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MODULO 1. PRODUCCIÓN Y VARIABILIDAD AMBIENTAL

INTEGRATED OVERVIEW OF THE OCEANOGRAPHY AND ENVIRONMENTAL VARIABILITY OF THE HUMBOLDT CURRENT SYSTEM, CHILE

This overview is a summary of the oceanographic knowledge of the Humboldt Current Large Marine Ecosystem (HCLME). It draws mainly on published scientific literature that demonstrates a healthy and sizeable knowledge increase during the last decade, due to the implementation of key oceanographic and fisheries related research programs. The aim of this overview is to combine the work from Chile with similar work from Peru to identify the issues, factors and threats affecting the HCLME.

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1. INTRODUCTION

The Humboldt Current Large Marine Ecosystem (HCLME) off Chile and Perú is one of the four major Eastern Boundaries Currents (EBCs) of the world oceans, being in many respects similar to the Benguela current running off the coast of west Africa, the California current off the west coast of U.S.A and the Canary current off north-west Africa (Mackas et al., 2006). The HCLME originates at the bifurcation of the West Wind Drift Current (~42°S), which generates the Cape Horn Current System (CHCS) to the south and Humboldt Current System (HCS) to the north and extends along the southwest coast of South America to Ecuador and the Galápagos Islands (Strub et al., 1998, Thiel et al., 2007). The bifurcation of the West Wind drift oscillates seasonally and from year to year between 35°S to 45°S (Montecino et al., 2006; Thiel et al., 2007) (Fig. 1).

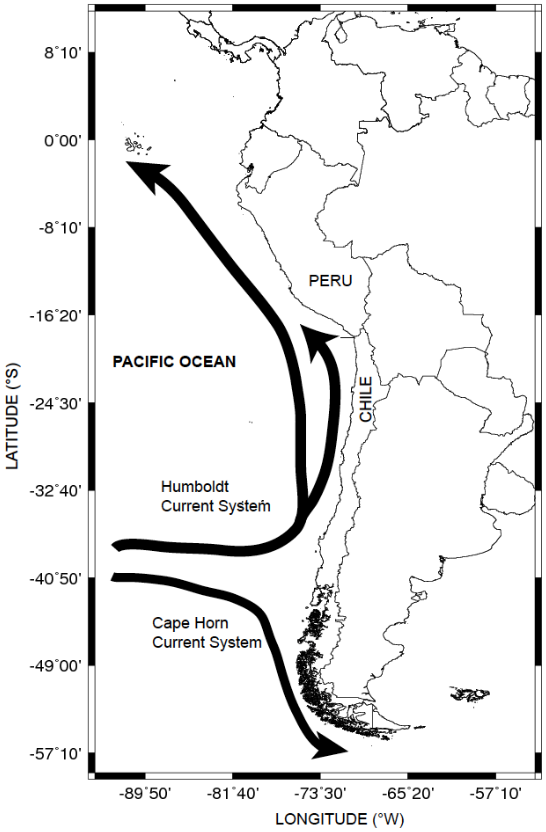

Figure 1. The Humboldt Current Large Marine Ecosystem showing at ~40°S the bifurcation of the West Wind Drift Current, forming the HCS and the CHCS respectively.

The HCS is a highly productive large marine ecosystem supporting one of the largest fisheries of the world oceans, representing about 10% of the world fish catch (Chavez et al., 2008, Montecino & Lange, 2009). This high productivity is closely associated with the occurrence of coastal upwelling that brings nutrient rich subsurface waters to the surface and the El Niño Southern Oscillation (ENSO) interannual resettings (Bakun & Weeks, 2008). Consequently, at the smaller scales, upwelling promotes high phytoplankton yield and associated food chains (Daneri et al., 2000; Thiel et al., 2007, Chavez et al., 2008). This process is also influenced by other smaller and larger scale perturbations (Rutllant & Montecino, 2002; Bakun & Weeks, 2008).

The high biomass and species richness of marine organisms in the HCLME supports important benthic, demersal and pelagic fisheries (Montecino et al., 2006a; Montecino & Lange, 2009). As a result of this, a significant part of the population and economy of Chile and Peru depends directly or indirectly on the HCLME. In the last three decades however environmental changes, coupled with an increase in fishing pressure, has resulted in dramatic fluctuations and loss of stock of marine natural resources in the HCLME (Thiel et al., 2007; Montecino & Lange, 2009).

The HCLME is not only under threat from overfishing but also from other human activity along the coastal fringe that generates pollution and habitat degradation problems. Petroleum spills, emission of organic and inorganic residuals of domestic and industrial processes, habitat degradation through bentho-demersal fisheries, aquaculture activities and the physical alteration of the coastal border by urban developers are increasingly threatening fragile coastal habitats that can be important nursery areas of both benthic and pelagic marine species (Ahumada et al., 2000).

Based on an ecosystem approach that considers different time and space scales of environmental changes, this work will update a transboundary overview and diagnosis of the main environmental and human dimension issues. These issues should be included in a Strategic Action Plan (SAP) for integrated and sustainable management of the HCLME.

1.1. Objective

This overview is an updated revision of the published oceanographic knowledge about the HCLME. It draws mainly on open data bases and scientific publications that have shown a healthy increase in recent decades, due to the implementation of some key oceanographic and fisheries related research programs. The overview starts with a brief discussion of the main historical events and programs that have had a measurable impact on the state of the art of HCS knowledge. It continues with a discussion of the main physical features and processes–the bathymetry, wind field, temperature, salinity, water masses, upwelling and circulation. Key aspects of the chemistry and chemical processes follow, including a discussion of nutrient dynamics and the importance of the oxygen minimum zone (OMZ). The next section deals with pelagic components such as bacterioplankton, phytoplankton, zooplankton and ichthyoplankton, including red tides and harmful algal blooms (HABs). Following this is a section on the biogeographic partitioning of the HCLME. Finally we provide some perspectives on various issues, problems and threats facing the HCLME, also identifying some of the major gaps in its knowledge and understanding.

1.2 A Brief history on the development of oceanographic and environmental knowledge in the Humboldt Current Large Marine Ecosystem.

The early story of the HCLME begins with the first measurements of a cold current by Alexander von Humboldt in 1846 in the southern South Pacific, named by Vasco Nuñez de Balboa, 'Mar del Sur' in 1513, and 'Océano Pacífico' in 1520 by Hernando de Magallanes (Gunther 1936).

After Humboldt, several expeditions in the 20th century investigated the local biodiversity (Thiel et al. 2007). From the perspective of oceanography, the last 30 years have been the most productive in relation to knowledge development and publication rates. Two major events marked the beginning of a significant increment in the quality and frequency of the information acquired. One was the acquisition of two research vessels: the Abate Molina and the Vidal Gormáz; the second was the substantial increment in the funds allocated to marine science programs such as the Fondo de Fomento al Desarrollo Científico y Tecnológico FONDEF, the Fondo de Financiamiento de Centros de investigación en areas prioritarias FONDAP, and the

Fondo de investigación pesquera FIP. Among the more important oceanographic initiatives are: the Joint Global Ocean Flux Studies JGOFS-SAREC project, the Sectorial Biomass (Fondo de investigación científica y tecnológica FONDECYT-CONICYT), the CIMAR PROGRAM from the National Oceanographic Comitee CONA, the FONDAP-HUMBOLDT PROGRAM and the FONDAP-COPAS and CASEB PROGRAM (Montecino & Lange 2009). From the standpoint of fisheries oceanography it is important to mention the grants supported by FIP (Fisheries Research Fund) in the period from 1991 to the present, after the first “Fishery law”.

2. PHYSICAL FEATURES AND PROCESSES

2.1 Geographical Aspects

The Chilean coast extends from about 18°20’ to 57°30’ latitude south, along the western coast of South America. This region of the Pacific is one of the Eastern Boundary Current Systems (EBC’s), mentioned above as the HCS (Mackas et al., 2006). The West Wind Drift current (WWDC), located in the subantarctic zone at 42-43° S, reaches the continent creating: a) an equatorward surface coastal current (the Humboldt or Peru-Chile current) and an equatorward deep-ocean current, separated by a poleward countercurrent; and b) a poleward flow known as the Cape Horn Current (Fig. 1). The WWDC carries the Subantarctic Water mass (SAAW). The southern boundary of the HCLME is set at the bifurcation of the Wind West Drift current shifting between 35°S to 45°S. The northern limit of HCLME is set at the boundary with the Equatorial Current near the Galapagos Islands, while the western boundary of the HCLME extends far beyond the 200 nm Exclusive Economic Zone off Chile and Peru. In oceanographic terms, it is difficult to set the western limit of the HCLME, particularly at the extremes where the current originates in the south and in the northern segment were it turns to the open ocean (but see Hormazábal et al., 2004).

The Chilean north-central coastline located approximately from 18°20’ S to 41°30’ S, is an extended and straight, west-facing shoreline, with few embayments along the coast (Ahumada et al., 2000; Thiel et al., 2007). The continental shelf is narrow in the northern zone (<10 km) and has a depth of 100 to 150 m (Figueroa, 2002) (Figure 2). The shelf off Valparaiso is an exception, where a deep hanging shelf is around 70 km wide and 800 m deep (Figueroa 2002). The widest part of the shallower coastal shelf is found off Talcahuano (35°-37°S), being 45 km wide and 150 m deep (Figueroa, 2002), flanked by two submarine canyons: the Itata canyon and the Bio-Bio canyon; both originated from active rivers during the Quaternary period. In the southern area the shelf is narrower from 37-39°S, then widening with maxima of 50-70km between 39-42°S (Fig. 2). Some insular areas (Yañez et al., 2009), seamounts (Castilla, 1987; Freelander et al., 2013) and adjacent zones (Pizarro et al., 2006; Andrade et al., 2012) have been also recently studied.

Regarding bathymetry, the HCS is located in the area of subduction of the Nazca plate under the South American plate (Strub et al., 1998). This tectonically active and highly seismic plate boundary is associated with the presence of the deep trench (~6500 m) and the narrow shelf (Fig. 2).

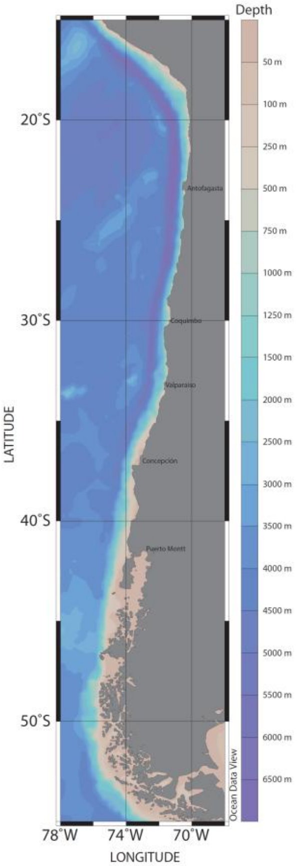

Figure 2. Bathymetry of HCLME with dark/light blue for the deeper/shallower zones (figure made using Ocean Data View software, Tyberghein et al., 2012).

2.2 Meteorological Conditions

The marine climate off the west coast of South America arises from the interaction of basin scale atmospheric systems, combined with regional and local effects introduced by the land sea boundary and the orography (Strub et al., 1998). For the HCLME area the most influential large-scale system is the southeastern Pacific subtropical anticyclone, which drives equatorward winds along the coast for most of the year (Montecino et al., 2006). The equatorward direction is favorable for upwelling processes (Blanco et al., 2001). Coastal alongshore winds become poleward in Autumn and Winter south of approximately 38°S, as the atmospheric anticyclone shifts to the north and allows synoptic storms to pass through (Müller and Figueroa, 1996; Figueroa and Moffat, 2000; Figueroa, 2002). Associated with the anticyclone there is a subsidence inversion at the top of the marine boundary layer that comes closer to the surface near the coast, creating onshore-offshore gradients in wind stress and cloudiness. The inversion and the inland mountain ranges parallel to the coast support the poleward propagation of trapped atmospheric disturbances (e.g. coastal lows) that modulate the upwelling-favorable winds, generating variability on a scale of a few days (Rutllant, 1993; 1997; Lefevre et al., 2002). Due to the influence of regional and local wind forcing factors, maximum wind speeds along the coast are found in the austral Spring-Summer, while offshore equatorward winds in the north off Perú (the southeastern trades) peak during the austral Winter (Strub et al., 1998).

The average monthly climatology in northern Chile between 18°-26°S has little seasonal variability, with nearly constant equatorward alongshore winds of 2 – 3 m/s. South of 26°S, seasonality increases, although monthly mean alongshore winds remain equatorward during most of the year north of 38°S. Between 26°-30°S average monthly alongshore winds have minima between 2 – 4 m/s in Winter (June and July) and maxima between 4 – 6 m/s in Spring and Summer (December to March). Between 30°-38°S, minima in monthly winds may be near zero in AAutumn and maxima reach 6 – 8 m/s in Spring and Summer. Maximum equatorward winds of nearly 10 m/s occur between 36°-37°S in Summer (Figueroa, 2002). Thus, the mid-latitudes have the strongest upwelling-favorable winds in Spring-Summer and the largest seasonal range.

Onshore-offshore winds are less intense and their seasonal variations are smaller. Between 20°-33°S, the mean monthly winds are onshore with magnitudes that increase in magnitude from 1 to 2 m/s, moving from north to south. The mean magnitude of the onthsore winds increases to 3-4 m/s south of 33°S (Figueroa, 2002). The colors in Fig. 3 show the magnitude of the wind stress, maximum around 36-37°S in Summer and near 30°S in Winter. It also shows the Winter maximum off Peru and the minimum wind stress off Northern Chile.

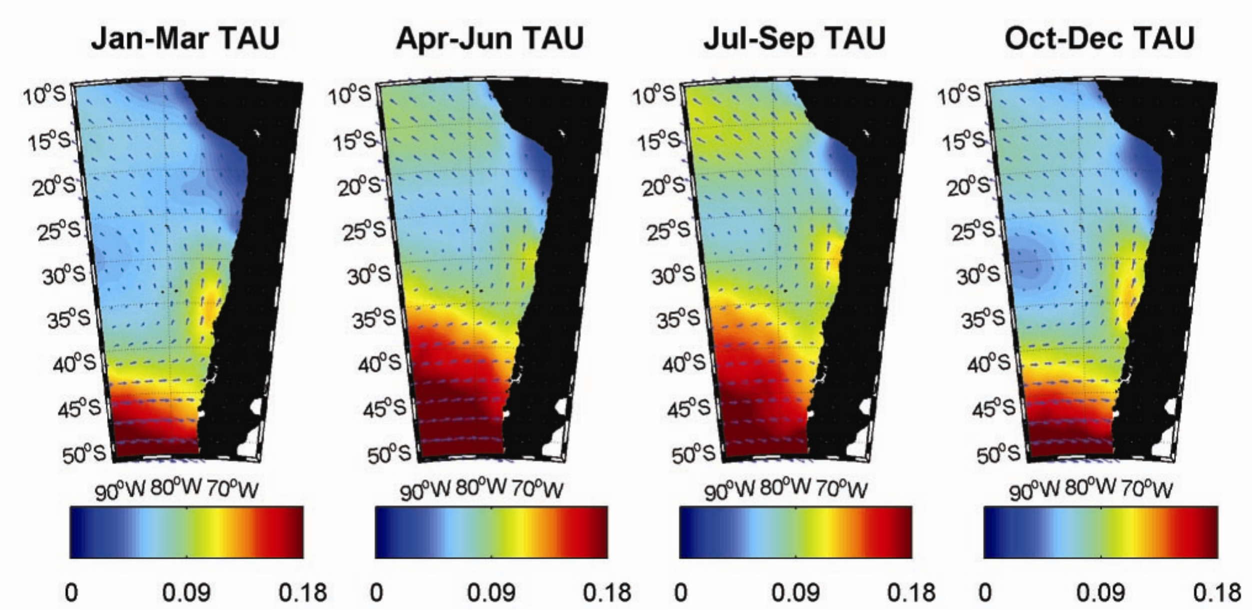

Figure 3. Seasonal (3-month) mean surface wind stress data from Jet Propulsion Laboratory archive, based on eight years of QuikSCAT scatterometer data. Magnitudes are shown by the colors at full resolution (0.25 degree gridding). Vectors are plotted every two degrees. TAU is the meridional wind stress (Daniel Varela at NOAA is acknowledged for this Figure jointly with Ted Strub at Oregon State University, USA for his contributions).

Regarding precipitation, the northern zone of Chile presents extremely arid conditions with a predominance of South and Southwest wind throughout the year, but peaking with more intensity in southern Spring and Summer (Thomas et al., 1994, Pizarro et al., 1994). The southern zone of Chile present a more pronounced seasonality, with a great quantity of precipitation during Winter (Strub et al., 1998).

2.3 Water Masses

The oceanography of the HCS off northern Chile (18.5-30°S), between the coast and 200 nm offshore, is characterized by the presence of five water masses. Between the surface and approximately 35 m depth the Subtropical Water (STW) mass has a well-defined superficial nucleus, particularly north of 23°S. The STW is characterized by temperatures of 16-24°C and salinity of 34.9-35.3 (Silva and Konow, 1975; Robles, 1976, Escribano et al., 2002, Montecino et al., 2006). South of 30°S the (Superficial) Subantarctic Water (SAW) is found, between the surface and 120 m depth. The SAW is defined by temperatures of 9-15°C and salinity of 33.0-34.3 (Silva & Konow, 1975; Robles, 1976). The area between 23°S and 30°S is a transition zone where the SAW is located below the STWs, forming an upper minimum of salinity (Gunther, 1936; Wyrtki, 1963; Reid, 1965, 1973a, 1973b; Brandhorst, 1971). At the subsurface between approximately 150 and 350 m, Equatorial Subsurface Water (ESSW) is characterized by a salinity maximum (34.4-34.9) and a dissolved oxygen minimum (0.2 and 3 ml l^{-1}) (Reid, 1965; Silva & Konow, 1975). In the intermediate layer between, 400 and 1000 m depth the Antarctic Intermediate Water (AIW) mass is characterized by temperatures of 4-6.5°C and salinity of 34.2-34.5 (Reid, 1965; Silva & Konow 1975). The AIW flows equatorward between 500 and 1500 m depth and is characterized by low temperature and low and constant salinity (Strub et al., 1998). Pacific Deep Water (PDW) is characterized by low temperatures and higher salinities, with a poleward flow. These waters have an ascending movement to the south and reach the surface at the Antarctic divergence. Additional variability is found in the Chile Coastal Current, where fresh water (32.7< S <34.2) from the fjord region around 42-45°S is advected northward at the surface in Summer while saltier Poleward Undercurrent Water is mixed into the surface water next to the coast during coastal upwelling.

Table 1. Water masses in the Humboldt Current System (modified from Cañon & Morales 1985, Strub et al., 1998; Escribano et al., 2002).

Water mass	Temperature (°C)	Salinity (UPS)	Depth (m)
Subtropical Water	16 - 24	>34.9	0 - 35
Subantarctic Water	11 – 15	34.1 – 34.8	20 - 80
Equatorial Subsurface Water	8 – 14	34.5 – 34.8	300 - 370
Antarctic Intermediate Water	5.5	34.3 – 34.5	500 – 600

The Subtropical Water mass (STW), characterized by superficial, oceanic, warm and saline waters, moves seasonally towards the northern coast of Chile and southern Peru. During "El Niño" events, the STWs can reach the coast as a superficial water mass between 0 and 50 m depth, causing temperature increases of 3 to 4°C at the coast in a layer 30 to 50 m depth. The SAW has a higher density than the STW and when these two water masses converge to the coast, the STW reaches the surface. Differences in the water masses next to the coast create changes in the physical and chemical features of seawater, which induce clear changes in intertidal and subtidal coastal species. The flow of the SAW is equatorward and has two branches: the oceanic and coastal current, both referred to as the HCS. Usually, this water moves between 0 to 300 m depth along the coast, with some temperature and salinity changes due to the exchange of heat and water vapor with the atmosphere. The Equatorial Subsurface Water mass (ESSW) is a poleward flow characterized by low temperature, medium level salinity and low concentrations of dissolved oxygen (less than 0.5 ml/l) (Strub et al., 1998).

2.4 Temperature and Salinity

The most interesting features of the HCLME are the marked latitudinal gradients of sea surface temperatures (SST) and salinities. The average of the monthly fields of SST from 2002-2009 show high SST from northern Chile (27 – 21 °C) and low values in southern HCLME (13 – 9 °C) (Fig. 4a). In the same way, the average of monthly fields of salinity from 2002-2009 show high values from northern Chile (35.8 – 34.6 psu) and low values in southern HCLME (31.9 – 29.1 psu) consequence of the high intromission of freshwaters from rivers and fjords (Fig. 4b).

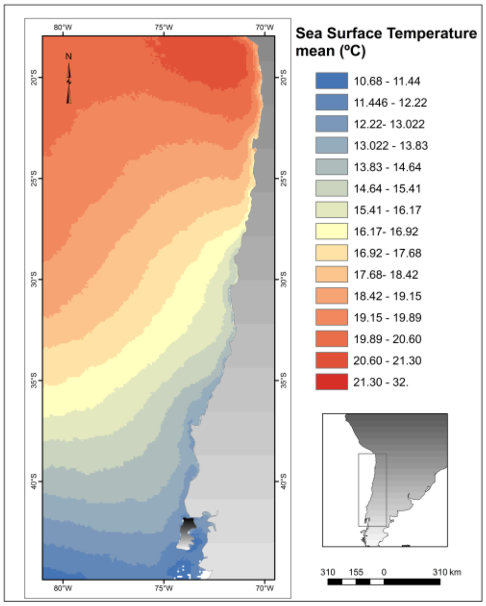

Figure 4a. Latitudinal changes in temperature (°C) at the surface (data from Bio-Oracle, Tyberghein et al., 2012).

Blanco et al. (2001) describe the seasonal patterns of surface temperature, salinity and the depth of 15°C isotherm along northern Chile. Their study shows that surface temperature and salinity have strong annual cycles with maximum offshore values in Summer (>24°C and 35.3 psu) and minimum values during Winter (16-17°C and 34.8-35.0 psu). Within 100 km of the coast, isopleths are generally parallel to the shore even during Winter because of upwelling of cooler, less saline subsurface water. This upwelling moderates the annual cycle of both temperature and salinity near shore. Within 100 km of the coast, Summer minimum temperatures and salinity are 19-30°S and 34.8-34.9 psu, respectively, and Winter values are 16-17°C and 34.8-34.9 psu. The cross-shelf gradients of both temperature and salinity are highest during the Summer and decreases from north to south. Offshore of the coastal upwelling influence area (west of ~72°W) the temperature and salinity isopleths run perpendicular to the coast as a response to the latitudinal gradients in solar heating. The vertical structure of temperature shows that vertical stratification is maximum in Summer, and weakest in Winter. Near –surface isotherms (>14°C) tilt upward towards the coast throughout the year, in response to the continuous upwelling-favorable winds. Below 150 m, isotherms deepen as they approach the coast indicating the poleward geostrophic flow associated with the undercurrent (Blanco et al., 2001).

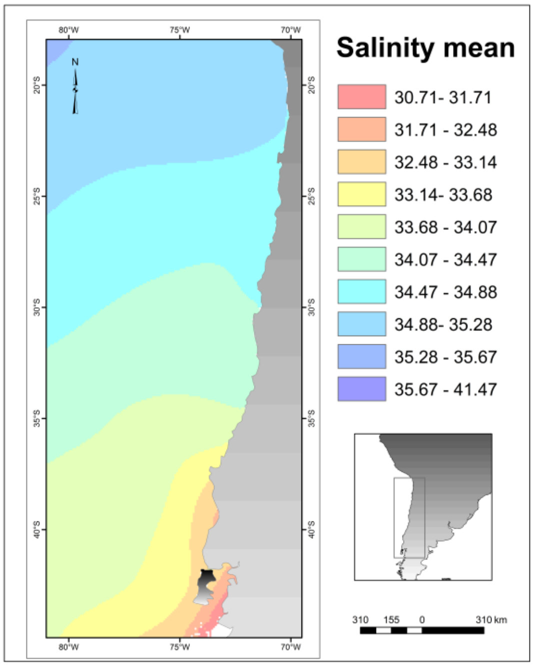

Figure 4b. Latitudinal changes in salinity (psu) at the surface (data from Bio-Oracle, Thyberghein et al., 2012).

The vertical salinity structure (first 800 m) is determined by the distribution of four principal water masses in northern Chile (AIW, ESSW, SAW, and STW). The freshest water mass is influenced by AIW, which is defined by a salinity minimum at a mean depth of 700 m. Between 100 and 300 m adjacent to the coast a salinity maximum is associated with the ESSW. A relative salinity minimum located above and offshore of ESSW is due to SAWs. Highest salinities are found offshore in STWs (>35.1 psu), present at the surface in Summer and Fall and seen as a wedge of warm, saline waters at the surface, extending southward and toward the coast, with minimum presence in Winter. Salinity values in the upper 50 m indicate that upwelling brings water with lower salinity to the surface near the coast throughout the year, but is weaker in Winter. Upwelled water is either ESSW or SAW or a combination of the two (Strub et al., 1998).

2.5 Circulation

The HCS carries a net transport of 11.04 Sv to the north; calculated from the Caldera to Easter Island transect (Fuenzalida et al., 2007). The geostrophic circulation relative to 2500 db presents the greatest velocity between the surface and 1000 m, with alternating currents to the north and south directions, typical of the Southeast Pacific Ocean. Below 1000 m the flux is slower and predominantly toward the pole. The general circulation pattern derived from geostrophic measurements is consistent with direct current measurements obtained by Shaffer et al. (1995) through the deployment of deep current-meters in the offshore area of Coquimbo. The poleward flow of the Peru-Chile Undercurrent (220 m) has an average velocity of 12.8 cm/s. The AIW flows toward the equator with a velocity of 1.1 m/s. The flow directed to the Pole near the bottom is stronger in Spring and decreases and weakens in the Winter. Near the bottom of the AIW (700 m), the seasonal variability is less intense. However, in the water column the interannual variability along the Chilean coast is strong (Shaffer et al., 1999).

Where upwelling brings denser water to the surface next to the coast, it creates lower sea surface height (SSH) over that water. This creates downward sloping SSH across the front that developes between the offshore water and the upwelled water next to the coast. A narrow, nearly geostrophic jet flows along the upwelling front at the surface, separating the more productive upwelling ecosystem inshore of the jet from the more oligotrophic deep-ocean ecosystem offshore of the jet. The jet can move off of the shelf and develop non-linear instabilities, meanders and eddies, which move westward into the deep ocean, which is the natural direction of propagation of the eddies (Chaigneau & Pizarro , 2005b) .

2.5.1 Upwelling

In the HCLME three well-defined upwelling subsystems are recognized: (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 (Montecino & Lange, 2009).

Wind-driven upwelling causes the ESSW to be upwelled into the euphotic zone from depths deeper than 200 m near the coast (Strub et al., 1998; Blanco et al., 2001). The ESSW contains large concentrations of nutrients, which promote high productivity in coastal waters (Marín et al., 1993; Escribano & Hidalgo, 2000).

The intensity of the upwelling along the coast is not only due to the wind stress, but also to topographic effects. In general, the local topography and the geometry of the coast have important effects on the currents along the coast, inducing or changing upwelling (Figueroa & Moffat, 2000; Atkinson et al., 2002). The curl of the wind stress also contributes to the strength of upwelling in offshore regions and can change the location of the upwelling-front jet (Aguirre et al., 2012).

Several upwelling centers are commonly identified along the Chilean coast: including Antofagasta (23°S), Coquimbo (30°S), Concepción (37°S) and Punta Galera (40°S). Looking at one location, the main upwelling center in northern Chile at Antofagasta has been described by many authors (Blanco et al., 2001; Escribano & Hidalgo, 1998; Sobarzo & Figueroa, 2001; Morales et al., 2001). In addition to physical oceanographic investigations, there have been detailed studies of chlorophyll-a (Chl-a) and primary production (Marín et al., 1993, Morales et al. 1996, 2001, Thomas et al. 2000, Pizarro et al., 2002,) and secondary production (zooplankton) (Escribano & Mc Laren, 1999; Morales et al., 1997). Similar studies have been conducted during anomalous periods associated with El Niño and La Niña conditions (Ulloa et al., 2001; González et al., 2000; Escribano & Hidalgo, 2001; Blanco et al., 2002). The Antofagasta upwelling center has also been described by Morales et al. (1997), Escribano & Hidalgo (2000) and Marín et al. (2001) as a favorable area for larval retention due to circulation patterns. Although a few studies of the geostrophic circulation based on hydrographic ship surveys have been reported (Silva & Sievers, 1991), more detailed fields of mean surface currents have been obtained recently from satellite-tracked drifters deployed from 1991 to 2005 (Chaigneau & Pizarro, 2005a).

The dominant circulation patterns near the coast along Chilean upwelling regions are controlled by the baroclinic density field created by upwelling and downwelling. The development of a mostly geostrophic jet along the upwelling front is described above, leading to unstable meanders and eddies that propagate westward. Where the Winter winds force onshore Ekman transport and downwelling, a baroclinic polward flow is also created, which has not been studied in as much detail as the Summer upwelling systems, either in the HCS or in other EBCs. During upwelling (seasonal or perennial), the offshore movement of the jet is due to multiple factors, including simple offshore Ekman transport and Rossby Wave vorticity dynamics. Aguirre et al. (2012) present a model study that shows the ability of the negative wind stress curl to move the upwelling jet westward, off of the shelf and into the deep ocean. This has the ecological consequence of spreading the coastal upwelling ecosystem over a wider area, including the otherwise oligotrophic deep ocean. Without the curl of the wind stress, the jet and upwelling system stays trapped over the shelf. These dynamics are most important in the south-central zone of Chile, where the strongest coastal upwelling is induced by wind and has a strong seasonal cycle. This zone also receives a contribution of freshwater by rivers, which contributes to the strong stratification in Summer. Stratification is so strong in some places that the wind is not able to destroy the stratification during the upwelling process and the upwelled water does not even reach the surface (Atkinson et al., 2002; Dávila et al., 2002).

2.6 Coastal Trapped Waves

The first measurements of free coastal trapped waves (CTW's) in the Chilean portion of the HCS were made by Shaffer et al. (1995; 1997). During the El Niño event in 1991-1992 (a moderate event), free CTWs with periods of ~ 50 days were recorded. Several flow reversals with poleward directions occurred above the continental shelf, reaching velocities of about 12 cm/s. These waves originated as equatorial Kelvin waves, forced by a series of pulses of the west wind in the Equatorial Pacific, an expression of the Madden-Julian oscillation in the atmosphere during the beginning of El Niño (Shaffer et al., 1999, Pizarro et al., 2001). Similar changes in the flow direction are reported by Blanco et al. (2002) for the El Niño during 1997-1998, as observed through geostrophic calculations using hydrographic surveys. The presence of CTWs was also observed by Hormazábal et al. (2001) offshore of Valparaiso (33°S), who found a significant relation between sea surface temperature and adjusted sea level, consistent with CTW dynamics. On seasonal time scales, the intra-seasonal variability associated with the CTWs is weaker during the Winter; on interannual time scales, the CTW variability is stronger during El Niño and weaker during La Niña events (Shaffer et al., 1999). To the south of 20°S, a portion of intraseasonally variation is forced by local winds associated with atmospheric teleconnections and the atmospheric coastal lows described above (Hormazabal et al., 2002).

The ecological significance of the low frequency oscillations is their capacity to change the mean depth of the coastal thermocline/nutricline and modulate the effectiveness of nutrients pumping in the euphotic zone during the local upwelling events. The consequence is a change in productivity in the coastal zone, unrelated to local winds (Morales et al., 2001; Rutllant & Montecino 2002; Montecino et al., 2006).

2.7 Mesoscale eddies

Mesoscale eddies, generated locally or in other regions, are responsible for energy and material transports from and to the coast, including larval retentions and dispersions. Offshore of the coast of Chile, these eddies have been described by various authors (Silva & Sievers, 1981; Barbieri et al., 1987; Fonseca & Farias, 1987 among others), who observed eddies using data from oceanographic cruises or sea surface temperature from satellites. For example, eddies off Talcahuano and Antofagasta are described by Cáceres (1992) and Sobarzo & Figueroa (2001). Over larger areas, Blanco et al. (1998) and Pizarro et al. (2000) observed and described mesoscale eddies in the zone between Peru and north of Chile using SSH anomaly fields from altimetry data. Continuing these ideas, Narváez (2000) and Chaineau et al. (2008) analyzed oceanographic cruises and satellite altimeter sea level measurements off northern Chile and Perú, describing their principal characteristics and recurrence. The horizontal scale of these eddies are approximated 100-150 Km, extending in the vertical over 600 m depth.

3. CHEMISTRY AND RELATED PROCESSES

3.1 Dissolved Oxygen and the Oxygen Minimum Zone

Latitudinally, from north to south, dissolved oxygen in surface waters show a clear increase in concentration (Fig. 5).

In northern Chile the vertical structure of oxygen concentration is characterized by strong gradients in the first 100 m year round, from concentration ranging from 5 ml/l to 1 ml/l

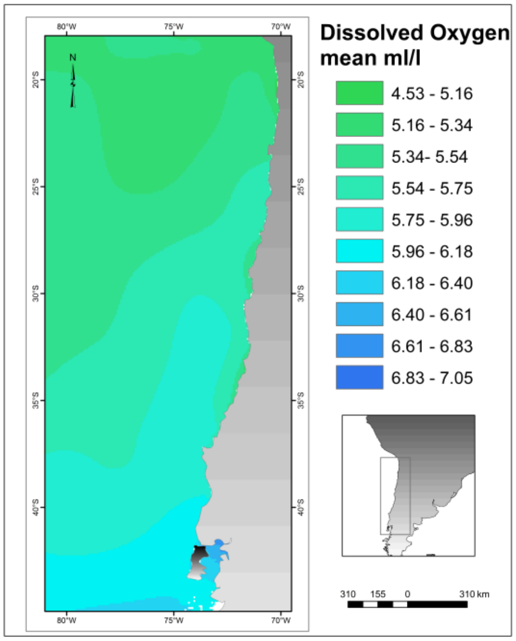

Figure 5. Latitudinal changes in oxygen structure (ml/l) at surface (data from Bio-Oracle Thyberghein et al., 2012).

whereas below the depth of 1ml/l, the concentration decreases even to values <0.25 ml/l. Off southern Peru, the veering of the main limb of the HC offshore creates ventilation, and is the primary driver of this oxygen minimum layer (OMZ) from sub-surface to intermediate depths, attributed to sluggish circulation, and a high demand of oxygen by microbial aerobic respiration (Codispoti et al., 2005, Paulmier & Ruiz-Pino 2008; Ulloa et al., 2013). The sinking and remineralization of surface-derived organic matter further contribute to the OMZ. At the northern end, the equatorial undercurrent ventilates the OMZ and, at the southern end, the poleward Peru–Chile undercurrent advects the low oxygen waters poleward (Montecino & Lange, 2009). This layer with concentration < 0.5 ml/l dominate the water column from 100 to 450 m, and is associated with ESSW.

The upper limit of the OMZ, defined by the oxycline, present a great vertical variability intra and interannually associated with the dynamic processes of the HCS. The oxygenated surface layer is deeper offshore and decreases towards the coast by continuous upwelling processes in this zone. According to time series data obtained in northern Chile (1980-1997; JGOFS and FONDAP-Humboldt projects), the oxycline is located at 50 m depth at the coast, and at oceanic waters it deepens to 100 m. However, this limit has been detected in shallower waters at 10 m during strong EN, such as the 1997-1998 event. Overall, in the HCLME the OMZ is observed between 5 and 800 m water depth (Paulmier et al., 2006) having large impact over the structure and dynamics of the pelagic and benthonic communities, as well in the biogeochemistry cycles a regional level. Off Chile the OMZ structure is maintained everywhere over the shelf with an intense oxycline (>1 μM/m) and minimum concentrations reaching $O_2<1$ μM in the OMZ core (Paulmier et al., 2006). Global time series (1960-2008) reveal vertical expansion of the intermediate-depth low-oxygen zones in Eastern Pacific from 0.09 to 0.34 mmol $kg^{-1}year^{-1}$ and from 300 to 700 m depths (Stramma et al., 2008).

The OMZs are located under oxygenated waters and in these areas the microbial respiration is based on the support of sulfate as alternative oxidizing agent (Codispoti et al., 2005). In addition to small oxygen concentration, chemical features of water column suboxia typically include nitrite and nitrate minima (Codispoti et al., 2005). The OMZs have been mainly known for playing an essential role in the global nitrogen cycle, in which various chemical species, according to their degree of oxidation (e.g. ammonium, NH_4^+; nitrite, NO_2^-; nitrate, NO^- ^{3}; nitrous oxide, N_2O; dinitrogen, N_2), where different microbial processes have been identify. Under oxic conditions, but also at the upper OMZ boundary (oxycline), nitrification transforms NH_4^+ into NO_3^-. But OMZs are especially associated with denitrification, which is a bacterial process occurring only in O_2-deficient regions (e.g., Codispoti et al., 2001; 2005; Paulmier & Ruiz-Pino, 2009), where nitrate serves as the main terminal electron acceptor for the oxidation of organic matter (Lam & Kuypers, 2011 fide in Ulloa et al., 2013). In such cases, denitrification and anaerobic ammonium oxidation (Anammox) contributes to the removal of fixed nitrogen as N_2, with resulting impacts on global nutrient cycles and the climate system (Codispoti et al., 2001., Farías et al., 2007).

The effect of El Niño over the OMZ and the influence in the whole system is shown in Fig. 6; under normal conditions the ESSW mass lift upwards at the coast transporting nutrients to the surface layers and favoring gases exchange between the atmosphere and the ocean.

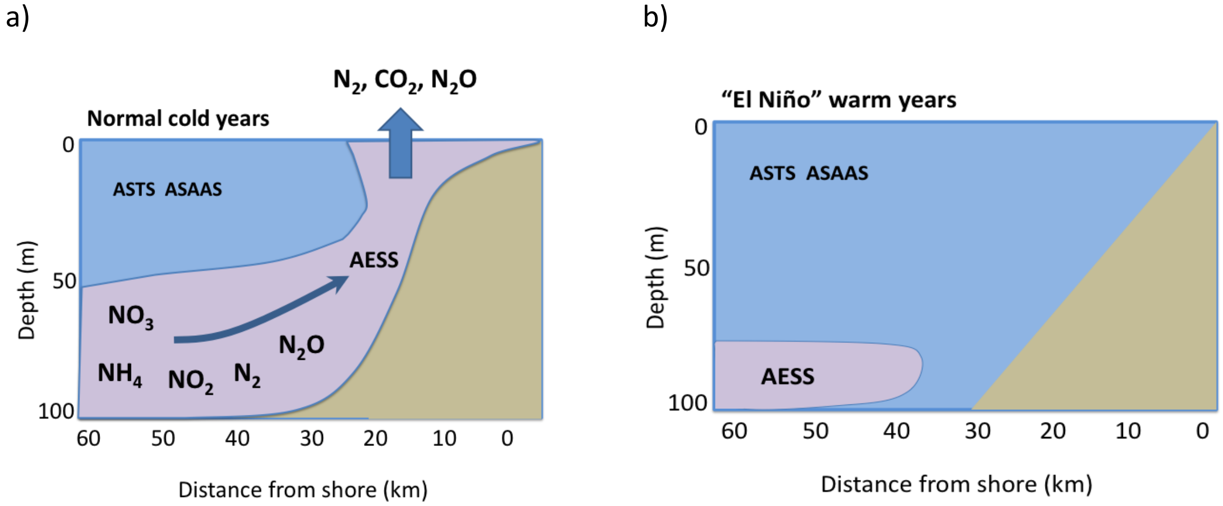

Figure 6. Transversal representation of the vertical displacement of the OMZ in northern Chile a) in normal cold years b) as consequence of El Niño. ASAAS: Subantarctic Surface Waters; ASTS: Subtropical Surface Waters; AESS: Equatorial Subsurface Waters. (Modified from Gallardo et al., 2001).

3.2 Nutrients

Macro and micronutrients effects (FIG. 7 a, b, c)

Nutrients and trace metals play a key role in controlling phytoplankton biomass over the Pacific basin (Thomas et al., 2012) and in the overall upper-ocean productivity (Redfield, 1934; de Baar, 1994: Morel et al., 2003). Changes in nutrient supply are felt at every trophic level, with consequences in the carbon transfer pathways (microbial web vs. classical trophic chain) (Montecino & Lange, 2009).

The primary production in marine ecosystems is supported by "new" and "regenerated" nitrogen. The "new" nitrogen mainly represented by nitrate (NO_3^-), is injected into the euphotic zone by mixing and vertical advection (upwelling), whereas ammonium (NH_4^+), the most common form of "regenerated" N, is mainly released during bacterial remineralization of dissolved organic matter (DOM) in the water column as well as by zooplankton excretion (Alcaraz et al., 1994; Bronk, 2002; Mopper & Kieber, 2002; all fide Fernández & Farías, 2012). The new nitrogen is the most important because it should be quantitatively equal to the organic matter exported below the surface ocean (Dugdale & Goering, 1967; Eppley & Peterson, 1979 all fide in Fernández & Farías, 2012).

The nutrient dynamics in the HCLME starts in the upper coastal ocean off Perú, where the high biological productivity creates a downward flux of organic material that decomposes at depth, which further depletes the already-low oxygen concentrations in the Poleward Undercurrent (PUC) which becomes extremely anoxic, with values < 1 µM Kg^{-1} as it moves to the south. Furthermore, this process causes heavy phosphate, nitrate and methane-hydrate deposits. The upwelling brings nutrients back into the equatorward surface layer, fueling productivity and creating a semi-closed "nutrient trap" that further enhances productivity. In general, the distribution of nitrate showed low subsurface concentrations (Pantoja et al., 2004) associated with high nitrite concentrations (>2 µM; Morales et al., 1996b) and coincident with low oxygen concentrations (<0.5 ml L^{-1}) (Thiel et al., 2007). The low oxygen conditions favors anaerobic denitrification by bacteria that uses nitrate as an electron source, reducing nitrate to nitrite (depleting nitrate and increasing nitrite) and ultimately reducing nitrite to nitrous oxide (Codispoti et al., 1989; Naqvi et al., 2004; all fide in Montecino et al., 2006). This implies that denitrification is an important process in the nitrogen recycling, as has been recognized for other OMZ regions (Codispoti & Christensen, 1985; Codispoti et al., 1986; Cornejo et al., 2006; all fide in Thiel et al., 2007).

Off southern Perú (15ºS) and north of Chile, warm and salty Subtropical Surface Water (SSW) at the surface with high values of oxygen and low values of nitrate is overlying the Equatorial Subsurface Water (ESSW) (high nitrate, low oxygen) below depths of 100-150m in the offshore regions (Montecino et al., 2006). The upwelling-favorable winds rises to the surface of these nitrate enriched waters, but also mixing and the Coastal-Trapped Waves (CTW'S) by uprising the nutricline, increases the efficiency of nutrient fueling into the euphotic zone (Hormazabal et al., 2001; Rutllant & Montecino, 2002; all *fide in* Montecino et al., 2006). Because upwelling is more intense within 50 km off the coast, the nitrate concentrations in the upper 50m are higher with respect to offshore. Below 50m next to the coast nitrate diminishes due to the presence of the (PUC), with relatively low nitrate and extremely low dissolved oxygen. At approximately 200km and 700km off the coast, subsurface nitrate minima are coincident with deeper regions of higher salinity and shallower regions of low oxygen. Next to the coast between 200km and 700km offshore and from 100 to 200m depth the minimum values of nitrate and also the maximum values of nitrite are found (Montecino et al., 2006).

The distribution of nutrients shows high variability associated with upwelling pulses and mixing processes (Thiel et al., 2007), meanwhile high-low pigment concentrations follow the same trend (Escribano et al., 2003; Marín et al., 2003; Thiel et al., 2007). The average of the monthly data of nutrient concentrations from 2002-2009 are show in the Fig. 7. High nutrient concentrations occur usually inshore decreasing offshore, which is more pronounced for phosphate and silica which is more marked for phosphate and silica when considering the monthly averages of the concentrations (Fig 7 a y b). In contrast, the nitrate concentration increases toward higher latitudes (Fig 7 c). Additionally, off 30°S, high surface concentrations of nitrate, phosphate and silicate have been reported by other authors i.e. ~5–15, 0.5–1 and 5–8 µM, respectively (Peñalver, 2004, fide in Thiel et al., 2007), and ~17 µM of nitrate and silicate during the austral Spring of 2007 (September) concentrations that were positively correlated (Torres & Ampuero, 2009). Besides, in the central-southern coastal areas with intense seasonal upwelling, values up to 10-25 µM of NO_3^- have been reported (Escribano et al., 2004; Montecino et al., 2004). In central Chile off Concepcion (36°30.8'S; 73°07.75'W), surface fertilization and the development of subsurface hypoxia occurs in austral Spring and Summer, and the rates of NO_3^- uptake that have been measured during seasonal upwelling were 5 times higher than in the non-upwelling season. Otherwise the NH_4^+ uptake rates was almost half of NO_3^- uptake rates during upwelling periods, and similar to NO_3^- uptake rates in the absence of upwelling (Fernández & Farias, 2012). The nutrient distribution at this latitude is also affected by the topography of the area, where several islands reduce the circulation and mixing of the water column (Thiel et al., 2007). In northern Chile, between 20°S and 22°S, high concentrations of nitrate were also observed nearshore below 100 m deep (0–20 µM; Escribano et al., 2004; Pantoja et al., 2004, Herrera & Escribano, 2006).

In general, rivers play an important role in the fluxes of trace metals, nutrient and particulate matter to coastal waters, and some of these components are considered to be important factors determining primary productivity (PP) in the water column (Thiel et al., 2007).

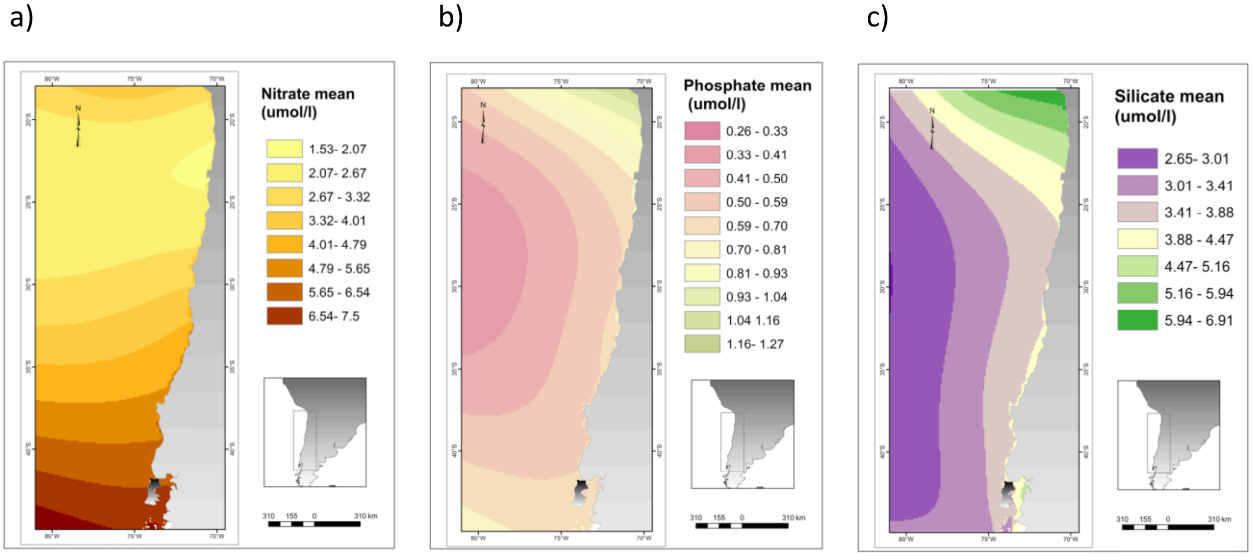

Figure 7. Monthly mean (2007-2009) of mean nutrient concentration (μmol L^{-1}) along the HCLME (data from Bio-Oracle Thyberghein et al., 2012): a) Nitrate, b) Phosphate, c) Silicate.

For example, iron often limits productivity where subsurface nutrient supply is enhanced, including the main oceanic upwelling regions of the Southern Ocean and the eastern equatorial Pacific (Martin & Gordon, 1988; Martin et al., 1993; Coale et al., 1998; Moore et al., 2013). The systems in the Humboldt Current are limited by Iron with ambient concentrations of 0.1 nM, and to measure the consequences of these low concentrations of Fe phytoplankton Fe limitation experiments were carried off Peru using shipboard incubation experiments (Hutchins et al., 2002) adding Fe up to 2.5 nM. The results of these experiments indicated that Chl- a, photosystem II, photosynthetic efficiency, and nitrate and phosphate drawdown increased in proportion to the amount of Fe added; the algal communities after Fe additions included colonial and flagellated *Phaeocystis globosa* and large pennate diatoms and Fe limitation decreased net $NO_2:PO_4^{-3}$ utilization ratios well below Redfield values.

Torres et al. (1999) showed that the deep upwelling of normally cold and already CO_2-supersaturated subsurface waters in the HCLME leads to an immediate outgassing of CO_2 at the coastal divergence. Outgassing is prevented by the inorganic carbon sequestration of phytoplankton, reducing the fugacity of CO_2 (fCO_2) and thus reducing or even reversing the CO_2 flux at the air–sea interface and being higher during periods of upwelling (Simpson & Zirino, 1980). Nevertheless, it has been shown that the iron limitation of phytoplankton growth (mainly diatoms) plays a role in maintaining high-CO_2 outgassing by preventing rapid interception of upwelled CO_2 (Torres & Ampuero, 2009).

Other microelements such as Cd and Co may also play an important role in biological processes. Measures of dissolved Cd in the water column in Mejillones Bay (23ºS; ~0.4–1.6 nM) shows a typical micronutrient-like distribution in the same way that the distribution of Co in Peru (Thiel et al., 2007). In the other hand, in surface sediments there are very high Cd concentrations (~60 µg g^{-1}; Valdés et al., 2003 fide in Thiel et al., 2007). It is probable that in other coastal waters of northern-central Chile, high Cd values in sediments are associated with biological uptake and subsequent deposition in the sediments (Thiel, et al., 2007).

4. PLANKTON

4.1 MICROBIOLOGICAL COMPONENTS

Microbiological components of the oceans consist of protists (eukaryotic), prokaryotic autotrophic bacteria and heterotrophic bacteria, Archaea, Fungi and Viruses. Each one of them is involved in the production processes taking different routes and occurs at different scales. The relative importance of each very different size components depends on factors such as environmental conditions and trophic interactions. Moreover, PP, the transfer of carbon to higher levels through microbial and classical pathways depends on the size structure of phytoplankton, the heterotrophic community structure, and the feeding preferences of the grazers (González et al., 2004a; Vargas & González, 2004a,b; Morales et al., 2007; Vargas et al., 2007a; Chavez et al., 2008; Pavés & González, 2008).

4.1.1. BACTERIOPLANKTON AND THE BACTERIAL SECONDARY PRODUCTION

The high fish production in upwelling systems has been primarily associated with recurrent upwelling pulses and to the predominance of short, thermodynamically efficient food chains (Ryther, 1969; Ryther et al., 1971). However, it has now been established that bacterioplankton constitutes an important fraction of the total carbon biomass in pelagic ecosystems in a variety of marine environments (McManus & Peterson, 1988). In oligotrophic waters bacterial biomass can be 2-3 times more abundant than phytoplankton (Cho & Azam, 1990) and in meso and eutrophic environments 0.5 to 2 times greater (Azam et al., 1983). Bacteria are an important pelagic mineralizer of organic matter. Actually it is accepted that a high proportion of the organic carbon produced by phytoplankton may flow through the bacteria in a variety of marine environments including upwelling areas and in the HCS (Montero et al., 2007). A significant amount of carbon flowing through the bacterioplankton may imply that the carrying capacity for fish in upwelling ecosystems is considerably less than that which may be anticipated for a simple herbivore-dominated food chain (Newell & Turley, 1987). It has been reported that depending on environmental conditions, bacterial secondary production (BSP), as a percentage of primary production, can fluctuate between 2 to 1101% (Fuhrman & Azam, 1982). This may represent an underestimation as most of the estimates of BSP/PP % do not take into consideration that bacterial activity continues at night (Mc Manus & Peterson, 1988).

BSP and bacteria abundances in coastal upwelling ecosystems is similar to that reported for other coastal environments and seems to be closely coupled to upwelling cycles, and consequently associated with water column stratification processes (McManus & Peterson, 1988; Vargas et al., 2007a; Daneri et al., 2012). In the HCS, BSP has been shown to increase a few days after the peak in phytoplankton production (McManus & Peterson 1988; Daneri et al., 2012). A similar decoupling between PP and BSP has been reported for the Benguela upwelling system (Painting et al., 1993). Furthermore, off Concepción (36° S), bacterial activity is higher during non-upwelling periods (e.g. 5–29.2 μg C L^{-1} h^{-1}), compared to upwelling periods (<0.1 μg C L^{-1} h^{-1}) considering short timescales (days), differences probably underestimated in the past (Daneri et al., 2012). The close relationship observed between primary productivity and bacterial production suggests tight coupling between the organic matter produced during photosynthesis (fresh material) and bacterial utilization (Kuznar et al., 2007; Montecino & Lange, 2009), so that the organic substrate availability is an important factor determining the bacterial activity (Vargas et al., 2007a;b).

Troncoso et al. (2003) quantified bacteria as one of the most fundamental components of the pelagic planktonic community from Antofagasta 23°S to Concepción 36°S upwelling ecosystems off Chile. In these areas, the upper values of BSP reported by these authors were greater than any reported in the literature for a variety of marine environments (Troncoso et al., 2003 and references therein). Moreover, latitudinal, longitudinal and seasonal differences reported indicate the highest BSP values measured in Antofagasta (1722 ± 1362 mg C m^{-2} d^{-1} in Summer), and the lowest BSP values in Coquimbo upwelling area (294 ± 160 mg C m^{-2} d^{-1} in Spring). The higher levels of BSP during Spring -Summer is a consequence of increased upwelling during this period, which is associated to the seasonal strengthening of the Pacific Anticyclone. During the Winter a weakening of the Pacific anticyclone coupled with a reduced light field results in four to six fold drops in BSP. For example, the data measured in coastal areas of Antofagasta and Coquimbo, showed that BSP values fell to 490 ± 178 mgC m^{-2} d^{-1} and 77± 56 mgC m^{-2} d^{-1} in the Winter (Troncoso et al., 2003). In general in the HCLME, BSP is two to five fold higher inshore than offshore under more oligotrophic conditions, such as those encountered in the Winter, but in less productive areas such as the Coquimbo upwelling area, the coast to offshore BSP gradient become less pronounced while interannual variations were also reported to diminish during pre El Niño conditions (Troncoso et al., 2003). Off Chile a very significant fraction of the organic matter produced by phytoplankton activity is being channeled through the bacteria (Daneri et al., 1994). Such that the proportion of carbon utilized by bacteria, taken as a percentage of PP, range from 16% to 96% (ca. 63%-96% in Antofagasta, 16%-34% in Coquimbo and 10%-24% in Concepción). Assuming a conservative bacterial growth yield of 0.25 (Daneri et al., 1994), the overall carbon utilization by bacteria often seems to be in or excess of the in situ PP. These results are in agreement with reported data for other upwelling systems (Brown et al., 1991; Ducklow, 1993; Weibinga et al., 1997) and for the Concepción shelf upwelling area (McManus & Peterson, 1988) bacteria are an important component of upwelling ecosystems capable of processing an important fraction of the organic carbon fixed by algal activity, as reflected in the low (<1%) rain rate of organic carbon at the sediment–water interface (Pantoja et al., 2008 fide in Montecino & Lange, 2009).

Bacteria biomass transfer carbon to higher trophic levels when consumed by heterotrophic or mixotrophic flagellates (e.g. Barbosa et al., 2001; Cuevas et al., 2004; Cuevas & Morales, 2006; Kuznar et al., 2009). The importance of these processes depends on the environmental conditions and the resources available to phytoplankton. In coastal upwelling systems, when upwelling cycles are relaxed, bacterial carbon demand in primary production is higher (Montecino & Lange, 2009). However, in global, the bacterial populations are significantly regulated by the consumption of heterotrophic microorganisms in a variety of systems, including the HCLME (i.e. McManus & Fuhrman, 1988; Hlaili et al., 2007; Montecino & Lange, 2009). In northern Chile, the grazing pressure of heterotrophic nanoflagellates controls bacterial production in the suboxic layers, which is relevant in areas with relatively shallow OMZ (Cuevas & Morales, 2006). In addition, indirect measurements from an area around Mejillones Bay (23°S) revealed high rates of ingestion of heterotrophic organisms (including nanoflagellates, ciliates and dinoflagellates) (Vargas & Gonzalez, 2004).

Most studies have attributed to bacteria the major role in processing organic matter in the microbial loop off central Chile however; there is evidence that Archaea (Microbes that have no cell nucleus or any other membrane-bound organelles within their cells) are also responsible for an important fraction of microbial secondary production (Levipán et al., 2007; Quiñones et al., 2009).

4.1.2. PHYTOPLANKTON COMPOSITION, SIZES AND PRIMARY PRODUCTIVITY

The microphytoplankton is the most conspicuous and dominant size class in most water systems (> 20 μm), including temperate and coastal upwelling systems. Diatoms are the most abundant component in numbers and biomass of this size fraction whereas dinoflagellates are the second largest group (Rodríguez et al., 2004 and references therein). Rivera (1995) indicated that in Chile 84 genera and 563 species of diatoms of marine phytoplankton, and 42 genera and 295 species of dinoflagellates are known. In these numbers, phytoplankton from the Humboldt Current, Oceanic Islands, Horn Cape Current and fjords of Chile are included. In the coast of north and central Chile phytoplankton species are typical from upwelling systems, between diatoms and dinoflagellates around 200 species from 5 taxonomic groups can be found (Avaria & Muñoz, 1991; Santander et al., 2003). Chain forming diatoms seem to be best adapted in upwelling environments presenting faster growth due to its higher efficiency to capture light and nutrient uptake (Avaria & Muñoz, 1991; Mackey et al., 1998). The diversity and dominant species may vary according to the season, the geographical location of the upwelling zone and the upwelling intensity, but generally it is mentioned in the literature that dominant and more frequently diatoms belong to the genera *Leptocylindrus, Rhizosolenia, Detonula, Nitzschia, Chaetoceros, Thalassiosira, Eucampia* and *Skeletonema*, while the dominant dinoflagellate are: *Ceratium, Prorocentrum* and *Gymnodinium* (Avaria & Muñoz, 1991; Iriarte et al., 2012). In general, when biomass is high in central and southern Chile the larger and long-chain-forming diatoms are the most abundant (Vargas et al., 2007a).

The microphytoplankton community structure is coupled to an intermittent upwelling regime in the HCLME, because they respond to these changes in the physical environment ("bottom-up" control) (Santander et al., 2003; Aguilera et al., 2009; Kuznar et al., 2009). Along the Chilean coast, the ecological successions of microphytoplankton show a pattern of dominance of diatoms in or immediately after upwelling events. On these systems, diatom assemblages undergo successional processes among r and K selected species (Avaria; Kuznar et al., 2009), according to their ability to colonize empty niches and persist in the environment (Margalef, 1978; Reynolds, 2006). *Detonula pumila*, *Chaetoceros debilis*, *Leptocylindrus danicus* are species considered as r-selected, and are characterized by their small cell size, high reproductive rates and high efficiency to obtain and use resources, so they usually start ecological succession. k-selected diatoms, are larger in size with lower growth rates, but are skilled using scarce resources, such as *Guinardia delicatula* (Kuznar et al., 2009). The diatoms are followed by an increased presence of dinoflagellates and other phytoflagellates during relaxation periods, which usually occur during Summer in the central-southern areas (Avaria, 1971; Alvial & Avaria, 1982; Avaria & Muñoz, 1982; Avaria et al., 1989; Avaria & Muñoz, 1991 in Santander et al., 2003; Thomas et al., 2001), which is less pronounced in the northern areas due to weak seasonality of the wind-driven upwelling events. Comparatively off more southern areas and during the Winter period there is a dominance of autotrophic and heterotrophic smaller sized groups (Iriarte et al., 2012). In relation to the upwelling phases and species richness it has been observed that during the Spring, in the northern coastal area (Iquique, 20°14'-20°18' S), relaxed periods are characterized by low species diversity, with increased diversity when winds promote active upwelling (Santander et al., 2003). In this case, salinity was the determining factor in the microphytoplankton community structure, which is linked to the type of water mass. The microphytoplankton (>20 μm) are, in general, dominant in coastal zones (>37 km) whereas pico- and nanophytoplankton (pico: 0.7–2.0 µm; nano: 2.0–20 µm) predominate in the offshore, mostly oligotrophic zone (Morales et al., 1996a; Iriarte & González, 2004). The dominant functional group of microphytoplankton also depends on the longitudinal position, as diatoms are dominant in coastal zones (< 10 nm) while in the oceanic zone the dinoflagellates dominate, although the total abundance is lower in neritic areas (Avaria & Muñoz, 1983; 1991).

The microphytoplankton total biomass in the HCLME is usually associated with dominant functional group. Thus, greater biomass is achieved when the diatoms dominate, i.e. during the warmer seasons in the central- southern coastal areas with high solar radiation and high concentration of nutrients. In cooler conditions, less light and oligotrophy, lower values of biomass are found and a dominance of small flagellates increasing the importance of microbial food webs and the carbon flux to the bottom (Rodríguez et al., 2004 and references therein, Iriarte et al., 2012). Changes in biomass are much less variable in northern Chile and the seasonality in Chl-a concentration showed slightly higher values during the Winter and early Spring (Thomas et al., 2001).

The HCS as one of the most productive large marine ecosystems (Mackas et al., 2006; Montecino et al., 2006; Montecino & Lange, 2009; Escribano & Morales, 2012), achieves high levels of PP (Daneri et al., 2000; Troncoso et al., 2003; Montero et al., 2007; Rodríguez et al., 2010; Iriarte et al., 2012), with integrated values of gross primary production > 15 g C m^{-2} during active upwelling off Concepción (36°30’80”S–73°07’70”W) (Montero et al., 2007), although, as with the biomass and size structure, there is great spatial and temporal variability, with higher mean values in coastal areas than oceanic areas (Fig. 8 and 10) and highest variability in central-southern of Chile than northern of Chile (Fig. 8) .

In the HCS high fish productivity has been associated with this high productivity of phytoplankton, for example, in central Chile (32° S), it has been reported that the period of maximum spawning for hake coincides with the period of maximal proliferation of phytoplankton (Avaria & Avial, 1985).

The close relationship between biomass and PP, wind regimes and coastal upwelling processes are determined by the variability of the pycnocline–nutricline–oxycline depth, which modify the light, nutrients and oxygen availability for the cells (Montecino & Lange, 2009). This is associated with the width of the shelf (which defines the amplitude of the coastal area) and the frequency of upwelling driven by winds, due that together determine the amount of nutrients exported from the seabed to the surface layers (Strub et al., 1998). In the central-southern coastal areas intense upwelling of nutrient-replete waters fertilize the euphotic zone (e.g., NO_3^- up to 10-25 μM) (Escribano et al., 2004b; Montecino et al., 2004) creating suitable conditions for large-size primary producers, and in turn causing profound effects on the water column processes such as carbon flow through the pelagic food web and carbon export toward deeper layers of the ocean (Gonzalez et al., 1998; Jacob et al., 2011). In northern Chile (21°-23°S, off Iquique and Antofagasta), permanent upwelling sustains high PP throughout the whole year (3-9 g C m^{-2} d^{-1}; Daneri et al., 2000; Montecino & Quiroz, 2000; Pizarro et al., 2002; Iriarte & González, 2004; Thiel et al., 2007; Montecino & Lange 2009).

Each of these processes (PP, PB) is modified by climatic conditions such as wind direction and intensity at different spatial and temporal scales (Montecino et al., 2006a,b, and references therein). Thus considering a multi-scale approach it have seen that the cold-warm phases and transitions determine the supply of limiting nutrients to the euphotic zone, which, in turn, regulates overall productivity (Table 2) (Montecino et al., 2006b). Previously, McManus & Peterson (1988) showed that PP was lowest during periods of active upwelling and highest during subsequent periods of calm or light northerly winds.

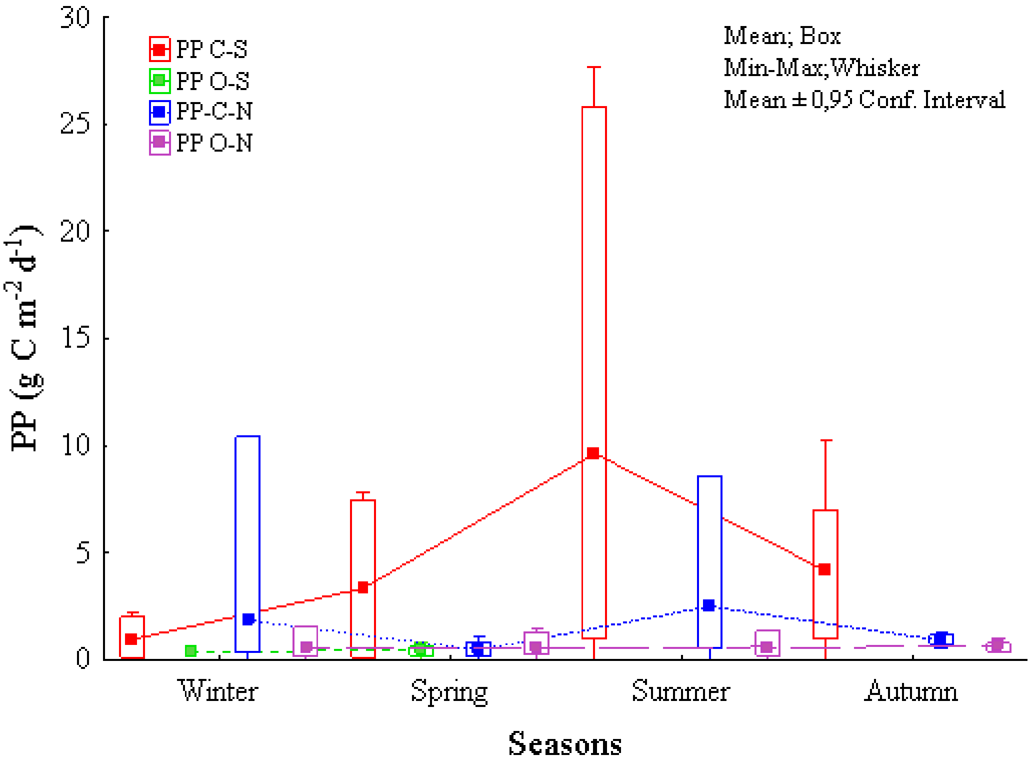

Figure 8. Coastal (C) and oceanic (O) primary productivity (Net/gross PP) in gC m^{-2} d^{-1} in northern (N) and central-southern (S) Chile during different seasons between years 1998-2007 (n=130 measurements) during five occasional cruises and one time series (Pizarro et al., 2002; Montecino et al., 2004; Montero et al., 2007; González et al., 2009 and Jacob et al., 2011). Mean values in S coastal areas (red) are highest in Summer and in N coastal areas in Winter and Summer (blue).

Table 2 Coastal environmental conditions from warm to cold (from deep to shallow thermo-nutricline due to interannual, annual and intraseasonal variability) and consequences in primary productivity (PP) and phytoplankton size composition (phyto size) and the carbon transfer pathway, microbial trophic web (Tweb) vs classical trophic chain (Tchain) (modified from Montecino & Lange 2009).

Conditions	Primary productivity (PP)	Phytoplankton cell size	Carbon transfer pathway	ENSO-Season
Warm	<<PP	<< phyto size	Tweb	EN-Late Summer
Cold	>>PP	>> phyto size	Tchain	LN-Early Spring

In the EBCS coastal band in South America, the HCLME characterized by strong upwelling-based nutrient enrichment with low wind-induced turbulence generation and relatively extended mean ‘‘residence time” within the favorable upwelling-conditioned near-coastal habitat is also under the cyclic ‘‘re-setting” of the system by ENSO perturbations, that may tend to interrupt adverse self-amplifying feedback loops within the nonlinear biological dynamics of the ecosystem (Bakun & Weeks, 2008). The relationships of Chl-a anomalies to forcing were explored through correlations to local upwelling anomalies and three indices of Pacific Ocean basin-scale variability, the Multivariate El Niño Index (MEI), the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO) by Thomas et al., (2009) finding a much stronger domination of El Niño conditions on HCS anomaly relationships over this 10-year period. This interannual variability recurrently exposes these ecosystems to disruption and re-setting. For example, during the Winter a weakening of the Pacific anticyclone coupled with a reduced light field results in a decrease in the productivity of the system, which has been reflected in overall two to five, fold drops in PP (Daneri et al., 2000). During upwelling events, high frequency wind regimes changes constitute probably an important intermediate perturbation ecologically favorable for high biological productivity. This adds to the idea that phytoplankton and PP patterns are driven by multiscale upwelling forcing (Rutllant & Montecino, 2002; Montecino et al., 2006b; & Montecino & Lange, 2009).

The effect of light availability on PP, has been explained by climatological analysis of low cloud frequency derived from visible GOES imagery during the Spring, and it was shown that immediately north of upwelling centers, on average, more clear of low cloud cover is found (Tongoy -Coquimbo, Fig. 9a). These results can elucidate increased primary production due to higher temperatures, nutrient input from the upwelling centers and thermal stratification (Garreaud et al., 2011). Additionally, similar patterns can be observed in the monthly mean (2007-2009) low cloud percentages along the HCLME i.e. Concepción and Antofagasta (Fig 9b).

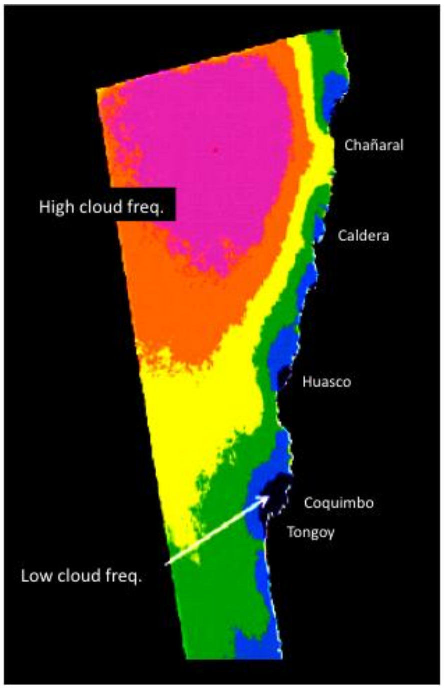

Figure 9a: Spring climatology of low cloud frequency derived from visible GOES imagery (pink is >80%; blue is less than 30%). Adapted from Gonzalez et al. (2007), and modified from Garreaud et al., 2011.

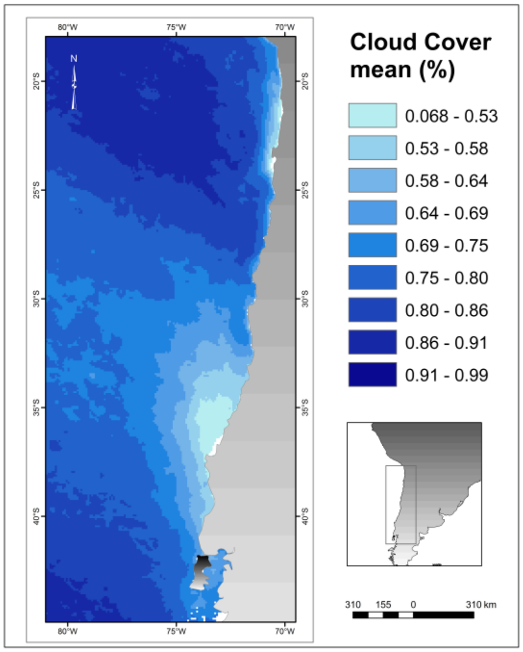

Figure 9b. Monthly mean (2007-2009) of cloud percent along the HCLME (data from Bio-Oracle, Thyberghein et al., 2012).

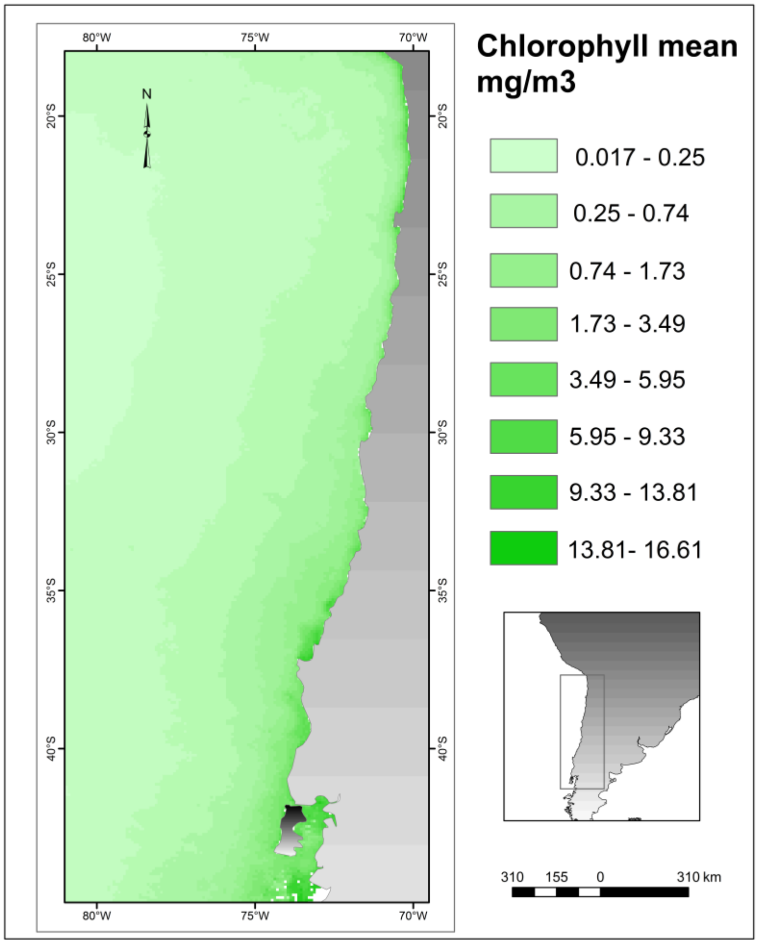

Figure 10 Monthly mean (2007-2009) of Surface Chlorophyll concentration (Cl-a) along the HCLME (data from Bio-Oracle, Thyberghein et al., 2012).

4.1.3 Red tides and Harmful Algal Blooms

The term red tide, referring to a change in the color of seawater, is caused by population growth of certain phytoplankton species as a result of an increase in the rate of cell division or by mechanical accumulation, producing a color ranging from brown-yellow to deep red, depending on the concentration and pigmentation of the species involved (Guzman & Campodónico, 1978; Avaria, 1999a). Because most red tides are harmless (Lopez et al., 1999), currently the term Harmful Algal Bloom (HAB) is used to refer to those blooms that cause a negative effect on the biota, human health, aquaculture, tourism or other economic activity, regardless of whether they cause discoloration of seawater (Avaria, 1999b; NRC, 1999; Frangópulos, 2002). One ecologically important effect is that the HABs modify the structure of ecosystems by altering marine food webs (Fleming et al., 2006).

In general, algal blooms are HABs if they produce high biomass or species are toxic. In the first case, a disproportionate increase in cell density could lead to a depletion of oxygen concentration, resulting in hypoxia or anoxia conditions for biota, or the diatoms frustules can cause mechanical damage to the gills of fish, which could result in economical problems for marine farming and fisheries (Fleming et al., 2006). Among the bloom-forming species in northern Chile are the dinoflagellates *Prorocentrum micans*, *Gymnodinium spp. Glenodinium spp*. and the ciliate *Mesodinium rubrum* (Avaria et al., 1999b). The presence of the latter is associated with upwelling processes, whereas dinoflagellate blooms in this region are related with ENSO (Rodríguez, 2004; Krock et al., 2009).

Likewise, the potent toxins produced by dinoflagellates or diatoms can be transmitted to human consumers through shellfish and fish food, and generate allergic or intoxications producing gastrointestinal and neurological pathologies, and in extreme cases, death (Hallegraeff, 2003; Varela et al., 2012; Fleming et al., 2006).

Phycotoxins that have been detected in Chile include saxitoxins (STXs) and more than 20 structurally- analogue compounds (Bricelj & Shumway, 1998). This neurotoxin group is known as Paralythic Shellfish Toxins (PST), formerly known as Paralythic Shellfish Poison (PSP), due to the paralyzing effects acting as blockers of the sodium channel. Microorganisms synthesizers of PST toxins in Chile are the dinoflagellates *Alexandrium catenella* and *A. tamarense* (Burkholder, 1998), but It is unknown if *A. oftenfeldii* is STXs producer (Guzmán et al., 2002; Molinet et al., 2003). The STXs also are attributed to some *Gymnodinium* and *Pyrodinium* species (Burkholder, 1998).

Others recurrent toxins that had been detected in Chilean waters are okadaic acid (OA) and dinophysistoxin (DTX), which are known as diarrhetic toxins (DST). It is assumed that dinoflagellates synthesizing these toxins are *Dinophysis acuta* and *D. acuminata* (Blanco et al., 2007a; Krock et al., 2009). Blanco et al. (2007a) have also detected pectenotoxins (PTX) in *D. acuminata*, but some studies suggest that their oral toxicity is very limited in humans (Miles et al., 2004). Using mass spectrometry, some investigations have also detected yessotoxins (YTX) in

Arica Bay (18°S), a lipophilic phycotoxin, maybe produced in Chile by the dinoflagellates *Gonyaulax spinifera*, *Protoceratium reticulatum* and *Lingulodinium polyedrum* (Krock et al. 2009; Pizarro et al. 2010a). Recently, in Coquimbo Bay (30°S), lipophilic marine toxins the azaspiracids (AZPs) and espirolides (SPXs), have been documented which share similar characteristic with OA, DTX, PTX and YTX (López et al., 2009; Alvarez et al., 2010), however the species that synthesize these toxins have not yet been identified.

The domoic acid is a neurotoxin amino-acid responsible for amnesic shellfish poisoning (ASP) in humans and its production has been attributed to some diatoms of the genus *Pseudo-nitzschia*, specifically in *P. australis* and *P. calliantha* and not found in *P. subfraudulenta* isolated from mixed blooms occurring in Northern Chile (Álvarez et al., 2009a). More research is needed to evaluate the potential for toxin production in *P. pseudodelicatissima*, while other species recorded along Chile have presented toxicity in other regions of the world (Álvarez et al., 2009a and references therein).

The understanding of the biogeography and ecology of key species and their toxins in relevant due the high impacts at different levels from health to economics. Thereto, it is relevant to sustain monitoring and research programs to evaluate the role of physical, chemical and biological variables in the occurrence of HABs, their frequency and distribution (Cembella et al., 2010; Thomas et al., 2010**;** Varela, 2012). In Chile examples of monitoring programs are "Sanidad de Moluscos Bivalvos" run by Sernapesca from 1997 to 2004 and the project "Difusión Programa Marea Roja en la XII Región" funded by the Fondo Nacional de Desarrollo Regional (FNDR). These programs and other research projects have produced the following information about HABs species biogeographic distribution.

From all dinoflagellates, the genus *Alexandrium* is the most widespread in the world; they occur mainly in temperate regions but have also been reported from tropical and subarctic locations (Varela et al., 2012). In Chile, *A. catenella* appears frequently in samples of phytoplankton of the southern regions, but this species has progressively expanded its distribution in the last four decades. The first report was in the Magellan region (53°S) in 1972 (Guzmán et al., 1975) and since then it distribution has expanded northward (up to 42°S), associated with recurrent toxic outbreaks along the channels and fjords of Chile's austral regions (Lembeye, 1981; Uribe, 1988; Guzmán et al., 2002; Molinet et al., 2003; Mardones et al., 2010). Through morphological, toxicological and phylogenetic analyses, Varela et al. (2012) have found significant intraregional variability strains of *A. catenella*, which showed twenty-two strains isolated from different localities along the wide distribution area of this species (from 42°S to 55°S). Nevertheless, recently, blooms of *Alexandrium* were detected in several aquaculture sites in northern Chile i.e. Mejillones, Guanaqueros and Tongoy Bays, between 13°55'S and 33°5'S, comprising the subtropical zone of the southeastern Pacific Ocean (Álvarez et al., 2009b).

In de HCLME the dinoflagellate *Dinophysis acuminata* has been reported in an area of ca. 350 Km from Bahía Inglesa - Bahía Tongoy in northern Chile, in the vicinity of scallop harvesting (Blanco et al., 2007a). *D. acuminata* and low amounts of *D. rotundata* cells (possibly toxic *Dinophysis* species), were identified at 18°29.986'S–18°38.431'S and 70°19.463'W–70°21.492'W (Krock et al., 2009).

Records of diatoms of the genus *Pseudo-nitzschia* covering more than 1000 km, having been found from northern to southern Chilean waters; Bahía Antofagasta (23°01'S, 70°25'W) (Rodríguez, 2004), in mixed blooms of phytoplankton from Bahía Inglesa (27º7'S, 70º52'W), Bahía Tongoy (30º15'S, 71º20'W) and Bahía Guanaqueros (Suárez-Isla et al., 2002; Álvarez et al., 2009a), in central Chile in Bahía Valparaíso (33º01'S, 71º38'W) (Avaria, 1962), in South Chiloé (Suárez-Isla et al., 2002), and between 36ºS-41ºS (Rivera, 1985). It is important to consider that the identification of the species in this genus is very difficult using only optical microscopy, being necessary to use more sophisticated techniques such as electron microscopy or molecular methods. Furthermore, the attribution of toxicity to a concrete species requires, in addition to its identification, the demonstration of the presence of the toxins in cultures or isolated cells (Álvarez et al., 2009a and references therein).

Toxins affect humans through consumption of contaminated seafood. These toxins are tasteless, odorless, and heat and acid stable. Furthermore the contaminated organisms have normal aspect and food preparation procedures will not prevent intoxication if the fish or shellfish is contaminated (Baden et al., 1995). Most affected shellfish can have a mixture of various toxins, depending on the species, the toxin-producing organism and the geographic area affected. The toxins are accumulated in the digestive gland of shellfish, and once consumed by humans are rapidly absorbed by the gastrointestinal mucosa. Poisoning depends on the ingested dose, intoxicated individual susceptibility and the rate of elimination of toxins (Blanco *et al.*, 1997; Bougrier et al., 2003). Some toxins can be extremely lethal.

Marketing regulations of seafood for human consumption state that these may contain very low levels of these compounds, without compromising the health of consumers. For PST toxins the maximum limit should be 80 μg STX eq/ 100 g of tissue. DST is the semi-quantitative detection, since it is considered the number of mice that were injected with digestive gland extract shellfish and die within 24 hours. The regulatory limit of domoic acid concentrations is 20 μg g^{-1} of shellfish meat, higher values lead to the banning of shellfish harvesting from both wild populations and aquaculture sites, with the resulting negative effect on the local economies (Álvarez et al., 2009a).

The vectors of all these toxins are herbivores and mostly planktivorus shellfishes, principally bivalves mollusk mostly fished in the three austral regions of Chile, however, scallop *Argopecten purpuratus* and the mussel *Semimytilus algosus* contaminated with PST have been detected in three aquaculture sites in northern Chile (13°55’ S and 43°5’S) (Álvarez et al., 2009b). The ASP are has also been found in the tunicate *Pyura chilensis*, which has a high commercial value (López-Rivera et al., 2006), next to *A. purpuratus* aquaculture sites (Suárez-Isla et al., 2002). Krock et al. (2009) carried out the first report of PTXs and YTX from planktonic samples in the Chilean coast, from Arica Bay, and Pizarro et al., 2010 have detected them in the Los Lagos Region. Moreover, lipophilic toxins AZPs and SPXs were detected in razor clam (*Mesodesma donacium*) and taquilla clam (*Mulinia edulis*) in Coquimbo Bay in Spring 2008 (Alvarez et al., 2010). These many issues deserve different lines of research that should be supported permanently in the HCLME.

In a global scale during the last three decades a notorious increase of HABs has been reported in frequency, intensity and geographical spread (Sellner et al., 2003). Among the probable causes of these problems are increasing human activities such as aquaculture (Hallegraeff, 1993; Hallegraeff & Bolch, 1992), eutrophication by increased concentrations of nitrogen and phosphorus (Anderson et al., 2002) or the breakdown in the macronutrient ratio that favours harmful species (Smayda, 1990). Physical factors such as water temperature and consequently stratification, may also in some cases promote the explosive growth of dinoflagellates (Hallegraeff, 2010). In other cases, it also depend on hydrodynamic processes related to transport of vegetative cells or resting cysts surviving during ballasting process, the voyage in the dark ballast tank, and subsequent ballast water discharge (inoculation), with posterior successful germination of cysts, sustained growth and reproduction of planktonic cells. Additionally, the inoculums may be spreading via coastal currents, or by local shipping (Hallegraeff, 1998).

4.1.4. VIRUSES

Viruses are biological components ubiquitous, abundant, dynamic, and present in all ecosystems on the planet (Egaña, 2012). In one milliliter of seawater can be found up to 108 viral particles (Wommack & Colwell, 2000 fide in Egaña, 2012) and an estimated abundance in the oceans is 1030 virus with a biomass of about $2x10^{11}$ kg of carbon, which is surpassed only by the bacterial biomass (Sutlle, 2007; Hambly & Suttle, 2005). In the ocean viruses infect all biota, from bacteria to whales (Suttle, 2005 fide in Egaña, 2012), but the most abundant are bacteriophages (Weinbauer, 2004), which explains its high relation to the abundance and bacterial activity.

The pool of viruses in the ocean is very dynamic due to their high rates of reproduction and mortality. Furthermore, their presence in the water column responds to the abundance of their hosts, and the system input with deep-water reaching the mixing zone through upwelling and river inputs (Egaña, 2012). The few studies of marine viruses in Chile indicate their abundance and sometimes some ecological aspects. At Valparaíso Bay (32º57’ S - 71º34’ W) in HCLME system, have been measured concentrations of viral particles of $0.1 x10^7$, 1.5×10^7 and 7×10^7 mL-1 virus before, during and after the upwelling, respectively, where the maximum values were measured after phytoplankton blooms (Kuznar et al., 2009). While virus measured obtained in the water column over the continental shelf (36°30'18" S, 73º 00'75" W) and Coliumo Bay (36°31'79 "S, 72º57'02" W) indicated 4.1×10^7 and 5.87×10^7 viral particles mL^{-1}, respectively (Chiang et al., 2007). Further south, between 41°39' S and 43°49' S in the inner sea of Chiloé, the range detected is 7.5×10^5 - 2.19×10^7 viruses mL^{-1}, values that correlated with the concentration of heterotrophic bacteria and showed a positive trend with the concentration of photosynthetic pigments (Egaña, 2012).

Viruses have great influence on the composition of communities in all environments, including upwelling systems, since they act as regulators of the diversity and abundance of bacterioplankton and phytoplankton. Viruses also modified microbial food webs affecting primary and bacterial productivity because participate in the flow of carbon and nutrients influencing (Suttle, 2007; Kuznar et al., 2009). Nutrient enrichment in areas of upwelling produces high productivity of phytoplankton and bacterioplankton, while the abundance and dynamics of viruses respond to changes in the populations of the first two, being its main hosts. Generally, after an upwelling event, significant increases occur in the abundance of these components microbiological (Santander et al., 2003; Kuznar et al., 2009; Rohwer, 2003 fide in Egaña, 2012) and the common sequence ecological successions begin with an increase in the concentrations of phytoplankton, heterotrophic bacterioplankton followed then by virus (Kuznar et al., 2009).

4.1.5. FUNGI

Fungi could play a major role in the detrital food web in coastal marine ecosystems, but there is a lack of global knowledge in the world's oceans. Studies on fungi in HCLME in Chile are also few and only the coastal zone off central, near Conception Bay (~ 36ºS) (Gutiérrez et al., 2010; 2011). These analyzes shows a temporal pattern in fungal biomass in the water column during a year cycle like a reflection of their capacity to hydrolyze organic polymers and, in consequence, fungal biomass and activity respond to a seasonal cycle of upwelling in this ecosystem. Furthermore, found a relationship between fungal biomass and microplankton biomass and upwelling cycles. During active upwelling periods there are higher fungal biomass, being comparable to that of prokaryotes (bacteria plus Archaea) and was associated with an increase in phytoplankton biomass and in extracellular enzymatic hydrolysis in waters from the depth of maximum fluorescence (Gutiérrez et al., 2010; 2011). The fungal biomass recorded ~6 µg C L^{-1} in surface waters during austral Summer 2008 (Gutiérrez et al., 2010) and ≥ 4 μg C L^{-1} during the austral Spring and Summer 2009 with a maximum value of ~40 μg C L^{-1} (Gutiérrez et al., 2011).

4.2.- Zooplankton.

4.2.1.- Biodiversity of holoplankton

The zooplankton is taxonomically and structurally diverse in size and shape (Lalli & Parson 2006). In the HCLME the most studied taxa of zooplankton are Copepoda (e.g., Heinrich, 1973; Arcos, 1975; Vidal, 1976; Hidalgo & Escribano, 2001; Escribano et al., 2003; 2009; 2012; Morales et al., 2010; Grunewald et al., 2002) and Euphausiacea (Antezana 1970, 1978, 2002, 2009, Fernández et al., 2002, Escribano et al., 2000, Riquelme-Bugueño et al., 2012). Nearly 60 species of copepods have been identified, of which the dominant in the coastal zone are *Calanus chilensis*, *Centropages brachiatus*, *Paracalanus parvus*, *Acartia tonsa*, *Eucalanus inermis*, *Oithona similis*, *Oncaea conifera* and *Corycaeus typicus*. *Calanoides patagoniensis* and *Calanus chilensis*, are endemic species of the HCLME (Marín et al., 1994, Morales et al., 2010), whereas *Centropages brachiatus*, *Paracalanus parvus*, *Acartia tonsa* and *Oithona similis* are cosmopolites and widely distributed along the Chilean coast (Thiel et al., 2007). Euphausiids in the HCLME is composed of 42 species since the most abundant and endemic species is *Euphausia mucronata* (Antezana, 1978). The gelatinous, principally the ctenophorous and siphonophorous, are an important group of species in HCLME. In the central Chile Palma & Rosales (1995) identify 45 species of gelatinous: hydrozoa (17), siphonophorous (12), ctenophorous (4), chaetognaths (10) and thaliaceans (2), the dominant are *Muggiaea atlantica*, *Obelia* spp., *Phialidium* spp., *Sagitta bierii*, *S. enflata* and *Thalia democratica*. Aravena & Palma (2002) publish a taxonomic identification of 15 species of appendicularians off northern Chile, the dominants species are: *Oikopleura longicauda*, *O. gracilis*, *O. albicans*, *O. cophocerca, Fritillaria pellucida typica*, *F. pellucida omani* and *F. venusta*. Palma & Apablaza (2004) find in northern Chile (33°S) 44 species of gelatinous zooplankton (23 siphonophores, 17 hydromedusae, and 4 ctenophores). Eight species, *Sphaeronectes irregularis*, *Rhizophysa eysenhardti*, *Amphogona apicata*, *Proboscidactyla stellata*, *Sarsia coccometra*, *Pleurobrachia bachei*, *Thalassocalyce inconstans* and *Velamen parallelum*, were recorded by the first time in HCLME. The more recent revision of marine biodiversity mentioned 22 species of chaetognaths, 135 species of Hydrozoa, 14 Scyphozoa, 31 Appendicularia, 6 Ctenophora and 25 Thaliacea (Sielfeld & Guzman, 2006). Most of these species are important components of the zooplankton in HCLME.

Table 3 Number of zooplanktonic species ranked according to taxonomic groups

Taxonomic group	**Species number**
Copepoda	60
Euphausiacea	42
Appendicularia	31
Thaliacea	25
Chaetognatha	22
Scyphozoa	14
Siphonophora	12
Ctenophora	6

4.2.2.- Abundance of holoplankton

Copepod dominate in relative abundance (>60%) over other taxonomic groups (e.g., euphausiids, gelatinous) in Central-Chile (off Concepción) during August 2002 to December 2005. Appendicularia (345.1 ind. m^{-3}) and siphonofora (397.7 ind. m^{-3}) followed copepods (1587.8 ind. m^{-3}) in relative abundance. Euphausiids were much less abundant (31.18 ind. m^{-3}), but were considered to be important in the total biomass (Escribano et al., 2007). In central-Chile (Arauco Gulf) in the zooplankton the copepods is dominated by only a few species (*Paracalanus parvus*, *Calanus chilensis*, *Calanoides patagoniensis*, *Centropages brachiatus*) with densities higher than 6000 individuals m^{-2} during January 1985 (Castro et al., 2007). In northern Chile (off Iquique) *Eucalanus inermis* (473.2 ind. m^{-3}) and *Paracalanus* cf *indicus* (158.8 ind. m^{-3}) are the copepods more abundant during March 2000 representing 47.6% and 16% of relative abundance respectively (Escribano et al., 2009). Twenty year time series (1988-2008) of copepod abundance in northern Chile (off Antofagasta) and central-Chile (off Concepción) showed that *Paracalanus* cf *indicus* is the dominant species in both locations with similar relative abundance of 43% in Antofagasta and 45% in Concepción but different densities (Antofagasta 1846.4 ind. m^{-3}, Concepción 142.1 ind. m^{-3}) (Escribano et al., 2012). In northern Chile (off Iquique) *Euphausia mucronata* is the euphausiid more abundant (103 ind. m^{-3}) during

March 2000 representing 10.4% of relative abundance (Escribano et al., 2009). The most abundant species off Central/South Chile is *E. mucronata* reaching an average of 205.9 individuals per 1000 m^{-3} (from April 2007 to November 2008) (Riquelme-Bugueño et al., 2012). In July–August 1974 the density of this species reached 16,500 individuals per 1000 m^{-3} (Antezana, 2009). Gelatinous zooplankton in northern Chile show seasonal trends in density, increasing in Spring and Summer, with the highest aggregations (> 2600 ind.·100 m^{-3}) of *Aglaura hemistoma*, *Solmundella bitentaculata*, *Muggiaea atlantica* and *Pleurobrachia bachei* in October and *Obelia* spp. in February (Apablaza & Palma, 2004). In central-Chile (35-37°S) the Ctenophores *Pleurobrachia bachei* and *Beroe cucumis* are the most abundant species (>1000 ind. 100 m^{-3}) (Pavez et al., 2010).

4.2.3.- Holoplankton variability

The euphausiid *Euphausia mucronata* is closely associated with upwelling centers off northern Chile (Escribano et al., 2000) and performs an extensive vertical migration into the OMZ daily (Antezana, 2009). Gelatinous zooplankton is known to form dense aggregations in the coastal upwelling zones (Pagès et al., 2001). Copepod species appear strongly constrained to the upper layer (<100 m) over the OMZ (Escribano & Hidalgo, 2000a). Zooplankton populations tend to aggregate in upwelling zones in northern Chile and they are very patchily distributed (González & Marín, 1998; Escribano & Hidalgo, 2000a). Dominant zooplankton, which usually aggregates near the upwelling centers in this region (Escribano & Hidalgo, 2000b), must cope with such low-oxygen conditions. The options are both avoiding the OMZ and restricting the population to the upper oxygenated layer, as earlier reported for some dominant copepods (e.g. Escribano, 1998). The most abundant species of gelatinous zooplankton in central-Chile (35-37°S) occur in well-oxygenated waters; however, high abundances (10–100 ind. 100 m^{-3}) were also observed in suboxic waters (Pavez et al., 2010).

Recent results on the distribution of plankton along an inshore–off shore off Concepción (36°S) show that large copepod species, which are dominant in the upwelling area (i.e., *Calanus chilensis* and *Rhincalanus nasutus*), also display a secondary abundance maximum associated with the presence of a Chl-a and cyclonic eddy (Morales et al., 2007). Other species that are common in the upwelling area off Concepción affected by offshore advection include: *Centropage brachiatus*, *Pleuromamma gracilis*, *Acartia tonsa*, *Paracalanus parvus*, *Corycaeus typicus*, *Triconia* (*Oncaea*) *conifer*, *Oithona nana*, and *Oncaea similis* (Arcos, 1975; Peterson et al., 1988; 1998; Escribano et al., 2007; Morales et al., 2007).

4.2.4.- Diel vertical migration

It has been observed that several abundant epipelagic species concentrate in the upper 50 m without exhibiting diel vertical migration (Escribano, 1998; Escribano & Hidalgo, 2000a), although some euphausiids, such as *Euphausia mucronata*, may temporarily enter the OMZ (Antezana, 2002), or some others like the copepod *Eucalanus inermis* may even reside in it (Hidalgo et al., 2005a). In the upwelling region off northern Chile, the most abundant species are usually closely related to coastal upwelling plumes (Escribano et al., 2000; Giraldo et al., 2002). These species have been well identified (Heinrich, 1973; Hidalgo & Escribano, 2001). Among dominant ones, the studies of horizontal and vertical distribution have been focused on the calanoids *Calanus chilensis* (Escribano, 1998), *Centropages brachiatus* (González & Marín, 1998) and *Eucalanus inermis* (Hidalgo et al., 2005a) and on the euphausiid *Euphausia mucronata* (Escribano et al., 2000; Antezana, 2002). The available information indicates that *Calanus chilensis* and *Centropages brachiatus* are mostly restricted to the upper layer without performing substantial diel vertical migration (Escribano, 1998; Escribano & Hidalgo, 2000a). By contrast, *Eucalanus inermis*, the dominant species among a complex of four to five species of the genus *Eucalanus* that coexist in this region, may remain in the upper boundary of the OMZ with limited excursion into surface waters (Hidalgo et al., 2005a). Meantime, *Euphausia mucronata* has been suggested as actively and daily migrating into the OMZ (Antezana, 2002).

4.3. Meroplankton

Coastal zones around the world represent the habitat for many benthic marine species with a dispersive larval phase. The study of their populations is particularly difficult because of the generally poor information regarding basic aspects of the distribution, abundance and fate of their larvae. The importance of physical factors affecting the variability of larval supply has also been emphasized; however, there is still need for research, mainly focused on the identification and quantification of the transport mechanisms operating near the time of settlement.

Brachyuran decapod crustaceans represent a common group of invertebrates along the coast of Chile, with benthic (juvenile and adults) as well as planktonic stages (zoeas and megalopae) that are easily quantified. Larval stages of brachyuran decapods spend a variable period of time in the plankton (on the order of weeks) and are generally capable of long-distance dispersal; mortality is typically high during this period. In a study of the importance of coastal morphology, and its influence on the magnitude of larval delivery and subsequent recruitment patterns of brachyuran decapods, Palma et al. (2006) found that (1) in general, the abundance of *Paraxanthus barbiger*, the most abundant species throughout, was greater at all locations in 2003 compared with 2004 and it was also greater (particularly >1 yr individuals) at protected sites; (2) for most of the species, the abundance of megalopae and young-of-the-year (YOY) was highly seasonal, with peaks during the austral Spring and Summer months; and (3) for at least 2 of the 4 species considered in the southernmost peninsula, the abundance of YOY and >1 yr individuals exhibited higher abundance at the protected site. Therefore, at least for *Cancer setosus* and *Paraxanthus barbiger*, longer retention times at protected sites may provide a mechanism driving the pattern of elevated YOY abundance at the protected site.

In relation to mesoscale processes, crustacean decapods such as *Libidoclaea granaria* larvae are mainly released during Spring, the period of intensified upwelling (Yannicelli et al., 2006a). *L. granaria* occupies the continental shelf in south-central Chile, and usually turns up as bycatch of the squat lobster *Pleuroncodes monodon* fishery trawling at depths around 100 m. This seasonal timing of larval release also appears to coincide with that of *P. monodon* (Palma & Arana, 1997). There is very little information regarding larval distribution of crustaceans whose adults inhabit depths around 100 m, and their association with upwelling cycles. For larvae released over the shelf area, the upwelling season might imply onshore transport, and enhanced feeding conditions. The facts that zoea I appeared widely distributed (especially during downwelling winds) and zoea II approached the coast (especially during upwelling) support this idea. Large proportion of larvae occurred in low oxygen ESSW and in a spatially limited study, *L. granaria* larvae had been reported in deep intruding waters in the gulf of Arauco during upwelling conditions (Yannicelli et al., 2006b).

From the other extreme of adult habitat depth range, zoea of *Emerita analoga* show a contrasting pattern (Yannicelli et al., 2006a). Larvae are released in the intertidal zone and although highest concentrations of Stage I are found close to shore, high offshore advection is evident even for this first stage. *E. analoga* increases its offshore distance at intermediate stages, and approaches the coast again during Stage V. The behavioural mechanism that accomplishes return to coastal habitat is usually a deepening of late zoeas. More recently, Diaz-Cabrera et al. (2012) evaluates the presence of mesoscale spatial patterns in meroplanktonic stages of decapods and stomatopods in central southern Chile. The observed spatial patterns suggested decreased larval transport with distance, which ultimately has consequences for the species composition of zoeae at each sampling site, limited and restricted larval transport between nearby sites, and source–sink dynamics in the spatial structure of species richness of zoeae larvae. Based on the increase in β diversity with distance, they infer limited dispersion potential of zoeae larvae in the study area (~400 km2, 40 km of coast). Therefore, larvae remain near their original spawning areas and recruit to their original population or to nearby subpopulations, increasing self-recruitment.

A biophysical mechanism that may increase self-recruitment in intertidal species is a reverse diel vertical migration (DVM) during upwelling events, as it has been suggested by Poulin et al. (2002) for *Concholepas concholepas* larvae. When upwelling favorable winds begin to intensify, larvae would be first advected offshore as a consequence of Ekman transport of the surface layer. At night, active or passive downward migration would allow larvae to cross the thermal front (located no deeper than 20–25 m) and enter into the cold water being upwelled shoreward. The following day, and depending on their initial position, larvae would reach the surface again, on either side of the front. During the course of the upwelling event, the repetitive occurrence of the 24-h migration cycle would lead to a progressive incorporation of larvae in the upwelled water and the retention of larvae between the upwelling front and the shore. The rate at which larvae cross from the warm waters into the cold upwelled waters will vary depending on the surface and bottom current velocities. Considering a general case, when surface offshore current velocity is faster than onshore flow of the bottom layer, the net displacement of larvae will also be offshore but at a slower rate than that of the front because of the time that larvae spent at the bottom layer during night hours. Thus, larvae would be progressively incorporated into the upwelled zone, but the effectiveness of the mechanism will depend on the offshore surface current velocity, the time spent in each layer, and their initial position.

High frequency processes (semidiurnal tides, diurnal fluctuations) superimposed onto others of lower frequency (3–8 day period of wind-driven upwelling) may contribute significantly to variations in the transport of meroplankton from bays in upwelling areas (Yannicelli et al. 2006b). Larval vertical distribution in the two layer circulation at embayment entrances can enhance or preclude retention within the bay. During upwelling periods, Yannicelli et al. (2006b) hypothesized that group of surface dwelling larvae (e.g. *Cancer* spp., *Emerita analoga*) would be exported offshore from the gulf of Arauco (37°S). A second group (e.g. *Pagurus* spp., Porcellanids and *Pinnixa* spp.) would be retained nearshore; *Neotrypaea uncinata* zoea would be widespread during the first stages, and later stages should tend to concentrate nearshore. A third group (e.g. *Pleuroncodes monodon*, *Libidoclaea granaria*) would possibly approach the coast in the subsurface in successive instars from their offshore hatching areas.

Diurnal onshore winds associated with the summertime sea breeze promote shorter term variability in the cross-shelf transport of surface material, including the larvae of intertidal barnacles (Vargas et al., 2006), and nearshore accumulation of warm surface waters (Kaplan et al., 2003). Thus, changes in the geometry of wind forcing at a given site may alter the balance of meso- and small-scale forcing of the surface ocean, and produce drastically different patterns of

Onshore transport, accumulation, and retention of surface water. Consequently, patterns of larval delivery to intertidal habitats may change drastically as well (Tapia & Navarrete, 2010).

4.4.- Ichthyoplankton

4.4.1 Ecology of littoral fish larvae in the Humboldt Current System

In upwelling ecosystems, spatio-temporal variability in larval fish abundance has mainly been related to meteorological and oceanographic seasonal features, especially at mid latitudes. However, the location and abundance of larval stages may in some cases exhibit a strong relationship with the type of habitat or spawning grounds of the adult segments of those populations, and their reproductive strategies. Therefore, it is expected that those fishes with benthic eggs and parental care may be forced by different oceanographic features than marine fishes showing pelagic spawning in the water column, say epipelagic and demersal fishes.

In the very nearshore coastal waters (<2 nm offshore) of central Chile there is a seasonal reproductive pattern of intertidal, subtidal and epipelagic fishes, varying among them (Hernández-Miranda et al., 2003). While larvae of epipelagic fishes such as anchoveta *Engraulis ringens* show a seasonal pattern on their abundance (larger during Winter and Spring), larvae of intertidal fishes occurs throughout the year. Additionally, the spatial distribution of intertidal fishes is restricted to coastal waters with less than 60 m depth (Hernández-Miranda et al., 2003). One exception is the blenny *Hypsoblennius sordidus*, whose larvae can be collected in seawater from the continental slope (Landaeta et al., 2008), because of their large pelagic duration (around 5 months, Plaza et al., 2013).

During the developmental period, larvae of intertidal fishes must spend a long time in the water column before reaching a competent stage to settle. This ontogenetic stage has been defined as pelagic larval duration (PLD) (Kohn & Clements, 2011). PLD seems to be directly related to larval growth rates because it is indicative of the physiological interactions of the individuals with physical and biological factors that directly or indirectly influence larval growth rates (Suthers, 1998). Because of the influence of the upwelling of cold waters to surface, fish larvae experience slow growth rates in nearshore waters of central Chile (El Quisco, 33.4°S); larval triplefin *Helcogrammoides chilensis* grow at 0.21 mm day^{-1}, while clingfishes grow at 0.24 mm day^{-1} (*Gobiesox marmoratus*) and 0.14 mm day^{-1} (*Sicyases sanguineus*) (Palacios-Fuentes et al. 2012, Contreras et al., 2013). Slow growth rates retard recruitment, increasing the PLD of a cohort. Estimations of PLD for blenny *Scartichthys viridis* are around 90 and 100 days (Hernández-Miranda et al., 2009).

Self-recruitment of coastal fishes can be achieved by physical variables (site isolation, coastal complexity, flow variability). Physical factors that result in a departure from unidirectional, depth-uniform water flow provide the opportunity for retention of larvae, and therefore of self-recruitment (Sponaugle et al., 2002). For example, clingfish *Gobiesox marmoratus* from central Chile hatch coupled to a lunar periodicity, showing larger hatch events during first-quarter moon (Contreras et al., 2013). A hatching pattern related to the first-quarter moon is associated to neap tides, which implicate the reduced effects of tidal export from coastal waters to offshore (Robertson et al., 1990). On the other hand, other clingfish, *Sicyases sanguineus* showed a semi-lunar periodicity in the hatching events (Contreras et al., 2013). If we consider that *S. sanguineus* larvae experience slow larval growth rates and hatch near a full moon, it is predicted that this species has enhanced their potential geographical dispersion more than has *G. marmoratus.* This enhanced dispersion is because one of the hatching pulses (during neap tide and first-quarter moon) may increase the nearshore retention potential, whereas the remaining pulse (during Spring tide and full moon) may increase the probabilities of offshore advection and colonization of distant habitats.

Although having large PLD, the blenny *Scartichthys viridis* seems to self-recruit. In a study of otolith microchemistry (Hernández-Miranda et al., 2009) by using the ratio between trace elements and the calcium present in the nuclei and edges of *S. viridis* otoliths, evidence was found supporting spatial segregation between the specimens collected in the intertidal zone off Los Molles and Isla Negra (at a distance of 200 km). These results suggest that both groups of recruited fish originated from different areas at this spatial scale could act as demographically independent entities with distinct dynamics (i.e. different populations). Nevertheless, the occasional arrival of specimens from separate sources within these distances would allow both populations to maintain the characteristic features of the species.

The apparent spatial segregation of both locations may be due to larval behavior during ontogeny. Recently hatched larvae are found in surface waters during night (Hernández-Miranda et al., 2009), however large (flexion, postflexion) larvae are extremely scarce in the plankton samples over shelf and nearshore waters (Landaeta, pers. obs.), suggesting that they may behave as epibenthic schools (within 0.5 m of the bottom, Leis, 1985; Breitburg 1989;

Steffe, 1990). Possible advantages include avoidance of dispersal, availability of certain food organisms such as epibenthic mysids, avoidance of pelagic predators and avoidance of unfavorable physical and biological conditions at the surface in stratified waters. Possible disadvantages include increased exposure to demersal predators and possible damage due to contact with the bottom, and increase of parasitism by ecto and endoparasites.

For those fish species with a bipartite life cycle, the infection of larvae with ecto- and/or endoparasites affecting larval growth may increase the PLD, the time that an individual spends in the vulnerable larval stages before settlement. Then, small length-at-age and/or low individual growth rates (the latter generally based on measurements of otolith microstructure) due to parasitism can serve as a proxy for estimating individual survival probabilities (Dower et al., 2009). Coastal fish larvae from central Chile, such as labrisomids, clinids, triplefin, clingfishes and anchovies are likely to be parasitized by Caligidae and/or Pennellidae copepods (Herrera 1984, 1990). Recently, Palacios-Fuentes et al. (2012) detected that otolith microstructure reveals the negative effect of parasitism by Chalimus pennellids on the recent growth and condition of larval triplefin *Helcogrammoides chilensis* in the coastal waters of central Chile during the austral Spring season. Note, nevertheless, that parasitism by Pennellidae in adult *H. chilensis* has not yet been observed (Muñoz & Delorme, 2011). This apparent absence could indicate that these larvae are only intermediate and/or alternative hosts in the life cycle of pennellids. Or this could mean that there is variability in the preference for a specific host.

The effects of attached ectoparasites on larvae include an increase in hydrodynamic drag. This increase affects the swimming ability of the larvae. Because it is harder for the larvae to swim, they have more difficulty-escaping predators (Herrera, 1990). Moreover, attached ectoparasites may increase the visibility of larvae to predators. All the effects cited above produce greater energetic costs for the larvae and retard their growth. These effects on larval energetics and growth will indirectly affect the settlement of the larvae and increase their PLD. During the additional time the larvae must spend in the plankton, they are susceptible to predation and have difficulty foraging. These factors jeopardize their survival. In conclusion, pennellids can indirectly affect the survival rates of individual *H. chilensis* larvae.

4.4.2. Reproductive tactics of marine fishes during the upwelling and non-upwelling seasons

Transport and retention are physical processes responsible for moving early pelagic life stages from the spawning site toward an appropriate nursery ground (Pineda et al. 2000) and can play a role in the regulation of recruitment and year-class strength. Biophysical coupling between reproductive tactics of marine fish species and upwelling events vary among fish species, latitude and even among spawning seasons. For the bigeye flounder *Hippoglossina macrops* (Paralichthyidae), Landaeta et al. (2006) described a seasonal depth gradient in the spawning moving from the continental shelf during late Winter, over the shelf-break during mid Spring, and at the continental slope during late Summer (34-37°S). Also, transport of diverse larval stages from the shelf break to nearshore probably occurs through the compensatory onshore flow (50 m thickness) that balances the surface onshore transport in the Ekman layer. Studies off the Talcahuano area (37°S) on the early life history of hake *Merluccius gayi* (Vargas et al., 1997, Vargas & Castro 2001, Landaeta & Castro 2006), squat lobster *Pleuroncodes monodon* (Yannicelli et al., 2006) and lightfish *Maurolicus parvipinnis* (Landaeta & Castro, 2002) show reproductive tactics similar to those observed for the big eye flounder *H. macrops*. In these species, spawning occurs offshore and at depths above 100 m during the wind-induced upwelling season (September to March). For hake, onshore transport may occur from the slope to the continental shelf (Vargas & Castro 2001) and/or from continental shelf to gulfs and bays (Landaeta & Castro, 2006) through the intrusion of poorly oxygenated waters (< 1 mL L^{-1}), producing daily losses of 8-11% (Landaeta & Castro, 2006).

In late Summer and early Autumn, when rapid changes in the wind direction and speed occur and wind-driven upwelling reduces its intensity and warm waters occurs off-shelf, small and medium-sized hakes (<55 cm TL) migrate to the coast and even into the bays (Landaeta & Castro, 2006), spawning smaller eggs (<1.15 mm) in the mixed layer (<25 m). Small yolk-sac larvae hatch with relatively large yolk reserves (Landaeta & Castro 2012) and plankton samples revealed that larval hake persist in surface waters up to 7 mm NL, when they begin DVM. What triggers the DVM in hake larvae is still unknown, but it may be related to changes in meteorological conditions (wind-generated turbulence), water column structure (mixed vs. stratified conditions), foraging behavior, advective transport and/or topography. Upwelling fronts (Vargas & Castro, 2001) and abrupt changes in wind direction and speed in March and April may reduce chances in offshore advection of hake eggs and larvae during late Summer, producing lower mortality rates (0.065 day^{-1}; Landaeta & Castro, 2006) than in Spring (0.1–0.38 day^{-1}; Vargas et al., 1996).

Cubillos et al. (2001; 2007) concluded that the reproductive strategy of anchovy *Engraulis ringens* and common sardine *Strangomera bentincki* is to spawn at the end of the austral Winter (August), when oceanographic conditions are producing retention and concentration of eggs and larvae near the coast (i.e. onshore transport and convergence by northerly winds). These conditions are alternating with moderate southerly winds, which are able to produce moderate upwelling events. Nonetheless, river plumes may also affect the spatial distribution of eggs and larvae of these species in coastal areas of central Chile (Soto-Mendoza et al., 2010).

Other small pelagic fish, such as the mote sculpin *Normanichthys crockeri*, show a different reproductive tactic along central Chile. This species spawn in coastal protected sites mostly during transitional periods, eggs and larvae are located in the top 50 m of the water column, and larvae grow at a rate of 0.15-0.20 mm day^{-1} (Landaeta et al., 2010). Because of larvae of *N. crockeri* are vertically distributed in surface waters and feed on microplankton (mostly copepod eggs, copepods and tintinids, Balbontín et al., 1997), protected sites around headlands along central Chile are optimal locations where the feeding success and larval growth of *N. crockeri* can occur (Landaeta et al., 2010).

In northern Chile, the persistence of upwelling events increase not only the primary production, but also the potential prey availability (i.e., microzooplankton) for the feeding of neritic fish larvae, such as anchovies. This species show low mortality rates by starvation in coastal areas (2.9%), analyzed by histological criteria (Pizarro et al., 1998). However, in central-southern Chile, mortality rates during early life stages is rather high, particularly during the non-upwelling season (96% daily in Winter 1995, 98% daily in Winter 1996, Castro & Hernández 2000). The most important factors affecting egg and larval survival are probably the fluctuations in oceanographic conditions generated by wind switches in early Winter that induced cross-shelf transport (Castro et al., 2000). These wind switches (i.e., north to south) occurred mainly when spawning activity was at its maximum and when the cohort mortality estimates were the highest. The results are intriguing because they suggest that the environmental conditions were not favorable for larval survival at the beginning of the spawning season in 1995 and that they may have improved as the Winter season progressed (Castro & Hernández, 2000). This interpretation certainly poses a puzzle, considering the anchoveta's reproductive strategy of Winter spawning.

Other source of mortality for early life stages of anchoveta is predation. Among pelagic invertebrate predators, euphausiids have long been considered important consumers of fish eggs and larvae. In the Humboldt Current euphausiids (i.e., *Euphausia mucronata*) are very abundant, and anchoveta eggs proteins have been detected in the digestive tract of this species (Krautz et al., 2003). The potential consumption of *E. mucronata* of eggs of *Engraulis ringens* in the northern Chilean Humboldt Current is around 4 x 10^{12} eggs d^{-1}, accounting for 24 to 27% of natural mortality (Krautz et al., 2007).

Because growth may be dependent on environmental factors, seasonal variations in growth and mortality rates is expected among the cohorts spawned during the year. Hernández & Castro (2000) documented potential differences in growth rates of groups of cohorts spawned a few weeks apart during the main spawning season (Winter). For coastal species living in upwelling areas, changes in growth rates among cohorts may be beneficial because environmental conditions may change markedly in short time scales (from days to few weeks).

Upwelling plumes or filaments may also transport phytoplankton and microplankton offshore, supplying food for the larvae in adjacent oceanic areas. For example, Rodríguez-Graña et al. (2005) detected high number of the lanternfish *Diogenichthys laternatus* larvae with gut contents found in open ocean, coinciding with a cold upwelling filament extending from the coast to ca. 90 nautical miles offshore off Mejillones Península.

4.4.3. The effects of the OMZ

Although the interaction of OMZ and the spatial distribution of eggs and larval fishes have been studied in several upwelling zones, there is a lack of studies of such topic for the Chilean area of the Humboldt Current ecosystem. Morales et al. (1997) suggested the occurrence of a barrier to the vertical distribution of anchovy larvae, determined by a concentration of ca. 0.75 ml 0_2 L^{-1}. Although it was not possible to distinguish clearly between the effects of temperature and dissolved oxygen (DO) because of the high correlation between these two variables, the limiting concentration above suggested that the base of the thermocline (15 °C) may not, in fact, constitute their main barrier since DO, concentrations between 3 and 4 ml L^{-1} are associated with it.

Other species, such as hake, are capable to spawn at depths inside the OMZ (off central-southern Chile). Vargas & Castro (2001) suggested that spawning at these depths may be beneficial because of eggs and larvae may be transported onshore, and because avoids egg and larval predation by extremely abundant clupeiform populations typical of coastal upwelling areas. In northern Chile, particularly off Mejillones Península, the presence of OMZ below 80 m depth seems not to affect the abundance of mesopelagic fish larvae (myctophids *Diogenichthys atlanticus* and *D. laternatus*, bathylagids *Bathylagus* sp.) (Rojas et al., 2002; Rodríguez-Graña & Castro, 2003).

5. ENVIRONMENTAL VARIABILITY AND FISHERIES

5.1 Large spatio-temporal variability of ichthyoplankton

Variations in egg size among populations located along a latitudinal gradient or during the spawning season have been reported for a number of demersal and pelagic fishes. In general, larger eggs are spawned at higher latitudes, egg size tends to decrease as the spawning season progresses, and eggs produced in Winter are larger than those spawned in Summer. In anchoveta *Engraulis ringens*, the egg size, larval length at hatching, and yolk sac volume of recently hatched larvae increase with latitude, and instantaneous yolk sac larval growth rates may differ between latitudes (Llanos-Rivera & Castro, 2006). Seasonal variations in size have also been reported in eggs of the southern (36°S) anchoveta population (Llanos-Rivera & Castro, 2004). At this latitude, larger eggs are generally spawned in Winter, and smaller eggs, in Summer. Analyses of the biochemical characteristics of eggs during the spawning season also showed differences between populations. Total lipid contents and TAGs occurred in much higher concentrations in the southern eggs that in those from the northern stock (Castro et al., 2009).

The large interannual changes in abundance and composition of the northern Chilean ichthyoplankton can to a certain extent be related to interannual changes of hydrographic conditions in the Humboldt Current. This has been demonstrated through correlations of ranked temperature and salinity values and abundances of coastal species, sardine (*Sardinops sagax*), and *Lampanyctus parvicauda*. The shift from relatively large percentage contributions by *Lampanyctus parvicauda* and *Triphoturus oculeus* to larger proportions of *Diogenichthys laternatus*, *D. atlanticus*, *Bathylagus nigrigenys,* and *Vinciguerria lucetia* after 1969 was notable. The abundances of these mesopelagic species, unlike those of anchoveta and sardine, are not directly influenced by man's fishing activities and so may be interpreted as indicators of environmental change. Furthermore, the timing of these species absolute and relative abundance changes preceded by several years the dramatic changes in anchoveta and sardine stocks off of northern Chile and so cannot be directly related to biological consequences of change in the dominant pelagic schooling fish stocks (Loeb & Rojas, 1988).

Off the Mejillones' coast, there is a complex spatial and temporal hydrographic system where ichthyoplankton of coastal and oceanic fish species coexist. Despite both short-term and longer-term disruptive oceanographic processes (e.g., mesoscale filaments, El Niño events), it seems that the numerically dominant species persist in the area due to their various behavioral strategies and physiological adaptations (Rojas et al., 2002; Rodríguez-Graña & Castro, 2003).

For coastal fish species, ENSO events may affect egg and larval abundance, growth, survival and recruitment. The cohort somatic growth rates of herbivores (*Scartichthys viridis*), omnivores (*Girella laevifrons*) and carnivore (*Graus nigra*, *Auchenionchus microcirrhis*) fish species are low for those recruited during El Niño and high for those recruited during La Niña events. Also, cohort mortality rates are highest during El Niño and lower during La Niña and transitional years. Hernández-Miranda & Ojeda (2006) proposed that productivity (as a bottom-up driver) acts as a primary exogenous factor upon annual cohort mortality rates.

In a study of nearshore ichthyoplankton off Valparaíso Bay (33°S) during the 1997-2000 ENSO cycle (1997-1998 El Niño, 1999-2000 La Niña), among larval fish with epipelagic adults, larvae of sardine *S. sagax* showed higher densities during the beginning of 1997 in the warm phase of ENSO. In constrast, larval anchoveta *E. ringens* were collected in higher abundance during La Niña (Landaeta et al., 2009). Highest larval densities of *M. gayi* were collected at the onset and the end of the El Niño phase, but during La Niña, larval hake appeared more frequently in the samples; the highest value of larval abundance obtained during this cold period occurred when Ekman transport was low.

In northern Chile, Rojas et al. (2011) suggested that El Niño 1997-1998 triggered an abrupt change in the spatial distribution of eggs and larvae of *E. ringens*, and consequently the distribution patterns of anchoveta larvae were altered as part of a strategy to cope with strong environmental changes., Claramunt et al. (2012) postulate that instead of searching for certain temperatures, *E. ringens* accommodate their offspring characteristics (*e.g*., egg size, fecundity) according to the prevalent environment. In that case, the anchoveta reproductive system response to temperature might be in the scale of spawning frequency, *i.e*., weeks, matched with upwelling frequency

Most recently, for the common sardine (*S. bentincki*) Gomez et al. (2012) established the impact of Spring upwelling variability on larval recruitment. They found that interannual changes in both Spring upwelling intensity and SST from the Niño 3.4 region are related to changes in remotely sensed Chl-a over the continental shelf. In turn, year-to-year changes in coastal Chl-a abundances are tightly coupled to this species srecruitment; therefore, *common sardine* recruitment is modulated by phytoplankton food supply during their pre-recruitment period. It is expected that upwelling variability exerts a strong impact in the survival of early life stages.

No detailed studies about *S. bentincki's* diet in the prerecruitment period exist but it is known as a planktivorous fish, feeding on both phyto and zooplankton (Espinoza et al., 2009). In a plausible first approximation, coastal Chl-a can be considered an index of food abundance for this species. Thus, weak Spring upwelling conditions limit food abundance for common sardine, decreasing prerecruit survival, whereas the opposite occurs with strong upwelling conditions. In this context, further studies on diet variability and seasonal plankton dynamics are required to identify the underlying mechanism affecting prerecruit survival.

5.2. Components, processes and regimen shift.

Air-Sea interaction is one of the most relevant processes in EBCs driving upwelling frequency in close interplay with primary and secondary production (Fig. 11). Wind controls seasonality of upwelling along the HCLM. Regime shifts modulations of changes in fish abundances at different scales are affecting fish landings differentially depending on population habitats, i.e. pelagic vs. demersal. Yañez et al. (2008) referred to the different scales affecting fish landings .

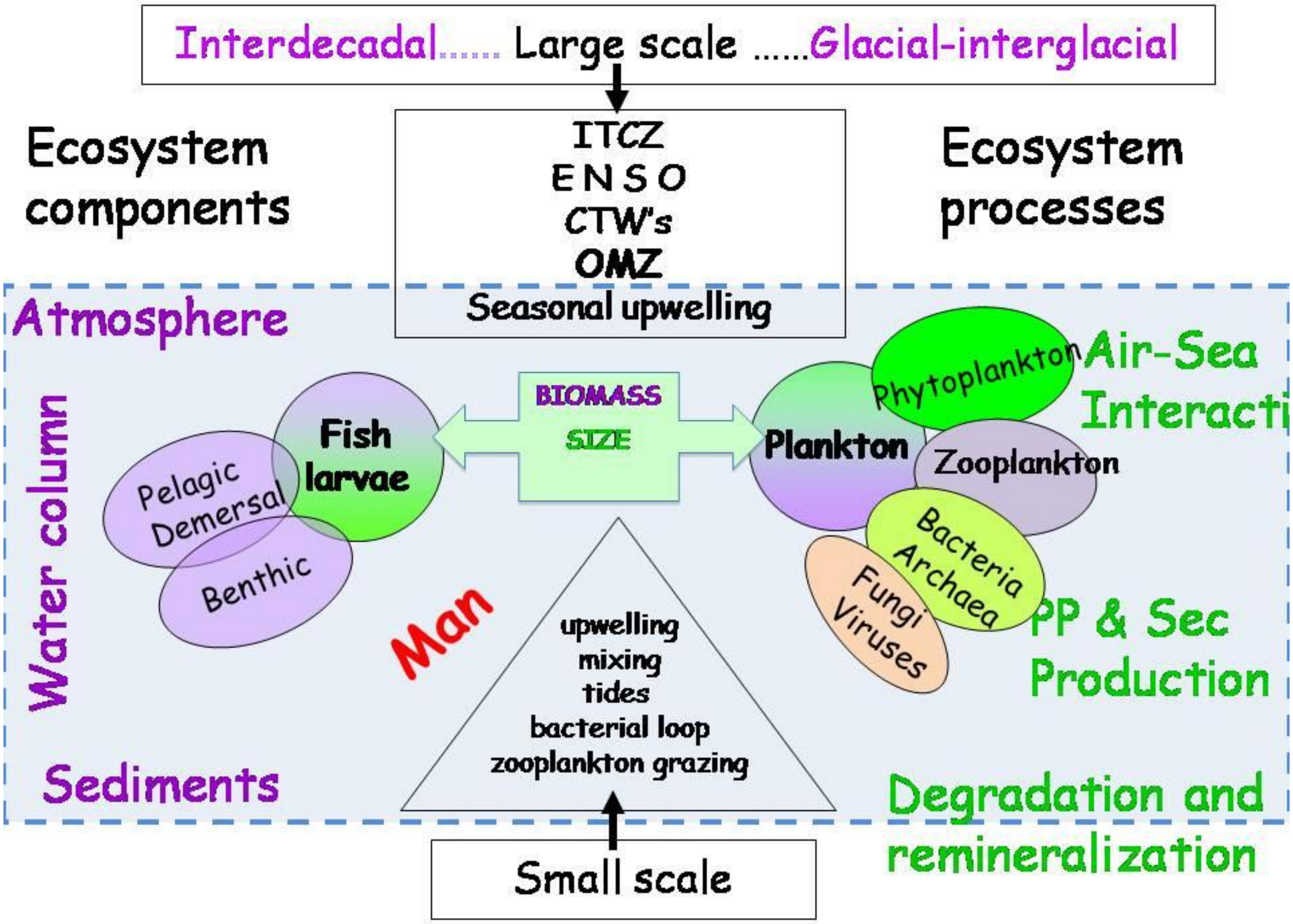

Figure 11. Ecosystem components in the vertical gradient (left) and ecosystem processes in these components (right), different scales (top and bottom) acting over biological communities, biological, chemical and physical processes.

5.3 El Niño Southern Oscillation (ENSO)

Climate changes in physical oceanographic variables have been clearly linked with oceanic ecosystem changes on many temporal and spatial scales. This physical forcing is also evident on interannual timescales associated with ENSO events (El Niño and La Niña episodes), when the Southeastern Pacific is remotely forced by the concomitant oceanic and atmospheric teleconnections (Maturana et al., 2004). The mechanisms by which physical forcing affects oceanic ecosystems range from those associated with the smallest scales of dissipation, turbulent mixing and diffusion, to those acting on the mesoscale associated with fronts, eddies, and upwelling, to those operating on the basin scale associated with gyres, El Niño, and the thermohaline convective circulation (Denman et al., 1996).

The regional and local manifestations of this physical forcing on the marine organisms can occur instantaneously or with a time lag. In this context the ENSO impacts may induce changes in population survival and/or recruitment, producing variations in the local abundance, geographical distribution and gene flow structure of populations (Camus, 2008). Predicted that Taxa with high connectivity and large geographical ranges should be less affected by ENSO than others characterized by low connectivity and/or narrow distribution ranges (Thiel et al., 2007).

The principal fisheries (benthic, demersal and pelagic) of the HCLME have been affected by ENSO events (Thiel et al., 2007). Physical forcing related to ENSO in the coastal and oceanic habitat caused biological (e.g., growth and reproduction) and ecological (e.g., migration, distribution and abundance) changes in the pelagic fish populations like sardine (*Strangomera bentincki*), anchovy (*Engraulis ringens*) and jack mackerel (*Trachurus murphy*) (Arcos et al., 2001, 2004). This oceanographic variability plus the high fishing intensity during the previous years to the 1997-98 El Niño contributed both to the alteration in the spatial pattern of the jack mackerel population (Arcos et al., 2001, 2004). The El Niño 1997–1998 also affected the small pelagic fish (anchovy and sardine) habitat off central-south Chile, and this changed the on recruitment of common sardine, while anchovy did not seem to have been affected by the environmental changes observed in the 1990s (Cubillos & Arcos, 2002).

In benthic habitats the disruption of upwelling conditions during El Niño events, resulted in the enrichment of food chains and impacting directly on the recruitment of mollusk benthic species with planktonic larvae like *Choncholepas concholepas* and *Tegula atra* (Moreno 2004). Benthic communities change their structure and organization during and after ENSO events (Vásquez & Vega, 2004; Thiel et al., 2007; Camus, 2008). The destruction of the seaweed beds in northern Chile after the main expression of the 1997-98 ENSO was the result of an increase in the densities of grazers and the disappearance of a guild of high-level predators, the sea-stars (Vásquez & Vega, 2004).

5.4 Effects of Global Climate Changes

The Intergovernmental Panel for Climate Change (IPCC) reports that Global Environmental Changes (GEC) is occurring quicker than at any other time over the last 25 million years and impacting upon marine environments (Bellard et al., 2012). There is also an overwhelming evidence showing that GEC are affecting both the quality and quantity of the goods and services provided by a wide range of marine ecosystems (Turra et al., 2013).

Among the environmental factors that have been identified related global changes are; increase in atmospheric and seawater temperature and increase concentration of greenhouse gases like CO_2 and N_2O. The effects of these changes may have on ecosystems organisms and coastal economies are varied and are acting through multiple direct and indirect mechanisms. In coastal upwelling systems it is known that the OMZ, full of CO_2 and N_2O is comparatively shallower than in other marine ecosystems, facilitating wider diffusion of these gases into the atmosphere (Paulmier et al., 2008; Stramma et al., 2008; Gilly et al., 2013). Climate models predict an overall decline in oceanic dissolved oxygen concentration with a consequent expansion of the OMZ under global warming conditions (Matear, R.J. & Hirst, 2003). In the Chilean OMZ area, the mean N_2O fluxes are 5–10 times higher than the previous historical maximal in the OMZ open area of the Pacific (Paulmier et al., 2008). Shoaling of the upper boundaries of the OMZs accompanies OMZ expansion, and decreased oxygen at shallower depths can affect all marine organisms through multiple direct and indirect mechanisms. Effects include altered microbial processes that produce and consume key nutrients and gases, changes in predator-prey dynamics, and shifts in the abundance and accessibility of commercially fished species (Gilly et al., 2013).

Harmful algal blooms, partially related to temperature increase, have negative impacts on the quality of coastal areas as a whole (Turra et al., 2013). Ocean acidification in response to rising atmospheric CO_2 partial pressures is widely expected to reduce calcification by marine organisms seriously reducing the ability of edible shellfish, such as mussels and oysters, to produce shells, thereby threatening local aquaculture activities and food security (Turra et al., 2013; Iglesias-Rodriguez et al., 2013). Coccolithophores are major calcium carbonate producers in the world's oceans, today accounting for about a third of the total marine $CaCO_3$ production. The calcification and net primary production in the coccolithophore species *Emiliania huxleyi* are significantly increased by high CO_2 partial pressures, which has important implications for biogeochemical modeling of future oceans and climate (Iglesias-Rodriguez et al., 2013).

It is more likely that extreme events and not trends will affect communities (Thomson et al., 2013) and these authors recognized that an understanding of physiological, ecological and evolutionary processes will underpin the relationship between climate and biodiversity.

Elevated temperatures associated with climate change accelerate the life-histories of invertebrates, increasing their growth rates and shortening their life-spans (Pecl & Jackson 2007, Hoegh-Guldberg & Bruno 2010). This life histories changes could modify the population size-structure and destabilized the population dynamics resulting in a shift in abundance and distribution (in patterns of occurrence with latitude and depth) of marine species (Stenseth & Dunlop 2009, Rijnsdorp et al., 2009). From an evolutionary point of view the global climate change can impact of genetic diversity of populations (Pauls et al. 2012).

5.5. Species Biodiversity and introduced species

The biota of HCLME is a mixture of tropical, temperate and austral components (Camus, 2001). In a recent review, Miloslavich et al. (2011) report a total of 10201 species with a density of 140 species in 100 km^2. From a biogeographic point of view the HCLME is located into Peruvian Province (3°S – 42°S), but some studies distinguish a transition zone between 30°S-42°S (Lancellotti & Vásquez, 2000; Camus, 2001; Thiel et al., 2007; Ibáñez et al.,, 2009). Temperature and continental shelf area are the most important factors that determine the latitudinal gradients of species richness along the Chilean coast (Astorga et al., 2003, Valdovinos et al., 2003, Fernández et al., 2009, Rivadeneira et al., 2011).

Invasive or nonindigenous species in the HCLME are poorly studied and reported. Miloslavich et al. (2011) reported 77 introduced species in HCLME, principally composed by fishes (35 species), seaweeds (10 species), Annelida (8 species) and Mollusca (7 species). In a high percentage these species has been introduced as a consequence of the rise of aquaculture (Camus, 2005; Miloslavich et al., 2011). National and international regulations to control these activities seem to be either insufficient or scarcely efficient, and they might be against large economic interests (Camus, 2005).

6. ISSUES AND GAPS IN KNOWLEDGE

There are many issues considered to be relevant for management purposes in the context of a Large Marine Ecosystem approach and that reflect our major gaps in knowledge. The following processes are suggested to be key study targets, and they are not presented in an order of priority:

1. Restricted spatial studies on physical, chemical and biological oceanography due to non existing or paucity of base lines.
2. Insufficient explanations about ecosystem behavior.
3. Few studies on the effect of seasonal changes on abundance and distribution of marine resources, key species and trophic structure.
4. To improve the knowledge on the main environmental forcing factors affecting population and ecosystem dynamics.
5. The effect of variability of the OMZ for the functioning of the trophic web and distribution and abundance of resources.
6. To improve knowledge on mesoscale circulation and other oceanographic features (e.g. eddies, filaments, jets) relevant to the survival or early life history stages and migration patterns of adults fish stocks.

7. Coastal upwelling variability. This is certainly a key process to understand why the HCS, subjected to a high fishing pressure, still has the capacity to maintain large biomasses of clupeids, jack mackerel and other biological resources. Changes in the rate of nutrient pumping by upwelling into the euphotic zone and air sea interaction in both space and time relevant for ecosystem production studies and management

8. Support a monitoring program to make continuous estimates of primary production rates and their variability along the HCS is a priority. The monitoring of oceanographic variables although important is clearly not sufficient to understand ecosystems responses to climate and ENSO variability and process studies and estimates of rates are key issues.

9. Biological diversity and trophic interactions are certainly relevant aspects of ecosystem studies. Nevertheless, it is necessary to connect components and process.

10. The need to develop integrated models of the HCLME to improve our understanding on the ecosystem and as a tool to better manage the system.

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