Chapter 10. BIO-PHYSICAL INTERACTIONS OFF WESTERN SOUTH-AMERICA

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1. Introduction

In this chapter, we describe biophysical interactions in the marine ecosystems off Perú and Chile, with some information off Ecuador. This extends a previous review of the physical oceanography of the region (Strub et al., 1998). It also builds upon a long history of interdisciplinary studies of the coastal ocean off Perú, Chile and Ecuador, including their fisheries and responses of those fisheries to El Niño (Barber and Smith, 1981; Brink et al., 1980,1981; Richards, 1981; Bernal et al., 1982; Barber and Chavez, 1983, 1986; Brink et al, 1983, and other papers in the same volume; Parrish et al., 1983; Neshyba et al., 1989; Walsh, 1981, 1991; Arntz and Faahrbach, 1996; Chavez, et al., 2003). See also Bakun (2004), Chavez (2004) and other papers in Robinson and Brink (2004)

We refer to this large and complex oceanographic domain as the Perú-Chile Current System (PCCS), which makes the geographic scope of our review clear. Other names include the Humboldt Current and Perú Current. Like other eastern boundary current (EBC) systems, the PCCS includes large regions of coastal upwelling, both year-round (from the equator to approximately 30ºS) and seasonal (approximately 30ºS-40ºS). For reasons not yet understood, however, the productivity of the PCCS, in terms of total fish catch, far exceeds (by weight) the catches of the other EBC's. Large

interannual and interdecadal fluctuations in that catch also remain to be understood.

The general structure of this chapter is to move up the trophic levels, from physics to plankton to fish to humans. Section 2 reviews of the system's physical characteristics. Section 3 examines the patterns of variability for nutrients and phytoplankton, followed by zooplankton in Section 4. Variability in the commercially important pelagic fish is described in Section 5. Section 6 moves to the sediment and benthic ecosystems of the deep ocean and shelf, then to the nearshore and intertidal ecosystems. The effects of humans on these systems are briefly discussed in Section 7, followed by conclusions. Further details of interdisciplinary studies from several regions can be found in the Appendix.

2. Physical characteristics and overview

It is often useful to divide this large domain into latitudinal and onshore-offshore regions. These divisions are mostly conceptual, vary in time and may be different for physical, chemical and biological characteristics. The largest depiction of latitudinal biogeographic regions is of a tropical or "Panamic" province, extending from the tip of Baja California to the Ecuador-Perú border, a "Perú-Chile" province that extends from northern Perú to approximately 42°S, and a "Magellanic" province in the south (Boschi, 2000). Considering only Chile, Camus (2001) divides Chile into a "Perú" province in the north; a Magellanic region in the south, covering the fjords; and a "non-transitional Intermediate Area" (Perú-Chile) in the middle, which includes a mix of species from the other two regions. Some disagreement exists in the definition of these boundaries (Lancelotti and Vazquez, 2000). Figueroa (2002) defines four zones along the Chilean coast based on physical characteristics. Northern Chile has a very narrow shelf (<10km), weak equatorward winds and little river inflow. From 33.5º-36ºS the shelf broadens slightly and winds increase, strongest in spring. The shelf continues to widen (up to 70km) between 36º-42ºS, with strongest equatorward winds in summer, poleward winds and greater river inflow in winter. South of 42ºS, winds are poleward (strongest in winter), freshwater inflow is greater than in the north and the shelf width is complicated by the presence of fjords and islands, forming the Inland Sea. Although not discussed by Figueroa (2002), the narrow shelf off northern Chile broadens to the north, off Perú and Ecuador.

On land, the Andes mountains are oriented approximately parallel to the coast from central Chile to Ecuador. Off central Chile, the Andes are separated from the coastal mountain range (the Coastal Cordillera), by a narrow (100km) central valley (**Fig. 10.1**). Off northern Chile, the region between the Andes and the ocean consists of a high desert (pampas), which plunges abruptly to the ocean in cliffs over 1 km high. A deep trench is found at the base of the continental slope. Another coastal mountain range is present off Perú, Ecuador and Colombia. In all regions, the coastal mountain ranges and cliffs influence the coastal winds and precipitation (Rutllant et al., 1998). On the ocean bottom, the Nazca Ridge separates the Chilean and Perúvian basins.

Surface forcing by fluxes of momentum, heat and freshwater are affected by movements of the Intertropical Convergence Zone (ITCZ) and trade winds in the north, the South Pacific High at mid-latitudes, with increasing effects of cyclonic storms as one moves to the south (Rutllant and Fuenzalida, 1991). **Fig. 10.2a** shows the annual mean cycle of atmospheric sea level pressure (SLP). Mid-latitude seasonality is shown by the across-coast pressure gradient in summer between approximately 30º-40ºS. Off central Chile, atmospheric variability is augmented by the excitation of coastal low pressure systems that are trapped by the intersection of the marine boundary layer and the coastal mountains, propagating poleward from 27º to as far as 42ºS (Rutllant, 1997; Garreaud et

al., 2002). **Fig. 10.2b** depicts equatorward coastal winds (arrows), the South Pacific Anticyclone ("A"), and mid-latitude cyclonic storms that reaches the coast from offshore ("B" near 40º-45ºS). Another coastal low has been generated near 25º-30ºS and will propagate to the south, causing fluctuations in the equatorward winds with "synoptic" time scales of several days.

Off Ecuador and Perú (0ºS-15ºS), the northward displacement of the ITCZ in austral winter creates a winter maximum in upwelling-favorable winds (Zuta et al., 1978; Bakun and Nelson, 1991; Halpern, 2002; Carr et al., 2002). Southward movement of the ITCZ in austral summer creates a summer maximum in precipitation at the equator and to the north, decreasing to very low rainfall off Perú (Cucalón, 1987). In **Fig. 10.3**, we present the Coastal Upwelling Index (offshore Ekman transport) from the coast of South America between 5º-55ºS, which shows the maximum in upwelling centered around August off Perú and on January at 45ºS. The increased offshore Ekman transport in winter results in weak stratification over the shelf (Guillen and Calienes, 1981), leading to weaker oceanographic fronts and frontal jets than found at mid-latitudes.

Along northern Chile, winds are also persistently equatorward but weak, with a mild spring maximum (Bakun and Nelson, 1991; Thomas, 1999; Blanco et al., 2001; Carr et al., 2002). Satellite altimeter estimates of oceanographic eddy kinetic energy off northern Chile are also weak, compared to similar estimates of the ocean south of 30ºS (Hormazabal et al., 2004). A 30-year climatology for northern Chile, presented by Blanco et al. (2001), shows: (1) The weak upwelling of fresher and colder water is confined to a narrow coastal region. The fresher water is usually SubAntarctic Water (SAW), which moves onshore at approximately 100m depth under the top layer of much saltier Subtropical Surface Water (SSW, sometimes also called Subtropical Water or STW), and over somewhat saltier Equatorial Subsurface Water (ESSW). The tongue of fresh SAW is stronger in the south off Antofagasta (23ºS) than in the north off Arica (18ºS). (2) Geostrophic surface currents next to the coast are weakly equatorward all year, strongest in fall. The seasonal cycle of surface currents is better defined in the south and very weak north of 20ºS, although the seasonal cycles of surface heat flux and upper ocean stratification are strong. (3) Subsurface currents are generally poleward, strongest in the poleward undercurrent (PUC) next to the coast (Neshyba et al., 1989; Pizarro et al., 2002). On interannual time scales, El Niño events cause substantial deepening of the thermocline, nutricline and oxycline off Perú and northern/central Chile (Morales et al., 1999; Blanco et al., 2002). These modulate the annual cycles described above.

On diurnal scales at mid-latitudes (30ºS), winds on land reach a maximum around 17:00-18:00 h. Nocturnal cooling increases atmospheric pressure on land, decreasing winds during early morning. This effect fades quickly and is negligible about 12 km offshore. Because of this diurnal cycle, afternoon upwelling is primarily due to offshore Ekman transport, while early morning upwelling is due to wind-stress curl. Thus, the daily strength of upwelling-favorable winds is better represented by measured winds from the afternoon, rather than daily means (Rutllant and Montecino, 2002). When this is done, records of daily upwelling strength reveal upwelling strengthening and relaxations with "synoptic" periods of several days. Strong upwelling-favorable wind events (UFWE's) are those with two or more consecutive days with equatorward wind speeds greater than one standard deviation (5-6 m s^{-1}). These occur during all seasons, although the longer events tend to be concentrated in late-spring and early-summer. Typical periods between UFWE's are 40 days for 2-day UFWE's and one per season for 3-day UFWE's (Rutllant and Montecino, 2002). The alternation of stronger and weaker upwelling (or downwelling) produces fluctuations in the depth of the thermocline on synoptic scales.

Off Chile between 30º-40ºS, seasonal changes in winds include a spring-summer maximum and a winter minimum in equatorward winds, or a reversal to poleward winds (**Fig. 10.3**). Winter precipitation increases and summer surface heat fluxes decrease toward the south. The PUC continues to be seen in velocity measurements and to be identified by water properties (Silva and Neshyba, 1979; Fedele, 1993). Equatorward winds in summer create moderate-to-strong density fronts in the coastal ocean (Moraga, 1996) and surface-jets along the fronts. These jets develop instabilities (Leth and Shaffer, 2001; Hormazabal et al., 2004) and meanders that carry long filaments of cold water, phytoplankton and zooplankton far from the coast, with a coastal band of cold water that expands and contracts back toward the coast during synoptic fluctuations of equatorward winds. Upwelling occurs preferentially around a number of "upwelling centers" and reduces oxygen concentrations to values less than 0.5 ml l^{-1} over the shelf, creating anoxic benthic ecosystems (Morales et al., 1999).

In addition to locally-induced upwelling and downwelling, intraseasonal coastal-trapped waves (CTW's) of equatorial origin propagate poleward into the region along the coasts of Perú and north-central Chile, raising and lowering the thermocline as they pass. A wide range of periods is possible for CTW's and early studies off Peru emphasize periods of days-weeks (Smith, 1978; Cornejo-Rodriguez and Enfield, 1987; Enfield et al., 1987). Off northern and central Chile, Shaffer et al. (1997) emphasize waves with periods of 30-60 days. By rising the nutricline, the CTW'S increase the efficiency of wind-induced upwelling and mixing in raising nutrients into the euphotic zone (Hormazabal et al., 2001; Rutllant and Montecino, 2002). Energy levels of these waves appear to increase during El Niño periods, at both the higher frequencies (Cornejo-Rodriguez and Enfield, 1987; Enfield et al. [1987]) and the lower frequencies (Shaffer et al., 1997). See also Hormazabal (2002, 2004), Leth and Shaffer (2001), Pizarro et al. (2001, 2002) and Vega et al. (2003). The biological effects of the CTW's are discussed in Section 3.

South of 40ºS, winds become persistently poleward and downwelling favorable, maximum in fall-winter (**Fig. 10.3**). The characteristic water properties of the PUC disappears as one moves south from the equatorward PCCS into the poleward Cape Horn Current (Silva and Neshyba, 1979). The flow in the "Inland Seas" is complicated by its geometry but often forms an estuarine circulation (offshore flow of surface fresh water, over onshore flow of oceanic water). This flow delivers oceanic nutrients to the nearshore region below the surface waters, which are usually devoid of nutrients other than silicate. Mixing processes are then necessary to bring nutrients up into the euphotic zone in the otherwise stratified (due to salinity) fjord region. The latitudinal pattern of salinity is negatively correlated with river discharges (Dávila et al, 2002).

3. Lower trophic level bio-physical-chemical interactions.
3.1 Patterns and interactions in space

The combination of low-latitude upwelling, high primary productivity, equatorward surface flow and the poleward undercurrent have far-reaching effects on the chemical and biological fields in the PCCS. These effects are observed from the equator to the northern portions of the Chilean Inland Sea, and from the coast to several hundred kilometers offshore. This combination undoubtedly plays a role in the high fishery yields in the PCCS, although the details of the physical-chemical-biological interactions and energy flows in the food web still need to be determined.

Phytoplankton PPr values off Perú and northern and central Chile are presented in **Table 10.1**. Although the range of measured values is large, there is a general pattern of higher values of PPr in nearshore regions, decreasing offshore (Calienes et al., 1985; Montecino et al., 1996; Daneri et al.,

2000). Integrated PPr measurements at different times and locations produce mean values as high as 3,700-5,200 mg C m^{-2} d^{-1} off Perú and 3,000 – 7,000 mg C m^{-2} d^{-1} off Chile (**Table 10.1**). Chávez et al. (1989) use PPr measurements from 1975 to 1987 to calculate a grand mean of 3,200 mg C m^{-2} d^{-1} (1.2 kg C m^{-2} y^{-1}) for the coast of Perú, consistent with the value estimated by Walsh (1981). Similar estimates of total integrated annual PPr rates of 0.93 kg C m^{-2} y^{-1} reported by Daneri et al. (2000) for the Chilean area is off Concepción (36ºS). Comparing studies in upwelling centers within both Chile and Perú, the lowest biological activity is found during several cruises off north-central Chile (Coquimbo, 30ºS), as reported by Montecino et al. (1996). Daneri et al. (2000) state that this is consistent with lower fish catch off Coquimbo, which is about one third the catch off Antofagasta to the north and off Concepción to the south.

The onshore-offshore vertical structure in temperature, salinity, nitrate and dissolved oxygen off Perú and Chile are provided in **Figs. 10.4 and 10.5**. Off southern Perú (15ºS), warm and salty SSW at the surface has high values of oxygen and low nitrate, overlying ESSW (high nitrate, low oxygen) below depths of 100-150m in the offshore regions (**Fig. 10.4**). The broad-scale effects of upwelling can be observed out to 400km from shore in raised isopleths of all variables. A narrower region of more intense upwelling is indicated in the upper 50m by rising contours of temperature, nitrate and oxygen within 50km of the coast. Below 50m next to the coast, contours of temperature, salinity and nitrate slope downward toward the coast, consistent with the presence of a poleward undercurrent (PUC). Water in the PUC is warmer and saltier than the water surrounding it, with relatively low nitrate and extremely low dissolved oxygen. At approximately 200km and 700km from the coast, subsurface nitrate minima are coincident with deeper regions of higher salinity and shallower regions of low oxygen. Nitrite data from the same WOCE transect (not presented) show isolated nitrite maxima exactly where the nitrate minima are found in **Figure 10.4**, i.e., right next to the coast and in the features 200km and 700km offshore between 100-200m depth.

Biological productivity in the upper coastal ocean off Perú creates a downward flux of organic material that decomposes at depth and further depletes the already-low oxygen concentrations in the PUC as it moves to the south. Upwelling brings nutrients back into the equatorward surface layer, fueling productivity and creating a semi-closed "nutrient trap" that enhances productivity further. The net result is that the PUC off Perú is extremely anoxic, with values less than 1 µM Kg^{-1}. The low oxygen favors anaerobic denitrification by bacteria. These bacteria use 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). This explains the lower nitrate and oxygen next to the coast in **Fig. 10.4**. The interpretation of the offshore regions of low nitrate and oxygen, high salinity (and high nitrite) is not as clear. These may represent the offshore Perú-Chile Countercurrent (PCCC), with connections to a branch of the EUC that separates at the Galápagos Islands and connects to the PCCC at around 10ºS (Lukas, 1986). The PCCC is visible in hydrographic sections presented by Huyer et al. (1987). Alternatively, these nitrate minima may represent subsurface-intensified eddies, spun off from the PUC, such as found in the California Current by Huyer et al. (1998).

Off Chile at 33ºS (**Fig. 10.5**), the structure is somewhat changed by the presence of SAW, which intrudes from offshore between 100-200m depth, creating a salinity minimum (stronger in the offshore region) that lies between the saltier water above and the salty ESSW in the PUC next to the coast between 100-400m depth. Underneath the ESSW is the fresher Antarctic Intermediate Water (AIW). The PUC is clearly marked by a salinity maximum and an oxygen minimum layer (OML). Unlike the severe oxygen minimum off Perú, concentrations rarely drop below 20 µM Kg^{-1} (0.46 ml

l^{-1}). Nutrients are higher in and beneath the PUC (Davies and Morales, 1998). A thin subsurface maximum in nitrite concentrations is sometimes found in the thermocline. Little is known about the causes of this maximum. It may be a remnant of the main secondary nitrite maximum (MSNM) described north of 23ºS by Codispoti et al. (1989); or it may be related to more normal photosynthesis processes.

Anaerobic bacterial denitrification, described above, occurs when oxygen concentrations fall below a critical level (ca <0.2 ml l^{-1}). This creates the MSNM at depths of 100-300m (Codispoti et al., 1989). **Fig. 10.6**, adapted from Helly and Levin (2004), shows the OML (defined as the layer in which oxygen concentrations are below 0.5 ml l^{-1}). The OML becomes shallower and narrower from north to south (Levin et al., 2002; Helly and Levin, 2004). When the depth of the thermocline and the oxycline are nearly the same, low oxygen concentrations above the base of the thermocline may act as barriers to downward vertical motion by zooplankton and ichthyoplankton (Morales et al., 1996b 1999, Eissler and Quiñones, 1999), as discussed in the next section. According to Codispoti et al. (1989), the northern boundary of the MSNM area is near 10ºS, where the PCCC joins the PUC. The southern boundary is near 23ºS, where the intrusion of SAW raises oxygen concentrations above the level where anaerobic bacteria can operate. However, the OML, the nitrate deficit, a thin subsurface nitrite maxima and other perturbed nutrient relationships continue to be found in the undercurrent as far south as 43ºS (Silva and Neshyba, 1979), serving as tracers of the PUC.

High bacterial secondary production (BSP) values are present in the PCCS, closely coupled with upwelling cycles (Daneri et al., 2000). Off Chile, Troncoso et al. (2003) estimate that the fraction of organic matter being channeled through BSP varies from 90% in Antofagasta (23ºS, near the southern boundary of the MSNM), 34% in Coquimbo (30ºS) and 20-45 % in Concepción (36ºS). Comparing these locations, daily BSP rates reach a maximum off Antofagasta (4999 mg C m^{-2} d^{-1}) and a minimum off Coquimbo. Mean values for the two locations are 1,721 ± 1,361 and 77.4± 56.2 mg C m^{-2} d^{-1} respectively, with a strong onshore-offshore gradient, similar to primary production (PPr) and Chl-a (see below). The presence of seasonal variability in BSP suggests coupling between bacterial consumption and PPr.

SeaWiFS satellite Chl-a concentrations (**Fig. 10.7**) provide a more complete picture of surface Chl-a (not of PPr) and suggest approximately 4 different regions in the PCCS. Off Perú, there is a wide region of moderately high pigment concentrations, which decreases off Ecuador as the region of high pigment concentration extends offshore toward the Galápagos Islands (not shown). Off northern Chile ($\cong$ 20ºS), the region of high Chl-a surface pigment concentrations is narrower, widening off central Chile (approximately 33º-41ºS), especially around Coquimbo (30ºS) and the Gulf of Arauco and Concepción. South of 41ºS in the fjord region, it remains to be determined whether the apparently high values of satellite-derived Chl-a are real or biased by non-chlorophyll colored material.

Fig. 10.8 shows onshore-offshore sections of nitrate concentration at 5º, 10º and 12 ºS, while **Fig. 10.9a** shows offshore transects of Chl-a concentrations at 5º, 10º, 12º and 33ºS. Off Perú, Chl-a concentrations greater than 1 mg m^{-3} are found in the upper 50m, extending 200km or more offshore. Nitrate does not appear to be limiting, especially at 5ºS. This is the region where a band of moderately high Chl-a concentrations sometimes connects with the band of higher Chl-a along the equator, similar to the equatorial cold tongue extending from Perú to the Galápagos Islands in

austral winter. Chl-a concentrations off Perú are high throughout the year and higher than those in corresponding inshore water in the California Current (Chavez, 1995). Average surface Chl-a content within 100 km of the Perúvian coast vary from 1 to 12 mg m^{-3}. Integrated Chl-a content in the euphotic layer ranges from 5 to 200 mg m^{-2} in the same area. Higher values (>5 mg m^{-3} surface Chl-a, >100 mg m^{-2} integrated Chl-a) are found within upwelling waters (Calienes et al., 1985). Tongues of surface Chl-a > 0.5 mg m^{-3} are observed in satellite data >400 km offshore.

Field surveys off northern Chile indicate that the highest chlorophyll-a pigments (> 1 mg Chl-a m^{-3}) are confined within 50 km of the coast and mostly in the upper 25-50 m (e.g. Montecino et al., 1998). Outside of bays, high surface pigment concentrations do not extend far offshore in the few ship surveys available. However, an offshore transect at 30ºS using continuous underway in situ fluorescence did find a subsurface chlorophyll maximum within the thermocline that extended far offshore (**Fig. 10.9b**, from Torres et al. [2002]). Other surveys have also found similar subsurface chlorophyll maxima, following the thermocline as in **Fig. 10.9b**. This is a recurrent pattern found in other eastern boundary currents, such as the California Current (Barth et al., 2004). This feature was apparently missed by standard sampling at discrete stations and depths in **Fig. 10.8**. Temporal averages of satellite-derived surface pigment concentrations in **Fig. 10.7** support the ship findings that the enriching effects of upwelling off northern Chile are closely confined to the coast, while off Perú and south of 33ºS the regions of higher surface pigment concentrations are wider.

Individual images of surface pigment and SST, however, often show filaments extending one to two hundred kilometers from coastal upwelling centers off Chile (Fonseca and Farias, 1987), including northern Chile around the Mejillones Peninsula (23ºS) (Thomas, 1999) and Concepción (Grünewald et al., 2002). Sobarzo and Figueroa (2001) describe filaments reaching 100 m depth and 170 km from the coast which appeared in satellite SST images in January, 1997. Shipboard sampling of these filaments shows that the water can be SAW, ESSW or a mixture of the two, varying in response to changes in upwelling strength which draws water from different depths. Filaments rich in particulate organic matter (POM) act as vehicles for the transfer of POM to the oligotrophic ocean off northern Chile (González et al., 2000a). Farther south at 36°S, Grünewald et al. (2002) measured grazing rates which indicated that offshore zones are sustained by horizontal export from adjacent upwelling zones and behave as recycling systems with little export to depth.

As in all eastern boundary currents, phytoplankton productivity and biomass are related to cell size patterns and species assemblages with –larger cells associated with higher biomass (Iriarte et al., 2000; Montecino and Quiroz, 2000; Dellarossa et al., 2001; Montecino, 2001). Offshore regions of lower biomass in northern and central Chile are characterized by higher percentages of smaller cells, occasionally modified by the advection of larger cells, which results in short term biomass increases. The opposite occurs near the coast, associated with circulation and turbulence changes. This also helps to explain seasonal changes. Morales et al. (2001) report that in summer when concentrations are higher than 1.0 mg Chl-a m^{-3} and confined to 20 km of the coast, larger phytoplankton (>20 um) are dominant; at lower concentrations (<1.0 mg Chl-a m^{-3}) the smaller phytoplankton are dominant. In autumn both size fractions are equally important.

3.2. Patterns and interactions in time

Phytoplankton dynamics in the PCCS have a wide range of time scales, due to the combined influence of local forcing by synoptic wind systems (periods of several days) and distantly forced coastal trapped waves (CTW's), with periods of 30-60 days (Shaffer et al., 1997; Hormazabal et al., 2001). Starting at the shortest time scales, water upwelled due to local winds "ages" rapidly over a

several day period, during which phytoplankton utilize newly upwelled nutrients for growth (Abbott and Zion, 1985; MacIssac et al., 1985; Peterson et al., 1988). During relaxation of upwelling, water flows back onshore and restratifies, concentrating the phytoplankton biomass and nutrients, which increases primary production over a narrow near-shore region over a several-day period (Marín and Olivares, 1999). This pattern of upwelling and relaxation repeats during the upwelling season or occurs more or less continuously where upwelling is the normal condition.

"Intraseasonal" (30-60 days) fluctuations in the thermocline and nutricline depth are caused by CTW's arriving from the north. Hormazabal et al. (2001) found phase relationships between temperature and sea level, whereby SST anomalies lag sea level perturbations by 12 days (1/4 cycle). Thus SST is decreasing when sea level is low, coldest when sea level is rising, etc. This relationship cannot be explained with a 1-D model, implying that horizontal advection is important in these waves (Hormazabal et al., 2001). These intraseasonal CTW's have been studied most off north-central Chile and may decrease in strength as they move poleward to mid-latitudes around Concepción (35°-37°S), where wind forcing is stronger.

Seasonal variability in SST occurs off Perú as the coastal upwelling system expands and cold SST connects to the Equatorial cold tongue during austral winter (Strub et al., 1998). Changes in Chl-a over annual periods are moderate in strength off Perú, weak off northern Chile and stronger off Chile at mid- and high latitudes (Thomas et al., 2001b). A time-latitudinal plot of monthly surface chlorophyll concentrations derived from SeaWiFS pigment estimates between September 1997 and March 2004, averaged over the 100km next to the coast, extends the time series of Thomas et al. (2001b) and shows both the seasonal pattern and interannual variability (**Fig. 10.10**). The 1997-1998 El Niño produced a large area with values less than 1.0 mg Chl-a m^{-3} between 15°-30ºS. Over this 6-year period, the pigment concentrations generally increase north of 35ºS, reducing the extent of the region with low-pigment concentration to 5°-10° of latitude and producing peak concentrations off Perú in austral summer with values over 5 mg m^{-3} .

The seasonal minimum of spatially averaged surface chlorophyll concentrations off Perú in austral winter (June-August) of each year is a puzzle, as equatorward winds tend to be stronger at that time. Strong upwelling events occur during the austral winter along the Perúvian coast (Chavez and Barber, 1985, 1987, Chavez, 1995). Field data by Guillén and Calienes (1981) and Calienes et al. (1985), however, support the observation that the seasonal variation of plankton biomass and primary production within 100 km of the coast is 180° out of phase with the variation of upwelling intensity. Guillén and Calienes (1981) suggest that higher primary production during summer/fall is explained by the dynamics of the depth of the mixed layer and of solar radiation. Chávez (1995) finds Chl-a concentrations in the offshore region (100-250km) to be maximum during winter and suggests that the stronger winds and Ekman transport disperse the phytoplankton over a wider region in winter, reducing the average concentration in this 100km wide band. This question remains to be answered.

As with estimates of PPr, field measurements of Chl-a concentrations cover a wide range over even short time and space scales. Off northern Chile between 16-23°S during the summer of 1994, Morales et al. (2001) measured Chl-a concentrations of 0.1-20.3 mg m^{-3} at the surface, with the highest values (>1 mg m^{-3}) associated with newly upwelled water in a 10 km band next to the coast. During autumn this range diminished to 0.1-11.7 mg Chl-a m^{-3}, with the higher values occurring in patches and extending 20-80 km from coast. Mean values of 1.5-1.6 mg Chl-a m^{-3} were not

significantly different between the two seasons. At 25 m depth, the Chl-a distribution was similar, with an offshore extension of higher values in the summer. Subsurface chlorophyll maxima occurred in the top 25 m during both seasons, with slightly higher values (16-20 mg Chl-a m^{-3}) in summer than in autumn (10-15 mg Chl-a m^{-3}). Mean 25 m integrated Chl-a values were also similar to those found in the previous winter and spring (Morales et al., 1996a). At 30°S, integrated Chl-a concentrations (0-30 m) were lower than around Mejillones Peninsula (23°S), with the lowest values measured at both an oceanic station (6.9 mg m^{-2} in winter) and a coastal station (8.1 mg m^{-2} in spring) (Montecino and Pizarro, 1995). These measurements add the temporal component to the spatial pattern noted previously: the very narrow and shallow region of high phytoplankton biomass off northern Chile has virtually no seasonal cycle. The unique topography of the Mejillones peninsula may be the anomaly in this northern region, creating topographically induced upwelling, filaments and eddies that produce higher Chl-a concentrations than found at other locations along northern Chile.

Farther south in the region around Concepción (35°-37°S), the satellite data in **Figs. 10.7** and **10.10** show the clear mid-latitude seasonal cycle. Maximum pigment concentrations occur in austral spring and summer, coincident with the annual cycles in solar radiation and upwelling wind intensity. In situ measurements generally support this seasonality, although they contain considerable short term variability. Sources of this variability include the large temporal and spatial variability in the hydrographic features associated with precipitation and runoff of the Bio-Bio River (Faúndez et al., 2001). Because both seasonal variability and locally-forced upwelling are stronger than off northern Chile, the effect of intraseasonal fluctuations on PPr and phytoplankton biomass is less obvious and needs further study.

On interannual scales, ENSO fluctuations create strong environmental variability at low and mid-latitudes in both the ocean and atmosphere. The 1997-1998 El Niño was perhaps the best documented on record and produced increased sea levels at tide gauges as far south as 33°S, highest off Perú (Blanco et al., 2002). Altimeter data document increases in sea level that spread rapidly to the southernmost tip of Chile, but were strongest and most persistent off Perú (Strub and James, 2002). Winds measured by satellite remained upwelling-favorable throughout the time period for most of the area and actually increased in strength during November 1997 – March 1998 (Halpern, 2002; Carr et al., 2002). Despite these winds, the thermocline was strongly depressed off Perú and off Chile at 20.5°S and 23°S (Blanco et al., 2002; Thomas et al. 2001a, Ulloa et al., 2001). Satellite derived surface Chl-a (OCTS and SeaWiFS) dropped in May-June 1997 (OCTS failed in June, 1997) and was low from December 1997 – January 1998 (SeaWiFS started in September, 1997). The decrease in pigment levels was strongest off Perú and central Chile and it affected the offshore regions more than the very nearshore. The extreme narrowing of the upwelling region was documented by in situ and satellite data off northern Chile (Rocha, 2001; Thomas et al., 2001a; Blanco et al., 2002; Carr et al., 2002).

In situ measurements from nearshore regions present a less clear picture of El Niño effects. During the transition to El Niño in 1997, Pizarro et al. (2002) reported no change in integrated Chl-a concentrations between January 1997 (pre-El Niño) and July 1997 (during the El Niño) at either oceanic or coastal stations off Antofagasta outside of the bays. They did find a significant decrease in mean PPr values in the coastal stations, dropping from 3,129 mg C m^{-2} d^{-1} in January (summer) to 942 mg C m^{-2} d^{-1} in July (winter), but overall concluded that any El Niño effect was "masked" by "prevailing space and seasonal variability." Similarly, Ulloa et al. (2001) report no change in general phytoplankton or zooplankton abundance very close to shore in Antofagasta Bay from June

1996 to January 1998, although water was 4°C warmer and twice as oxygenated. One herbivorous zooplankton population (a species that does not tolerate low oxygen levels) actually increased in abundance. Farther north off Iquique (20ºS), Herrera and Santander (2002) also found that phytoplankton species assemblages changed in response to changing environmental conditions during the El Niño. Torres et al (2002) showed that strong upwelling-favorable wind anomalies at 23°S resulted in outgassing of CO_2 during the first pulse of El Niño conditions in 1997, while the upwelled water was substantially warmer (3-4°C) than during La Niña period. These studies point out that changes in water properties during ENSO events in nearshore regions can be stronger and more complex than the patterns found offshore. These can produce both beneficial and deleterious effects on nearshore ecosystems.

3.3 Interactions of multiple time scales

Noting the more complex reaction to ENSO changes in the nearshore regions of north-central Chile described above, Rutllant and Montecino (2002) argue that it is the interactions of processes with different time (and space) scales, rather than individual events, that control changes in primary production and integrated Chl-a concentrations. This interaction is accomplished by the superposition of changes in the depth of the thermocline/nutricline/oxycline.

The new element in this argument is the recognition, due to a decade of moored current meter measurements from north-central Chile (Shaffer et al., 1995, 2004), that intraseasonal (30-60 day) changes in currents and thermocline depths due to CTW's can be stronger than changes due to local upwelling and similar in magnitude to ENSO signals (Shaffer et al, 1997; Pizarro et al., 2001, 2002; Hormazabal et al., 2002, 2004). Especially where the seasonal signals are weak (off southern Perú and northern Chile), this adds a third forcing to the previously considered balance between local upwelling and ENSO changes in pycnocline depths and allows "warm" and "cold" phytoplankton patterns to arise from a larger number of combinations. For example, an increase in temperature and deepening of the pycnocline associated with the ENSO warm signal could be offset by an intraseasonal rise in the euphotic zone depth, allowing upwelling to bring nutrients to the surface and drive phytoplankton growth next to the coast. However, the intraseasonal CTW's have narrower scales than ENSO effects. So phytoplankton growth and integrated Chl-a measured in bays and over the narrow shelf may find no differences between El Niño and La Niña periods, despite the fact that interannual Chl-a changes are discernible in satellite images of oceanic areas farther offshore.

Table 10.2 presents examples of the scales of modulation of biological response over a full upwelling cycle from two cruises off Cruz Grande bay (29.5ºS). The first took place during the *warm* phase of the ENSO cycle in November 1987 (which is also during the *warm* season), while the intraseasonal fluctuation of sea-level was rising. Since sea level leads SST by ¼ period, this is the *coldest* phase of the intraseasonal signal. During this cruise, integrated Chl-a increased more than three times from the active to the relaxed phase of the local wind forcing, while primary production (PPr) had a slight decrease. The interpretation is that PPr was maintained during the active upwelling by both the upwelling and the intraseasonal wave, which continued to favor productivity (with a slight drop) when upwelling stopped. The major change when upwelling relaxed was the movement of the enriched water back toward the coast, where the phytoplankton occupied a deep mixed layer (due to ENSO effects) and produced the high values of integrated Chl-a. Conversely during the La Niña (*cold*) phase of the ENSO cycle, in November 1988 (again seasonally *warm*), the sea level was steady on intraseasonal time scales. In this case, when upwelling relaxed, integrated Chl-a increased only moderately (due to the shallow pycnocline during La Niña), while primary production increased by almost a factor of three (Rutllant and

Montecino, 2002). The shallower pycnocline limited the integrated Chl-a values, but allowed the injection of nutrients into the euphotic zone during the upwelling and concentrated the nutrients in a shallower euphotic zone.

The basic argument is simple: Frequent (synoptic scale) upwelling, superimposed on the slower intraseasonal variability, must push the system toward active upwelling in nearshore regions during the part of each intraseasonal period, when the pycnocline is closest to the surface. This is especially effective in countering the (very real) El Niño effect on the pycnocline, if El Niño's also bring increases in both the strength of upwelling wind-forcing off Perú and northern Chile (as argued by Halpern [2002] and Carr et al. [2002]) and in the strength of intraseasonal CTW's (as argued by Shaffer et al. [1997]). Thus, the simple picture of low-nutrients during El Niño conditions becomes episodic over the shelf, although the mean productivity of the offshore area is reduced. The mix of forcing also affects what happens when upwelling relaxes: "Warm" (El Niño and decreasing intraseasonal sea-level) conditions favor deeper mixed layers and an increase in integrated Chl-a when upwelling relaxes. Conversely, "Cold" (La Niña and rising intraseasonal sea-level) conditions favor a decrease in mixed layer depth and an increase in primary production when winds relax, without a significant increase in integrated Chl-a.

The same processes also control the flux of CO_2 between the atmosphere and ocean, as argued by Codispoti et al. (1989). In an average sense and over long time scales, Torres et al. (2002) use the regional minimum in wind forcing off northern Chile to point out that both wind forcing and ventilation of CO_2-rich waters increase as one moves from 23ºS and 30ºS, implying that the latitudinal gradient in CO_2 outgassing is due to wind forcing. Estimates of the rates of CO_2 outgassing from specific cruises (**Fig. 10.11**) demonstrate how upwelling increases CO_2 concentrations in the upper ocean and leads to fluxes of CO_2 from ocean to atmosphere (Copin-Montégut and Rimbault, 1994; Torres et al., 1999, 2002; Torres and Lefevre, 2001; Lefevre et al., 2002; McNeil et al., 2003). On shorter timescales, however, phytoplankton uptake of CO_2 as the upwelled water ages can draw down surface CO_2 concentrations in the ocean, leading to a flux of CO_2 from the atmosphere to the ocean within chlorophyll-rich upwelling filaments (Torres and Lefevre, 2001, Lefevre et al., 2002). Thus, estimating overall rates of CO_2 transfer between the atmosphere and ocean in the PCCS requires careful sampling, considering the same combinations of temporal and spatial scales that Rutllant and Montecino (2002) describe as controlling PPr and integrated Chl-a concentrations.

4. Holozooplankton and merozooplankton.
4.1. Zooplankton composition, distribution, abundance and behavior
In reviewing zooplankton distributions off Perú and Chile, we consider only the coastal upwelling regions (0º-40ºS), ignoring the two other major biogeographic provinces: the high-latitude Inland Sea and the coasts of offshore islands (Antezana, 2001). Most studies of zooplankton in these coastal regions focus on one or more of several inter-related themes: (1) the association of different species with certain water mass types or depths; (2) the relationship between vertical migration/distribution and the OML; (3) the distribution of zooplankton with respect to mesocale fields of velocity, temperature and phytoplankton biomass; and (4) changes caused by ENSO or lower frequency signals. Herbivorous zooplankton commonly exhibit diel vertical migration (DVM), both as a feeding/predation avoidance mechanism and also to maintain their latitudinal and cross-shelf position. Off Perú and northern Chile, however, the presence of a shallow OML makes deep DVM difficult or impossible. ENSO and lower frequency climate signals can affect zooplankton populations by altering the depth of the oxycline, the mix of water mass types at a

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given location (along with changes in predators associated with those water mass types) and the mesoscale circulation fields.

Off Perú, the available data are usually expressed as total integrated zooplankton biomass or zooplankton volume, which reaches its maximum in spring off northern Perú (3.5º-6ºS), associated with ESSW. Carrasco and Lozano (1989) estimate average zooplankton volumes from 1964 to 1983 off the Perúvian coast, giving grand seasonal means from $0.38 - 1.75$ ml m^{-3}, with higher values during spring. A 30-40% decline in zooplankton biomass after the 1972-1973 El Niño coincided with the decrease of the anchoveta stock and the increase of other (larger) fish predators, such as sardine, horse mackerel and mackerel (Carrasco and Lozano, 1989). The authors imply that increased grazing is responsible for the decline in zooplankton biomass. During the 1982-1983 El Niño, an apparent change in zooplankton composition and a decrease in abundance (Carrasco and Santander, 1987) may be due to the continued sampling at only two standard depths (0 and 50 m), while the pycnocline deepened substantially. ENSO effects at higher latitudes include the deepening of the oxycline (Morales et al., 1999), which would increase the vertical region over which zooplankton and ichthyoplankton are distributed, decreasing their density but not their total abundance

In Chilean coastal waters, the dominant zooplankton taxa are copepods, euphausiids and the large holozooplankton such as salps, appendicularia (tunicata), siphonophores (cnidaria) and chaetognaths. Epipelagic and mesopelagic holozooplankton are found in the upper 200m to 400m of the ocean and are often associated with specific water mass types. As an example, Ulloa et al. (2000) characterize the distributions of the dominant chaetognath species off Valparaíso as either epipelagic or mesopelagic. Epipelagic species are associated with the SAW or SSW in the upper 100m. Mesopelagic species are associated with ESSW between 100-400m (mostly in the 100-200m range). Gelatinous zooplankton are also associated with specific water masses. When siphonophores are the dominant species, they are often associated with SSW (>19ºC). In one survey where siphonophores were dominant off Mejillones Peninsula, *Bassia bassensis* was the most important secondary predator in the top 50m of the water column, exerting a significant trophic impact on the small copepods present during the sampling period (Pages et al., 2001). Ctenophores (represented by *Pleurobracia sp.*) were found in SAW (higher oxygen concentrations), while salps (such as *Salpa fusiformes*) were associated with ESSW. In general, there was a low occurrence of gelatinous taxa in upwelled ESSW.

Reviewing the distribution of smaller zooplankton (<200 μm) along the northern coast of Chile (18º-23ºS), González and Marín (1998) found that *Calanus chilensis* and *Centropages brachiatus* are the most abundant species in number within 80 km of the coast, with the highest abundance within 10 km of the coast (**Fig. 10.12**). Both species are more abundant where SAW is upwelled. They reproduce throughout the year, with no evidence of seasonal or diurnal vertical migrations. Both *C. chilensis* and *C. brachiatus* may be found more than 40km from the coast, a result of reproduction in coastal upwelling areas, followed by offshore advection by mesoscale features.

Among crustacean macro-zooplankton off Chile, the endemic euphausiid, *Euphausia mucronata,* has been identified as a key indicator species by Antezana (1981) and plays a major role in channeling primary production to higher trophic levels. This species can be limited in the nearshore by the shoaling of the OML. For example, around the Mejillones peninsula, Escribano et al. (2000) found *E. mucronata* everywhere, with greater aggregations in the southern area, where the top of

the OML was deeper. There was no correlation with other water properties (T, S, Chl-a), only with deeper OML layers. Abundances were also greater around upwelling filaments. Marín et al. (2001) and Marín and Moreno (2002) also find a lack of DVM in the dominant endemic species around the Mejillones peninsula.

Escribano et al. (2002) consider other mechanisms that can act to retain passive or vertically swimming plankton within the upwelling zone: gyres, current reversals and lateral thermal fronts. Their results indicate that late stages of copepods located outside of upwelling plumes develop faster and gain greater weight, size, better condition indices and ovary development (adult females) than those inside the cold plumes, presumably because their metabolism is significantly slowed by colder temperatures. The ability to maintain positions just outside the plume, entering the plume to feed and then leave, would provide the best combination of conditions for growth. Escribano et al. (2001) further note that a fairly substantial fraction of a zooplankton population can be advected offshore and removed from the breeding population (20% in the case of *C. chilensis*), with little effect, if these losses are compensated by very high daily production rates.

Considering interannual time scales off northern Chile (18°-24°S), Bernal et al. (1982) analyze data from fisheries (IFOP) cruises between 1964-1973 to show: 1) a spring and/or summer maximum during a majority of the years; and 2) a decrease in zooplankton biomass and ichthyoplankton species around 1969-1970, which was not related to ENSO changes and continued for at least several years (**Fig. 10.13**). Loeb and Rojas (1988) analyzed ichthyoplankton surveys off northern Chile and southern Perú during this same period (1964-73) plus 1983, a period that included the decline and collapse of the anchoveta fisheries in the mid 70's and increase of sardine, mackerel (*Scomber*) and jack mackerel (*Trachurus*) stocks. They found changes in the zooplankton biomass and in larval fish taxa composition that were consistent with a subtle, large scale (low frequency) environmental transition during the 1969-1970 period.

The zooplankton community includes the eggs and larvae of economically important higher trophic levels, whose distribution, survival and recruitment depend on same physical-biological interactions, while they are in their more passive stages. For example, anchovy eggs are spawned near the coast and remain near the surface during their development, where they are subject to strong advection, temperatures, oxygen levels, etc. Morales et al. (1996b) describe the effects of a sequence of cold and warm events between 1990-1995. Temperatures were favorable for anchovy larvae in the coastal zone between 18°-24°S, whereas changes in the depth of the OML did not show a direct influence on their survival. They hypothesize that changes in fishery yields in this region may be directly related to the expansion and contraction of their preferred habitat.

Besides anchovy and sardine, other economically important larval forms in the meroplankton include the demersal *Pleuroncodes monodon* (Squat lobster) and *Cervimunida johni*, the most important of the eight endemic species of Galatheidae (Crustacea) (Bahamonde et al., 1986). *P. monodon* is distributed between Perú and Chile, whereas *C. johnni* has a more restricted distribution. In terms of relative catch, *C. johnni* was more abundant until 1970, when *P. monodon* catches increased and gradually expanded southward (37°S). Note that the year of the change is the same as found for changes in zooplankton biomass and ichthyoplankton species.

4.2. Grazing, growth and secondary production

Several studies have attempted to link zooplankton biomass, composition and seasonal development to primary production and phytoplankton biomass (Hidalgo and Escribano, 2001). Zooplankton

grazing consumed between 5-40 % of primary production in a study off Perú (Boyd and Smith, 1983) and between 6-58 % off northern Chile (González et al., 2000b). Looking at vertical fluxes of POC (fecal material, micro and phytoplankton) off Antofagasta, González et al. (2000b) conclude that fluxes in the pelagic ecosystem are dependent on a combination of three factors: zooplankton composition, the abundance of cyclopoid copepods and the composition and size spectrum of phytoplankton. When euphausiids are abundant, there is a fast vertical export; when copepods are dominant, there is more recycling.

González et al. (2000b) compare the grazing impacts of crustacean and pelagic tunicates during El Niño and non-El Niño years. Although the deepening of the thermocline leads to generally lower nutrient and Chl-a concentrations during El Niño period, upwelling of ESSW in the vicinity of the upwelling centers fertilized the euphotic zone and enhanced the rate of PPr. Upwelling filaments were rich in POC and Chl-a, transferring organic matter to the oligotrophic ocean. Ingestion of phytoplankton exceeded respiratory demands for copepods, but failed to supply the respiratory needs of euphausiids, which must utilize detritus, micro and mesozooplankton. Grazing by crustacean zooplankton had a significant impact on phytoplankton, removing from 10 to 34% of the estimated PPr. Salps consumed up to 60% and Euphausiids removed between 1 to 19%. There were no differences in zooplankton biomass between January 1997 (non-El Niño) and January 1998 (El Niño) (24.6 and 21.4 mg dry wt m^{-3} respectively). A similar result was found within Mejillones Bay, where secondary production of *Calanus chilensis* showed no evidence of food limitation during the 1997-98 El Niño (Ulloa et al., 2001). These studies extend the conclusions based on PPr and Chl-a concentrations to a higher trophic level, i.e., that in nearshore regions, El Niño periods do not necessarily result in lower secondary productivity for zooplankton.

Most plankton grazing studies measure only metabolic rates of adult stages of the dominant copepods species. Studying the grazing pressure (GP) of whole assemblages of the upwelling zone off Concepción, Grünewald et al. (2002) found values that were relatively low (<6%), and did not vary with season. Considering just the coastal zone, however, they found GP to be significantly higher during spring (> 17%) than in other seasons.

Studies of respiration (oxygen consumption) in the water column are also scarce. Nevertheless, Eissler and Quiñones (1999) report a strong seasonal signal off Antofagasta in northern Chile. Because of the lower percentage of primary production respired by the phytoplankton in winter, more fixed carbon is available for higher trophic levels and export production. Estimates of mean integrated respiration in the mixed layer range from 50-95 μM O$_2$ m^{-2} day^{-1}. These are similar to those found in the Benguela current, while lower and less variable than those reported off Perú (estimates of 28-590 μM O$_2$ m^{-2} day^{-1} by Setchell and Packard, 1979; Boyd et al.,1980; Hendrikson et al., 1982).

Considering sedimentation as a "final" product of the coastal ecosystem around the Mejillones Peninsula in January and July 1997, González et al. (1998) calculate values of 104 and 123 mg C m^{-2} d^{-1} (40-45 g C m^{-2} y^{-1}), prior to and during El Niño. Their estimate of pelagic consumption rates on an annual basis is approximately 90 g C m^{-2} y^{-1}, including potential horizontal export from the coastal system. They conclude that only a small proportion of the primary production is metabolically used by the coastal ecosystem.

Moving offshore to the oceanic region (150km from the coast) near 30ºS, Marchant et al. (1998) report large vertical fluxes of planktonic foraminifera, measured by moored sediment traps at 2300 and 3700m. Between 1991-1994, daily average fluxes of shells >150 um were 4000 shells m^{-2} d^{-1}. Even during the moderate El Niño period of 1991/1992, the daily average of 3000 shells >150 um m^{-2} is high. In this same area (30ºS, 73.11ºW) and for the same period, Hebbeln et al. (2000) measured a downward export flux of 20-400 mg C m^{-2} d^{-1} (7-146 g C m^{-2} y^{-1}), with the maximum occurring during the spring upwelling season. They interpret the timing of the export flux maximum (during upwelling) to indicate the effect of upwelling in enriching the ocean to at least 150km from the coast on a seasonal basis.

The above, order-of-magnitude estimates of PPr, secondary production, respiration and sedimentation serve as a beginning in considerations of regional oceanic carbon budgets. The discussion of scales of variability, however, makes it clear that a great deal of further work is required to quantify more complete carbon budgets, along with their variability in time and space. These budgets also need to include the higher trophic levels (fish), if we are to understand the underlying mechanisms responsible for the large mean and fluctuating values of the fish catches in the PCCS (next section).

5. Pelagic fish distribution and abundance patterns off Perú and Chile

This section concentrates on the economically and ecologically important populations of small pelagic fish off Perú and Chile. The production, life histories and food web dynamics of these species are discussed in the context of the patterns of distribution and abundance associated with large interannual and interdecadal fluctuations in their overall catches. In regions adjacent to the coast, there are also important artisanal (small vessel) fisheries, which supply most of the fish and shellfish bought in markets and restaurants for direct consumption. The artisanal fisheries typically produce 10-20% of the total catch from this region and are very important to the economies of coastal communities. The industrial fisheries for small pelagics, however, have values listed for Perú and Chile as $1.1 billion U.S. and $1.7 billion U.S., respectively (FAO, http://www.fao.org/sof/sofia/). Thus, the dramatic increases and declines in fish catches over interannual and interdecadal time scales described below have significant impacts on both national and local economies. See also Chavez (2003, 2004) and Bakun (2004) for discussions of the same topics on a global scale.

The significance of these populations is illustrated by their effect on interannual variability in global catch. The global capture of marine species was 93 million metric tons (MMT) in 1996, falling to 86 MMT in 1998, reflecting the drop in the SE Pacific from 17.1 MMT to 8.0 MMT (FAO). This represents a response to the 1997-98 El Niño. During the same period, the total catch of all oceanic species in the NE Pacific (California Current, Gulf of Alaska) was 2.8MMT and 2.9MMT, showing the difference in productivity of the two systems.

Perú and Chile can be divided latitudinally into four regions of fisheries productivity: northern and central Perú; southern Perú and northern Chile (S. Perú-N. Chile); central Chile from 30º-40ºS; and southern Chile in the Inland Sea. The primary commercial catch off north-central Perú is from a single anchovy stock (anchoveta, *Engraulis ringens*) with a significant but lesser contribution from a sardine stock (sardina, *Sardinops sagax*). Other species present in the system include hake (*Merluccius gayi*), chub mackerel (caballa, *Scomber japonicus*), and bonito (*Sarda chilensis*). In the south Perú- and north Chile region, important commercial species include the sardine, a second

stock of anchovy, jack mackerel (Jurel, *Trachurus symmetricus murphi*), tuna (Atún, *Thunus sp.*), and swordfish (Albacora, *Xiphias gladius*). Off Central Chile, the primary commercial fish are Jack Mackerel, anchovy and a sprat called the common sardine (Sardina común, *Strangomera bentincki*). Hake (Merluza, *Merluccius magellanicus*) are also present. Off Southern Chile, the fishery is concentrated on demersal fish such as hake.

The generalized locations of the regional fisheries off Perú and Chile are shown in **Fig. 10.14a** with respect to anchovy, sardine, hake and the Chilean jack mackerel. This provides a very broad outline of the distribution of fish habitats. The pelagic habitat can be further divided into three onshore-offshore regions (not indicated on figure): tuna and swordfish are found offshore in the clear oceanic waters; jack mackerel stocks are associated with the transitional zone between oceanic and coastal waters; and sardine and anchovy are found in the cooler coastal zone with the sardines normally found farther offshore. For example, the highest catches per effort (CPUE) for anchovy off northern Chile are located within 20nm of the coast in the more recently upwelled water, while the highest CPUE for sardine is located in waters advected farther offshore (Yañez et al., 1995; Yañez et al., 2001）.

The fluctuations in catches off Perú and Chile appear to reflect a rough alteration in abundance (biomass) of the anchovy and sardine populations (**Fig. 10.14b**) at the interdecadal time scale (Lluch-Belda et al., 1989; Schwartzlose et al., 1999; Chavez, et al., 2003; Bakun, 2004). The yearly combined catches of sardine and anchovy are larger off Perú (8-14 MMT) than off Chile (4-6 MMT). In the south Perú-north Chile region, the catch is usually greater off northern Chile than off southern Perú. Considering Perú and Chile together, the combined catch of small pelagics typically ranges from 4-12 MMT but may drop to lows of under 4 MMT (Schwartzlose et al., 1999). For example, as result of the 1997-1998 El Niño, total catch of anchovy alone dropped from 8.9 MMT in 1996 to 1.7 MMT. The Perúvian anchoveta fishery recovered quickly, however, and produced the largest single species catch (> 11 MMT) in the year 2000.

The larger catches (above 6 MMT) are comprised mainly of the anchovy off northern and central Perú. The anchovy stock off southern Perú and northern Chile makes a relatively small contribution to the overall catches (**Fig. 10.14c**). The sardine catches that peaked in the 1980s (**Fig. 10.14b**) were comprised of roughly equal parts from the region off northern and central Perú and the region off southern Perú and northern Chile with only a relatively small contribution from the stock off central Chile.

The mechanisms responsible for the alternation of anchovy and sardine abundances over the last 50 years of catch records are still not well understood, despite much consideration and conjecture. The paleo record of sardine and anchovy scale deposition off southern California suggests that alternation has occurred frequently over the past 1700 years (Baumgartner et al., 1992), although this record also reveals periods when both species were thriving together or had declined simultaneously. A shorter paleo record beginning in the 1870s off central Perú indicates that periods of low anchovy scale deposition during the first half of the 20th century was accompanied by the appearance of sardines in the scale record, indicating that the alternation may result from natural and regular phenomenon in the Perú-Chile region.

The approximately simultaneous changes in several fish populations in different regions of the North and South Pacific Ocean over interdecadal periods are referred to as regime shifts (Lluch-

Belda et al., 1989, Chavez et al., 2003). The timing of these changes has been linked to interdecadal shifts in the climate and physical environment (Mantua et al., 1997). In particular, anomalies in sea surface temperature of one sign over a wide coastal region in the eastern Pacific in both hemispheres, with some extension along the equator, is called the Pacific-Decadal Oscillation (PDO). When these regions show one sign of anomaly, the mid-latitude central Pacific regions in both hemispheres show the opposite sign in the SST. A "warm regime" is identified by a warmer eastern boundary and colder interior, reversing these signs during a "cool regime." In general, the periods of greater anchovy CPUE have been associated with cool regimes (prior to 1975), while the period of greater sardine abundance (1975-1990) in the SE Pacific was a warm regime (Schwartzlose, 1999). There is some debate concerning whether the regime changed from warm to cold around 1990, when anchovies replaced sardines in the PCCS. Chavez et al. (2003) suggest another possible shift in 1998. See also Bakun (2004) and Chavez (2004).

Estimates of changes in fish population sizes and distributions based on fish catch records are biased by uneven fishing efforts. Massive harvesting of the fish stocks also makes it difficult to assess the effects of the large-scale environmental changes. For example, catches of 12 MMT and 10 MMT in 1970 and 1971, respectively, may have contributed to the decline in anchovy abundance. Patterns found by combining stocks can also be misleading. For instance, both anchovy stocks (northern and central Perú and S. Perú - N. Chile) generally fluctuated in phase, but separating the sardines into four stocks shows a lag in the peak in the S. Perú – N. Chile region compared to the stock of northern and central Perú. Individual landings at Coquimbo and Talcahuano (both in the Central Chile) have alternating peaks during 1978-1990 (Schwartzlose et al., 1999). This may represent changes in distribution of the stocks, rather than in overall population.

To overcome these limitations, estimates of adult biomass and recruitment attempt to more accurately determine the timing of changes in the responses of fish populations to environmental conditions. Data from Schwartzlose et al. (1999) (**Fig. 10.15)** reveal high anchovy recruitments off North-Central Perú prior to 1970, lower recruitment from after 1970, with a few years with moderate values (1978, 1983, 1986, 1990-1991). Estimates of sardine recruitment started in 1974 and show moderate (northern and central Perú) to high (S. Perú – N. Chile) values (1983-1989), declining in both regions in the early 1990s. Thus, both recruitment and catch data agree on the dramatic collapse of the anchovy around 1970. Replacement of anchovy catch with sardine catch lagged the decline of the anchovy by several years (recruitment data are lacking), beginning in earnest around 1976-77. The peak in the sardine catch in the mid-1980s corresponds to a period of relatively high recruitment in the S. Perú – N. Chile region. This period also had peaks of moderate anchovy recruitment while anchovy catches increased in the second half of the 1980s (with sardine catches still high). Sardine catches declined sharply after 1990, when sardine recruitment fell to very low values. The fact that anchovy recruitment and catches began to increase during the mid-1980s makes it difficult to argue that the alteration between species was due to an abrupt change of state favoring one or the other species (Schwartzlose et al., 1999). Rather it appears that a more gradual shift in the habitat conditions favoring the anchovy over sardine occurred during the period from the mid-1980s to the mid 1990s.

A number of physical and biological mechanisms, interacting with harvesting, have been suggested to explain aspects of these population changes. These include: (i) physical changes in surface fluxes of momentum, heat and precipitation, wind-induced turbulence and vertical mixing that cause significant changes in temperature, salinity and stratification, as well as changes in thermocline,

nutricline and oxycline structures that alter ecosystem function and habitat conditions (Gargett, 1997; Yáñez et al., 2001); (ii) advection of water masses with anomalous properties (Loeb and Rojas, 1988; Ñiquen et al., 1999); (iii) advection of warm oceanic water toward the coast, which concentrates the organisms that prefer cold water, increasing density-dependent processes (Csirke, 1988; Alheit and Bernal, 1993) and allowing increased catchability and predation; (iv) warmer coastal water also allows new, warm-water predators to exploit the concentrations of fish; (v) the above changes in environmental factors lead to changes in the dominant phytoplankton and zooplankton sizes, usually moving to smaller phytoplankton and zooplankton during warm regimes and El Niño's (favoring more the adult sardines). As discussed in previous sections, these processes operate over a wide range of time scales. Determining the role of these interacting mechanisms is the subject of ongoing investigations off Perú and Chile, where prediction of the changes in these populations has a large economic and social impact (Carr and Broad, 2000).

The commercial importance of its anchoveta harvest has focused attention on the ecosystem off Perú. Adults of anchovy and sardine can both feed on phytoplankton as well as zooplankton, with adult sardines favoring smaller particles (including anchovy eggs). Egg cannibalism by the anchoveta is considered to be an important density-dependent mechanism. Jack and chub mackerel may exert significant predation pressure on anchovy when oceanic waters approach the coast (during El Niño events); the same is true for hake, when oxygenated waters extend further southward than normal (Muck, 1989). In turn, anchovies may exert a strong control on sardine and hake populations by feeding on their eggs (Muck, 1989). Other important predators of anchovy are bonito, guano birds, sea lions and fur seals (Muck, 1989).

Jarre-Teichmann (1998) investigated the ecosystem trophic structure by means of top-down, steady-state mass-balance models. **Fig. 10.16** compares the results for the warm regime favoring sardines (right) and the cold regime favoring anchovy (left). Without worrying about absolute values, it suggests that anchovy appear to covary in phase with the lower components of the ecosystem (zooplankton and, to some extent, phytoplankton and detritus) while sardines are out of phase. This may be a clue to important differences in the life histories of the two species and related to the difference in mobility of the two populations, with sardines relying on their better swimming capability for movements over significant distances to find suitable forage during periods of decreased productivity at lower trophic levels. The mean transfer efficiency (from herbivores to top predators) was calculated as 4-6%. Total fish production of the five dominant species (anchovy, sardine, chub mackerel, jack mackerel and hake) is consumed by predators in the following order: by fish predators (jack mackerel, chub mackerel, hake and other demersal species), by the human fishery, by mammals and other top predators (seabirds and other large pelagic fish).

Off Central Chile, the common sardine and the anchovy have similar life histories, living in the coldest waters. Their reproductive strategy is to spawn at the end of winter, in order to enhance survival of eggs and larvae during moderate upwelling, low turbulence and weak offshore Ekman drift. During spring and summer, they use the period of upwelling and enrichment of the coastal ocean to grow and store energy for reproduction. Energy storage is critical, due to the rigorous winter conditions of food availability for adults (Cubillos et al., 2001). The jack mackerel, on the other hand, move offshore to spawn. Juvenile mackerel then move north to the Perú-Chile region and onshore to the Central Chile region, with the highest catch offshore of the sardine and anchovy.

Considering only a subset of the fish and euphausiid species off Central Chile, Antezana (2001) proposes a fairly simple conceptual model of the food-web dynamics. In this model, hake, sardine,

anchovy and other small pelagics increase when jack mackerel are under full commercial exploitation, keeping their numbers low. When jack mackerel numbers increase, populations of the small pelagics decline. Looking at energy requirements off Central Chile, Cubillos et al. (1998) find a high value of primary production required to sustain the fish biomass. This region is dominated by jack mackerel, which are highly migratory and have access to smaller fish and zooplankton over a wide range of ecosystems, as they travel along the coast. This points to the difficulty of considering food web dynamics within small, isolated regions.

Mortality of the larval sardine and anchovy are thought to be a key factor in determining year-class population sizes. Off Perú, anchovy larvae have larger mouths but smaller guts, compared to sardine larvae of the same size. Species compositions in the guts of first feeding larvae show that anchovy feed almost exclusively on small, flagellate phytoplankton, while sardine larvae feed almost exclusively on small zooplankton such as copepod eggs and nauplii (Muck, 1989). Thus, anchovies spawn closer to shore, where phytoplankton biomass is greater, and sardine spawn farther from shore, where zooplankton are more abundant. Further evidence for this is given by Hernández et al. (2003), who show that anchovy larvae are the most abundant of over 30 species collected within 5 km of the coast at two sites near 33.5ºS. This suggests that conditions which favor small phytoplankton over zooplankton could put anchovy larvae at an advantage.

Adults also differ in their diets, due to the fact that sardines are capable of filtering smaller particles, including phytoplankton as well as zooplankton. Because of this, adult anchovies depend more on zooplankton than adult sardines, which are more likely to survive periods with low zooplankton biomass in El Niño conditions. It has been suggested that conditions that move the system from large diatoms and zooplankton to smaller phytoplankton and copepods for a long period of time would favor adult sardines (Alheit and Bernal, 1993; González et al., 2000a; R. Escribano personal communication). Off North-Central Perú, however, Pauly et al. (1989) find that anchoveta rely on zooplankton less than do their counterparts on the south. Near the coast, phytoplankton is a larger part of the diet the fraction of zooplankton in the mixed diet increases with distance from the coast, latitude and temperature.

The jack mackerel fishery is also affected by stronger El Niño events. Landings in Chile ranged from 2.5 to 4.4 MMT from 1990-1997, with no apparent effect from the moderate 1991-1992 El Niño. During the strong El Niño that extended from mid-1997 to mid-1998, landings off Chile alone fell from 2.9 MMT (1997) to 1.6 MMT (1998) and 1.2 MMT (1999 and 2000). Arcos et al. (2001) report that most of the fish caught during 1998 were juveniles and interpret this to mean that the normal migration paths to the northern Chile region were interrupted by warmer than normal water. They state that they find a direct relation between the latitude of the 15ºC isotherm and the proportion of juvenile jack mackerel in the catch during normal years. Since the 15ºC isotherm was at its most southward position during and following the 1997-1998 El Niño, the juveniles were presumably unable to reach their normal northern habitat. Arcos et al. (2001) speculate that it would take several years for the nursery habitat north of 30ºS to be "restored." See also Salinas et al. (1999), for a description of post-El Niño environmental conditions and their relation to pelagic fisheries in south-central Chile.

Finally, although it does not constitute a large part of the harvested biomass, the 3-7 thousand MT caught in the swordfish fishery is economically important and also appears to respond to changes in the SST distributions. Gatica et al. (2002) examine the relation between the catch of swordfish in the region south of 27ºS-38ºS and the latitude of the West Wind Drift (WWD), which is determined

from the location of the bifurcation of the 14ºC isotherm. They find a significant increase in the CPUE when the WWD is farther south. Using data from the entire time series (1982-1995 for total catch, 1989-1996 for CPUE), they conclude that: (i) the macroscale conditions become favorable for swordfish off south-central Chile (in the 200 mile EEZ) when the WWD is south of a "threshold latitude" (approximately 40ºS); and (ii) that the WWD is a thermal barrier for the southern migration of swordfish.

6. The benthic, nearshore and intertidal ecosystems
6.1 Sedimentation, nutrient regeneration and the benthic continental margin habitat
Sediment types off western South America are related to the hydrological characteristics of each climatic region, the geology of the adjacent land and the nature of the overlying marine ecosystem. As repositories for detritus from the overlying marine ecosystems, they preserve layers that include foraminifera shells and fish scales. In anoxic regions, these may be present in varved layers that allow paleo-oceanographers to reconstruct climatic changes in the overlying ecosystems, with fairly high temporal resolution. On the shelves, biogeochemical interactions in the sediments play active roles in the marine ecosystems. The nature of the physical climate affects the mode of sediment input: by the wind (eolian) in dry regions or by rivers (fluvial), if present. It also affects the grain size of the source material (physical vs. chemical weathering). Given the range of latitudes and climates along the west coast of South America, sedimentation is fairly complex and has also been sparsely sampled. Here we give only a brief overview.

From Concepción (36ºS) to the south in the fjord region, the fluvial sedimentation rates are extremely high, due to the heavy precipitation on the Andes Mountains. On the continental margin one finds rates of meters per 1000 years, rather than the normal tens of centimeters on other ocean margins (Markgraf et al., 2000). South of Concepción (away from upwelling centers) the sediments are more fine-grained (not sand), coming from the scouring of the Andes mountains. In this region, there is not a high proportion of organic matter, especially in comparison to elsewhere off Perú and Chile. The sediments here can be characterized as hemipelagic mud (Lamy et al., 1998).

Along much of Chile there are complex canyons and ridges. Flows of turbidity currents down the canyons leave coarse-grained deposits in the deep trench that runs parallel to the coast at the base of the continental slope. Thick sediments cover the deepest portions of the Perú-Chile trench south of ~27ºS. South of ~40ºS, the high sediment input is sufficient to fill the trench with >1 km of sediment, such that no topographic expression of this tectonic feature is observed. The trench is mostly sediment starved off Northern Chile, due to aridity of the source regions. Sediment again appears in the trench north of ~20ºS. The topographic highs between the canyons accumulate hemipelagic sediment with significant biogenic components falling out of the water column. This feature is useful for paleo-oceanographers, who want to sample pristine sediments that have arrived from the water above in stratigraphic sequence, rather than coming horizontally from elsewhere through turbidity flows (Schweller, et al., 1981).

North of Concepción, the climate becomes drier and stays relatively dry north of 35ºS to near the Equator. Here sediments are more likely to be eolian than fluvial, except in very localized regions around the few rivers. The abundance of clay minerals in sediments is strongly affected by variations of source-rock compositions on the continent. Around upwelling centers (along most of the Chilean coast in the nearshore regions), a large amount of organic matter is delivered to the bottom. Anoxic conditions are often found in the sediments, even if the overlying water is not anoxic. Over time, this material decomposes and leaves large deposits of sulphate, as well as

methane-hydrate deposits. The anoxic conditions in the sediments favor the growth of anaerobic bacteria and may inhibit bioturbation.

As one moves to the north, the decreasing oxygen concentrations in the poleward undercurrent eventually drop below a critical value ($\sim$0.2 ml l^{-1}) and demineralization becomes anaerobic up into the water column, as described previously. Off Perú north of 10ºS, the year-round upwelling produces an even richer rain of organic material to the sediment, again creating heavy phosphate and methane-hydrate deposits. The region between 11º-16ºS was studied by Reimers and Suess (1981). They found preferential organic matter accumulation on the outer shelf and upper slope in 100-450 m of water depth. Organic carbon and fine grained clays accumulate at 15ºS at maximum rates ($>$9 gCm^{-2} 1000 y^{-1}). Surprisingly, this is not reflected in the carbon content of the sediments ($<$ 10%) at that latitude. They estimated that long term mean PPr is highest north of Chimbote (9ºS) and Callao (12ºS) and south of Pisco (14ºS). Quartz distribution between 7-11ºS may reflect cross-shelf Ekman transport in the bottom boundary layer under the PUC, moving westward from the shallow shelf to the slope. In addition, up to 20% of the non-biogenic sediment offshore reflects the input of eolian quartz originating from the Atacama Desert. Highest concentrations of eolian quartz occurs between $\sim$20º and 5ºS, in a plume that follows the trade winds westward to about 110ºW near the equator (Molina-Cruz,
1977).

Higher rainfall near the equator, with rivers draining the Andes of Ecuador and Colombia, yields substantial increases in the sediment accumulation rates of terrigenous material off the northwestern coast of South America (Lyle, 1992). In the same area, high biogenic production associated with upwelling both along the coast and near the equator results in high percentages and accumulation rates of organic matter from 10ºS to the equator, extending westward beyond the Galápagos Archipelago. Biogenic opal content increases to the west, as the dilution with terrigenous material decreases. Similarly, biogenic calcite accumulation increases to the west, especially on topographic rises such as Carnegie Ridge, Cocos Ridge, and the Galapagos Platform, because carbonate minerals are generally better preserved at shallower water depths.

Although low oxygen level is a negative factor for most animals, it is a positive factor for some bacteria and other prokaryotes. Off both Perú and Chile, the extremely low oxygen concentrations in the benthic layer over the slope and outer shelf (sometimes extending to the shore) has led to several metabolic adaptations, which allow organisms to thrive in these regions. Thus, dense concentrations of deep-sea macrofauna ($>$300 µm) are found in the benthic system (300-1000 m depth) off Perú, under very low oxygen conditions (Fossing, 1990).

Spatial patterns across the continental shelf off Chile, in which *Beggiatoa* and *Thioploca* mats occupy the anoxic regions, provide habitat for other species, allowing different degrees of bioturbation and reworking of the primary structure of the sediment layers (Arntz et al., 1991, Gallardo et al., 1995, Schulz et al., 1996, Gutiérrez et al., 2000). These mats store nitrate that is used in the sulfide oxidation, so the bacteria may grow autotrophically or mixotrophically using acetate or other organic molecules as a carbon source and favoring denitrification.

The filaments of *Thioploca* stretch up into the overlying seawater, from which they take up nitrate, and then extend down 5-15 cm deep into sediments to oxidize sulfide formed by intensive sulfate reduction. The very high sulfate reduction rates contribute further to anoxic conditions of the

bottom water. *Thioploca* mats are responsible for converting new nitrogen into biologically available substrate in the seabed of the eastern Pacific shelf, catalyzing reactions like nitrite amonification, a metabolic pathway not considered before for *Thioploca*. This would explain the high ammonium fluxes in the sediments in which the NO_3^- consumed may be reduced to NH_4^+, rather than to N_2, which increases the oxidative capacity of the NO_3^- pool by 60% (Farías, 1998).

In the Bay of Concepción, the increase in ammonium fluxes contributes to low CO_2: NH_4^+ accumulation ratios in the shelf sediments and confirms the extremely high carbon oxidation rates, in which sulfate reduction is the dominant pathway near the surface sediments. As iron distribution decreases with depth, the importance of SO_4^{2-} reduction increases and Fe^{2+} reduction becomes the second most important pathway in carbon oxidation of continental margin sediments (Thamdrup and Canfield, 1996). Ammonium fluxes obtained from the flocculent layer and *Beggiatoa* mat cultures, represent about 39% of total ammonium out-flux during the spring-summer period bloom. Products of this process are mainly ammonia, nitrite, di-nitrogen, and elemental sulfur. (Fossing, 1990; Fossing et al., 1995; Jøergensen and Gallardo, 1999). Bacterial mats could also contribute to nitrogen losses in upwelling areas, through their burial in the sediments and biomass preservation (Farías, 1998).

Large interannual variability exists in this anoxic biogeochemical cycling due to perturbations of the depth of the thermocline and oxycline, associated with the ENSO cycle. During El Niño years, especially close to the coast, the significantly deeper oxycline subjects the shallow sediments to strong oxygenation. During `normal' (or `transition) years, and especially during La Niña years, the rise of the oxycline extends anoxic conditions over the same shallow sediments. During this time, *Thioploca* act as an efficient benthic habitat detoxifier, removing acid H_2S (Arntz et al., 1991). The organic matter accumulated during the more productive La Niña period is oxidized by the more oxygenated waters related to deeper mixed layers during El Niño. This cycle is demonstrated at Callao (**Figure 10.17a,b**) by the increase of *Thioploca* biomass during 1995-1997 (La Niña conditions), while there was a decrease of macrofauna biomass and species richness, followed by dramatic macrofauna increases and *Thioploca* decreases during and after the 1997-98 El Niño. This pattern appears to have reversed again (a delayed (La Niña effect?) around 2000. The time series for macrofauna species richness is extended back in time by a time series from Ancon Bay (**Fig. 17c**) that extends from 1982 – 1998 and shows the increases associated with the El Niño years of 1982-83, 1986-87, 1991-92 and 1997-98.

6.2 The nearshore links
Nearshore intertidal ecosystem processes are regulated by the coupling between physical forcing and biogeographic patterns, keystone species and life history. They have been more extensively studied than pelagic ecosystems along the west coast of South America. However, studies of the effects of oceanic processes on nearshore ecosystems are scarce.

On the large-scale, there are general coincidences among the biogeographic boundaries of nearshore ecosystems across taxonomic groups. Breaks, discontinuities and diversity hotspots encompass at least three provinces: Panamic, Perú-Chile and Magellanic (the southern Fjord region). Fernández et al. (2000) divides the latitude band along Chile alone into the three regions shown in **Fig. 10.18**: Perúvian or Chilean off northern and central Chile, and Magellanic in the south. These nearshore provinces apply not just to animals, but also to sea weeds and even phytoplankton Chl-a concentrations in nearshore waters. Explanatory models for latitudinal patterns have considered

availability of solar energy, habitat complexity, resource exploitation and historical factors (Wieters, 2001).

Biogeographic and floristic studies on the seaweeds of Perú and Chile indicate an effective isolation from the Western Pacific, the Central Pacific Islands and the Eastern Tropical Pacific. Contributions of tropical and subantarctic elements, combined with high endemism are the principal characteristics of this isolated flora. This combination of tropical and subantarctic influence extends to littoral fish diversity off Chile, which remains fairly constant along the coast down to 40ºS, declining south of this latitude (Camus, 2001). Ojeda et al. (2000) note that diversity in these nearshore fish increases again south of 54ºS. Diversity and distribution ranges appear to be related. As diversity increases, a progressive decline in species' mean latitudinal range size has been observed. Different factors may account for these latitudinal patterns and care must be taken when testing explanatory models. For example, the often cited relation that species richness peaks in the tropics decreases sharply towards the poles (presumably due to temperature) is contradicted by the increase in littoral fish diversity south of 54ºS. Increased communication with the Atlantic has been cited as the cause of this increase.

Nearshore ecosystems processes are found to be mainly driven by differential reproductive seasonality and larval recruitment. Recruitment, in turn, may be affected by oceanic advection, depending on whether the larvae of a species exhibit exclusively planktonic, non-planktonic or mixed development modes. The advection is driven by nearshore circulation, which varies on scales from synoptic to interdecadal. Thus advection may affect the diversity and distribution ranges of different taxa on these same time scales. For instance, during warm El Niño periods, the range of broadcasting species with warm water affinities may expand to the south. In this way, the locations of biogeographical boundaries for a broad range of functional groups may be changed. However, as with phytoplankton biomass, latitudinal gradients and local effects must be considered. For example, Navarrete et al. (2002) find little effect on intertidal organisms off central Chile during the 1997-1998 El Niño.

One method used to understand the links between the pelagic ocean and nearshore ecology has been to look at the settlement of benthic invertebrates, changes in their abundance, biomass, and community structure, comparing rocky or sandy beaches (Menge et al., 1997). Many conceptual models have been proposed, from those that use a physical oriented analysis and treat organisms as passive particles, to those emphasizing the behavior of the organisms. Poulin et al. (2002) found the epineustonic larvae of the gastropod *Concholepas concholepas* to be restricted to the region between the shore and the upwelling front. During calm periods, these larvae performed reverse vertical migration. Thus their retention is influenced by both physical and biological (behavior) factors. Stratification may also modulate onshore larval transport and settlement, by providing conditions favorable for internal waves. In the comparable California current system, it has been reported that internal waves and tidally-generated solitons are important in the onshore transport of some benthic invertebrate larvae (Pineda and López, 2002).

A comprehensive set of articles concerning the shelf, the nearshore intertidal region and bays is found in Castilla and Largier (2002). These include discussions of the dispersal, retention and settlement of larvae and planktonic organisms in relation to wind driven flows. In general there are numerous possible biological-physical couplings. Wind driven transport and Langmuir circulation may advect larvae of some species from areas 1-3 nm offshore to the rocky intertidal (Marín and Moreno, 2002). In some specific cases recruitment requires rough seas to free rocky substrate (i.e.

Choromitylus chorus at 40ºS). Other species (i.e. *Concholepas concholepas*) require the presence of competent larvae near the coast in autumn and winter, when downwelling may transport them onshore. Others (gastropods Fisurella and Tegula) recruit mostly during summer, when thermal fronts collapse toward the shore during upwelling relaxations. Given the variety of specific mechanisms, the consensus is that there is a need to develop realistic 3-D circulation models to investigate the various processes. To resolve the fronts and small scale features of importance, these models must have fine horizontal resolution (10's to 100's of meters). This requires use of either telescoping grid structures (finite volume models) or multiple nestings, since the larger-scale coastal circulation must form the offshore boundary conditions, including CTW's, forced by even larger-scale models.

Recruitment of meroplankton is also affected by strong interactions of the coastal currents with headlands and bays, such as found around Mejillones Peninsula. In 2000, many sites along the Chilean coast were studied, including the Bay of Antofagasta. It was found that recruitment rates for chtamaloid barnacles were higher inside of bays than in open coastal areas. Sites located towards the south were favored by cyclonic circulation and by the closeness of the frontal zone to the shore. The contribution of thermal gradients and fronts to an increase in recruitment rates for intertidal invertebrates was also studied by estimating advection patterns from SST images, with some agreement between these advection estimates and *in situ* measurements (Lagos et al., 2002). Spatial patterns of recruitment were in approximate agreement with models that predicted the distribution of the benthic (barnacle) populations. Using spatial statistics, a degree of integration of oceanographic processes and ecological patterns was achieved.

To add to the mix of local and distant factors affecting macroinfaunal community structure, substrate must also be included. Thus, although the El Niño has an effect on recruitment of the keystone carnivore, *Concholepas concholepas*, along the northern part of Chile and Perú, it has little effect on the central-south Chilean coast. The most important interannual factor there appears to be the presence of upwelling (Moreno et al., 1998). However, in the case of sandy beaches, neither upwelling nor El Niño appear to induce differences in the macroinfaunal community structure (Jaramillo, 2001a), nor does it change linearly with changes in beach morphodynamics along a 3000 km latitudinal gradient (Jaramillo, 2001b). For sandy beaches, these authors suggested that the highest abundances and biomass relate to the seasonal dynamics of bottom up effects, competitive interactions and beach/sand dynamics. Thus, to formulate a general model that would explain changes in distributions and abundances within a macroinfauna community, the range of processes that must be included in the model is daunting.

7. Anthropogenic influences

The previous sections describe natural environmental variability and some of the primary physical and biological coastal processes. Here we briefly look at some of the effects caused by human actions on these same ecosystems. In all but the most extreme cases, however, it is usually difficult to identify anthropogenic influences with certainty, due to the complexity of the processes that couple pelagic, benthic and intertidal communities to environmental variability. Identification of anthropogenic effects in marine benthic communities is comparatively more advanced than studies of pelagic communities in the PCCS (Castilla, 1997; Castilla and Largier, 2002; Arcos et al., 1993; Jumars, 2000). In general, the primary stress factors considered are industrial and domestic wastes (both toxins and nutrients) and human harvest. The motivating factor is economics, directing most research to issues related to fisheries and aquaculture.

To manage these resources, we need an understanding of natural variability and how human activities (harvesting and various types of pollution, disruption of habitat, etc.) affect species resilience within the pelagic communities. In the "simpler" pelagic systems, a "bottom up" approach to ecosystem management might take, as a first goal, the ability to predict rates of primary production and phytoplankton abundance, then zooplankton and higher trophic level production. As described in several sections above, however, the determination of nutrient concentrations depends on complex microbial processes, chemistry and physics with multiple time and space scales in much of the region. For these reasons, even prediction of PPr and phytoplankton biomass from basic principles remains a challenge, despite over a decade of using "NPZ" models within increasingly complex physical models (Fasham, et al., 1990; Robinson et al., 1993; Hofmann and Lascara, 1998). Moving from there to the prediction of secondary production and fish biomass in pelagic ecosystems is an even more distant goal, although one that is being addressed in ongoing research (Batchelder et al., 2002).

Unfortunately, use of alternative, linear statistical models for pelagic ecosystems is also limited, because the response of populations to anomalous ocean conditions does not result from simple linear processes (the cessation of upwelling, the monotonic depression of the nutricline and decrease in nutrients), as shown above. In addition, catch-ability also increases during the onset of warm conditions in some coastal regions, leading to interactions between human harvest efforts and ocean conditions (Csirke, 1988; Carr and Broad, 2000). This leaves the optimal management strategies for pelagic resources as an important, unsolved problem.

In intertidal ecosystems, recruitment and settlement are important issues, as are predation and competition within the ecosystem. Recruitment and settlement are dependent on water circulation processes, interacting with behavior and life history strategies of the species in question. After settlement, several keystone species play major roles in community dynamics, structure, productivity and diversity, through predation and competition. Along much of the Chilean coastline, heavy pressure from human harvesting strongly affects the distribution of intertidal resources. As a result, we rarely have a reliable picture of what those distributions would be without human effects. An exception is an examination of the effects of eliminating humans as predators in small intertidal regions (Castilla and Duran, 1985; Godoy and Moreno, 1989). The result of excluding humans is the return of the dominant keystone predator (*Concholepas concholepas*). These experiments resulted in the restoration of an entirely different community, presumably more like the pristine community.

Fisheries management of the near-shore (intertidal and diving depths) species usually uses a traditional single-species approach (as in pelagic systems). Territorial use rights become the issue for management and exploitation of these resources. As an alternative, Castilla and Fernández (1999) propose a multispecies, community-ecosystem management approach. This approach is based on the establishment of a mix of "take" (harvested) versus "non-take" areas (marine reserves), in a spatially structured coastal network defined by the known dispersal characteristics of the larvae. This could enhance the rational use and management of coastal species, merging conservation and fishery management objectives.

Many patterns in the intertidal can also be related to patterns of human harvesting. The actual effect depends on what they humans harvest, i.e., whether the humans act as herbivores or carnivores. Moreno (2001) describes community patterns and harvesting in rocky shores and proposes three main patterns, which may be used as a way of evaluation of the state of conservation of the Chilean

rocky intertidal shores. When the humans act as herbivores, adult plants of *Durvillea antarctica* disappear from the mid-littoral exposed and semi-exposed habitats. When humans harvest the carnivorous gastropods "Fisurella," a red algae (*Mazaella laminaroides*) covers 100% of the mid-littoral rocks. Finally when humans act as top predators by collecting the carnivorous gastropod *Concholepas concholepas*, bivalves (mainly *Perúmitylus purpuratus*) cover the rocks in multiple layers.

In the Chilean Inland Sea (South of 42º), human activities have increased at unprecedented rates for economic reasons related to salmon farming, industrial fishing and tourism. Aquaculture activities have produced 200,000 metric tons of salmon (Soto and Jara, 1999). Biodiversity losses are one of the typical ecological consequences of aquaculture, caused by eutrophication. These authors demonstrate the possibility of enhancing nutrient utilization through native food webs, thus reducing eutrophication. This is accomplished by enhancing bottom heterogeneity (using filter feeders), and by providing habitat for free-living fish populations around pens. Another possible effect of eutrophication and high loading of nutrients and organic matter is oxygen depletion. Initial analyses of oxygen concentrations in the water column and sediments in the salmon farming regions (the northern fjord areas) have not identified significant oxygen depletion due to salmon-culture activities. Monitoring of these sites is just beginning, however, and needs to continue as the industry expands.

There are also indirect effects of salmon aquaculture. One example is the introduction of exotic species of salmonids into the wild at 41º-46º S (Chiloé and Aysen Inner seas) after a major storm in 1995. All salmonids are exotic in the Southern Hemisphere; these specific species are rainbow trout, Coho and Atlantic salmon. Methods to address this problem have been evaluated by Soto et al. (2001). They propose that artisanal fishing would be the most efficient way to remove these individuals and control escaped salmon. These authors also conclude that Coho salmon are the most probable competitor of the southern hake and mackerel, due to a higher chance to complete natural maturation cycle for the Coho.

The southern fjord region is a very heterogeneous system, raising the possibility of unknown (as yet) problems caused by the growing salmon aquaculture in a largely unexplored region (Antezana, 1999). Carbon and nitrogen concentrations and distributions serve as one measure of the heterogeneity, as characterized by Silva and Prego (2002) in nine regions of the Inland Sea. Three out of nine areas had comparatively high organic carbon (>1·6%) and organic nitrogen (>0·2%) abundance, associated with geographically protected inlets and productive planktonic zones. There were four areas of comparatively low organic carbon (<0·8%) and nitrogen (<0·2%). These were largely due to the influence of glacial inputs and were associated with low planktonic production. Finally, two areas were associated with carbonate-rich sediments. Studies such as this need to be conducted in more regions and the potential effects of aquaculture evaluated.

A very real environmental problem exists in the form of the periodic occurrence of Harmful Algal Blooms (HAB's, also called Red Tides) in the Inland Seas of Southern Chile. This phenomenon, reported for the first time in 1972 in the Magellanic region (Muñoz and Avaria, 1997), has increased its frequency, geographic coverage and intensity. After occurrences in 1972, 1981 and 1989, HAB outbursts have been reported in the Magallanic-Aysén region on a yearly basis (Guzmán et al., 2002). Ongoing biophysical research has revealed a suite of toxins produced by different microalgal populations (Guzmán et al., 2002). These are concentrated by filter feeding organisms that are harvested intensely for human consumption and distributed both locally and in

distant markets. These episodes and their lethal consequences to nearby and distant human consumers have caused permanent closed seasons, with a resulting economic loss of shellfish fisheries in the region.

In response to this problem, there is an active program for monitoring HAB's from 41º30' to 56ºS. Hypotheses for the cause of these events include natural origins, increases in nutrient loading of terrestrial sources due to clear cutting and erosion, aquatic sources such as aquaculture, etc. Continuous input of seed populations by sources such as ballast water has been suggested. At present there are not enough data to discriminate between these hypotheses.

Red tides also occur off northern Chile. Spring blooms of *Mesodinium* spp. in the Bay of Mejillones have reached concentrations of more than 300 mg Chl-a m^{-3} (Marín et al., 1993), while in summer (January, 1997) Pizarro et al. (2002) found a similar bloom at 5 nm offshore of the Mejillones peninsula in the upper 2m, reaching 108 mg Chl-a m^{-3}. Of the 133 red tide events reported by Muñoz and Avaria (1997) between 1827 and 1996, 49% of them occurred off northern Chile between 18º- 23ºS. Blooms of *Mesodinium* spp. have also been reported in Perúvian waters (Tarazona and Arntz, 2001). Thus, this is a widespread and growing problem in the PCCS and Inland Sea, as in many coastal regions of the world.

8. Conclusions

- Coastal upwelling, high primary productivity, equatorward surface flow and the poleward undercurrent interact to shape the distributions of nutrients and biological populations over the system between the Equator and the Inland Sea (42ºS).

- The system is strongly affected by interactions with the Equatorial Current System, on scales ranging from intraseasonal (CTW's) to interannual (ENSO). The primary mechanisms for communicating larger-scale fluctuations to local-scale conditions involve the depth of the pycnocline and the advection of different water mass types into the local region.

- In the poleward undercurrent, anoxic conditions in the oxygen minimum layer determine the nature of denitrification off Perú and northern Chile.

- Nutrients are concentrated in the PUC and it serves as the major source of upwelled water in many locations. Chemical signatures of the PUC extend from the equator past 40ºS.

- CO_2 outgassing occurs during upwelling and increases with wind speed. It may decrease or reverse after a period of strong photosynthesis in phytoplankton-rich filaments and patches.

- Much of the chlorophyll biomass is found within 10-50km of the coast, although some effects of upwelling can be detected as far offshore as 150-400km. The maximum in surface chlorophyll in the region within 100 km of the coast occurs in austral summer off both Perú and Chile, although the maximum upwelling winds occur in winter off Perú and summer off central Chile.

- A multi-scale approach is needed to understand phytoplankton and zooplankton patterns. A key factor is the depth of the pycnocline-nutricline-oxycline.

- Off Perú and south-central Chile, the vertical migration of zooplankton is inhibited by the depth of the oxygen minimum layer, removing one common mechanism for retention of zooplankton found in other eastern boundary currents. Mesoscale circulation features may provide other means for retention near favorable habitat for zooplankton

- The abundance and catch of small pelagic fish is greater than in other eastern boundary currents. Even in the absence of fishing harvests, these appear to undergo multi-decadal and interannual fluctuations, with instances of alternating species (anchoveta and sardine). Fishery harvests may amplify these fluctuations. The reasons for the natural high abundance and the fluctuations are not fully understood.

- South of 42ºS in the Inland Sea region, precipitation increases stratification. This region is used for an expanding salmon aquaculture industry, although studies of the natural ecosystems of the region have only recently begun. Continued research and monitoring is needed to quantify the effects of this industry on the natural ecosystems in the Inland Sea.

- Harmful algal blooms are a growing problem in the regions off southern and central Chile and are also present off northern Chile and Perú.

- Although components of the basic carbon budget have been estimated for specific locations and times, the details of regional carbon budgets, along with their spatial and temporal variability, remain to be determined. These may help to explain the abundances and fluctuations of the fish populations.

- Fisheries activities interact with the marine ecosystem at the whole coastal ecosystem level, affecting benthic and pelagic organisms through processes that are not well understood. The economic consequences of mismanagement are severe, however, providing the motivation for continued research.

9. Appendix: Examples of biogeochemical and trophic links in specific regions

Equatorial Latitudes

The largest (and probably unique) low latitude EBC estuarine ecosystem of the Pacific coast off western South America is the Gulf of Guayaquil, with input from a 51,230 km^2 watershed (outer estuary) and an inner river estuary comprised of the Guayas River. This system is located in the transition zone (3ºS) of tropical and subtropical water masses forming the equatorial front (Cucalón, 1983, 1986). The large seasonal and interannual variations that are present in this system are tightly coupled to oceanographic processes (Twilley et al., 2001). During the summer, the ESSW moves from the south into the Gulf, increasing productivity. During El Niño conditions, abnormally warm and less saline waters move into the Gulf from the Colombia coast. Accordingly, Cardenas (1995) reported large temporal differences in the distribution of suspended particulate matter, which supports populations of filter feeders.

Primary production appears to be controlled by denitrification processes, while organic matter input from the mangroves is related to the tides and the mangrove crab populations. The crab population plays an important role in the mangrove leave litter dynamics, decreasing five folds their average residence time. Moreover, links with the coastal ocean are tightly related to the migration life cycle of shrimp. These mangrove areas have been negatively affected by shrimp aquaculture, urbanization

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and land use in upland and intertidal water-sheds (Twilley et al., 2001).

Central and Southern Perú (10º — 14 ºS)
Along the central Perúvian coast, cold and nutrient-rich waters from year-round upwelling are responsible for extremely high productivity. Nixon and Thomas (2001) estimated the size of the nutrient enhanced productive habitat associated with the upwelling to be between $120\text{-}220 \times 10^3$ km^2 , even considering the ENSO cycle. Nutrient-rich waters are transported towards the north by the coastal Perúvian current, enriching regions without local upwelling, for example in bays such as Bahía Independencia. In this zone, tides are frequently semidiurnal, with mean amplitudes of 0.6 m. The euphotic zone and mixing depth are typically less than 20 m, restricting zooplankton distributions to the upper 30 m (Tarazona and Arntz, 2001). This area has low biological diversity in the pelagic ecosystem, which is dominated by just a few species. The high productivity creates a rich benthic region, with a high degree of endemism. Due to periodic El Niño events, some tropical species extend their distribution to the south and find a refuge there for a period of several years (Tarazona et al., 1985; Tarazona and Valle, 1998).

In nearshore rocky substrates many important commercial species can be found, such as conspiquos bivalves (*Aulacomya ater* with a biomass reaching 40 000 g $\times$ m^{-2}*, Gari solida, Semele solida, Argopecten purpuratus*), gastropods i.e. *Thais chocolata*; crustacea such as *Cancer setosus*, *C. porteri*, *Platyxanthus orbignyi*; the sea-urchin *Loxechinus albus*; and the large macroalgae *Lessonia* spp. and *Macrocystis pyrifera*. These species provide kelp forests that are good refuges and nursery grounds for larval fish, as is true along much of the South American coast (Fernández et al., 2000).

Deepened oxyclines during El Niño conditions reduce the effects of hypoxia, leading to changes in many populations **(Fig. 10.17).** For example, since early 1998 there have been higher densities of macrofauna along the Perú margin (Levin et al., 2002) and these have been accompanied by growth of the hake population (in response to the higher densities of food supply). This creates a negative relation between hypoxic conditions and predation on macrofauna. In the Bay of Ancon, a time series of macrobenthos density from 1981-1997 revealed an overall tenfold density change in 1982-1983 **(Fig. 10.17c)**, although it was also found that each of the different species had a specific behavior (Tarazona and Arntz, 2001).

Some nearshore species do better in the warm and rich environment off Perú than elsewhere (Urban, 1994). Research on bivalve populations of *Gari solida* by Urban and Tarazona (1996) found that this taxa had a biannual reproductive cycle at 14º S and only one reproductive cycle at 36ºS. This demonstrates an opportunistic reproductive strategy, taking advantage of favorable conditions such as higher temperature and perhaps higher concentrations of food particles.

The Mejillones Peninsula and Associated Bays
The most conspicuous coastal feature in northern Chile is the Mejillones Peninsula (23°S), with a large bay to the north (the Bay of Mejillones) and another to the south (the Bay of Antofagasta). These have been the subject of many studies (Ortlieb et al., 1994; Rodriguez et al., 1996; Marín and Olivares 1999; Escribano et al., 2000, 2001). The Bay of Mejillones is a semi-enclosed bay with low currents and low export capacity (Navea and Miranda, 1980). During the summer of 1965, Ramorino and Muñiz (1970) obtained the first quantitative measurements of the benthic fauna in relation to the type of substrate down to the 200 m isobath. Between 3-20 m the highest biomass was found in muddy-sandy bottoms. At 80 m because of persistent low oxygen concentrations,

macro-invertebrate abundance decreases significantly and as a result of the low bio-perturbation, varved sediment layers with high resolution (decadal to centennial) have been found. Low oxygen conditions have been present in this bay for at least the last 2000 years, under changing (warm/cold) oceanographic conditions. These are documented by changes in the planktonic foraminifers (Ortlieb et al., 2000).

 Due to the coastal morphology associated with capes, the bays are influenced by the frequent upwelling along the western coast of the Mejillones Peninsula. This is especially true for the northern bay (Mejillones). The upwelled, nutrient-rich waters along the long, north-south coast of the peninsula are carried northward in a persistent upwelling plume into the bay (Marín et al., 2001), inducing a cyclonic circulation pattern (northward flow along the western shore and poleward flow along the eastern shore). The strength of the cyclonic gyre is positively correlated with the equatorward wind stress, with time scales of 3-7 days (Escribano et al., 2002). Retention of planktonic organisms within this gyre is enhanced by reversals of the winds (from south-west to north winds), creating extremely high Chl-a (and surface oxygen) concentrations. The highest phytoplankton biomass have been found during the relaxation of upwelling, with a maximum reported surface Chl-a value (373.5 mg m^{-3}) in October 1990 (Marín and Olivares, 1999). At the bay entrance at depths of over 90m, integrated mean values of 182 ± 97 mg Chl-a m^{-2} have been reported (Ulloa et al., 2001). Similar values (175.4 mg Chl-a m^{-2}) have been found offshore of the Mejillones Peninsula in summer (January 1997) by Pizarro et al. (2002).

The bay and surrounding shelf show little systematic seasonal variability in phytoplankton biomass, as described in Section 3. This has been attributed to higher zooplankton grazing rates on the typical small phytoplankton during the austral summer compared to the winter (González et al., 1998; Pizarro et al., 2002). A similar dominance of small phytoplankton and weak seasonality is found farther north (Morales et al. 1996a, 2001). Although phytoplankton biomass does not show a clear seasonality, seasonal patterns in species composition have been reported in the Bay of Antofagasta. Rodríguez et al. (1996) identified four different groups of species, including some that were always present (the diatom *Leptocylindrus* is a prominent member of this group). Others were present only in certain periods. For example, *Planktoniella* and *Eucampia* were only prominent during the winter.

Similarly, (but on longer time scales) the lack of change during El Niño 1997-1998 in zooplankton biomass in the Bay of Mejillones next to the coast does not mean there are no effects on zooplankton. Vertical distributions of zooplankton are affected by the deepening of the OML (Morales et al., 1999). The upper limit of the oxygen minimum layer ($\cong 44.7$ µmol m^{-3}) was measured during pre-El Niño summer at 45m and 89 m in the coastal and offshore zones, respectively. These deepen during El Niño winter to 84m and 126 m respectively (Eissler and Quiñones, 1999), expanding the vertical habitat for the zooplankton.

Around the peninsula, the more saline and colder ESSW in the anoxic PUC sometimes reaches the surface during strong upwelling events, where it contributes to high CO_2 degassing (**Fig. 10.11**). During these events, the phytoplankton efficiency is kept low and Chl-a concentrations remain below 0.4 mg m^{-3}. With less intense but more constant winds, phytoplankton are advected from the adjacent bays, leading to rapid consumption of both nutrients and CO_2 in the upwelling center. This decreases the lag in CO_2 consumption along the peninsula during upwelling and reduces CO_2

outgassing (Torres et al., 2002). Thus, the main process that drives the short term variability of CO_2 fluxes is the intermittent changes in the wind forcing (Torres et al., 1999, 2001, 2002).

The effects of wind forcing do change seasonally due to increased summer stratification. Numerical model studies indicate that similar winds during extreme seasons produce a more intense circulation in summer, partially due to stronger stratification, which allows the creation of thermal fronts and associated jets. This changes residence times, the spatial distribution of planktonic organisms, their dispersion, aggregation and rates of carbon export to the open ocean (Escribano et al., 2002). An example of the effect of wind and thermal structure on larval retention is found in the Bay of Antofagasta. A persistent warm-water patch develops inside the bay in summer, with a cyclonic circulation and a thermal front that restricts exchanges across the mouth of the bay. This helps to retain the larvae of the large and spatially restricted sea squirt, *Piura preaputialis* (a tunicate) in the periphery of the cyclonic gyre. These larvae must stay in the nearshore region during their very short pelagic phase (2 hours). Wave-driven flow within the surf zone creates a convergent zone that further retains the larvae in the very near-shore region. Details of this ubiquitous species and its localized distribution can be found in Castilla and Camaño (2001).

Valparaíso Bay
Although Valparaíso Bay is one of the most important ports for commercial shipping and fishing, there are few integrated studies of its circulation and ecology. Two studies found seasonal changes in water mass properties, which may have biological consequences. Avaria et al. (1989) and Sievers and Vega (2000) report that SAW fills the bay when winds are mild and is replaced by ESSW during upwelling periods. The higher nutrient concentrations in the ESSW presumably leads to higher productivity and changes in species composition. A separate biological study of meroplankton looked at more than 300 wide-spread species of decapod crustacea, including plankton composition, community structure and abundance of specific groups such as Porcellanidae (Ulloa and Palma, 1998). This analysis identified an increase in species richness within Valparaíso Bay, compared to other coastal locations. The authors suggest that this is due to the influence of open ocean biota and to changes in water mass properties due to large-scale advective processes, such as found during El Niño conditions. It seems likely that the seasonal changes in water mass properties and their associated biota play a strong role in maintaining this increased species richness.

The Gulf of Arauco, Bay of Concepción and Other Bays off Central Chile
Farther south near Concepción (~36ºS), there are a number of bays, often oriented with their mouth facing north, similar to the Bay of Mejillones. The largest of these is the Gulf of Arauco. The Bay of Concepción has also been well studied, due to its proximity to the Universidad de Concepción, which houses several departments and institutes with a focus on oceanographic studies and marine ecosystems. In addition, the fishing industry has its private research institute, the Instituto de Investigación Pesquera, in nearby Talcahuano. It may also be easier to study a smaller semi-enclosed bay than a much larger system, such as the Gulf of Arauco. At this latitude, the year is divided into an upwelling season (spring-summer) and a downwelling season in fall-winter. There are only small mean temperature differences (12.8-13.5 ºC) between these seasons, due to the presence of ESSW during the spring, that replaces SAW found during the winter (Cubillos et al., 1998; Ahumada, 2002).

The fall-winter rainy seasonal is also called the "estuarine" season, due to the increase in fresh water inflow from land, which creates opposing offshore and onshore flow in the surface and lower water column, respectively. Residence times within the bays are increased during the downwelling season. For example, in the Bay of Concepción, residence times are typically 22 days during the estuarine season. During the upwelling season, residence times are typically 2-3 days, as colder, denser, oxygen poor and nutrient rich ESSW enriches the bay and leads to high PPr. The seasonal (or longer La Niña period) hypoxic or anoxic conditions favor the release of NH_4^+ from the sulphidic sediments, providing a regenerated nitrogen source and further maintaining high PPr (Graco et al., 2001). With the short residence times, large amounts of organic matter is advected from the bay to deep shelf sites, which experience permanent hypoxia because of the influence of the OML and this contribution of organic material (Gutiérrez et al., 2000).

Higher levels of export from the bays may be partially due to low grazing pressures of zooplankton on phytoplankton within the bays, as measured in the Bay of Concepción during spring 1998 and winter 1999, while measurements in oceanic waters outside the bay showed significantly larger consumption of primary production (Grünewald et al., 2002). These consumption rates are consistent with, though slightly higher than, previous observations in the region during the upwelling season (Peterson et al., 1988) and other upwelling systems (Boyd and Smith, 1983, González et al., 2000a). Particulate organic carbon flux estimates off Concepción are also in the range of those reported (above) off north-central Chile (41-123 mg C m^{-2} d^{-1} and 20-400 mg C m^{-2} d^{-1} at 23ºS and 30º S respectively), but are much lower values than the 9000 mg C m^{-2} d^{-1} found by Reimers and Suess (1981) off Perú.

Other studies of bays in this region have investigated a variety of forcing mechanisms. Sobarzo (2002) considered winds, tides and external circulation and found tides to be the dominant mechanism in Bahía San Vicente, just south of Concepción. Faundez et al. (2001) found low spatial variability in several bays near the large Bio-Bio River, while Sobarzo et al. (2001) looked at the influence of the Bio-Bio submarine canyon. At this latitude, Figueroa and Moffat (2000) found that the topographic effects are not dominant in upwelling processes when compared to the wind stress. The environmental influences on pelagic fish spawning has also been studied in relation to coastal upwelling and the presence of river plumes (such as the Bio-Bio), which produce rapid transport of larvae from the coast. Young anchovies are found nearshore, either within or outside of the river plume. Presumably, this forms part of the reproductive strategy of this species (Castro et al., 2000, 2002).

The largest bay is the Gulf of Arauco (36.3º-37ºS), with scales of 40-60km, fairly gentle bottom topography, opening to the north with depths of 100-200m at the mouth. There is an island along the west side, with a small, shallow opening between the island and the southwest corner of the Bay. The southern and eastern coasts are fairly regular. The Bio-Bio River discharges at the northeast corner of the bay and the relatively deep (500m) Bio-Bio River Canyon cuts across the northern edge of the bay, running from east to west.

Parada et al. (2001) previously found a one-layer anticlockwise circulation, forced by intense upwelling events, becoming more complex during relaxations. Mesias et al. (2001, 2003) modeled the larger-scale coastal region covering 600km centered on the Gulf of Arauco. While the resolution is not fine enough to define the circulation within the Gulf, it demonstrates the intense jet that forms along the coast south of the Gulf (along Punta Lavapié), extending offshore of the north-facing Gulf

as a separated jet. In this way it is similar to the flow next to the Mejillones Peninsula and the Bay of Mejillones. Valle-Levinson et al. (2003) followed-up an earlier study by Djurfeldt (1989) with a several days of high resolution transects across the main mouth and a one-day set of transects across the smaller opening. This is probably the highest-resolution study to date, during the upwelling season (December, 2000), although limited in duration. From their measurements, they hypothesize a double gyre circulation, with southward inflow across the middle of the mouth, where depths are greatest, and outflow through the shallower edges of the mouth. The inflowing water was characteristic of upwelled water (low in oxygen and high in nutrients). They also saw large internal vertical displacements (10m range) near the northeast corner of the bay, repeated diurnally, and hypothesized that this disturbance would propagate clockwise around the bay and dissipate around the smaller opening. They suggest that inflow of the rich, upwelled water, combined with mixing by the internal wave dynamics, contribute to the high productivity in the bay (some of the highest values of PPr reported by Daneri et al. [2000] were in Gulf). Given a number of northward-facing bays along the coast of Chile, the further studies of this type would be worthwhile, especially including nutrient and biological rate measurements (some were taken during this study but were not reported in this paper). Use of studies of these bays may also be advantageous for model validation, since there is a greater chance of balancing budgets in semi-enclosed systems than on open shelves.

Acknowledgments

Table 1

Integrated primary production measured through ^{14}C (unless other indicated) at different sites listed with increasing latitude. Only mean surface gross primary production in shown for the oceanic region

Reference	Year/publication	Site and dates	mean	min	max
			mg C m^{-2} d^{-1}		
Twilley	2001	Bay of Guayaquil	300	200	1000
Guillen & Calienes	1981	Chimbote, Perú	1100		
Chavez & Barber	1987-1985	Perú	2290-4820		
Chavez et al.	1989	Perú	3200[a]		
Mendo et al.	1989	Perú	3700-5200[a]		
Chavez	1995	Perú	3500		
Daneri et al.	2000	Antofagasta, Chile 1997		120-800[b]	5100-9300[b]
Pizarro et al.	2001	Antofagasta, Chile 1997		539	5811
Montecino et al.	1996	Coquimbo, Chile		140	2950
Daneri et al.	2000	Coquimbo, Chile 1997		660[b]	2800[b]
Daneri et al.	2000	Concepción, Chile 1989-91		320[b]	5900[b]
Montecino et al.	unpublished	Concepción, Chile	630w-1920sp	200	7480
Pizarro et al.	2000	Chilean fjords		98	1380
Daneri et al.	2000	Nazca ridge & oceanic region	mg C m^{-3} h^{-1}		
		1995		0.7	1.8

a=new production
b=Gross PPr (Oxygen)
w= winter
sp=spring

Table 2

Phytoplankton patterns (response of mean daily primary production (PPr, in mg C m^{-2} d^{-1}) and Zeu-integrated Chl-a (B, in mg m^{-2}) over a full local forcing cycle in Cruz Grande Bay (30ºS). Interannual, seasonal and intra-seasonal conditions are respectively indicated. PPr and B values are space (2 to 5 stations) and time (1 to 3 days) averaged. (simplified from Rutllant and Montecino 2002)

Date	ENSO cycle	Seasonal cycle	Intraseasonal cycle (sea level)	UPWELLING Active PPr	Relaxed PPr	Active B	Relaxed B	PHYTOPLANKTON PATTERN PP	B
Nov. 1987	Warm	Spring (+)	Rising	620	439	28	107	PP ⇒ ↓ PP	B ⇒ ↑↑ B
Nov. 1988	Cold	Spring (+)	Stationary	222	622	36	56	PP ⇒ ↑↑ PP	B ⇒ ↑ B

(+) = Strong (ENSO)/seasonally late
↓ ↑ = small changes up or down; ↑↑ = large changes up
⇒ = transition from the active to the relaxed phase of the upwelling.

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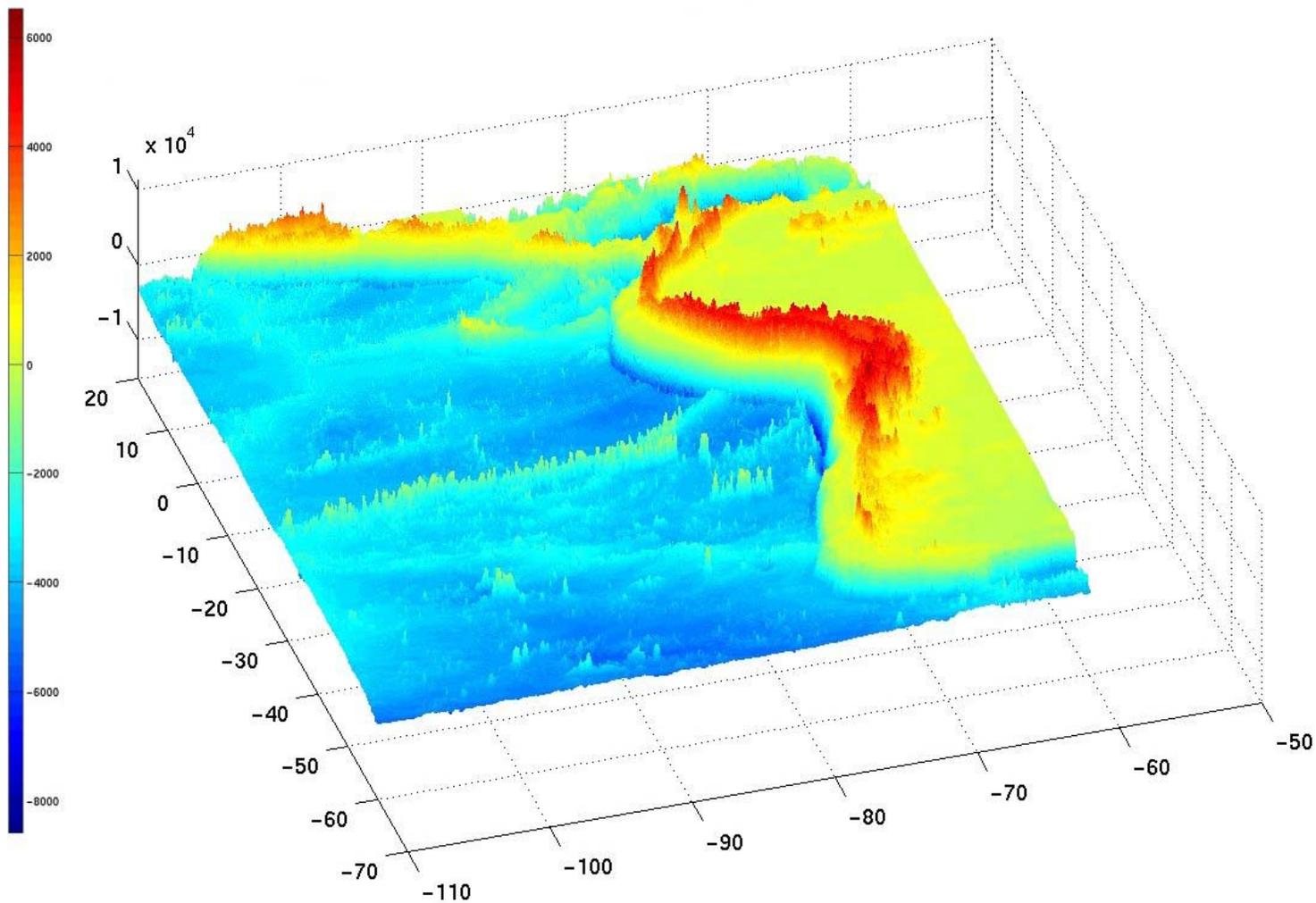
Figure 10.1 Topography. 3-D view of the land and ocean topography of western South America. Mountains higher than 2000m appear in red (the Andes). In the ocean, the prominent features are the Nazca ridge (light green), intersecting the coast off southern Perú, and the deep trench next to the shelf along Perú and Chile (deep blue). (Figure courtesy of Oscar Pizarro and Gabriel Yuras [Universidad de Concepción]).

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Figure 10.2a Climatological seasonal cycle of the atmospheric pressure fields at sea level in the SE Pacific (National Centers for Environmental Prediction). Austral summer is DJF, etc.

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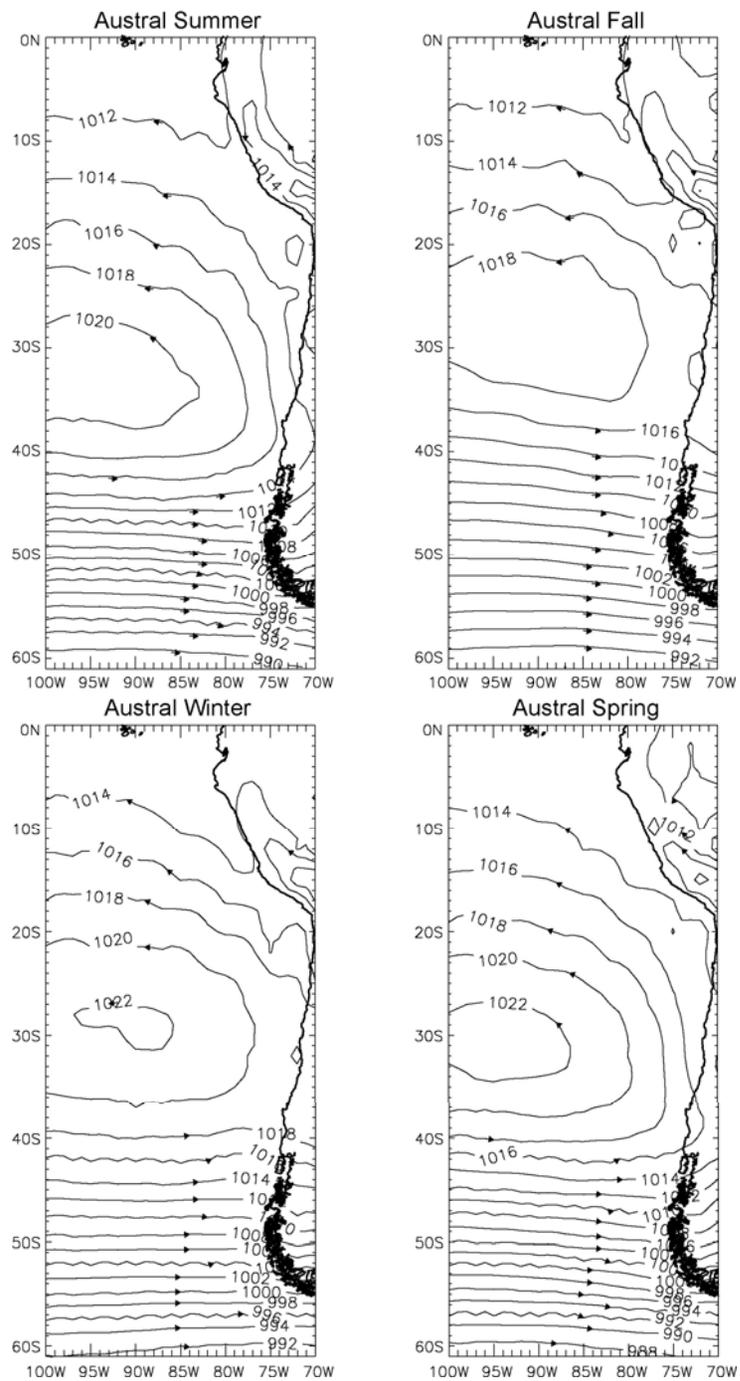
Figure 10.2b Cartoon of the synoptic meteorological factors that create and modulate upwelling favorable winds (Figure adapted from Rutllant 1997).
CT: Thermal contrast between the warm land and cold ocean.
AI: The maximum in upwelling caused by the subtropical anticyclone in austral winter.
AA: Year-round upwelling due to the subtropical anticyclone.
AV: The maximum in upwelling caused by the subtropical anticyclone in austral summer.
BC: The region where coastal lows propagate toward the pole.
B: The movement of extratropical cyclones to and along the coast. The northernmost B is a coastal low near its location of formation, propagating poleward and modulating the underlying equatorward winds (arrows).
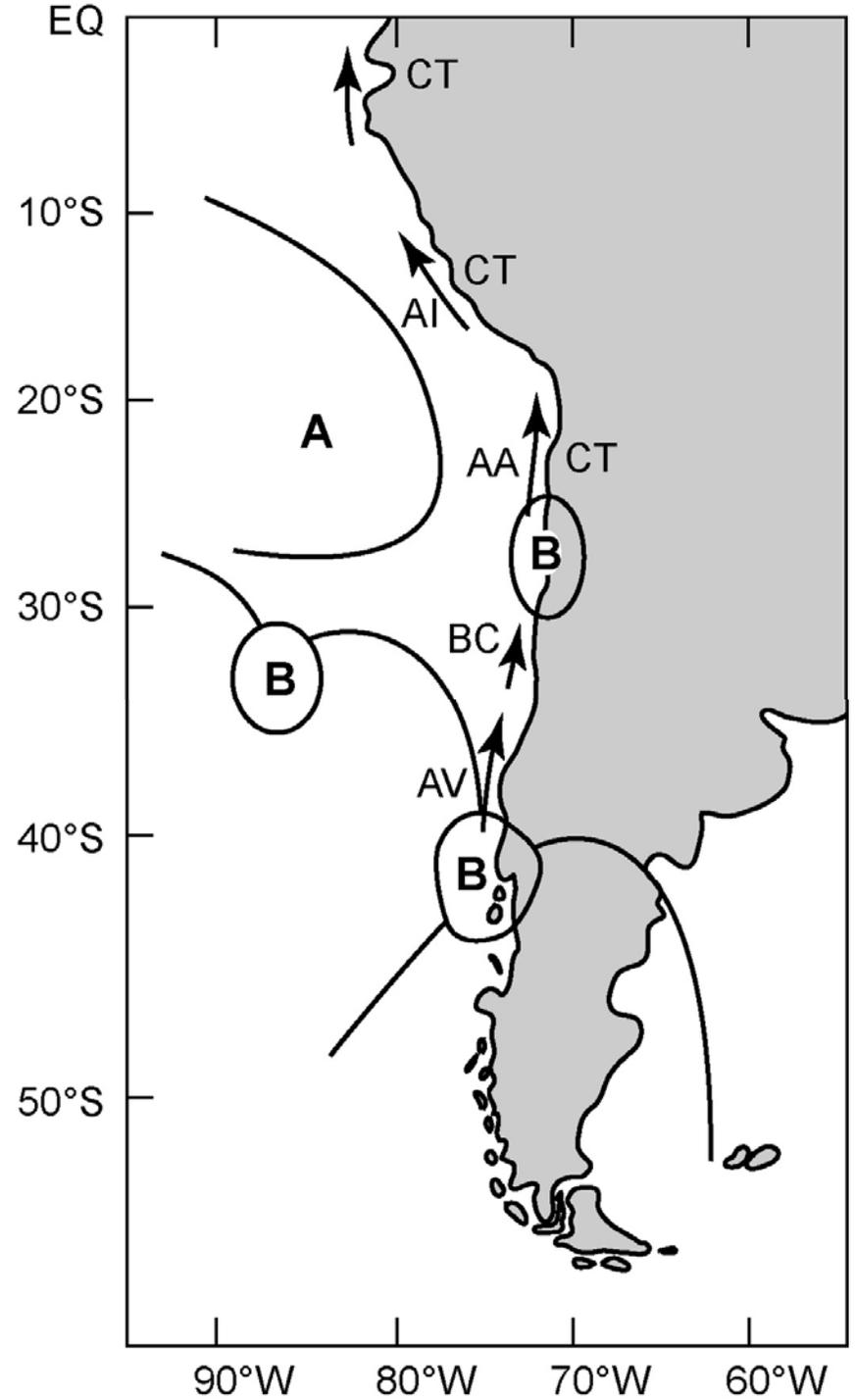
Figure 10.3 Coastal Upwelling Indices along the coast of Perú and Chile (Schwing et al., 1996) from September 1997 through March 2004. Monthly mean sea level pressure fields are calculated from 6-hourly pressure fields from the atmospheric forecast model run at the U.S. Navy Fleet Numerical Meteorological and Oceanographic Center (FNMOC), Monterey, CA. Monthly derived winds are calculated from the pressure fields and used to generate monthly values of offshore surface Ekman transport. Positive values indicate equatorward winds and upwelling.
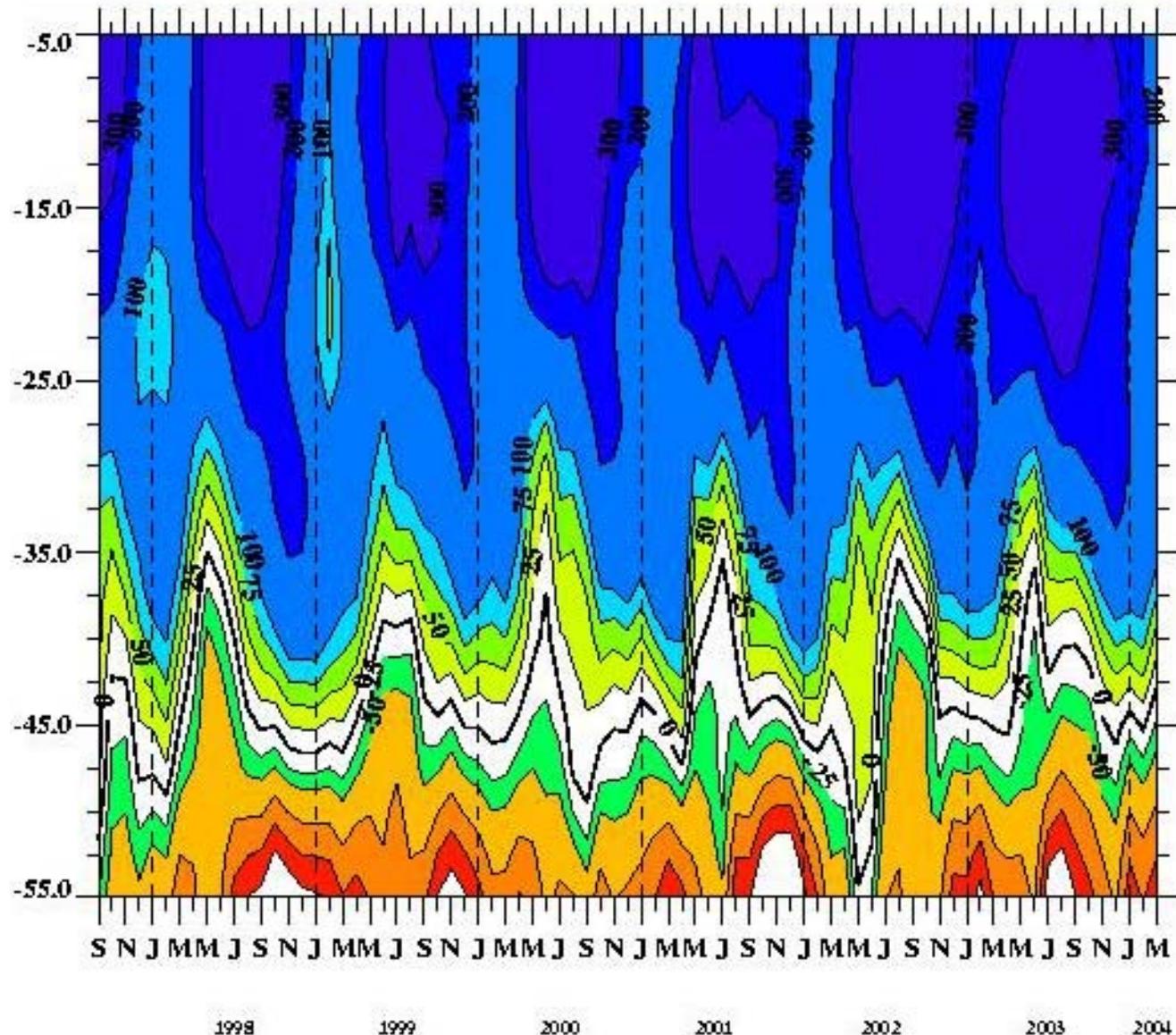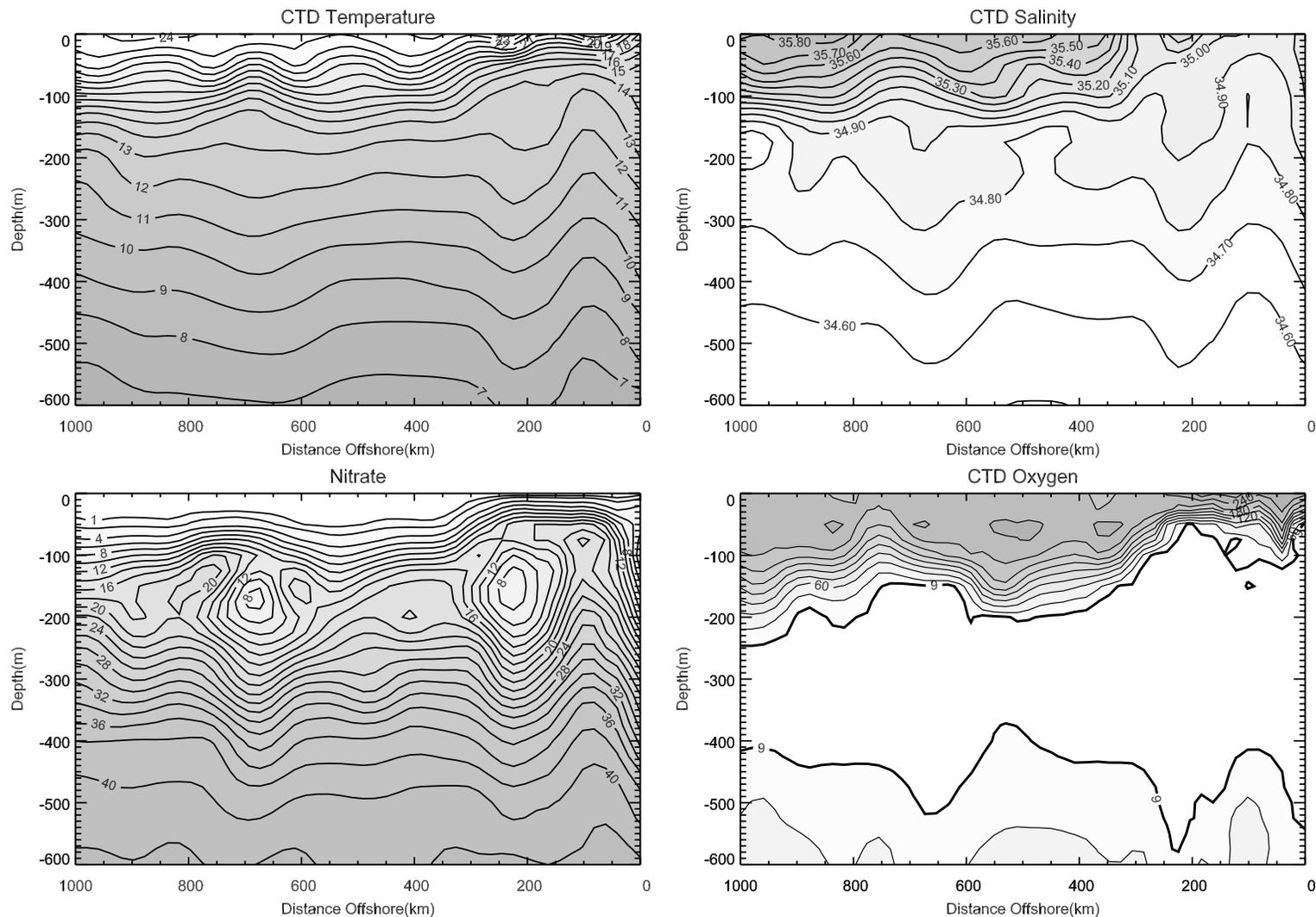
Figure 10.4. Offshore sections of temperature, salinity, nitrate and dissolved oxygen off Perú at 14.5ºS (WOCE section P21). Units for T, S, nitrate and oxygen are ºC, psu, µM, and µM Kg-1. The contour intervals of 30 for oxygen correspond to approximately 0.7 ml l-1. Values less than 9 µM Kg-1 (0.2 ml l-1) occupy the water column between 50-500m depth next to the coast. Station spacing is approximately 6-10 km along the 100 km next to the coast, increasing to approximately 60 km for the rest of the transect.
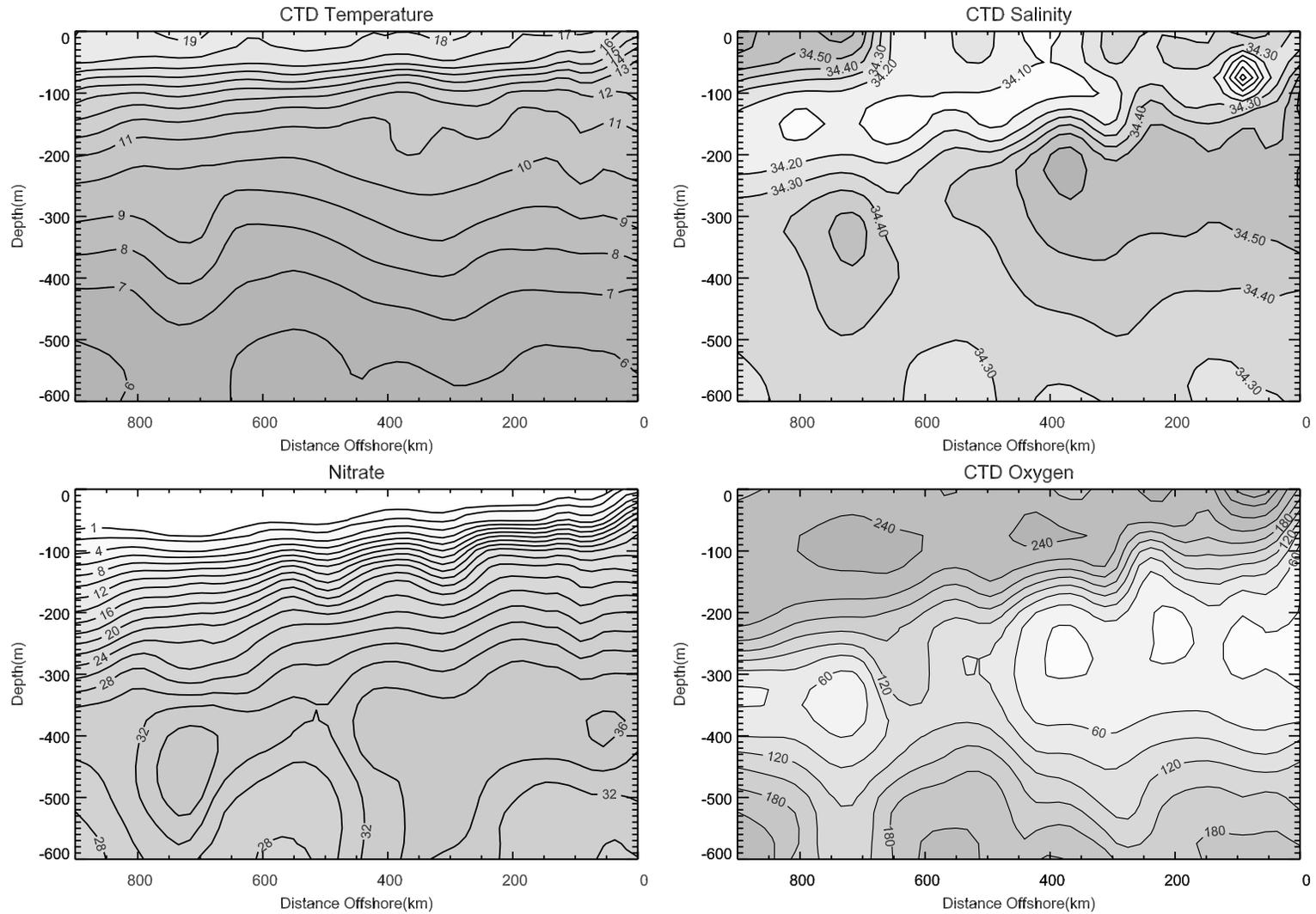
Figure 10.5. Offshore sections of temperature, salinity, nitrate and oxygen off Chile at 32.5ºS (WOCE section P06). Units and station spacing are as in Figure 10.4.

Vertical Extent of the Oxygen Minimum Layer
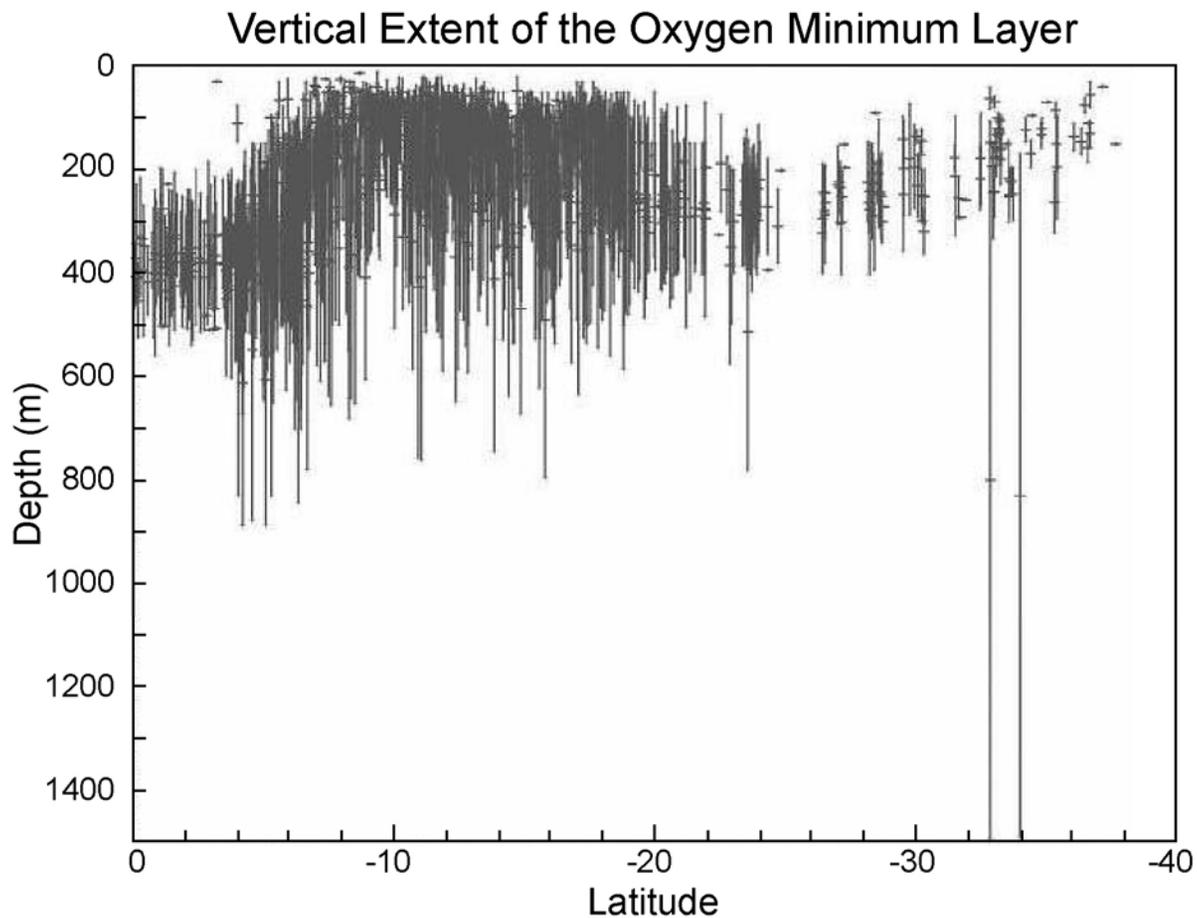
Figure 10.6.   Depth range of the oxygen minimum layer (OML, concentrations less than 0.5 ml/L dissolved oxygen) for the eastern Pacific from the Equator to 40°S. Each vertical bar connects the upper and lower OML depth value for a given hydrocast. The upper boundary of the OML was estimated by the first quartile of depth (25% of the shallowest observations were shallower) and the lower boundary was estimated by the fourth quartile (25% of the deepest observations were deeper) (Figure courtesy of John Helly [University of California at San Diego] and Lisa Levin [Scripps Institution of Oceanography]).
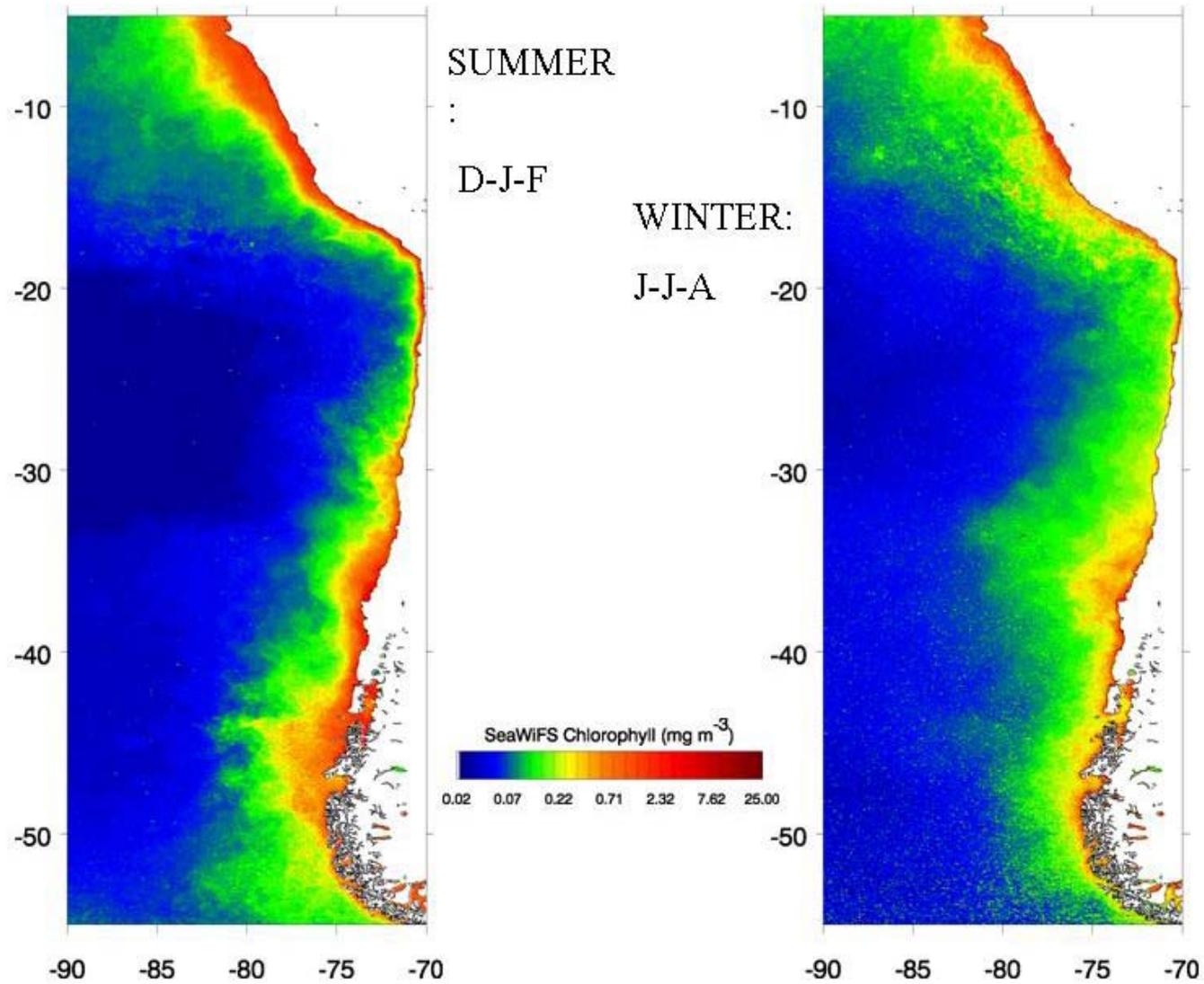
Figure 10.7.   Surface Chlorophyll-a pigment concentrations estimated from the first five years of SeaWiFS ocean color measurements –

Left: Summer (December-February); Right: Winter (June-August).
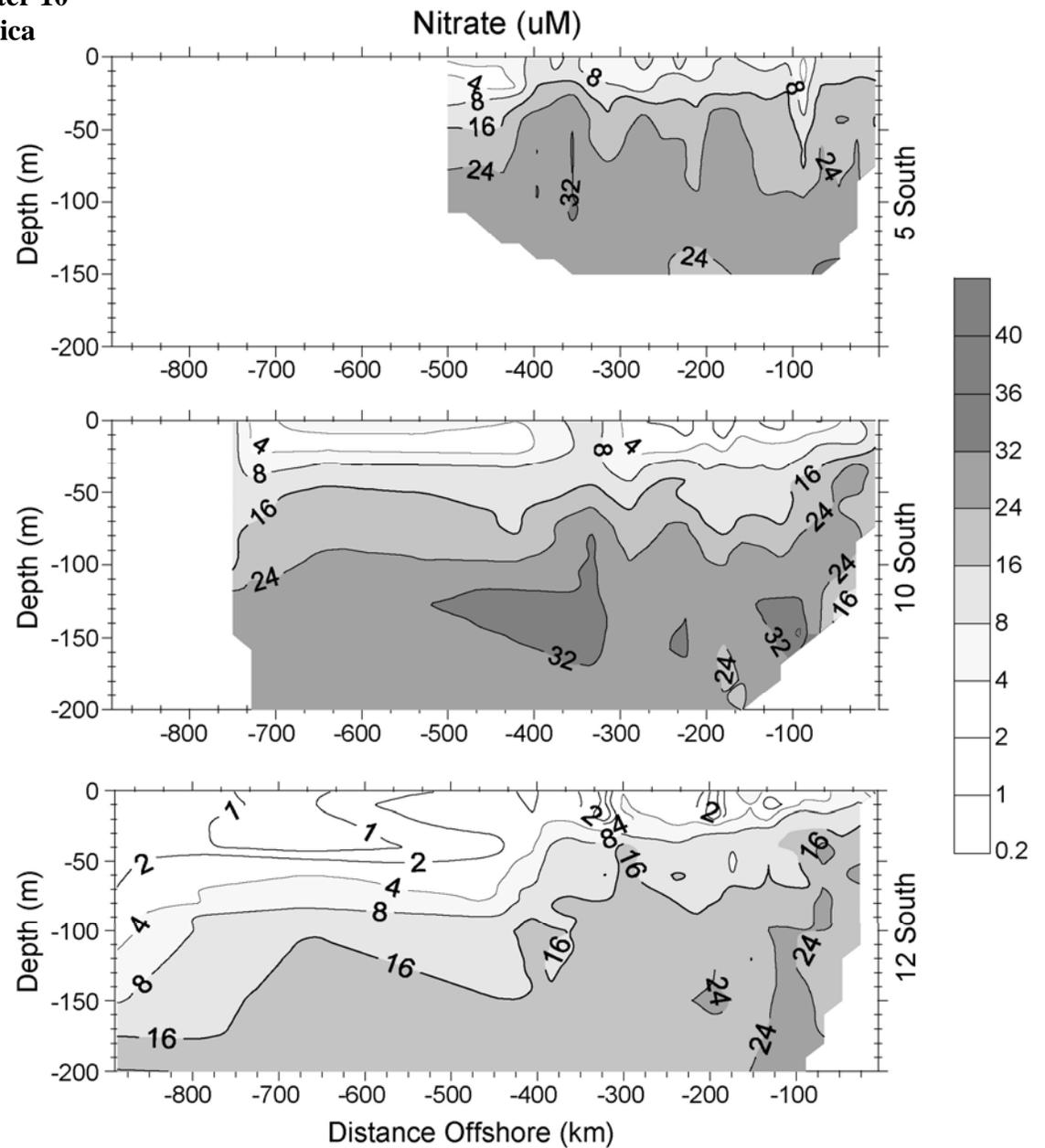
Figure 10.8. Nitrate sections off Perú at 5°, 10°, 12° S, showing the mean fields from many sections. Station separation is of order 20km and standard depths sampled are 0, 10, 20, 40, 60, 80, 100, 150 and 200m.

Figure 10.9a. Chl-a pigment sections off Perú and Chile at 5º, 10º, 12º and 33ºS. The data off Perú are means from the same cruises used to make Figure 8. The data off Chile are from a single cruise in October 1999 (spring), with wider spatial separation than off Perú and discrete bottle measurements at 8 depths (0, 5, 10, 20, 50, 75 and 150 m), hence the smoothness. (Data off Chile are courtesy of Gemita Pizarro [IFOP]). Units are mg m-3.
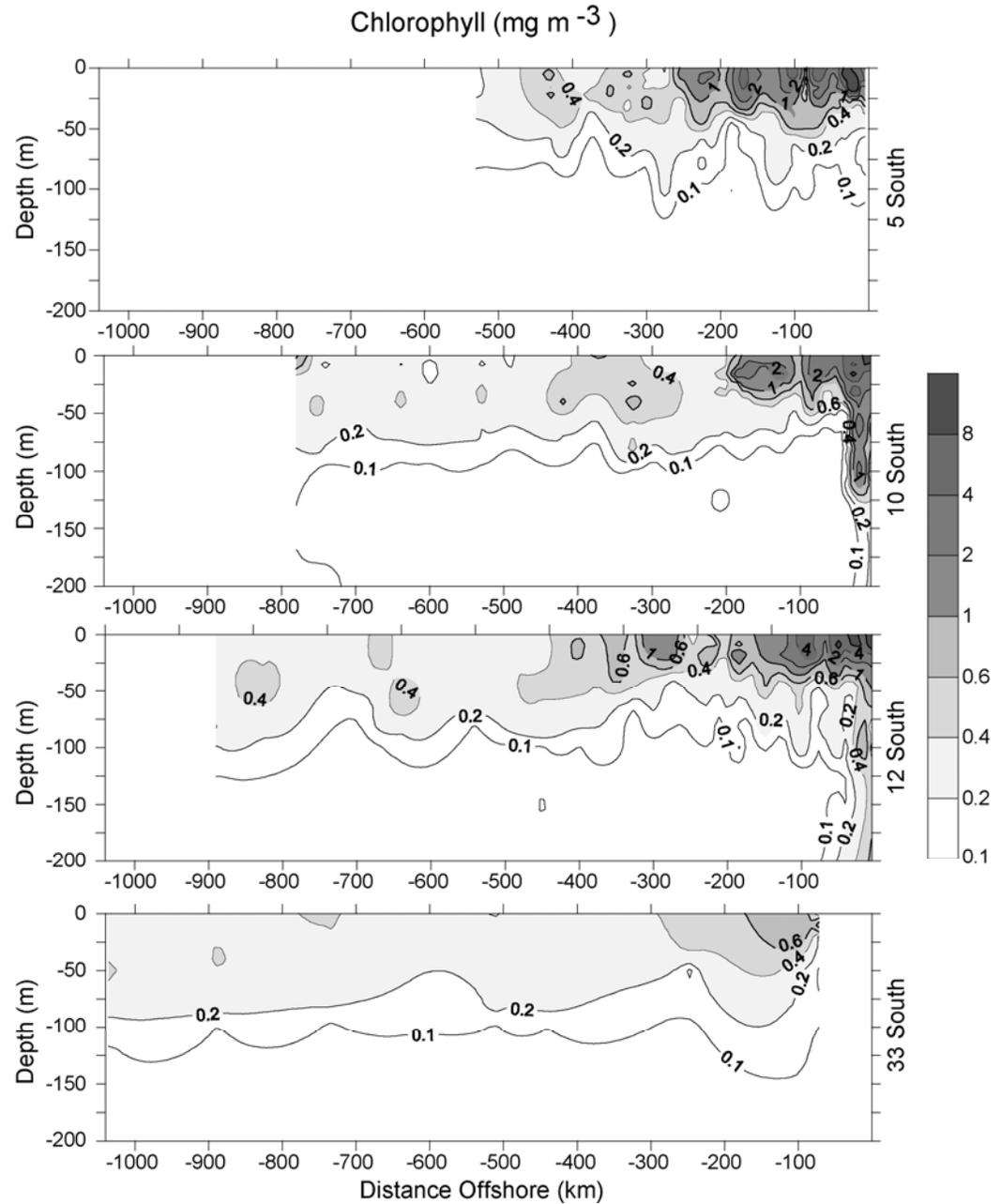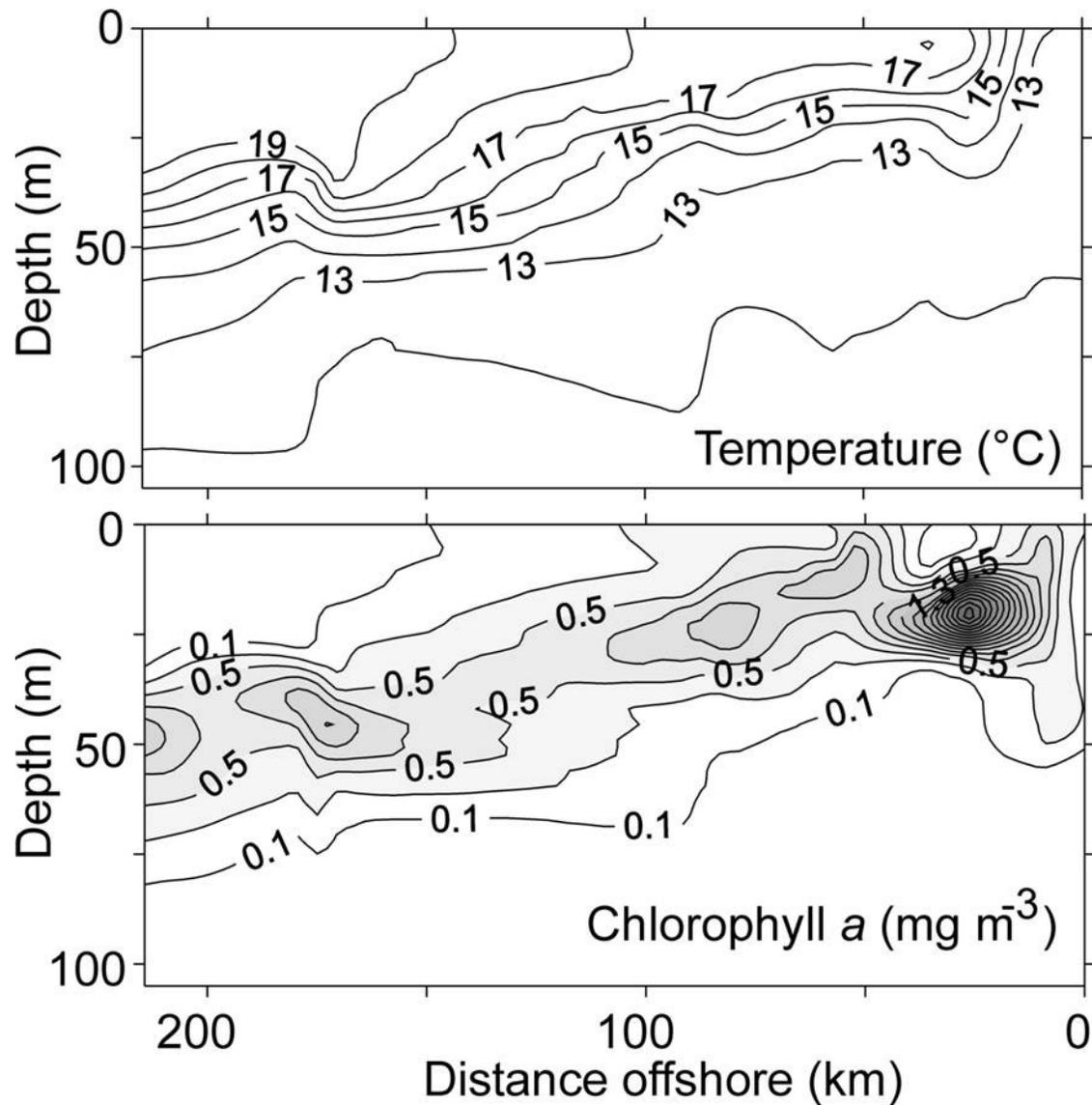
Figure 10.9b. Temperature and Chl-a pigment section at 30ºS during February 1997 (JGOFS – Chile) from continuous in situ fluorescence (Figure adapted from Torres et al. [2002]). Units are degrees C and mg m-3.

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MONTH Composite 100km Cross Shelf Mean
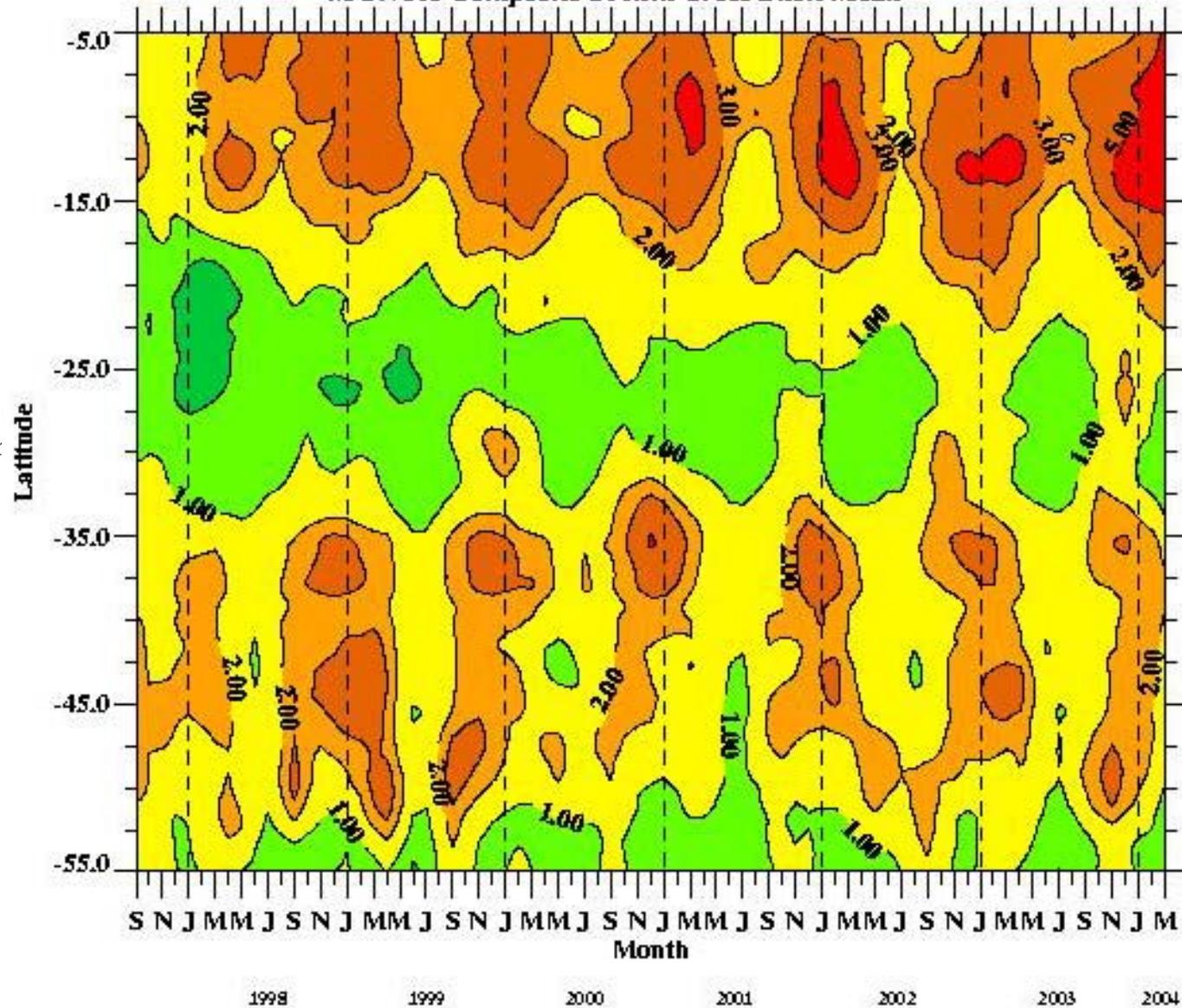
Figure 10.10. Time-latitude plot of satellite-derived Chl-a pigment concentration from SeaWiFS; monthly averages over the 100 km next to the coast along Perú and Chile, September 1997 – March 2004. Units are mg m-3; the domain is the same as in Fig. 10.7.
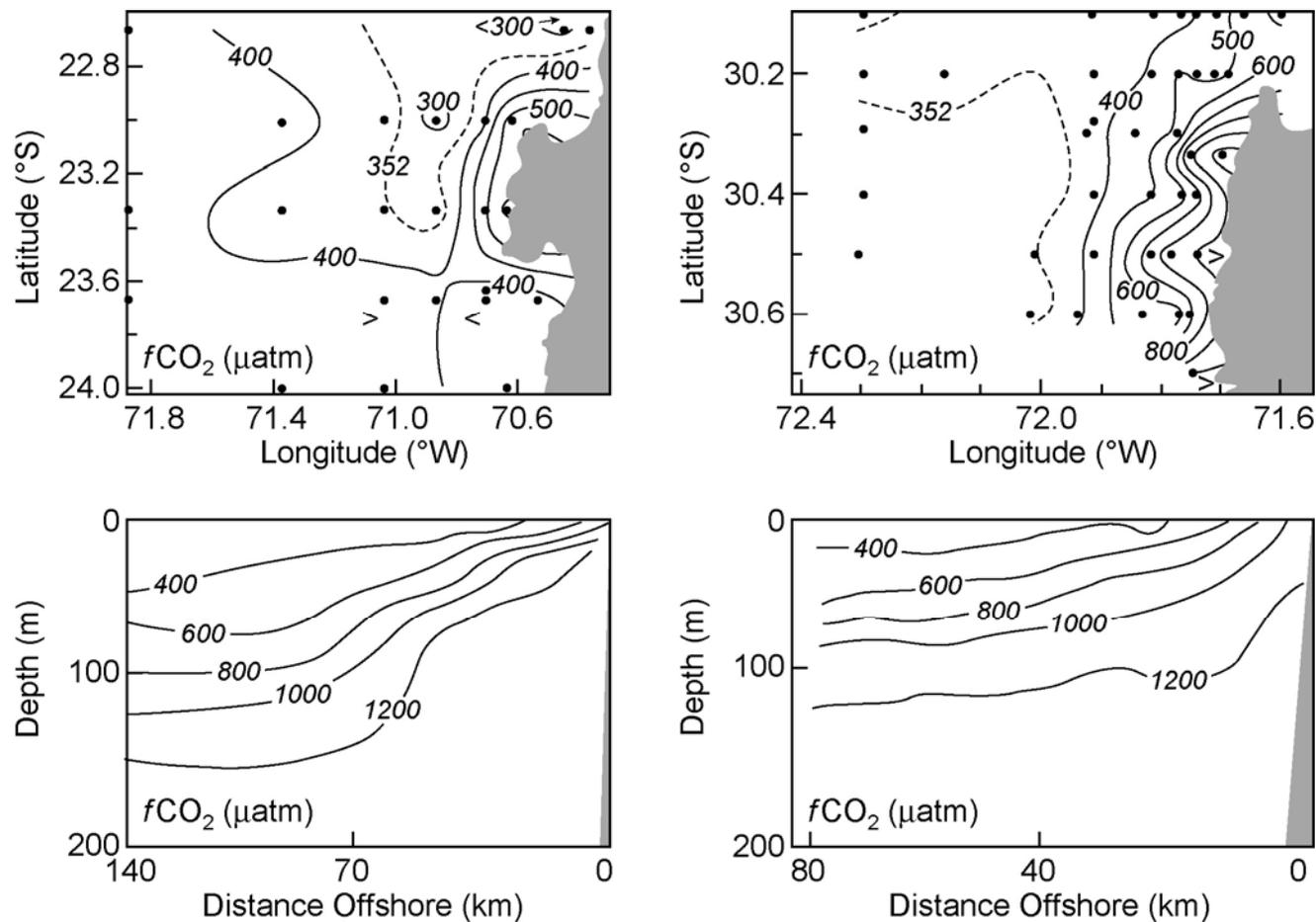
Figure 10.11.   Surface distribution of carbon dioxide fugacity (fCO2) off Antofagasta (left, 23º4'S) and off Coquimbo (right, 30ºS) during austral summer (January and February 1997 respectively). Across-shore section from the same grids and transect are shown in the lower panels. (Figure adapted from Torres et al. [2002]).
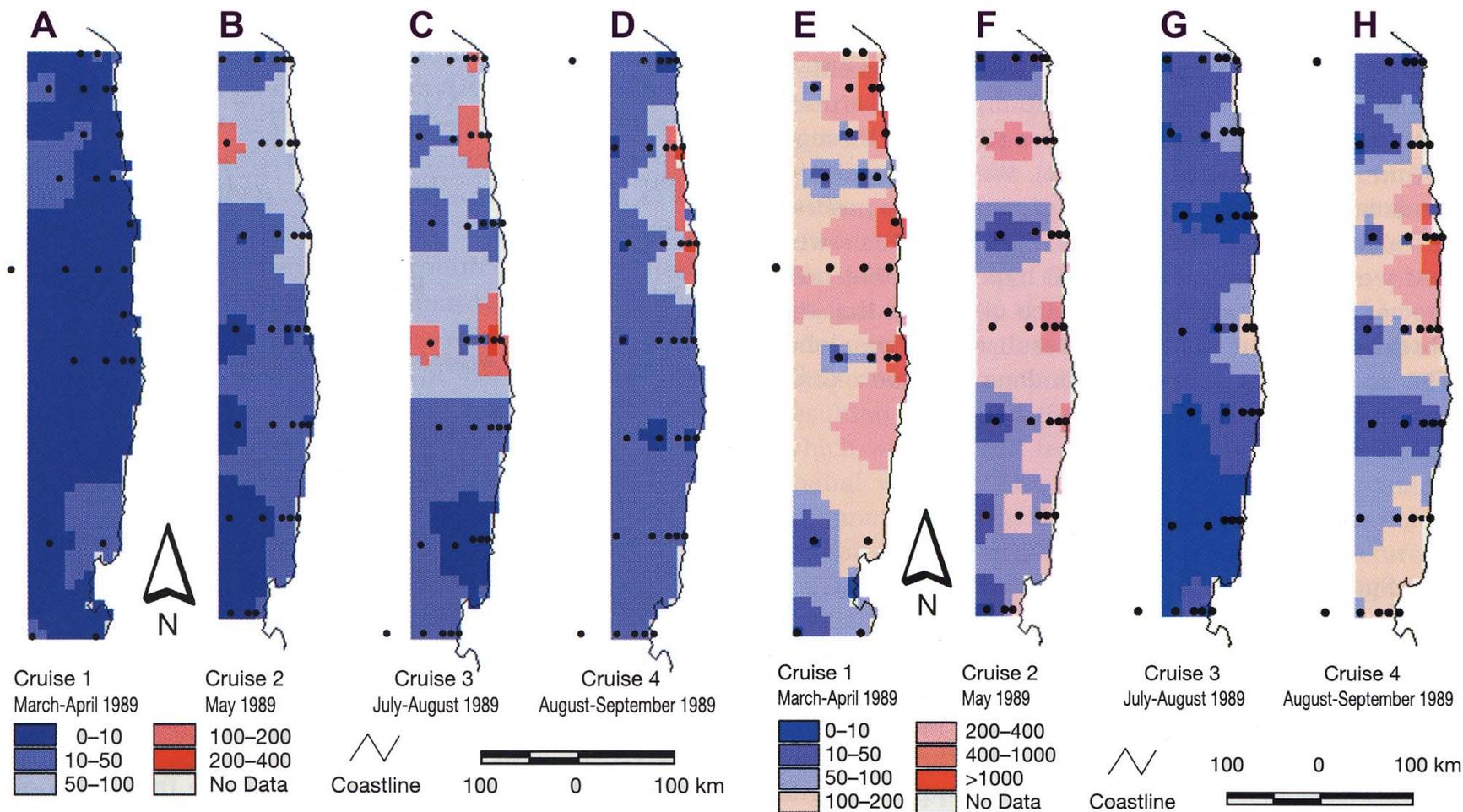
Figure 10.12.   Spatial distribution of the abundance of copepods off Chile during 4 cruises in 1989.

(a-d) Calanus chilensis; (e-h) Centropages brachiatus. Units are (copepods m-3). Grids were averaged using a spatial weighted moving average (IDW) technique. (Figure adaped from González and Marín [1998]).
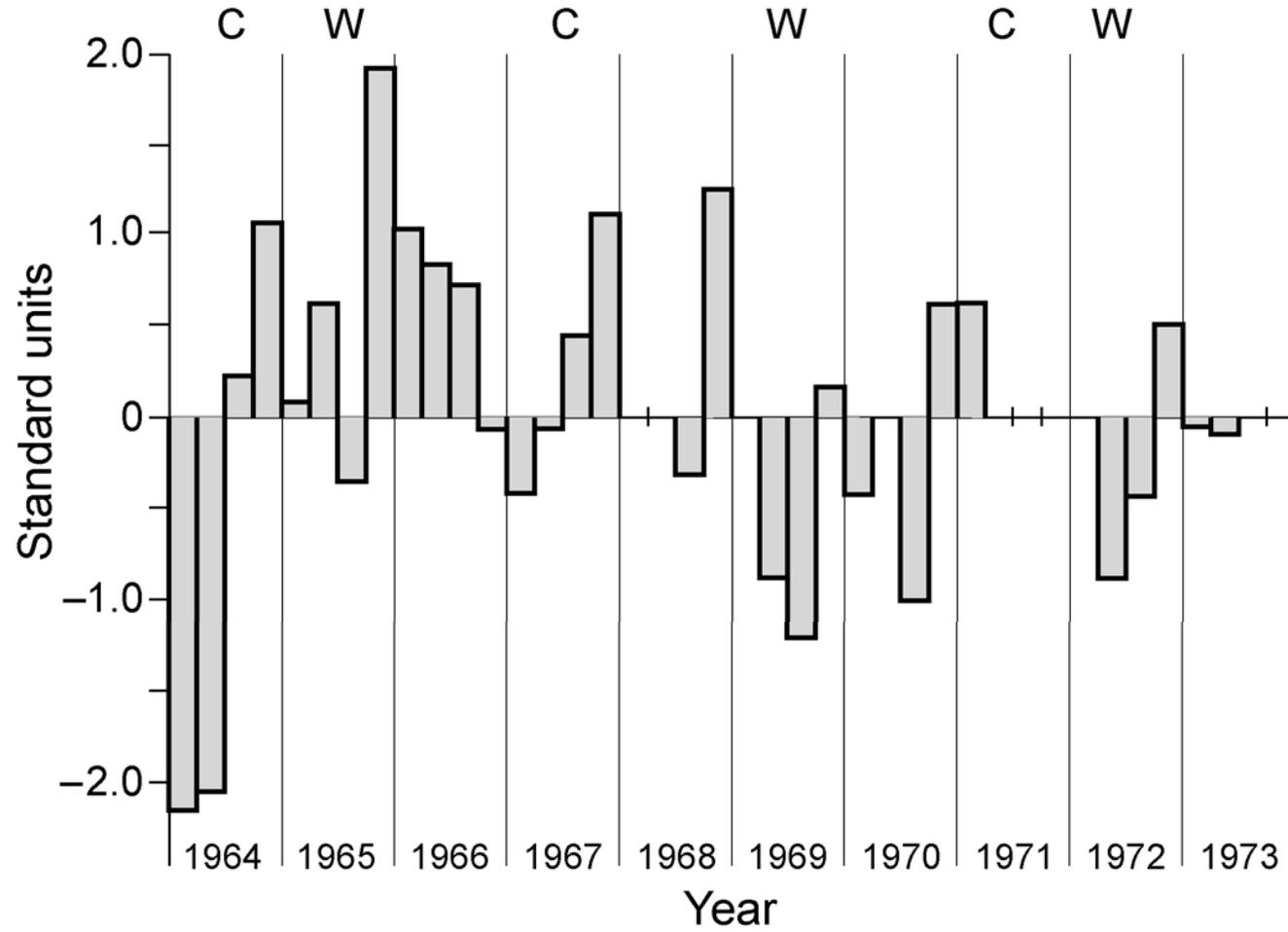
Figure 10.13.   Long-term changes in zooplankton biomass off northern Chile, 1964-1973 (Figure adapted from Bernal et al., [1982]).
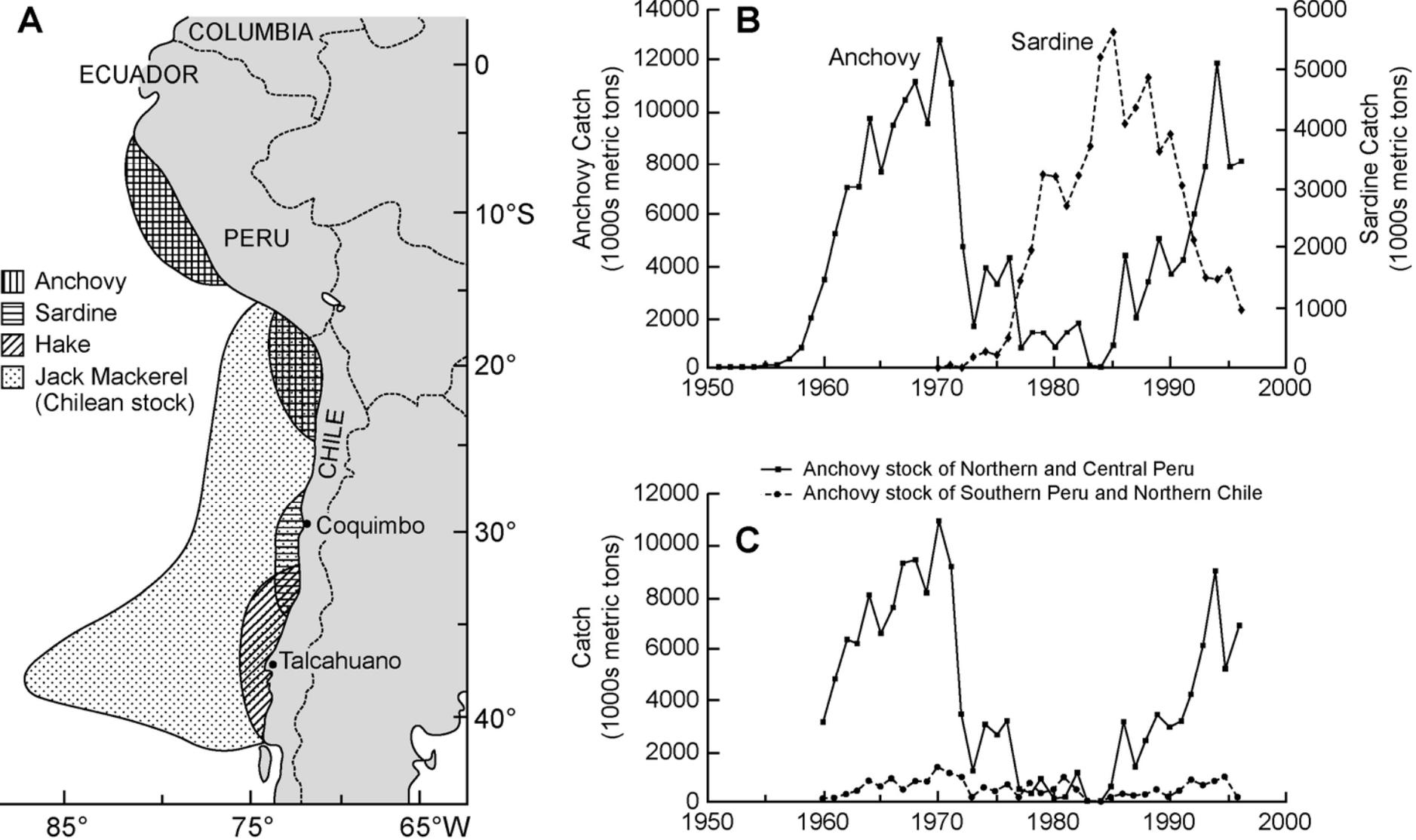
Figure 10.14. a) Generalized locations of the anchovy, sardine, hake and jack mackerel fisheries off Perú and Chile. b) Catch series of the anchovy and sardine off Perú and Chile from 1950 through 1996. c) Comparison of catch series of the anchovy stocks from northern and central Perú and from southern Perú and northern Chile, 1960-1996. (Figure adapted from Schwartzlose et al. [1999]).
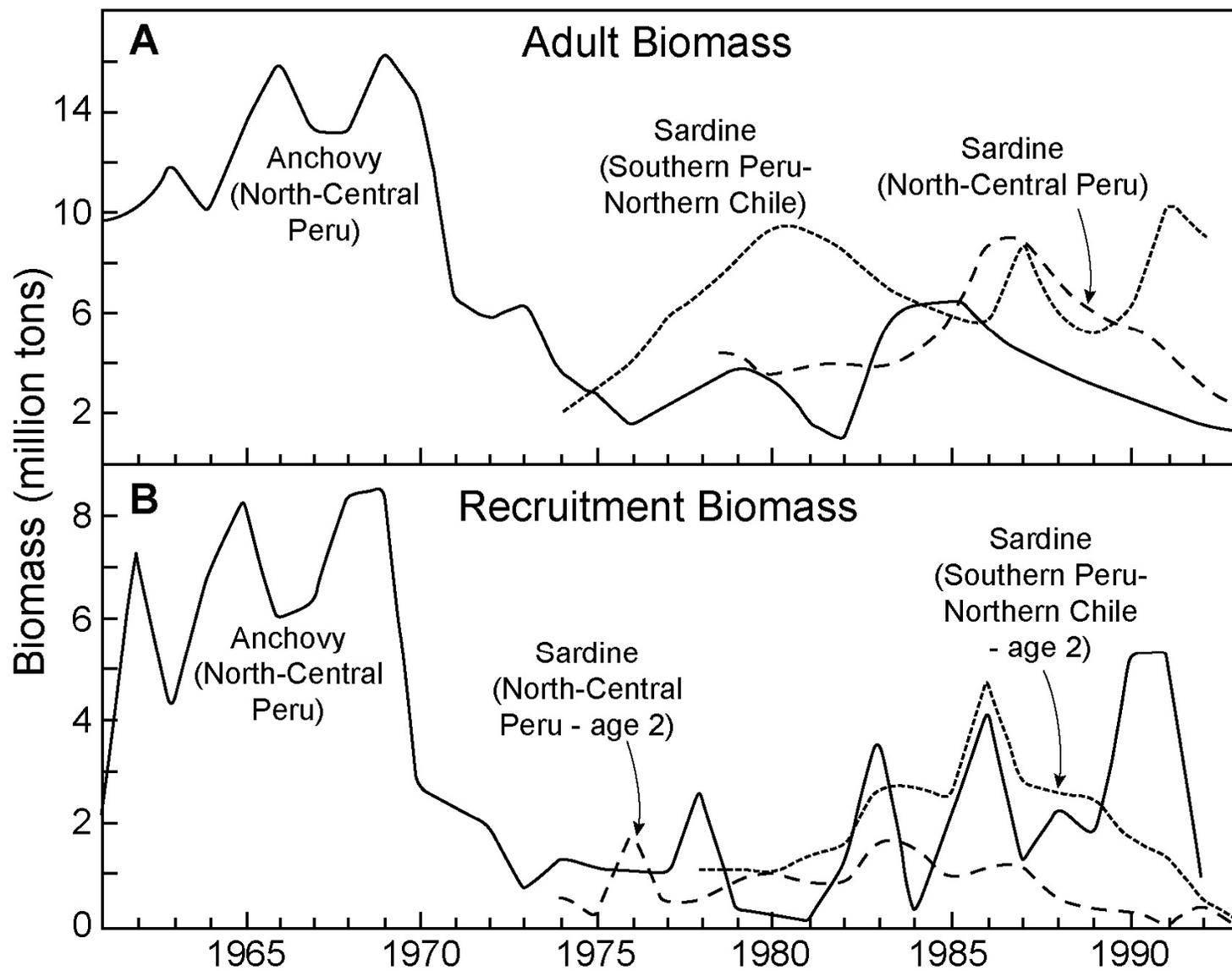
Figure 10.15. Estimates of the a) adult biomass of the sardine and anchovy stocks off Perú and Chile from 1961 through 1993, and b) recruitment biomass to those stocks. Sardine recruits are age two fish; anchovy recruits are young of the year. The different stocks are noted on the two plots. (Figure adapted from Schwartlzlose et al. [1999]).
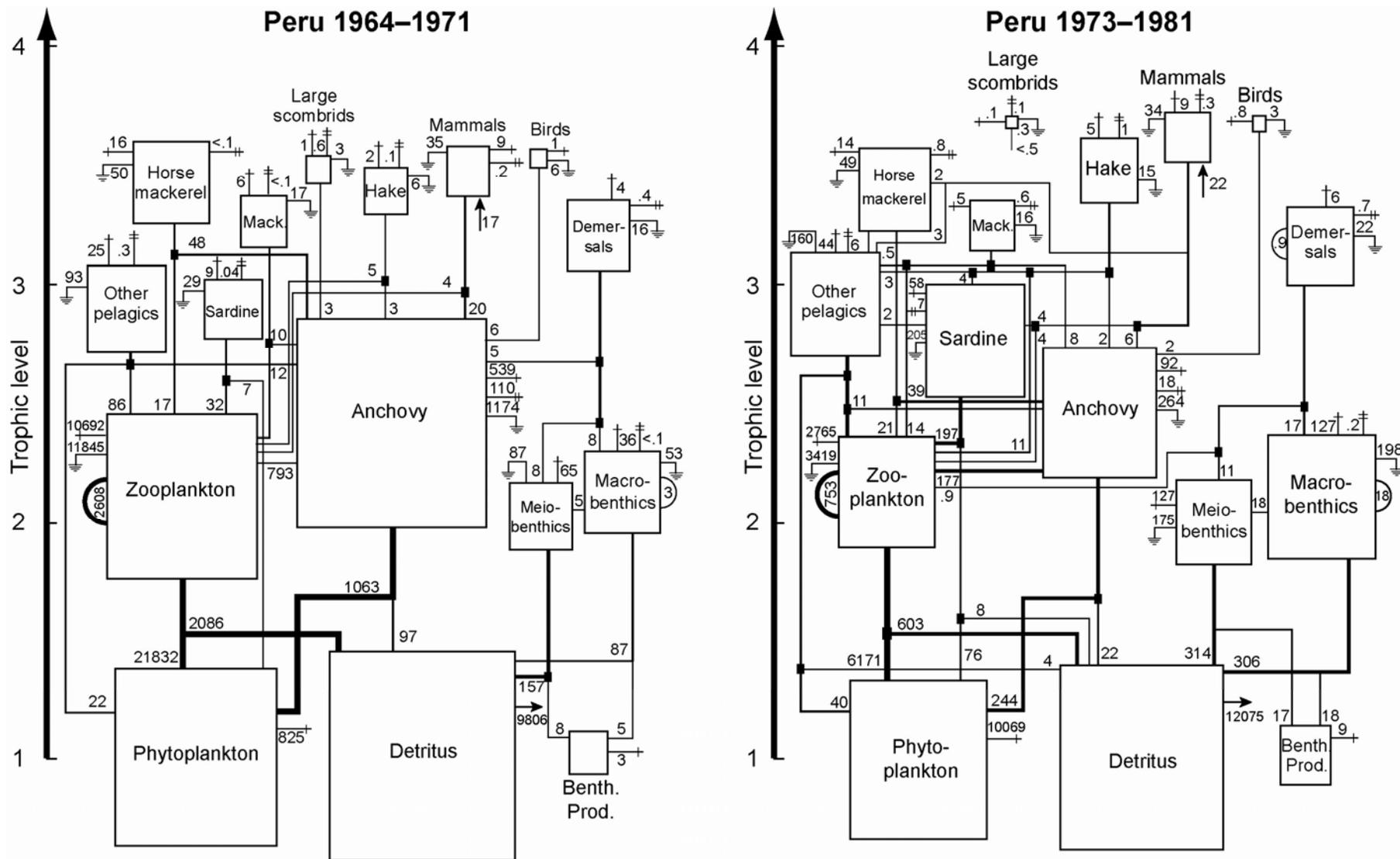
Figure 10.16. Ecosystem trophic structure obtained from steady-state mass-balance model runs for cool (left side) and warm (right side of figure) regimes off Perú. (Figure adapted from Jarre-Teichmann [1998]).
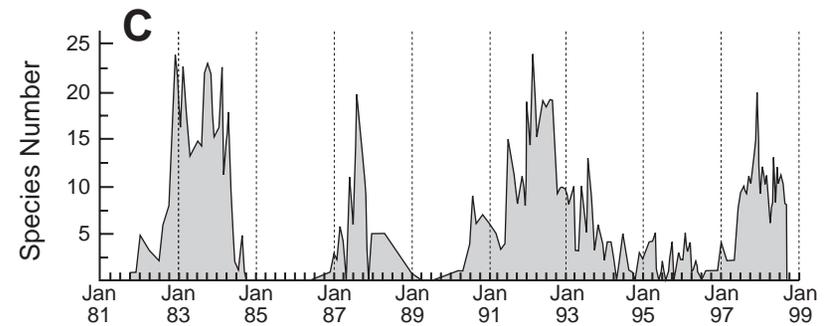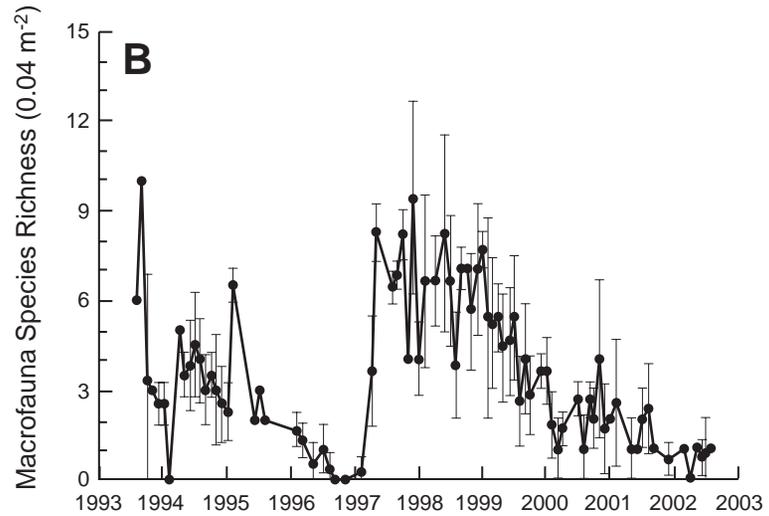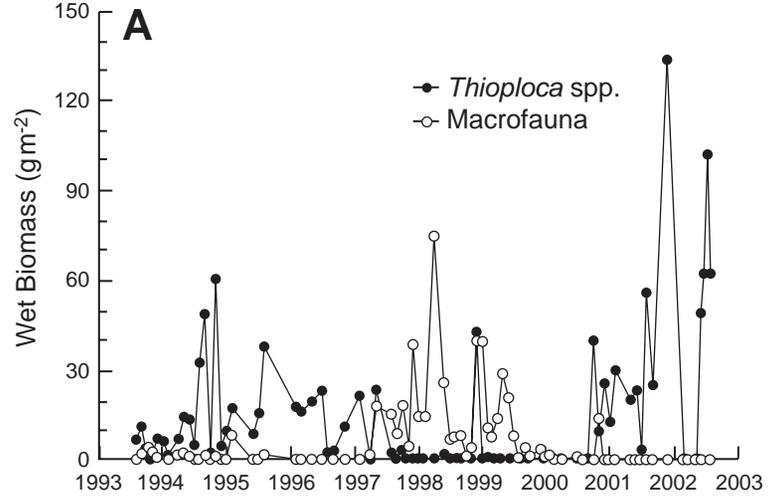
Figure 10.17.   Temporal variability of benthic communities in
Perú:

a)   Biomass of macrofauna and *Thioploca spp.* in Callao
(93m depth), 1993-2002;

b)   b) Macrofauna species richness in Callao, 1993-2002;

c)   c) Macrofauna species richness in Ancon Bay, 1982-1998
(Unpublished data courtesy of Dimitri Gutierrez).
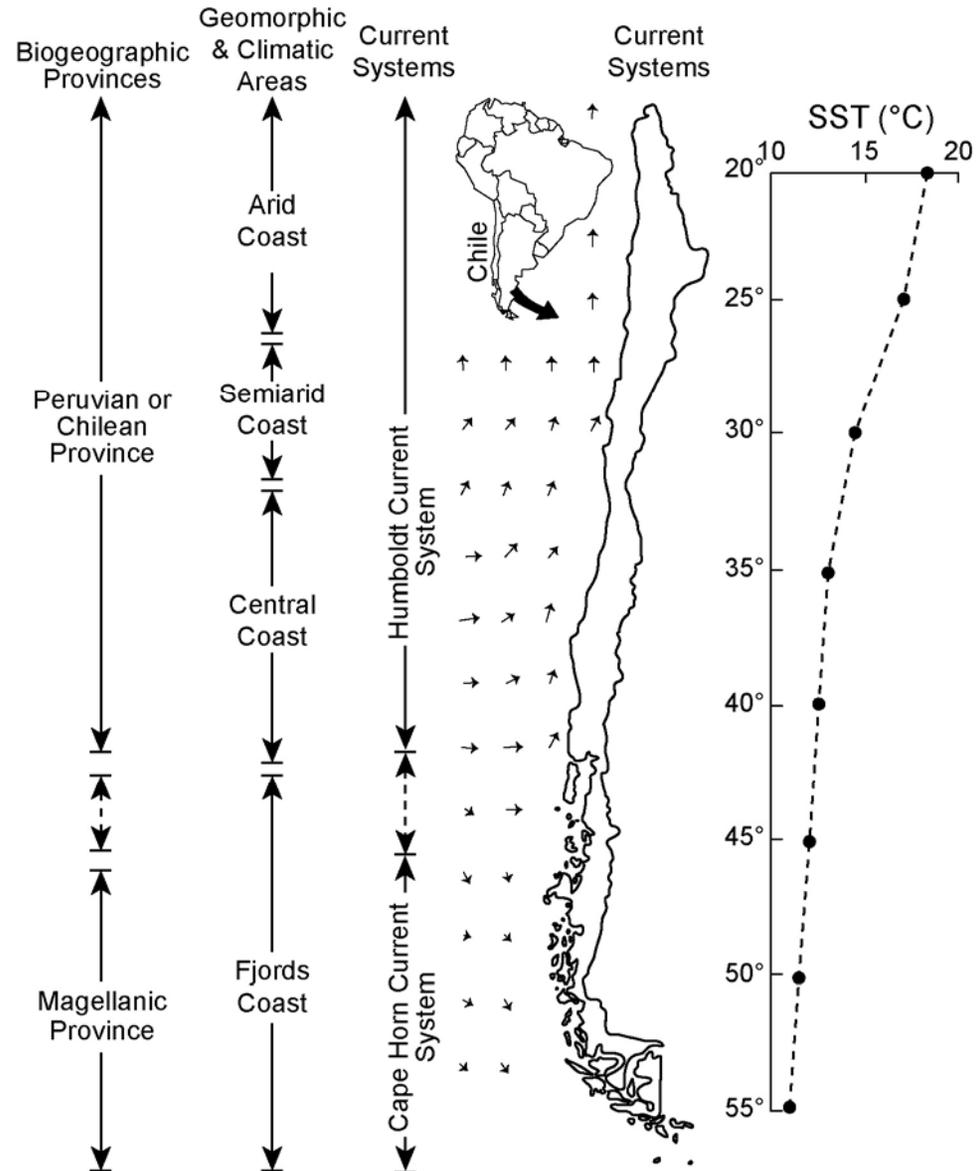
Figure 10.18. Several latitudinal subdivisions (biogeographic, physical, etc.) of the regions off Chile. (Reproduced with the authorization of the editors of *Revista Chilena de Historia Natural*, from Fernández et al. [2000]).