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Carbon export and regeneration in the coastal upwelling system of Monterey Bay, central California

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ABSTRACT

In order to quantify the role of coastal upwelling regions as source or sink areas for carbon, the relationships between particulate organic carbon (POC) production, export, remineralization, and accumulation were examined in Monterey Bay from 1989 through 1992. During a normal upwelling year (1989–90), a high positive correlation ($r = 0.91$) is observed between biweekly primary production and POC export at 450 m. Primary production values range from 500 mgC m^{-2} d^{-1} during the winter, to 2600 mgC m^{-2} d^{-1} in the spring and summer upwelling months. Corresponding deep-water (450 m) POC fluxes vary from a minimum of 10 mgC m^{-2} d^{-1} in December, to 120 mgC m^{-2} d^{-1} in May. In contrast, the mid-1991 through 1992 data sets obtained during the '91–92 El Nino period, show a relatively poor correlation ($r = 0.23$) between productivity and carbon export. Calculated ratios of POC export to POC production (defined as *e*-ratios) display a trend for the three-year data sets in which the *e*-ratio values are greatest during periods of low productivity and decrease to minimal values when surface production is high. Upwelling-induced, offshore Ekman transport of organic matter and probable seasonal changes in the planktonic community structure are the mechanisms likely to be responsible for the *e*-ratio trends. Based on the data sets reported from this work, a simple box model of the annual export and regeneration of particulate organic carbon is presented for the Monterey Bay region. An appreciable advective and/or recycling "loss" from the euphotic zone of 362.8 gC m^{-2} y^{-1} is estimated, representing primarily algal material transported offshore and/or recycled within the upper 100 m of the water column. Annual mid-water (~100–450 m) and deep-water (>450 m) POC remineralization rates of 71.8 gC m^{-2} y^{-1} of 7.2 gC m^{-2} y^{-1}, respectively, are reported for Monterey Bay. The average POC rain rate to the underlying slope sediments is sufficient to satisfy reported benthic utilization requirements without invoking an additional input source of POC via deep lateral advection and/or the downslope movement of particulate material.

1. Introduction and background

Although it is widely accepted that coastal and marginal oceans account for a significant portion of global primary production, we are less certain as to the quantitative role of the

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margins as source regions of various organic and inorganic materials for the adjacent open ocean. Therefore the significance of continental margins to the global ocean flux and storage of biologically active elements continues to be a topic of much interest and debate (Walsh *et al.,* 1981, 1991; Rowe *et al.,* 1986, 1994; Falkowski *et al.,* 1988; Jahnke *et al.,* 1990; Jahnke and Jackson, 1992, pp. 295–307; Toggweiler and Carson, 1995, pp. 337–360).

In an attempt to balance the global carbon budget, Walsh *et al.* (1981) proposed that a majority of the spring bloom carbon produced on the shelf must be exported to the adjacent continental slope and open ocean where a substantial portion would be buried, therein representing a major sink term in the global budget. The hypothesis was widely embraced as it helped to explain a broad spectrum of phenomena, such as the absence of organic-rich, fine-grained particle matter on the shelves, the relatively high accumulation of organic carbon in slope sediments, and the fate of the "excess" carbon resulting from lower than expected rates of macrozooplankton grazing and ingestion of spring bloom carbon occurring on the shelf (Walsh *et al.,* 1988; Biscaye *et al.,* 1994). To independently quantify the importance of continental margins in the marine biogeochemical cycling of carbon and nitrogen, Walsh (1991) and Walsh *et al.* (1991) provided estimates and a two-dimensional model of the source and fate of organic debris on continental margins, drawing upon organic carbon data sets from 32 moored sediment trap deployments. The above studies calculated that the annual supply of onwelling nutrients (e.g., new production) from the open ocean to the continental shelves via coastal upwelling, cyclonic eddy-induced upwelling, and estuarine-type exchange, could result in relatively high *f*-ratios of 0.25–0.54, thus balancing an offshore flux of dissolved and particulate carbon (Eppley and Peterson, 1979; Walsh *et al.,* 1981).

However, results from the SEEP I and II programs, whose major focus was to quantify the particulate carbon storage and/or export occurring in the Middle and South Atlantic Bight continental margins, showed that in fact there was little measured export of continental shelf organic matter to the adjacent continental slope and open ocean (Biscaye *et al.,* 1994; Falkowski *et al.,* 1988; Rowe *et al.,* 1986). The conclusions from SEEP I and II were that less than 10% (SEEP I) to less than 1% (SEEP II) of the annual primary production occurring on the Mid and South Atlantic shelf is exported, with the majority being recycled on the shelf by bacteria and micro/macro-organismal consumption (Biscaye *et al.,* 1994). In a carbon budget presented for the mid-slope depocenter of the SEEP II/Mid-Atlantic Bight region, Anderson *et al.* (1994) showed that the relatively small portion of labile, shelf-derived carbon arriving on the deep slope is rapidly remineralized primarily by bacteria, with the result that the organic carbon-rich sediments (1–2%) of the depocenter actually consist of old, refractory carbon. Extrapolation of the offshore flux of shelf-produced carbon obtained in the SEEP experiments to the entire North American coastline suggests that the shelf-derived carbon contribution to the North Atlantic represents approximately 1% of the new production in that ocean basin (Biscaye *et al.,* 1994).

Obviously the magnitude of contributions to global elemental budgets made by various geochemical processes occurring on continental margins will vary from margin to margin.

Coastal upwelling represents a highly dynamic margin process whose influence on the adjacent interior ocean in terms of nutrient input and particulate nutrient cycling may be significant. Walsh (1991) noted that on a global scale, the annual nitrate input onto continental shelves from the deep sea occurring via upwelling along eastern boundaries, exceeds that occurring on shelves influenced by estuarine exchange or by cyclonic eddies in western boundary current regions. Using a phytoplankton carbon:nitrogen ratio of 5:1, the dissolved nitrogen input via upwelling could fuel a maximum carbon export from coastal upwelling shelves of 1.1×10^{15} gC y^{-1}. Another strong indication of the potential global significance of POC and PON cycling processes occurring within eastern boundary/coastal upwelling margin regions was presented by Jahnke *et al.* (1990). Reporting on results from *in-situ* benthic exchange and metabolism experiments conducted off the coast of central California, Jahnke *et al.* (1990) argued that at least 50% of the total flux of organic carbon to the northeast Pacific sea floor occurs in the eastern boundary upwelling margin areas within 500 km of the continental slope.

Several studies of sedimentary oxygen consumption and demand have provided strong evidence that greater rates of detrital POC delivery and benthic remineralization exist in the Pacific Basin as compared with the Atlantic (Jahnke and Jackson, 1992, pp. 295–307; Rowe *et al.*, 1994). Inter-basin variability in the supply rate (and lability) of organic matter transferred to the adjacent interior ocean from continental margins may be in part responsible for the significant differences observed between the Pacific and Atlantic basins in terms of sea floor organic carbon delivery and remineralization rates. Coastal upwelling, a process typically associated with elevated rates of new production, POC production, and carbon burial, is prevalent along the eastern boundaries of both the Pacific and Atlantic basins. However, we do not have a comprehensive understanding of the role that coastal upwelling systems, or continental margins overall, play in terms of their contribution of particulate and dissolved organic matter to adjacent ocean basins. If significant offshore fluxes of POM and DOM exist across particular continental margins, such processes may in fact provide a way to balance the frequently observed mismatch between new production estimates and sediment trap-measured POM export (Toggweiler, 1989, pp. 65–83).

The foregoing discussion leaves one with the question: "What is the quantitative coupling (or decoupling) between the production, export and burial occurring in the highly productive waters of coastal upwelling regions, and do such regions represent carbon source areas for the open ocean?" The primary focus of this study was to provide POC source and sink measurement terms within the context of a box model for the Monterey Bay coastal upwelling region in order to help answer this question.

2. Study site

Monterey Bay, located on the central coast of California, is the largest open bay along the U.S. west coast with unrestricted communication to the adjacent open Pacific (Rosenfeld *et al.*, 1994). The Bay is also the site of the Monterey Submarine Canyon, one

of the deepest and most extensive submarine canyon systems in the world (Shepard, 1973). Between March and October, upwelling occurs more or less continually with intermittent periods of enhancements and relaxations in response to local wind forcing and interactions with a meander of the California Current (Rosenfeld *et al.,* 1994). Water upwelled north of Monterey Bay at Pt. Ano Nuevo and advected alongshore has been identified as the source of cold, salty, nutrient-rich water frequently documented near the surface in the bay during periods of maximum upwelling from March through July (Rosenfeld *et al.,* 1994). Offshore-trending tongues of the water upwelled at the coastal headland result in filaments of cold water that extend hundreds of kilometers and have been documented in high-resolution satellite infra-red imagery (Breaker and Mooers, 1986; Chelton *et al.,* 1987; Tracy, 1990).

During normal upwelling years (as opposed to El Nino conditions), primary production off central California is greatest in the spring and summer, coincident with the shoaling of the thermocline and nutricline (Bolin and Abbott, 1963; Chavez, 1996). In Monterey Bay during the months of March through July, high rates of integrated primary production exceeding 1000 mgC m^{-2} d^{-1} are measured within the euphotic zone, coincident with enhanced chlorophyll levels and elevated surface water nitrate concentrations (Chavez, 1996). The productive, upwelling ecosystem of Monterey Bay is well known for its unique and diverse biological community which has resulted in a significant amount of public and scientific interest in the area. Such interest led to the development of the Monterey Bay Aquarium Research Institute in 1987 and the designation of the region in and around Monterey Bay as a National Marine Sanctuary in 1991. The research and results presented here are in direct response to one of the major scientific objectives outlined in the original "Scientific Initiatives Statement" of the Monterey Bay Aquarium Research Institute, namely to: "Determine the time-varying production and flux of carbon and associated biogenic elements in the eastern boundary current of the Pacific and evaluate the exchange of such elements with the deep-sea and the underlying sediments."

3. Methods

Measurements of time-series biogeochemical fluxes and primary production were completed at two stations located near the western edge of the Bay where water depths range from 650 to over 1000 m (Fig. 1). Samples of settling particulate matter were obtained using a cone-shaped, baffled sediment trap (produced by AMI, Aquatic Monitoring Institute, Anderson, 1977) deployed from August 1989 through November 1992 at an average depth of 450 m on a subsurface mooring located approximately 20 km offshore (Station S1, Fig. 1). Particulate samples were collected in a plexiglass sample tube attached to the base of the trap cone and pre-poisoned with a 4% density-adjusted formalin solution, buffered to pH 7.9–8.0 at 4°C (Pilskaln and Paduan, 1992; Fig. 2). Individual biweekly flux events were separated within the sample tube by layers of teflon beads that were dispensed every two weeks from an intervalometer instrument suspended inside the trap cone (Anderson, 1977; Fig. 2). The steep-angled cone design of the AMI traps, coupled with a

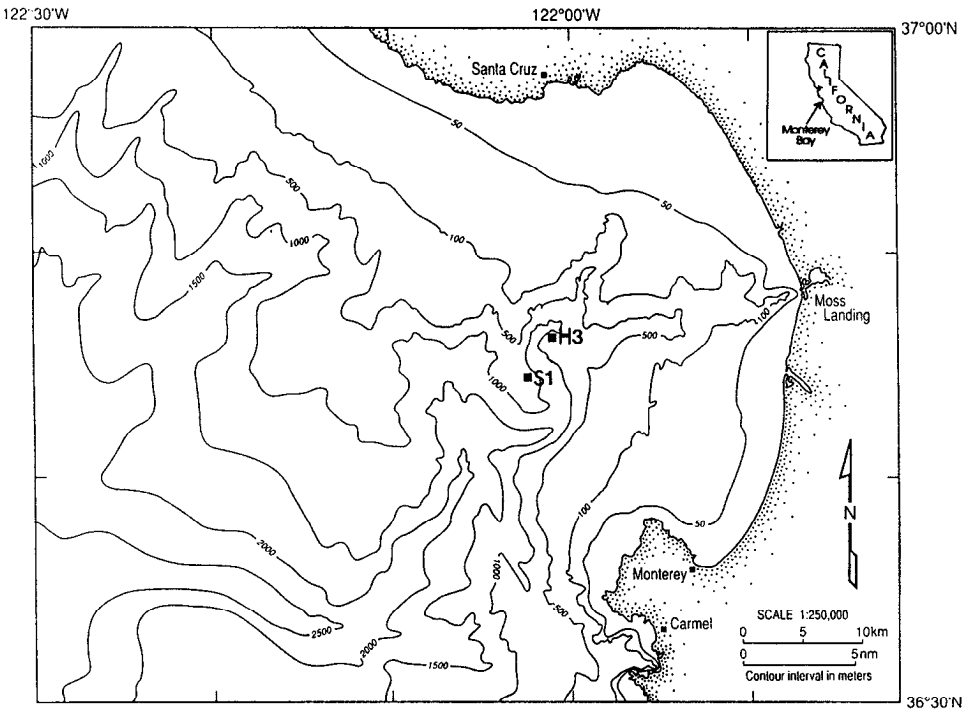

Figure 1. Study region. Locations in Monterey Bay of the S1 time-series sediment trap mooring site and the H3 station where biweekly to monthly measurements of primary production and new production were conducted. Depth contours are in meters.

baffled collection area of 0.05 m^2 and a small individual baffle cell diameter (approximately 12 mm), was found to solve a trap clogging problem encountered when we deployed a second cone trap on the mooring that had a larger collection diameter (0.5 m^2) and a greater baffle cell diameter. The AMI trap samples were retrieved every six months and processed and analyzed chemically according to the methods detailed in Pilskaln and Paduan (1992). Individual biweekly samples were sieved at 400 μm to remove the teflon beads, split into quantitative aliquots using a Honjo-Erez rotary precision sample splitter (Honjo, 1980), and carefully picked for swimmers under a dissection microscope prior to chemical analysis. Total, organic, and inorganic carbon composition of particle samples was measured using a UIC, Inc. Coulometrics Full Carbon System Coulometer, organic CHN analyses were performed on acidified samples with a Carlo Erba CHN Analyzer, opaline silica was determined using a sodium carbonate extraction method adapted from Eggimen *et al.* (1980) and Mortlock and Froelich (1989) and measured spectrophotometrically, and lithogenic content of the trap material was obtained by subtraction of the opaline silica value from the total noncombustible fraction of the sample (Honjo, 1980; Pilskaln and Paduan, 1992).

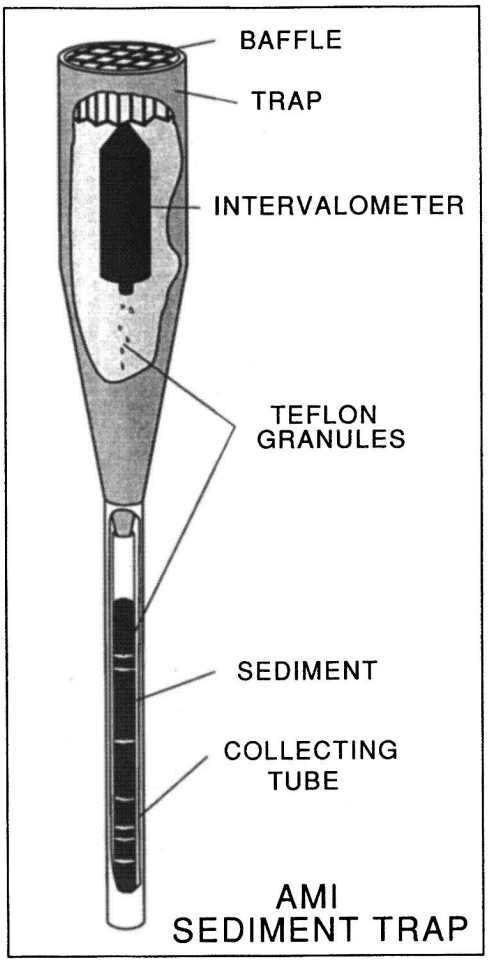

Figure 2. Schematic of the AMI intervalometer sediment trap deployed at the S1 site depicting the location of the teflon granule-dispensing intervalometer suspended within the cone. Teflon granules were dispensed every two weeks, creating a 0.5–1.0 cm layer between each biweekly accumulation of particulate material within the 2.3 cm diameter acrylic collecting tube at the base of the trap cone. Collection area of the trap was 0.05 m^2, individual baffle cell size was 12 mm.

Biweekly measurements of primary productivity reported in this paper were conducted between August 1989 and December 1992 at Station H3, a long time-series CalCOFI site in Monterey Bay located approximately 4 km northeast of Station S1 (Bolin and Abbott, 1963; Fig. 1). Radiocarbon (^{14}C) uptake measurements utilizing 24 hour deckboard incubations were completed on water samples obtained at Station H3, from which euphotic zone, depth-integrated primary production rates (in mgC m^{-2} d^{-1}) were calculated following the procedures described in Chavez *et al.* (1991). Detailed information on the radiocarbon uptake measurements completed in Monterey Bay are the subject of another

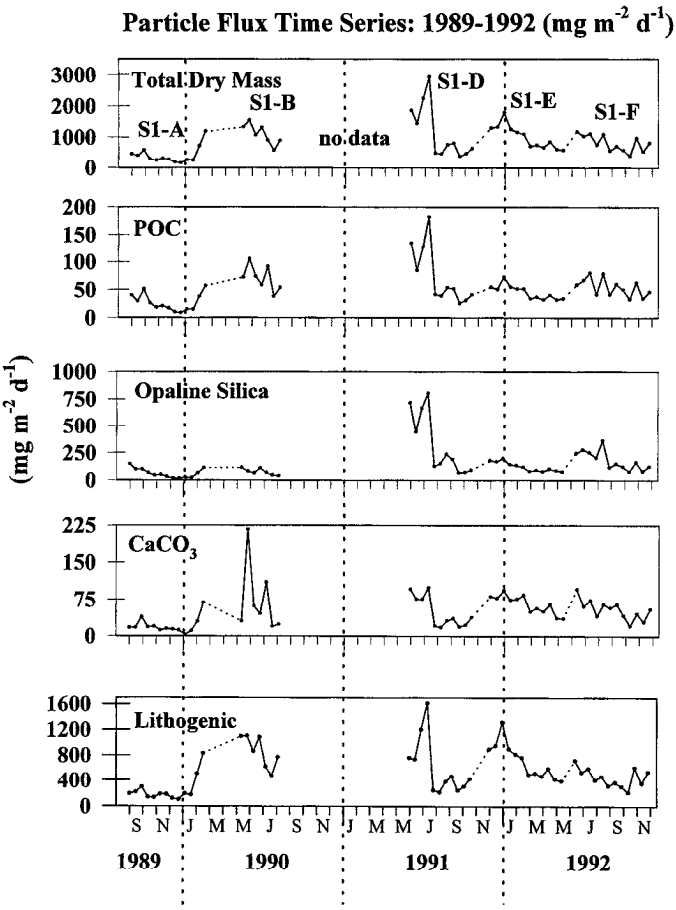

Figure 3. 1989–1992 time-series biweekly fluxes of POC, opaline silica, $CaCO_3$, and lithogenic material obtained from the sediment 450 m trap.

paper specifically addressing the time-series primary productivity study in Monterey Bay (Chavez, 1996).

4. Results

Time-series plots of total dry particle mass flux in Monterey Bay and the fluxes of major geochemical components, are shown in Figure 3 and Table 1 along with the dates of the biweekly trap collections. The sediment trap was initially deployed in August 1989 and retrieved in February 1990 (designated deployment S1-A). Redeployment did not occur until May 1990 when the system was moored until August 1990 (designated deployment S1-B). An eight-month hiatus in the collection of the time-series particulate samples occurred between August 1990 and May 1991 due to a trap malfunction and was designated deployment period S1-C for which no data exist. Trap turnarounds and

Table 1. Monterey Bay time-series sediment trap data.

Event #	Dates	Dry Mass Flux (mg/m²/d)	% Total Carbon	% $CaCO_3$	$CaCO_3$ Flux (mg/m²/d)	% Organic Carbon	POC Flux (mg/m²/d)	% Opal	Opal Flux (mg/m²/d)	% Litho-genic	Litho. Flux (mg/m²/d)
					Monterey Bay S1-A: 1989–1990						
1	8/23/89–9/6/89	458.0	9.4	3.7	16.9	8.7	39.8	32.1	147.3	40.9	187.5
2	9/6/89–9/20/89	406.6	7.9	4.2	17.1	7.1	28.9	23.6	96.1	52.3	212.5
3	9/20/89–10/4/89	574.0	10.1	6.8	39.0	8.8	50.5	17.3	99.0	51.2	294.2
4	10/4/89–10/18/89	290.2	10.1	6.3	18.3	8.9	25.8	21.9	63.6	47.1	136.6
5	10/18/89–11/1/89	244.0	9.1	7.9	19.3	7.6	18.5	17.0	41.6	52.6	128.2
6	11/1/89–11/15/89	310.0	7.5	3.7	11.5	6.8	21.1	16.0	49.5	58.4	181.1
7	11/15/89–11/29/89	279.7	7.1	5.3	14.8	6.1	17.1	10.5	29.3	63.7	178.2
8	11/29/89–12/13/89	183.4	6.9	7.4	13.6	5.5	10.1	9.1	16.6	64.3	118.0
9	12/13/89–12/27/89	157.7	6.8	7.4	11.7	5.4	8.5	9.1	14.3	63.9	100.8
10	12/27/89–1/10/89	263.1	6.0	1.1	2.9	5.8	15.3	9.7	25.5	70.5	185.5
11	1/10/90–1/24/90	250.0	6.7	4.2	10.5	5.9	14.8	8.4	20.9	68.1	170.4
12	1/24/90–2/7/90	711.4	6.1	4.2	29.9	5.3	37.7	8.8	62.4	70.7	503.2
13	2/7/90–2/21/90	1182.3	5.9	5.8	68.6	4.8	56.8	9.4	111.4	70.1	828.6
					Monterey Bay S1-B: 1990						
1	5/5/90–5/19/90	1322.0	5.9	2.3	30.4	5.5	72.4	8.5	111.8	82.9	1096.0
2	5/19/90–6/2/90	1546.0	9.5	14.0	216.0	6.8	105.6	5.1	79.2	71.4	1103.5
3	6/2/90–6/16/90	1068.0	8.0	5.7	60.9	6.9	74.0	5.8	62.4	80.5	859.3
4	6/16/90–6/30/90	1303.0	5.2	3.5	45.6	4.5	58.4	8.3	108.3	83.0	1081.3
5	6/30/90–7/14/90	904.0	12.4	12.1	109.4	10.1	91.4	7.4	66.8	68.1	615.7
6	7/14/90–7/28/90	578.0	7.2	3.4	19.7	6.6	37.9	7.7	44.5	81.7	472.2
7	7/28/90–8/11/90	888.0	6.6	2.7	24.0	6.1	54.0	4.2	37.7	86.5	767.7
8	8/1/90–8/20/90	2440.0	6.6	3.7	90.3	5.9	143.0	12.3	300.0	77.4	1888.7
					Monterey Bay S1-D: 1991						
1	5/24/91–6/06/91	1858.0	7.9	5.2	96.4	7.3	134.9	38.6	716.3	40.9	759.4
2	6/06/91–6/20/91	1443.0	6.5	5.3	75.8	5.9	84.8	30.7	443.0	50.8	733.7
3	6/20/91–7/04/91	2231.0	6.1	3.4	75.8	5.7	126.7	29.9	667.1	53.8	1200.9
4	7/04/91–7/18/91	2930.0	6.6	3.4	98.9	6.2	181.8	27.5	804.3	55.0	1611.7
5	7/18/91–8/01/91	484.0	8.9	4.4	21.4	8.4	40.5	25.7	124.4	50.8	245.8
6	8/01/91–8/15/91	469.0	8.8	3.9	18.4	8.3	38.9	32.4	152.0	45.5	213.2
7	8/15/91–8/29/91	761.0	7.6	4.0	30.8	7.1	54.0	31.1	236.3	49.2	374.8
8	8/29/91–9/12/91	806.0	7.0	4.5	35.9	6.5	52.2	23.3	187.4	57.6	464.3
9	9/12/91–9/26/91	385.0	7.3	4.9	18.8	6.7	26.0	17.2	66.2	62.7	241.5
10	9/26/91–10/10/91	466.0	7.3	4.9	22.9	6.7	31.2	15.3	71.3	65.4	304.6
11	10/10/91–10/24/91	640.0	7.1	6.0	38.1	6.3	40.6	14.0	89.3	66.1	423.1

Table 1. Monterey Bay time-series sediment trap data. (Continued)

Event #	Dates	Dry Mass Flux (mg/m²/d)	% Total Carbon	% $CaCO_3$	$CaCO_3$ Flux (mg/m²/d)	% Organic Carbon	POC Flux (mg/m²/d)	% Opal	Opal Flux (mg/m²/d)	% Litho-genic	Litho. Flux (mg/m²/d)
					Monterey Bay S1-E: 1991–1992						
1	11/21/91–12/06/91	1294.0	5.0	6.3	81.4	4.3	55.2	13.9	179.2	69.4	897.6
2	12/06/91–12/21/91	1325.5	4.6	5.9	77.6	3.9	51.3	12.7	167.7	71.8	951.6
3	12/21/91–1/05/92	1778.0	4.7	5.3	93.3	4.1	72.6	11.1	196.5	73.8	1311.7
4	1/05/92–1/20/92	1251.5	5.1	5.9	74.3	4.4	55.1	11.4	142.7	71.9	900.2
5	1/20/92–2/04/92	1149.5	5.4	6.6	76.4	4.6	52.4	11.6	132.8	71.0	816.0
6	2/04/92–2/19/92	1092.0	5.7	7.7	84.4	4.8	52.2	10.8	117.9	69.7	761.5
7	2/19/92–3/05/92	704.5	5.6	7.1	50.0	4.8	33.6	11.2	78.9	70.1	493.9
8	3/05/92–3/20/92	749.0	5.9	7.6	57.0	4.9	37.0	12.1	90.3	68.8	515.1
9	3/20/92–4/04/92	669.5	5.7	7.5	50.5	4.8	31.9	11.5	77.0	69.6	466.2
10	4/04/92–4/19/92	846.0	5.6	7.6	64.5	4.7	39.8	11.9	100.3	69.3	586.2
11	4/19/92–5/04/92	614.5	6.0	6.0	36.9	5.3	32.5	14.1	86.3	67.6	415.2
12	5/04/92–5/19/92	583.5	6.6	6.2	36.3	5.9	34.2	12.9	75.0	66.7	389.3
					Monterey Bay S1-F: 1992						
1	6/04/92–6/19/92	1173.9	6.0	8.1	95.6	5.0	58.8	20.9	245.3	61.0	716.3
2	6/19/92–7/04/92	1031.5	7.2	5.9	60.8	6.5	67.2	26.9	277.5	51.3	529.3
3	7/04/92–7/19/92	1111.2	8.0	6.6	73.4	7.2	79.9	22.5	250.0	53.3	592.8
4	7/19/92–8/03/92	750.2	6.2	5.4	40.6	5.5	41.3	27.0	202.5	53.8	403.4
5	8/03/92–8/18/92	1084.5	8.0	6.0	65.1	7.3	78.8	33.4	362.2	42.5	460.5
6	8/18/92–9/02/92	570.7	8.4	10.1	57.7	7.2	41.2	20.2	115.3	54.7	312.0
7	9/02/92–9/17/92	709.3	9.6	9.2	65.0	8.5	60.1	20.7	146.8	51.3	364.1
8	9/17/92–10/02/92	585.4	9.4	7.2	42.0	8.6	50.1	20.9	122.3	51.7	302.7
9	10/02/92–10/17/92	396.6	9.0	5.3	21.1	8.3	33.1	19.3	76.5	54.0	214.2
10	10/17/92–11/01/92	971.5	7.0	4.7	45.7	6.5	62.7	16.7	162.2	62.3	605.7
11	11/01/92–11/16/92	544.0	6.9	5.3	28.7	6.2	33.9	14.4	78.3	65.0	353.3
12	11/16/92–12/01/92	816.3	6.5	6.7	54.6	5.7	46.2	15.1	123.3	65.7	536.5

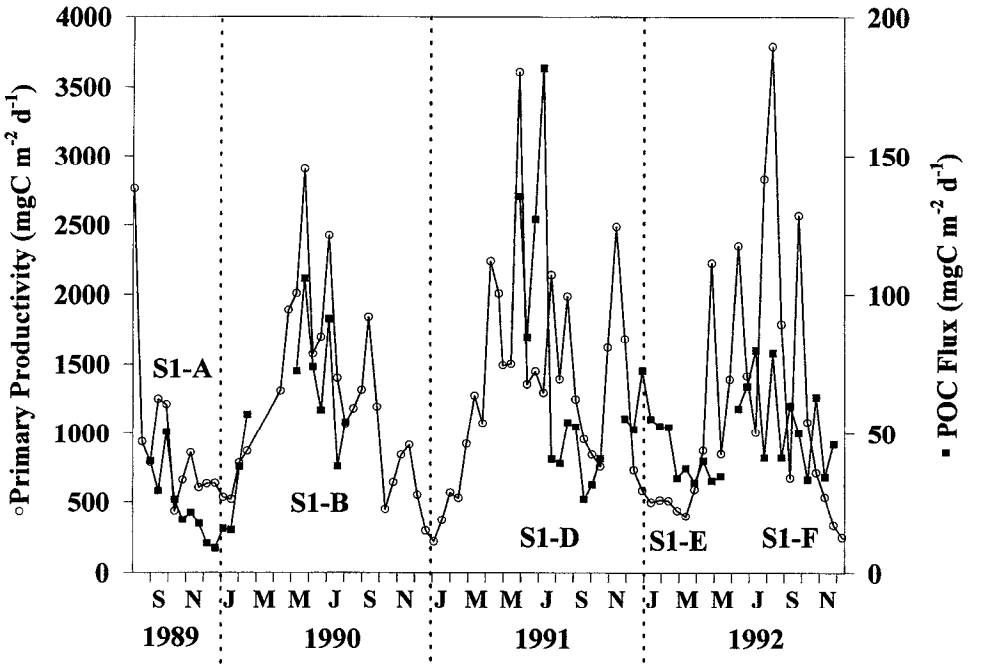

Figure 4. Three year time-series plot of daily POC flux at 450 m (solid squares) and primary production at Sta. H3 (open circles) in mgC m^{-2} d^{-1}. Calculated from biweekly POC fluxes and biweekly primary production measurements.

redeployments (e.g., S1-D-S1-F) occurred every 5–6 months from May 1991 to December 1992 (Table 1).

With the exception of 1992, all particulate flux components measured—total mass, opaline or biogenic silica, organic carbon, calcium carbonate, and lithogenics—display strong seasonal variations, with primary flux peaks occurring during the spring/summer upwelling months and minimal flux values obtained in the late fall and winter months (Fig. 3). The total mass flux over the three years varied by an order of magnitude (e.g., 158–1560 mg m^{-2} d^{-1}) and the individual geochemical component fluxes varied by factors of two to three between upwelling versus nonupwelling months (Fig. 3, Table 1). The particulate samples consisted of 40–50% biogenic material (e.g., $CaCO_3$, opaline silica, organic carbon and nitrogen) and 50–60% lithogenic matter in the form of clay and fine silt particles (Table 1).

Primary production in Monterey Bay exhibits a strong seasonal pattern, with low and uniform rates of approximately 500 mgC m^{-2} d^{-1} from October to February, and higher, more variable rates on the order of 1500 mgC m^2 d^{-1} during the upwelling and summer months of March–July/August (Chavez, 1996; Fig. 4). The onset of El Nino conditions off central California in 1991–92 was associated with an anomalous and extensive warming of the subsurface and surface waters beginning in late 1991, documented by time-series

temperature data sets obtained from two meteorological instrument moorings located in the Monterey Bay (Chavez *et al.,* 1994; Chavez, 1996). Sea surface temperature measured 14°C in March 1992 compared to 11°C in March 1990 (Chavez *et al.,* 1994; Chavez, 1996). Significant effects of the 1992 El Nino were seen in the March '92 surface water nitrate levels, total phytoplankton abundance, and primary production rates, all of which were reduced by factors of three to four compared to March 1990 (Chavez, 1996). March 1992 primary productivity levels were on the order of only 500 mgC m^{-2} d^{-1} whereas productivity values exceeded 1000 mgC m^{-2} d^{-1} in March 1990 and 1991 (Fig. 4). The difference between the March 1990 and 1992 productivity levels is a reflection of the delay in the onset of spring bloom conditions of approximately two months (e.g., April versus February) occurring in 1992 relative to previous years (Fig. 4).

A pronounced abundance of centric diatom valves as well as centric valve fragments contained within zooplankton fecal pellets was observed in the trap material collected during the spring and summer upwelling periods and documented by SEM (Fig. 5). Diatom valve counts completed on the majority of the 1989–1992 trap samples show a significantly higher average diatom valve flux occurring during the upwelling months of 8.7×10^6 valves m^{-2} d^{-1}, compared with an average valve flux of 2.5×10^5 valves m^{-2} d^{-1} calculated for the nonupwelling season. A comparison of mean diatom valve fluxes to the 450 m trap in 1989–1990 versus late 1991–1992 reveal slightly higher fluxes in the 1989–90 period of 8.2×10^6 valves m^{-2} d^{-1} compared with 4.7×10^6 valves m^{-2} d^{-1} for the 1991–92 El Nino period. Zooplankton fecal pellets larger than 50 μm (measured as pellet diameter) were also counted in the 1989–92 time-series trap samples to determine seasonal pellet flux values. Average pellet fluxes are slightly higher during the upwelling season (4.0×10^5 pellets m^{-2} d^{-1}) versus 2.5×10^5 pellets m^{-2} d^{-1} calculated for the nonupwelling season. No significant difference in zooplankton fecal pellet fluxes was observed between the normal upwelling year (e.g., 1989–90) compared to the 1991–92 El Nino period, as determined by the Student's *t*-test analysis of variance ($P < 0.05$).

Both $CaCO_3$ and opaline silica display a strong positive correlation with the POC flux throughout the time-series data set (Fig. 6). Peak fluxes of opal and POC occur during periods of diatom blooms between March and June, 1990–1992 (Figs. 3 and 4, Table 1), with the largest peaks observed in the spring of 1990 and 1991 following large blooms of colonial centric diatoms (Chavez, 1996).

Secondary peaks in POC and opal fluxes occur during the fall of 1989 and 1991 and are attributed to blooms of the pennate diatom *Nitzschia* based on microscopic examination of the trap particulate samples and filtered water samples, the latter obtained on primary productivity measurement cruises (Chavez, 1996; Fig. 5). Radiolarians and silicoflagellates settling into the trap also contribute to the opaline silica flux, with the most frequent observations of these biogenic components noted in samples that were obtained during the upwelling season (Fig. 5). The opaline silica content of the collected particulate matter (reported as percent dry weight), displays the widest range of all analyzed components over the time-series, varying from a low of 4% to high of 30% (Table 1). Maximum contribution

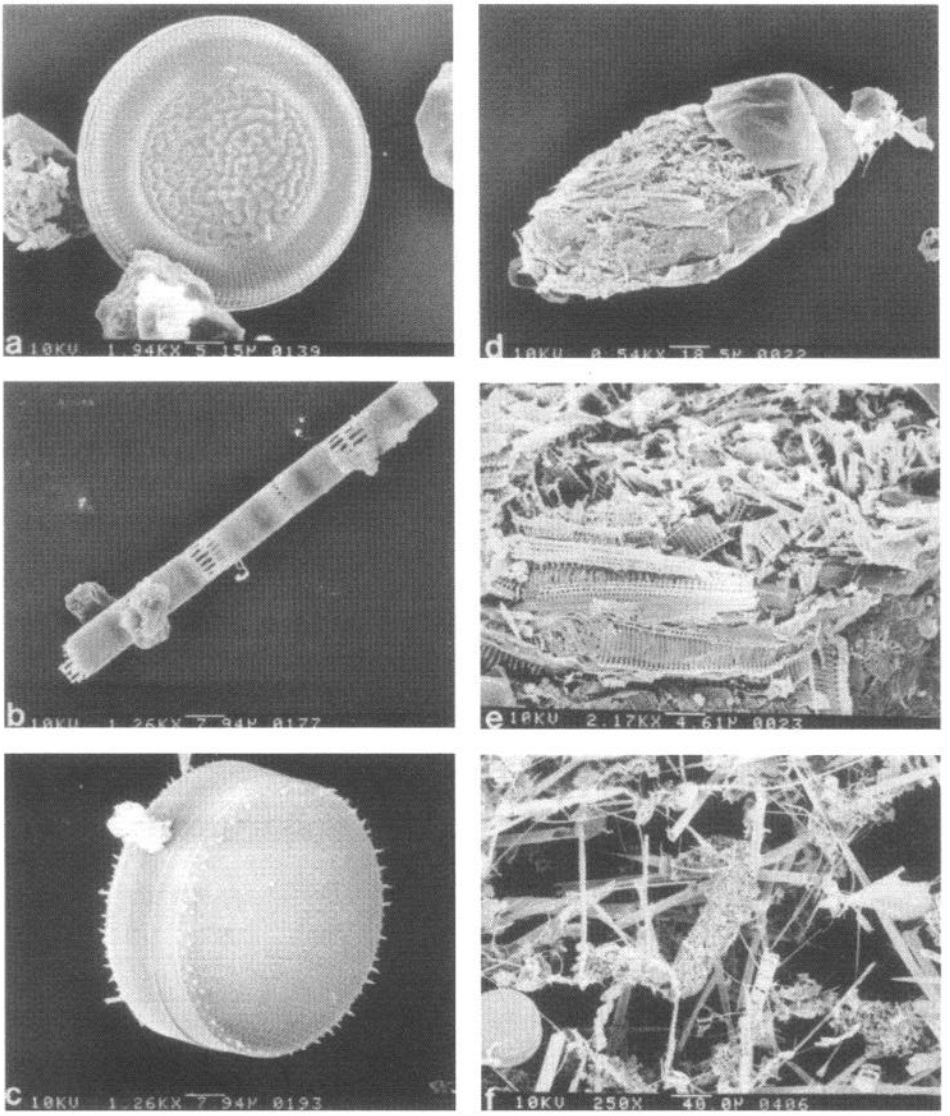

Figure 5. SEM micrographs of the major biogenic skeletal components collected in the sediment trap. Scales noted on each micrograph. (a–c) Large chain-forming centric diatoms typical of late spring/summer Monterey Bay sediment trap collections. (d–e) Zooplankton fecal pellet and pellet surface. Collected 9/89 during a fall *Nitzschia* and *Pseudonitzschia* bloom. Note dominance of diatom fragments contained in pellet. (f) Sediment trap particulate material obtained in mid-August 8/91, showing high abundance of *Nitzschia* and *Chaetocerous*. (g–i) Radiolarians and silicoflagellates were moderately common components of the trapped particulate matter, with relatively greater occurrences in samples collected during the upwelling months. (j) A rare planktonic foraminifera obtained from the 2/90 particulate sample. The rarity of these protozoans in the trap samples was not due to post-collection dissolution as the tests were in good to excellent condition and the sample pH measured upon recovery was generally above 7.7. (k) Tintinid obtained from the 9/89 trap sample. Note *Chaetocerous* spines as major lorica component (l) Lorica of tintinid consisting exclusively of cococcoliths. The tintinid was obtained from the late May '90 trap particle sample which contained numerous coccoliths, occasional coccospheres, and a relatively high calcium carbonate content of 14%.

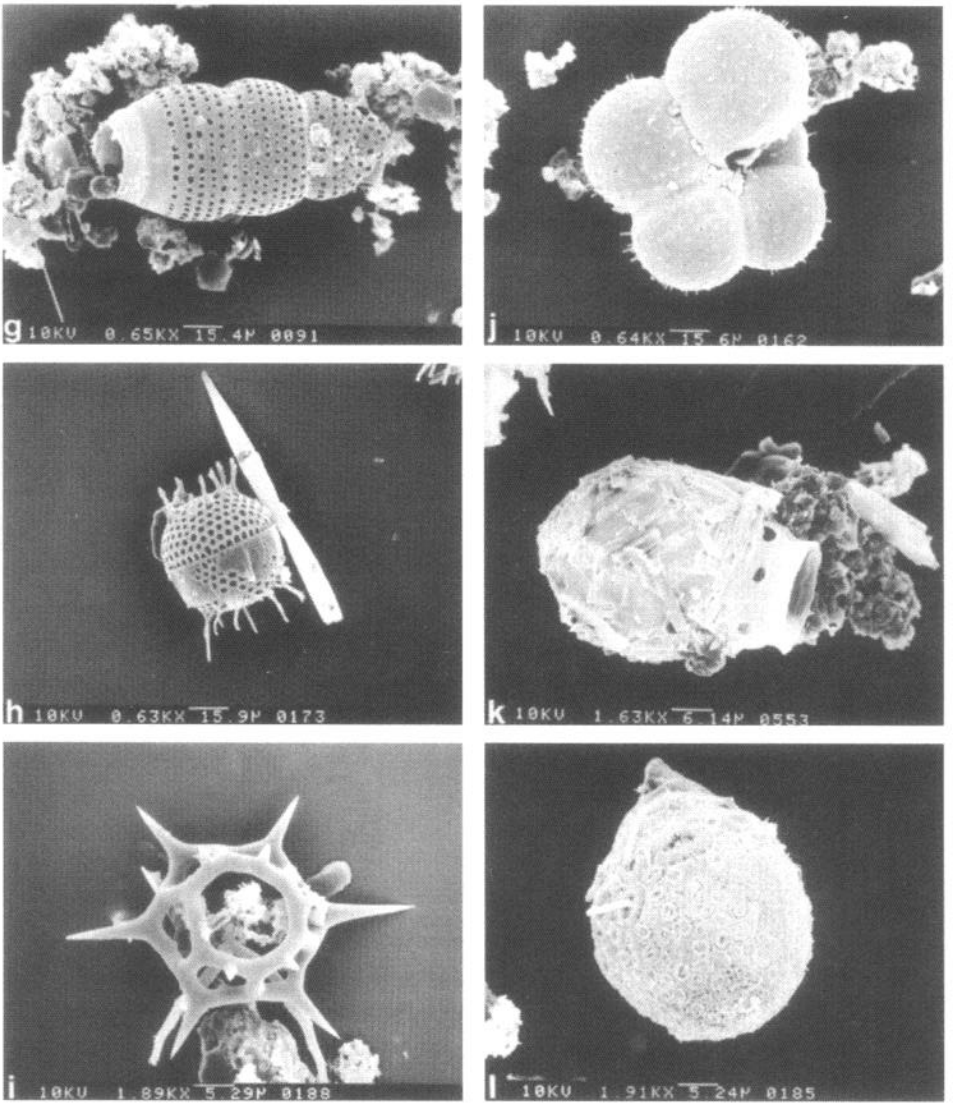

Figure 5 (Continued)

of opal to the mass flux of particle material is seen between the months of June and September in 1991 and 1992, and in the 1989 August–September time period (Table 1). Chemical analysis of the top 1–2 cm of surface sediments collected in 1990 with a box core deployed 1.8 km from the S1 trap mooring location, reveals appreciable opal preservation within the near-surface sediments reflected by a mean sedimentary opaline silica content of 36% (two samples analyzed in triplicate; Pilskaln, unpublished data).

The percentage of organic carbon in the trap particulate material varies over the time

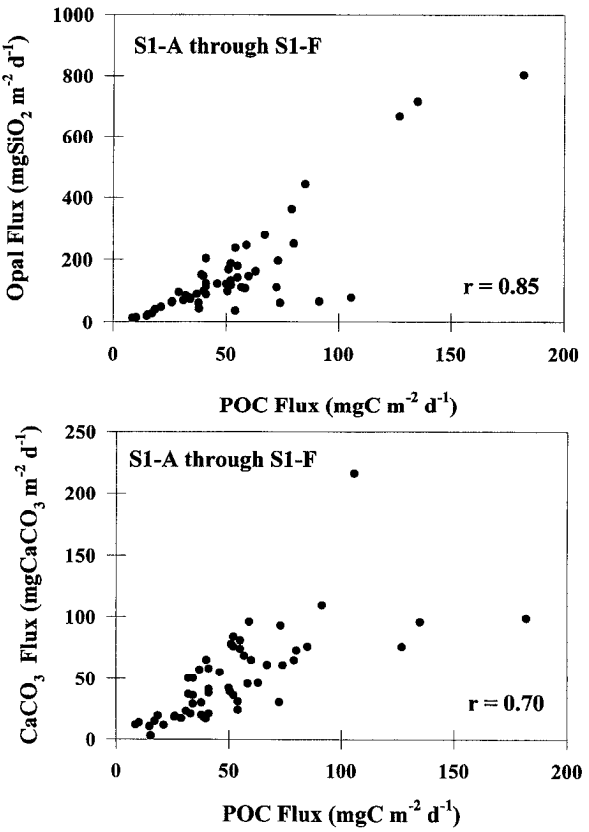

Figure 6. Regression plots of POC flux vs. opaline silica and $CaCO_3$ fluxes for the complete time series. Each point corresponds to a biweekly-collected sample.

series, with values of 4–5% and fluxes of 10–30 mg POC m^{-2} d^{-1} typical of winter month/nonupwelling samples, and 7–8% POC in the spring–summer/upwelling periods, representing organic carbon fluxes of 50–182 mg m^{-2} d^{-1} (Table 1). The average POC content of the particulate material collected in the 1989–90/upwelling years was 7%, only slightly higher than the value of 6% POC obtained for the material collected during the El Nino period of late 1991 through 1992 (S1-E and F; Table 1). Resultant POC fluxes to the 450 m trap in late 1991–1992 display a substantially smaller range (32–80 mgC m^{-2} d^{-1}) than those measured in 1989–90 which vary from a low of 10 mgC m ^{2} d ^{1} to a high of 143 mgC m^{-2} d^{-1} (Table 1).

Previously reported POC fluxes obtained at depths of 250–700 m in the Monterey Bay region from the VERTEX MULTITRAP experiments, range from 25–252 mg POC m^{-2} d^{-1} measured at stations located 30–80 km off the Monterey Peninsula during upwelling and nonupwelling periods (Knauer *et al.*, 1979; Martin *et al.*, 1987; Knauer and Martin, 1981). Variations in the trapping efficiencies of the cylindrical MULTITRAPS versus that

of moored, cone-shaped traps, as well as substantial differences between the VERTEX trap experiments and ours in terms of sample poison, swimmer removal techniques, and length of trap sampling periods, are all factors which could contribute to potentially large differences in the POC fluxes measured in the two studies (Gardner, 1980; 1985; Knauer and Asper, 1989; Buesseler, 1991; Honjo *et al.,* 1992). Considering these factors, it is encouraging to see similar POC flux data from the two Monterey Bay particle trap programs.

Calcium carbonate content of the trapped particulates in the form of coccolithophores, coccolith-covered tintinnid lorca, and occasional planktonic foraminifera, represent less than 8% of the sinking particle matter collected between 1989–1992 (Table 1). Occasional increases in the carbonate content of the trap samples are attributed to an influx of coccolith carbonate during the summer months, observed with SEM (Fig. 5). Our results are substantially different from the calcium carbonate fluxes reported from a time-series sediment trap study conducted in 1990 in the southern California Borderland Basin region where the average $CaCO_3$ content of biweekly-collected particulate matter obtained with a moored, cone-style trap deployed for six months at 500 m in the San Pedro Basin was 19%, as compared to 8% in Monterey Bay (Thunell *et al.,* 1994). This difference is believed to be due to the relative abundance of planktonic foraminifera collected in the southern California trap as compared to the Monterey Bay particulate samples in which planktonic forams are quite rare. Surface sediment analyses on a Monterey Bay box core confirms the lack of foraminiferal carbonate as a major component of the sediments in this region. Calcium carbonate content of the top 1 cm of box core sediments obtained near the S1 trap mooring site are less than or equal to 1%, whereas San Pedro Basin surface sediments contained 5–10% calcium carbonate (Pilskaln, unpublished data; Thunell, personal communication; Schwalbach and Gorsline, 1985; Berelson *et al.,* 1987).

The lithogenic content of the trap particulates and the resultant lithogenic fluxes are extremely high, generally representing over 50% of the material collected in the trap over the time series (Table 1). This finding is not surprising considering the continental margin location of the mooring site and the high potential for periodic resuspension and lateral advection of fine sediments from the adjacent shelf and upper slope. Additionally, seasonal increases in the river inflow into Monterey Bay could result in substantial influxes of suspended matter into the deep waters of the bay. Typical winter-time maxima in river flow into the Bay are coincident with frequent observations of brown turbid plumes adjacent to the Salinas, Pajaro, and Carmel Valley Rivers, extending out from the Monterey Bay coast several kilometers (Pilskaln, personal observation). Such an event of high influx into the bay of sediment-laden run-off may explain the winter peak observed in the 1991 lithogenic flux at which time coastal California began to experience high rainfall levels, marking the end of the several year drought (National Weather Service, personal communication). Similar high percentages of lithogenic material were also reported from the San Pedro Basin trap experiment and were attributed to the periodic resuspension and advective

offshore transport of shelf sediments during winter periods of increased rainfall and river flow (Thunell *et al.,* 1994).

5. Discussion

During a normal upwelling year in Monterey Bay (e.g., 1989–1990: S1A-S1B), we observe a tight temporal coupling between depth-integrated, euphotic zone primary production and deep water POC delivery, reflected in the strong positive correlation ($r = 0.91$) between primary production and biweekly POC export measured below the euphotic zone at a depth of 450 m (Figs. 4 and 7). These data, in addition to the positive correlation observed between opaline silica and POC fluxes throughout the time series (Fig. 6), are indicative of the overall control which seasonal phytoplankton blooms (largely dominated by diatom species) exert over carbon export in this system. This relationship is also reflected in the composition of the trapped particle matter which we found to be overwhelmingly dominated by mucoid diatom flocs in 1989–90, but not in 1992.

The strong positive relationship between carbon production and export begins to weaken significantly however in mid-1991 (S1-D) through 1992 (S1E-F), with the result that by the 1992 El Nino period, a poor positive correlation ($r = 0.23$) exists between productivity and mid-water carbon export (Fig. 7). This change in the POC production and export relationship in Monterey Bay is primarily linked to the significant change observed in the 1991–1992 plankton community structure. According to Chavez (1996), the plankton community in Monterey Bay was transformed in 1991–92 from a normally diatom-dominated system to one in which picoplankton and flagellates represented the major planktonic components, with a conspicuous absence of diatoms in 1992 until late April/May. The change in the plankton community resulted in significantly lower surface chlorophyll *a* levels (0.5 $\mu g\ l^{-1}$) and primary productivity rates (500 $mgC\ m^{-2}\ d^{-1}$) as compared with previous years (Chavez, 1996). Lower mean algal carbon production rates in 1992 and a concomitant decrease in the abundance and deep-water delivery of fast-settling phytodetritus would contribute to the decoupling of carbon production and particulate carbon export measured on a relatively fine-scale, biweekly basis.

The temporal decoupling between productivity and export peaks suggests that a change in the particle type and sinking rate occurred between 1989–90 and 1991–92. To account for the almost synchronous occurrence of the 1989–90 peaks in the biweekly primary production and POC fluxes at 450 m, surface-produced particulate matter sinking below the euphotic zone would have to exhibit sinking rates of 45–90 m per day (for arrival at 450 m in 5–10 days). The 4–6 week time difference between the occurrences of POC production and export peaks in mid-1991 through 1992, indicates a decrease in particle sinking rate to 10–15 m per day (Fig. 4). These lower particle sinking rates are within the range reported for small (0.5–1.0 mm) marine snow (Asper, 1987; Alldredge and Gotschalk, 1988; Pilskaln *et al.,* 1991). Pilskaln *et al.* (1991) determined from quantitative, video-based surveys of marine snow size and abundance in Monterey Bay (conducted between 1990–92) that this small size class of marine snow with an *in-situ* measured average

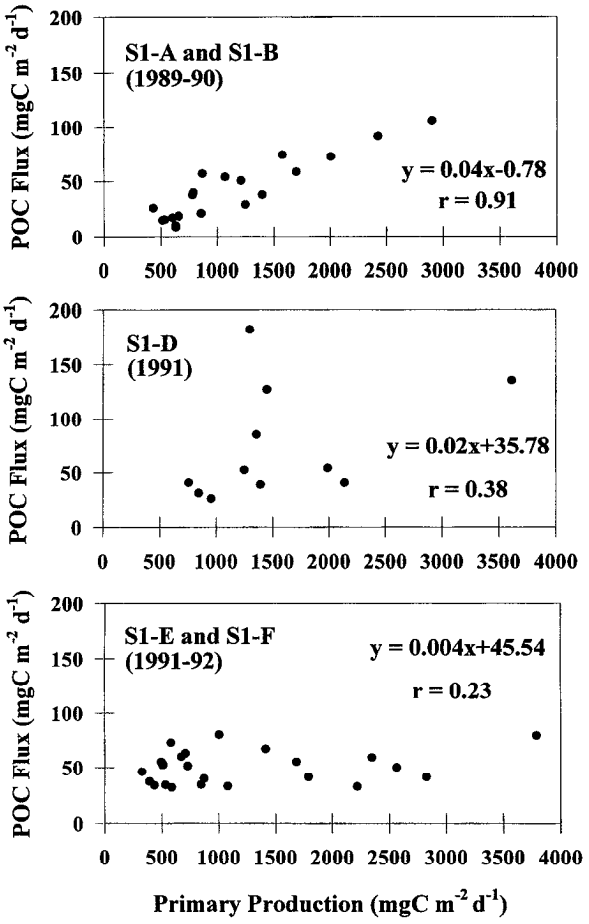

Figure 7. Regressions of daily POC flux (450 m) and primary production for various sediment trap deployment periods over 1989–1992: (a) S1-A and B (8/23/89–8/11/90), (b) S1-D (5/24/91–6/06/91), (c) S1-E and F (11/21/91–12/01/92).

sinking rate of 16 m d^{-1}, was the dominant class of marine aggregates within the upper 500 m of the water column during the spring and summer upwelling months of 1992, as compared to a significantly greater abundance of larger (>1 mm) marine aggregates in 1990 and early 1991.

Phytoplankton populations in Monterey Bay are observed to vary from a diatom-dominated to picoplankton-dominated community, moving from the spring/summer upwelling months to the winter nonupwelling months (Chavez, 1996). As previously noted, a similar variation in the composition of the phytoplankton community was observed between 1990 (a normal upwelling year) and 1992, the El Nino year (Chavez, 1996). Examination of the Si:C ratios of the trap material reveals seasonal and interannual variations that reflect changes in the phytoplankton community. Atomic ratios (in mM

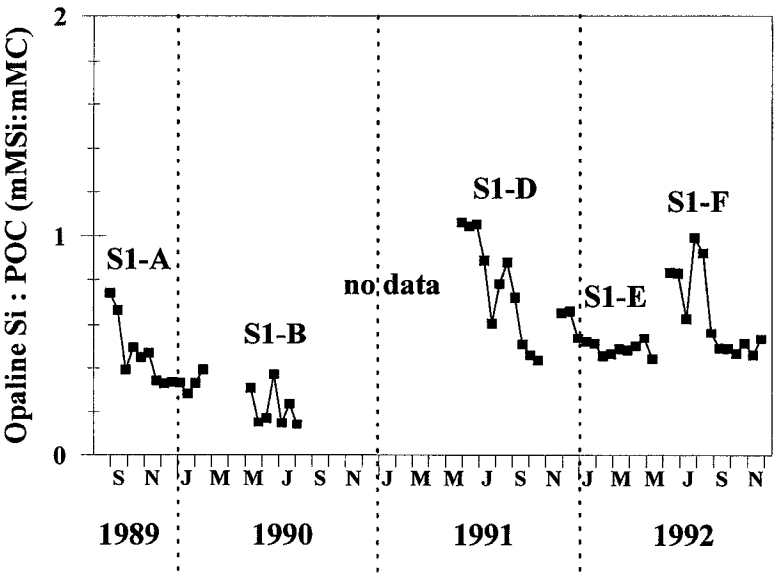

Figure 8. Time-series plot of opaline silica: POC ratio in the trap-collected particulate material.

units) of opaline silica:organic carbon in the biweekly-collected trap material display elevated values in the early summer months of each year when centric colonial diatoms dominate the plankton and are actively growing (Fig. 8). Reduced Si:C ratios occur during the latter half of the year when diatom populations decrease and smaller cell-size phytoplankton, flagellates, and picoplankton are relatively more abundant. Somewhat puzzling however is the fact the average atomic particulate Si:C ratio for samples obtained between August 1989–1990 (a normal upwelling/high diatom production year) of 0.35, is substantially less than that calculated (0.60) for August 1991–1992 when relatively low diatom production and El Nino conditions prevailed (Chavez, 1996). A possible explanation for the higher amounts of silica relative to organic carbon in the 1991–92 trap material is that the diatoms which bloomed relatively late in the 1992 upwelling season may have rapidly moved into a resting cell stage, producing heavily silicified resting cells, as the already low nutrient levels were further depleted. Additionally, the silica-producing picoplankton that dominated the 1992 primary producer community have a large surface area:cell volume ratio and would produce more particulate silica relative to organic carbon if cell division occurred rapidly (Brzezinski, 1985).

Calculations of *e*-ratios (defined as the ratio of carbon export:production; Murray *et al.*, 1989) completed on the time-series carbon production and 450 m export data sets reveal an *e*-ratio trend which is inversely proportional to the depth-integrated primary production (Fig. 9). The values range from 0.02 to 0.14 and are higher during the low productivity/ winter months in Monterey Bay, not the high productivity/upwelling season (Fig. 9). A similar *e*-ratio/productivity trend was reported from a two-year time-series data set

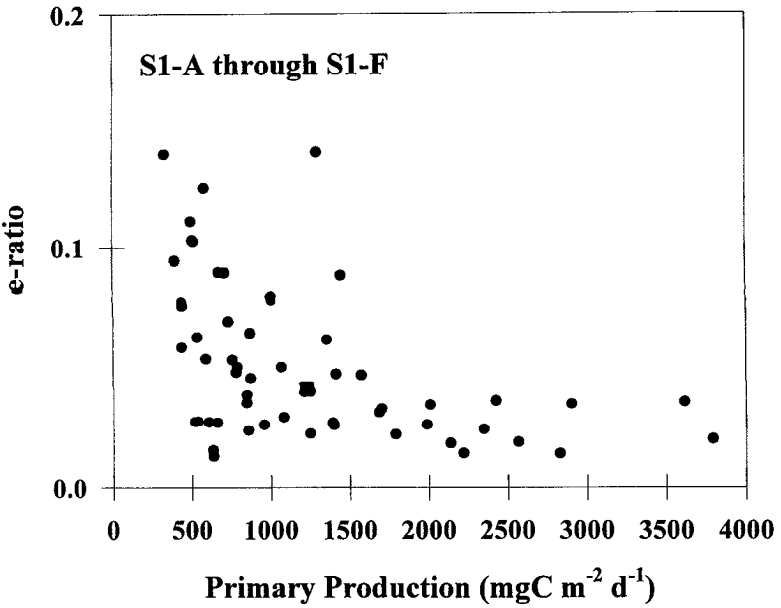

Figure 9. *e*-ratio (calculated as ratio of daily POC export:primary production) vs. primary production, 1989–1992.

obtained at the BATS JGOFS site in the northwestern Sargasso Sea (Lohrenz *et al.,* 1992). Additionally, the mean *e*-ratio value calculated for the 1991–92 low production/El Nino time period in Monterey Bay of 0.06 is twice as high as that calculated for normal upwelling period between 1989–90. Our range of *e*-ratio values compare reasonably well with previously published values from sediment trap experiments conducted in the same central California coastal region. Knauer and Martin (1981) reported values of 0.03–0.04 for the calculated *e*-ratios at 500–750 m from a floating VERTEX MULTITRAP array deployed in the upwelling waters 80 km off the Monterey Peninsula for six days during the early winter season. Knauer *et al.* (1979) provided *e*-ratio values of 0.14 and 0.18 for upwelling and nonupwelling periods, respectively, from a three-week moored, pre-VERTEX MULTITRAP experiment at 700 m in coastal waters 30 km off central California. Thus the range of *e*-ratios reported in this study are not significantly different from those obtained in other Monterey Bay studies.

Our *e*-ratio trend indicates that relative to the daily primary production of carbon, there is less export of organic material to depths below the euphotic zone during the upwelling season compared to the nonupwelling months. Two mechanisms may be responsible for the low *e*-ratio values during the upwelling season: one physical and one biological. The first mechanism concerns the physical flow dynamics in the upper 100 m of this eastern boundary, coastal upwelling system. Net offshore Ekman transport of surface/near-surface waters typifies eastern boundary coastal upwelling regions, with the result that particle matter may be entrained and advected out of the local regime (Suess, 1980; Smith, 1981,

pp. 13–36). Suess (1980) presented such an explanation to reconcile the difference between his empirically derived POC flux for the base of the euphotic zone off Peru and that which had been measured with sediment traps (Staresinic *et al.,* 1978; Barber and Smith, 1981, pp. 366–371; Smith *et al.,* 1981, pp. 400–410; Staresinic *et al.,* 1982, 1983, pp. 225–240). In his 1980 paper, Suess predicted the carbon export through the base of the euphotic zone in a variety of environments, one of which was coastal Peru, using an empirical relationship for estimating POC flux from water depth and primary production. He found that the predicted POC flux off Peru was an order of magnitude greater than the actual measured value. Near-surface, offshore lateral advection of a substantial portion of the primary produced algal carbon was presented by Suess (1980) as the mechanism behind the mis-match between the predicted and measured POC export values off Peru. Suess (1980) suggested that such a mismatch should also be observed in other coastal upwelling systems.

In the case of the Monterey Bay region, numerous data sets exist which characterize the surface water flow regime obtained from various drifter, ADCP and CODAR studies (Strub *et al.,* 1987, 1991; Neal, 1992; Rosenfeld *et al.,* 1994). Results from these studies indicate a predominant southward (equatorward) surface flow on the order of 10–20 cm s^{-1} occurring during the prime upwelling months (March–May) when northwesterly, upwelling-favorable winds are strongest. Detrital algal and mucoid material produced within the euphotic zone of Monterey Bay during the spring and summer take the form of large flocs or aggregates that sink at maximum rates of 45–90 m d^{-1} (Asper, 1987; Alldredge and Gotschalk, 1988; Pilskaln *et al.,* 1991). Near-surface, offshore flows of 10–20 cm s^{-1} could easily transport such aggregates horizontally out of the local system prior to their sinking out of the upper water column.

Additional support for the high probability of substantial offshore transport of detrital algal carbon occurring in the upper water column of Monterey Bay during the upwelling season, comes from results of the Coastal Transition Zone (CTZ) experiment completed north of Monterey Bay (37.5–41.5N) in a region extending from San Francisco to Point Arena, CA (Brink and Cowles, 1991). The CTZ study results suggest a significant offshore transport of particulate carbon may occur via filaments of water extending offshore. These structures are frequently observed in satellite images of the northern and central California coastal regions between the spring and early fall months of the year (Brink and Cowles, 1991; Strub *et al.,* 1991; Jones *et al.,* 1991). Conversion of the across-shelf chl *a* transport values reported by Strub *et al.* (1991) and Jones *et al.* (1991) to carbon equivalents (assuming a chlorophyll to carbon ratio of 0.025; mg chl a:mg C), results in an appreciable offshore transport of POC of 1.1–1.3 gC s^{-1} occurring within the upper 100 m of the offshore-directed, cold-water, coastal filaments. Similarly, in a number of studies examining the carbon budget of the upwelling ecosystem off Peru, Walsh (1981) and Walsh *et al.* (1985) calculated a carbon export off the narrow Peruvian shelf via offshore, wind-induced surface flows of 82 and 591 gC m^{-2} y^{-1} for the years between 1966–69 and 1976–79, respectively.

A second explanation for the low *e*-ratios observed in Monterey Bay during high productivity/upwelling periods concerns the seasonal abundance of detritus feeders and the POC recycling rates within the midwater column. This biological explanation or mechanism implies higher rates of midwater organic matter regeneration occurring during the upwelling season due to increases in the midwater micro and macro-consumer abundance levels. Counts of protozoans (tintinnids, radiolarians, and foraminifera), ciliates, and bacteria completed on water samples obtained at depths of 100–500 m in Monterey Bay over a three year period (1990 through 1992) displayed seasonally varying abundances, with spring/summer counts being several-fold to an order of magnitude greater than those obtained in the late fall/winter (Silver *et al.,* in prep.). Additionally, the abundance (in numbers per liter) of marine snow aggregates that provide a habitat and food source for midwater, planktonic detritus consumers, increases by a factor of ten or more from nonupwelling to upwelling months within the 100–500 m depth zone in Monterey Bay (Pilskaln *et al.,* in prep.). On a larger regional scale, examination of the CalCOFI plankton tow survey data on the seasonal and interannual abundance of zooplankton and micronekton within the California Current System indicates a spring/summer increase in the total zooplankton biomass in the upwelling months as compared to the winter months (Smith, 1971; Bernal and McGowen, 1981, pp. 381–399).

A box model carbon budget for Monterey Bay summarizing the results of this study is presented in Figure 10. The model is constructed using the data presented in this paper and previously published benthic flux and sediment accumulation data sets obtained near our trap mooring site. The values of primary carbon production and POC flux at 450 m in the box model represent annual means obtained by averaging the time-series measurements of these parameters obtained between 1989 and 1992. The POC flux out of the euphotic zone (100 m in Monterey Bay) is calculated by dividing the opaline silica:organic carbon ratio of each biweekly particulate sample collected in the moored trap at 450 m by 0.13 (= Si:C ratio of diatoms growing under nutrient replete conditions; Brzezinski, 1985), and multiplying this product by the particulate organic carbon flux measured at 450 m. The calculation is based on the assumption that opaline silica is a conservative tracer between 100 m and 450 m and that the majority of the POC flux in the bay is associated with siliceous diatom material. This latter assumption is supported in part by the strong positive correlation which we observe between POC and opal fluxes throughout the time-series trap experiment. We completed the above calculation of POC export at the base of the euphotic zone for each collection period and report a mean value in the box model. The annual mean POC flux at 100 m of 86.2 gC m^{-2} y^{-1} (Fig. 10), compares reasonably well to those POC export values at 100 m of 85.2 gC m^{-2} y^{-1} and 54.7 gC m^{-2} y^{-1} predicted by the Martin *et al.* (1987) power function equation and the Pace *et al.* (1987) empirical model, respectively, using VERTEX data sets.

Values presented in the box model for sea floor carbon flux, sediment carbon burial, and deep water carbon regeneration due to animal respiration are taken from Jahnke *et al.* (1990), Jahnke and Jackson (1987; 1992), Reimers *et al.* (1992), and Berelson *et al.* (1996).

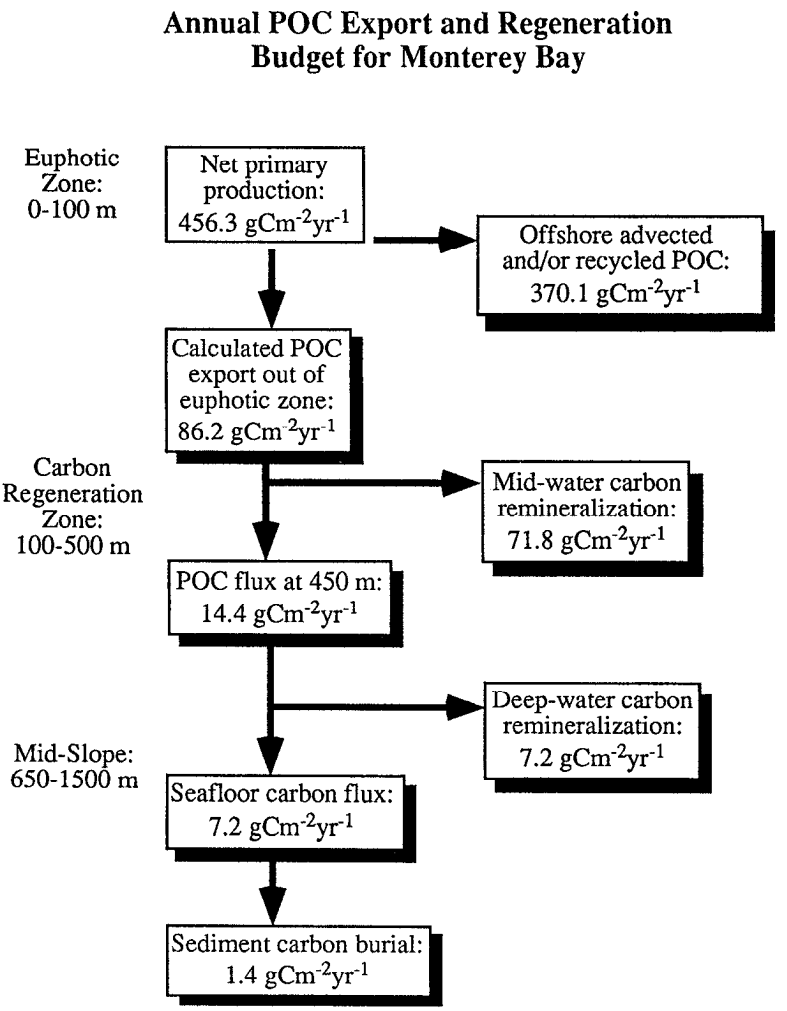

Figure 10. Box model of annual POC budget for Monterey Bay. Data sources described in text.

The difference between the net annual primary production value of 456.3 gC m^{-2} y^{-1} and the calculated annual POC flux at the base of the euphotic zone of 86.2 gC m^{-2} y^{-1} must be equal to the amount of carbon removed via offshore lateral advection in the upper 100 m plus that which is recycled within the euphotic zone. POC regeneration via respiration in the upper 100 m of such a substantial amount of POC (370.1 gC m^{-2} y^{-1}) representing 81% of the annual primary production, is extremely unlikely with near-surface carbon respiration losses being on the order of a few percent to 20% (Parsons *et al.*, 1984). Therefore we believe that the majority of the calculated particulate carbon loss in the upper 100 m of Monterey Bay is due to the lateral, offshore advection of a significant portion of locally produced, labile POC, prior to sinking below the euphotic zone.

Offshore advection of POC contained in near-surface waters, a process that is maximized during the upwelling months in the Monterey Bay region, would explain the minimal *e*-ratios observed during such periods. For comparison, our value of 370.1 gC m^{-2} y^{-1} for the predicted offshore export of POC falls within the middle of the range reported by Walsh (1981) of 82–591 gC m^{-2} y^{-1} for offshore POC export from the Peruvian shelf. The large offshore export of POC from west coast/Pacific upwelling systems is in stark contrast to the results of the SEEP program showing that only a very small fraction of the spring bloom phytodetritus is exported off the eastern U.S./Atlantic continental shelf (Falkowski *et al.,* 1988; Anderson *et al.,* 1994; Rowe *et al.,* 1994). Substantial offshore export of POC from the western U.S. and South American upwelling coasts may provide an explanation for the reportedly higher sediment oxygen demand in the Pacific versus the Atlantic (Jahnke and Jackson, 1992; pp. 295–307; Rowe *et al.,* 1986).

Chavez and Smith (1995, pp. 149–164) report a mean new primary production rate of 1750.0 mgC m^{-2} day^{-1} and a mean *f*-ratio value of 0.89 for the 1991 spring upwelling period in Monterey Bay. If we assume that POC export flux at the base of the euphotic zone approximates the nitrate-driven new production (e.g., Eppley and Peterson, 1979), comparing our calculated POC flux at 100 m for spring/early summer 1991 (= 1009.1 mgC m^{-2} d^{-1}) with the mean new production rate of 1750 mgC m^{-2} d^{-1}, indicates that the calculated POC export accounts for only 52% of the new production. The imbalance or mis-match between the nitrate-driven new production and the downward flux of POC may be resolved if one considers the idea put forth by Toggweiler (1989, pp. 65–83) and Toggweiler and Carson (1995, pp. 337–360) that large, dissolved organic matter (DOM) pools represent a substantial sink for upwelled nitrate. Using a coupled biological/physical ecosystem model of nitrogen cycling in the Equatorial Pacific, Toggweiler and Carson (1995, pp. 337–360) demonstrated that if a significant portion of upwelled nitrate resides in the ocean as biota-produced DOM that is advected away from the upwelling region via surface flows, the nitrogen budget could be closed without the necessity of a large sinking flux of particles. They suggested that this DOM pool must have a lifetime on the order of months to years so that it may be laterally exported in fairly substantial quantities prior to being remineralized back to nitrate and CO_2. If an appreciable fraction of the nitrate-driven new production in Monterey Bay exists as DOM with a relatively low C:N ratio (~6) and a lifetime on the scale of years, this material could be moved offshore by strong surface flows during the upwelling season, mixed into the deeper layers of the ocean, and remineralized below the thermocline. Such a process would provide a plausible explanation for the imbalance between the 1991 spring new production value and calculated POC export for the base of the euphotic zone reported above for the bay.

The 100–500 m depth interval underlying the euphotic zone in our box model represents the carbon regeneration zone, the depth stratum in the ocean where measured POC fluxes generally decrease over an order of magnitude and where organic carbon remineralization rates are maximized (Suess, 1980; Betzer *et al.,* 1984; Martin *et al.,* 1987). The daily POC flux at 450 m in Monterey Bay varies from 14.8–181.8 mgC m^{-2} day^{-1}, with a calculated

annual mean flux of 14.4 gC m^{-2} y^{-1} representing 3.2% of surface-fixed carbon measured as primary production (Table 1, Fig. 10). Our mid-water POC flux values from the west coast slope range more widely and are higher than those reported from similar trap depths in the 1988–1989 Mid-Atlantic Bight SEEP II experiment. In the latter program, the daily POC fluxes to traps deployed at 400 m on the slope ranged from 23.0–33.0 mgC m^{-2} day^{-1} and the annual mean POC flux was 10.2 gC m^{-2} $year^{-1}$ (Biscaye and Anderson, 1994). The annual POC flux to 450 m reported in this study compares reasonably well to the results from several other studies in the coastal upwelling region off central and southern California where reported POC export at comparable depths represents 3–14% of surface water production (Knauer *et al.,* 1979; Knauer and Martin, 1981; Nelson *et al.,* 1987; Thunell *et al.,* 1994). According to the Martin *et al.* (1987) normalized power function for determining annual carbon flux as a function of depth and primary production, the annual carbon flux at 450 m for a near-coastal site is estimated to be 24 gC m^{-2} y^{-1}. For comparison, the calculated carbon flux at the same depth would be 18 gC m^{-2} y^{-1} using the Pace *et al.* (1987) model. We suggest that the longer duration of our time-series trap program, encompassing normal upwelling as well as El Nino years with semi-continuous measurements made throughout a three year sampling period, renders our annual mid-water POC flux value more representative of the Monterey Bay system relative to those provided in Martin *et al.* (1987) and Pace *et al.* (1987) where the temporal sampling coverage was less.

We calculate an average annual regeneration of sinking POC occurring within the mid-water column (100–450 m) of Monterey Bay of 71.8 gC m^{-2} y^{-1} (Fig. 10). The value is determined as the difference between the calculated carbon export at the base of the euphotic zone and the measured POC flux at 450 m. Mid-depth POC regeneration is most likely mediated by a community of free-living and particle-attached micro- and macro-consumers that have been shown to convert sinking POC to slow-sinking, small particle matter pools and/or dissolved organic matter (Childress, 1975; Sherr *et al.,* 1986; Asper, 1987; Alldredge and Gotschalk, 1988; Alldredge and Silver, 1988; Toggweiler, 1989, pp. 65–83; Alldredge *et al.,* 1990; Azam *et al.,* 1993; Steinberg *et al.,* 1994).

The benthic POC delivery rate to the mid-slope, sediment/water interface in Monterey Bay is based on benthic chamber and microelectrode measurements of oxygen, TCO_2, and carbonate alkalinity fluxes converted to benthic organic carbon degradation rates to approximate carbon flux to the seafloor (Fig. 10; Jahnke *et al.,* 1990; Jahnke and Jackson, 1992, pp. 295–307, pp. 295–307; Reimers *et al.,* 1992; Berelson *et al.,* 1996). Although the above studies were conducted at a series of stations located slightly south of Monterey Bay, a number of the mid-slope sampling depths are comparable to the bottom depths in the vicinity of the Monterey Bay S1 trap mooring. The mean benthic carbon fluxes from the above studies is 1.6 mmolC m^{-2} d^{-1} or 7.2 gC m^{-2} y^{-1} for depths ranging from 500–1000 m (Fig. 10). For comparison, the SEEP II program reported benthic carbon flux values for the Mid-Atlantic slope that ranged from 5.6–14.4 gC m^{-2} y^{-1} obtained from lander deployments (Rowe *et al.,* 1994). If we assume that the annual POC flux of 14.4 gC

$m^{-2}\ y^{-1}$ measured at 450 m on the western edge of Monterey Bay is generally representative of mid-water POC fluxes in the slope region off central California (excluding the Monterey Submarine Canyon axis that is affected by slumping and turbidity events), then we may conclude that the POC delivery rate satisfies the average annual oxygen requirements on the slope. We do not need to invoke an additional input source of carbon in order to balance the sedimentary oxygen budget, as in the case of the southern California Borderland Basins (Thunell *et al.,* 1994; Berelson *et al.,* 1996). Additionally, in contrast to the Mid-Atlantic continental margin where a small portion of the spring bloom POC is transported offshore prior to deposition and where the slope deposited organic matter is primarily refractory, Monterey Bay slope sediments appear to receive pulsed inputs of highly reactive organic matter produced in the overlying, high productivity surface waters (Anderson *et al.,* 1994; Berelson *et al.,* 1996).

The difference between the sea floor carbon delivery rate to the bottom sediments (located at 700 m at the S1 mooring site) and the measured POC flux at 450 m, represents the deep-water remineralization of sinking POC occurring below the 100–500 m carbon regeneration zone prior to actual seafloor deposition (Fig. 10). This value is 7.2 $gC\ m^{-2}\ y^{-1}$ (Fig. 10). It is purely coincidental that the seafloor carbon flux number obtained from the benthic chamber measurements, and the calculated deep-water carbon remineralization value are identical; the former value was directly measured and the latter estimated by difference. A 50% loss of the POC rain within the deep Monterey Bay water column prior to benthic delivery is not surprising given the reasonable assumption of a highly active, near-bottom community of micro- and macro-consumers under this region of relatively high production and export. Support for this assumption comes from numerous studies reporting on the POC remineralizing activity of near-bottom zooplankton and microbial detritivor communities (Smith, 1982; Lampitt, 1985; Rowe and Deming, 1985; Smith *et al.,* 1987; Jahnke and Jackson, 1987; Wishner and Gowing, 1987; Jumars *et al.,* 1989; Lampitt, 1992).

The carbon burial rate for Monterey Bay of 1.4 $gC\ m^{-2}\ y^{-1}$ is calculated using the mean carbon burial efficiency of 19% obtained by Reimers *et al.* (1992) and Berelson *et al.* (1996) for central California slope sediments between 500–1000 m (Fig. 10). Our study indicates that 2% of the total primary production is deposited at the sediment/water interface on an annual basis, with approximately 0.3% being preserved in the underlying sediments. These rates compare reasonably well to the carbon accumulation and burial rates of $<2\%$ and $<1\%$, respectively, previously reported for other Pacific and Atlantic continental slope sediments (Walsh *et al.,*, 1985; Reimers *et al.,* 1992; Jahnke and Jackson, 1992, pp. 295–307, pp. 295–307; Anderson *et al.,* 1994).

6. Conclusions

To date, this study represents the only multi-year, high-resolution, time-series examination of the biogeochemical cycling of particulate carbon in a coastal upwelling/continental margin system. The results indicate that coastal upwelling regimes produce and export

potentially significant quantities of organic carbon to the adjacent open ocean through physical mixing and advection processes that are unique to these coastal systems. Additionally, the Monterey Bay time-series study of POC production and export allowed us to examine the seasonal and interannual variability in the *e*-ratio parameter relating midwater POC export to euphotic zone production. The trend of minimal *e*-ratios observed during upwelling periods of maximal productivity is primarily explained by enhanced Ekman offshore transport of near-surface algal carbon during upwelling months, and secondarily by an increase in the abundance of water column detritus feeders in the upwelling season.

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REFERENCES

Alldredge, A. L. and C. Gotschalk. 1988. *In situ* settling behavior of marine snow. Limnol. Oceanogr., *33,* 339–351.

Alldredge, A. L., T. C. Granata, C. C. Gotschalk and T. D. Dickey. 1990. The physical strength of marine snow and its implications for particle disaggregation in the ocean. Limnol. Oceanogr., *35,* 1415–1428.

Alldredge, A. L. and M. W. Silver. 1988. Characteristics, dynamics and significance of marine snow. Prog. Oceanogr., *20,* 41–82.

Anderson, R. F., G. T. Rowe, P. F. Kemp, S. Trumbore and P. E. Biscaye. 1994. Carbon budget for the mid-slope depocenter of the Middle Atlantic Bight. Deep-Sea Res. II, *41,* 669–703.

Anderson, R. Y. 1977. Short term sedimentation response in lakes in western United States as measured by automated sampling. Limnol. Oceanogr., *22,* 423–433.

Asper, V. L. 1987. Measuring the flux and sinking speed of marine snow aggregates. Deep-Sea Res., *34,* 1–17.

Azam, F. T., T. Fenchel, J. G. Field, J. S. Gray, L. A. Meyer-Reil and F. Thingstad. 1983. The ecological role of water column microbes in the sea. Mar. Ecol. Prog. Ser., *10,* 257–263.

Barber, R. T. and W. O. Smith. 1981. The role of circulation, sinking and vertical migration in physical sorting of phytoplankton in upwelling center at 15S, *in* Coastal Upwelling, *1,* F. A. Richards, ed., American Geophysical Union Monograph Series on Coastal and Estuarine Science, Washington, DC, 529 pp.

Berelson, W. M., D. E. Hammond and K. S. Johnson. 1987. Benthic fluxes and the cycling of biogenic silica and carbon in the two southern California Borderland Basins. Geochim. Cosmochim. Acta, *51,* 1345–1363.

Berelson, W. M., J. McManus, T. E. Kilgore, K. H. Coale, K. S. Johnson, D. H. Burdige and C. H. Pilskaln. 1996. Biogenic matter diagenesis on the sea floor: A comparison between two continental margin transects. J. Mar. Res., *54,* 731–762.

Bernal, P. A. and J. A. McGowen. 1981. Advection and upwelling in the California current, *in* Coastal Upwelling, *1,* F. A. Richards, ed., American Geophysical Union Monograph Series on Coastal and Estuarine Science, Washington, DC, 529 pp.

Betzer, P. R., W. J. Showers, E. A. Laws, C. D. Winn, G. R. DiTullio and P. M. Kroopnick. 1984. Primary productivity and particle fluxes on a transect of the equator at 153W in the Pacific Ocean. Deep-Sea Res., *31,* 1–11.

Biscaye, P. E. and R. F. Anderson. 1994. Fluxes of particulate matter on the slope of the southern Middle Atlantic Bight: SEEP II. Deep-Sea Res. II, *41,* 459–510.

Biscaye, P. E., C. N. Flagg and P. G. Falkowski. 1994. The shelf edge exchange processes experiment, SEEP-II: an introduction to hypotheses, results and conclusions. Deep-Sea Res., *41,* 231–252.

Bolin, R. L. and D. P. Abbott. 1963. Studies on the marine climate and phytoplankton of the central coastal area of CalCOFI Rept., *9,* 23–45.

Breaker, L. C. and C. N. K. Mooers. 1986. Oceanic variability of the central California coast. Prog. Oceanogr., *17,* 61–135.

Brink, K. H. and T. J. Cowles. 1991. The Coastal Transition Zone Program. J. Geophys. Res., *96,* 14637–14648.

Brzezinski, M. A. 1985. The Si:C:N ratio of marine diatoms: Interspecific variability and the effect of some environmental variables. J. Phycol., *21,* 347–357.

Buesseler, K. O. 1991. Do upper-ocean sediment traps provide an accurate record of particle flux? Nature, *353,* 420–423.

Chavez, F. P. 1996. Forcing and biological impact of onset of the 1992 El Nino in central California. Geophys. Res. Lett., *23,* 265–268.

Chavez, F. P. and R. T. Barber. 1987. An estimate of new production in the equatorial Pacific. Deep-Sea Res., *34,* 1229–1243.

Chavez, F. P., K. R. Buck, K. H. Coale, J. H. Martin, G. R. DiTullio, N. A. Welshmeyer, A. C. Jacobson and R. T. Barber. 1991. Growth rates, grazing, sinking, and iron limitation of equatorial Pacific phytoplankton. Limnol. Oceanogr., *36,* 1816–1828.

Chavez, F. P., R. Herlien and G. Thurmond. 1994. Oasis—acquisition system for moorings/drifters. Sea Technol., *35,* 51–60.

Chavez, F. P. and S. L. Smith. 1995. Biological and chemical consequences of open ocean upwelling, *in* Upwelling in the Oceans; Modern Processes and Ancient Records, C. P. Summerhayes, K.-C. Emeis, M. V. Angel, R. L. Smith and B. Zeitzschel, eds., John Wiley and Sons Ltd., NY, 422 pp.

Chelton, D. B., R. L. Bernstein, A. Bratkovich and M. Kosro. 1987. The Central California coastal circulation study. EOS, Trans. Amer. Geophys. Union, *68,* 1, 12–13.

Childress, J. J. 1975. The respiratory rates of midwater crustaceans as a function of depth of occurrence and relation to the oxygen minimum layer off Southern California. Comparative Biochem. Physiol., *50,* 787–799.

Dugdale, R. C. and J. J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnol. Oceanogr., *12,* 196–206.

Eggimen, D. W., F. T. Manheim and P. R. Betzer. 1980. Dissolution and analysis of amorphous silica in marine sediments. J. Sed. Petrol., *50,* 215–225.

Eppley, R. W. and B. J. Peterson. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature, *282,* 677–680.

Falkowski, P. G., C. N. Flagg, G. T. Rowe, S. L. Smith, T. E. Whitledge and C. D. Wirick. 1988. The fate of a spring phytoplankton bloom: export or oxidation? Cont. Shelf Res., *8,* 457–484.

Gardner, W. D. 1980. Field assessment of sediment traps. J. Mar. Res., *38,* 41–52.

—— 1985. The effect of tilt on sediment trap efficiency. Deep-Sea Res., *32,* 349–361.

Garfield, N., T. A. Rango, K. J. Schnebele and C. A. Collins. 1994. Evidence of a turbidity current in Monterey Submarine Canyon associated with the 1989 Loma Prieta earthquake. Cont. Shelf Res., *14,* 673–686.

Honjo, S. 1980. Material fluxes and modes of sedimentation in the mesopelagic and bathypelagic zones. J. Mar. Res., *38,* 53–97.

Honjo, S., D. W. Spencer and W. D. Gardner. 1992. A sediment trap intercomparison experiment in the Panama Basin, 1979. Deep-Sea Res., *39,* 333–358.

Jahnke, R. A. and G. A. Jackson. 1987. Role of sea floor organisms in oxygen consumption in the deep North Pacific Ocean. Nature, *329,* 621–623.

—— 1992. The spatial distribution of sea floor oxygen consumption in the Atlantic and Pacific Oceans, *in* Deep-Sea Food Chains and the Global Carbon Cycle, G. T. Rowe and V. Pariente, eds., Kluwer Academic Publishers, Dordrecht, 400 pp.

Jahnke, R. A., C. E. Reimers and D. B. Craven. 1990. Intensification of recycling of organic matter at the sea floor near ocean margins. Nature, *348,* 50–54.

Jones, B. H., C. N. K. Mooers, M. M. Rienecker, T. Stanton and L. Washburn. 1991. Chemical and biological structure and transport of a cool filament associated with a jet-eddy system off northern California in July 1986 (OPTIMA21). J. Geophys. Res., *96,* 22207–22225.

Jumars, P. A., D. L. Penry, J. A. Baross, M. J. Perry and B. W. Frost. 1989. Closing the microbial loop: Dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. Deep-Sea Res., *36,* 483–495.

Knauer, G. A. and V. L. Asper. 1989. Sediment trap technology and sampling. U.S. GOFS Planning Rept., No. *10,* 94 pp.

Knauer, G. A. and J. H. Martin. 1981. Primary production and carbon-nitrogen fluxes in the upper 1,500 m of the northeast Pacific. Progr. Oceanogr., *26,* 181–186.

Knauer, G. A., J. H. Martin and K. W. Bruland. 1979. Fluxes of particulate carbon, nitrogen, and phosphorus in the upper water column of the northeast Pacific. Deep-Sea Res., *26,* 97–108.

Lampitt, R. S. 1992. The contribution of deep-sea macroplankton to organic remineralization: results from sediment trap and zooplankton studies over the Madeira Abyssal Plain. Deep-Sea Res., *39,* 221–233.

—— 1985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. Deep-Sea Res., *32,* 885–897.

Lohrenz, S. E., G. A. Knauer, V. L. Asper, M. Tuel, A. F. Michaels and A. H. Knap. 1992. Seasonal variability in primary production and particle flux in the northwestern Sargasso Sea: U.S. JGOFS Bermuda Atlantic Time-series Study. Deep-Sea Res., *39,* 1373–1391.

Martin, J. H., G. A. Knauer, D. M. Karl and W. W. Broenkow. 1987. VERTEX: carbon cycling in the northeast Pacific. Deep-Sea Res., *34,* 267–285.

Mortlock, R. A. and P. N. Froelich. 1989. A simple method for the rapid determination of biogenic opal in pelagic marine sediments. Deep-Sea Res., *36,* 1415–1426.

Murray, J. W., J. N. Downs, S. Strom, C. Wei and H. W. Jannasch. 1989. Nutrient assimilation, export and production and 234Th scavenging in the eastern equatorial Pacific. Deep-Sea Res., *36,* 1471–1489.

Neal, T. C. 1992. Analysis of Monterey Bay CODAR-derived surface currents, March to May 1992. M.S. Thesis, Naval Postgraduate School, Monterey, CA. 96 pp.

Nelson, J. R., J. R. Beers, R. W. Eppley, J. A. Jackson, J. J. McCarthy and A. Soutar. 1987. A particle flux study in Santa Monica-San Pedro Basin off Los Angeles: Particle flux, primary production, and transmissometer survey. Cont. Shelf Res., *7,* 307–328.

Pace, M. L., G. A. Knauer, D. M. Karl and J. H. Martin. 1987. Primary production, new production and vertical flux in the eastern Pacific Ocean. Nature, *325,* 803–804.

Parsons, T. R., M. Takahashi and B. Hargrave. 1984. Biological Oceanographic Processes, Pergamon Press, Oxford, 330 pp.

Pillsbury, R. D., C. H. Pilskaln, G. Pittock and R. E. Still. 1992. Deep water flow characteristics of Monterey Bay: a two year current meter data set. Oregon State University Data Rept., No. 143/92-2, 66 pp.

Pilskaln, C. H. and J. B. Paduan. 1992. Laboratory techniques for the handling and geochemical analysis of water column particulate and surface sediment samples. MBARI Technical Rept., No. 92-9, 22 pp.

Pilskaln, C. H., M. W. Silver, D. L. Davis, K. M. Murphy, S. A. Lowder, B. R. Gritton and L. M. Lewis. 1991. A quantitative study of marine aggregates using specialized ROV instrumentation. Inst. Electrical and Electronic Engrs. (IEEE) Proc. 91CH3063–5, Oceans '91, 1175–1182.

Reimers, C. E., R. A. Jahnke and D. C. McCorkle. 1992. Carbon fluxes and burial rates over the continental slope and rise off Central California with implications for the global carbon cycle. Global Biogeo. Cycles, *6,* 199–224.

Rosenfeld, L. K., F. B. Schwing, N. Garfield and D. E. Tracy. 1994. Bifurcated flow from an upwelling center: a cold water source for Monterey Bay. Cont. Shelf Res., *14,* 931–964.

Rowe, G. T., G. S. Boland, W. C. Phoel, R. F. Anderson and P. E. Biscaye. 1994. Deep seafloor respiration as an indication of lateral input of biogenic detritus from continental margins. Deep-Sea Res., *41,* 657–668.

Rowe, G. T. and J. W. Deming. 1985. The role of bacteria in the turnover of organic carbon in deep-sea sediments. J. Mar. Res., *43,* 925–950.

Rowe, G. T., S. Smith, P. Falkowski, T. Whitledge, R. Theroux, W. Phoel and H. Ducklow. 1986. Do continental shelves export organic matter? Nature, *324,* 559–561.

Schwalbach, J. R. and D. S. Gorsline. 1985. Holocene sediment budgets for the basins of the California Continental Borderland. J. Sed. Petrol., *55,* 829–842.

Shepard, F. P. 1973. Submarine Geology, Harper and Row, NY, 517 pp.

Sherr, E. B., B. F. Sherr, R. D. Fallon and S. Y. Newell. 1986. Small aloricate ciliates as a major component of the marine heterotrophic nanoplankton. Limnol. Oceanogr., *31,* 177–183.

Smith, K. L. 1982. Zooplankton of a bathyal benthic boundary layer: In situ rates of oxygen consumption and ammonium excretion. Limnol. Oceanogr., *27,* 461–471.

Smith, K. L., A. F. Carlucci, R. A. Jahnke and D. B. Carven. 1987. Organic carbon mineralization in the Santa Catalina Basin. Deep-Sea Res., *34,* 185–211.

Smith, P. E. 1971. Distributional atlas of zooplankton volume in the California region, 1951 through 1966. CalCOFI Atlas, *13,* 144 pp.

Smith, R. L. 1981. Circulation pattern in upwelling regimes, *in* Coastal Upwelling: Its Sediment Record, Part A: Responses of the Sedimentary Regime to Present Coastal Upwelling, E. Suess and J. Thied, eds., Plenum Press, NY, 604 pp.

Smith, S. L., K. H. Brink, H. Santander, T. J. Cowles and A. Huyer. 1981. The effect of advection on variations in zooplankton at a single location near Cabo Nazca, Peru, *in* Coastal Upwelling, *1,* F. A. Richards, ed., American Geophysical Union Monograph Series on Coastal and Estuarine Science, Washington, D.C., 529 pp.

Staresinic, N., J. W. Farrington, R. B. Gagosian, C. H. Clifford and E. M. Hurlburt. 1983. Downward transport of particulate matter in the Peru coastal upwelling: Role of the anchoveta *Engraulis ringens, in* Coastal Upwelling: Its Sediment Record, Part A: Responses of the Sedimentary Regime to Present Coastal Upwelling, E. Suess and J. Thied, eds., Plenum Press, NY, 604 pp.

Staresinic, N., G. T. Rowe, D. J. Shaughnessy and A. J. Williams, III. 1978. Measurement of the vertical flux of particulate organic matter with a free-drifting sediment trap. Limnol. Oceanogr., *23,* 559–563.

Staresinic, N. J., K. von Brockel, N. Smodlaka and C. H. Clifford. 1982. A comparison of moored and free-drifting sediment traps of two different designs. J. Mar. Res., *40,* 273–292.

Steinberg, D. K., M. W. Silver, C. H. Pilskaln, S. L. Coale and J. B. Paduan. 1994. Midwater zooplankton communities on pelagic detritus (giant larvacean houses) in Monterey Bay, California. Limnol. Oceanogr., *39,* 1606–1620.

Strub, P. T., J. S. Allen, A. Huyer and R. L. Smith. 1987. Seasonal cycles of currents, temperature, winds and sea level over the northeast Pacific continental shelf: 35N to 48N. J. Geophys. Res., *92,* 1507–1526.

Strub, P. T., P. M. Kosro and A. Huyer. 1991. The nature of cold filaments in the California Current. J. Geophys. Res., *96,* 14743–14768.

Suess, E. 1980. Particulate organic carbon flux in the oceans—surface productivity and oxygen utilization. Nature, *288,* 260–263.

Thunell, R. C., C. H. Pilskaln, E. Tappa and L. R. Sautter. 1994. Temporal variability in sediment fluxes in the San Pedro Basin, Southern California Bight. Cont. Shelf Res., *14,* 333–352.

Toggweiler, J. R. 1989. Is the downward dissolved organic matter (DOM) flux important in carbon transport? *in* Productivity of the Ocean: Present and Past, W. H. Berger, V. S. Smetacek and G. Wefer, eds., John Wiley and Sons, Chichester, 471 pp.

Toggweiler, J. R. and S. Carson. 1995. What are upwelling systems contributing to the ocean's carbon and nutrient budgets? *in* Upwelling in the Ocean: Modern Processes and Ancient Records, C. P. Summerhayes, K.-C. Emeis, M. V. Angel, R. L. Smith and B. Zeitzschel, eds., John Wiley and Sons Ltd., NY, 422 pp.

Tracy, D. E. 1990. Source of cold water in Monterey Bay observed by AVHRR satellite imagery. M.S. Thesis, Naval Postgraduate School, Monterey, California, 114 pp.

Wakeham, S. G. 1985. Wax esters and triacylglycerols in sinking particulate matter in the Peru upwelling area (15 degrees S, 75 degrees N). Mar. Chem., *17,* 213–235.

Walsh, J. J. 1981. A carbon budget for overfishing off Peru. Nature, *290,* 300–304.

—— 1991. Importance of continental margins in the marine biogeochemical cycling of carbon and nitrogen. Nature, *350,* 53–55.

—— 1994. Particle export at Cape Hatteras. Deep-Sea Res., *41,* 603–628.

Walsh, J. J., P. E. Biscaye, and G. T. Csanady. 1988. The 1983–1984 Shelf Exchange processes (SEEP)-I experiment: hypotheses and highlights. Cont. Shelf Res., *8,* 435–456.

Walsh, J. J., D. A. Dieterle and J. R. Pribble. 1991. Organic debris on the continental margins: a simulation analysis of source and fate. Deep-Sea Res., *38,* 805–828.

Walsh, J. J., E. T. Premuzic, J. S. Gaffney, G. T. Rowe, G. Harbottle, R. W. Stoenner, W. L. Balsam, P. R. Betzer and S. A. Macko. 1985. Organic storage of CO_2 on the continental slope off the mid-Atlantic bight, the southeastern Bering Sea, and the Peru coast. Deep-Sea Res., *32,* 853–883.

Walsh, J. J., G. T. Rowe, R. L. Iverson and C. P. McRoy. 1981. Biological export of shelf carbon is a sink of the global CO_2 cycle. Nature, *291,* 196–201.

Wishner, K. F. and M. M. Gowing. 1987. In situ filtering and ingestion rates of deep-sea benthic boundary-layer zooplankton in the Santa Catalina Basin. Mar. Biol., *94,* 357–366.

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