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The Humboldt Current System: Ecosystem components and processes, fisheries, and sediment studies

Vivian Montecino [a,*], Carina B. Lange [b]

[a] Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Chile
[b] Departamento de Oceanografía y Centro FONDAP-COPAS, Universidad de Concepción, Chile

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ABSTRACT

In the Humboldt Current System (HCS), biological and non-biological components, ecosystem processes, and fisheries are known to be affected by multi-decadal, inter-annual, annual, and intra-seasonal scales. The interplay between atmospheric variability, the poleward undercurrent, the shallow oxygen minimum zone (OMZ), and the fertilizing effect of coastal upwelling and overall high primary production rates drive bio-physical interactions, the carbon biomass, and fluxes of gases and particulate and dissolved matter through the water column. Coastal upwelling (permanent and seasonally modulated off Peru and northern Chile, and markedly seasonal between 30°S and 40°S) is the key process responsible for the high biological productivity in the HCS.

At present, the western coast of South America produces more fish per unit area than any other region in the world ocean (i.e. $\sim 7.5 \times 10^6$ t of anchoveta were landed in 2007). Climate changes on different temporal scales lead to alterations in the distribution ranges of anchoveta and sardine populations and shifts in their dominance throughout the HCS. The factors affecting the coastal marine ecosystem that reverberate in the fisheries are crucial from a social perspective, since the economic consequences of mismanagement can be severe. Fish remains are often well-preserved in sediment settings under the hypoxic conditions of the OMZ off Peru and Chile, and reveal multi-decadal variability and centennial-scale changes in fish populations.

Sediment studies from the Chilean continental margin encompassing the last 20,000 years of deposition reveal changes in sub-surface conditions in the HCS during deglaciation, interpreted to include: a major reorganization of the OMZ; a deglacial increase in denitrification decoupled from local marine productivity; and higher deglacial and Holocene paleoproductivities compared to the Last Glacial Maximum in central-south Chile (35–37°S) while this scheme is reversed for north-central Chile.

Multi-scale, interdisciplinary approaches and focused research groups are needed to understand air–sea interactions, plankton dynamics, biomass removal by fisheries, and the transformation and fluxes of matter across the different HCS components. In this paper, we present a multidisciplinary synthesis of the HCS that covers its physics, atmosphere, primary and secondary production, medium and high trophic levels, fisheries including management aspects, and relevant sedimentary studies.

1. Introduction

The Humboldt Current System (HCS) is a major Eastern Boundary Upwelling Ecosystem and is most notable for its amazing production of small pelagic fish (Chavez et al., 2008). The domain extends from southern Chile (~45°S), where the West Wind Drift intersects the South American continent, to northern Peru and Ecuador (~4°S), where cool upwelled waters collide with warm tropical waters forming the Equatorial Front. The domain is by no means uniform, encompassing three well-defined upwelling subsystems: (1) a productive seasonal upwelling system in central-southern Chile; (2) a lower productivity and rather large "upwelling shadow" in northern Chile and southern Peru; and (3) the highly productive year-round Peru upwelling system. How these subsystems are inter-connected and/or dependent on each other remains uncertain. In addition to the high productivity of small pelagic fish, the HCS is notable for its clear connectivity to large-scale basin-wide dynamics associated with El Niño, decadal and centennial variability, and a large and dynamic oxygen minimum zone (OMZ).

This review attempts a multidisciplinary synthesis of the HCS that focuses on three specific aspects: (1) ecosystem processes,

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* Corresponding author. Address: Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile Las Palmeras 3425, Casilla 653, Santiago, Chile. Tel.: +56 2 9787405; fax: +56 2 2727363.

E-mail addresses: vivianmontecino@uchile.cl, vivian.montecino@gmail.com (V. Montecino), clange@udec.cl (C.B. Lange).

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components, and scales; (2) fisheries; and (3) sediment studies. It is by no means exhaustive; rather the work highlights novel findings and recent advances, thereby extending and updating previous reviews on the HCS (e.g. Tarazona et al., 2003; Morales and Lange, 2004; Montecino et al., 2006a; Pennington et al., 2006; Thiel et al., 2007; Bertrand et al., 2008a). Therefore, the literature cited herein is purposefully restricted mainly to papers published from 2003 onwards.

The paper begins with background information on the HCS, including fishery resources. The second section about ecosystem processes pays special attention to the fact that the HCS is influenced by factors on different time scales and by the presence of the OMZ. In the third section, we examine contemporary fisheries activities, research, and management. Longer term changes in the HCS derived from sediment studies are presented in the fourth section. Finally, we discuss end-to-end shifts and the need for further research.

1.1. Some historical background

Long before contemporary times, ancestral populations developed along the arid coast of the eastern South Pacific (Thiel et al., 2007). Native South Americans used and knew much about marine resources. Marine resources were collected for multiple purposes, including trade. The native people made use of coastal near-shore species, salt, guano, and whales (Antezana and Bahamonde, 2002). In the 19th century, the German naturalist Alexander von Humboldt reported the measurements of the cold current in 1846 in his book Cosmos, so the Humboldt Current (HC) was named in his honour.

As a consequence of the increasing economical importance of the marine resources in the HCS, public institutions aimed at the study of fisheries fluctuation, oceanography, and ecosystem dynamics (e.g. Instituto Nacional de Pesca, INP, in Ecuador; Instituto del Mar del Peru, IMARPE, in Peru; Instituto de Fomento Pesquero, IFOP, in Chile) have been of crucial scientific importance for the past half century (for more information, see Tarazona et al., 2003; Thiel et al., 2007; Chavez et al., 2008). In Peru, international oceanographic cooperation strengthened in the 1970s after the collapse of the anchovy fishery, in the 1980s with the creation of WorldFish Center (previously ICLARM) and German collaboration (GTZ), and, more recently, through ties with the Institut de Recherche pour le Développement (IRD, France). In Chile, multi- and interdisciplinary marine research has increased significantly through the building of focused research groups (JGOFS-Chile; IAI; the FONDAP Program of the Scientific & Technological National Commission; CONICYT; the Center for Oceanographic Research in the eastern South Pacific, COPAS; and the Center for Advanced Studies in Ecology and Biodiversity, CASEB).

1.2. Fishery resources

Latitudinally, Peru and Chile can be divided into fishery regions that coincide with the upwelling subsystems of northern and central Peru; southern Peru and northern Chile (S. Peru–N. Chile); and central Chile from 30°S to 40°S; plus the most southern region of Chile in the Inland Sea (Montecino et al., 2006a). The three Chilean regions are similar to those described by Escribano et al. (2003), who also identify a Northern Upwelling Region, a Central/Southern Upwelling Region, and the Austral Fjords Region. Moreover, these authors incorporate characteristics from three larger-scale systems: the Trade Wind, the Westerlies, and the Polar biomes. The Pacific Trade Wind biome corresponds to the tropical ocean and the Westerlies biome is considered to be a transition zone between the Trade Wind and Polar biomes. The diversity patterns of benthic and pelagic marine communities in the eastern South Pacific support the existence of these biogeographic units.

The names of the principal artisanal and industrial resources are listed in Table 1. Additionally, the relative importance of the recent landings of the different taxa is shown.

2. Scales and processes in the Humboldt Current System

2.1. General characteristics of the HCS

On the large scale, the trade wind system is the primary driver of ocean circulation. The trade winds are set up by the permanent South Pacific High centred off northern Chile and the low pressure region over Indonesia. Variability in this system is driven by latitudinal shifts of the Intertropical Convergence Zone (ITCZ) and trade winds in the north, the South Pacific High at mid-latitudes, and the increasing effects of cyclonic storms and Southern Westerlies as one moves south. Therefore, recurrent coastal features are due to equatorward coastal winds, the South Pacific High, and mid-latitude cyclonic storms that reach the coast from offshore. Off central Chile, atmospheric variability is augmented by the excitation of coastal low pressure systems that are trapped by the intersection of the marine boundary layer and the coastal mountains, propagating poleward from 27°S to as far as 42°S (Montecino et al., 2006a, and references therein).

In the upper ocean, the HC, also known as the Peru–Chile Current, is characterized by an equatorward flow of fresh, cooler Sub-Antarctic Surface Water northward of ~45°S along the eastern rim of the subtropical gyre (Fig. 1, left). The main flow of the HC veers offshore in southern Peru and a weaker coastal limb continues equatorward (Chaigneau and Pizarro, 2005a). The fresher waters mix with the very salty and warmer Subtropical Surface Waters (SSW) beginning at ~18°S and are partially subducted. At the northern end, the cool (and saltier) coastal (upwelled) waters off Peru collide with the fresh, warm Tropical Surface Waters (TSW) (Swartzman et al., 2008). Below the surface circulation and water masses, the equatorial undercurrent (EUC) flows eastward along the equator and feeds the poleward Peru–Chile undercurrent (PUC). This poleward undercurrent lies over the slope and continental shelf from northern Peru to about 42°S off Chile. A more ephemeral surface poleward Peru–Chile Countercurrent is sometimes found between the two equatorward limbs of the HC (Strub et al., 1998; Chaigneau and Pizarro, 2005b).

Mesoscale variability, meanders or fronts, and squirts and filaments are characteristic features superimposed on the large-scale HCS circulation in the eastern South Pacific. Chaigneau et al. (2008) studied the mesoscale dynamics of the Peruvian oceanic region (between 3°S and 19°S and 70°W and 90°W), observing that eddies are more frequent south of 15°S and off Chimbote (9°S) than in the rest of the study area. Long-lived energetic eddies, or those having a lifetime exceeding 3 months, are principally generated near the coast and can propagate long distances offshore (Chaigneau and Pizarro, 2005c; Chaigneau et al., this issue). On the other hand, Hormazábal et al. (2004) defined a coastal transition zone (CTZ) off central Chile that is characterized by high eddy kinetic energy associated with mesoscale eddies and meanders and extends from the coast to ~600 to 800 km offshore. Based on daily SeaWiFS chlorophyll data, Correa-Ramirez et al. (2007) showed that this CTZ can be separated into three regions, with higher chlorophyll-*a* (Chl-*a*) concentrations occurring in wider regions next to the coast off Peru (10–15°S) and central Chile (30°S), and very narrow regions off northern Chile (Montecino et al., 2006a).

Coastal upwelling is the key process responsible for the high biological productivity of the HCS (Fig. 1 centre and right). Its seasonal and spatial dynamics have been well described by Strub et al.

Table 1
Common and scientific names of principal artisanal and industrial resources in the Humboldt Current System (HCS) separated by fish (pelagic and demersal), Crustacea (Crust), molluscs (Moll), echinoderms (Echin) and macroalgae (Seaweeds). List is based on geographical distributions in the HCS, species mostly under special or quota regimes, and landings in Peru and Chile (available from FAO, IFOP, IMARPE, SERNAPESCA, SUBPESCA and PRODUCE).

	Common name		Scientific name	Landings in 2007 (t)		
	English	Spanish		Peru	Chile	Total
Fish	Anchovy	Anchoveta	*Engraulis ringens*	6,159,802	1,392,408	7,552,210
	Jack mackerel	Jurel	*Trachurus murphyi*	254,426	1,302,784	1,557,210
	Chub mackerel	Caballa, macarela	*Scomber japonicus*	62,387	298,123	360,510
	Sardine, common sardine	Sardina común	*Strangomera bentincki*[b]		281,382	281,382
	Patagonian grenadier	Merluza de cola	*Macruronus magellanicus*[b]		61,819	61,819
	Common hake	Merluza común	*Merluccius gayi gayi*		43,571	43,571
	Common hake	Merluza común	*Merluccius gayi peruanus*	31,634		31,634
	Mullet	Lisa	*Mugil cephalus*	10,549	79	10,628
	Bonito	Bonito	*Sarda chilensis*	9706	4	9710
	Corvina drum	Corvina, lorna	*Cilus gilberti*	6530	564	7094
	Patagonian toothfish	Bacalao de profundidad	*Dissostichus eleginoides*	126	4995	5121
	Yellow-fin tuna	Atún aleta amarilla	*Thunnus albacares*	4080	121	4201
	Barndoor skate	Raya	*Raja chilensis*	974	3203	4177
	Pomfret	Reineta	*Brama australis*[b]		3850	3850
	Swordfish	Pez espada	*Xiphias gladius*	57	3741	3798
	Snoek	Sierra	*Thyrsites atun*	91	976	1067
	Sardine	Sardina	*Sardinops sagax*	4	979	983
	Besugo	Besugo	*Epigonus crassicaudus*[b]		931	931
	Elephant fish	Pejegallo	*Callorhynchus callorhynchus*	13	650	663
	Ling, kinglip	Congrio negro, c. colorado	*Genypterus maculatus; G. chilensis*	–[a]	654	654
	Cusk eel	Congrio	*Genypterus* spp.	423		423
	Flat fish	Lenguado	*Paralichthys* spp., *Hippoglossina* sp.	204	34	238
Crust	Shrimp	Camarón nailon	*Heterocarpus reedi*	–[a]	4456	4456
	Yellow prawn	Langostino amarillo	*Cervimunda johni*	–[d]	4197	4197
	Red prawn, squat lobster	Langostino colorado	*Pleuroncodes monodon*	–[a]	1545	1545
	Crab	Jaiba, cangrejo	*Cancer* spp., *Homalaspis* sp.,	843	186	1029
	Brown shrimp	Langostino café	*Farfantepenaeus californiensis*[c]	524		524
Moll	Squid	Pota, jibia	*Dosidicus gigas*	427,591	124,389	551,980
	Scallop, Peruvian calico	Ostión, concha abanico	*Argopecten purpuratus*	43,286	19,584	62,870
	Chilean clam	Almeja	*Venus antiqua*	–[e]	15,816	15,816
	Cholga mussel	Cholga	*Aulacomya atra*	8769	3974	12,743
	Chilean abalone	Loco, chanque	*Concholepas concholepas*	2543	2939	5482
	Gastropods	Caracoles	*Tegula* spp; *Prisogaster* spp.	2838	1592	4430
	Pacific clam	Culengue, almeja blanca	*Gari solida*	478	3673	4151
	Top shell	Locate, caracol	*Stramonita chocolata*	2838	654	3492
	Razor clam	Macha	*Mesodesma donacium*	–[a]	2882	2882
	Limpet	Lapa	*Fissurella* spp.	218	2264	2482
Echin	Red sea urchin	Erizo	*Loxechinus albus*	1932	38,526	40,458
Seaweed	Bull kelp	Huirales	*Macrocystis* spp.; *Lessonia* spp.	$\sim$18,000	178,726	196,726

[a] No data.
[b] Only in southern HCS.
[c] Only in northern HCS.
[d] Crustacea = 4148 t.
[e] Clams = 13,409 t.

(1998), Montecino et al. (2006a), and Thomas and Brickley (this issue) and so will be only briefly covered here. In central-southern Chile, upwelling is highly seasonal with maximum upwelling-favourable winds and biological productivity in austral summer (January–March). This productive region "merges" with the highly productive, seasonal, subtropical front. Off central Chile (starting at $\sim$35°S) and extending to 16°S in southern Peru, the oligotrophic subtropical gyre impinges on the coast, creating a narrow but productive coastal upwelling zone. This region is reminiscent, with some differences, of the Southern California Bight in the California Current System (CCS). A transition from seasonal to permanent upwelling occurs off central Chile ($\sim$33°S) and off northern Peru ($\sim$4°S) (Fig. 1); off Peru upwelling forcing peaks in austral winter (July–September). Somewhat paradoxically, biological productivity is out of phase with upwelling-favourable wind forcing (Pennington et al., 2006); iron and light limitations have been implicated as the cause of lower productivity during the winter season (Hutchins et al., 2002; Chavez et al., 2008; Echevin et al., 2008; Friederich et al., 2008).

High Chl-*a* is typically restricted to within 50 km of the coast, although the effects of upwelling can be detected far offshore through the offshore advection of filaments (Correa-Ramirez et al., 2007). Moreover, in a narrow coastal band, the annual Chl-*a* cycle is strong along the entire latitudinal extension (Yuras et al., 2005), contrasting with previous observations that showed a weak seasonal cycle of Chl-*a* averaged over a 100-km band next to the coast off northern Chile (Montecino et al., 2006a).

Off southern Peru, the veering of the main limb of the HC offshore creates ventilation, and is the primary driver of an intense OMZ from sub-surface to intermediate depths. The sinking and remineralization of surface-derived organic matter further contribute to the OMZ. At the northern end, the EUC ventilates the OMZ and, at the southern end, the PUC advects the low oxygen waters poleward into northern Chile. Of the six permanent hypoxic regions in the world oceans, the eastern South Pacific OMZ is volumetrically the fourth largest, occupying $2.18 \pm 0.66 \times 10^6$ km^3 and accounting for 11% globally. Its core is centred off Peru, where the upper boundary is shallow ($\leqslant$100 m) and the vertical extension may reach 600 m (Fuenzalida et al., 2008). Off Peru and northern Chile in the PUC, low dissolved oxygen conditions (<0.5 mL L^{-1} or <22.3 mM O_2) in the OMZ determine the nature of denitrification (aerobic or anaerobic). Chemical signatures of the PUC extend from

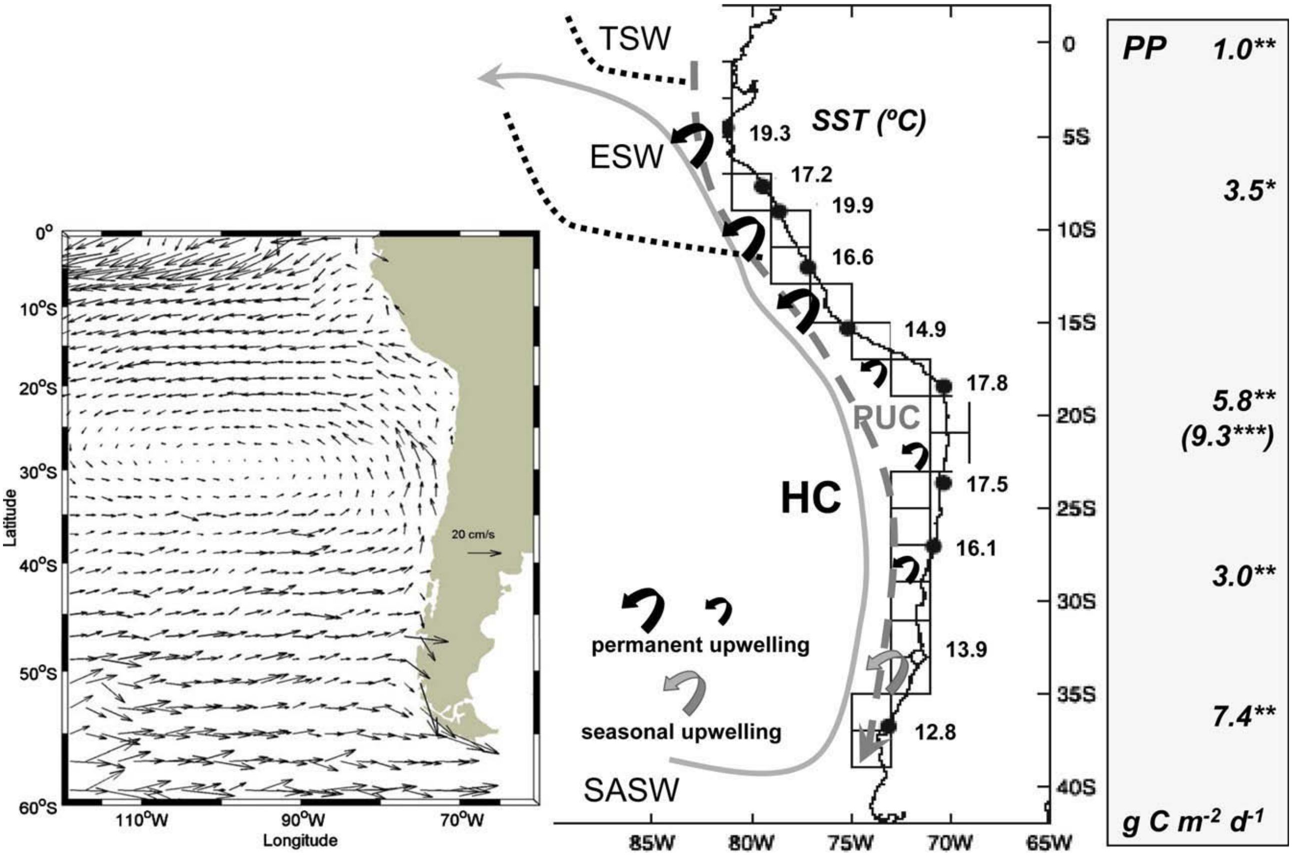


Fig. 1. Main characteristics of the Humboldt Current System (HCS). Left: Mean surface currents obtained from surface satellite-tracked drifters from 1991 to 2005 (map provided by O. Pizarro, University of Concepción). Centre: Water masses and currents (Strub et al., 1998; Graco et al., 2007); schematic representation of permanent and seasonal upwelling (black and light grey arrows, respectively; Mackas et al., 2006); and long-term mean values of sea surface temperatures (SST in °C) at different locations from Montecinos et al. (2003). Right: Primary production (PP) mean (*) maximum (**) and gross (***) daily values based on Tarazona et al. (2003), Montecino et al. (2006a), Henríquez et al. (2007), and Montero et al. (2007). Grey solid and broken lines represent the Humboldt Current (HC) and the Poleward Undercurrent (PUC); TSW, Tropical Surface Waters; ESW, Equatorial Surface Waters; SASW, Sub-antarctic Surface Waters.

the Equator past 40°S, shaping the distribution of nutrients and biological populations throughout the system (e.g. Montecino et al., 2006a; Farías et al., 2007; Graco et al., 2007; Stevens and Ulloa, 2008).

The HCS is strongly affected by interactions with the equatorial dynamic on scales ranging from intra-seasonal (coastal trapped waves, CTWs), annual (Rossby waves), inter-annual (El Niño/La Niña), to multi-decadal (Pacific Decadal Oscillation, PDO) (i.e. Chavez et al., 2003; Montecinos et al., 2007; Ramos et al., 2008). The primary mechanisms for communicating larger-scale fluctuations to local-scale conditions involve basin-scale changes in the depth of the pycnocline and the advection of different water mass types into the local region (Rutllant and Montecino, 2002; Pizarro and Montecinos, 2004; Ramos et al., 2006; Graco et al., 2007).

2.2. Phytoplankton, primary production, and bio-physico-chemical interactions

Among the key elements in the dynamics of upwelling ecosystems, the pycnocline–nutricline–oxycline depth is fundamental for interpreting phytoplankton productivity and growth associated with the efficiency of any particular upwelling wind event. Along the coast of the HCS, the thermo-nutricline depth changes according to the phase of intra-seasonal CTWs, the annual cycle (seasons), and the inter-annual El Niño/Southern Oscillation (ENSO) cycle (Montecino et al., 2006a,b, and references therein). A multi-scale approach is advisable for studying these ecosystems since all these cold-warm phases and transitions determine the supply of limiting nutrients to the euphotic zone, which, in turn, regulates overall productivity (Fig. 2). Moreover, off northern Chile, wind reversals occur during the relaxation of upwelling conditions, often in connection with the trailing edge of coastal atmospheric lows. These wind reversals result in the fertilization of poleward-facing bays from adjacent upwelling centres (Marín and Moreno, 2002).

Changes in nutrient supply are felt at every trophic level, with consequences in the carbon transfer pathways (microbial web vs. classical trophic chain). This transfer of carbon to higher levels through microbial and classical pathways depends on the size of the phytoplankton components, the heterotrophic community structure, and the feeding preferences of the grazers (González et al., 2004a; Vargas and González, 2004a,b; Morales et al., 2007; Vargas et al., 2007a; Chavez et al., 2008; Pavés and González, 2008).

Multi-scale changes in the oceanographic conditions, i.e. inter-annual scale (EN) and at higher frequencies (seasonal, intra-seasonal), also drive changes in the OMZ. During EN events, the thermocline and upper boundary of the OMZ deepen off northern Chile and Peru, with recognized implications for the pelagic system related to nitrogen losses and carbon export. In contrast, during non-EN years, the oxycline at the upper boundary of the OMZ often occurs at 20–40 m off central Peru (M. Graco pers. comm.). The OMZ core reaches its maximum thickness (~100 to ~350 m) and extension (~300 to 400 km) off central Peru (Fuenzalida et al., 2008). Non-EN years are characterized by high productivity, high nutrients, high N recycling, denitrification, high carbon export, and remineralization (Morales et al., 1999; Graco et al., 2006; Gutiérrez et al., 2006; Paulmier and Ruiz-Pino, 2008).

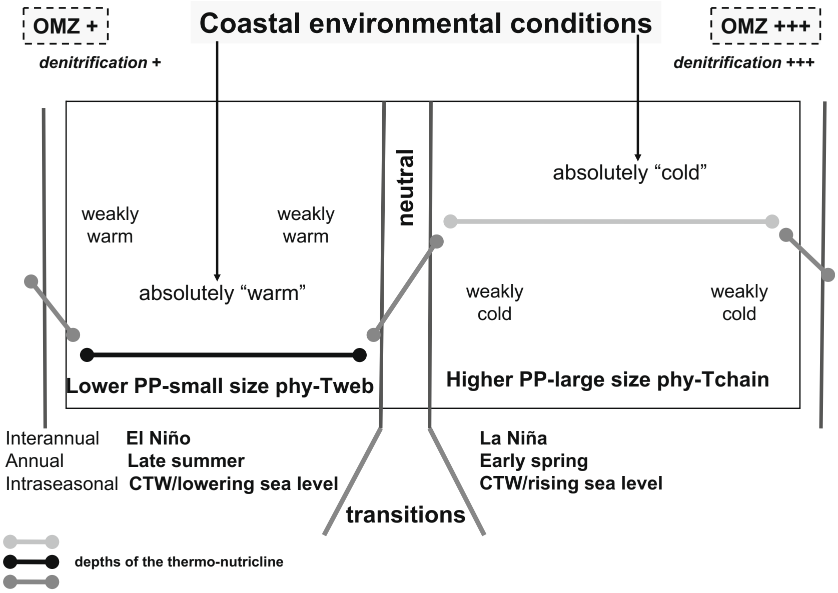


Fig. 2. Schematic representation of coastal environmental conditions from warm to cold, including transitions (neutral conditions), due to changes in the thermo-nutricline depth (black, grey, light grey lines refer to deep, lowering/rising, shallow, respectively), and consequences in the carbon transfer pathways (microbial trophic web (Tweb) with lower PP/small-sized phytoplankton on left vs. classical trophic chain (Tchain) with higher PP/large-sized phytoplankton on right). The depth of the thermo-nutricline changes on different time-scales: inter-annual El Niño/Southern Oscillation (ENSO) cycle, annual cycle (seasons), and the phase of intra-seasonal cycle of lowering/rising sea level associated with coastal trapped waves (CTWs) (modified from Montecino et al., 2006b).

2.3. Residence times, dispersal, and resetting

2.3.1. Zooplankton and fish

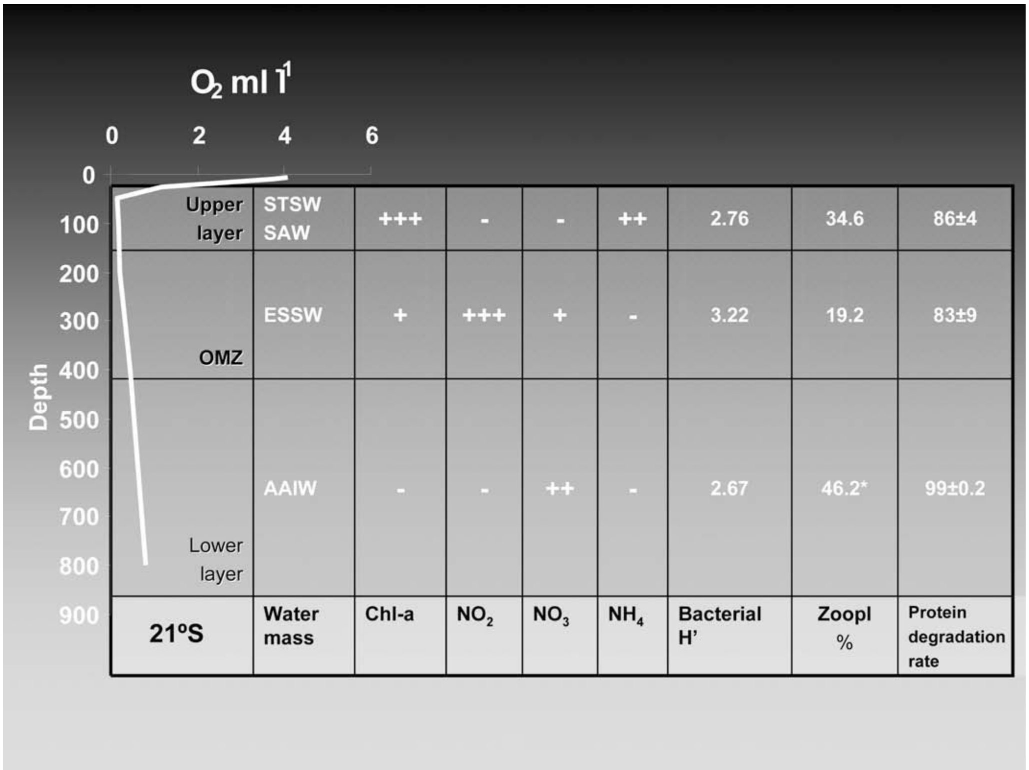
The recruitment of small pelagic fishes is related to the environmental variability in upwelling ecosystems through processes of enrichment, concentration, and transport/retention known as the ocean triad proposed by Bakun (1996). Marín and Delgado (2007) concluded that the near-inertial motion and alongshore changes in current direction may serve as mechanisms of coastal water residence time enhancement. This extended mean "residence time" within the favorable upwelling-conditions of the near-coastal habitat prevents losses of planktonic organisms, which are more critical for species with complex life cycles (Bakun and Weeks, 2008). Mesoscale circulation features may provide other means for retaining zooplankton near favorable habitats. Similarly, the survival of small pelagic fishes over a range of different spatial–temporal scales is thought to be mediated mainly by environmental conditions rather than by density-dependent processes (Bertrand et al., 2004). However, although it is known that environmental conditions largely influence the survival of early life stages, forecasting environmentally-driven fluctuations in irregular recruitment remains problematic (Brochier et al., 2008; this issue). Field egg and larval abundances indicating spawning locations and periods were used to investigate, through modelling and simulations, the factors driving variability in survival rates; for this, larval retention associated with phytoplankton-rich coastal areas was evaluated. Discrepancies between the seasonality of enrichment (winter) and high primary production in summer are discussed by Lett et al. (2007) in relation to anchovy egg and larva distributions in the northern HCS. Furthermore, off Peru and north-central Chile, the vertical migration of part of the zooplankton, in particular fish eggs and larvae, is restricted by the presence of the shallow OMZ.

Zooplankton vertical migration is also associated with the OMZ (Fig. 3). Escribano et al. (2008) provide a complete assessment of copepods and euphausiids in northern Chile (20°S) for March 2000, revealing that the whole sampled water column (0–600 m) is occupied by distinct species having well-defined habitats, some of which occupy the OMZ on a daily basis. Ontogenetic migrations were evident in Eucalanidae and *Euphausia mucronata*. Estimates in terms of biomass showed a substantial daily exchange of carbon between the euphotic layer and the OMZ, with over 75% of the total zooplankton biomass moving into and out of the OMZ. This crustacean zooplankton biomass participates actively in carbon exchanges through respiration, mortality, and the production of faecal pellets within the OMZ. The strong inter-annual variability recurrently exposes these ecosystems to disruptions or resetting (Bakun and Weeks, 2008; Chavez et al., 2008).

2.3.2. Intertidal communities and benthos

Wind-driven coastal ocean circulation is crucial for the dispersal of marine benthic invertebrates and the recruitment and settlement of intertidal species (Broitman et al., 2001; Narváez et al., 2006; Vásquez et al., 2006). In conjunction with wind stress, buoyancy fronts produced by river plumes, common from about 30°S southward in the HCS, can also play a role in delivering larvae to shore (Vargas et al., 2006a).

Since retention is influenced by both physical and biological (behaviour) factors (Marín and Moreno, 2002; Montecino et al., 2006a; Rykaczewski and Checkley, 2008), larval dispersal studies rely on two different approaches: those with physical orientations and those based on organism behaviour. The former approach does not emphasize the biological characteristics, but treats larvae as passive particles. Thus, settlement variability for intertidal species in time has been associated with summer storms and circulation features such as the advection of warm waters that moves frontal zones onshore. Nevertheless, biological-oceanographic models are needed for a better understanding of larval transport beyond the passive particle approach. Mesoscale processes may shape recruitment patterns by way of modulating invertebrate larval dispersal. This has been reported by Lagos et al. (2007) by studying the spatial synchrony in species with contrasting dispersal potential. Spatially, the coastal morphology (i.e. bays, head-lands, coastline configuration) influences the magnitude of larval delivery and subsequent recruitment patterns, as reported for a variety of brachyuran crab species (Palma et al., 2006). Narváez et al. (2006) reported on the effect of what they called 'large warming events', which



21ºS	Water mass	Chl-a	NO_2	NO_3	NH_4	Bacterial H'	Zoopl %	Protein degradation rate
Upper layer	STSW SAW	+++	-	-	++	2.76	34.6	86±4
OMZ	ESSW	+	+++	+	-	3.22	19.2	83±9
Lower layer	AAIW	-	-	++	-	2.67	46.2*	99±0.2

Fig. 3. Synoptic diagram summarizing novel information on the vertical structure of water column features off northern Chile, including the OMZ. Oxygen distribution in a 900 m water column (Farías et al., 2007); water masses (Leth et al., 2004; Graco et al., 2007); chlorophyll-*a* (Chl-*a*) biomass abundances (Montecino et al., 2006a); nitrite, nitrate, and ammonia (Farías et al., 2007); bacterial diversity (*H*′) (Stevens and Ulloa, 2008); crustacean zooplankton percentage for a total of 26 species that live exclusively in the upper layer above the OMZ, within the OMZ, and those that enter the OMZ from above or below; (∗) patterns represent the day-dominant habitat (modified from Escribano et al., 2008). The last column shows percent degradation (%) for decay of sinking protein within each layer (Pantoja et al., 2004). STSW, Subtropical Surface Waters; SASW, Sub-antarctic Surface Waters; ESSW, Equatorial Sub-surface Waters; AAIW, Antarctic Intermediate Waters.

occurred a few times in spring-summer in association with episodic downwelling-favourable (northerly) winds. During these events, the authors observed significant synchrony in the recruitment of several invertebrate taxa (decapods, gastropods, polychaetes, mussels, sea urchins), suggesting that larvae could be entrained in these advective fronts and delivered onshore. The intensity of local upwelling and the distance downstream from an upwelling centre are also factors influencing the succession and structure of hard-bottom communities (Broitman et al., 2001; Castilla and Largier, 2002; Castilla et al., 2002; Wieters et al., 2003; Navarrete et al., 2005; Blanchette et al., this issue).

Benthic hypoxic zones and the sediments also offer examples of recruitment changes as does the cyclic "resetting" of the system on the scale of ENSO perturbations. Indeed, these regions host specific benthic fauna together with giant sulphur bacteria during normal "colder" La Niña conditions. During EN events, better oxygenated conditions prevail and some species proliferate, whereas others emigrate or die. All these changes affect local small-scale fisheries; i.e., increase in shrimp abundance or modifications in the population distribution of other invertebrates (Arntz et al., 2006).

2.4. Trophic interactions and size structure

Scaling and allometric approaches based on the well-accepted concepts of the pyramids of biomass and numbers are useful for studying ecological systems. Moreover, the size and numerical abundance of different organisms are tightly coupled (Damuth, 1991). Determination of biomass distribution by size in pelagic systems has been a significant step in the search for generalizations in aquatic ecology (Marquet et al., 2005, and references therein). In addition, the consideration of body size as a state variable has been a useful tool for specific modelling efforts (i.e. size-based simulation model of carbon and nitrogen flows in plankton communities). Changes in the taxonomic composition along the community size spectrum can explain the relationship between photosynthetic efficiency and the phytoplankton size structure off Chile, as is also the case for the fate of carbon on inter-annual scales (Montecino and Quiroz, 2000; Iriarte and González, 2004).

Recent studies about the relative importance of microbial and classical food webs in permanent and seasonal upwelling loci in the HCS have yielded novel information on quantitative grazing interactions that may be the controlling factor in the size, abundance, and biomass of coastal assemblages. One of the few attempts to analyze both the abundances of microorganisms and grazing processes under oxic and suboxic conditions of marine areas characterized by a relatively shallow OMZ, or hypoxic environments, is the study of Cuevas and Morales (2006) off northern Chile. These authors found that heterotrophic nanoflagellate (HNF) consumption controls bacterial production in the suboxic layer. Previously, Vargas and González (2004b) indirectly estimated protozoan ingestion rates (including HNF, ciliates, and heterotrophic dinoflagellates) from an area around Mejillones Bay (23°S), concluding that the HNF were largely bacterivorous. A study of seasonal variations in the trophic pathways of carbon at 36°S over the shelf off Concepción provided evidence that the energy available for larger omnivorous and carnivorous metazoans, and even for commercially exploitable pelagic fishes, may be considerably larger than that estimated from a simple herbivore-dominated food chain model (Vargas et al., 2007a).

In upwelling ecosystems, high bacterial rates are related to labile dissolved organic carbon (DOC) availability during relaxed upwelling cycles; depending on seasonality, carbon bacterial demand on primary production is high and can be efficiently transferred to higher levels through the trophic microbial web (G. Daneri, pers. comm.). Despite the fact that biological processes could be synoptically and locally important, on the large-scale, the relationship between bottom-up forcing, zooplankton, and foraging fish species has been corroborated in Peruvian waters (Ayón et al., 2004, 2008). Apparently, the observed multi-year, large-scale, bottom-up control occurs at the same time as the smaller-scale depletion of zooplankton when and where anchoveta are locally abundant. This effect was observed over a wide range of anchoveta abundances.

2.5. Fluxes of carbon and nitrogen, bacterial activity, and the OMZ

In the oceans, it is clear that natural climate variability can have a large impact on the ecosystem structure and biological productivity (Chavez, 2006). Net primary production in the global ocean is thought to be in the range of 40–70 Pg C per year and is accomplished by a phytoplankton biomass of about 1 Pg C. Consequently, on average, the phytoplankton biomass turns over on the order of once per week (Marra, in press).

In the HCS, carbon fixation has been reported to reach very high values (1.0–9.3 mg C m^{-2} d^{-1} with an overall mean of 3.5 g C m^{-2} d^{-1} for Peru) (Fig. 1), varying widely between inshore and offshore, and changing with seasonal upwelling and bio-optical variability (Montecino et al., 2004). Many efforts have been undertaken to understand the role of key species or functional groups in global carbon sequestration. The high fluxes of $CaCO_3$ (maximum ~180 mg m^{-2} d^{-1}) at 30°S represent a potential sediment reservoir, as they result in significant accumulations in the underlying deep sediments (8–9 weight% in continental slope cores), and therefore in carbon sequestration (González et al., 2004b; Marchant et al., 2004). Also, the crucial role that euphausiid faecal material plays in the total organic carbon export flux to the sediments has been recently assessed by González et al. (this issue) along the HCS between 19°S and 42°S.

Phytoplankton is continually stirred and mixed by ocean processes and air-sea interactions, playing a role in the exchange of chemical species (i.e. gases and aerosols). Studies of CO_2 dynamics (sources and sinks) in the eastern South Pacific are important for a better understanding of the interplay between global climate change and the CO_2 budget. The upwelling areas off Peru and Chile are considered important areas for CO_2 exchange with the atmosphere, and the Peruvian upwelling system has been found to be a source of CO_2 to the atmosphere during all seasons (Friederich et al., 2008). Measurements of carbon dioxide fugacity (fCO_2) during upwelling may reach >400 μatm, and there is a latitudinal gradient in CO_2 outgassing between northern and central Chile caused by increased wind speeds in the south. It appears that, for western South America, the crossover from source to sink occurs between 21°S and 27°S (Friederich et al., 2008). However, fCO_2 may decrease or reverse after a period of strong photosynthesis in phytoplankton-rich filaments and patches (Montecino et al., 2006a). In some cases, suboptimal levels of dissolved iron may prevent a rapid biological uptake of the upwelled, supersaturated CO_2 waters, contributing to the continued outgassing of the excess CO_2 (Torres and Ampuero, in press).

Upwelling also promotes N_2O outgassing as measured from 2002 to 2007 (36°S) and 2000 to 2004 (~21°S) by Cornejo et al. (2007) and Farías et al. (2007), respectively. At 21°S, N_2O displayed sharp, shallow peaks with concentrations of up to 124 nM (1370% saturation) in association with a strong oxycline that impinges on the euphotic zone; N_2O levels at these peaks were highly variable and depended on the development of a physical gradient evidenced by the presence of the surface mixed layer associated with the Eastern South Pacific Intermediate Water. Thus, part of this high, shallow N_2O accumulation can be lost towards the atmosphere, making a high potential greenhouse contribution. At 36°S, Cornejo et al. (2007) confirmed that the continental shelf off central-south Chile is an important source of N_2O to the atmosphere, with a mean annual N_2O flux of 30.2 μmol m^{-2} d^{-1}. The authors found that increasing N_2O concentrations agree with the appearance of upwelling-favourable wind stress and a strong influence of oxygen-poor, nutrient-rich ESSW.

In these coastal upwelling areas, autotrophic activity is generally high, with high incorporation and degradation rates of dissolved organic carbon (DOC) coupled with high mineralization rates. The strong relationship between primary productivity (PP) and bacterial productivity (BP) suggests tight coupling between the organic matter produced during photosynthesis (fresh material) and bacterial utilization. The above conclusions, coupled with the lack of correlation with temperature, seem to confirm that organic substrate availability is an important factor affecting bacterial activity in upwelling areas (Vargas et al., 2007a,b). Within the 36°S seasonal upwelling system, bacterial activity was low during non-upwelling periods; consequently, the relationship between PP and BP can be associated with water column stratification processes (Vargas et al., 2007a).

Bacterial secondary production (BSP) has been differentially evaluated from non-bacterial prokaryotes in the OMZ off central Chile (Levipan et al., 2007). This time series of prokaryote secondary production (PSP) showed that BSP accounted for the majority of the PSP with maximum values of ~600 μg C m^{-3} h^{-1}. Moreover, Van Wambeke et al. (2007) reported heterotrophic bacterial production coupling with primary production on a larger scale in the eastern South Pacific.

The OMZ is an important sink for fixed nitrogen, contributing 30–50% of the oceanic nitrogen removal, mainly through the process of pelagic denitrification. In this low-oxygen zone, anaerobic denitrification by bacteria that use nitrate as an electron source reduces nitrate to nitrite (depleting nitrate and increasing nitrite) and ultimately reduces nitrite to nitrous oxide (Montecino et al., 2006a). Strong gradients and a high vertical structure of nitrogen species exist on a scale of meters. The biological and functional diversity of microorganisms living in the OMZ have been studied recently along the oxygen gradient in the HCS (Molina et al., 2007; Stevens and Ulloa, 2008). These studies were related to the characterization of functional genes involved in nitrogen cycling in the OMZ of the HCS and showed shifts in the structure of ammonia monooxygenase (*amoA*) genes and nitrite reductase (*nirS*) genes. Anammox is the microbially catalyzed anaerobic oxidation of ammonium coupled to nitrite reduction, with the production of nitrogen gas. Observations by Thamdrup et al. (2006) off Chile indicated that ammonium was oxidized and nitrite was reduced through the anammox reaction, whereas denitrification was generally not detected and, therefore, the area was a minor sink for nitrite. In these environments, anammox is the only documented anaerobic pathway of ammonium oxidation and it provides a second route from fixed nitrogen to N_2 along with microbial denitrification, which was previously thought to be the only important process to convey such a conversion.

The high decay rates of organic carbon in the water column and high bacterial growth efficiency result in a generally low (<1%) rain rate of organic carbon at the sediment–water interface. No acceleration of the particulate flux of sinking organic matter due to the presence of the OMZ has been observed (Pantoja et al., 2008).

A summary of the main characteristics described above is shown in Fig. 3, superimposed on the vertical structure of the water column features, including the OMZ defined by the oxygen vertical gradient.

3. Fisheries activities, research, and management

An ecological understanding of the ocean is essential for many disciplines (Rykaczewski and Checkley, 2008) and fisheries constitute one of the most complex anthropogenic effects. Recent ecosystem-based management directives, as recommended by many experts, require considering both direct and indirect fishery effects (Crowder et al., 2008). Although the indirect effects of fisheries are predicted to lead to an unprecedented decline in marine top predators and the initiation of trophic cascades (Heithaus et al., 2008), these topics have not been studied much in the HCS (Taylor and Wolff, 2007; Taylor et al., 2008). By-catch constitutes an additional concern because, during fishing operations, such catches are often discarded (i.e. seabirds, sharks, rays, chimaeras, turtles). Worldwide discards have declined over about a ten-year period from 27 to 7 million t (Zeller and Pauly, 2005). This global reduction might have been caused by an overestimate (of about 7 million t) in the original figure and a switch to more selective gear, but there are also indications that an increased portion of the by-catch is now being retained and used. The demersal crustacean fishery produces the highest levels of by-catch in Chile (www.oceana.org, Document 11, June 2005).

Today, emergent deep-sea fishing methods in the eastern South Pacific that target species and habitats of seamounts and canyons also give cause for conservation and regulatory concerns; long-lived species with restricted habitats and high concentrations (i.e. orange roughy) are highly vulnerable to depletion. When addressing the issue of deepwater fisheries in the HCS, trawling poses another problem because it affects the fragile cold-water benthos. The enforcement and compliance of regulations regarding these issues at sea is not only technologically but also legally difficult (FAO, COFI/2007/Twenty-seventh Session, Rome, Italy, 5–9 March 2007).

3.1. Fisheries in the Humboldt Current System

The primary commercial catch off northern-central Peru is taken from a single anchovy (anchoveta) stock, with a historical but lesser contribution from a sardine stock. Other species exploited include chub mackerel and bonito. In the S. Peru–N. Chile region, important commercial species include sardine, a second anchoveta stock, jack mackerel, tuna, and swordfish. In central Chile, the primary commercial fish are anchoveta, jack mackerel, and common sardine. Total landings of species like chub mackerel, common sardine, hake, and squid are much smaller (Table 1).

The Chilean fjord region is an important area for trawl and long-line fisheries based on gadiform fishes such as Patagonian grenadier and southern hake; the latter has supported annual catches of 30,000 t in the past decade (Bustos et al., 2007).

Industrial demersal fisheries are actually comparatively small in the HCS (<1% of total fish landings in Peru). The hake (*Merluccius gayi peruanus*) fishery in Peru has shown a significant decline in the last 15 years, attributed to overfishing, and a diminished reproductive capacity and increased population vulnerability to environmental stress (Ballón et al., 2008; Guevara-Carrasco and Lleonart, 2008). The Chilean hake (*Merluccius gayi gayi*) fishery, which is concentrated in central-south Chile, has reached maximum catches of >100,000 t but has currently decreased to less than 44,000 t (Table 1).

3.1.1. Small to medium-sized pelagic fish

Along with sardine, anchoveta experience well-known periodic changes in population size and distributions, with anchoveta found in more recently upwelled waters closer to the coast and sardines normally found farther offshore. The shifting abundance between anchoveta and sardine populations (Niquen and Bouchon, 2004) throughout the upwelling system has been explained by the habitat-based hypothesis related simply to the range of habitat available forced by climatic changes on different temporal scales (Bertrand et al., 2004; Gutiérrez et al., 2007). The specific mechanisms by which climatic changes affect the distribution and abundance of the fishes are still a subject of debate. Anchoveta are a main prey of marine mammals, seabirds, fish, and fishers, being an important component of matter and energy processing in the HCS.

Three major fishing stocks are recognized throughout the anchoveta distribution range (4–42°S); the largest stock is off northern Peru, a medium-sized one is found off southern Peru–northern Chile, and a smaller stock exists off central Chile (Castro et al., 2001). In terms of population studies and recruitment variability (Yáñez et al., 2001), stock units must be carefully identified, especially to improve management regulations. Anchoveta large-scale spatio-temporal dynamics, considering the concentration, percent occupancy of space, and clustering of high-fish abundances in relation to environmental variables from 1983 to 2003 in Peru, showed transition periods with associated high biomasses of anchovy and sardine, but with different spatial aggregation patterns (Gutiérrez et al., 2007). Latitudinal variations in environmental characteristics off northern and central Chile during the anchoveta spawning season are correlated and crucial for larval survival, as are transport, retention, and food limitations during their early life history (Castro et al., 2001).

A synchronous fluctuation pattern has been quantified in the three anchoveta fisheries from the northern to southern upwelling ecosystems; these were found to be out of phase with large-amplitude sardine (*Sardinops sagax*) fisheries (Cubillos et al., 2007). In the southernmost spawning population of the HCS, the reproductive strategies of common sardine (*Strangomera bentincki*) and anchoveta take advantage of the effects of seasonal upwelling (Cubillos et al., 2001); spawning at the end of the winter enhances egg and larva survival during moderate upwelling, low turbulence, and the weak offshore Ekman drift.

Gutiérrez et al. (2008) indicated that, off Peru, there is an ecological overlap between anchoveta and the squat lobster or red prawn, *Pleuroncodes monodon*. Whereas red prawn are restricted to the coldest coastal waters, anchoveta occur over a wider temperature range. It is worth noting that *P. monodon* inhabits the HCS from 7°S off Peru to Chiloe Island (43°S) in Chile, where it has a bottom habitat. The demographic explosion of red prawn off Peru since the mid-1990s is concomitant with colder conditions and was accompanied by a change toward more pelagic behaviour. M. Gutiérrez et al. (2008) linked this change to the shallower oxycline off Peru, as compared to that off Chile.

The high degree of plasticity in the feeding behaviour of anchoveta (Espinoza and Bertrand, 2008) and clupeoids in general (van der Lingen et al., 2006) is a matter of ongoing study in the context of ecosystem functioning. This will help to re-adjust and resolve ecosystem models and predictions for these small pelagic fishes. Trophodynamic anchoveta studies using the conversion of stomach contents to carbon equivalents and generalized additive models (GAMs) indicate that zooplankton (with euphausiids contributing 67.5% of the dietary carbon, followed by 26.3% from copepods) was by far the most important dietary component. Foraging behaviour relates to the diel cycle, distance from the coast, sea surface temperature, and latitude, thereby illustrating the capability of anchoveta to forage at any time and place (Espinoza and Bertrand, 2008).

Jack mackerel or "jurel" is the second largest fishery in the HCS. Jurel spawning is a large-scale process and the population is considered to be composed of a single stock based on the seasonality of the fishery and migrations, known spawning grounds, similarity of the size composition of catches, and genetic convergence throughout the HCS (Poulin et al., 2004; Cubillos et al., 2008). Jurel is considered to be a straddling species (distributed both inside and outside the 200-mile economic exclusive zone, EEZ) for reproduction and feeding. Jurel has been studied in Chile by more than 80 projects and is subject to constant direct assessment.

The jurel fishery became important in the early 1970s, when it developed as an alternative to that of anchoveta, which decreased as shown by catch statistics since 1950. After the jurel poor recruitment in the 1980s and its overexploitation (catches reached 4.5 million t in Chile), restrictions were imposed in 1998. Given favourable recruitment from 1996 to 2002, jurel is now under full exploitation. Although in 2007 the most important landing in Chile was anchoveta (30%), it was closely followed by jurel (26%). In contrast, jurel catches in Peru declined markedly in recent years.

3.1.2. Small-scale or artisanal fisheries

In the highly productive region of the HCS, IFOP in Chile, IMARPE in Peru, and INP in Ecuador have been collecting data on landings by species, weight, and gear in the major ports of artisanal fisheries since 1969. Commercially and ecologically important species include molluscs (bivalves, gastropods and cephalopods), crustaceans (crabs, prawns, shrimps), and fishes like hake, barndoor skate, pomfret, and other bentho-demersal resources (Table 1). Small-scale fisheries have exclusive rights to commercial landings within a region extending from 3 to 5 miles from the coast.

Interestingly, management decisions have been most commonly based on sustained landings in small-scale fisheries. Also, although a long-term decline of economically important species in fisheries could motivate some fishers to leave the fisheries, which would lead to a decline in fishing effort, this has not occurred. On the contrary, there has been a long-term trend of increasing fishing effort attributed to socio-economic-cultural issues and livelihood adaptability (Salas et al., 2007).

3.2. Management

The challenge of managing fisheries has gone through phases of state regulation at the national or at least stock level. Present steps, especially in the management of benthic resources, relate to building local capacity for self-regulation and the establishment of equitable access and rights to fisheries resources among stakeholders.

3.2.1. Benthic resources: territorial use rights for fisheries and open access

The co-management of benthic resources is based on territorial use rights for fisheries (TURF) and was developed to improve the management status of benthic fisheries (mainly dive fisheries for invertebrates and algae). The TURF is combined with open access areas. Historically, open access fisheries only need an authorization to exploit mostly resident stocks; from a practical point of view, the fishery has free access.

In Chile, the TURF system was initiated at the beginning of the 1990s but was only legally established in 1997 (Bernal et al., 1999; Thiel et al., 2007). TURF areas are exploited by fishermen under the permanent supervision of the administrative authority according to a base study proposal and a management plan developed by a team of experts and qualified professionals. This type of management directly affects 12,000 small-scale fishermen, involving more than 300 TURF areas. The mid-term tendencies show an increase in the number of these areas. Thus, TURFs have proven to be a good tool for increasing stocks and recovering depleted fisheries.

Experience with incentives for the participation of fishers in the monitoring and management of artisanal fisheries around southern South America has resulted in the conclusion that, overall, centralized monitoring, assessment, and control of these fisheries are unrealistic (Parma et al., 2003). On the contrary, it has been found that delegating much of the monitoring and management only to the local fishers' organizations to conserve their resources has serious risks and consequences. Therefore, co-management experiments should be based on agreements between fishers, scientists, and managers, aiming at the development of sustainable management plans for specific situations. For example, Wolff and Mendo (2002) proposed that co-management plans for the scallop in Peru should be at the level of metapopulations. In addition, the Chilean National Commission of the Environment (CONAMA) has been promoting the development of a model for marine coastal protected areas of multiple uses that would allow both ecosystem connectivity and the conservation of marine biodiversity (CONAMA, 2007).

3.2.2. Fisheries regulations

The total allowable catches (TAC) for benthic and pelagic resources are discussed yearly by the Chilean National Fisheries Council with the participation of fisheries authorities, scientists, and representatives of industrial and artisanal fisheries. In Peru, the same TAC is assigned or adjusted at the beginning of each fishing period and, for anchoveta, a new individual quota system is also being implemented (Chavez et al., 2008). According to Fréon et al. (2008), Peru has a huge overcapacity problem with purse-seiners and fishmeal factories, leading to a very inefficient fishing strategy and with an increase in productions costs. For the fishing fleet, a certain level of overcapacity is advantageous to adjust to high abundance periods, but the present fishing capacity of the Peruvian pelagic fleet is at least three times higher than the average TAC (Fréon et al., 2008).

In the Chilean pelagic fishery, the system of individual transferable quotas (ITQ) was introduced in 2001 and had an immediate impact on the operation of the industrial fleet. The number of active vessels fell from 132 vessels in 2000 to 65 in 2002. Additionally, there were also benefits due to lower capital and operating costs, eliminating chronic overinvestment. Stopping the "Olympic race" also allowed fishermen to catch less fish in a given trip, improving the quality of the landings and allowing diversification in processing and marketing. After December 1997 to December 2000, when the hake (*M. gayi gayi*) fishery was closed for biological reasons, the authorities allowed 'experimental' fishing expeditions to keep the fleet active under controlled conditions. These special expeditions worked as a pseudo-individual quota system and facilitated the formal introduction of an ITQ system later on (P. Barría, IFOP, pers. comm.).

Biological bases and the monitoring of fish and shellfish resources in Peru and Chile can be found at the web sites of IMARPE, IFOP and the Chilean Fisheries Research Fund (FIP). Recently, the results of an overall analysis of the FIP projects (Yáñez et al., 2008), through a structural matrix analysis of some of the resources shown in Table 1, indicated that the focus was on fisheries biology, with little emphasis on oceanography and no interest in economic, social, or governability factors. Evidently, an integrated framework can lead to an adequate protection of marine ecosystems and the sound use of marine resources, including fisheries (Crowder et al., 2008) in the specific case of the HCS.

4. Long-term changes in the Humboldt Current System

Bakun (1990) proposed that the major coastal upwelling systems of the world have been experiencing increased upwelling intensity since the mid-20th century in response to anthropogenic greenhouse forcing. He suggested that elevated atmospheric CO_2 concentrations could intensify coastal ocean upwelling by heating the land surface more than the ocean, enhancing the spring and summer land–sea contrast that drives near-shore upwelling in eastern boundary currents (EBC) regions. Temporal trends in upwelling have been considered by different authors. Recent findings show increased upwelling in the 20th century for the Iberian Peninsula (in winter with a possible negative impact on the recruitment of small pelagic fishes; Santos et al., 2005); the Arabian Sea, where it is accompanied by an increase in phytoplankton biomass (Goes et al., 2005); and parts of the CCS and HCS (Bakun, 1990; Vargas et al., 2007c). For the Canary Current, although upwelling increased in one area (the Moroccan upwelling off Cape Ghir; McGregor et al., 2007), a study of spatio-temporal trends in upwelling patterns for the period 1967–2006 shows a strong decrease in all seasons, particularly summer (Gómez-Gesteira et al., 2008). For the HCS, positive trends of inferred primary production (from organic carbon content in sediments) coincide with increasing upwelling-favourable winds in instrumental records and take place both off central Peru and northern Chile, suggesting that these positive trends occur on a regional scale (Gutiérrez et al., 2006; Vargas et al., 2007c).

4.1. The sedimentary record, decadal, and multi-decadal time scales

Geochemical, micropaleontological, and mineralogical analyses of laminated sediment cores from Mejillones Bay in northern Chile (23°S) and from the central Peruvian continental slope (off Pisco and Callao, 13°43′S and 12°02′S, respectively) combined with 20th century instrumental data, suggest intensification and cooling of coastal upwelling regimes along northern Chile and central-southern Peru since the late 19th century (Vargas et al., 2007c; Siffedine et al., 2008) as well as changes in ecosystem properties, terrestrial runoff, and the oxygenation state of the water column (Gutiérrez et al., 2006, 2008a,b; Díaz-Ochoa et al., 2008; Sifeddine et al., 2008) (Fig. 4).

Vargas et al. (2007c) proposed that the intensification of upwelling-favourable coastal winds appears to have been driven by enhanced solar heating over land (Atacama) through a decrease in low-cloud cover, and that the increased land-sea thermal contrast along this arid coast intensifies the equatorward wind stress resulting in enhanced primary and export production during inter-decadal EN-like conditions. The authors suggest that this mechanism overcompensates for the overall effect of a regional surface warming secular trend in the HCS. The secular intensification of ENSO-like variability from the 19th century closely matches the onset of the modern ENSO teleconnection patterns between tropical and subtropical western South America, implying regional hydrological changes (Vargas et al., 2006b). The results for northern Chile and Peru contrast with a general warming trend over the past ~250 years at the upwelling centre off Concepción (36°S) (Vargas et al., 2007c).

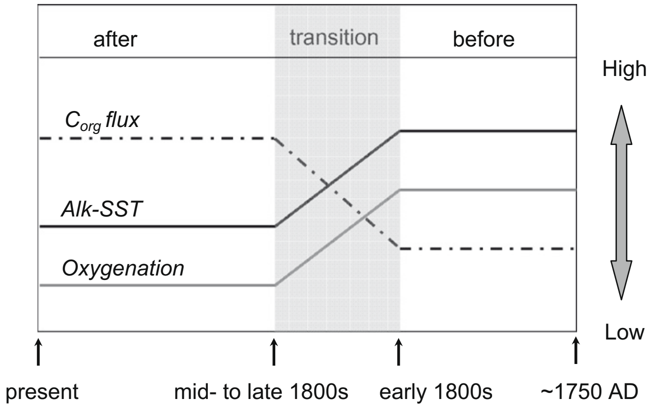


Fig. 4. Schematic representation of changes in sea surface temperature (alkenone-derived, Alk-SST) interpreted as the strength of the Ekman pumping; organic carbon fluxes (Corg flux) used as an indicator of primary/export production; and oxygenation of the bottom environment based on ratios of redox-sensitive trace elements (Cu/Al, Mo/Al, Ni/Al, Zn/Al, V/Al), bulk sedimentary δ^{15}N, and information on the preservation of calcareous foraminifera; data taken from sediment cores collected in upwelling centres off northern Chile (23°S, Mejillones Bay) and central Peru (12–15°S). This drawing simplifies and summarizes information published by Vargas et al. (2007c), Valdés et al. (2008), Díaz-Ochoa et al. (2008), and Siffedine et al. (2008).

4.2. Accumulation of fish scales in sediments under the OMZ

Because of their high economic value, relatively long time-series of abundance records (e.g., landings, recruitment, etc.) are available for pelagic fishes such as anchoveta, sardine, and jack mackerel in some highly productive EBC settings. Recent shifts between alternating anchoveta and sardine regimes have been described for the Pacific and have been linked to large-scale atmospheric and oceanic changes such as the PDO (Chavez et al., 2003). In the HCS, these regime shifts (a cool "anchoveta regime" and a warm "sardine regime") are attributed to long-term periods of warm or cold temperature anomalies related to the advance or retreat of warm subtropical oceanic waters toward the coasts of Peru and Chile (Alheit and Ñiquen, 2004). The recent time series, however, include both environmental influences as well as the impact of fishing. Most landing time series generally extend less than 50 years, limiting our capacity to detect natural multi-decadal scale variability. A "sediment approach" is particularly useful since it provides longer timescales, including periods before the onset of intense commercial fishing (Baumgartner et al., 1992).

The accumulation of fish debris (bones and scales) in sediment settings of the continental shelf and upper slope off Peru and Chile under the hypoxic conditions of the OMZ has received attention over the past 25 years. Fish remains are often well-preserved in these environments, thus providing a record of past changes in fish populations (Milessi et al., 2005, and references therein). Off Callao (Peru), Schwartzlose et al. (1999) provided a ~100-year history (AD 1875–1974) of anchoveta and sardine abundances. Recently, Sandweiss et al. (2004) demonstrated the usefulness of archaeological data in tracking multi-decadal changes between anchoveta and sardines along the coast of Peru. Also, a multi-proxy study, including fish scales from laminated sediments collected off Pisco and Callao (Gutiérrez et al., 2008b), revealed dramatic centennial-scale changes related to the Little Ice Age, with overwhelming multi-decadal variability.

There is evidence that spatial and temporal variations in the extension and strength of OMZs may lead to oxygenation changes in the underlying sediments, and that these variations could greatly affect the preservation of fish remains. The potential preservation biases of fish remains due to variable redox conditions has been recently addressed by Valdés et al. (2008) for Mejillones Bay in northern Chile and by Díaz-Ochoa et al. (2008) and Gutiérrez et al. (2008a) off Peru. Valdés et al. (2008) found that the anchoveta scale deposition rate was probably influenced by dissolution processes linked to higher oxygenation of the bottom environment prior to ca. AD 1820. Díaz-Ochoa et al. (2008) observed an increase in the redox-sensitive trace elements in the early to mid-1800s (Fig. 4) and concluded that the change to more reducing (and probably more anoxic) conditions since the early 19th century might have led to better preservation of fish remains and several biogenic proxies. Gutiérrez et al. (2008a,b) associated this biogeochemical regime shift in the early 19th century with an expansion of the nutrient-rich, oxygen-depleted EESW, which resulted in overall higher diatom and pelagic fish productivity.

4.3. Changes in productivity since the Last Glacial Maximum

Information about paleoceanographic changes and the history of productivity in the HCS has grown over the past two decades. Efforts have focused on the reconstruction of paleoproductivity since marine biological productivity might be one of the mechanisms responsible for glacial/interglacial pCO_2 changes (Broecker, 1982). On glacial–interglacial scales, primary productivity in the upwelling ecosystem off northern Chile has varied with the precessional cycle (~20,000 years) during the last 100,000 years, and with inputs of iron from the continent due to changes in precipitation patterns. This provides evidence for iron control of past productivity in the region (Dezileau et al., 2004; Mohtadi and Hebbeln, 2004). Experimental work has demonstrated that iron limitation is a major constraint on phytoplankton growth along the eastern South Pacific in present times (Hutchins et al., 2002).

Planktonic foraminiferal faunal changes off Chile and sedimentary nitrogen isotope composition ($\delta^{15}N$) data between 11°S and 36°S indicate important and synchronous changes in sub-surface conditions in the HCS during deglaciation (Fig. 5), interpreted as a major reorganization of the OMZ that affected a large region of the eastern South Pacific (Higginson and Altabet, 2004; De Pol-Holz et al., 2006; Robinson et al., 2007; Mohtadi et al., 2008). Sedimentary $\delta^{15}N$ has been widely used as a tool for reconstructing past variations in water column denitrification over timescales from hundreds to million of years, and near-surface NO_3^- drawdown (see Altabet, 2006 for a review). Results from several ^{14}C-dated cores from the upwelling regions of the Peru and Chile margins reveal remarkable similarities among geographic areas with low glacial sedimentary $\delta^{15}N$ values followed by an abrupt rise at ~17 ka (5‰ increase off Peru and northern Chile; 3.5‰ increase off central-southern Chile), a gradual decline until the mid-Holocene, and then an increase toward the present (Fig. 5). The unique deglacial increase in denitrification seems to be decoupled from local marine productivity (Altabet et al., 2004; De Pol-Holz et al., 2006; Chazen et al., 2007; Mohtadi et al., 2008). In Peru, it coincides with the onset of stronger El Niño activity (Rein et al., 2005) and increased coccolithophorid:diatom production between 18.0 and 15.5 ka (Higginson and Altabet, 2004).

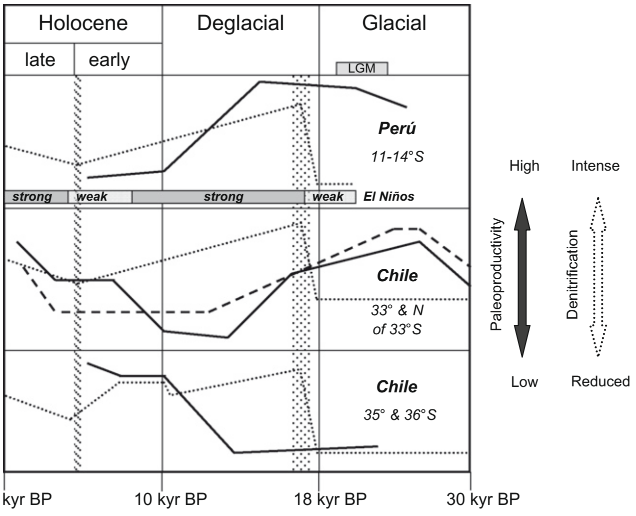


Fig. 5. A simplified latitudinal view of past changes in productivity [based on opal/$CaCO_3$ ratio for cores off Chile, and on $CaCO_3$ accumulation rates for Peru (core 69TC from the Nazca Ridge)], and water column denitrification (as inferred from downcore $\delta^{15}N$ records) in the HCS for the period between 30 ka BP and the present, from sediment cores collected at upwelling centers off Peru (11–14°S), north-central Chile [at 24°S, 27.5°S, and 30°S (solid line), and at 33°S (dashed line)], and south-central Chile (35°S and 36°S). This cartoon simplifies and summarizes information published by Dezileau et al. (2004), Altabet et al. (2004), Higginson and Altabet (2004), Mohtadi and Hebbeln (2004), De Pol-Holz et al. (2006), Robinson et al. (2007), and Mohtadi et al. (2008). The dashed vertical rectangle indicates the onset of modern El Niño manifestations at ca. 5500 cal yr BP (after Vargas et al., 2006b, and references therein); the dotted gray vertical rectangle denotes the time (ca. 17 ka) when paleoceanographic conditions changed abruptly in the HCS (see Mohtadi et al., 2008, and references therein). The dark and light gray horizontal bar refers to El Niño variability off Peru, after Rein et al. (2005). LGM, Last Glacial Maximum. Black lines: solid and dotted, paleoproductivity; grey dotted lines, denitrification.

Paleoproductivity changes encompassing the Last Glacial Maximum (LGM) and the Holocene in mid-latitudes off western South America are associated with the latitudinal migration of the Southern Westerlies (SW), and the strength and position of the Southeast Pacific anticyclone. Climate reconstructions based on marine and continental archives of the Southern Hemisphere assume a 5–6° northward shift of the SW during the LGM. This would have prevented coastal upwelling in central-southern Chile, where productivity did not increase until 13–14 ka in coincidence with the Meltwater Pulse 1a (35°S and 36°S, Fig. 5). Mohtadi et al. (2008) linked these higher deglacial and Holocene paleoproductivities, compared to the LGM, with the onset of active upwelling off central-southern Chile and increased export production. In contrast, at 33°S and farther north, stronger hemispheric meridional winds caused enhanced upwelling intensity and paleoproductivity during the last glacial compared to the Holocene (Mohtadi and Hebbeln, 2004; Mohtadi et al., 2008, and references therein).

5. End-to-end shifts

On large scales, regime shifts, or drastic changes vs. gradual changes in climate, nutrients, and temperature, can contract/expand the area of high/low productivity (Thomas and Brickley, this issue) and fish distribution in the HCS (i.e. coastal-oceanic patterns associated with EN; Chavez, 2006; Chavez et al., 2008; Swartzman et al., 2008). The "colder" coastal ecosystem occupies an area of ~200 km from shore with mesoscale filaments, whereas an "oceanic" nutrient-limited, low biomass and primary productivity ecosystem with an efficient recycling system is found offshore. During warm years, the productive coastal area is reduced dramatically in its offshore extension and the oceanic ecosystem dominates. Trophic changes, as a consequence of the coastal multi-scale environmental "warmer" conditions, result in a microbial web with smaller-sized organisms vs. the classical trophic chain during "colder" multi-scale environmental conditions. All these ocean states have large repercussions for the whole ecosystem, including benthic-pelagic coupling.

The most challenging question is whether coastal upwelling will intensify/decrease as greenhouse gases increase. Bakun and Weeks (2008) apply the comparative method to identify the specific factors underlying the fishery productivity of the marine ecosystem off Peru. The Peru system is the one located at lowest latitudes and is susceptible to extreme inter-annual ecosystem disturbances associated with EN and other ENSO-related episodes. These authors argue that this could be regarded as favourable considering that, in such systems, non-linear processes interact in intricate ways to move them to configurations that may be much more difficult to reverse than to establish.

A difficult issue, though intriguing and stimulating, is the separation of anthropogenic effects from natural variability. This type of issue is more common globally every day in different disciplines. For example, fishing is considered to be the main threat to marine ecosystems, and Pauly et al. (1998) showed that landings from global fisheries have shifted in the last 45 years from large piscivorous fishes toward smaller invertebrates and planktivorous fishes. This may imply major changes in the structure of marine food webs, possibly explaining the decline of landings in recent decades. This top-down control is a major concern in the HCS.

Working in coordination with the fishery fleet was recommended for guiding adaptive management decisions on shorter time scales in pelagic fisheries, and this has been done with the entire fleet of Peruvian anchoveta purse-seiners using the Peruvian satellite Vessel Monitoring System (Bertrand et al., 2007, 2008b). Neira et al. (this issue) used long-term simulations to conclude that fishing in the southern HCS is more likely to exceed ecological thresholds and induce regime shifts of low recovery than decadal-scale bottom-up forcing. The authors recommended considering fishing and environmental variability on the decadal scale rather than simply focusing on inter-annual variability.

6. Conclusions and further needs

The HCS is a large marine ecosystem whose dynamics permeate the social and economic sectors of the bordering countries. It is subject to large fluctuations in climate, ecosystems, productivity, and fisheries on all time scales. For centuries, coastal communities have developed around and depended (and still do) heavily on its marine resources.

The HCS is characterized by the upwelling of cold, nutrient-rich waters; extremely high biological productivity; and a shallow OMZ with unique biology and complex biogeochemical processes. The continued collection of time series and satellite data, *in situ* observations and experiments, modelling, biogeography and biodiversity descriptions, and the sedimentary record have only recently helped understand ocean variability at the regional level.

One important fact is that the abundance and catches of small pelagic fishes in the HCS are greater than in any other EBC. These abundances appear to undergo natural multi-decadal and inter-annual fluctuations, even in the absence of fishing harvests. Secondly, fisheries activities reverberate through entire marine ecosystems, affecting benthic and pelagic organisms through processes that are not yet well understood. The economic consequences of mismanagement are severe, providing the motivation for continued research. Therefore, we propose that further efforts should address: (i) the connections between upwelling variation and large-scale remote forcing; (ii) how upwelling strength and productivity in the HCS have changed in the recent and geological past; (iii) how size structure and trophic interactions are organized spatially; (iv) the role of mesoscale oceanographic features in further supporting biological production beyond the shelf break area; (v) carbon retention and export through grazing removal rates and fish ingestion rates under different environmental scenarios using multi-scale approaches; and (vi) regional carbon budgets, along with their spatial and temporal variability.

Since comparative studies among EBCs have been promoted at all levels, it is encouraging that there is an ongoing UNDP/GEF-LME-Humboldt Project focusing on ecosystem-based management in the HCS-Large Marine Ecosystem through a coordinated framework that provides for improved governance and the sustainable use of living marine resources and services. Hopefully, initiatives such as this will result in ecological, social, economical, and technological improvements and will promote the viability for integrated management, since they are crucial issues for preventing further deterioration of the coastal zone habitats.

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