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Editorial The northern Humboldt Current System: Brief history, present status and a view towards the future

1. Introduction

The tropical ocean off the west coast of South America is notable for several reasons. First, it is unusually cool for an ocean that is so close to the equator with sea surface temperatures at 5 °S off Peru as cool as 16 °C when most other tropical locations are in excess of 25 °C. Upwelling of cool waters brings phytoplankton nutrients to the surface, dramatically increasing biological productivity in this low-latitude region of few storms. Second, as a result of the enhanced productivity, the northern Humboldt Current System (HCS) off Peru produces more fish per unit area than any other region in the world oceans (Fig. 1), representing less than 0.1% of the world ocean surface but presently producing about 10% of the world fish catch. Third, as a result of sinking and decay of surface-derived primary production and poor ventilation, surface oxygenated waters overlie an intense and extremely shallow Oxygen Minimum Zone (OMZ). The OMZ forms a barrier to some animals, concentrating living resources near the surface. At the other end of the spectrum different forms of marine life have adapted to this harsh environment, some utilizing it as a refuge from predation. The OMZ also affects global nutrient budgets, as nitrate instead of oxygen is used by bacteria as a terminal electron acceptor. Fourth, beneath the OMZ, in layered continental shelf sediments the absence of oxygen preserves dead organisms, creating a record of past ecosystem and climate changes. Fifth, through ocean/atmosphere coupling, the northern HCS is intimately linked to equatorial Pacific dynamics and is subject to large interannual to multidecadal fluctuations in climate, ecosystems and its fisheries.

New in situ and satellite observing capabilities, long-term and multi-variable data series, improved analysis, and modelling have opened new windows into the dynamics of the northern HCS. Fishery management is also evolving from a single-species approach towards one that where the ecosystem is the unit of management. This holistic approach, likely to be embraced in the 21st century, appears to be particularly appropriate for the northern HCS where strong temporal variability including El Niño, the Pacific Decadal Oscillation (PDO, or El Viejo/La Vieja) and global change, constitutes a major challenge. In this context, there was a clear need to begin a new integration and synthesis of the Humboldt Current System. The present collection of research papers resulted from the "International Conference on The Humboldt Current System: Climate, ocean dynamics, ecosystem processes, and fisheries" organized by the Institut de Recherche pour le Développement (IRD), the Instituto del Mar del Perú (IMARPE) and the Food and Agriculture *Organisation* (FAO) in Lima in late 2006 and highlight these developments. The focus of this special issue is on the northern Humboldt Current System (HCS) off Peru and complements a 2007 compilation in the same journal for the central and southern upwelling region off Chile (Escribano and Schneider, 2007). In this introductory paper we provide a brief overview of the "ecological and socio-economic" history of the northern HCS. The papers are then introduced in the context of: (1) the impacts of natural environmental rhythms and human exploitation; (2) new observations and models; and (3) the ecosystem as the management unit. A section on future research directions concludes the introduction to the special issue. The papers in the special issue are organized starting with physics and chemistry, then lower trophic biology to fish. These mostly data papers are followed by modelling and then socio-economic papers.

2. A brief history of ecology and exploitation of living marine resources

The first "artistic" descriptions of the biological richness of the northern HCS and its importance to humans can be found in the pottery left behind by native South Americans well before America was discovered by the Europeans (Rostworowski, 2005). Coastal pre-Inca and Inca communities depended heavily on ocean resources for their survival. The modern world became aware of the incredible biological productivity of the northern HCS with the discovery of tremendous deposits of seabird droppings or guano (Cushman, 2003). The extraction of the seabird excrement (guano, derived from an Inca word, comes primarily from the cormorant Phalacrocorax bouganville, common name Guanay) for fertilizer, played an important role in the Peruvian economy. The guano was exported worldwide and played a role in the survival of Europeans during the 19th century. The first marine biology scientific research entity in Peru was the Marine Biology Laboratory (Laboratorio de Biología Marina) established by the Compañia Administradora de Guano to study and preserve this important resource. With the aid of international scientists the first ecosystem perspective of the HCS was published in 1948 with the seabirds occupying a central role (Fig. 2). During the 1940s and 1950s a fishery developed on species like bonito (Sarda chilensis chilensis) and tuna (primarily Thunnus albacore) driven by the high demand of the liver oil of these species in the US market during World War II and later the Korean war. The end of the Korean War increased demand for guano and coincidentally the strong El Niño of



Fig. 1. Fish catch versus primary productivity for the four main eastern boundary coastal upwelling ecosystems for the years 1998–2005. It was assumed that the reported fish catches (Fish and Agriculture Organization, FAO) were made within 100 km from the coast. The catches were then normalized by area. Primary productivity was estimated from satellite remote sensing of chlorophyll and the Behrenfeld and Falkowski (1997) model. Even during the El Niño year of 1998 Peru fish catch still exceeded that from the other areas by several fold. Is Peru exceedingly efficient in the transfer of primary production to fish or are Benguela and Northwest Africa exceedingly inefficient?

1957–1958 led to a dramatic decrease in seabird populations. The present day anchovy or anchoveta (*Engraulis ringens*) fishery started around the same period in 1955. This was an important period for the ecosystem as managers pondered if the primary objective was seabirds (guano) or anchoveta (fish meal). In 1954 the Peruvian Navy with input from the Compañía Administradora de Guano and the government entity that managed fishing and hunting established the Consejo de Investigaciones Hidrobiológicas (CIH). The CIH was directed to coordinate and intensify hydrobiological studies with the goal of improving the use and



Fig. 2. First "ecosystem-based" diagram for the northern Humboldt Current System developed when seabirds were the focus of management (from Vogt, 1948).

sustainment of living marine resources. In 1959, as the anchoveta fishery continued to develop, Peru requested technical assistance for CIH from the Food and Agriculture Organization of the United Nations (FAO) to develop a National Fishery Plan. Soon after the Instituto de Investigaciones de los Recursos Marinos (IREMAR) was created with programs dealing with oceanography, fisheries biology, biology of whales, fishery economics and fishery technology. In their final report FAO recommended the fusion of CIH and IREMAR into a single institution. Accordingly in July of 1964 the Instituto del Mar del Perú (IMARPE) was created and began operation in September of 1965. A number of the early IMARPE scientists traced their roots to the Biology Department of the Compañía Administradora de Guano. IMARPE continues to conduct research on the northern HCS and its fisheries today.

The anchoveta fishery continued to grow during the 1960s to a peak harvest of 12 million tons per year in 1970 accounting for 20% of the world catch. The seminal paper of Ryther (1969), regarding primary productivity, trophic levels and fish productivity in coastal upwelling ecosystems, was developed based on an expedition to Peru during this period of record harvest. A number of international expeditions to the northern HCS followed and continue to present. However, seven years after IMARPE's formation, the anchoveta population collapsed during the 1972 El Niño. An outstanding synthesis of the dynamics of the Peruvian Upwelling Ecosystem focused on anchoveta and its crash was produced by IMARPE in conjunction with ICLARM (now World Fish Center) and the Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) during the mid 1980s and published as conference proceedings in 1987 and 1989 (Pauly and Tsukayama, 1987; Pauly et al., 1989a,b). These publications continue to serve as major references for the northern HCS. Since the 1980s, important technical and conceptual advances have transformed many areas of marine sciences. These advances have clarified important links and feedbacks between climate, ocean circulation, biogeochemical cycles, trophic webs and fish production. In addition, decades-long time series data are now revealing environmental and climactic variability bevond the interannual scale of El Niño.

3. Impacts of natural environmental rhythms and human exploitation on the ecosystem

The northern HCS is the region where El Niño, and climate variability in general, is most notable (Fig. 3); sea surface temperature (SST) anomalies greater than 10 °C have been observed during strong El Niño events (Barber and Chavez, 1983). The modern strong El Niño events include those beginning during 1925, 1941, 1957, 1982 and 1997. It was the strong 1957-1958 El Niño that led to the realization that El Niño was more than just the intensification of a tropical coastal current (Chavez, 1986) but was linked to changes in the global atmosphere (Bjerknes, 1966). The 1957-1958 El Niño resulted in strong declines in seabirds (see Fig. 1 of Chavez et al., 2003; Jahncke et al., 2004) and contributed, as described above, to the development of the most intense and successful fishery in the world. It was another El Niño in 1972 that was associated with a large and persistent decline in anchoveta. The collapse led to a vigorous scientific debate regarding causes: natural climate variability or over-fishing. The following 15-20 years saw a dramatic rise in sardine (Sardinops sagax) populations. It took over 10 years for scientists to notice that the same type of variability was also being experienced off California and Japan (Kawasaki, 1983; Lluch-Belda et al., 1992) and 30 years before a longer period (~50 year) natural climate phenomena (Mantua et al., 1997) was implicated in the fluctuations of anchoveta and sardine (Chavez et al., 2003; Alheit and Niquen, 2004). These large-scale, long-term changes in Pacific ecosystems became widely known as "regime shifts". The topic remains hotly debated; did the Pacific transition



Fig. 3. Top panel shows the trend in sea surface temperature (SST) for the global ocean in 2×2 degree bins from 1875 to 2007. The warming over the last several decades is notable. The first empirical orthogonal function (EOF) of the SST time series was calculated after the trend and the seasonal cycle were removed (a la Mantua et al., 1997 for the Pacific Decadal Oscillation). The second panel shows the spatial pattern of the EOF with the northern HCS showing the highest variance relative to any coastal area of the world ocean. The time series of the EOF is shown in the third panel with a warm eastern Pacific from the mid 1970s to the mid 1990s. The bottom panel shows the trend of SST in 1×1 degree bins from 1981 to June 2008. Over this period, and primarily over the last decade the eastern Pacific, and the northern HCS in particular, has cooled (negative trend) while the majority of the ocean warmed. The long term SST records are from Woodruff et al. (2008) and the recent SST trend from Reynolds et al. (2007).

from a cool eastern Pacific (La Vieja) to warm eastern Pacific (El Viejo) in the early 1970s and then to a cool eastern Pacific again in the early to mid 1990s (Fig. 3)? Several papers in this issue examine changes that occurred during this period (Ayón et al., 2008b; Bakun and Weeks, 2008; Bertrand et al., 2008b; Guénette et al., 2008; Swartzman et al., 2008). Finally, information collected from anoxic sediments off Peru and Chile have uncovered even longer term and more dramatic changes (Gutiérrez et al., 2008; Sifeddine et al., 2008; Valdés et al., 2008). During the 400 years of the Little Ice Age (LIA) primary productivity was low in the northern HCS, the OMZ region was more oxygenated, and the abundance of small pelagics was greatly reduced. This changed at the end of LIA, circa 1820, to the present condition: high primary productivity, a very intense and shallow OMZ, and abundant small

pelagic fish. This super regime shift showed that both anchovies and sardines were favoured after 1820. Multi-decadal variability (Chavez et al., 2003) was still apparent, but overwhelmed by the centennial scale changes. Are these trends continuing, what will happen with climate change (Fig. 3) and how will future changes influence the harvest of marine living resources? Will there be other tipping-points like the one at the end of LIA in the near future? Are ecological disturbances associated with large interannual to multi-decadal climate fluctuations responsible for the extremely high levels of fish production? Does environmental variability explain the Peruvian 'anchoveta paradox', that is why are fish abundance and production in the northern HCS so much higher than other coastal upwelling ecosystems (Fig. 2)? These questions will form the basis of future research.

4. New observations and models

This section highlights new findings regarding living marine resources and the environment that they are an integral part of Bertrand et al. (2008a) integrate observations and show how anchoveta are impacted by processes occurring along a spectrum of temporal and spatial scales. These processes include internal waves with periods of minutes and sizes of meters to the global climate variations described in the previous section with periods ranging from the interannual to centennial. A multi-scale (meter to entire coastline) observational effort allowed Bertrand et al. (2008a) to construct a conceptual model with management implications. The new and revealing aspects came from the small scale surveys that showed how anchoveta and other members of the living ecosystem "organize" around the rapidly varying environmental landscape. The animals leave their imprint on the physical environment, as evidenced by measurements of the partial pressure of carbon dioxide (pCO_2) . Another example of a small scale but important observation, with significant impacts on ecosystem dynamics, concerns anchoveta diet. Earlier studies had shown an overwhelming numerical dominance of phytoplankton in stomach contents (e.g. Pauly et al., 1989b; Rojas de Mendiola, 1989) and led to the belief that the large populations of anchoveta were supported by an unusually short and efficient food chain (Ryther, 1969). From the analysis of a large number of stomach contents and, most importantly, by conversion of the contents to carbon equivalents, Espinoza and Bertrand (2008) show that the most important source of calories for anchoveta are zooplankton - primarily euphausiids and large copepods. Anchoveta, as indicated by its long intestine typical of herbivorous organisms, still consumes phytoplankton for important nutrients but zooplankton for energy. This new information changes previously developed and widely held paradigms for the northern HCS. Questions that immediately come to mind are: Are there more zooplankton off Peru than in any of the other coastal upwelling systems? Or perhaps, are zooplankton more concentrated and available to anchoveta? Ayón et al. (2008a) provide a review of zooplankton research for the northern HCS and leave it clear that new technologies are required to deal with the difficulties of zooplankton sampling.

One model for colonization of pelagic habitat suggests that fish first colonize favourable habitat then move to less favourable habitat as populations expand (MacCall, 1990). Information collected for anchoveta suggest a tight link to particular water masses, irrespective of population size (Bertrand et al., 2004; Swartzman et al., 2008). Salinity is a good proxy for the anchoveta-favoured water mass, Cold (upwelled) Coastal Wasters (CCW), as anchoveta is abundant and well fed over a wide (14-23 °C) temperature range (Gutiérrez et al., 2008b). Sardines seem to have greater affinity for the high salinity Subtropical Surface Waters (SSW) although not as strong as anchoveta for CCW (Swartzman et al., 2008). CCW are associated with a shallow oxycline that may favour anchoveta. Plankton size-structure is also different with larger plankton being favoured in the CCW (high nutrients) and smaller plankton in the SSW (more oligotrophic). What combination of properties selects for anchoveta and sardine is still under investigation.

Within the CCW habitat (Swartzman et al., 2008), anchoveta (i) forage efficiently under a variety of different environmental conditions (Espinoza and Bertrand, 2008), (ii) utilize food from various trophic levels and select high energy food types (Espinoza and Bertrand, 2008), (iii) concentrate in refuge areas when conditions are adverse (Bertrand et al., 2004), (iv) adapt their reproductive behaviour (Buitrón and Perea, 2000), and (v) distribute its population over a large temperature range (Gutiérrez et al., 2008). This combination of characteristics may help explain the Peruvian 'anchoveta paradox': how anchoveta achieves such enormous concentrations when they (i) are only capable of very short migrations and therefore cannot actively escape adverse conditions, and (ii) are mainly distributed in dense surface aggregations, have very slow avoidance reactions and are highly accessible to predators (fish, cephalopods, birds, mammals and fishers) (Gerlotto et al., 2006).

Bakun and Weeks (2008) suggest two processes that might explain the dramatic fish productivity of the northern HCS. The northern HCS is the upwelling system that is nearest to the equator and is also a region of relatively weak but steady upwelling favourable winds. Because of the proximity to the equator the area of upwelling is large so even with weak winds large quantities of nutrients are upwelled but turbulence is low. Under these conditions the so called environmental window (Cury and Roy, 1989) for fish production is optimized. Second, Bakun and Weeks postulate that the close connection between Peru and the equatorial Pacific exposes the region to strong interannual variability. These sporadic and recurrent disruptions or ecosystem 're-sets' could keep the northern HCS from mature successional states and favor the rapidly growing 'r' populations like anchoveta (Chavez, 1987). Chaigneau et al. (2008) are the first to analyze eddy activity from 15 years of altimeter data off Peru; somewhat surprisingly they find highest activity during the strong El Niño of 1997-1998. A next step would be to compare eddy activity for the major coastal upwelling systems.

The role of the ocean in modulating increasing concentrations of CO₂ in the atmosphere has led to an explosive growth of regional measurements of sea surface pCO₂. Based primarily from observations off Oregon, Hales et al. (2005) suggested that coastal upwelling systems were sinks for atmospheric CO₂. The comprehensive observations from the coast of Peru reported by Friederich et al. (2008) sharply disagree with that generalization and show that the northern HCS is a strong source of CO₂ to the atmosphere. The authors suggest several factors that could contribute to the maintenance of sea surface pCO₂ levels well above those of the atmosphere in spite of elevated uptake of CO₂ by phytoplankton: (1) upwelling source waters are affected by OMZ denitrification. contain low concentrations of pre-formed nitrate and have excess inorganic carbon relative to nitrogen; (2) iron limitation of primary production enhanced by offshore upwelling, driven by the curl of the wind stress, that does not recruit continental shelf iron (Johnson et al., 1999) and (3) rapid sea surface warming that reduces CO₂ solubility. In a modelling study Echevin et al. (2008) were able to reproduce a seasonal chlorophyll cycle that is out of phase with the upwelling seasonal cycle and nutrients (Pennington et al., 2006). The authors conclude that either (or both) light limitation by deeper mixing (first suggested by Calienes et al., 1985) during strong upwelling or iron limitation could be responsible for the out of phase relationship. Clearly the topic of regulation of primary productivity in the northern HCS requires further study.

In another combined observation and modelling study, Bertrand et al. (2008b) show the impact of equatorially-generated Kelvin Waves (KW) on the distribution of anchoveta and its primary consumer, the fishers. New tools like satellite vessel monitoring systems (VMS) are now routinely deployed on fishing vessels and in the northern HCS provide real-time positions of anchoveta seiners. Bertrand et al. (2008b) combine VMS information, oceanographic data and model output to show that large-scale oceanic KW forcing is both detectable and significant in the spatial organization of the ecosystem, including the distributions of anchoveta and the fishers. These results provide evidence for a bottom-up control of the system via "behavioural cascades" (see Frontier, 1987; Russel et al., 1992) that can produce contrasting 'ecosystem scenarios' under upwelling or downwelling KW conditions.

Bottom-up forcing in the northern HCS is evident at interannual (Barber and Chavez, 1983), multidecadal (Chavez et al., 2003; Alheit and Niquen, 2004) and now at centennial time scales (Gutiérrez et al., in press; Sifeddine et al., 2008; Valdés et al., 2008). This bottom-up control observed with in situ data was also simulated with trophic models at the scale of a bay (Taylor et al., 2008b) and for the entire northern HCS (Taylor et al., 2008a). The example provided by Bertrand et al. (2008b) makes it abundantly clear that there is also strong bottom-up forcing in the northern HCS at the intraseasonal time scale, but what about top-down effects? The large concentrations of plankton foraging fish in the northern HCS, and the other coastal upwelling ecosystems (Fig. 2 and 4), could drive a top-down control of zooplankton, the socalled wasp-waist hypothesis (Cury et al., 2000, 2003). Ayón et al. (2008b) combined zooplankton data (1961-2005) with simultaneous acoustic fish observations from 40 pelagic survevs (1983–2005) and Peruvian landing statistics (1961–2005). They showed that on a regional scale zooplankton and anchoveta fluctuated in phase (i.e. bottom-up forcing), but in dense schools anchoveta often induced a local reduction in zooplankton abundance.

An area of explosive progress during the last several decades has been in the development and use of numerical models. The role of models in research and management is several-fold. First, they serve as tests of our understanding of how ecosystems function: what are the drivers, why they are the way they are, why they change, etc. Models lead to new observations, improved understanding, new ecosystem rules, and iteratively to improved models. Second, models serve as integrators and interpolators of sparse information. The ocean, because of its challenges to observation (opacity to light, corrosive water, etc.), will always remain under sampled; models can interpolate the sparse data and generate views of the system that are in many ways analogous to satellite images but in three dimensions. Finally, given enough scientific



Fig. 4. Landings of anchoveta (*Engraulis ringens*), sardine (*Sardinops sagax*), jurel or jack mackerel (*Trachurus murphy*i), caballa or mackerel (*Scomber japonicus*), merluza or hake (*Merluccius gay*i) and Pota or the jumbo squid (*Doscidicus gigas*) for the period of 1950 to the present. The landings likely reflect fluctuations in abundance after 1965 for anchoveta, early 1970s for the remainder of the species and perhaps later for jack mackerel, mackerel and the jumbo squid.

progress the models can forecast the future and predict ecological responses to natural climate variability and global change. While models are an integral part of the future, it is also important to consider their present-day shortcomings. The quality (here defined as the ability to realistically simulate the ecosystem) of a model is directly proportional to the amount of available *in situ* data. The northern HCS, with its rich data, is an ideal region for model development and use. Physical (ocean and atmosphere) modelling is currently far ahead of ecological modelling. This is partly driven by the number of variables needed for physics (temperature and salinity), compared to biology (a potentially unlimited number), which increases complexity and cost. Finally, the models are only able to simulate known processes for which equations have been developed; new processes or significant errors in ecological theory are obviously problems for accurate predictions. A case in point is provided by Espinoza and Bertrand (2008) who show that euphausiids and large copepods are the dominant caloric prev for anchoveta. Yet trophic models can be tuned to simulate long-term dynamics of the ecosystem using phytoplankton as the major source of food for anchoveta. Either what the anchoveta eats is not particularly important to the ecosystem or there are still fundamental problems with the models. It is evident that modelling will continue to advance in parallel to and with the advent of new observations.

The models can be organized into several categories. First are physical ocean models. These models are driven by atmospheric forcing (wind and heat) typically provided by data-assimilating atmospheric models or model-aided reanalysis of observations. The resolution of the model (meters to kilometres in the horizontal and meters in the vertical) is usually constrained by computational power and the resolution of the atmospheric forcing. A widely used model in the northern HCS is the Regional Ocean Modelling System (ROMS; Colas et al., 2008) although it is certainly not the only one (see Dewitte et al., 2008). Simple pelagic ecosystem models (referred to as NPZ for Nutrient, Phytoplankton, Zooplankton) were first conceptualized in the 1940s (Riley, 1946) and have more recently directly coupled to physical circulation models such as ROMS (see Echevin et al., 2008, for example). Original formulations had one phytoplankton and one zooplankton group but in order to simulate global satellite chlorophyll there was a need to include two size classes each of phytoplankton and zooplankton. This type of ecosystem model is presently the most common and able to simulate a small-sized tightly coupled (oceanic) food web and a large-sized decoupled (coastal) food web. Adding NPZ to a physical model increases computational requirements by at least five fold. A present-day weakness of the coupled models is the lack of zooplankton data for validation. The output of the coupled models can be used to drive Individual Based Models (IBM) where a single species is followed over time: the coupled model provides physiological (temperature) and energetic (PZ) growth constraints; predatory losses are provided externally (see Brochier et al., 2008 as an example). The final group of models focus on trophic interactions with the most popular being those of the ECOPATH family (Christensen and Pauly, 1992; Walters and Christensen, 2007). Several papers in this issue apply these models (Guénette et al., 2008; Tam et al., 2008; Taylor et al., 2008a,b). These models are able to deal with a large number of trophic levels (hence the use of the descriptor) and components but because of their complexity are not able to resolve time or space with the necessary resolution. Time and space are typically treated discretely, for example El Niño versus normal (see, for example, Tam et al., 2008; Taylor et al., 2008a). Newer versions include the ability to treat time and space more explicitly but not at the level of the coupled models. Available in situ data for many, if not most, of the trophic components and their rates is sparse. A new generation of models attempts to embed "trophic" fishery models in the three dimensional coupled circulation models described above (Fulton et al., 2004; Travers et al., 2007) but these have yet to be applied to the northern HCS.

5. The northern Humboldt Current System as a management unit

Research over the past decades in the northern HCS has focused on exploited living resources, i.e. a few number of species like anchoveta, sardine, jurel or jack mackerel (Trachurus murphyi), caballa or mackerel (Scomber japonicus), merluza or hake (Merluccius gayi) and more recently the jumbo squid or 'pota' (Doscidicus gigas) (Fig. 4). As can be gleaned from Fig. 4, landings have fluctuated quite dramatically over the last decades driven by the large year to year variability of the northern HCS (Fig. 3). Is the ecosystem more sensitive to the environmental variability as a result of human exploitation of the resources? The Ecosystem Approach to Fisheries (FAO, 1995) stresses the importance of managing the resources by considering the whole ecosystem that the exploited populations and their fishers are an integral part of. The expectation is that such informed management system will facilitate the long term sustainability of fish stocks by understanding and protecting the ecosystem of which the fish are dependent, while at the same time maximizing economic and societal benefits and preventing wasteful overinvestment of economic resources. EAF and its close relative Ecosystem-Based Management (EBM) have and will continue to be daunting tasks given that resources, technologies and management theory are not yet at a level needed to implement these systems effectively. Given the unique monitoring system, the well understood climate variability and the developing ecological theory (summarized well in this special issue) the northern HCS is a strong candidate for this approach. Routine physical (temperature, salinity), chemical (nutrients and oxygen) and biological (chlorophyll, zooplankton biovolume) oceanographic information has and continues to be collected. An even more intense observation effort is in place for the marine living resources. Evolving technical capabilities, including tagging and tracking individual animals (modern tags can also record environmental data), will go a long way in improving our knowledge of the abundance and distribution of the so-called charismatic and sometimes threatened species (i.e. seabirds, marine mammals, turtles, etc.). The final frontier lies in the mero and macro zooplankton (copepods, euphausiids, larger crustaceans, fish larvae) and smaller fish all with behavioural attributes.

Technological advances in acoustics have facilitated collection of information on the mero and macro zooplankton (copepods, euphausiids, larger crustaceans, fish larvae) and smaller fish. Acoustics can now provide qualitative and quantitative data on diverse species from zooplankton to large fish (and even mammals), and given well-designed surveys, can document their interactions (Bertrand et al., 2008a). Acoustics have been used to document the dramatic changes in the pelagic red crab or 'munida' Pleuroncodes monodon (a macro-zooplankton) population, after the 1997-98 El Niño (Gutiérrez et al., 2008b). Munida has been exploited for decades in central Chile where its adult population is demersal. High munida concentrations were rarely reported off Peru but recently its populations experienced exponential growth, presumably in response to the cooling trends shown in Fig. 3; 1998-2005 acoustic biomass estimates range from 0.6 to 3.4 million tons. The increase in population and range was accompanied by a change in the crab's ecology, going to a complete pelagic life cycle in Peru because the intense OMZ in this region restricts its demersal habitat. As described above the munida not only increased in abundance but extended its range towards the equator as the eastern Pacific cooled during La Vieja (Fig. 3). But is it really La Vieja or the beginning of the effects of man-induced global

warming? Global warming may differentially heat land and sea, intensify coastal upwelling winds (Bakun, 1990) and perhaps cool coastal upwelling regions in the face of a general global warming trend (Fig. 3). Acoustics allowed Gutiérrez et al. (2008b) to simultaneously observe anchoveta and munida and the data clearly show that they often share the same habitat. Climatic changes have resulted in an environment where these two species now overlap even though munida is restricted to the very cold CCW whereas anchoveta tolerates a much broader temperature range. Anchoveta and munida are both prey for apex predators, they both feed on the same planktonic organisms and munida forages on anchoveta eggs and larvae so their affinity for the same habitat has important ecological consequences. More information on euphausiids, the key prey of anchoveta, is critically needed. Presently acoustic devices can only be deployed routinely on ships but there is hope that acoustic devices or other technologies for sensing zooplankton can be made routinely available for autonomous platforms like floats, gliders and moorings.

Anderson et al. (2008) has shown that commercial fishing results in a decrease in average body size and age of maturity of the exploited fish stock. This can lead to age-truncated or juvenescent populations that can become increasingly unstable. Peruvian hake (Merluccius gayi peruanus) have been intensively fished since the early 1970s (Fig. 4C) and show juvenescent characteristics: a drastic reduction in mean hake size, an early age of maturation, with the percentage of mature hake at 2 years changing from \sim zero during the 1980s to >60% in the early 2000s. Additionally the proportion of females in catches increased from $\sim 40\%$ at the beginning of 1990 to \sim 100% at the beginning of 2000 (Guevara-Carrasco and Lleonart, 2008; Ballón et al., 2008). Ballón et al. (2008) showed that the few remaining large females in the population currently make low investments in egg production. The lack of males in the population could mean sperm limitation. In addition the lack of male pheromones should impact female spawning and lead the large females to reallocate resources from reproduction to growth or survival. Not surprisingly, large females had high condition factors and low gonosomatic indices when large males were scarce. The hake habitat is restricted to northern Peru (typically north of 6 °S) where waters are ventilated (and oxygenated) by the Equatorial Undercurrent. Ballón et al. (2008) also show that El Niño negatively affects hake's condition factor and reproduction even though El Niño increases geographical range and habitat of hake by oxygenating the central and southern Peru coastal waters (Espino, 1990). These results with hake illustrate how fishing and environmental variability can interact and impact populations in unexpected and complex ways.

In addition to the above factors, the jumbo squid, an important predator of hake (Zeidberg and Robison, 2007) seems to have increased in abundance over the past decade (Fig. 4C). Argüelles et al. (2008) showed that during 1989-1999, mature jumbo squid (Dosidicus gigas) where of medium size (\sim 40 cm), but from 2001 on, mature squid were larger (\sim 80 cm). Argüelles et al. (2008) hypothesize that the change in size and the increase in numbers was caused by a parallel increase in mesopelagic (lanterfish in particular) fishes that are prey for the jumbo squid. The size increase also suggests that squid are not over-exploited in the northern HCS. Unlike hake, squid is an 'r' species that grows very fast (like anchoveta) and is therefore more resilient to fishing pressures. Jumbo squid have not only increased rapidly off Peru but also off Chile, Mexico and the United States (Zeidberg and Robison, 2007; Bograd et al., 2008). Bograd et al. (2008) suggest that changes in the geographical distribution of the jumbo squid may be related to the expansion of eastern Pacific OMZ. If true hake may be further impacted since the small area of high productivity and oxygen off northern Peru (4-6 °S) where hake thrive may be shrinking.

In northern HCS off Peru, fisheries decisions are made in quasi real-time using the most recent observations. It is probably the only place in the world where this rapidly 'adaptive' management style is possible. Government bureaucracy and slow data analysis usually mean that management decisions are implemented for yesterday's conditions and problems. However, there is still a need for reliable predictors of future conditions to support the decision making process. These must include our developing understanding of interannual, multidecadal and centennial climate variability. Forecasting climate effects on fishery stocks clearly is a daunting task, but this should be an area of continued emphasis. Kelvin waves (KW) and interannual variability are areas where immediate gains are possible. As Bertrand et al. (2008b) have shown there is a predictable northern HCS ecosystem response to coastal KWs of equatorial origin. These KWs are excited in the western equatorial Pacific, are observed by the TOGA-TAO array and satellite altimetry, and travel across the Pacific to the northern HCS in about two months. To the extent that there is a predictable response, this two month window could be used to make management decisions. If environmental conditions could be predicted six to nine months in advance, such as predicting El Niño, further measures could be taken. Jarre et al. (2008) compared two knowledge-based systems (rule-based Boolean and fuzzy logic models) that would use multiple data sets and indices to aid the decision support system. The comparison was made for fisheries in the southern Benguela but it has applications for the northern HCS. These new efforts could be implemented into an easy to use "dashboard" to support the decision makers.

The satellite vessel monitoring systems (VMS) have provided unique data regarding fishery effort and as Bertrand et al. (2008c) show, on the spatial distribution of resources. VMS data provide robust, reliable, real-time, and low-cost information for scientific and management purposes (Bertrand et al., 2007). Bertrand et al. (2008c) used artificial neural networks (ANN) with VMS data to estimate the position of fishing operations for the entire fleet of Peruvian anchovy purse-seiners. The ANN was trained on a sample of fishing trips with known fishing set positions from an at-sea observer program. The ANN correctly identified 83% of the real fishing sets and largely outperformed comparative linear models. Bertrand et al. (2008c) quantified the extent to which the distribution of purse-seine sets describes anchovy distribution and found that location yields valuable information on the distribution of the Peruvian anchoveta stock and ultimately on its vulnerability to the fishery. A fishery that at present has too much capacity: Fréon et al. (2008) estimated the present overcapacity of the Peruvian purse seiner anchoveta fleet at over 300%, in other words the fleet has the capacity to capture over 30 million tonnes per year even though current quotas have ranged from 5 to 8 million tons. This overcapacity was economically driven by the classical "tragedy of the commons" i.e. the race to catch a larger share of a global annual quota and its roots can be traced to the inability of fisheries managers, under several administrations, to enforce laws controlling the expansion of the fleet and fish processing plants.

Under the present system the fishing year is divided into two semesters (April–September and October–March) or fishing seasons, with long-established closures coinciding with the two main spawning periods in winter and summer. The quota or total allowable catch (TAC) was assigned or adjusted by management at the beginning of each fishing period, formerly by season and over the last few years by month. When the TAC for a period is reached (or the period ends) the fishery is closed. Several periods make up the fishing season. Since there is a single quota for all there is a premium on skilled captains and high capacity. A new individual quota (IQ) system, where the TAC is distributed among registered fishing vessels holding a valid fishing license, is about to be implemented. Removing the need to race to harvest as much as possible is expected to eventually result in a significant reduction in the size of the fleet, but may also lead to new socio-economic, biological and ecosystem challenges especially if, as in the past, the system is not properly enforced. If properly administered the IQ system should result in similar economic benefits to the fishery as do individual transferable quotas (ITQs) (Costello et al., 2008) but perhaps not to the shortcomings: concentration of ownership into a few large companies, the loss of fishery benefits to local communities, and the development of speculative bubbles (see Hilborn et al., 2005 for a review). The implementation of the IQ system provides an opportunity to study how anchoveta and the ecosystem respond to a measured change. Under the present system the effective fishing season is about 50 days a year (Fréon et al., 2008) and one would expect the duration of the fishing season to increase under the IQ system. The consequences could be positive or negative and as far as we know no such "controlled" experiment has been carried out. For example, longer, less intense fishing might not be as traumatic to anchoveta but more days at sea may lead to more stress on the ecosystem as a whole. After several years of data collection the pros and cons of the IQ system should be evaluated.

The examples given above illustrate the challenge of implementing a management system that is ecosystem focused. It is noteworthy that this special issue has no contributions regarding the so-called called charismatic and sometimes threatened species (i.e. seabirds, marine mammals, turtles, etc.) and how they fit into the management equation needs to be considered. Although the challenge is monumental if it can be accomplished anywhere it might be in the northern HCS.

6. Future directions

Several future research problems have been highlighted throughout this introduction to the special issue on the northern HCS. Many can be linked to the unique features of this region: (1) intense primary productivity and an efficient but still poorly defined "trophic" transfer to small pelagic fish that supports the largest fishery in the world (Fig. 1); (2) the greatest level of interannual variability for any coastal region in the world ocean (Fig. 3); and (3) an intense, shallow and 'acidic' oxygen minimum zone (OMZ; Fig. 5). While these three processes, high biological productivity, interannual variability and oxygen minima, are not independent, we treat each separately in the following paragraphs.

Several hypotheses have attempted to explain the uniquely high productivity of small pelagic fish productivity in the northern HCS – or what has been termed the 'Peruvian anchoveta paradox': (1) the northern HCS may simply have higher levels of primary productivity and therefore fish productivity than other coastal upwelling ecosystems; (2) anchovy off Peru, but not the other upwelling ecosystems, have been suggested to feed directly on phytoplankton, primarily diatoms, and hence there is a very short and efficient food chain: (3) the combination of high primary productivity and relatively weak winds may lead to longer residence times, a less turbulent environment, and optimal conditions for fish growth, reproduction and egg and larval retention (Bakun and Parrish, 1982; Bakun and Weeks, 2008); (4) the OMZ could concentrate prey and at the same time reduce predation on zooplankton and small pelagic fish; and (5) the high levels of northern HCS interannual variability lead to a the pelagic ecosystem that is always in an 'r' state favouring fast growing fish like anchoveta (Chavez, 1987) and keeping long-lived ocean dwelling predators (on the small pelagic) from getting established (Bakun and Weeks, 2008). As Bakun and Weeks (2008) remind us the spectre of climate change is on the horizon making them wonder if the changes it brings will "shift Peru's marine ecosystem out of its current sweet-spot?"

The first hypothesis regarding increased fish production off Peru can now be safely rejected as estimates of primary productivity (Carr, 2001) and nutrient supply (Messie et al., 2008) indicate that



Fig. 5. Global distributions of 50 meter oxygen (µmol/kg, top) and pH (bottom). Note the very low oxygen and pH at this shallow depth off the northern HCS. The oxygen is from Conkright et al. (2002). The pH was calculated from total carbon dioxide and alkalinity found in the GLODAP database (Key et al., 2004) and temperature, salinity and nutrients in Conkright et al. (2002).

the Northwest Africa and Benguela coastal upwelling ecosystem have greater or similar levels as Peru (Fig. 1). Is Peru exceedingly efficient in the transfer of primary production to fish or are Benguela and Northwest Africa exceedingly inefficient? Paradoxically primary productivity off Peru appears limited during the winter months (Pennington et al., 2006), either by iron or light (Echevin et al., 2008; Friederich et al., 2008); Peru appears to be the only coastal upwelling ecosystem where upwelling and primary productivity are out of phase. The second, 'short food chain' hypothesis has now been discredited by Espinoza and Bertrand (2008), who show that anchovy get most of their caloric energy from zooplankton as in other upwelling ecosystems. One difference is that in the northern HCS euphausiids are the favoured prey of anchoveta, in contrast to Northwest Africa and Benguela. The Peruvian anchoveta paradox must be explained by some combination of the remaining hypotheses which concern (1) the efficient transfer of primary production to fish through zooplankton, in particular euphausiids, via an optimal environmental window, (2) the OMZ impacts predation on prey and predators of the small pelagic fish and (3) the high interannual variability.

There is growing awareness that environmental variability plays a dominant role in the functioning and structure of marine ecosystems and that this variability is much greater than previously thought. El Niño has been and remains the classic example of the impact of climate variability on ocean ecosystems (Barber and Chavez, 1983). However, longer and more subtle changes in the environment seem to drive stronger and more profound changes on marine living resources (Lluch-Belda et al., 1992; Chavez et al., 2003; Alheit and Niquen, 2004) leading to the so-called "regime-shifts." New time series from cores from the marine sediments underlying the Peru OMZ have revealed dramatic and sustained shifts (Gutiérrez et al., 2008; Sifeddine et al., 2008). It appears as if the current "sweet-spot" of fish productivity has come and gone in the past before the advent of anthropogenic influences. Will similar tipping-points (Gladwell, 2000) be reached in the future? And if so, when will they occur and will we predict them? Management plans will have to developed considering this shifting environmental baseline.

Environmental variability leaves its imprint on the ecosystem and the OMZ. Benthic communities on the continental shelf shift dramatically from those dominated by the few organisms capable of withstanding the dominant anoxic conditions to a diverse community during El Niño when oxygen levels over the shelf increase dramatically (Arntz et al., 2006; Gutiérrez et al., 2008a; Tarazona et al., 1988). The oxygenation during El Niño "cleans" not only the benthic but pelagic ecosystem on interannual scales (Chavez, 1987). Similar changes occur at multidecadal and centennial time scales. However, during recent centuries, the northern HCS OMZ has confined most oxygen-requiring animals to shallow surface waters, providing a refuge from predation and competition to those that can cope with low oxygen conditions. The impacts of the OMZ on benthic communities are relatively well documented but as discussed above the full impact of the intense and shallow OMZ on the pelagic ecosystem remains unclear. For example, the role of the OMZ on zooplankton growth and survival remains unresolved given the paucity of studies in the northern HCS. An early study suggests that a large fraction of the zooplankton community is limited in its vertical distribution by the OMZ (Judkins, 1980). In northern Chile on the other hand a large number of zooplankton can penetrate the OMZ as part of their vertical migrations while a smaller fraction is restricted to the upper oxygenated layer (Escribano et al. in press). Are the zooplankton further protected from grazing while in the OMZ? Are they eventually more accessible to the anchoveta? A number of bacterial processes and biogeochemical cycling, not discussed in this special issue, are enhanced in the OMZ making this region important for global nitrogen budgets for example (Codispoti et al., 1986).

Recent reports suggest that OMZs are growing either in response to the longer term centennial scale changes (Gutiérrez et al., 2008) or anthropogenic influences (Stramma et al., 2008). Such an expansion must certainly have consequences for the global nitrogen cycles discussed above, further removing nitrate via denitrification. Can this expansion help explain the shrinkage of the habitat of hake and other demersal fauna in northern Peru? The natural process of photosynthesis, carbon fixation and oxygen production, at the surface and sinking and decay of surface-derived primary production to depth, where oxygen is consumed and carbon dioxide respired, act to "acidify" the deep ocean. Regions of low oxygen are therefore regions of low pH (Fig. 5). How fast will the slow diffusion of anthropogenically-derived atmospheric CO_2 into the ocean (Feelv et al., 2008) further acidify northern HCS ecosystems and what will be the consequences? Is the acidic northern HCS OMZ a window into the future of other ecosystems that currently have higher oxygen and pH?

In summary, the northern HCS off Peru is intensively studied because of its unusual dynamics and astounding fish productivity. It is a turbid green-to-brown ecosystem with more "substance" than "beauty" - very different than stereotypical tropical systems where diversity and colour dominate. Indeed, in the northern HCS productivity is high at the expense of diversity. Interannually and multidecadally, the northern HCS changes from higher biological productivity and lower diversity during cool periods to lower productivity and higher biodiversity during warm periods (El Niño and El Viejo). In terms of marine living resources, the northern HCS is perhaps the best monitored large ecosystem in the world, allowing for unusually effective management of fisheries in spite of internal (economic) and external (environmental) challenges. The continued collection of time series data is strongly encouraged together with the application of new and evolving technologies for observation, modelling and management. In the present environment scientific/management strategy iterates between observations, basic ecosystem rules and single-purpose models or management practices. In the future fully integrated and adaptive observation, modelling and management systems will be required with greater reliance on autonomous observing systems like floats, gliders and moorings. We wonder what changes, in the environment, and the integrated management system, the next decades will bring, and hope that the next synthesis will be as positive as this one.

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