(vi) Oxygen minimum zones and biogeochemical 01 cycling in the EBCS: Oxygen minimum zones (OMZ) 02 are regions of the global ocean, located at intermediate 03 depths (50-1000 m), with dissolved oxygen concentra-04 tions less than 0.5 mL L^{-1} (i.e. about 7.5% saturation, 05 $<22 \,\mu$ M) due to reduced ventilation and the high res-06 piration rates of the settling organic matter produced 07 in the surface waters (Levin 2003). Of the four EBCS, 08 three (Benguela, California, Humboldt) have an impor-09 tant OMZ (Kamykowski and Zentara 1990). Recent 10 and comprehensive reviews of the OMZ can be found 11 in Levin (2003), Karstensen et al. (2008), and Paulmier 12 and Ruiz-Pino (2008). Oxygen minimum zones play a 13 crucial role in the ecology and biogeochemistry of the 14 EBCS. They constitute an important physical barrier 15 for aerobic respiration, making oxygen levels a critical 16 factor for the distribution and survival of the pelagic 17 biota (e.g. Boyd et al. 1980, Morales et al. 1996, 18 González and Quiñones 2002, Chan et al. 2008), espe-19 cially in those regions of the EBCS with an intense and 20 shallow OMZ. 21

The co-existence of oxic-suboxic gradients in the 22 OMZ involves rather complex biogeochemical pro-23 24 cesses such as strong organic matter remineralization, nitrate removal, and nitrite release (Paulmier and 25 Ruiz-Pino 2008). Furthermore, OMZ are important 26 sources of the greenhouse gases carbon dioxide (CO_2) 27 and nitrous oxide (N_2O) (Ward et al. 1989, Cornejo 28 et al. 2006, Farías et al. 2007). On the other hand, accu-29 mulating evidence indicates that the microbial com-30 munities inhabiting the OMZ of the EBCS are very 31 active metabolically (e.g. Kyupers et al. 2005, Molina 32 et al. 2005, González et al. 2007, Levipan et al. 2007) 33 and present high diversity (e.g. Molina et al. 2007, 34 Woebken et al. 2008, Quiñones et al. 2008, Stevens and 35 Ulloa 2008). Despite the importance of the OMZ in the 36 global nitrogen cycle, little is known about the struc-37 ture and functioning of its microbial communities. The 38 physical dynamics and the mechanisms by which the 39 OMZ are maintained in the Benguela, California, and 40 Humboldt systems are also poorly understood. 41

The high spatial and temporal variabilities as well as 42 the open nature of the EBCS boundaries are important 43 limitations for the carbon and nutrient budgets esti-44 mated therein (Sects. 2.2, 2.3, 2.4, 2.5, and 2.6). An 45 improved modeling approach (e.g. Baird et al. 2007) 46 is an important step toward achieving better carbon 47 and nutrient estimates. However, what is really nec-48 essary in order to confront some of the issues listed 49

above is a more thorough integration of population– community and process–functional approaches (sensu O'Neill et al. 1986).

2.2 The Northern and Central California Coastal Upwelling System

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2.2.1 Introduction

2.2.1.1 The Carbon Cycle: CO₂, the Greenhouse Effect, and the Biological Pump

Over the past 150 years, carbon dioxide (CO₂) has accumulated in the atmosphere and the partial pressure of CO₂ (pCO₂) has increased from approximately 280 to 370 ppm primarily due to the burning of fossil fuels, currently at a rate of about 6.5 gt carbon yr^{-1} (see overview in Miller, 2004). Because CO₂ absorbs infrared radiation, increased atmospheric CO₂ decreases radiative heat loss to space – the 'Greenhouse effect' – leading to the prediction that human activity is warming the earth's climate. While data confirm that climate is warming, many associated rates, patterns, and interactions remain poorly understood. These uncertainties have prompted considerable study of carbon cycles, of which this article and book are part.

The atmospheric accumulation of CO_2 is moderated by the existence of CO_2 sinks such as the oceans. The increase of atmospheric CO_2 has produced disequilibrium between the surface ocean and the atmosphere, which on average forces CO_2 to diffuse into the ocean (Bates, 2001; Bates et al., 2001; Sabine et al., 2004). About 1.7 gt carbon yr⁻¹ or 30% AQ2

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of the annual atmospheric CO₂ input is estimated 01 to dissolve in the surface ocean (see Miller, 2004; 02 Sabine et al., 2004). Biological processes play a piv-03 otal role in determining sea surface pCO₂ (see Hay-04 ward, 1991). When phytoplankton convert CO₂ into 05 organic molecules and their cellular constituents via 06 photosynthesis (carbon 'fixation'), near-surface pCO₂ 07 levels are reduced and the gradient between atmo-08 sphere and ocean is, on average, increased. When phy-09 toplankton are eaten or die, a portion of their fixed 10 carbon sinks, thus removing carbon from the lighted 11 euphotic zone. These two processes, carbon fixation 12 by photosynthesis and sinking, are termed the 'bio-13 logical pump' and in combination they maintain low 14 near-surface pCO₂, promoting carbon transfer from the 15 atmosphere into the oceans by diffusion. Beneath the 16 euphotic zone, organism respiration converts phyto-17 plankton organic carbon back into CO2 and other inor-18 ganic carbon species ('remineralization'), and this CO₂ 19 is isolated from the atmosphere for hundreds to thou-20 sands of years (Falkowski et al., 1998). The biological 21 pump is also regulated by iron, nitrate, and other fac-22 tors, but in its absence CO₂ concentration in the atmo-23 sphere would be substantially higher (Miller, 2004; 24 Sabine et al., 2004). 25

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There are strong spatial and temporal variations in 26 ocean/atmosphere CO₂ interactions. Ocean temperature change is important due to its effect on gas solubility. In regions with equatorward flowing and thus warming surface currents, gas solubility decreases and 30 CO_2 is in general vented to the atmosphere; the con-31 verse occurs in regions with poleward-flowing cur-32 rents. Biology interacts with physics to complicate 33 matters. In the equatorial upwelling regions, subsur-34 face water supersaturated in CO₂ is drawn to the sur-35 face, the biological pump operates slowly due to iron 36 limitation, and about 1 Gt carbon is vented into the AQ4 37 atmosphere annually (Chavez et al., 1999). Climac-38 tic variations, such as El Niño and El Viejo (Chavez 39 et al., 2003), further alter these processes. For many 40 parts of the oceans such as the coastal margins, CO₂ 41 fluxes into and from the ocean have not been measured 42 at all (see Liu et al., 2000), and the cycles and rates that 43 control the biological pump have not been examined 44 or synthesized. These processes are important, espe-45 cially as feedbacks to climate change phenomena. Do 46 coastal upwelling systems contribute to atmospheric 47 CO₂ as does equatorial upwelling? Studies to exam-48 ine the contributing elements of carbon cycles in such 49

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locations are badly needed. One such location is the coastal upwelling region of the northeast Pacific.

2.2.1.2 The Northeast Pacific Eastern Boundary and Coastal Upwelling System

The Pacific Ocean off western North America is a classic eastern boundary current region (Fig. 2.2.1; see Barber and Smith, 1981; Thurman and Trujillo, 1999). In this system near-surface flow of the gyral circulation can be divided into three regions. Offshore, in the central Pacific beyond about 1300 km from North America, warm and salty North Pacific Central Gyre (NPCG) waters form a southward-flowing layer about 250 m deep (reviewed by Karl and Lucas, 1996). Second, between the NPCG and 150-200 km west of North America, the California Current (CC) also flows southward at $0.6-1.2 \text{ km h}^{-1}$ (U.S. Hydrographic Office, 1947) as a 1200 km broad and 250 m deep surface current (Reid et al., 1958). CC isolines (thermocline, halocline, nutricline; Fig. 2.2.2A-F) shoal toward the east due to a basin-scale geostrophic adjustment termed 'pycnocline tilting', caused by the interaction of the flow with Coriolis (Chelton et al., 1982). Maximum velocity occurs near the CC's eastern margin, on average only 150–200 km offshore (Fig. 2.2.3), and this 'CC jet' or core transports the CC's lowest salinity water (see Fig. 2.2.2C, D; Lynn and Simpson, 1987; Strub and James, 2000; Collins et al., 2003). Spring and summer maxima in CC jet velocity are associated with seasonal maxima in CC pycnocline tilting (Collins et al., 2003). Third, inshore of the CC jet, the CC interacts with the North American continent in a region we call the coastal upwelling system (CUS), where coastal currents and mesoscale phenomena dominate (Barber and Smith, 1981; Collins et al., 2003). In spring and summer, seasonal northwesterly winds drive a coastal upwelling circulation in the CUS characterized by equatorward flow of near-surface coastal upwelling jets with associated eddies and fronts that extend offshore to the CC jet (Fig. 2.2.3). During upwelling, isolines in the CUS shoal and inshore near-surface waters become colder and saltier (Fig. 2.2.2A-D; reviewed by Pennington and Chavez, 2000; Chavez et al., 2002, 2003) - distinct from CC jet waters offshore (Fig. 2.2.2A-D; Collins et al., 2003). This wind-driven equatorward circulation overlies the poleward-flowing California



Fig. 2.2.1 NE Pacific composite SeaWIFS surface chlorophyll image, with schematic currents overlain. The carbon budget is assembled for the CUS (Region A), which is defined as a 60 m deep Ekman layer reaching from Cape Mendocino to Point Conception and 170 km offshore along CalCOFI Line 67 (L67; *green dots*). Monterey Bay is at the NE terminus of L67. The Behrenfeld and Falkowski (1997) net primary production model (Table 2.2.3) was run for the CUS (Region A), the central CC

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(Region B), a portion of the NPCG (Region C), and the larger CC (Region D). The inset compares monthly surface chlorophyll values for the regions of Fig. 2.2.1 and L67. L67 and the CUS (Region A) are very similar (*upper panel*), the larger CC including the CUS (Region D) is much lower but still exhibits a spring/summer maximum (*lower panel*), while the offshore CC (Region B) and the NPCG (Region C) exclude the CUS and lack a spring/summer chlorophyll maximum (*lower panel*)

Undercurrent, which has maximum velocity near 31 100 m but reaches to at least 1000 m (Collins et al., 32 33 2000). In winter, the northwesterly winds weaken or are replaced by southerly storm winds. Under these 34 conditions the California Undercurrent surfaces (Sver-35 drup et al., 1942; Reid and Schwartzlose, 1962), where 36 it is called the Inshore Countercurrent or Davidson 37 Current which flows northward 0-100 km offshore 38 39 (Collins et al., 2000). The CC and CUS with its California Undercurrent, Inshore Countercurrent and 40 coastal upwelling circulation are together termed the 41 California Current System (CCS; Collins et al., 2003). 42 43 Biologically, the CUS, CC, and NPCG progress from eutrophic coastal to oligotrophic central waters 44 (Barber and Smith, 1981). During the spring and sum-45 mer in the CUS, wind-driven upwelling draws the 46 nutricline into the euphotic zone (Fig. 2.2.2E-F) and 47 the enhanced nutrient flux supports prolific phyto-48 49 plankton growth (Fig. 2.2.2G–J), in particular of large

cells such as diatoms (Pennington and Chavez, 2000; see Chavez et al., 2002, for El Niño perturbations). This upwelling season primary production in turn supports stocks of zooplankton (Hopcroft et al., 2002; Marinovic et al., 2002), fishes (Chavez et al., 2003), and cetaceans (Benson et al., 2002). The CC jet may act as a barrier which separates the productive CUS waters from offshore CC waters where levels of primary production are intermediate between those of the upwelling circulation and the oligotrophic NPCG (Figs. 2.2.3, 2.2.5; Collins et al., 2003). CC phytoplankton has variously been suggested to be supported by nutrients (1) advected from the north (Chelton et al., 1982), (2) uplifted from depth via isopycnal tilting (Chelton et al., 1982; Collins et al., 2003), or (3) injected into the CC by the jets, eddies, and fronts that form the western edge of the CUS's coastal upwelling circulation (Barber and Smith, 1981; Collins et al., 2003).



2.2.1.3 Carbon Budget for the NE Pacific Coastal Transition Zone

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Here we assemble a first-estimate carbon budget for
the (1) near-surface CUS and (2) flux to the inshore

jet or core region of the CC (Fig. 2.2.1). The budget is based on a simple schematic flow diagram (Fig. 2.2.4). The purpose is to initiate a synthesis of carbon flow within this nearshore domain and to highlight processes for which well-founded estimates are lacking.



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JMMJSN Fig. 2.2.3 Annual cycle of surface layer dynamic height along L67 (from Collins et al., 2003). Dynamic height was calculated for 0/200 m and plotted against distance offshore (*vertical*) and month (*horizontal* axis) based on 9 years of quasi-quarterly cruises 1988–2001. The CC and CUS at top and bottom, respectively, are both in *darker shades*. The CC jet is the horizontal band of tight *light-colored* contours, implying high velocity, that oscillate offshore in winter/spring and onshore in summer/fall; its inshore margin is near the 0.45 dynamic meter contour and is approximately 170 km offshore. This distance has been used in the budget calculations as an offshore boundary for the CUS

2.2.5). The budget includes estimates for rates of air/sea CO_2 exchange and in-water carbon cycling. The in-water estimates include (1) nitrate imports and exports, (2) particulate organic carbon (POC) exports via diffusion, advection, sinking, conversion to dissolved organic carbon (DOC) and fisheries, and (3) total, new, and recycled primary production.

2.2.2 Budget Components

2.2.2.1 Spatial Domain

The budget estimates surface layer carbon fluxes for the central 750 km of the North American coastal upwelling region between Cape Mendocino and Point Conception in California (40.5–34.4°N; Region A of Fig. 2.2.1), where upwelling dominates the system during spring and summer. L67 lies near the center of this domain.

We rely heavily on time-series data collected by our laboratory at MBARI in Monterey Bay and along Cal-COFI Line 67 off central California (L67; Figs. 2.2.1,

For L67, Collins et al. (2003) defined the 'CC jet' as a band of strong equatorial surface flow marked by the tightest gradient of dynamic height for the 0–200 m surface layer (Fig. 2.2.3). The jet exhibits a seasonal offshore/onshore oscillation (winter–spring/



Fig. 2.2.4 Schematic diagram of the CUS and its carbon
 fluxes. The CC and CUC extend deeper than indicated, and the
 upwelling indicated includes both geostrophically driven 'pyc nocline tilting' (Collins et al., 2003) and wind-driven coastal
 upwelling. Nitrate and CO₂ are upwelled and partly converted

to phytoplankton (POC) via primary production. While moving offshore and southward, the POC sinks, is grazed and converted to dissolved organic carbon (DOC); the remaining nitrate and POC eventually diffuses or advects into or beneath the CC. Estimates for these sources and sinks are presented in Table 2.2.2



25 Fig. 2.2.5 Detail composite SeaWIFS surface chlorophyll 26 image showing Monterey Bay (near 36.7° N, 122° W), our Monterey Bay time-series stations occupied each 3 weeks since 27 1989 (inshore blue and pink circles), and L67 Stations (all cir-28 cles). Most data used to construct the Table 2.2.2 carbon bud-29 get were collected at these stations. Sediment trap data used in 30 the POC flux calculation were obtained at the pink (traps S1 and S2) and red circles (traps PREVTX and VTX#1 of Mar-31 tin et al., 1987) and at Station M (not shown, at 34.8° N, 123° 32 W). The M1 mooring/station is not shown but adjacent to the 33

ern *pink circle*. The inshore margin of the CC jet and CC as described in Fig. 2.2.3 and Collins et al. (2003) is shown as *white dashes*, 170 km offshore. The coastal upwelling system or CUS is defined as inshore of the CC jet. The CUS includes stations in three subregions: Monterey Bay, 0–20 km offshore (*blue circle*); an active upwelling region, 20–52 km offshore (*pink circles*); and the coastal transition zone or CTZ, 52–170 km offshore (*black circles* inshore of the *dashed line*)

eastern pink circle; the M2 mooring/station adjacent to the west-

summer-fall) as well as interannual variations (see
Collins et al., 2003), but its inshore margin is near
the 0.45 dynamic meter isostere which averages about
170 km offshore (Fig. 2.2.3). This distance has been
used as the offshore margin of the CUS for budget calculations.

Ten L67 stations thus lie within the CUS and 41 these fall into three subregions: (1) Monterey Bay, 42 43 0-20 km offshore, with one inshore L67 station (blue circle, Fig. 2.2.5); (2) an active upwelling region, 44 one 36° N Rosby Radius wide, 20-52 km offshore, 45 with two L67 stations (pink circles, Fig. 2.2.5; see 46 also Chavez, 1989; Pennington and Chavez, 2000); 47 and (3) a mesoscale mixing region called the Coastal 48 49

Transition Zone (CTZ; Brink and Cowles, 1991), 52– 170 km offshore, with seven L67 stations (black circles inshore of the dashed white line, Fig. 2.2.5). Eight offshore stations on L67, typically within the CC jet, are excluded from the CUS in this analysis (black circles offshore of the dashed line, Fig. 2.2.5).

Budget calculations are restricted to a 0–60 m surface layer, with 60 m being representative of winddriven Ekman layer depth in mid-latitudes (see Mann and Lazier, 1996). This layer typically includes both the euphotic (lighted) zone and, except in winter, the mixed layer. Upwelling source waters originate from about 60 m (Barber and Smith, 1981; see Fig. 2.2.2A–F).

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Fig. 2.2.6 (A) Mean temperature and nitrate profiles based
 on ship occupations of the M1 mooring site. The nitrate: temper ature equation was derived by Olivieri and Chavez (2000) from
 below-thermocline profile data and used to convert daily 60 m
 mooring temperatures to the nitrate values used in the calcula tion of upwelled nitrate. (B) POC flux profile. Black circles are
 data points as labeled from sediment trap programs cited in the

text; the *grey circles* are 60 and 100 m fluxes predicted from the data points with the Martin et al. (1987) power function shown in the figure. Flux values are summarized in Table 2.2.1. (C) Mean TOC profile from three CUS stations. TOC has been taken as equivalent to DOC for this winter profile, and the 0–60 m difference as the amount of DOC produced in the euphotic zone per m^3 of water upwelled

relationship to convert 60 m daily average tempera-01 tures from the M1 mooring to nitrate values. These 02 nitrate values were then multiplied by daily upwelling 03 volumes per meter of shoreline based on upwelling 04 indices for Monterey Bay (also computed by Olivieri 05 and Chavez, 2000) and the 32,000 m broad upwelling 06 subregion defined above, producing a daily estimate of 07 nitrate flux. This flux was summed over the year and 08 divided by the 170,000 m breadth of the CUS, produc-09 ing a m⁻² yr⁻¹ estimate for imported or new nitrate, 10 and then converted to carbon equivalents as described 11 above. If the imported nitrate were completely used by 12 CUS phytoplankton, the import could be taken as an 13 estimate of new production. However, it turns out that 14 significant nitrate is exported to the CC by diffusion 15 and advection; these losses are estimated below.

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2.2.2.5 Nitrate and POC Exports

22 Export by Horizontal Diffusion

The rate of diffusive transport of nitrate and particu-24 late organic carbon from the CUS into the CC was 25 estimated as follows. L67 0-60 m mean nitrate and 26 chlorophyll were regressed against distance offshore 27 across the CC jet (96-240 km offshore; Fig. 2.2.7). 28 Values for the active upwelling subregion and the off-29 shore CC were not included because surface layer 30 nitrate and chlorophyll trends are not linear across all 31 of L67 (Fig. 2.2.7); the regression's purpose was to 32





estimate decreases per unit distance offshore across

of interest; the above value was chosen as appropriate for horizontal mixing across the CUS/CC boundary (\sim 100 km; Fig. 2.2.7). Export of nitrate and chlorophyll represents loss of potential and realized new production, respectively.

Export by Advection Offshore

The above calculation pertains to mixing, not advection. Net offshore flow across the CUS/CC jet boundary is driven by Ekman transport and is balanced by onshore flow at depth (see Fig. 2.2.4; reviewed by Mann and Lazier, 1996). If the volume of water upwelled in the active upwelling subregion (Fig. 2.2.5) also approximates the volume-advected offshore across the CUS/CC jet boundary, a simple estimate for the percent of upwelled nitrate exported by advection is (1) the daily upwelling volume times the mean 0–60 m nitrate concentration at the CUS border ($3.2 \mu M NO_3$; Fig. 2.2.7A), divided by (2) the daily upwelling volume times the M1 mooring.

A similar calculation was performed to estimate POC export at the CUS boundary $(0.45 \text{ mg Chl m}^3;$



Fig. 2.2.7 Regressions of 0–60 m mean nitrate (A) and
 chlorophyll (B) against distance offshore across the CUS/CC jet
 boundary (170 km; *dotted vertical lines*). A few high data points were omitted for clarity. The slopes were multiplied against CUS

surface layer diffusivity (Okubo, 1971) to estimate nitrate and POC loss by diffusion. In addition the CUS/CC boundary nitrate $(3.2 \,\mu\text{M})$ and chlorophyll (0.45 mg m⁻³) values were used to estimate upwelling-driven loss due to offshore advection

Fig. 2.2.7B), but with chlorophyll export and nitrate import converted to carbon equivalents (POC).

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POC Export by Sinking

06 POC export by sinking was estimated by averaging 07 60 m fluxes calculated from six central California car-08 bon flux programs (Table 2.2.1). Martin et al. (1987) 09 deployed sediment traps at two coastal sites, PREVTX 10 and VTX#1 (Fig. 2.2.5, red circles), and produced 11 power functions that estimate coastal POC flux with 12 depth > 35 m. We combined the functions for these sta-13 tions and used the average to estimate 60 and 100 m 14 fluxes from measured fluxes and trap depths (aver-15 aged equation on Fig. 2.2.6B). Berelson et al. (1996, 16 2003) estimated 100 m POC flux off central Califor-17 nia, and we extrapolated this flux to 60 m. Pilskaln 18 et al. (1996; Station S1), Chavez (unpublished; Sta-19 tion S2), and Smith et al. (1992; Station M) produced 20 flux data with traps at various depths off central Cal-21 ifornia (S1 and S2 - pink circles, Fig. 2.2.5; Sta-22 tion M – 34.8°N, 123.0°W). POC fluxes at each trap 23 (Fig. 2.2.6B) were again extrapolated to 60 and 100 m. 24 The mean of the extrapolated 60 m fluxes was taken as 25 an estimate of the sinking of POC from the CUS sur-26 face layer (Tables 2.2.1 and 2.2.2). Extrapolated 100 m 27 fluxes were included in Table 2.2.1 for comparison 28 with other sediment trap work. 29

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2.2.2.6 POC Conversion to DOC

³³ Dissolved organic carbon (DOC) data are not routinely ³⁴ collected along L67. However, three total organic car-³⁵ bon profiles (TOC; Fig. 2.2.6C) were obtained in

Table 2.2.1 POC sinking. Fluxes from the trap programs described in the text. Measured fluxes at trap depth were extrapolated to 60 and 100 m with the Martin et al. (1987) power function (Fig. 2.2.6C) averaged for their coastal stations PRE VTX and VTX#1 (Fig. 2.2.5) The 100 m fluxes as estimated

the CUS during a February 2003 cruise (stations M1 and M2 – pink circles, Fig. 2.2.5; station UC1 – 36.0° N, 121.8°W). DOC production was estimated on the assumption that the increase in TOC from 60 m to the surface represents the DOC produced in water upwelled into the euphotic zone. POC contribution to TOC was ignored in this winter data. The DOC production estimate was multiplied by the daily upwelling volumes as calculated for new production above and summed to produce an estimate of DOC production $m^{-2} \text{ yr}^{-1}$.

2.2.2.7 Loss to Fisheries

Chavez (1989) estimate that 2–3% of total primary production per year became anchoveta biomass during peak years in the Peruvian upwelling system. If these fish or their feces are recycled in the surface CUS, no flux results. However, if they are removed by fisheries, a carbon export occurs. Lacking fisheries estimates for L67 and the CUS, we use 3% estimate as a placeholder in the current budget.

2.2.2.8 Atmosphere/Ocean CO₂ Exchange

The atmospheric and surface ocean partial pressure of CO₂ (pCO₂) has been measured on over 30 L67 and 140 C1-M2 cruises across the CUS. These and additional atmospheric data (Globalview-CO₂, 2004) were used to estimate the sea surface/air pCO₂ difference (Δ pCO₂) for 1 km binned data for the cruises. A long-term wind and air–sea gas exchange relationship (Wanninkhof, 1992; Wanninkhof and McGillis, 1999)

by Martin et al. (1987) and Berelson et al. (2003) have also been included here; these values were also extrapolated to 60 m. The mean of the 60 m fluxes was entered in the carbon budget, Table 2.2.2. Units are g C m⁻² yr⁻¹

Trap	Trap depth (m)	Measured flux	100 m flux	60 m flux	Data source
PVTX, VTX1	50-2000	_	63	98	Martin et al. (1987)
_	100	-	45	69	Berelson et al. (2003)
S2	300	18.8	48	74	Chavez (unpublished)
S1	450	14.4	52	80	Pilskaln et al. (1996)
S2	1200	14.7	121	186	Chavez (unpublished)
М	3500	1.7	34	52	Smith et al. (1992)
Mean (g C m ⁻¹	2 yr ⁻¹)		60	93	

⁰¹ **Table 2.2.2** Annual carbon budget for the northern and central California coastal upwelling system, with budget estimates expressed as g Carbon m^{-2} yr⁻¹. Nitrate import minus exports

is new production, and total production minus new production is recycled production. POC exports are the budgeted portion of new production

	g carbon per m ²	Metric tons carbon per m shore	Metric tons carbon entire CUS	Percent of upwelled nitrate	Percent of new production	Percent of total production
Nitrate flux						
Import - upwelling	204	35	25,995,182	100	121	59
Export - diffusion	2	0.4	301,080	1	1	1
Export - advection	33	6	4,181,244	16	19	10
POC exports						
Diffusion	0.2	0.04	30,108	0.1	0.1	0.1
Advection	5	1	590196	2	3	1
Sinking	93	16	11,857,500	46	55	27
DOC	22	4	2,805,000	11	13	6
Fisheries	10	2	1,317,866	5	6	3
Air/sea CO ₂ exchange	0	0	0	0	0	0
Total production	345	59	43,928,850	169	204	100
New production	169	29	21,512,857	83	100	49
Recycled production	176	30	22,415,993	86	104	51
POC exports	130	22	16,600,670		77	_
POC+nitrate exports	165	28	21,082,995	81	-	_

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²³ was applied to the ΔpCO_2 values and smoothed 30-²⁴ day winds from the M1 mooring to estimate sea to ²⁵ air flux of carbon. Results from all cruises were com-²⁶ bined to derive the mean spatial distribution of the flux. ²⁷ Monthly means can be derived for the C1-M2 region ²⁸ and seasonal means for the L67.

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2.2.3 Results and Discussion

Results are presented in Table 2.2.2 and are expressed 34 as g carbon yr^{-1} for each m^{-2} of the CUS, for 35 each m^{-1} of coastline from shore to the CC jet, and 36 for the total CUS as defined above (Region A in 37 Fig. 2.2.1). The fluxes are also expressed as percent-38 39 ages of upwelled nitrate, new, and total production. 40 Nitrate and chlorophyll have been converted to carbon equivalents (POC). 41

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44 2.2.3.1 Primary Production

46 Total Production

Total production within the CUS is 345 g carbon m⁻² yr⁻¹ or 4.4×10^7 metric tons of carbon yr⁻¹. CUS total production is overestimated by 39% by a SeaWIFSbased net primary production model (Table 2.2.3; Behrenfeld and Falkowski, 1997) as has been noted previously for L67 (MacFadyen, 1998). Nevertheless, using the model estimates on a per m² basis for the boxes in Fig. 2.2.1, CUS total production is nearly threefold higher per m² than that in the CC, and fourfold higher m⁻² than in the NPCG. However, the CUS contributes only $\sim 0.4\%$ of North Pacific primary production and 0.1% to global production. Similarly, the CCS as a whole (Region D of Fig. 2.2.1) contributes 2.9 and 0.7% to North Pacific and global primary production, respectively (Table 2.2.3). In Fig. 2.2.1, regions containing the CUS (A, D) show a pronounced spring/summer SeaWIFS chlorophyll maximum (inset), while offshore CC and NPCG regions (B, C) do not. L67 appears representative of CUS surface chlorophyll (Fig. 2.2.1, inset).

New Production

New production is that supported by 'new' nutrients – typically nitrate – imported into the system and is distinct from 'recycled' production supported by nutrients – typically ammonia – cycled within the euphotic

Table 2.2.3 SeaWIFS-derived total depth-integrated net primary production (TP) for the boxes in Fig. 2.2.1, calculated as in Behrenfeld and Falkowski (1997). 1 gt = 10^{15} g

$a C m^{-2} vr^{-1}$	2		Zone total g t C yr ⁻¹	Percent of NPac	Percent of Global
$g C m^{-2} yr^{-1}$	(m ²)	g C yr ⁻¹			
481.57	1.71E+11	4.93E+13	0.05	0.4	0.1
180.34	5.21E+11	9.40E+13	0.09	0.7	0.2
122.06	4.92E+11	6.00E+13	0.06		
212.56	2.06E+12	3.64E+14	0.36	2.9	0.7
			12.73		
			52.22		
	481.57 180.34 122.06 212.56	481.57 1.71E+11 180.34 5.21E+11 122.06 4.92E+11 212.56 2.06E+12	481.571.71E+114.93E+13180.345.21E+119.40E+13122.064.92E+116.00E+13212.562.06E+123.64E+14	481.57 1.71E+11 4.93E+13 0.05 180.34 5.21E+11 9.40E+13 0.09 122.06 4.92E+11 6.00E+13 0.06 212.56 2.06E+12 3.64E+14 0.36 12.73 52.22	481.57 1.71E+11 4.93E+13 0.05 0.4 180.34 5.21E+11 9.40E+13 0.09 0.7 122.06 4.92E+11 6.00E+13 0.06 212.56 2.06E+12 3.64E+14 0.36 2.9 12.73 52.22

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12 zone (Dugdale and Goering, 1967). In the CUS, most 13 new nitrate is supplied to the euphotic zone from below 14 by coastal upwelling (Olivieri and Chavez, 2000). Ver-15 tical diffusion and Ekman pumping driven by off-16 shore wind stress curl (see Mann and Lazier, 1996) 17 have not been considered here. If a system's biomass 18 remains constant, then new production is also the frac-19 tion of total production available for export, termed the 20 'f-ratio' (Dugdale and Goering, 1967). Recycled pro-21 duction is taken as the difference between total and 22 new production.

23 CUS upwelling of new nitrate can support 204 g 24 carbon m^{-2} yr⁻¹ or 59% of the total annual primary 25 productivity along L67 in the CUS (Table 2.2.2). This 26 estimate remains essentially unchanged if one uses a 27 constant 20 μ M nitrate input (206 g carbon m⁻² yr⁻¹) 28 instead of the nitrate:temperature relation employed to 29 produce the estimate in Table 2.2.2. However, it turns 30 out that 17% of the upwelled nitrate is not assim-31 ilated by phytoplankton in the CUS, but is apparently exported to the CC by diffusion and advection 32 33 (equivalent to 35 g carbon $m^{-2} yr^{-1}$). The remain-34 ing 169 g carbon $m^{-2} yr^{-1}$ thus represents our esti-35 mate of CUS new production (Table 2.2.2). Chavez 36 and Smith (1995) estimated new production for coastal 37 upwelling regions based on one Sverdrup upwelling 38 per 1000 km coastline and year and 20 μ M nitrate 39 source waters. When scaled to our spatial domain, their 40 estimate for new production is almost twice as large 41 as ours $(322/169 \text{ g carbon } \text{m}^{-2} \text{ yr}^{-1})$. This substan-42 tial difference is due to their higher, and less accurate, 43 estimated upwelling rate (1 vs. the ~ 0.5 Sv calculated 44 here) and to their assumption of complete utilization of 45 upwelled nitrate.

In spring and summer due to strong equatorward
 winds, CC and CUS isopycnals shoal (Fig. 2.2.2) as
 CC velocity and coastal upwelling increase. If new

production is calculated based on upwelling season isopycnal tilting rather than on upwelling indices, a much lower estimate is obtained – only 19% of total production (66/345 g carbon m^{-2} yr⁻¹; calculation not shown). Similarly, Collins et al. (2003) calculated that only 20% of Ekman transport is accounted for by isopycnal tilting. Apparently, spring and summer upward displacement of CUS isopycnals is responsible for less than half of the new nitrate brought into the surface layer each year (39% or 66/169 g carbon m^{-2} yr⁻¹). The remainder must be imported by recirculation and along-isopycnal flow.

Our estimate for an f-ratio of 0.49 (151/345 g carbon $m^{-2} yr^{-1}$) is lower than previous estimates for coastal upwelling regions. Chavez and Smith (1995) report a Monterey Bay *f*-ratio of 0.89 with a new production rate of 638 g carbon $\text{m}^{-2} \text{ yr}^{-1}$ for inshore waters during the spring of 1991. The present calculation, however, is reduced by nitrate exports and is for a much larger domain which includes considerable mesotrophic CTZ water offshore of the Monterey Bay observations of Chavez and Smith (1995). Additionally, although we have not produced seasonal estimates, CUS production rates and *f*-ratios are likely higher during the upwelling months than reflected in the annual means of Table 2.2.2. For the Peruvian upwelling system, Dugdale (1985) estimated an f-ratio of 0.75 and Chávez et al. (1989) estimated new production at 844 g carbon m^{-2} yr⁻¹, five times greater than our per m² estimate for California. This difference is partly procedural. For California the per m² rate of new production was effectively reduced by budgeting (1) the broad non-upwelling CTZ as part of the CUS and (2) advective and diffusive nitrate exports. It nevertheless remains true that the active upwelling region of the Peruvian CUS is much broader than that in California due to the increase in Rosby radius at low latitude (121 vs. 32 km at 9° vs. 36° latitude). Consequently, total CUS nitrate imports and new production
 are almost certainly several times larger off Peru than
 California.

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07 2.2.3.2 POC losses

09 Conversion to DOC

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DOC production was estimated as the TOC increase 11 in water upwelled to the surface from 60 m, and 12 accounts for 13 and 6% of CUS new and total produc-13 tion, respectively (Table 2.2.2). This estimate could be 14 increased to 21 and 9% of new and total production if 15 the larger 0-80 m mean TOC difference (32 g carbon 16 $m^{-2} yr^{-1}$) is used in the calculation, as may be justi-17 fied by the shape of the profile in Fig. 2.2.7C. In either 18 case the values are based on three wintertime CUS pro-19 files (M1, M2, UC1) – an exceedingly limited data set. 20 We have little concept of DOC cycling or export rates, 21 although one must imagine that like POC, CUS DOC is 22 exported to the CC by both diffusive and advective pro-23 cesses as suggested by Toggweiler and Carson (1995). 24 Our 13% DOC/new production estimate nevertheless 25 compares well with the 10-20% estimates of Hansell 26 and Carlson (1998) and Hansell (2002). 27

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30 Vertical POC Export by Sinking

Vertical POC export by sinking is substantial and flux 32 through 60 m accounts for 55% of new production. 33 This 93 g carbon $m^{-2} yr^{-1}$ is the mean of extrapola-34 tions from six sediment trap programs (Table 2.2.1) 35 using a power function derived from coastal flux mea-36 surements (see Methods). This function is data con-37 strained to 35 m (Martin et al., 1987, their Table 2.2.1). 38 Because our budget is for the surface Ekman layer, we 39 extrapolated to a 60 m flux horizon which is shallower 40 than the 100 m (shelf depth) flux typically calculated 41 by sediment trap workers. For comparison with previ-42 ous work we have included 100 m extrapolated fluxes 43 in Table 2.2.1; these average 60 g carbon $m^{-2} yr^{-1}$ or 44 36% of new production. The flux reaching 100 m is, 45 as expected, substantially less than that at 60 m, but 46 falls within the wide range of 100 m exports previ-47 ously estimated for the CUS. Martin et al. (1987) esti-48 mated 100 m fluxes of 42 and 85 g carbon $m^{-2} yr^{-1}$ for 49

their coastal stations, Pilskaln et al. (1996) calculated a 100 m flux of 86 g carbon $m^{-2} yr^{-1}$ and Berelson et al. (2003, eqtn. 4) estimated that about 45 g carbon $m^{-2} yr^{-1}$ sinks to the shelf at 100 m. These estimates average 64.5 g carbon $m^{-2} yr^{-1}$, in agreement with our 100 m value.

If POC sinking flux is normalized to total primary production as 'export-' or 'e-ratios' and plotted against total production, larger percentages of production are exported by sinking when productivity is low (Fig. 2.2.8). This result is true for the 450 m fluxes reported by Pilskaln et al. (1996) and for the mixed-layer modeled values produced by Olivieri and Chavez (2000). Pilskaln et al. (1996) suggest that when strong upwelling produces high productivity values, rate of advection is also high, minimizing POC flux to sediment traps within the CUS. The 100 m e-ratio based on our POC sinking flux from Table 2.2.1 and total production from Table 2.2.2 is 18% - similar to the 19% estimated by Pilskaln et al. (1996; Fig. 2.2.8). Our 60 m e-ratio for the base of the Ekman layer is substantially higher at 28%, and Pilskaln et al.'s (1996) 450 m ratio is lower, both as expected. It is not clear, however, why the modeled Olivieri and Chavez (2000) mixed-layer ratios are about half (mean $\sim 9\%$) the 100 m values and about one-third the 60 m e-ratio (Fig. 2.2.8).

Horizontal Export by Diffusion

Although meandering and often deflected or penetrated by upwelling-associated jets and plumes of the CUS (Figs. 2.2.3; Collins et al., 2003), the CC jet on average flows southeastward, parallel to the coast. CUS carbon is exported horizontally by (1) eddy diffusion and (2) advection of CUS waters into the CC. If upwelling supplies nutrients primarily within the active upwelling subregion (20-52 km of shore), then further offshore all flux terms combined should produce an offshore decline in nutrients (e.g., nitrate) and POC. If the slope of the decline is shallow, diffusive mixing will result in minor net transport across the area for which the slope was determined, which in the present calculation includes the CUS/CC boundary (Fig. 2.2.7). A steep slope implies that diffusion mixes substantial material offshore. Using a CUS diffusivity of 10⁶ cm² s⁻¹, nitrate and chlorophyll diffusive export accounts for 2 and 0.2% of new production

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Fig. 2.2.8 Percent export or *e*-ratios (POC flux/total production) plotted against total production, with representative of 450 m data from Pilskaln et al. (1996), mixed-layer model data from Olivieri and Chavez (2000), and CUS L67 data from this paper (100 m extrapolated flux/mean production at individual L67 stations). The *triangles* are mean ratios calculated

26 (Table 2.2.2), respectively. This diffusivity was chosen 27 as appropriate for a 100 km length scale (see Okubo, 28 1971), roughly matching the breadth of the CUS or 29 the CUS/CC boundary (Fig. 2.2.7). Our diffusivity is 30 nevertheless almost 100-fold less than the value esti-31 mated by Brink et al. (1991) for the CC jet. If the Brink 32 et al. (1991) value is used ($8.62 \times 10^7 \text{ cm}^2 \text{ s}^{-1}$), diffu-33 sion is estimated to remove an impossibly large frac-34 tion (220/169 g carbon $m^{-2} yr^{-1}$ or 130%) of new pro-35 duction from the CUS. The diffusive export of nitrate 36 represents 1% of that upwelled nearshore (Table 2.2.2). 37

³⁹ Export by Advection

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41 During the upwelling season, surface water of the CUS 42 is colder, saltier, and denser than CC surface water 43 (Fig. 2.2.2; reviewed by Pennington and Chavez, 2000; 44 Collins et al., 2003). Net offshore advection of sur-45 face CUS waters occurs due to wind-driven Ekman 46 drift and is balanced by onshore flow at depth (see 47 Fig. 2.2.4; reviewed by Mann and Lazier, 1996). Based 48 on the amount of nitrate present in surface waters at 49 the CUS/CC boundary and the rate of offshore flow,

from Tables 2.2.1 and 2.2.2 and from Pilskaln et al. (1996). The Pilskaln et al. (1996) data and Olivieri and Chavez (2000) model results suggest that higher percentages of production are exported when production is low. The *e*-ratios decrease with depth, as expected, except for the modeled mixed-layer values which are lower than the 100 m extrapolated ratios

we have calculated that, on average, 16% of nitrate upwelled into the surface 60 m is exported across the CUS/CC boundary (Table 2.2.2). In carbon equivalents this export represents 33 g carbon $m^{-2} yr^{-1}$ of potential new production or 19% of new production (Table 2.2.2). A similar calculation based on chlorophyll at the CUS/CC jet boundary suggests that 3% of new production or 5 g carbon $m^{-2} yr^{-1}$ POC may be exported as POC by advection (Table 2.2.2).

Taken together, diffusive and advective export of nitrate across the CUS/CC boundary account for 17% of upwelled nitrate – nitrate apparently not utilized in the CUS and which could increase new production by some 21% (Table 2.2.2). Surface nitrate in the offshore CUS and CC may be underutilized due to iron limitation (Johnson et al., 1999, 2001). If combined with diffusive and advective POC flux, we estimate 20% of CUS potential new production is exported to the CC (40/204 g carbon m⁻² yr⁻¹). This 20% does not include DOC export to the CC.

Such nutrient and POC advective export may take place at the surface or may occur by subduction at fronts along the CUS/CC jet boundary or inshore. Barth et al. (2002) documented a subduction event

associated with downwelling driven by cyclonic curva-ture in the flow of a CUS upwelling jet. They estimated that (1) 20% of CUS chlorophyll or 2400 tons of car-bon were advected into or beneath the CC during this event and (2) such events occur several times annually. While we note that 246 events of this magnitude would be needed to export 3% of CUS new production - our estimate for advective export of POC - subduction may nevertheless represent an important export process.

Loss to Fisheries

POC is grazed by heterotrophic zooplankton, which in turn are grazed by fish and higher trophic level organisms. Some portion of this POC is excreted by zooplankton as soluble nutrients and is recycled within the euphotic zone – we estimate 51% of CUS total production is supported by such recycled nutrients (176/345 g carbon m⁻² yr⁻¹; Table 2.2.2). Another portion of grazed POC is defecated – often packaged as fecal pellets – and will be represented in sediment trap estimates of POC sinking. A third portion becomes animal biomass. Some of this biomass is exported by fisheries mortality. Chávez et al. (1989) estimated that 3% of total production is converted into fish biomass (anchoveta) in the coastal upwelling system of Peru. If a similar fraction of total production is converted into fish off northern and central California, then CUS waters could theoretically produce roughly 1,300,000



metric tons of fish carbon – or 17,000,000 metric tons of fish (carbon to wet weight conversion as in Chavez, 1989) – annually. Lacking estimates of fish or fisheries production in the CUS, we have included the Chavez (1989) 3% in Table 2.2.2 as a placeholder.

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2.2.3.3 Atmosphere/Ocean CO₂ Exchange

10 Measured sea surface pCO₂ values along L67 are high 11 and variable inshore, and lower and less variable in 12 the CC (Fig. 2.2.9A). Within Monterey Bay, shore-13 ward of active upwelling, there is a band between the 14 coast and 20 km offshore that has an average CO₂ 15 flux of about 1 g carbon $m^{-2} yr^{-1} CO_2$ into the ocean 16 (Fig. 2.2.9B). Within the first Rosby Radius region of 17 active upwelling (20-52 km), CO₂ is on average vented 18 from the ocean on an annual basis (9 g carbon m^{-2} 19 yr^{-1}). The venting occurs primarily in spring and sum-20 mer; flux reverses and CO₂ diffuses into the ocean in 21 fall (Fig. 2.2.9A). Further offshore in the CUS (52-22 170 km), CO₂ diffuses into the ocean year round. The 23 net effect of these variations is that, on an annual basis, 24 CUS CO_2 fluxes between the ocean and atmosphere 25 are balanced (Table 2.2.2), with net ocean/atmosphere 26 flux representing less than 0.1% of new production. 27 The physical upwelling of CO₂ nearshore in spring 28 and summer is balanced by biological production and 29 drawdown offshore and in fall and winter. 30

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2.2.4 Conclusion

35 The carbon budget outlined here is a first attempt to 36 parameterize flow of carbon within the NE Pacific 37 CUS. The partitioning of carbon losses appears fairly 38 reasonable, as the independent estimates for the export 39 components fall within the bounds obtained by oth-40 ers, and when summed, account for 81 and 77% of 41 upwelled nitrate and new production, respectively. The 42 generalization of the L67 budget to the northern and 43 central California CUS provides some idea of regional 44 or system fluxes. An obvious refinement would be the 45 use of latitude-variable upwelling volumes. Except for 46 the pCO2, total and new production estimates along 47 L67, the estimates are at least partly deficient and 48 require more data and better derivation. Our DOC con-49

Nevertheless, several conclusions emerge: (1) on an annual basis, CUS air/sea CO_2 flux is near-zero, so that in-water processes dominate carbon flow; (2) sinking represents the largest POC loss term within the CUS, at 55% of new production; and (3) fully 17% of upwelled nitrate is not assimilated by phytoplankton within the CUS. Some portion of CC production is supported by this export, or conversely, this nitrate could increase CUS new production by 21%. The causes and consequences of these results need further exploration.

It is of some interest to consider the budget in relation to climate change. We have presented estimates for mean annual conditions. However, seasonally restricted estimates might be used to gauge the effects of climate change. For example, El Niño enhances and prolongs fall and winter conditions in the CUS (see Chavez et al. 2002). Although we have not prepared such seasonal model budgets, an El Niño (e.g., winter model) budget might be expected to show lower new and total production, lower DOC production, high POC e-ratios, less advective export of production to the CC, and a net flux of CO₂ into the ocean (see Chavez et al., 2002). Potential fisheries production should be less. Conversely, La Niña or a cold/anchovy phase of the PDO (see Chavez et al., 2003) (e.g., spring model) could cause increased new and total production, high DOC production, low POC e-ratios, more advective export of POC and nitrate to the POC, and perhaps a net flux of CO₂ from the CUS. Fisheries production might increase. CUS width would likely also decrease in the winter model and increase in the spring model (Collins et al., 2003; Chavez et al., 2002), affecting flux totals. Iron supply and the amount of sunlight or fog could also change.

While such predictions can be made for seasonal climate change analogues, it is not clear how global warming – the motivation for this book – might affect the CUS. Bakun (1990) suggested that a warmer earth will result in increased northwesterly wind in the NE Pacific. If so, an enhanced spring model may apply. A spring model may also apply if the subtropics spread poleward, suppressing winter and producing a longer upwelling season in the CUS, as presently occurs in the weakly seasonal, low-latitude Peruvian CUS. Whatever the effects of global warming, it seems likely they will alter carbon cycling by changing the strength or duration of upwelling within the CUS.

The carbon budget and the considerations above are 01 simplistic and highly speculative. We present them as a 02 framework for discussion and encourage others to syn-03 thesize their ideas and refine the questions that will be 04 needed to clarify carbon flow processes in NE Pacific 05 and its CUS. 06

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2.3 The Humboldt Current System²

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21 The Humboldt Current System (HCS) is one of the 22 most productive marine systems of the world (Fossing 23 et al. 1995, Daneri et al. 2000). Nevertheless, its role 24 in global biogeochemical cycling is still poorly known. 25 The scarcity of data on biogeochemical processes, the 26 strong interannual variability of the HCS and the open 27 nature of its physical borders have severely limited the 28 capacity to generate carbon and nutrient budgets for 29 this region.

30 The HCS extends, from a latitudinal perspective, 31 from central-south Chile ($\sim 42^{\circ}$ S) to northern Peru 32 $(\sim 4-5^{\circ}S)$. On its northern limit there is a dynamic 33 boundary with the Pacific Central American Coastal 34 Ecosystem (Bakun et al. 1999) and corresponds to the 35 transition zone between the Humboldt Biogeographic 36

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Province and the Panamian Biogeographic Province. This boundary is displaced at seasonal and interannual scales and it is also affected by ENSO phases (Strub et al. 1998).

The southern border of the HCS is related to the West Wind Drift Current (WWDC), which corresponds to the meridional edge of the subtropical gyre which has a permanent anticyclonic circulation in the southern Pacific. In fact the WWDC constitutes the origin of the northward Chile-Peru Current and the southward Cape Horn Current (Reid 1965, Wyrtki 1975, Silva and Neshyba 1977). The WWDC impinges upon the continent from west to northwest direction centred at about 42°S (Nuñez 1996) causing a stagnation point at 44°S around 30 miles from the coast (Dante Figueroa unpublished data). The north-south variability of the bifurcation near the coast results from local wind which, in turn, depends on the interaction between the South Pacific anticyclone and the subpolar lows (Nuñez 1996).

The offshore limit of the HCS is also variable and a matter of discussion. If only the physical domain of upwelling is taken into account the average extension of the ecosystem would be around 120 km off the coast, giving an area of 182 000 km², from 4 to 18°S (Chávez and Barber 1987). Nixon and Thomas (2001) used the surface Chl *a* contour line of 1 mg m^{-3} as a criterion to estimate the limit of the ecosystem off the Peruvian coast and found a total area of 220 000 km² (140 km width on average) for the 1998/1999 La Niña period, and an area of 120 000 km² (80 km width on average) for the 1997/1998 El Niño period. A similar temporal pattern for the whole HCS was observed by Carr (2002), noting a 50% increase of active area in the 1998/1999 annual period with respect to the 1997/1998 annual period for the Peruvian coast. Seasonal change of the extension of productive waters is also observed from maps of surface Chl a average distribution (Calienes et al. 1985). Nevertheless, the upwelling influence may extend further offshore. For instance, if a Chl a surface concentration of 0.5 mg m^{-3} is used as a threshold level that would give an offshore extension of 250 km or a total area of $400\,000\,\mathrm{km}^2$ for the 1998/1999 period (Nixon and Thomas 2000). A rather similar value is obtained if it is followed by the concept of a 'biological width' (Cushing 1971) as 2.5 times the physical width of upwelling (300 km and 450 000 km² of width and total area, respectively). AQ7