HAL
open science

El Niño and similar perturbation effects on the benthos of the Humboldt, California, and Benguela Current upwelling ecosystems

W. E. Arntz, V. A. Gallardo, D. Gutiérrez, E. Isla, L. A. Levin, J. Mendo, C. Neira, G. T. Rowe, J. Tarazona, M. Wolff

To cite this version:

W. E. Arntz, V. A. Gallardo, D. Gutiérrez, E. Isla, L. A. Levin, et al.. El Niño and similar perturbation effects on the benthos of the Humboldt, California, and Benguela Current upwelling ecosystems. Advances in Geosciences, 2006, 6, pp.243-265. hal-00296946

HAL Id: hal-00296946

https://hal.science/hal-00296946

Submitted on 18 Jun 2008

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Advances in Geosciences, 6, 243–265, 2006
SRef-ID: 1680-7359/adgeo/2006-6-243
European Geosciences Union
© 2006 Author(s). This work is licensed
under a Creative Commons License.

Advances in Geosciences

El Niño and similar perturbation effects on the benthos of the Humboldt, California, and Benguela Current upwelling ecosystems

W. E. Arntz[1], V. A. Gallardo[2], D. Gutiérrez[3], E. Isla[4], L. A. Levin[5], J. Mendo[6], C. Neira[5], G. T. Rowe[7], J. Tarazona[8], and M. Wolff[9]

[1]Alfred-Wegener-Institut für Polar- und Meeresforschung, Columbusstrasse, 27568 Bremerhaven, Germany
[2]Centro de Investigación Oceanográfica en el Pacífico Sur-Oriental (COPAS), Universidad de Concepción, P.O. Box 42, Dichato, Chile
[3]Instituto del Mar del Perú (IMARPE), P.O. Box 22, Callao, Peru
[4]Institut de Ciències del Mar/CSIC, Passeig Marítim de la Barceloneta 37-49, 08015 Barcelona, Spain
[5]Scripps Institution of Oceanography, La Jolla, CA 92093-0218, USA
[6]Universidad Agraria La Molina (UNALM), P.O. Box 456, Lima 100, Peru
[7]Texas A&M University, College Station, TX 77843, USA
[8]Universidad Nacional Mayor de San Marcos (UNMSM), P.O. Box 1898, Lima 100, Peru
[9]Zentrum für Marine Tropenökologie, Universität Bremen, Fahrenheitstr. 6, 28359 Bremen, Germany

Received: 26 August 2005 – Revised: 2 February 2006 – Accepted: 2 February 2006 – Published: 1 March 2006

Abstract. To a certain degree, Eastern Boundary Current (EBC) ecosystems are similar: Cold bottom water from moderate depths, rich in nutrients, is transported to the euphotic zone by a combination of trade winds, Coriolis force and Ekman transport. The resultant high primary production fuels a rich secondary production in the upper pelagic and nearshore zones, but where O_2 exchange is restricted, it creates oxygen minimum zones (OMZs) at shelf and upper slope (Humboldt and Benguela Current) or slope depths (California Current). These hypoxic zones host a specifically adapted, small macro- and meiofauna together with giant sulphur bacteria that use nitrate to oxydise H_2S. In all EBC, small polychaetes, large nematodes and other opportunistic benthic species have adapted to the hypoxic conditions and co-exist with sulphur bacteria, which seem to be particularly dominant off Peru and Chile. However, a massive reduction of macrobenthos occurs in the core of the OMZ. In the Humboldt Current area the OMZ ranges between <100 and about 600 m, with decreasing thickness in a poleward direction. The OMZ merges into better oxygenated zones towards the deep sea, where large cold-water mega- and macrofauna occupy a dominant role as in the nearshore strip. The Benguela Current OMZ has a similar upper limit but remains shallower. It also hosts giant sulphur bacteria but little is known about the benthic fauna. However, sulphur eruptions and intense hypoxia might preclude the coexistence of significant mega- und macrobenthos. Conversely, off North America the upper limit of the OMZ is considerably deeper (e.g., 500–600 m off California and Oregon), and the lower boundary may exceed 1000 m.

The properties described are valid for very cold and cold (La Niña and "normal") ENSO conditions with effective upwelling of nutrient-rich bottom water. During warm (El Niño) episodes, warm water masses of low oxygen concentration from oceanic and equatorial regions enter the upwelling zones, bringing a variety of (sub)tropical immigrants. The autochthonous benthic fauna emigrates to deeper water or poleward, or suffers mortality. However, some local macrofaunal species experience important population proliferations, presumably due to improved oxygenation (in the southern hemisphere), higher temperature tolerance, reduced competition or the capability to use different food. Both these negative and positive effects of El Niño influence local artisanal fisheries and the livelihood of coastal populations. In the Humboldt Current system the hypoxic seafloor at outer shelf depths receives important flushing from the equatorial zone, causing havoc on the sulphur bacteria mats and immediate recolonisation of the sediments by mega- and macrofauna. Conversely, off California, the intruding equatorial water masses appear to have lower oxygen than ambient waters, and may cause oxygen deficiency at upper slope depths. Effects of this change have not been studied in detail, although shrimp and other taxa appear to alter their distribution on the continental margin. Other properties and reactions of the two Pacific EBC benthic ecosystems to El Niño seem to differ, too, as does the overall impact of major episodes (e.g., 1982/1983(1984) vs. 1997/1998). The relation of the "Benguela Niño" to ENSO seems unclear although many

Correspondence to: W. E. Arntz
(warntz@awi-bremerhaven.de)

Pacific-Atlantic ocean and atmosphere teleconnections have been described. Warm, low-oxygen equatorial water seems to be transported into the upwelling area by similar mechanisms as in the Pacific, but most major impacts on the eukaryotic biota obviously come from other, independent perturbations such as an extreme eutrophication of the sediments ensuing in sulphidic eruptions and toxic algal blooms.

Similarities and differences of the Humboldt and California Current benthic ecosystems are discussed with particular reference to ENSO impacts since 1972/73. Where there are data available, the authors include the Benguela Current ecosystem as another important, non-Pacific EBC, which also suffers from the effects of hypoxia.

1 Introduction

This paper aims at a comparison of the benthic/demersal subsystems of Eastern Boundary Currents (EBCs) and the impact of El Niño or similar perturbations on interannual or lower time scales. It focusses on the Humboldt Current (Peru-Chile), HC, and California Current, CC, systems both of which receive direct impacts from El Niño (EN) and La Niña (LN), i.e. the warm and cold phases of the ENSO cycle. However, as the HC resembles the Benguela Current (BC) rather than the CC, the BC is included despite the fact that the existence of a "Benguela Niño" is not universally accepted (cf., for example, Shannon and Nelson (1996) vs. Hamukuaya et al. (2001)). There are, however, other perturbations such as H_2S outbreaks or intrusions of unusually warm equatorial water, which the BC has in common with the two other large upwelling systems. The Canary Current is a special case in that it does not have an oxygen minimum zone (OMZ), and does not seem to suffer from the kind of impacts investigated here. It is therefore excluded.

EBCs have obvious common properties (Blanco, 2001). Under "normal" conditions, in all three upwelling systems the main transport carries cold, well-oxygenated water from high towards low latitudes, whereas undercurrents take water with lower oxygen content poleward. There are also surface countercurrents in a poleward direction. Upwelling is caused by trade winds parallel to the coast and offshore water transport perpendicular to the coast, modified by the Coriolis force and Ekman transport (Arntz and Fahrbach, 1991). Upwelling normally draws cold, nutrient-rich bottom water from moderate depths into the photic mixed layer and thus fuels primary production and the pelagic food web. LN (very cold) phases of ENSO enhance these conditions. The abundant surface production leads to an extensive OMZ under the EBC, due to the fact that the organic material cannot be remineralised on the way to the seafloor and also exceeds the decomposition capacities of aerobic benthos.

EN conditions in the eastern Pacific, especially during strong and very strong events, are triggered by equatorial Kelvin waves. When these waves impinge on the continental margins, they are mainly converted into poleward coastal Kelvin waves. This process may lead to a drastic deepening of the pycnocline and nutricline along the E Pacific coasts, extending the warm surface water layer to considerable depths and making upwelling, which is then derived from the low-nutrient warm water sphere, unefficient (Barber in Canby, 1984). Fuelling of the pelagic system is largely interrupted, the pelagic upwelling food web breaks down and gives way to a tropical-oceanic web, which is advected with the Kelvin waves (Arntz, 1986). As surface production is reduced, there is less input of organic material to the seafloor during EN phases (Gutiérrez et al., 2000; González et al., 2000), and there is evidence that there is a shift in sedimentary organic matter composition, and a reduction of the biopolymeric organic carbon fraction, potentially available for consumers (Neira et al., 2001a).

These basic processes seem to be identical in the HC and the CC, and the same may hold for the reflected (Rossby) portion of the Kelvin waves, which can disturb the Pacific ecosystem a long time after EN while travelling between the continents (Lagos, 1999). System structure of the major EBCs is similar but there are differences in trophic structure (Moloney et al., 2005). Food chain efficiency is generally low (Jarre-Teichmann and Christensen, 1998) although productivity differs substantially (Jarre-Teichmann et al., 1998; Carr and Kearns, 2003). Latitudinally the HC is about 5° closer to the equator than the CC (Blanco et al., 2001). While off South America the enhanced poleward intrusion of saline, low-oxygen equatorial water leads to an oxygenation of the OMZ on the shelf and upper slope, with dissolved O_2 values at the seafloor at times multiplied by a factor of >10 (Guillen et al., 1985; Arntz et al., 1991; Levin et al., 2002), the much deeper OMZ off California and Oregon (see Helly and Levin, 2004) remains beyond the impact of the equatorial water mass. Instead, this intruding water lowers the O_2 concentrations on the shelf and upper slope. Thus flushing by the coastal Kelvin waves results in beneficial effects for the aerobic benthos off South America and potentially reverse effects off North America. This difference seems to be very important, however it explains only partly the different EN impact in the two hemispheres, which also depends on the season of onset, duration, severity, water depth and distance from the equator. While the very strong EN 1982–1983 and 1997–1998 were generally comparable (Enfield, 2001), differences in their impacts in the northern and southern hemispheres can be largely attributed to their different seasonal onset (Arntz, 2002). As is to be expected from the common origin, most stronger Pacific EN apply to both the NE and SE Pacific, however there are exceptions (Fig. 1). EN 1972–1973, considered a strong event in the HC, had almost no effect in the CC (Schimmelmann and Tegner, 1991). Generally, South America seems to receive earlier and stronger EN impacts than North America; for example, onset of anomalous conditions in the CC in 1997 and recovery in 1998–1999 lagged the equatorial events by four months (Bograd and Lynn, 2001). As observed in 1982–1983(1984) the effects may continue over another summer in the north while the episode weakens in southern hemisphere winter.

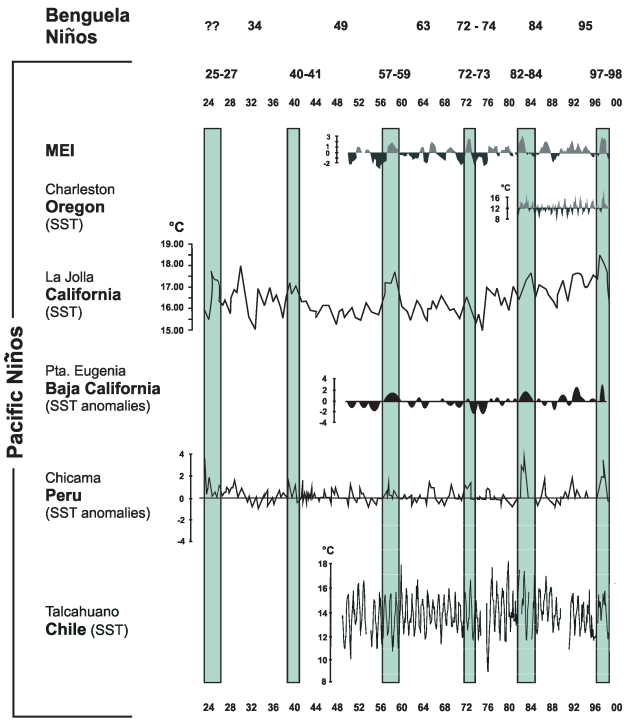

Fig. 1. Time series of the Multivariate ENSO Index, sea surface temperature SST (La Jolla, California/USA; Chicama, Peru; Talcahuano, Chile), and SST deviations (Charleston, Oregon/USA; Pta. Eugenia, Baja California/Mexico), indicating little delay in the arrival of the anomalies at the different latitudes except at the southernmost site, where the seasonal signal conceals the ENSO variation. Above the Pacific time series, some more important "Benguela Niños" are indicated, revealing only limited coincidence with the Pacific Niños. Sources (from above to below): Shannon et al. (1986); Pearcy (2002); Lea and Rosenblatt (2000); Lluch-Cota and Ponce-Díaz (2000); MIPE/IMARPE, Peru; CENDHOC/SHOA, Chile. All series redrawn, La Jolla data are 12-month, Talcahuano data 3-month moving mean.

"Benguela Niños" occur more seldom than Pacific EN and do not necessarily coincide temporally, as in the case of the very strong EN 1997–1998, which was not felt off Namibia and South Africa. However, the other very strong episode in the past century, in 1982–1983(1984), did occur as a Benguela Niño (in 1984), as did the episodes of the years 1963, 1972–1973 and 1991–1995, which also appeared only in the last year (Fig. 1). Some of the Benguela Niño impacts such as faunal migrations and mortalities resemble very much those of EN in the eastern Pacific (Gammelsröd et al., 1998) but seem to be restricted to shallower depths (Hamukuaya et al., 2001).

Changes caused by major EN have been documented since the beginning of the 20th century off Peru. However, the emphasis has been on the pelagic subsystem, in particular pelagic shoaling fish and the seabirds and marine mammals feeding on them. Information on the benthic system, which plays a much smaller economic role in EBCs, was largely anecdotal before the 1982–1983 EN and continues to receive less attention than the pelagic realm. As this review focusses on the benthic/demersal ecosystems in EBCs and the impact of EN in these systems, most of the impacts in the pelagic realm, on invertebrates, fish, birds and seals are not mentioned; these effects are summarised in specific (e.g., Chávez, 2003) or more general publications (e.g., Arntz and Fahrbach, 1991; Diaz and Markgraf, 2000). Other aspects we had to omit due to restricted space are the effects of ENSO in warm tropical regions (e.g., Glynn, 1990), the socioeconomic consequences and teleconnections of EN (e.g., Glantz et al., 1987; Glantz, 2001; Mendo and Wolff, 2002), and the palaeoaspects (Baumgartner, 1992; Macharé and Ortlieb, 1993; Ortlieb and Hocquenghem, 2001; Markgraf et al., 2000).

Table 1. Depth limits (m) of alongshore zones in the three EBC.

Zone	CC	HC	BC
O_2 saturated nearshore fringe	0-10	0-10	0-10
Intermediate zone	10-700 (Or) 10-50 (Pe)	10-50 (Pe) 10-150 (CCh)	10-50
Oxygen minimum zone	700-1100 (Or) 500-700 (Ca)	50-600 (Pe) 150-300 (CCh)	50-300
Deep-sea zone below OMZ	>1100 (Or) >700 (Ca)	>600 (Pe) >300 (CCh)	>300

CC California Current, HC Humboldt Current, BC Benguela Current; Or Oregon, Ca California, Pe Peru, CCh Central Chile
All depth limits refer to „normal" years and are approximate values, which are subject to seasonal and climatic changes

Within the three large EBCs considered for this comparison, four areas parallel to the coast have been distinguished (Table 1) based on their dissolved oxygen conditions (see Gallardo, 1963):

– the well-flushed nearshore strip, consisting of sandy beaches and rocky shores and mostly finer sediments in the upper subtidal. ENSO effects are manifested by other factors than by change in O_2, but lack of O_2 may play a role in the case of sulphidic eruptions. The lower boundary of this zone is arbitrarily put at 10 m but is variable.

– the intermediate zone between this coastal strip and the upper limit of the oxygen minimum zone (OMZ), extremely narrow but very productive off Peru/Chile and Namibia/South Africa, and broader in the CC, with important artisanal and recreational shallow-water fisheries in all areas and offshore fisheries off California and Oregon.

– the oxygen minimum zone ($<0.5\,\mathrm{ml\,O_2\,l^{-1}}$), off Peru/northern Chile mostly between 50 and 600 m, narrowing (ca. 150–300 m) towards central Chile and disappearing entirely at 43° S off Chiloe. In the CC the OMZ begins at ca. 500 m off California and ca. 700 m off Oregon and extends to about 700 m and 1100 m, respectively. In the BC it reaches from about 50 m to 300 m. This zone is dominated by bacterial (prokaryotic) populations but also houses a eukaryotic fauna

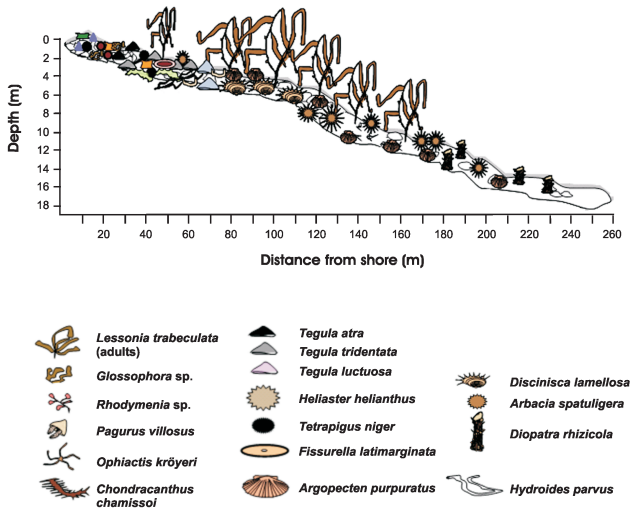

Fig. 2. Macrobenthic zonation of a rocky shore in central Peru (El Panteón, Bahía Independencia, Pisco). Original data.

specifically adapted to hypoxic conditions. Its benthic/demersal subsystem has no commercial importance for human consumption during normal and LN conditions.

– the deep sea below the OMZ, with oxygen concentrations increasing with depth, and a dominant benthic fauna as in shallow water. This zone has been explored for deep-sea fisheries but has scientifically been less studied than the OMZ. It is considered to be of lower importance in the context of this review, because EN effects should be faint if at all existent.

Literature used for this review could not always be clearly assigned to one of these depth zones, but most effects at the seafloor are depth- and oxygen-specific. In the following we will summarize typical conditions in the various depth zones, show ENSO or comparable effects, and try to explain why some of these effects differ in the three EBCs whereas others are similar.

2 Nearshore zone (intertidal, uppermost subtidal to 10 m)

This zone has high dissolved O_2 levels due to exchange with the atmosphere, wave action and abundant algal populations. Kelp beds along the American Pacific and African Atlantic coasts contribute substantially to biomass and habitat structure. The principal ecosystem engineers are *Macrocystis pyrifera*, *M. integrifolia* and *Lessonia trabeculata* along the South American Pacific coasts (Tarazona et al., 2003; Vásquez and Vega, 2004), *M. pyrifera* off California and Baja California, and *M. angustifolia* in the Benguela ecosystem. Benthic invertebrate and demersal fish production is very high due to favourable light and food conditions. In its pristine state, this zone may have had extremely high biomasses of all those valuable invertebrate stocks, which have been overfished and largely disappeared from shallow water (*Haliotis* spp., *Concholepas concholepas*, *Jasus lalandii*). However, there still remain very rich resources of kelp, clams, surf clams, mussels, snails, chitons, decapod crabs and lobsters, giant balanids, ascidians and sea urchins, together with numerous macroalgae and invertebrates which are not exploited. An example for the Peruvian coast is given in Fig. 2. Biomasses of these populations can be extremely high, e.g. for the surf clams *Mesodesma donacium* (Peru) and *Donax serra* (Namibia), an annual production of 2400 and 167–637 g ash-free dry mass m^{-2} has been reported, respectively (Arntz et al., 1987; Laudien et al., 2002). Similarly high values are known from mussels in the intertidal (HC, BC esp. *Semimytilus algosus*; *Choromytilus* spp.; CC *Mytilus* spp.). Among the demersal and coastal fish, most of which are also found in the next deeper zone, corvinas (Sciaenidae), congrios (Ophidiidae), sea bass (Serranidae), robalos (Centropomidae) and flatfish (Paralichthyidae), among others, play a dominant role, as do the "linefish" (kob *Argyrosomus hololepidotus* and *A. japonicus*, silver kob *A. inodorus*, steenbras *Lithognathus aureti*, blacktail *Diplodus sargus*, galjoen *Dichistius capensis*, and others) off southwest Africa. All these resources support important artisanal and recreational fisheries, although these areas are better known to most marine biologists for their wealth of shoaling fish in the pelagic zone. Benthic species richness is fairly high in this zone although not comparable to warm tropical regions, and diversity is moderate because of high dominance of some species.

Abiotic changes due to EN in this zone include a variety of factors, whose composition and severity depends on the characteristics outlined above (strength of the episode, time of onset, etc.). They include strong increases in temperature, less intense upwelling, changes in salinity, higher terrigenous, freshwater and sediment input, increased sea level, greater wave action, and increase of UV radiation, among others. Some of these impacts may work antagonistically; e.g., clear water of oceanic origin favours penetration of UV radiation, increased sediment input from rivers reduces it, and the two factors may change salinity in different directions.

Biotic responses to this altered environment include changes in species composition, abundance and biomass due to emigration, immigration, changes in reproductive success, larval dispersal and recruitment, as well as changes in food availability, competition and predation. These biotic responses trigger further effects in the biota. There is, however, a sad lack of physiological and experimental work to arrive at cause-and-effect explanations for the numerous changes that have been described. Generally, both negative and positive effects seem to be much more drastical in the HC than in the CC, where even very strong EN like those of 1982–1983(1984) and 1997–1998 did not have such consequences as off Peru, northern Chile and around the Galapagos Islands.

The best documented cases of EN impacts in shallow water are for the kelp forest communities (*Macrocystis* spp. and

associated species) in both hemispheres. In particular, giant kelp were heavily damaged in some areas during major EN (see also intermediate zone). Macroalgae are very sensitive to the reduction of nutrients that accompanies sea temperature rise and suffer high mortality during EN (Gunnill, 1985; Tegner and Dayton, 1987; Castilla and Camus, 1992; Dayton et al., 1999).

Off California, higher water temperatures >20°C and low nutrient concentrations had adverse effects during the 1982–1983 EN; the kelp canopy deteriorated rapidly after the onset of high temperatures and depletion of internal nitrogen reserves (Gerard, 1984). Photosynthetic capacity and growth rates were reduced. However, recovery after this very strong EN was fast; the kelp beds recovered 300 km of coastline in a period of only six months (Foster and Schiel, 1985; Hernández-Carmona et al., 1991). Shallow kelp beds off the west coast of Baja California again suffered high mortality during EN 1997–1998, depriving the invertebrate stocks of abalone, rock lobster, sea urchins and holothurians of their protection (Lluch-Cota et al., 1999). Invertebrate mortality in the intertidal and shallow subtidal off Peru was very high during EN 1982–1983, eliminating almost the entire assemblage of macrobenthic grazers and many suspension feeders and predators (Arntz, 1986) (Fig. 3).

The fish assemblages of intertidal rock pools off southern California experience major changes associated with EN and LN events. These include reduced recruitment and mortality of species with cold-water affinities and enhancement of those with subtropical affinities (Davis, 2000), altered population growth rates (Davis and Levin, 2002) and shifts in genetic structure as reflected in spot morphology (Davis, 2001).

Considering the effects on macroalgae and fish it is hard to understand why much literature dealing with invertebrate interactions in the Californian and Oregon intertidal does not refer to EN at all. A reason may be that the core of the CC is 300–400 km offshore off California and 200 km off Baja California (Lynn and Simpson, 1987 fide Aurioles-Gamboa and Pérez-Flores, 1997), and thus much further offshore than off South America.

The disastrous effect of storms associated to EN in the CC (Dayton and Tegner, 1984) on the kelp canopy has similar consequences. In September 1997, hurricane "Nora" struck the coast of Baja California and strongly affected the abalone banks of Natividad Island, where the *M. pyrifera* beds providing shelter for these gastropods were completely destroyed (Lavaniegos, 2003).

Off Lagunillas and other rocky sites along the central coast of Peru, giant kelp *Macrocystis* spp., *Lessonia* spp. and other brown and red algae were heavily reduced during the 1982–1983 EN. *L. trabeculata* disappeared from the central Peruvian coast during EN 1997–1998 (Fernández et al., 1999), and following this event the leading recruitment edge of *L. nigrescens* only advanced three km per year, much slower than off California (see above). Further south, in Chile the 1982–1982 EN caused mortality in kelp beds along 600 km of coastline (Castilla and Camus, 1992). Conversely, the 1991–1993 and 1997–1998 events did not cause massive

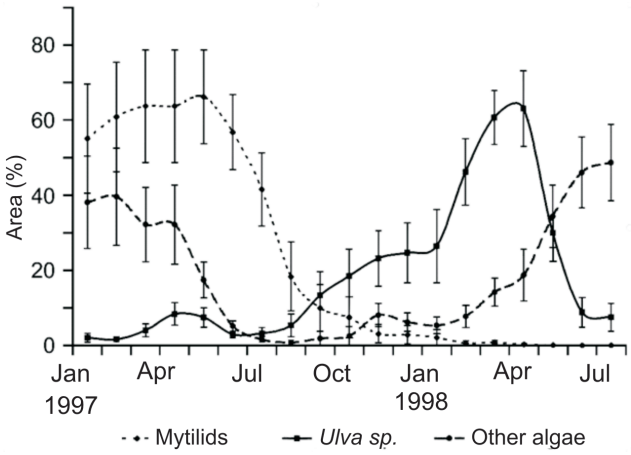

Fig. 3. Mean coverage of rocky shore species in Bahía Ancón (central Peru) during El Niño 1997–98. Source: Romero 2001.

mortality of *L. nigrescens* at these latitudes (Vásquez and Vega, 2004) but may have contributed to lower kelp production and limited recruitment.

Spatial-temporal distribution patterns of *M. integrifolia* and *L. trabeculata* in shallow water (2–15 m) off northern Chile during EN 1997–1998 were maintained by the continuity of coastal upwelling, which buffered and moderated superficial warming and nutrient depletion (Vega et al., 2005). Areas with continuous upwelling might thus serve as refuges during EN for those areas that lack upwelling at times, and suffer local extinctions. Intensification of upwelling after the 1998–2000 LN favoured productivity of the kelp assemblage. However, an abrupt increase of the sea urchin Tetrapygus niger, the most conspicuous grazer, produced local extinction of *M. integrifolia* and compression of the bathymetric range of *L. trabeculata*. Interannual variability in this ecosystem is thus triggered by oceanographic events (mainly upwelling) on different scales, biotic processes (change in grazer abundance) on local scales and the variability caused by warm and cold phases of ENSO (Vega et al., loc. cit.).

The slower recovery of the intertidal *L. nigrescens* off Chile as compared with the subtidal *M. pyrifera* off California seems to be due to a series of factors inhibiting recruitment of the former (Martínez and Santelices, 1998) or recruitment from dormant microscopic stages (Ladah et al., 1999).

Following local extinction of the former macroalgal and invertebrate dominants off Peru during EN 1982–1983, a successional process began immediately after EN with conspicuous green algae dominance in the intertidal followed by dominance of red and finally brown algae. This sequence took 2–3 years. The algal community developed a very different, long-bearded aspect, because the grazers had been eliminated as well (Arntz, 1986). Barnacles and small mussels were the first invertebrate colonists among the brown algae. In Independencia Bay, central Peru the recovery of the kelp forests (*Macrocystis*, *Lessonia*) took a little more

than two years. Dense initial coverage by calcareous algae was followed by efficient recolonisation by the two large brown algae and the mussel *Aulacomya ater*, which had also been wiped out in shallow water. Grazing gastropods, chitons and balanids returned later (Tarazona et al., 1988; Tarazona, 1990). Further north, in the Bay of Ancón, the mussel *Semimytilus algosus* was the first settler on the rocky shore after EN 1982–1983, presumably by recruitment from a sublittoral population that survived (Tarazona et al., 1988). A second fast colonizer was the brachiopod *Discinisca lamellosa*. In northern Peru (Islas Lobo) larvae of gooseneck barnacles (*Pollicipes elegans*) invaded the rocky shores during EN 1982–1983 and established large populations in the crevices, initiating a local fishery which lasted beyond the warm episode (Kameya and Zeballos, 1988).

The most conspicuous impact along the Peruvian sandy beaches during that event was the total mortality of the highly dominant surf clam *Mesodesma donacium*, whose distribution was set back poleward 7 degrees of latitude causing considerable shifts in the sandy beach community (Arntz et al., 1987). *M. donacium* did not recover to its former dominance in >20 years, during which the subdominants *Donax marincovichi* and *Emerita analoga*, which both survived the event, never attained the role of the former dominant at the study site (Tarazona, own obs.). Other shallow-water bivalves also suffered mortalities during EN, but to a much lower degree.

After EN, the rapid changes toward the LN cold regime caused further catastrophes among those organisms that either invaded the upwelling regions or, as local warm-tolerant species, were able to profit from the changes brought about by EN.

Whether the Benguela Niño is responsible at all for mass mortalities registered in shallow water off Namibia and South Africa (Table 2), or whether these were all due to hydrogen sulphide eruptions caused by other factors is not totally clear from the literature. Episodes of toxic H_2S and methane emission from "soupy" sediments are probably triggered by changes in atmospheric and oceanic pressure or precipitation-induced pressure signals from inland via fossil river beds (Emeis et al., 2004). They are more extensive, more frequent, and longer lasting than previously supposed; e.g. in April–March 2001 an area of >20 000 km^2 in Namibia was affected for over two weeks (Weeks et al., 2002, 2004). These sulphidic eruptions are commonest in the Walvis Bay-Swakopmund area, causing considerable economic damage (Bailey et al., 1985). Milky discolouration in these cases is accompanied by substantial amounts of hydrogen sulphide and O_2 concentrations <0.2 ml O_2 l^{-1} in surface waters right up to the beach (Brüchert et al., 2006; Weeks et al., 2002, 2004). The discolourations may be due to colloidal elemental sulphur produced by the oxidation of sulphide bubbles emerging from the sediment on encountering oxygenated column water (Jørgensen, pers. comm. fide Weeks et al., 2002).

Some data are available on the response of intertidal bivalves to sulphidic eruptions. *Semimytilus algosus*, *Donax serra* and *Perna perna* have developed mechanisms to survive such short-term events in the BC. *S. algosus* and *P. perna* survived 0.2 mM sulphide >6 days, and both started to produce energy anaerobically. Survival rate was higher, however, in the former species due to higher detoxification capacity (Schiedek and Currie, 2002). Under severe hypoxia juvenile *D. serra* survived for four days, but survival was significantly reduced under H_2S exposure (0.1 mM). The clams showed a high detoxification capacity by oxidising the penetrating sulphide to non-toxic thiosulphate. Despite these capabilities it is obvious that hydrogen sulphide must be considered an important community structuring factor in the BC (Laudien et al., 2002). Further effects of sulphidic outbreaks are given below for the fauna of the intermediate zone.

Milky discolourations ("aguas lechosas"), presumably of a similar kind, have occurred in the HC off Concepción (36° S) in past years, however only during cold (LN) ENSO phases with strong upwelling. The bivalve *Mulinia edulis* is floated during these sulphidic events by decomposition gases formed within the shell. The surface waters of Concepción Bay can be littered with these drifting clams, which are blown by the wind against the coast with their shells still closed, forming extensive accumulations on the beach (Gallardo, unpublished data). "Aguas lechosas" have also been reported from central Peru, where they can cause widespread mortality in the populations of *Semimytilus algosus* on rocky shores of the coast and the islands (Tarazona, unpublished).

3 Intermediate zone

During "normal" times and LN conditions, this zone between the littoral well-flushed strip and the OMZ reveals a broad range of oxygen concentrations. Its upper part can be as well-flushed as the nearshore zone (in fact, the shore may be only tens of metres away) whereas in the HC system its lower part may be characterized by low oxygen concentrations, although not as hypoxic as in the OMZ. For example off Peru, oxygen values can be quite low even at 15 m depth, where sheltered bays impede major water exchange (Tarazona et al., 1988a, b, 1991), but values do not reach the OMZ limit. In exposed areas (Independencia/Peru, central Chile) appreciable oxygen concentrations may be found beyond the 50 m depth limit. Conditions in the BC resemble very much those in the HC. On the other hand, off California and Oregon the much deeper position of the OMZ has the effect that the intermediate zone encompasses the entire shelf and upper slope to 400 or 500 m depth and comprises almost the total zone of demersal fisheries. The shelf is narrow and the slope is very steep in the CC system off California and Oregon, so that this zone may extend only few tens of kilometres from shore.

Giant kelp (*M. pyrifera* and *M. integrifolia* both in North and South America) also dominate the upper part of the intermediate zone. Off California, these areas (12–18 m) were opened for invasion by storms associated with the 1982–1983 EN, favouring *Desmarestia* and other algae whose canopies recovered much faster than that of *M. pyrifera* because

Table 2. Faunal mortalities recorded in the Benguela Current during the hypoxic events of March–May 1997 (Bailey, 1999).

Species name	Taxa	Common name
Clinus spp.	Decapoda	rock lobster*
Ovalipes trimaculatus	Decapoda	swimming crab
Donax serra	Bivalvia	surf clam
Choromytilus meridionalis	Bivalvia	mussel
Bullia laevissima	Prosobranchia	snail
Octopus vulgaris	Cephalopoda	octopus
Sepia vermiculata	Cephalopoda	cuttlefish
Loligo vulgaris	Cephalopoda	squid
Indet.	Polychaeta	worms
Solea bleekeri	Pisces	sole
Helicolemus dactylopterus	Pisces	
Agyrosomus sp.	Pisces	kob
Haploblepharus pictus	Pisces	
Pachymtopon blochii	Pisces	
Clinus spp.	Pisces	klipfish

* Rock lobster: 2000 t stranded during 6 hypoxic events at 4 discrete sites (from Cockcroft et al., 2000)

nutrients were enhanced at the seafloor whereas they were depleted in the water column where the *Macrocystis* canopy occurs (Dayton et al., 1992). While understory macroalgal populations were thus favoured by the 1982–1983 EN, they were outcompeted during LN 1988–1989 when giant kelp growth was extraordinary (Tegner et al., 1996). In 1997 the limits of macroscopic *Macrocystis* plants were shifted about three degrees of latitude to the north (Tegner, 2001). Deeper subtidal kelp partly escaped mortality during EN 1997-98 because individuals survived in cooler water (Martínez et al., 2003; Ladah and Zertuche-González, 2004). In the long run, *Macrocystis* remained the competitive dominant due to its capacity of recruiting effectively even during and after strong EN episodes. Off Peru and Northern Chile, the holdfast community of giant kelp *Macrocystis* spp. which consists of many species during normal periods and LN, was virtually wiped out during EN 1982–1983 (Arntz, 1986).

The intermediate zone is also of utmost importance for the artisanal fisheries in the HC and BC, and for artisanal and demersal (trawl) fishery in the CC. Many of the species mentioned among the resources of the nearshore zone extend their distribution into this zone and are joined by various important mussel, clam, scallop and gastropod species, as well as decapods (cancrid and xanthid crabs; spiny lobsters; shrimps and prawns). Some genera or even species are common to the two southern hemisphere EBC: the mussels *Semimytilus algosus, Choromytilus* sp. and *Aulacomya ater*, the crab *Pilumnoides* sp., the brachyopod *Discinisca* sp., several polychaetes and isopods. Various cancrid crabs (*Cancer edwardsi, C. coronatus, C. setosus*) are valued targets in the HC while *C. magister* plays an important role in the CC. On the other hand, commercial xanthid crab resources (*Homalaspis plana, Platyxanthus orbignyi*) seem to be restricted to the HC, while penaeid (warm water) shrimps usually live outside the upwelling areas under "normal" conditions. CC and BC have spiny lobsters (*Panulirus interruptus, Jasus lalandii*) and abalone (*Haliotis* spp.) in common whereas the species *Panulirus gracilis* stays outside cold upwelling water off Peru unless there is an EN (but the genus lives in the Galápagos Islands). Off Namibia, rock lobsters only occur until 15–30 m depth whereas off South Africa they are exploited to 55 m (Bailey et al., 1985). Squid (invertebrates but pelagic) are common fishery targets in all upwelling systems. Most of the demersal fish mentioned for the nearshore zone also live in the intermediate zone, together with hake (*Merluccius* spp.), which is predominantly semipelagic and tolerates extremely low O_2 concentrations (Cape hake in the BC to 0.25 ml l^{-1}), and other demersal or coastal fish. Due to the limited depth extension of this zone in the HC and BC, its importance for demersal fish (and shrimp) is much greater in the CC.

EN-induced changes in this zone may be quite strong and differ substantially from those in the nearshore zone. During (very) strong EN, the intermediate zone extends into the upper part of the area normally covered by the OMZ off Peru and Northern Chile due to flushing by the strengthened Peru-Chile Undercurrent (originating from the Cromwell Current; Strub et al., 1998), reducing the OMZ area substantially (Helly and Levin, 2004). This oxygenation during strong EN does not occur in the other EBC. Off North America, low oxygen equatorial water may even lead to oxygen-deficient conditions at upper slope depths. So many of the major EN effects in this zone off South America are due to oxygenation, whereas off North America EN may even induce oxygen deficiency.

Some of the effects on the biota described for the nearshore zone hold true also for the intermediate zone. Poleward invasions of (sub)tropical demersal fish and benthic invertebrate species during strong and very strong EN occur in both North and South America, but invertebrate invasions seem to be quantitatively more important in the south (Table 3). These poleward shifts involve both passive transport of eggs and larvae and active immigration of juveniles and adults. During EN 1982–1983 and 1997–1998 penaeid shrimps, mainly *Xiphopenaeus kroyeri* (=*riveti*), and rock lobsters from the Panamic Province appeared in the HC

Table 3. Invertebrate increases off Peru during and after EN 1982–1983.

Group	Species	Comments
Larval transport, active immigration:		
Shrimp	*Xiphopenaeus riveti*	Trawling and beach
	Penaeus spp.	seining introd.
	Sicyonia disdorsalis	market flooded, dumping prices
Swimming crabs	*Euphylax robustus*	Nuisance for fishermen,
	Callinectes arcuatus	not exploited
	Portunus acuminatus	Predatory impact
	Portunus asper	
	Arenaeus mexicanus	
	Euphylax dovii	
Gooseneck barnacles	*Pollicipes elegans*	Exploited, sold in markets, export to Spain
Spiny lobster	*Panulirus gracilis*	S range extension, in markets
Ghost shrimp	*Squilla panamensis*	No effect
Molluscs	*Pteria sterna*	No effect, rare
	Malea ringens	
Proliferation of local species:		
Scallop	*Argopecten purpuratus*	Boats and divers conc. in Paracas area. Market flooded, dumping prices. Export enhanced
Locate" snail	*Thais chocolata*	Incr. importance
Octopus	*Octopus mimus*	Incr. importance, feeding on scallops

Table 4. El Niño: Fish indicators off Peru during various El Niño years.

El Niño year	No. of „odd" fish spp.	Strength of EN
1972-73	39	S
1976-77	24	W
1982-83	58	VS
1986-87	22	W
1991-93	50	M (long)
1997-98	107	VS

Total no. of immigrant fish species registered so far off Peru: 157, thereof about two-thirds demersal and shallow water, rest oceanic or fully pelagic (Kameya et al. 2001). During EN 1982-83, Vélez et al. (1984) and Kong et al. (1985) registered 53 and 49 „odd" fish species off Peru and northern Chile, respectively. 24 of them were overlapping.

upwelling system, together with various species of swimming crabs and molluscs (Arntz, 1986; Arntz et al., 1988; Kameya et al., 2002). Interestingly, some of the shelled tropical invaders also appear in ancient kitchen middens in northern Chile and Peru, suggesting that these poleward range extensions are a common process in strong EN (Guzmán et al., 2001).

The immigrants from further north also included many demersal fish such as the gurnard *Prionotus stephanophrys*, which are normally restricted to tropical warm water (Table 4; for species cf. the refs. cited). Sharks and rays increased in importance and caused damage to drift and trammel nets (Arntz, 1986). Hake (*Merluccius gayi*), off Peru usually living north of Chimbote due to low oxygen further south, extended its area southward and beyond the slope margin, and switched to a demersal life style, because of the improved O_2 and food conditions at the seafloor (Espino et al., 1985, 2001; Wosnitza-Mendo and Espino, 1986; Espino, 1999).

On the other hand many cold-adapted benthic upwelling species, especially macroalgae, mussels, clams, snails, crabs and echinoderms in the upper part of the intermediate zone, suffered mass mortalities, although some managed to retreat in time to deeper, cooler water. Conversely, a few warm-tolerant local species such as the scallop *Argopecten purpuratus*, the purple snail *Thais chocolata* and the octopus *Octopus mimus* took advantage of the changed environment, reduced competition, perhaps improved food, and proliferated (Wolff, 1984, 1985; Arntz et al., 1988; Mendo and Wolff, 2002, 2003; Fig. 4; cf. Table 3). After EN 1982–1983, annual scallop landings in the ports of Pisco (Peru) jumped from normal <500 t to 50 000 t due to increased larval survival, improved recruitment, reduced mortality from predation and much faster growth. This species also extended its depth range from normally >20 m to 5 m in shallow water

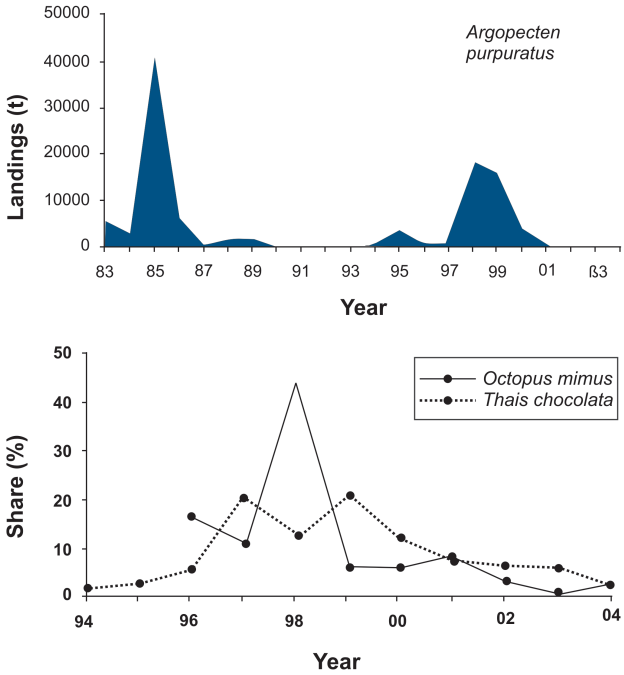

Fig. 4. Landings of the scallop *Argopecten purpuratus* 1983–2001 (above) and share of octopus *O. mimus* and the muricid snail *Thais chocolata* in the landings at Laguna Grande (Pisco, Peru) revealing the positive effect of El Niño on these species. Source of data: MIPE/IMARPE (Peru).

Table 5. "Unusual occurrences" of demersal and coastal fish off the Oregon coast during EN 1982–1984 and 1997001998 (Pearcy and Schoener, 1987; Pearcy, 2002).

Year	Scientific name	Common name
1983	*Symphurus atricauda*	California tonguefish
	Balistes polylepis	Finescale triggerfish
	Chilara taylori	?
	Remora remora	Common remora
	Synodus lucioceps	California lizardfish
	Echinorhinus cookei	Prickly shark
	Pristigenys serrula	Popeye catalufa
	Melichthys niger	Triggerfish
1997-98	*Seriola lalandi*	Yellowtail
	Sebastes rosaceus	Rosy rockfish
	Prionotus stephanophrys	Lumptail searobin
	Pseudopriacanthus serrula	Popeye catalufa
	Sphyraena argentea	California barracuda

Note: Other pelagic/oceanic spp. mentioned but not considered here

(Wolff, 1984, 1987, 1988). Another range extension into shallow water was noted off Callao in 1998 (Arguelles and Castillo, 2001). On the other hand, in northern Peru (Sechura Bay), where this scallop has become increasingly important, the effect of a strong EN differs markedly from that in the central and southern parts. In this tropical area EN-induced warming may exceed the temperature tolerance limits of *A. purpuratus*, and other changes such as a salinity decrease in the bay due to increased rainfall and river runoff may negatively impact the benthic communities. It thus seems that cold (La Niña) periods rather favour the scallops in this area, as reported also by IMARPE and scallop divers, who have increasingly operated in this northern zone during the past years of comparatively cool conditions. Both in central and northern Peru, however, overfishing is likely to reduce the stocks once they start proliferating, as was shown after EN 1982–1983 and 1997–1998, when this species was fished down in the Pisco area before it reached full market size.

Many more effects have been registered during strong EN, mainly off Peru and northern Chile. Compared with these effects in the HC, those in the CC appear rather moderate; attenuation seems to be the rule as in the strength of the interannual anomalies (Fiedler, 2002). The EN effects described above on giant kelp *Macrocystis* spp. and associated macroalgae also refer to the upper part of the intermediate zone in the CC. EN impact was found to be declining with depth from 12 to 18 m (Dayton et al., 1992). Strong EN, by destruction of kelp beds, introduce large amounts of kelp carbon into the coastal food web. Regrowth may last months to several years (Schimmelmann and Tegner, 1991).

Red sea urchin (*Strongylocentrotus franciscanus*) catches off Baja Califonia strongly decreased during the 1997–1998 EN (INP, 2000). Conversely, spiny lobsters (*P. interruptus*) produced large amounts of larvae and juvenile settlers (Guzmán-Próo et al., 2000) which resulted, however, in small reproductive females due to the accelerated development of the juveniles (Vega-Velázquez, 1999). Off the west coast of Baja California, unusually high catches of the shrimp *Farfantepenaeus californiensis*, which normally lives closer to the equator, during EN 1997–1998 brought some relief for those fishermen who were suffering from the disappearance of their normal invertebrate targets (Lluch-Cota et al., 1999). Ten decapod species showed northern range extensions into the Southern California Bight during and after EN 1991–1992 and 1997–1998 (Montagne and Cadien, 2001).

Poleward (northern) range extensions of (sub)tropical fish and invertebrates (Tables 5–7) in the CC are well documented. They included, for example, 2 species of triggerfish in 1983 (Pearcy and Schoener, 1987), gurnard *P. stephanophrys* (as in the southern hemisphere), hake *Merluccius productus* and some other coastal and demersal fish in 1998 (Pearcy, 2002; Swartzman and Hickey, 2003). Mearns (1988), in a review summarizing published records before EN 1982–1983 back to 1915, cites numerous "unusual occurrences" of fish and invertebrates north of their normal ranges (cf. Tables 6 and 7). In this analysis, tropical or warm temperate species migrating poleward are the largest group, with successive replacements on the latitudinal gradient. Equatorward migration of cold-water species, mostly in LN years, is also listed. The author cautions, however, that unusual occurrences are not restricted to major EN or LN events, but may sometimes also be consequences of more local environmental changes. Another long list of Panamic fish species occurring unusually far north during and after the 1997–1998 EN provided by Lea and Rosenblatt (2000) also contains demersal fish, and the Californian Dept. of Fish and Game (1999) mentions that in 1998 recreational fisheries were favoured by greater availability of fish normally found off Mexico. However, off Oregon fewer "unusual" species were noted during EN 1997–1998 than in 1982–1983 despite an "EN watch" (as in 1982–1983) by various organisations (Pearcy, 2002).

Another indication for EN effects are landings. Fishery landings from the Mexican Pacific decreased by 30% in 1998 (Lluch-Cota et al., 1999). In the same year, California fisheries landed 47% less fish and invertebrates from California waters than in 1997; market squid Loligo opalescens, red sea urchin, chinook salmon and numerous groundfish species declined, but spot prawn (*Pandalus platyceros*) and ridgeback

Table 6. Northward range extensions of tropical invertebrates off the western United States, 1914–1979 (Mearns 1988 based on numerous sources, mostly Californian Fish and Game).

Region	Scientific name	Common name
South of Mexican border – western U.S.	*Pleuroncodes planiceps*	Red crab, langostilla*
	Euphylax dovii	Swimming crab
	Panilurus gracilis	Pinto lobster
	Lophogorgia chilensis	White gorgonian
	Lyropecten subnudosus	Blunt-knobbed scallop
	Dosidicus gigas	Jumbo squid*
	Eucidaris thouarsii	Club-spined sea urchin
San Diegan region – Oregon	*Emerita analoga*	Mole crab*
	Loligo opalescens	Market squid
Additional northward range extensions during EN 1982-84 (Pearcy & Schoener 1987) and EN 1997-98 (Pearcy 2002)		
To Oregon	*Dosidicus gigas*	Jumbo squid (1997)
To Washington (1), British Columbia (2)	*Emerita analoga* (1,2)	Mole crab (1983)
	Loligo opalecens (1)	Market squid (1983)

* numerous individuals reported

prawn (*Sicyonia ingentis*), Dungeness crab (*C. magister*) and some demersal fish increased (Cal. Dpt. of Fish and Game, 1999). The increase of Dungeness crab landings is surprising as it is in contrast to the response of most crab populations to EN in the southern hemisphere, and also in contrast to findings and modelling results indicating that interannual recruitment variability of these crabs (as of red sea urchins and barnacles) depends on ENSO-related biological productivity and larval offshore transport, both of which are reduced during EN (Botsford et al., 1994; Botsford, 2001). Market squid decreased during both EN 1982–1983 and 1997–1998 and the razor clam Siliqua patula showed a decline in 1982–1983 (Pearcy and Schoener, 1987; Cal. Dpt. of Fish and Game, 1999). Northward incursions of the mole crab, *Emerita analoga*, by larval transport and northern range extensions of the red crab (langostilla) *Pleuroncodes planipes* seem to be consistent biological indicators of strong EN and have been registered since 1902/03 and 1941, respectively (Pearcy and Schoener, 1987).

To what extent occasional mass kills and strandings of *P. planipes* and jumbo squid *Dosidicus gigas* off California, with similar mass kills of these squid reported off Northern Chile (Tomicic, personal communication) may be related to diminished O_2 concentrations during EN is unclear. The most recent CC case of inner shelf (<70 m) hypoxia in July 2002 (Grantham et al., 2004), with massive die-offs of fish and invertebrates, was not related to EN. It was due to anomalous low O_2 levels (<2 ml l^{-1}) as a response to strong flow of Subarctic water off Oregon. This event caused high rockfish (*Sebastes* spp.) mortalities and widespread Dungeness crab mortality in the pots, as well as aggregation of deeper-water fish seeking refuge from O_2 depletion in shallow (<25 m) waters (Grantham et al., 2004).

Few effects in the BC can be clearly attributed to a Benguela Niño. In 1995 a Benguela Niño followed wide-scale advection of low-oxygen water into the northern BC from the Angola Dome. In March 1995, anomalously warm water, up to 8°C warmer in places, covered the entire shelf from Cabinda to central Namibia to >300 km offshore, causing mortalities, e.g. in silver kob, recruitment failures and declining catches (Gammelsröd et al., 1998). High levels of sediment loading in the river mouths (induced by rainfall during the Benguela Niño?) caused mortality in kob (Boyer and Hampton, 2001). On the other hand mass kills of rock lobsters, other benthos and demersal fish seem to be due rather to sulphidic outbreaks as mentioned above (cf. Table 2) for the nearshore zone, or to toxic algal blooms (Pitcher, 1998). Mass mortalities caused by sulphidic outbreaks have been described mainly for rock lobsters (*J. lalandii*), but holothurians, octopi, clams, mussels, limpets and other invertebrates, rock and reef fishes, and dogfish are also affected. Mortality is accompanied by "walkouts" of some inshore taxa, while others are washed up dead. Hake, in turn migrate offshore (Bailey et al., 1985; Bailey, MS 1999; Currie et al., 2006). Sulphide eruption episodes have been described since the 19th century (Currie, MS 1999) and include some spectacular rock lobster mass kills of thousands of tons, which combined with overfishing have decreased the stock dramatically (Grobler and Noli-Peard, 1997).

4 Oxygen minimum zone (OMZ)

The oxygen minimum zone, by definition, is the area with <0.5 ml O_2 l^{-1} (hypoxia); within the OMZ "severe hypoxia" areas have <0.2 ml (Levin, 2003; Helly and Levin, 2004). In fact, on a global scale, these are values which in other oceans

Table 7. Nortward range extensions of tropical inshore fish off the western United States. 1914–1979 (Mearns 1988 based on numerous sources, mostly CFG).

Region	Scientific name	Common name
Mexico into San Diegan region		
	Pronotogrammus gordensis	Threadfin bass
	Albula vulpes	Bonefish
	Ostracion diaphanum	Spiny boxfish (trunkfish)*
	Oligopus diagrammus	Purple brotula
	Chilomycterus affinis	Pacific burrfish
	Apogon atricaudus	Guadalupe cardinalfish
	Pseudopriacanthus serrula	Popeye catalufa
	Bagre panamensis	Chihuil
	Mulloidichthys dentatus	Mexican goatfish
	Pseudupeneus grandisquamis	Bigscale goatfish
	Mycteroperca xenarcha	Broomtail grouper
	Mycteroperca jordani	Gulf grouper
	Elops affinis	Machete
	Strongylura exilis	California needlefish*
	Calamus brachysomus	Pacific porgy
	Sphoeroides lobatus	Longnose puffer
	Doydixodon laevifrons	Rudderfish
	Citharichthys fragilis	Gulf sanddab*
	Scorpaenodes xyris	Rainbow scorpionfish
	Bellator xenisma	Splitnose searobin
	Dormitator latifrons	Pacific sleeper
	Ophichthus triserialis	Pacific snake eel
	Ophichthus zophochir	Yellow snake eel
	Lutjanus argentiventris	Amarillo snapper
	Lutjanus colorado	Colorado snapper
	Chaetodipterus zonatus	Pacific spadefish
	Kathetostoma averruncus	Smooth stargazer
	Balistes polylepis	Finescale triggerfish*
	Hermosilla azurea	Zebraperch*
San Diegan region into Oregonian region		
	Torpedo california	Pacific electric ray
	Sphyraena argentea	California *barracuda*
	Paralabrax clathrus	Kelp bass
	Synodus lucioceps	California lizardfish
	Peprinus simillimus	Pacific pompano*
	Atractoscion nobilis	White seabass*
	Amphistichus koelzi	Calico surfperch
	Symphurus atricauda	California tonguefish*
	Seriola lalandi	Yellowtail

*Numerous individuals reported

would cause mortality or emigration of the entire fauna (Diaz and Rosenberg, 1995). However, the benthic systems of EBC upwelling areas, while preserving specific modes and strategies of ancient non-aerobic life, have developed surprising adaptations also in their meio- and macrofaunal, protozoan and metazoan aerobic components, which enable these organisms to thrive at the limits. On the other hand, compared with most well-flushed regions, OMZ are low-diversity regions and inhospitable to most exploited resources (Helly and Levin, 2004).

In the E Pacific, intensity, spatial extension and thickness of the OMZ varies considerably. Restricting this review to EBC, the upper limit can be much shallower than 50 m off Peru whereas it is always deeper than 200 m, often >600 m off California and Oregon. In Peru hypoxic bottoms ($<0.5\,\mathrm{ml\,O_2\,l^{-1}}$) are found generally south of 6° S but below 200 m depth also north of 6° S. Southward the OMZ of the HC reaches to about 35° S but is no longer existent off Chiloé (about 40° S). Northward the OMZ of the CC extends beyond the Oregon northern border to Alaska. Only in the CC there is a poleward trend of OMZ upper limit depression. The lower margin is at 600–700 m off Chile and Peru and about 1100 m off North America. Affected areas under the CC are only half as large as those under the HC and BC, but there are large hypoxic areas off Mexico south of the CC. While hypoxia off South America is mostly very severe ($<0.2\,\mathrm{ml\,l^{-1}}$), most areas off North America are above the 0.2 ml limit (Helly and Levin, 2004).

The OMZ off Namibia and South Africa lies principally between ca. 100 m and 400 m depth but, as off Peru, may be much shallower in sheltered bays. Only areas south of 20° S are normally affected by severe hypoxia in this EBC (Helly and Levin, 2004). Persistent hypoxia in this ecosystem is usually restricted to within the 100 m isobath over

innershelf areas in the central region but low dissolved O_2 values $<3\,ml\,l^{-1}$ are common (Hamukuaya et al., 2001).

The most important organisms in the HC and BC OMZ under normal and LN conditions are prokaryotes, i.e. benthic sulphur bacteria (Gallardo, 1963, 1977; Schulz et al., 1996). In the HC the wet weight of *Thioploca* spp. can approach 1 kg (sheaths + trichomes) per m^2 (Gallardo, 1977; Arntz et al., 1991; Schulz et al., 1996). In all three upwelling systems sulphur bacteria have an important function in anaerobic respiration, which largely replaces aerobic respiration under the prevailing low oxygen conditions. However, *Thioploca* spp. seem to be dominant only in the HC, and only there mats with such exceptional biomasses have so far been found, although H_2S oxidizing bacteria cover the sediment surface also in the BC (Brüchert et al., 2006). O_2 concentrations $<0.3\,ml\,l^{-1}$ in the CC system occur mainly in the nearshore basins, such as the Santa Barbara and Santa Monica basins. Here large mats of sulphur bacteria (*Beggiatoa* spp.) cover the seafloor (Bernhard et al., 2000).

A suit of apparently new, large unsheathed filamentous bacterial morphs has recently been discovered in organically enriched post-EN 1997–1998 sediments off central Chile. Some of these bacteria appear to be associated with the most reduced conditions and bear sulphur granules, whereas others may roam widely within the first few millimetres. Spherical, pyriform, filiform and spirochaetal forms are common in this seemingly diverse community. Their presence has been confirmed also in sediments off northern Chile and Peru (Anonymous, 2005).

The continental margins beneath the OMZs are the sites of major carbon burial. In the Corg-rich sediments, H_2S is produced by bacterial sulphate reduction, which is the most important process for the oxidation of organic matter in coastal sediments (Ferdelman et al., 1997). The water above the sediments contains high amounts of nitrate (Fossing et al., 1995). Denitrification (reduction of nitrate NH_3^- in various steps to N_2) normally takes place at the benthic boundary layer where the bacteria in the OMZ (*Beggiatoa, Thioploca, Thiomargarita*) are sulphide-oxidizing denitrifiers (Otte et al., 1999; Schulz et al., 1999a) (Fig. 5). Sometimes H_2S production in the sediment is high but no H_2S can be detected in the pore water, because despite complete absence of O_2, H_2S is rapidly reoxidized in the sediment due to the reduction of NO_3^- by the *Thioploca* mat, or S is bound to iron forming iron sulphide. The sulphur bacteria thus have the ability to detoxify the surface sediment by taking up most of the toxic H_2S, a process observed both in the HC and BC (Fossing et al., 1995; Brüchert et al., 2006). This may facilitate life for those aerobic organisms that coinhabit this zone under conditions of severe hypoxia. Recently, Neira et al. (2001a) reported a positive correlation between *Thioploca* and total metazoan meiofaunal biomass off central Chile during non-EN conditions (May 1997) whereas no correlation was found at the end of EN (May 1998). It was suggested that during non-EN conditions, *Thioploca* might have a positive influence on the meiofauna (Neira et al., 2001 a). This observation supports the detoxifying role played by *Thioploca*. In the remote past, this process may have been important for the transition from anaerobic to first aerobic life (Gallardo et al., 1996).

Thioploca spp., which have been studied in detail, are dominant at oxygen concentrations between 0.2 and $0.3\,ml\,l^{-1}$ (Gutiérrez et al., 2000). In experimental flumes, they were able to shuttle between the nitrate-rich boundary layer and the sulphidic sediment (Fossing et al., 1995; Huettel et al., 1996). Their positive reaction to nitrogen overrules the negative response to oxygen; addition of nitrate induces the ascent of the trichomes in the sheaths whereas higher O_2 concentrations cause a descent. Thus *Thioploca* outcompetes other sulphur bacteria by taking advantage of the available H_2S and NO_3^- even when these are spatially separate (Fig. 5). *Thioploca* in the HC can store nitrate in the cell vacuole at concentrations of up to 500 mM, i.e., about 20 000 times higher concentrations than in seawater (Fossing et al., 1995). Similarly, in the BC *Thiomargarita namibiensis*, a related species, is vacuolated and also stores nitrate in high concentration, up to 300 mM (Schulz et al., 1999a). The Namibian *Thioploca* species collected so far (Gallardo et al., 1998) appeared similar to *T. chileae* and thus would also be a vacuolated, nitrate-storing species.

While the prokaryotic component seems to be particularly important under the conditions of the HC, specially adapted proto- and metazoan eukaryotes are also found elsewhere (Gallardo et al., 1994; Levin et al., 2002; Levin, 2003). Small organisms prevail, but the species inventory of OMZ comprises the whole range between micro- and megafauna. Macrofaunal adaptations include small, thin bodies, enhanced respiratory surface area, blood pigments, an increased number of specific enzymes, sulphide-oxydizing symbionts and biogenic structures to facilitate life in flocculent sediments (González and Quiñones, 2000; Levin, 2003). Calcareous forams, nematodes and some annelids tolerate severe hypoxia whereas agglutinated protozoans, harpacticoid copepods and calcified invertebrates (molluscs, echinoderms, but also cnidarians and crustaceans) are usually less tolerant. Disappearance of harpacticoids under severe hypoxia (Levin et al., 2001, 2002; Neira et al., 2001a, b) results in an even stronger dominance of nematodes in the meiofauna. Nematode numerical dominance can be >95% (Neira et al., 2001a, b; Levin et al., 2002; Sellanes et al., 2003). Nematode densities and biomasses are usually elevated in OMZ, which reflects adaptation to extreme low oxygen concentrations and high concentrations of sulphide, abundant food supply and indirectly, a release from predation and competition, but diversity is low (Neira et al., 2001b; Levin et al., 2001, 2002; Levin, 2003; Neira et al., 2005). Recent findings of exceptionally large nematodes of the family Epsilonematidae in bathyal sediments of the OMZ cores off Callao, Peru and Baja California, Mexico have revealed body structures which may represent specific adaptations to cope with almost anoxic, sulphidic, soupy sediments (Neira et al., 2001c, 2005).

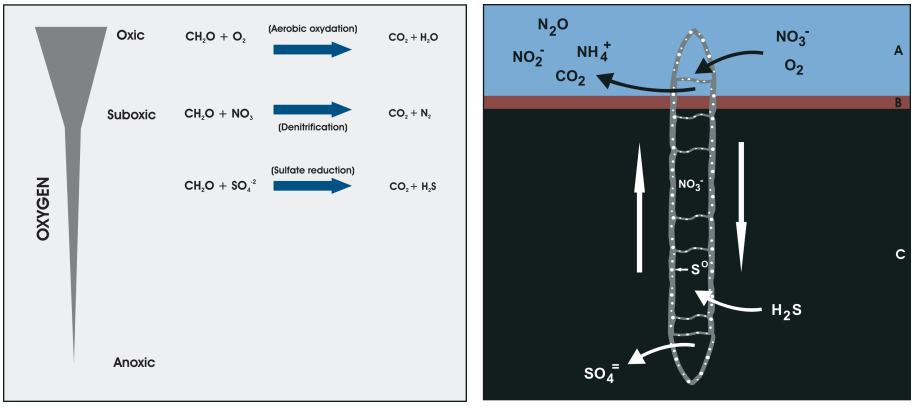

Fig. 5. Diagramme showing the function of the giant sulphur bacterium *Thioploca* spp. at the water column – sediment interface. A – hypoxic bottom water, B – oxydized interface, C – reduced sediment, rich in H_2S. The *Thioploca* trichome in the centre migrates between these horizons, taking advantage of the H_2S and NO_3^- even though they are spatially separate, and reoxydizing H_2S in the sediment via the reduction of NO_3^-. Nitrate is stored in the cell vacuole, and elementary sulphur granules are stored in the cell walls (see text). On the left, no chemical equations are presented but rather end products of the ongoing processes. (Source: Gallardo unpublished, developed from an older concept by Fossing et al. (1985) and Otte et al. (1999)).

Diversity of macrofauna off Peru is higher north of 6° N, where upwelling conditions change to warm tropical conditions. Within the OMZ, highest densities were registered between only 0.3 and 0.5 ml O_2, whereas biomass and species number of small macrofauna were found to be much higher outside the OMZ, between 1.2 and 1.5 ml. Above 1.5 ml O_2 the dominance of small macrofauna was ceasing, and at >2.5 ml the macrofaunal attributes were independent of the O_2 concentration (Gutiérrez et al., 2000). Macrofaunal biomasses in the OMZ, despite being low are clearly higher than those of meiofauna, but meiofaunal productivity (P/B) is 4.5 times higher (Sellanes et al., 2003). Macro- and megafauna exhibit low densities, reduced species richness and marked dominance of few species (and thus, low diversity) in the OMZ core; however, foraminiferans and larger metazoans such as polychaetes, crustaceans, molluscs and echinoderms may be quite abundant at OMZ boundaries (Levin, 2003). Small organisms are best able to cover their metabolic demands in the OMZ, and besides adaptation to low oxygen often have a capability to conduct anaerobic metabolism. *P. pinnata* is an aerobic oxygen conformer and has been shown to have high anaerobic activity of alanopine and strombine dehydrogenase (González and Quiñones, 2000). Based on observed respiration rates and measured population densities in situ, this species has been calculated to use about 8.6% of the total carbon flux to the seabed and contribute between 18 and 44% of the community oxygen consumption in the OMZ off Chile (Quiroga et al., in press). As off Peru (Tarazona et al., 1988a, b; 1991), polychaetes (71%) were found to dominate the macrofauna off Chile, with Cossuridae as the dominant family. Crustaceans contributed 16% whereas molluscs had only 2% share (Gallardo et al., 2004). During the PUCK RV "Sonne" expedition of 129 mostly inconspicuous macrozoobenthic taxa on two transects across the OMZ, 84 were annelids (Hebbeln and Wefer, 2003). In this study, the species *Cossura chilensis*, *Paraprionospio pinnata*, *Cirratulus cirratus*, *Magelona phyllisae* and an oligochaete dominated the OMZ annelid fauna on the shelf, constituting 80% of the macroinfauna (Palma et al., 2005), whereas the slope macrofauna was dominated by *Aphelochaeta monolaris*, *Aricidea strelzovi*, *Maldane sarsi* and *Paramphinome australis*. Also off Chile, the polychaete *Paraprionospio pinnata* and the "squat lobster" *Pleuroncodes monodon* were found under almost complete anoxia and very high production of H_2S (Gallardo, unpublished; Huettel et al., 1996), revealing that the *Thioploca* mats by taking up most of the H_2S had in fact produced a detoxification of the sediment surface and bottom water (see above). At very low O_2 concentrations <0.15 ml l^{-1} macro- and meiofaunal bioturbation is reduced (Gutiérrez et al., 2000; Levin, 2003), however oligochaetes (and other annelids) may bear bacterial symbionts (Giere and Krieger, 2001; Levin et al., 2003), which enable them to live in the sediment at almost anoxic conditions, at O_2 values much lower than those assumed to exclude bioturbation in fossil assemblages (Levin et al., 2003).

Under EN conditions, higher oxygen values in the bottom water transported by the Humboldt Undercurrent and lower fluxes of POM from the mixed layer create less reducing conditions, and the upper limit of the OMZ deepens off Peru and Chile by >100 m, improving oxygen concentrations in extreme cases (EN 1982–1983) to 300 m depth (Guillén et al., 1985; Arntz et al., 1991). During EN 1997–1998 this improvement seems to have been shallower, reaching hardly beyond 200 m (Sánchez et al., 1999; Levin et al., 2002). Helly and Levin (2004) calculated that this caused a 69% reduction in seafloor affected by the OMZ off Peru. In 1982–1983 dissolved oxygen just above the seafloor in Ancón Bay doubled to average values of 2.2 ml and 1.5 ml l^{-1}, with peak values surpassing 3.5 ml at 15 and 34 m depth, respectively. At

greater depths between 40 and 240 m, oxygen concentrations along the Peruvian coast showed an even greater increase, especially in the north to 10° S (Arntz et al., 1991).

In addition, the collapse of the pelagic food web due to the lack of nutrients in the mixed surface layer leads to reduced POM input to the seafloor (Muñoz et al., 2004; González et al., 2000). Off Concepción, reduced TOC, shifts in the sediment biochemical components, and a decrease in the "freshness" and quality of organic matter (sum of carbon, protein, carbohydrates, and lipids) were observed during EN 1997–1998 (Gutiérrez et al., 2000; Neira et al., 2001a; Sellanes and Neira, personal communication), together with increased dissolved oxygen in the bottom water (Gutiérrez et al., 2000). Conversely Levin et al. (2002), sampling at 305 m off Callao/Peru in January 1998, found at this depth only slight O_2 improvement, which they attributed to reduced production in the photic layer.

Both the oxygenation and the reduced organic input induce important changes in community structure at the seafloor in the HC OMZ, interrupting the "normal" prokaryotic dominance and changing the community from a predominantly prokaryotic reducing into a predominantly eukaryotic oxidative metabolic state (Gallardo, unpublished data).

During EN 1997–1998, the composition and size spectrum of phytoplankton and microzooplankton, reflecting to some extent the input from the water column, changed off northern Chile (González et al., 2000). Off central Chile, biogeochemical processes in the sediment-water interface of the continental shelf were also altered significantly during this period. Whereas during normal years ammonium production is higherduring the upwelling-favourable, oxygen-depleted spring and summer period, carbon fluxes to the sediment decreased to low normal autumn/winter levels during the entire 1997–1998 EN (Gutiérrez, 2000; Grunewald et al., 2002; Graco et al., 2005). Ammonium production and NH_4^+ fluxes during this period were lower than normal (Muñoz et al., 2004), indicating a tight pelagobenthic coupling during EN (Graco et al., 2005). *Thioploca* biomass was very low, and the filaments were withdrawn deeper into the sediment as a response to increased temperatures, oxygenation, reduced nitrate and lack of H_2S (Schulz et al., 1999b). The possibility that *Thioploca* might migrate in search of better conditions cannot be excluded; in fact their presence in widely separate regions would suggest they have a capacity of dispersal by currents. Significant reduction of *Thioploca* and *Beggiatoa* biomass has been observed during EN events in shallow water (15–34 m) of the Bay of Ancón, Peru (Tarazona and Arntz, 1986; Tarazona unpubl. data) and in continental shelf sediments off Callao (Gutiérrez et al., 2005). Unfortunately, all recent research directed specifically to sulphur bacterial behaviour was carried out before the strong EN 1997–1998, so we are lacking direct information on their performance during the process of oxygenation. However, inferences are possible from chemotactic responses in flumes (Huettel et al., 1996). Another open question is to what extent the deep OMZ off North America is influenced by the important changes recorded in the pelagic realm (Chávez, 2003; see also Progr. Ocean. 54), with consequences for the fluxes of nutrients and organic matter to the seafloor. Due to its recent recovery no information is available, either, on the variability of *Thiomargarita* populations in the BC during normal times, Benguela Niños and periods of sulphidic outbreaks. It would also be interesting to see whether *Thiomargarita* shows up in other coastal upwelling regions, as it has been reported from cold seeps in the Gulf of Mexico (Kalanetra et al., 2004).

Studies on the response of OMZ meiofauna to El Niño conditions are even more limited. Sampling during the 1997–1998 EN was carried out off central Chile along a transect of five sites, between the Bay of Concepcion (27 m) and the adjacent shelf (120 m) (Neira et al., 2001a; Sellanes and Neira, personal communication). Chloroplastic pigment equivalents (CPE) decreased towards the end of EN, sedimentary organic matter composition changed and the quality of the potential food for benthic consumers decreased. Labile organic matter in the top 1 cm decreased by 30% (Sellanes and Neira, personal communication) and by about 10% in the uppermost 15 cm (Neira et al., 2001a). Lipids declined by 40% at the end of EN. Along with these organic matter changes dissolved oxygen increased in the bottom water, and both altered the meiofaunal community structure. Meiofauna changed most drastically at those sites where during non-EN years oxygen-deficient conditions had prevailed. Total meiofaunal abundance and biomass increased towards the end of EN, copepods + nauplii increased in abundance at most sites, and nematodes penetrated deeper in the sediment. These studies revealed that during non-EN conditions, oxygen availability is the master factor off central Chile whereas during EN the influence of food quality increases in importance.

In another study off Callao (Peru) carried out in January 1998, when temperature anomalies were at their maximum, nematodes amounted to over 99% of total abundance in the core of the OMZ (305 m). About 70% of them were found subsuperficially (2–5 cm). Symbiont-bearing oligochaetes were found bioturbating the upper 5 cm of the sediment off Callao under the "slightly improved" conditions during EN 1997–1998 (Levin et al., 2002, 2003), however, still under extremely low O_2 concentrations (0.02 ml l^{-1}). Conversely, at deeper sites most nematods were restricted to the top 1 cm, and copepods + nauplii increased consistently. The success of nematodes in the OMZ was referred to reduction of predators and competitors in this zone and of high-quality food availability. Nematode abundance was strongly, positively correlated with food quality (represented by CPE and sedimentary protein, carbohydrates and lipids), and negatively correlated with oxygen. The authors suggested that improved sediment organic matter quality and shallow meiofaunal vertical distribution should prevail during non-EN conditions, whereas under conditions of increased oxygenation (i.e., EN), densities of predators and competitors should increase and nematode densities should decline (Neira et al., 2001b). In other cases where meiofauna was studied, O_2 was not measured (Sellanes et al., 2003).

An increased bioturbation potential was observed also in benthic macrofauna off central Chile during EN 1997–1998 due to subsurface deposit feeders (*Cossura chilensis*), which partly replaced the surface deposit feeders (*Paraprionospio pinnata, Ampelisca araucana*) dominant during LN and normal years (Gutiérrez et al., 2000). Bioturbators, taking advantage of the increased oxygenation and the concomitant reduction of H_2S, did not only penetrate deeper into the sediment but also contributed a greater share to the community.

A long-term time series on benthic macrofauna in shallow water (15 and 34 m) in the sheltered Bay of Ancón (Peru), which was started in 1981, reveals a very consistent positive response to the flushing and warming during the four EN that occurred during this period (Fig. 6). Contrary to the increase in temperature, oxygenation during EN is not a constant pattern but consists of different pulses, which maintain, however, the average concentration during (and sometimes after) the event much above the normal mean. Although there were notable differences in the composition and, particularly, the dominance of the small macrobenthic/large meiobenthic fauna among events, the community parameters changed in a very consistent manner (Tarazona et al., 1988a, b; 1996). The density increase of the fauna, which similar to the oxygen pulses appears in successive waves depending on the season, reproductive state of the species, or timely meroplankton advection, was almost immediately followed by an increase in biomass of the predominantly small fauna (Tarazona et al., 1988a, b; 1991). Most of these small settlers are local species, which opportunistically take their chance for enhanced population development when oxygen conditions increase. A notable example is the polychaete Sigambra bassi, which – as in 1997–98 – can become a dominant species in one event but may not show any conspicuous development in another. Modelling revealed that apart from abiotic factors such as temperature and oxygen, biotic interactions are responsible for the variable success of this polychaete (Peña et al., 2005). Overall, however, dominance decreased during EN and afterwards, and diversity in this shallow-water hypoxic community increased due to continuous colonisation by "new" species. The share of oceanic or tropical species registered was small in this study dealing with the small faunal component, but the formerly hypoxic zone was also invaded by large macro- and megafauna as described above for the intermediate zone. As these "aliens" contained many voracious predators, e.g. swimming crabs which were joined by local predators such as hake and brachyuran crabs, as well as other demersal fish and megabenthic species heading for deeper water, increased predation may have been responsible for the fact that there was not a similar increase of benthic infauna on deeper bottoms of the flushed OMZ (Arntz et al., 1985, 1991).

Even in the Bay of Ancón which generally shows a very consistent pattern, there may be significant exceptions to the overall picture of an enrichment of the small macro- and large meiofauna under EN, and an impoverishment under LN and "normal" conditions. Oxygenation pulses, e.g. in the 1995–1996 period, were not translated into density increases, and

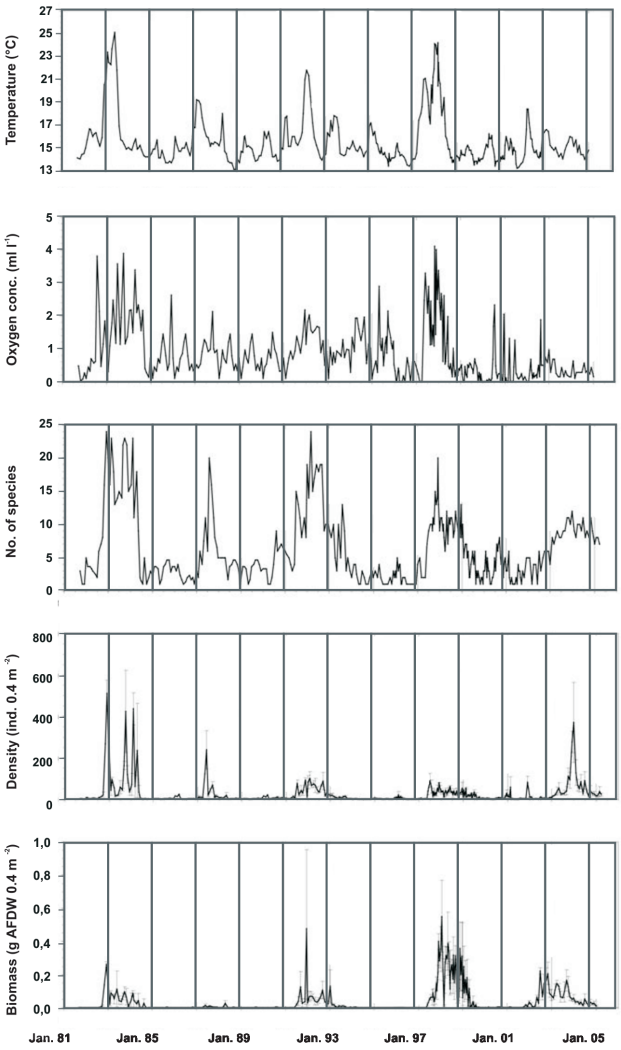

Fig. 6. Changes in temperature and dissolved oxygen, as well as in the number of species, density and biomass of a macrobenthic community (1981–2004) in central Peru (Bahía de Ancón, 34 m depth). Original data.

sometimes, as after 2003, high densities also developed under oxygen-poor conditions. Obviously, local processes in coastal areas and embayments such as upwelling strength, phytoplankton blooms followed by sedimentation providing fresh food for the macrofauna, and sediment resuspension due to increased sea roughness or erosion are also important in modulating the responses of the benthic fauna to ENSO or ENSO-like oxygenation events (Gutiérrez et al., 2005).

During the 1982–1983 event, the traditional target species among the demersal fish off Peru extended their distribution poleward into formerly hypoxic areas, offshore and even downslope. Semipelagic hake (Merluccius gayi) became demersal and fed on benthos (Espino et al., 1985), coastal lorna (*Sciaena deliciosa*) migrated offshore and fed on anchovies that had taken refuge at greater depths (Arntz and Tarazona, 1989 who also describe further trophic changes). However, due to the fact that the fish concentrations dispersed, direct

EN effects on demersal fisheries were detrimental despite oxygenation of the upper part of the OMZ. On the other hand, flushing of wide areas and improved feeding conditions favour recruitment in the medium term, so on longer time scales the effects of EN seem to be rather beneficial for these species as in the case of hake after the 1972–1973 event (Wosnitza-Mendo and Espino, 1986).

Immigrations of tropical and subtropical demersal and coastal fish such as the gurnard, *Prionotus stephanophrys*, selachians and lutjanids as described above for the intermediate zone also concerned the flushed upper OMZ, and during very strong EN as in 1982–1983 the whole demersal community shifted poleward (Herdson, 1984; Arntz and Fahrbach, 1991; Arntz and Tarazona, 1989; Kameya et al., 2001).

5 Zone below the OMZ

As indicated above, the lower margin of the OMZ in the three EBC varies considerably. The zone below the OMZ therefore comprises upper slope portions (off Chile, Namibia and South Africa) to lower slope and deep-sea areas (Peru, North America). Rowe's (1981) notion that benthic biomass usually is a function of surface productivity and tends to decrease with distance from shore and depth is somewhat upset in EBC areas, where medium water depths under the equatorward current core receive a surplus of organic matter resulting in extensive OMZ with a low biomass, e.g. $0.9\,\mathrm{g\,C\,m^{-2}}$ for both macroinfauna and sulphur bacteria, respectively (Rosenberg et al., 1983). With the distinct increase of O_2 concentrations below the OMZ, densities are often lower (Levin et al., 2002 but see Gallardo et al., 2004), particularly in the deep sea (Borowski and Thiel, 1998), but biomass increases (Levin et al., 2002; Gallardo et al., 2004). Rowe et al. (1994) found a "depocenter" due to the input of organic detritus on mid slopes around 1000 m. While most of these findings are derived from grabs and small corers, which emphasize the importance of polychaetes (especially Paraonidae, Maldanidae), isopods and tanaids, dredging and trawling below the OMZ of the HC also revealed an increase of macro- and megafauna (Romanova, 1972; Hebbeln and Wefer, 2003; Palma et al., 2005). Some megafaunal elements under the OMZ in Chile, in particular large decapods and echinoderms, strongly resembled a Subantarctic element during the PUCK expedition (own obs.), revealing the dominance of Subantarctic water (SAAW) under non-EN conditions. Large echinoids and decapods also dominate the lower slope off California (Thompson et al., 1993) most of which is, however, situated above the OMZ in this area.

Bathyal sites below the OMZ off central Chile studied in March 1999 were more diverse in higher meiofaunal taxa than a site located on the outer shelf (120 m) usually influenced by the OMZ. The vertical distribution pattern observed in the deep oxygenated sites (to 827 m) resembled that of the core of the OMZ off Callao (Peru) rather than Peruvian sites below the OMZ (Neira, unpublished data).

Methane (cold) seeps create particular conditions in this zone (and sometimes the OMZ) all along the American coasts (Levin, 2005). They occur from relatively shallow water <50 m until >5000 m depth. Many of them are spatially limited, with few chemoautotrophic symbioses (Levin, 2000, Levin and Michener, 2002) while others are dominated by various clam species with chemosynthetic endosymbionts (Stuardo and Valdovinos, 1988; Sellanes et al., 2004; Sellanes and Krylova, 2005). Cold-seep communities between 2630 and 5140 m depth off Peru have high biomasses and are quite diverse (Olu et al., 1996). The seep infaunal communities experience low O_2 and high H_2S concentrations and thus often resemble OMZ assemblages in composition (Levin, 2005).

We have no indications that the zone below the OMZ is affected by EN or similar impacts in any of the three EBC reviewed in this study, although only Hamukuaya et al. (2001) explicitly mention that the BC slope communities were not disrupted by the 1995 Benguela Niño. Boyer and Hampton (2001) suspect effects on monkfish (*Lophius* spp.) and other deep-water resources such as orange roughy (*Hoplostethus atlanticus*) but do not present details. Potentially, the reduction of pelagic production during EN could also have an effect on food availability at the deep-sea floor. Given the clear influence of surface production and climate change on benthos >4000 m off central California (Ruhl and Smith, 2004), it is likely that the large areas of the margin below the OMZ should respond to ENSO-related changes in hydrography and productivity.

6 Outlook and conclusions

The information available from the three EBCs differs substantially. For the Pacific coastal systems the Niño 3.4, reflecting processes occurring on the equator, predicts the impact to be expected only to a certain extent. The potential relation between the Pacific and Benguela Niños remains vague (Currie et al., 2002), although major events may coincide to some extent (cf. Fig. 1), and despite the notion that SST anomalies in the Pacific EN area are at least partly responsible for wind signal (Delecluse et al., 1995) and SST (Curtis and Hastenrath, 1995) anomalies in the tropical Atlantic. ENSO often (not always) has an effect on the formation of a "warm pool" in the northwestern Atlantic whose maximum typically appears in the boreal summer following the EN peak (Wang and Enfield, 2001, 2003), and Caribbean rainfall in the late season is also favoured by cold conditions in the tropical Pacific (Taylor et al., 2002). EN events in the Pacific and SST anomalies in the west African coastal upwelling region between 10° and 26° N are positively correlated with a lag of several months (Roy and Reason, 2001), leading to warm (cold) ENSO events being associated with a relaxation (intensification) of the NW Atlantic trade winds and the wind-driven coastal upwelling, with possible consequences for fish landings. Conversely, Latif and Barnett (1995), while recognising that ENSO-induced signals are

enhanced in the ocean and atmosphere of the Atlantic region, state that SST anomalies in the tropical Pacific force anomalies of the opposite sign in the Atlantic. In any case, effects of Pacific processes interact with those of the North Atlantic Oscillation, which might influence the BC in a similar way as the Pacific Decadal Oscillation (PDO) does with the HC, but in view of missing proof this connection remains speculative. Another potential link are associations between tropical monsoons around Africa and ENSO influencing zonal winds and rainfall (Jury et al., 2002).

Obviously the EN impact is strongest and lasts longest in the HC ecosystem, because of a shallower OMZ, greater proximity to the equatorial zone, less retardation and attenuation of the physical changes, and due to the fact that the upper part of the OMZ off Peru and Chile receives distinct oxygenation during major events. The OMZ off California (Alta and Baja) and Oregon is situated at too great depths to reflect obvious changes (and to stimulate the kind of research done in the OMZ of the HC). We know frustratingly little about the sulphur bacteria, meio- and macrobenthos of the deep OMZ off North America; are the bacteria as dominant, and as efficient as in the other EBCs? In general it seems as though, contrary to South America and with the exception of kelp and the fisheries sector, few changes in the NE Pacific Ocean benthos have been related to interannual climate fluctuations. Only recently conciousness has developed including decadal oscillations, in particular the PDO, as an important factor influencing life in the sea, especially concerning zooplankton and pelagic shoaling fish (Schwartzlose et al., 1999; Peterson and Schwing, 2003; Alheit and Niquen, 2004). Perhaps the very strong 1997–1998 EN may have stimulated studies on ENSO impacts in bathyal waters off North America, which are likely to be a fruitful area of pursuit for fisheries, metazoan, protozoan and microbial research.

Another aspect that should receive more attention are the positive effects of EN. It is still customary to refer to EN as a mere catastrophe, a disaster that merits attention only for the fact that it disrupts normal conditions in the sea and on land, and causes immense damage. This is true only to a certain extent; over 20 years ago the senior author already emphasized the numerous positive facets of EN (Arntz, 1984), and in a recent paper Bakun and Broad (2003) even suggested that in the long run EN may be a prime reason for the remarkable fishery productivity of the HC ecosystem.

In the CC it is not at all clear to what extent the intrusion of equatorial low oxygen water during EN contributes, at least in some cases, to the occasional mass kills of fish and invertebrates. It is obvious, however, that these events are associated with oxygen deficiency, as in the BC where oxygen depletion and occurrence of H_2S is usually not a consequence of the Benguela EN but of sulphide eruptions (Weeks et al., 2002, 2004) or toxic algal blooms (Pitcher, 1998). A clear EN (and LN) relation does exist in the case of poleward (and equatorward) migration and range extension of fish and invertebrates both in the HC and CC, whereas in the BC migrations towards shallow and deep water as a response to low oxygen have been described but no large-scale latitudinal displacements seem to occur.

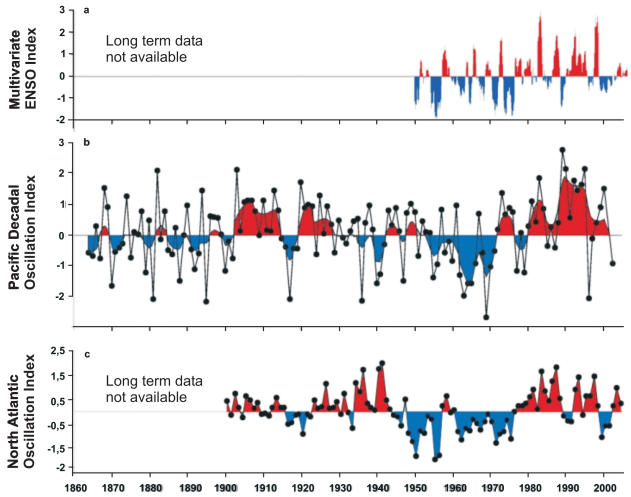

Fig. 7. Fluctuations in the Multivariate ENSO Index, the Pacific Decadal Oscillation Index, and the North Atlantic Oscillation Index showing a large degree of simultaneous warm and cold phases during the last two decadal regimes. Source: NOAA-CIRES Climate Diagnostics Center, Univ. of Colorado at Boulder (USA).

Answering the initial question as to the similarities and differences in the structure of the three EBC and in the impact of ENSO and similar perturbations, we conclude that there are important similarities mainly in the way that bacteria and aerobic benthos have adapted to oxygen deficiency and the defense against/use of H_2S and nitrate, and – at least between the HC and the CC – in the response to interannual variations of temperature. On the other hand, there are great differences regarding the positive/negative effect of the coastal Kelvin waves in the HC and CC although they come from the same source, whereas the Benguela Niño may be a different thing altogether. Finally it is likely that the effects of interannual variation in all EBCs are biased by those of decadal variation (Fig. 7) and global warming (Mc Phaden, 1999; Enfield, 2001), making a clear identification of ENSO effects increasingly difficult.

Acknowledgements. The authors would like to thank EGU and CIIFEN for an enjoyable symposium and the acceptance of this paper as a keynote, two referees for constructive criticism, and the editors for their patience. The Deutsche Forschungsgemeinschaft kindly provided a travel grant for the senior author. A. Bleyer and W. Mensing were very helpful in the preparation of the manuscript, tables and illustrations. SHOA (Chile) and IMARPE (Peru) contributed information on time series, and B. Currie, C. Bartholomae and J. Laudien helped with references and an illustration. To all of them go our sincere thanks.

Edited by: P. Fabian and J. L. Santos
Reviewed by: J. L. Santos and another anonymous referee

References

Alheit, J. and Niquen, M: Regime shifts in the Humboldt Current ecosystem, Progr. Oceanogr., 60, 201–222, 2004.

Anonymous: Filamentous bacteria off central/south Chile, COPAS Newsl., 7, 2–3, 2005.

Arguelles, J. and Castillo, G.: Talla, densidad y distribución de *Argopecten purpuratus* entre enero y septiembre de 1998 en la Bahía de San Lorenzo – Callao – Perú, in: El Niño en América Latina: impactos biológicos y sociales, edited by: Tarazona, J., Arntz, W. E., and Castillo de Maruenda, E., CONCYTEC, Lima, 163–167, 2001.

Arntz, W. E.: El Niño and Peru: positive aspects, Oceanus, 27, 36–39, 1984.

Arntz, W. E.: The two faces of El Niño 1982–83, Meeresforsch., 31, 1–46, 1986.

Arntz, W. E.: The role of El Niño, La Niña and climate change in the Pacific Eastern Boundary Currents: An integrated introductory view, in: Extended Abstracts of the Symposium "Impacts of El Niño and basin-scale climate change on ecosystems and living resources: A comparison between the California and the Humboldt current systems", edited by: Salinas, S., Urban, H.-J., and Arntz, W. E., Invest. Mar., 30, 81–82, 2002.

Arntz, W. E. and Tarazona, J.: Effects of El Niño 1982–83 on benthos, fish and fisheries off the South American Pacific coast, in: Global Ecological Consequences of the 1982–83 El Niño-Southern Oscillation, edited by: Glynn, P. W., Elsevier Oc. Ser., 52, 323–360, 1989.

Arntz, W. E. and Fahrbach, E.: El Niño – Klimaexperiment der Natur, Physikalische Ursachen und biologische Folgen, Birkhäuser, Basel, 1991, (Spanish edition 1996, Fondo de Cultura Económica, México D.F.).

Arntz, W. E., Landa, A., and Tarazona, J. (Eds.): "El Niño", Su Impacto en la Fauna Marina, Boletín IMARPE, vol extraord., 1985.

Arntz, W. E., Brey, T., Tarazona, J., and Robles, A.: Changes in the structure of a shallow sandy-beach community during an El Niño event, in: The Benguela and Comparable Ecosystems, edited by: Payne, A. I. L., Gulland, J. A., and Brink, K. H., S. Afr. J. Mar. Sci, 5, 645–658, 1987.

Arntz, W. E., Valdivia, J., and Zeballos, J.: Impact of El Niño 1982–83 on the commercially exploited invertebrates (mariscos) of the Peruvian shore, Meeresforsch., 32, 3–22, 1988.

Arntz, W. E., Tarazona, J., Gallardo, V. A., Flores, L. A., and Salzwedel, H: Benthos communities in oxygen deficient shelf and upper slope areas of the Peruvian and Chilean Pacific coast, and changes caused by El Niño, in: Modern and Ancient Continental Shelf Anoxia, edited by: Tyson, R. V. and Pearson, T. H., Geol. Soc. Special Publ. 58, 131–154, 1991.

Aurioles-Gamboa, D. and Pérez-Flores, R.: Seasonal and bathymetric changes in feeding habits of the benthic red crab *Pleuroncodes planipes* (Decapoda, Anomura, Galatheidae) off the Pacific coast of Baja California Sur, Mexico, Crustaceana, 70, 272–287, 1997.

Bailey, G. W., Ms 1999: Severe hypoxia and its effects on marine resources in the southern Benguela upwelling system, Intern. WS on Monitoring of Anaerobic Processes in the Benguela Current Ecosystem off Namibia (Orren, M., Bailey G., and O'Toole, M., conveners): Swakopmund, Namibia, 8–9 March 1999.

Bailey, G. W., de Beyers, C. J., and Lipschitz, K.: Seasonal variation of oxygen deficiency in waters off southern South West Africa in 1975 and 1976 and its relation to the catchability and distribution of the cape rock lobster *Jasus lalandii*, S. Afr. J. Mar. Sci, 3, 197–214, 1985.

Bakun, A. and Broad, K.: Environmental "loopholes" and fish population dynamics: comparative pattern recognition with focus on El Niño effects in the Pacific, Fish. Oceanogr., 12, 458–473, 2003.

Baumgartner, T. R., Soutar, A., and Ferreira-Bartrina, V.: Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, Calif. Coop. Oceanic Fish. Invest. Rep., 33, 24–40, 1992.

Bernhard, J. M., Buck, K. R., Farmer, M. A., and Bowser, S. S.: The Santa Barbara Basin is a symbiosis oasis, Nature, 403, 77–80, 2000.

Blanco J. L., Thomas, A. C., Carr, M. E., and Strub, P. T.: Seasonal climatology of hydrographic conditions in the upwelling region off northern Chile, J. Geophys. Res., 106, 11 451–11 467, 2001.

Bograd, S. J. and Lynn, R. J.: Physical-biological coupling in the California Current during the 1997–99 El Niño-La Niña cycle, Geophys. Res. Lett., 28, 275–278, 2001.

Borowski, C. and Thiel, H.: Deep-sea macrofaunal impacts of a large-scale physical disturbance experiment in the southeast Pacific, Deep-Sea Res. II, 45, 55–81, 1998.

Botsford, L. W., Moloney, C. L., Hastings, A., Largier, J. L., Powell, T. M., Higgins K., and Quinn, J. F.: The influence of spatially and temporally varying oceanographic conditions on meroplanktonic metapopulations, Deep-Sea Res. II, 41, 107–145, 1994.

Botsford, L. W.: Physical influences on recruitment to California Current invertebrate populations on multiple scales, ICES J. Mar. Sci, 58, 1081–1091, 2001.

Boyer, D. C. and Hampton, I.: An overview of the living marine resources off Namibia, in: A Decade of Namibian Fisheries Science, edited by: Payne, A. I. L., Pillar, S. C., and Crawford, R. J. M., Afr. J. Mar. Sci., 23, 5–35, 2001.

Brüchert, V., Currie, B., Peard, K.R., Lass, U., Endler, R., Dübecke, A., Julies, E., Leipe, T., and Zitzmann, S.: An integrated assessment of shelf anoxia and water column hydrogen sulphide in the Benguela coastal upwelling system off Namibia, in: Past and Present Marine Water Column Anoxia, edited by: Neretin, N. L., Jørgensen, B. B., and Murray, J. W., Springer, Berlin, 161–193, 2006.

California Department of Fish and Game: Review of some California fisheries for 1998: Pacific sardine, Pacific mackerel, Pacific herring, market squid, sea urchin, groundfishes, swordfish, sharks, nearshore finfishes, abalone, Dungeness crab, prawn, ocean salmon, white seabass, and recreational, Fisheries Rev, CalCOFI Rep., 40, 9–24, 1999.

Canby, T. Y.: El Niño's ill wind, Natl. Geogr., 165, 144–183, 1984.

Carr, M.-E. and Kearns, E. J.: Production regimes in four Eastern Boundary Current systems, Deep-Sea Res. II, 50, 3199-3221, 2003.

Castilla, J. C. and Camus, P. A.: The Humboldt-El Niño scenario: coastal benthic resources and anthropogenic influences, with particular reference to the 1982/83 ENSO, in: Benguela trophic functioning, edited by: Payne, A. I. L., Brink, K. H., and Mann, K. H., Afr. J. Mar. Sci., 12, 703–712, 1992.

Chávez, F. P., Ryan, J., Lluch-Cota, S. E., and Niquen, M.: From anchovies to sardines and back: Multidecadal change in the Pacific Ocean, Science, 299, 217–221, 2003.

Cockcroft, A. C., Schoemann, D. S., Pitcher, G. C., Bailey, G. W., and Van Zyl, D. L.: A mass stranding or walkout of west coast rock lobster *Jasus lalandii* in Elands Bay, South Africa: causes,

results and implications, Crustacean Issues, 11, 673–688, 2000.

Currie, B.: Marine chemical processes in nearshore waters of Namibia in relation to intertidal and shallow benthic fauna, in: Intern. WS on Monitoring of Anaerobic Processes in the Benguela Current Ecosystem off Namibia (Orren, M., G. Bailey and M. O'Toole, Conveners), Swakopmund, Namibia, 8–9 March, 1999 (mimeo).

Currie, B., Bartholomae, C., Noli-Peard, K., Kragstad, J.-O., and Kreiner, A.: Warm water events in the northern Benguela: a local perspective, in: Extended Abstracts of the Symposium "Impacts of El Niño and Basin-Scale Climate Change on Ecosystems and Living Resources: A comparison between the California and the Humboldt current systems", edited by: Salinas, S., Urban, H.-J., and Arntz W. E., Invest. Mar., 30, 94–95, 2002.

Currie, B., Peard, K., Brüchert, V., Emeis, K.-C., van der Plas, A., Endler, R., Salvanes, A., Weeks, S., Bakun, A., Chikwililwa, C, Skrypzeck, H., Goosen, A., and Bahlo, R.: Biogeochemical dynamics of hydrogen sulphide and methane in Namibian inner shelf sediments, with implications to the living marine resources, Afr. J. Mar. Sci., in press, 2006.

Dayton, P. K. and Tegner, M.: Catastrophic storms, El Niño and patch stability in a southern California kelp community, Science, 324, 283–285, 1984.

Dayton, P. K., Tegner, M. J., Parnell, P. E., and Edwards, P. B.: Temporal and spatial patterns of disturbance and recovery in a kelp forest community, Ecol. Monogr., 62, 421–445, 1992.

Dayton, P. K., Tegner, M. J., Edwards, P. B., and Riser, K. L.: Temporal and spatial scales of kelp demography: the role of oceanographic climate, Ecol. Monogr., 69, 219–250, 1999.

Davis, J. L. D.: Changes in a tidepool fish assemblage on two scales of environmental variation: seasonal and El Niño Southern Oscillation, Limnol. Oceanogr., 45, 1368–1379, 2000.

Davis, J. L. D.: Variability in spot pattern of *Girella nigricans*, the California opaleye: variation among cohorts and among climate periods, Bull. S. Calif. Acad. Sci., 100, 24–35, 2001.

Davis, J. L. D. and Levin, L.: Importance of pre-recruitment life-history stages to population dynamics of the woolly swculpin, *Clinocottus analis*, Mar. Ecol. Progr. Ser., 234, 229–246, 2002.

Delecluse, P., Servain, J., Levy, C., Arpe, C., and Bengtsson, L.: On the connection between the 1984 Atlantic warm event and the 1982–1983 ENSO, Tellus, 46A, 448–464, 1994.

Díaz, H. and Markgraf, V. (Eds.): El Niño and the Southern Oscillation: multiscale variability and global and regional impacts, Cambridge Univ. Press, 496 pp., 2000.

Díaz, R. J. and Rosenberg, R.: Marine benthic hypoxia: a review of ecological effects and the behavioural responses of benthic macrofauna, Oceanogr. Mar. Biol. Ann. Rev., 33, 245–303, 1995.

Emeis, K. C., Brüchert, V., Currie, B., Endler, R., Ferdelman, T., Kiessling, A., Leipe, T., Noli-Peard, K., Struck, U., and Vogt, T.: Shallow gas in shelf sediments of the Namibian coastal upwelling ecosystem, Contin. Shelf Res., 24, 627–642, 2004.

Enfield, D. B.: Evolution and historical perspective of the 1997–1998 El Niño-Southern Oscillation event, Bull. Mar. Sci., 69, 7–25, 2001.

Espino, M.: "El Niño 1997–98": su efecto sobre el ambiente y los recursos pesqueros del Perú, in: El Niño 1997–98 y su impacto sobre los ecosistemas marino y terrestre, edited by: Tarazona, J. and Castillo, E., Rev. Per. Biología, vol. extraord., 97–109, 1999.

Espino, M., Benites, C., and Maldonado, M.: Situación de la población de merluza durante "El Niño", in: El Niño. Su impacto en la fauna marina, edited by: Arntz, W. E., Landa, A., and Tarazona, J., Bol. Inst. Mar Peru-Callao, spec. vol., 159–162, 1985.

Espino, M., Samamé M., and Castillo, R. (Eds.): La merluza peruana *(Merluccius gayi peruanus)*, IMARPE, Callao, 1–120, 2001.

Ferdelman, T., Lee, C., Pantoja, S., Harder, J., Bebout B., and Fossing, H.: Sulfate reduction and methanogenesis in a *Thioploca*-dominated sediment off the coast of Chile, Geochimica et Cosmochimica Acta, 61, 3065–3079, 1997.

Fernández, E., Córdova , C., and Tarazona, J.: Condiciones de la pradera submareal de *Lessonia trabeculata* en la Isla Independencia durante El Niño 1997–98, in: El Niño 1997–98 y su impacto sobre los ecosistemas marino y terrestre, edited by: Tarazona, J. and Castillo, E., Rev. Per. Biología, vol. extraord., 47–59, 1999.

Fiedler, P. C.: Environmental change in the eastern tropical Pacific Ocean: review of ENSO and decadal variability, Mar. Ecol. Prog. Ser., 244, 265–283, 2002.

Fossing, H., Gallardo, V. A., Jørgensen, B. B., Hüttel, M., Nielsen, L. P., Schulz, H., Canfield, D. E., Forster, S., Glud, R. N., Gundersen, J. K., Küver, J., Ramsing, N. B., Teske, A., Thamdrup, B., and Ulloa, O.: Concentration and transport of nitrate by the mat-forming sulphur bacterium *Thioploca*, Nature, 374, 713–715, 1995.

Foster, M. and Schiel, D. R.: The ecology of giant kelp forests in California: A community profile, US Fish and Wildlife Service Biol. Rep., 85, 1–152, 1985.

Gallardo, V. A.: Notas sobre la densidad de la fauna bentónica en el sublitoral del norte de Chile, Gayana (Zool.), 10, 3–15, 1963.

Gallardo, V. A.: Large benthic microbial communities in sulphide biota under Peru-Chile Subsurface Countercurrent, Nature, 268, 331–332, 1977.

Gallardo, V. A., Cañete, J. I., Roa, R., Enríquez-Briones, S., and Baltazar, M.: Recruitment of the squat lobster *Pleuroncodes monodon* on the continental shelf off central Chile, J. Crust. Biol., 14, 665–669, 1994.

Gallardo, V. A., Roa, R., Carrasco, F. D., Cañete, J. I., Enríquez-Briones S., and Baltazar, M.: Bathymetric and seasonal patterns in the sublittoral megafauna off central Chile, J. Mar. Biol. Ass. U.K., 76, 311–326, 1996.

Gallardo, V. A., Klingelhöfer, E., Arntz W. E., and Graco, M.: First report of the bacterium *Thioploca* in the Benguela ecosystem off Namibia, J. Mar. Biol. Ass. U.K., 78, 1007–1010, 1998.

Gallardo, V. A., Palma, M., Carrasco, F. D., Gutiérrez, D., Levin, L. A., and Cañete, J. I.: Macrobenthic zonation caused by the oxygen minimum zone on the shelf and slope off central Chile, Deep-Sea Res. II, 51, 2475–2490, 2004.

Gammelsröd, T., Bartholomae, C. H., Boyer, D. C., Filipe, V. L. L., and O'Toole, M. J.: Intrusion of warm surface water along the Angolan-Namibian coast in February–March 1995: the 1995 Benguela Niño, in: Benguela Dynamics, edited by: Pillar, S. C., Moloney, C. L., Payne, A. I. L., and Shillington, F. A., S. Afr. J. Mar. Sci, 19, 41–56, 1998.

Gerard, V. A.: Physiological effects of El Niño on giant kelp in southern California, Mar. Biol. Lett., 5, 317–322, 1984.

Giere, O. and Krieger, J.: A triple bacterial endosymbiosis in a gutless oligochaete (Annelida). Ultrastructural and immunocytochemical evidence, Biol., 120, 41–49, 2001.

Glantz, M. H. (Ed.): Once burned, twice shy? Lessons learned from the 1997–98 El Niño, United Nations Univ., New York, 294 pp, 2001.

Glantz, M. H., Katz, R., and Krenz, M. (Eds.): Climate crisis: The societal impacts associated with the 1982–83 worldwide climate anomalies, Nat. Center Atm. Res., Boulder, 1987.

Glynn, P. W.: Global ecological consequences of the 1982–83 El Niño-Southern Oscillation, Elsevier Oceanography Series, 52, 563 pp, 1990.

González, R. R. and Quiñones, R. A.: Pyruvate oxidoreductases involved in glycolytic anaerobic metabolism of polychaetes from the continental shelf of central-south Chile, Est. Coastal Shelf Sci., 51, 507–519, 2000.

González, H. E., Ortiz, V. C., and Sobarzo, M.: The role of faecal material in the particulate organic carbon flux in the northern Humboldt Current, Chile (23° S), before and during the 1997–1998 El Niño, J. Plankton Res., 22(3), 499–530(32), 2000.

Graco, M., Gutiérrez, D., Farías, L., Yuras, G., and Montecinos, A.: Inter-annual variability of the "pelagic-benthic-pelagic" coupling in the upwelling system off central Chile, 1st Alexander von Humboldt Conference on the El Niño Phenomenon and its Global Impact, Guayaquil, 16–20 May 2005, Book of Abstracts, 50–51, 2005.

Grantham, B. A., Chan, F., Nielsen, K. J. Fox, D. S., Barth, J. A., Huyer, A., Lubchenco, J., and Menge, B. A.: Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific, Nature, 429, 749–754, 2004.

Grobler, C. A .F. and Noli-Peard, K. R.: *Jasus lalandii* fishery in post-independence Namibia: monitoring population trends and stock recovery in relation to a variable environment, Mar. Freshwater Res., 48, 1015–1022, 1997.

Grunewald, A., Morales, C., González, H., Sylvester, C., and Castro, L.: Grazing impact of copepod assemblages and gravitational flux in coastal and oceanic waters off central Chile during two contrasting seasons, J. Plankton Res., 24, 55–67, 2002.

Guillén, O., Lostaunau, N., and Jacinto, M.: Características del fenómeno "El Niño" 1982–83, in: "El Niño". Su Impacto en la Fauna Marina, edited by: Arntz, W. E., Landa, A., and Tarazona, J., Bol. Inst. Mar Perú-Callao, vol. extraord., 11–22, 1985.

Gunnill, F. C.: Population fluctuations of seven macroalgae in Southern California during 1981–1983 including effects of severe storms and El Niño, J. Exp. Mar. Biol. Ecol., 85, 149–164, 1985.

Gutiérrez, D.: Bioperturbación y macrofauna en fondos sublitorales hipóxicos de un área de surgencias, Chile central (36° 30′ S); variación estacional y espacial en el período 1997–1999, Ph.D thesis, Univ. Concepción, 221 pp, 2000.

Gutiérrez, D., Gallardo, V. A., Mayor, S., Neira, C., Vásquez, C., Sellanes, J., Rivas, M., Soto, A., Carrasco, F., and Baltazar, M.: Effects of dissolved oxygen and fresh organic matter on the bioturbation potential of macrofauna in sublittoral sediments off central Chile during the 1997/98 El Niño, Mar. Ecol. Prog. Ser., 202, 81–99, 2000.

Gutiérrez, D., Quipuzcoa, L., Enríquez, E., and Marquina, R.: ENSO-driven variability of sublittoral macrobenthos off Peru: modulation by local environmental settings along a latitudinal gradient, 1st Alexander von Humboldt Conference on the El Niño Phenomenon and its Global Impact, Guayaquil, 16–20 May 2005, Book of Abstracts, 2005.

Guzmán, N., Díaz, A., Ortlieb, L., and Clarke, M.: TAMAs, ocurrencia episódica de moluscos tropicales en el norte de Chile y evento El Niño, in: El Niño en América Latina: impactos biológicos y sociales, edited by: Tarazona, J., Arntz, W. E., and Castillo de Maruenda, E., CONCYTEC, Lima, 385–393, 2001.

Guzmán del Próom, S. A., Carreón-Palau, L., Belmar-Pérez, J., Carillo-Laguna, J., and Herrera Fragoso, R.: Efectos del fenómeno de "El Niño" sobre el reclutamiento de invertebrados bentónicos de Baja California, in: Los efectos del fenómeno El Niño en México, 1997–98, edited by: Escobar-Briones, E., Bonilla, M., Badán, A., Caballero, M., and Winckell, A., Consejo Nacional de Ciencia y Tecnología, México D. F., 231–239, 2000

Hamukuaya, H., Bianchi, G., and Baird, D.: The structure of demersal assemblages off Namibia in relation to abiotic factors, in: A Decade of Namibian Fisheries Science, edited by: Payne, A. I. L., Pillar, S. C., and Crawford, R. J. M., Afr. J. Mar. Sci., 23, 397–417, 2001.

Hebbeln, D.: Seasonal and interannual variability of the particle flux in the Humboldt Current off Chile, in: Extended Abstracts of the Symposium "Impacts of El Niño and Basin-Scale Climate Change on Ecosystems and Living Resources: A comparison between the California and the Humboldt current systems", edited by: Salinas, S., Urban, H.-J., and Arntz, W. E., Invest. Mar., 30, 168–170, 2002.

Hebbeln, D., and Wefer, G. (Eds.): Final report for the BMBF project PUCK – SO-156 "Interrelationships between productivity and environmental conditions along the Chilean continental slope", FB Geowiss. Univ. Bremen, 1–69, 2003.

Helly, J. J. and Levin, L. A.: Global distribution of naturally occurring marine hypoxia on continental margins, Deep-Sea Res. I, 51, 1159–1168.

Herdson, D.: Changes in the demersal fish stocks and other marine life in Ecuadorian coastal waters during the 1982–83 El Niño, Trop. Ocean-Atmos. Newsl., 28, 14–16, 2004.

Herdson, D.: Changes in the demersal fish stocks and other marine life in Ecuadorian coastal waters during the 1982–83 El Niño, Trop. Ocean-Atmos. Newsl., 28, 14–16, 1984.

Hernández-Carmona, G., Rodríguez-Montesinos, Y. E., Torres-Villegas, J. R., Sánchez-Rodríguez, I., and Vilchis, M. A.: Evaluación de los mantos de *Macrocystis pyrifera* (Phaeophyta, Laminariales) en Baja California, Mexico, I. Invierno 1985–1986, Ciencias Marinas, 15, 1–27, 1989.

Huettel, M., Forster, S., Klöser, S., and Fossing, H.: Vertical migration in the sediment-dwelling sulfur bacteria *Thioploca* spp. in overcoming diffusion limitations, Appl. Envir. Microbiol., 62, 1863–1872, 1996.

INP: Sustentabilidad y pesca responsable: Evaluación y manejo, Instituto Nacional de Pesca, Secretaría del Medio Ambiente, Recursos Naturales y Pesca, México, pp. 610, 2000.

Jarre-Teichmann, A. and Christensen, V.: Comparative modelling of trophic flows in four large upwelling ecosystems: global vs. local effects, in: Global vs. local changes in upwelling ecosystems, edited by: Durand, M. H., Cury, P., Medelssohn, R., Roy, C., Bakun, A., and Pauly, D., Proc. First Internat. CEOS Meeting, Orstom, Paris, 423–443, 1998.

Jarre-Teichmann, A., Shannon, L. J., Moloney, C. L., and Wickens, P. A.: Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems, in: Benguela Dynamics, edited by: Pillar, S. C., Moloney, C. L., Payne, A. I. L., and Shillington, F. A., S. Afr. J. mar. Sci., 19, 391–414, 1998.

Jury, M. R., Enfield, D. B., and Mélice, J.-L.: Tropical monsoons around Africa: Stability of El Niño-Southern Oscillation associations and links with continental climate, J. Geophys. Res., 107(C10), 3151, doi:10.1029/2000JC000507, 2002.

Kalanetra, K. M., Huston, S. H., and Nelson, D. C.: Novel, attached, sulfur-oxidizing bacteria at shallow hydrothermal vents possess vacuoles not involved in respiratory nitrate accumulation, Appl. Env. Microbiol., 70, 7487–7496, 2004.

Kameya, A. and Zeballos, J.: Distribuciones y densidad de percebes *Pollicipes elegans* (Crustacea: Cirripedia en el mediolitoral pe-

ruano (Yasila, Paita, Chilca, Lima), Bol. Inst. Mar Peru-Callao, 12, 1–22, 1988.

Kameya, A., Lleellish, M., and Caccha, L.: Patrones de occurrencia de indicadores biológicos del fenómeno El Niño desde 1972 a 1998, in: El Niño en América Latina: impactos biológicos y sociales, edited by: Tarazona, J., Arntz, W. E., and Castillo de Maruenda, E., CONCYTEC, Lima, 81–89, 2001.

Kong, I., Tomicic, J., and Zegers, J.: Ictiofauna asociada al fenómeno El Niño 1982–83 en la zona norte de Chile, in: Taller nacional fenómeno El Niño 1982–83, edited by: IFOP-Chile, Invest. Pesq. (Chile), 32, 215–223, 1985.

Ladah, L. B. and Zertuche-González, J. A.: Giant kelp *(Macrocystis pyrifera)* survival in deep water (25–40 m) during El Niño of 1997–1998 in Baja California, Mexico, Botanica Marina, 47, 367–372, 2004.

Ladah, L., Zertuche-González, J. A., and Hernández-Carmona, G.: Giant kelp *(Macrocystis pyrifera)* recruitment near its southern limit in Baja California after mass disappearance during ENSO 1997–1998, J. Phycol., 35, 1106–1112, 1999.

Lagos, P.: El Niño y el cambio climático en el Perú, in: Perú: Vulnerabilidad Frente al Cambio Climático, edited by: Marticorena, B., Consejo Nacional del Ambiente, Lima, 65–94, 1999.

Latif, M. and Barnett, T. P.: Interactions of the tropical oceans, J. Climate, 8, 952–964, 1995.

Laudien, J.: Population dynamics and ecology of the surf clam *Donax serra* (Bivalvia, Donacidae) inhabiting beaches of the Benguela upwelling system, Diss. Univ. Bremen, 1–99, 2002.

Laudien, J., Schiedek, D., Brey, T., Arntz, W. E., and Pörtner, H.-O.: Survivorship of juvenile surf clams *Donax serra* (Bivalvia, Donacidae) exposed to severe hypoxia and hydrogen sulphide, J. Exp. Mar. Biol. Ecol., 271, 9–23, 2002.

Lavaniegos, B. E., Gaxiola-Castro, G., Jiménez-Pérez, L. C., González-Esparza, M. R., Baumgartner, T., and García-Córdova, J. A.: 1997–98 El Niño effects on the pelagic ecosystem of the California current off Baja California, México, Geofísica Internacional, 42(3), 483–494, 2003.

Lea, R. N. and Rosenblatt, R. H.: Observations on fishes associated with the 1997-98 El Niño off California, CalCOFI Rep., 41, 117–129, 2000.

Levin, L. A., Gage, J. D., Martin, C., and Lamont, P. A.: Macrobenthic community structure wihtin and beneath the oxygen minimum zone, NW Arabian Sea, Deep-Sea Res. II, 47, 189–226, 2000.

Levin, L. A.: Ecology of cold seep sediments: interactions of fauna with flow, chemistry and microbes, Oceanogr. Mar. Biol. Ann. Rev., 43, 1–46, 2005.

Levin, L. A.: Oxygen minimum zone benthos: adaptation and community response to hypoxia, Oceanogr. Mar. Biol. Ann. Rev., 41, 1–45, 2003.

Levin, L. A. and Michener, R. H.: Isotopic evidence for chemosynthesis-based nutrition of macrobenthos: the lightness of being at Pacific methane seeps, Limnol. Oceanogr., 47, 1336–1345, 2002.

Levin, L. A., Etter, R. J., Rex, M. A., Gooday, A. J., Smith, C. R., Pineda, J., Stuart, C. T., Hessler, R. H., and Pawson, D.: Environmental influences on regional deep-sea species diversity, Annu. Rev. Ecol. Syst., 32, 51–93, 2001.

Levin, L., Gutiérrez, D., Rathburn, A., Neira, C., Sellanes, J., Muñoz, P., Gallardo, V. A., and Salamanca, M.: Benthic processes on the Peru margin: a transect across the oxygen minimum zone during the 1997–98 El Niño, Progr. Oceanogr., 53, 1–27, 2002.

Levin, L. A., Rathburn, A. E., Gutiérrez, D., Muñoz, P., and Shankle, A.: Bioturbation by symbiont-bearing annelids in near-anoxic sediments: implications for biofacies models and paleo-oxygen assessments, Palaegeogr., Palaeclimatol., Palaeoecol., 3175, 1–12, 2003.

Lluch-Cota, D., Lluch-Belda, D., Lluch-Cota, S., López-Martínez, J., Nevárez-Martínez, M., Ponce-Díaz, G., Salinas-Zavala, G., Vega-Velázquez, A., Lara Lara, J. R., Hammann, G., and Morales, J.: Las pesquerías y El Niño, in: Los impactos de El Niño en México. Where?, edited by: Magaña, V. O., 137–178, 1999.

Lynn, R. J. and Simpson, J. J.: The California Current system: the seasonal variability of its physical characteristics, J. Geophys. Res., 92, 12 947–12 966, 1987.

Macharé, J. and Ortlieb, L. (Eds.): Registro del fenómeno El Niño y de eventos ENSO en América del Sur, Bull. Inst. Franc. Etudes Andines, 22, 1–406, 1993.

Markgraf, V., Baumgartner, T. R., Bradbury, J. P., Diaz, H. F., Dunbar, R. B., Luckman, B. H., Seltzer, G. O., Swetnam, T. W., and Villalba, R.: Paleoclimate reconstruction along the pole-equator-pole transect of the Americas (PEP 1), Quatern. Sci Rev., 19, 125–140, 2000.

Martínez, E. A. and Santelices, B.: Selective mortality on haploid and diploid microscopic stages of *Lessonia nigrescens* Bory (Phaeophyta, Laminariales), J. Exp. Mar. Biol. Ecol., 229, 219–239, 1998.

Martínez, E. A., Cárdenas, L., and Pinto, R.: Recovery and genetic diversity of the intertidal kelp *Lessonia nigrescens* (Phaeophyceae) 20 years after El Niño 1982/83, J. Phycol., 39, 504–508, 2003.

McPhaden, M. J.: Genesis and evolution of the 1997–98 El Niño, Science, 283, 950–954, 1999.

Mearns, A. J.: The "odd fish": unusual occurrences of marine life as indicators of changing ocean conditions, in: Marine Organisms as Indicators, edited by: Soule, D. F. and Kleppel, G. S., Springer, New York, 137–176, 1988.

Mendo, J. and Wolff, M. (Eds.): Bases Ecológicas y Socioeconómicas para el Manejo de los Recursos Vivos de la Reserva Nacional de Paracas, Univ. Nac. Agr. La Molina, Lima, 1–244, 2002.

Mendo, J. and Wolff, M.: El impacto de El niño sobre la producción de concha de abanico *(Argopecten purpuratus)* en Bahía Independencia, Pisco, Perú, Ecología Aplicada, 2, 51–57, 2003.

Moloney, C. L., Jarre, A., Arancibia, H., Bozec, Y.-M., Neira, S., Roux, J.-P., and Shannon, L. J.: Comparing the Benguela and Humboldt marine upwelling ecosystems with indicators derived from inter-calibrated models, ICES J. Mar. Sci., 62, 493–502, 2005.

Montagne, D. E. and Cadien, D. B.: Northern range extension into the southern California Bight of ten decapod Crustacea related to the 1991/92 and 1997/98 El Niño events, Bull. Southern Calif. Acad. Sci, 100, 199–211, 2001.

Muñoz, P., Salamanca, M. A., Neira, C., and Sellanes, J.: Nitrogen sediment fluxes in an upwelling system off central Chile (Concepción Bay and adjacent shelf) during the 1997–1998 El Niño, Rev. Chil. Hist. Nat., 77, 305–318, 2004.

Neira, C., Sellanes, J., Soto, A., Gutiérrez, D., and Gallardo, V. A.: Meiofauna and sedimentary organic matter off central Chile: response to changes caused by the 1997–1998 El Niño, Oceanol. Acta, 24, 313–328, 2001a.

Neira, C., Sellanes, J., Levin, L. A., and Arntz, W. E.: Meiofaunal distributions on the Peru margin: relationship to oxygen

and organic matter availability, Deep-Sea Res. I, 48, 2453–2472, 2001b.

Neira, C., Gad, G., Arroyo, N. L., and Decraemer, W.: *Glochynema bathyperuvensis* sp.n. (Nematoda, Epsilonematidae): a new species from Peruvian bathyal sediments, SE Pacific Ocean, Contr. Zool., 70, 147–159, 2001c.

Neira, C., Decraemer W., and Backeljau, T.: A new species of *Glochinema* (Epsilonematidae, Nematoda) from the oxygen minimum zone off Baja California, NE Pacific and phylogenetic relationships at species level within the family, Cahiers Biol. Mar., 46, 105–126, 2005.

Olu, K., Duperret, A., Sibuet, M., Foucher, J.-P., and Fiala-Médioni, A.: Structure and distribution of cold seep communities along the Peruvian active margin: relationship to geological and fluid patterns, Mar. Ecol. Prog. Ser., 132, 109–125, 1996.

Ortlieb, L. and Hocquenghem, A.-M.: Reconstrucción del registro histórico de eventos El Niño en el Perú: un estado de avance, in: El Niño en América Latina: impactos biológicos y sociales, edited by: Tarazona, J., Arntz, W. E., and Castillo de Maruenda E., CONCYTEC, Lima, 361–379, 2001.

Otte, S., Kuenen, J. G., Nielsen, L. P., Pearl, H. W., Zopfi, J., Schulz, H. N., Teske, A., Strotman, B., Gallardo V. A., and Jørgensen, B. B.: Nitrogen, carbon and sulphur metabolism in natural *Thioploca* samples, Appl. Environm. Microb., 65, 3148–3157, 1999.

Palma, M., Quiroga, E., Gallardo, V. A., Arntz, W. Gerdes, D., Schneider W., and Hebbeln, D.: Macrobenthic animal assemblages of the continental margin off Chile (22 to 42° S), J. Mar. Biol. Ass. U.K., 85, 233–245, 2005.

Pearcy, W. G.: Marine nekton off Oregon and the 1997–98 El Niño, Progr. Oceanogr., 54, 399–403, 2002.

Pearcy, W. G. and Schoener, A.: Unusual occurrences of fish and invertebrates off Oregon during EN 1982–83, J Geophys. Res., 92(C13), 14 417–14 428, 1987.

Peña, T., Johst, K., Grimm, V., Arntz, W. E., and Tarazona, J.: Population dynamics of a polychaete during three El Niño events: disentangling biotic and abiotic factors, Oikos, 111, 253–258, 2005.

Peterson, W. T. and Schwing, F. B.: A new climate regime in northeast Pacific ecosystems, Geophys. Res. Lett., 30(17), 1896, doi:10.1029/2003GL017528, 2003.

Pitcher, G. C.: Harmful algal blooms of the Benguela Current, Sea Fisheries Res. Inst., Cape Town, South Africa, 21 pp., 1998.

Quiroga, E., Quiñones, R. A., González, R. R., Gallardo, V. A., and Jessen, G.: Aerobic and anaerobic metabolism of *Paraprionospio pinnata* (Polychaeta, Spionidae) in central Chile, J. Mar. Biol. Ass. UK, in press, 2006.

Romanova, N. N.: Investigaciones científico-pesqueras en las aguas del Océano Pacífico adyacentes a la costa del Perú durante el invierno de 1972, Distribución de bentos en la plataforma y en el talud continental de la costa peruana, Ser. Inf. Esp. Inst. Mar Perú-Callao, 128, 127–132, 1972.

Rosenberg, R., Arntz, W. E., Chumán de Flores, E., Flores, L. A., Carbajal, G., Finger, I., and Tarazona, J.: Benthos biomass and oxygen deficiency in the upwelling system off Perú, J. Mar. Res., 41, 263–279, 1983.

Rowe, G. T.: Benthic biomass and surface productivity, in: Fertility of the Sea, edited by: Costlow, J. D., Gordon and Breach, New York, 441–454, 1971.

Rowe, G. T., Boland, G. S., Phoel, W. C., Anderson, R. F., and Biscaye, P. E.: Deep-sea floor respiration as an indication of lateral input of biogenic detritus from continental margins, Deep-Sea Res. II, 31, 657–668, 1994.

Roy, C. and Reason, C.: ENSO related modulation of coastal upwelling in the eastern Atlantic, Prog. Oceanogr., 49, 245–255, 2001.

Ruhl, H. A. and Smith, K. L.: Shifts in deep-sea community structure linked to climate and food supply, Science, 305, 513–515, 2004.

Sánchez, G., Calienes, R., and Zuta, S.: The 1997–98 El Niño and its effects on the coastal marine ecosystem off Peru, CalCOFI Rep., 41, 62–86, 2000.

Schiedek, D. and Currie, B.: Metabolic responses of two macrobenthic species to naturally occurring hydrogen sulphide, SAMSS 2002, Currents Coasts Communities, Swakopmund, 1–5 July 2002.

Schimmelmann, A. and Tegner, M. J.: Historical oceanographic events reflected in 13C/12C ratio of total organic carbon in laminated Santa Barbara Basin sediment, Global Biogeochem. Cycles, 5, 173–188, 1991.

Schulz, H. N., Jørgensen, B. B., Fossing, H. A., and Ramsing, N. B.: Community structure of filamentous, sheath-building sulfur bacteria, *Thioploca* spp., off the coast off Chile, Appl. Environm. Microbiol., 62, 1855–1862, 1996.

Schulz, H. N., Brinkhoff, T., Ferdelman, T. G., Hernández Mariné, M., Teske, A., and Jørgensen, B. B.: Dense populations of a giant sulfur bacterium in Namibian shelf sediments, Science, 284, 493–495, 1999.

Schulz, H. N., Strotmann, B., Gallardo, V. A., and Jørgensen, B. B.: Population study of the filamentous sulfur bacteria *Thioploca* spp. off the Bay of Concepción, Chile, Appl. Env. Microbiol., 62, 1855–1862, 2000.

Schwartzlose, R. A., Alheit, J., Bakun, A., et al. (20 co-authors): Worldwide large-scale fluctuations of sardine and anchovy populations, Afr. J. Mar. Sci., 21, 289–347, 1999.

Sellanes, J. and Krylova, E.: A new species of *Calyptogena* (Bivalvia, Vesicomyidae) from a recently discovered methane seepage area off Concepción Bay, Chile (ca. 36° S), J. Mar. Biol. Ass. U.K., 85, 969–976, 2005.

Sellanes, J. and Neira, C.: ENSO as a natural experiment to understand environmental control of meiofaunal community structure, Mar. Ecol., in press, 2006.

Sellanes, J., Neira, C., and Quiroga, E.: Composition, structure and energy flux of the meiobenthos off central Chile, Rev. Chil. Hist. Nat., 76, 401–415, 2003.

Sellanes, J., Quiroga, E., and Gallardo, V. A.: First direct evidence of methane seepage and associated chemosynthetic communities in the bathyal zone off Chile, J. Mar. Biol. Ass. U.K., 84, 1065–1066, 2004.

Shannon, L. V. and Nelson, G.: The Benguela: Large scale phenomena and processes and system variability, in: The South Atlantic: Present and Past Circulation, edited by: Wefer, G., Berger, W. H., Siedler, G., and Webb, D. J., Springer, Berlin, 163–210, 1996.

Shannon, L. V., Boyd, A. J., Brundrit, G. B., and Taunton-Clark, J.: On the existence of an El Niño-type phenomenon in the Benguela system, J. Mar. Res., 44, 495–520, 1986.

Strub, T., Mesías, J., Montecino, V., and Rutllant, J.: Coastal ocean circulation off western South America, in: The Sea, edited by: Robinson, A. and Brink, K., 11, 273–313, 1998.

Stuardo, J. and Valdovinos, C.: A new bathyal *Calyptogena* from the coast of central Chile (Bivalvia: Vesicomyidae), Venus (Jap. J. Malac.), 47, 241–250, 1988.

Swartzman, G. and Hickey, B.: Evidence for a regime shift after the 1997–1998 El Niño, based on 1995, 1998, and 2001 acoustic surveys in the Pacific Eastern Boundary Current, Estuaries, 26,

1032–1043, 2003.

Tarazona, J.: Disturbance and stress associated to El Niño and their significance for the macrobenthos of shallow areas of the Peruvian upwelling system, Diss. Univ. Bremen, Germany, 181 pp. 1990.

Tarazona, J. and Arntz, W. E.: Bacterias filamentosas gigantes en fondos someros de la Bahía de Ancón, Rev. Ciencias UNMSM, 74, 178–180, 1986.

Tarazona, J., Salzwedel, H., and Arntz, W. E.: Oscillations of macrobenthos in shallow waters of the Peruvian central coast induced by El Niño 1982–83, J. Mar. Res., 46, 593–611, 1988a.

Tarazona, J., Salzwedel, H., and Arntz, W. E.: Positive effects of "El Niño" on macrozoobenthos inhabiting hypoxic areas of the Peruvian upwelling system, Oecologia, 76, 184–190, 1988b.

Tarazona, J., Canahuire, E., Salzwedel, H., Jerí, T., Arntz, W. E., and Cid, L.: Macrozoobenthos in two shallow areas of the Peruvian upwelling ecosystem, in: Estuaries and Coasts: Spatial and Temporal Intercomparisons, edited by: Elliott, M. and Ducrotoy, J.-P., Olsen and Olsen, 251–258, 1991.

Tarazona, J., Arntz, W. E., and Canahuire, E.: Impact of two "El Niño" events of different intensity on the hypoxic soft bottom macrobenthos off the central Peruvian coast, P.S.Z.N. I: Marine Ecology, 17, 425–446, 1996.

Tarazona, J., Gutiérrez, D., Paredes, C., and Indacochea, A.: Overview and challenges of marine biodiversity research in Peru, Gayana, 67, 206–231, 2003.

Taylor, M. A., Enfield, D. B., and Chen, A. A.: Influence of the tropical Atlantic versus the tropical Pacific on Caribbean rainfall, J. Geophys. Res., 107(C9), 3127, doi:10.1029/2001JC001097, 2002.

Tegner, M. J.: Biological impacts of the 1997–98 El Niño in the Californias: kelp forests were devastated, in: El Niño en América Latina: impactos biológicos y sociales, edited by: Tarazona, J., Arntz, W. E., and Castillo de Maruenda, E., CONCYTEC, Lima, 137–146, 2001.

Tegner, M. J. and Dayton, P. K.: El Niño effects on southern California kelp forest communities, Adv. Ecol. Res., 17, 243–279, 1987.

Tegner, M. J., Dayton, P. K., Edwards, P. B., and Riser, K. L.: Is there evidence for long-term climatic change in southern California kelp forests?, CalCOFI Rep., 37, 111–126, 1996.

Thompson, B., Tsukada, D., and Laughlin, J.: Megabenthic assemblages of coastal shelves, slopes, and basins off southern California, Bull. Southern Calif. Acad. Sci, 92, 25–42, 1993.

Vásquez, J. A. and Vega, J. M. A.: El Niño 1997–1998 en el norte de Chile: efectos en la estructura y en la organización de comunidades submareales dominadas por algas pardas, in: El Niño – La Niña 1997–2000 sus efectos en Chile, edited by: Avaria, S., Carrasco, J., Rutllant, J., and Yáñez, E., CONA, Valparaíso, 119–135, 2004.

Vega, J. M. A., Vásquez, J. A., and Buschmann, A. H.: Population biology of the subtidal kelps *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales, Phaeophyceae) in an upwelling ecosystem of northern Chile: interannual variability and El Niño 1997–1998, Rev. Chilena Hist. Nat., 78, 33–50, 2005.

Vega-Velázquez, A.: Reproductive pattern of *Panulirus interruptus* as related to sea temperature and Ekman transport in central Baja California peninsula: effects of the El Niño and La Niña during 1997–1999, Calif. Coop. Oceanic Fish. Invest. 50th Anniversary Conference, P-28, 1999.

Vélez, J. J., Zeballos, J., and Méndez, M.: Effect of the 1982–83 El Niño on fishes and crustaceans off Peru, Trop. Ocean-Atmos. Newsl., 28, 10 pp, 1984.

Wang, C. and Enfield, D. B.: A further study of the tropical western hemisphere warm pool, J. Climate, 16, 1476–1493, 2003.

Weeks, S., Currie, B., and Bakun, A.: Massive emissions of toxic gas in the Atlantic, Nature, 415, 493p, 2002.

Weeks, S., Currie, B., Bakun, A., and Peard, K. R.: Hydrogen sulphide eruptions in the Atlantic Ocean off southern South Africa: Implications of a new view based on SeaWiFS satellite imagery, Deep-Sea Res., 51, 153–172, 2004.

Wolff, M.: Impact of the 1982–83 El Niño on the Peruvian scallop Argopecten purpuratus, Trop. Ocean-Atmosph. Newsl., 28, 8–9, 1984.

Wolff, M.: Abundancia masiva y crecimiento de preadultos de la concha de abanico peruana *(Argopecten purpuratus)* en la zona de Pisco bajo condiciones de "El Niño" 1983, in: El Niño. Su impacto en la fauna marina, edited by: Arntz, W. E., Landa, A., and Tarazona, J., Bol. Inst. Mar Perú-Callao, vol esp., 87–89, 1985.

Wolff, M.: Population dynamics of the Peruvian scallop *Argopecten purpuratus* during the El Niño phenomenon of 1983, Can. J. Fish. Aquat. Sci., 44, 1684–1691, 1987.

Wolff, M.: Spawning and recruitment in the Peruvian scallop *Argopecten purpuratus*, Mar. Ecol. Prog. Ser., 42, 213–217, 1988.

Wosnitza-Mendo, C. and Espino, M.: The impact of „El Niño" on recruitment of the Peruvian hake *(Merluccius gayi peruanus)*, Meeresforsch., 31, 47–51, 1986.