical variation in the abundance, effort and investment in pelagic fisheries: (a) pseudo-cyclic variation; (b) long periods of collapse; (c) investment strategies related to pseudo-cyclic variation. The size of question marks reflects the uncertainty about the trend in abundance over the next 10-year period (from Fréon P., Cury, P., Shannon, L. and Roy, C., Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. *Fishery Bulletin*, 2005).

ACKNOWLEDGMENTS

We are grateful to Arnaud Bertrand for his contribution to the Humboldt Current section of this work and to Dave Checkley for reviewing the California Current section. We acknowledge the comments of two anonymous referees. This is a contribution of the IDYLE and Upwelling ecosystem programmes of IRD and of the EUR-OCEANS network of excellence (sixth Framework Programme of the European Community)

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