

# Assessing the importance of land and marine sources of organic matter to kelp forest food webs

Henry M. Page\*, Daniel C. Reed, Mark A. Brzezinski, John M. Melack,  
Jenifer E. Dugan

Marine Science Institute, University of California Santa Barbara, Santa Barbara, California 93106, USA

**ABSTRACT:** We used stable isotope analysis to investigate the relative importance of marine and terrestrial sources of organic matter to the food web of 4 nearshore reefs in the Santa Barbara Channel (California, USA) over a 4 yr period that included substantial variability in the availability of marine and terrestrial organic matter. We measured stable C and N isotope values of ocean- and land-derived sources of organic matter and of different types of consumers on reefs that varied in exposure to freshwater runoff and in biomass of giant kelp.  $\delta^{13}\text{C}$  values of suspended particulate organic matter (POM) on reefs tended to decrease following periods of significant rainfall at the reef most influenced by freshwater runoff, to increase with phytoplankton standing crop at all reefs, and generally to decline in both wet and dry years in late fall–early winter at all reefs. Stable isotope values of reef consumers indicated little direct use of terrestrially-derived POM. However, a pattern of  $^{15}\text{N}$ -enrichment in 2 common benthic-feeding species, the sea urchin *Strongylocentrotus purpuratus* and the annelid *Diopatra ornata*, with increasing influence of runoff indicated that terrestrially-derived nitrogen may enter the food web indirectly through a trophic intermediate (e.g. microbes, algae). The importance of giant kelp to the reef food web varied with consumer feeding mode. In contrast to previous studies,  $\delta^{13}\text{C}$  values suggested little use of kelp-derived material by suspension-feeders, based on the similarity in isotope values of these consumers among reefs when kelp biomass was low, and the absence of a directional shift in isotope values that would indicate the use of more  $^{13}\text{C}$ -enriched kelp when kelp biomass was higher at 2 of the reefs. However, isotope values for herbivores were generally  $^{13}\text{C}$ -enriched relative to suspension-feeders, reflecting the use of local giant kelp or other  $^{13}\text{C}$ -enriched benthic algal production. Thus, spatial and temporal fluctuations in the biomass of giant kelp would be least likely to impact the food resources of suspension-feeders and have greatest effect on benthic herbivores.

**KEY WORDS:** *Macrocystis pyrifera* · Kelp forest · Food web · Rocky reef · Stable isotopes

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Material exchange among ecosystems is recognized increasingly as an important determinant of many ecological patterns and processes (Valiela et al. 2001, Roberts et al. 2003). The movement of organic and inorganic materials across boundaries of discrete ecosystems is widespread and has been shown to influence population dynamics, community structure, food web complexity, and primary and secondary production (e.g. Polis et al. 1997, Bouchard & Bjorndal 2000,

Bishop et al. 2002). Much of what we know about the role of material exchange in coastal ecosystems originates from studies of estuaries where inputs from the ocean mix with those from rivers (e.g. Canuel et al. 1995, Deegan & Garritt 1997, Chanton & Lewis 2002). However, estuarine systems differ from open coastal systems in oceanographic conditions and in exposure to ocean-derived inputs.

Giant kelp *Macrocystis* spp. forests are among the most productive ecosystems in the world (Mann 2000). They occur on shallow subtidal rock outcrops (a habi-

\*Email: page@lifesci.ucsb.edu

tat hereafter referred to as 'reef') along the open coasts of western North and South America, southern Africa, Australia and most sub-Antarctic islands, including Tasmania and New Zealand (Womersley 1954). Because of their close proximity to shore, physical and biological processes that occur in the open ocean as well as on land potentially influence these reef ecosystems. Of interest in this regard is the relative importance of land- and ocean-derived sources of organic matter to reef food webs and the extent to which these inputs are affected by changes in natural environmental drivers (e.g. freshwater runoff, sea surface temperature, currents).

The shallow rocky reefs of the Santa Barbara Channel (southern California, USA) typically support beds of the giant kelp *Macrocystis pyrifera*. These kelp beds can be highly productive; field based estimates of productivity range from 20 to 30 kg wet weight m<sup>-2</sup> yr<sup>-1</sup> or 460 to 690 g C m<sup>-2</sup> yr<sup>-1</sup> (Coon 1982). Kelp production can enter the reef food web through the consumption of attached or dislodged plants by benthic grazers, or as detritus (Mann 2000), where microbial activity on older parts of kelp blades and on kelp POM may increase its food value to suspension-feeding benthic consumers (Duggins & Eckman 1997, Norderhaug et al. 2003). Several studies in different geographical settings have suggested that the contribution of kelp-derived POM to the diet of suspension-feeders can approach that of phytoplankton (Dunton & Schell 1987, Duggins et al. 1989, Kaehler et al. 2000). Phytoplankton abundance in the Santa Barbara Channel is generally highest along the mainland and peaks in the spring and summer months (Otero & Siegel 2004).

Riverine and terrestrial organic matter may also be incorporated into coastal food webs, as documented in some estuarine systems (Canuel et al. 1995, Chanton & Lewis 2002). Runoff from about 75 small catchments drains directly or through small estuaries into the Santa Barbara Channel from a coastal mountain range (Santa Ynez Mountains). The climate of southern California is Mediterranean and most of the annual discharge of freshwater and associated particulate material to the coast occurs within a few days to weeks each winter (Beighley et al. 2003). Storm runoff transports large amounts of suspended POM to the coastal ocean that could either be used immediately by reef consumers, or settle to the bottom and become available to consumers later through resuspension.

Stable isotope analysis has proven useful in revealing sources of production used by consumers in kelp forest food webs (Dunton & Schell 1987, Duggins et al. 1989, Kaehler et al. 2000, Fredriksen 2003). We used this technique to explore trophic linkages between consumers on rocky reefs in the Santa Barbara Channel and sources of production originating from beds of

*Macrocystis pyrifera*, phytoplankton, and neighbouring terrestrial (riverine and terrestrially-derived POM) ecosystems. The use of stable isotope analysis in food web studies is a well established technique, but there are potential limitations with its use that need to be recognized (e.g. Fry & Sherr 1984, Stephenson et al. 1984, Simenstad et al. 1993).

We hypothesized that land-derived inputs of particulate carbon will be distinguishable from marine sources on nearshore reefs by a pattern of <sup>13</sup>C depletion in suspended reef POM (Canuel et al. 1995, Fry 2002). Consumers incorporating appreciable amounts of land-derived carbon should have more negative  $\delta^{13}\text{C}$  values in years of highest rainfall and on reefs experiencing and/or retaining particulate inputs from land compared with reefs that are less influenced by freshwater runoff. Suspended POM consisting primarily of marine phytoplankton is typically more enriched in <sup>13</sup>C than terrestrially derived carbon (Fry & Sherr 1984, Gearing et al. 1984). Carbon isotope values of reef consumers using primarily kelp or other <sup>13</sup>C-enriched benthic macroalgal production might be expected to have even more positive carbon isotopic signatures (Dunton & Schell 1987, Duggins et al. 1989, Fredriksen 2003).

In this study, we investigated the relative importance of marine and terrestrial sources of organic matter to the food web of nearshore reefs. Specifically, we explored temporal and spatial variability in the stable C and N isotope values of ocean and land-derived sources of organic matter over a 4 yr period on 4 reefs that varied in exposure to freshwater runoff and in kelp biomass. We compared these data to the stable C and N isotope values of a diverse group of consumers on each of the reefs to determine the extent to which consumer diets were influenced by variation in the different sources of organic matter.

## MATERIALS AND METHODS

**Study reefs.** We characterized the stable C and N isotope values of sources of organic matter and of a diverse array of invertebrate consumers on 4 rocky subtidal reefs that we anticipated to vary in exposure to freshwater runoff and in the standing crop of giant kelp (Fig. 1). Carpinteria Reef (CA), located directly offshore (0.1 to 0.2 km) of a small salt marsh (93 ha) and coastal plain developed for intensive agriculture (Page et al. 1995, Robinson 2006) was expected to be more influenced by freshwater runoff and to possess a lower standing crop of giant kelp than the other reefs. The reefs at Arroyo Quemado (AQ) and Mohawk (MO) were located 0.1 to 0.2 km offshore and had historically abundant giant kelp, whereas Naples Reef (NA),

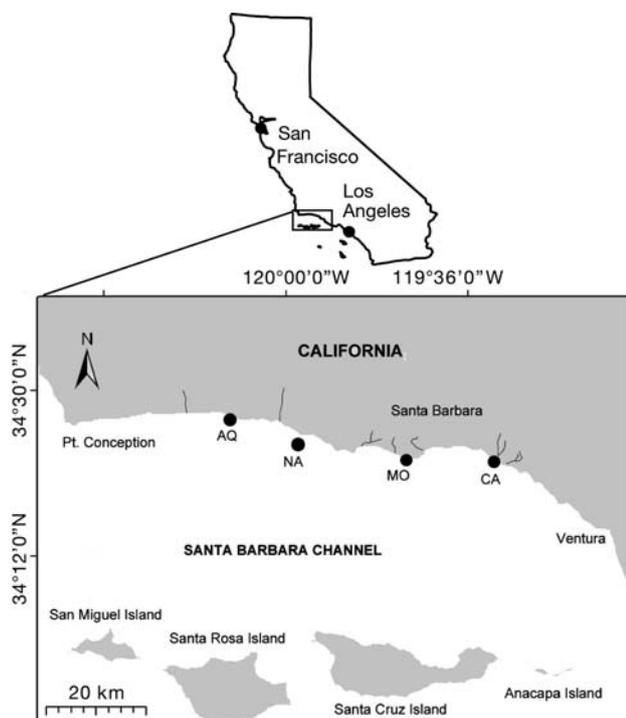


Fig. 1. Study reefs in the Santa Barbara Channel: Arroyo Quemado (AQ), Naples (NA), Mohawk (MO), and Carpinteria (CA). Sampled streams are marked

located further offshore (1.8 km), was anticipated to be less influenced by freshwater inputs and to have more variable giant kelp. The reef substrates are composed primarily of bedrock with relatively low topographic relief (i.e. <3 m) and overlap in water depth (AQ: 5–11 m; NA: 6–13 m; MO: 4–6 m; CA: 2–9 m).

AQ, NA, and CA were sampled monthly as part of the Santa Barbara Coastal Long Term Ecological Research Project (LTER), a multi-year program to investigate the relative importance of land and ocean processes in structuring giant kelp forest ecosystems. MO, which was sampled less frequently, was included in our study to provide additional data on the isotope values of consumers from a reef with historically abundant giant kelp.

**Sampling design. Sources of organic matter:** Temporal and spatial variability in the isotopic composition of reef suspended POM was investigated in water samples collected approximately monthly at CA and NA beginning in November 2000, and at AQ beginning in March 2001, through April 2005 (water samples were not collected at MO). Water samples were collected at depths of 1, 5, and 10 m using a Niskin bottle (10 m samples were not collected from CA because the bottom depth is <10 m). To obtain stable C and N isotope values of offshore suspended POM, we also collected water samples 8 to 20 km offshore of

the study reefs at depths of 1 and 5 m on 5 occasions from September 2002 to September 2004. These water samples were taken at different stations within an approximate 1100 km<sup>2</sup> rectangular area defined by latitudes 34° 10' to 34° 30' N and longitudes 119° 50' to 120° 10' W. Samples were either returned to the laboratory in Nalgene polypropylene bottles in a cooler where they were filtered (reef samples), or filtered on board ship (offshore samples, see 'Sample preparation' below).

To obtain stable C and N isotope values of land-derived POM, water samples were collected at nontidal locations in 8 coastal streams during storm events from November 2001 to March 2005. Stream water samples were collected manually in clean polyethylene bottles just below the water surface during periods of peak runoff and returned on ice to the laboratory where they were filtered. Values from 6 different storm events were averaged to obtain isotope values of suspended POM from each stream.

The stable isotopic signatures of the dominant benthic macroalgae were determined from tissue samples collected at the 4 study reefs. Samples of the giant kelp *Macrocystis pyrifera* were collected approximately monthly (less frequently from MO and CA) from the canopy of adult plants from 2002 through 2005. For this species only, both actively growing ('new') and senescent ('old') blades were collected during each sampling period to examine whether the isotopic composition of this macroalga varied with age of the tissue. Entire old blades, present on fronds in which the apical meristem had stopped growing, were sampled and processed whole. Entire new blades from actively growing fronds of the same plant were also sampled at the same time and processed whole. Tissue samples from 5 of the most common species of understory macroalgae were also collected annually at each reef in March–April of 2002 through 2005 (Table 1). Five replicate samples of each macroalgal species were collected from each reef and date.

**Kelp forest consumers:** Tissue samples from common species of benthic kelp forest invertebrates representing different trophic levels and feeding guilds (e.g. herbivores, suspension feeders, predators and scavengers) were collected by SCUBA divers at each reef once per year in March–April of 2002–2005 (Table 1). Five individuals of each invertebrate species were collected from each reef and date at depths of from 6 to 12 m. Samples of all consumers were kept on ice during transport to the laboratory and then stored frozen at –20°C until processing. We considered March and April a suitable time to test for the incorporation of terrestrially-derived POM by reef consumers because 92% of the annual rainfall in the Santa Barbara area has historically occurred from November through April

Table 1. Species and tissues of macroalgae and invertebrates sampled for isotopic analysis. n = 5 samples per species

Category	Species	Common name	Tissue sampled
<b>Macroalgae</b>			
Canopy forming	<i>Macrocystis pyrifera</i>	Giant kelp	Thallus tissue
Understory	<i>Chondrocanthus corymbiferus</i>		Thallus tissue
	<i>Corallina officinalis</i>	Coralline algae	Thallus tissue
	<i>Cystoseira osmundacea</i>	Bladder chain kelp	Thallus tissue
	<i>Gelidium robustum</i>		Thallus tissue
	<i>Rhodomenia californica</i>		Thallus tissue
<b>Macroinvertebrates</b>			
Suspension feeder	<i>Corynactis californica</i>	Strawberry anemone	Entire organism
	<i>Crassadoma gigantea</i>	Giant sea scallop	Adductor muscle, mantle
	<i>Cucumaria salma</i>	Salmon cucumber	Longitudinal muscle
	<i>Megabalanus californicus</i>	Giant acorn barnacle	Muscle
	<i>Ophiothrix spiculata</i>	Spiny brittle star	Entire organism
	<i>Styela montereyensis</i>	Stalked tunicate	Body wall
Herbivore	<i>Diopatra ornata</i>	Ornate tube worm	Entire organism
	<i>Lithopoma gibberosum</i>	Red turban snail	Foot tissue
	<i>Strongylocentrotus purpuratus</i>	Purple urchin	Lantern tissue
Predator/scavenger	<i>Asterina miniata</i>	Bat star	Tube feet
	<i>Conus californicus</i>	California cone snail	Foot tissue
	<i>Cypraea spadicea</i>	Chestnut cowry	Foot tissue
	<i>Pisaster giganteus</i>	Giant sea star	Tube feet

with most (44%) falling in January and February (Santa Barbara Flood Control, [www.countyofsb.org/pwd/water/downloads/hydro/234dailys.pdf](http://www.countyofsb.org/pwd/water/downloads/hydro/234dailys.pdf)).

**Rainfall, salinity, chlorophyll a concentration, biomass of giant kelp.** To explore relationships between the isotope values of suspended POM at the reefs and the timing and intensity of storm events, we obtained publicly available data on daily rainfall measured on the coastal plain at the Santa Barbara Flood Control District office, which lies 1 km inland from the coast (see above URL). Data on ocean salinity obtained from moored conductivity sensors (Seabird SBE 37) at AQ, NA, and CA were used as an indicator of freshwater runoff. Conductivity was sampled at a depth of ~4.5 m below mean lower low water every 20 min.

The isotopic composition of suspended reef POM depends not only on the sources of organic matter, but also on their relative abundances. We assessed the abundance of phytoplankton on the reefs by measuring the chlorophyll *a* (chl *a*) concentration of the same water samples that were analyzed for suspended POM at the reefs. We examined the biomass of giant kelp at our study reefs from 2001 to 2005 using data collected by ISP Alginates, a San Diego-based kelp harvesting company that has conducted aerial surveys of *Macrocystis* biomass in southern California since 1958 (see Reed et al. 2006 for a more detailed description of these data). We used data for the administrative kelp beds defined by the California Department of Fish and Game that contained our study reefs: bed

numbers 30 (AQ: 1.01 km<sup>2</sup>), 28 (NA: 1.54 km<sup>2</sup>), 24 (MO: 0.13 km<sup>2</sup>), and 20 (CA: 0.62 km<sup>2</sup>).

**Sample preparation.** Water samples used for chl *a* analysis were filtered under vacuum through 0.45 µm 47 mm HAWP Millipore filters. Filters were stored frozen in glass scintillation vials at -20° C until analysis. Chl *a* concentrations were determined following methods of Parsons et al. (1984). For isotopic analysis of suspended POM, water samples were filtered under vacuum through pre-combusted (450°C for 5 h) 25 mm GF/F filters. The filters were stored at -20°C in pre-combusted foil pouches. In the laboratory, filters were thawed, transferred to clean scintillation vials, exposed to dilute HCl fumes to remove carbonates, and dried at 65°C.

Macroalgal samples were rinsed in deionized water (DI), gently scrubbed to remove adhering material, and submerged in 10% HCl until bubbles ceased forming to remove any remaining calcified epiphytes, or (in the case of the coralline red alga *Corallina officinalis*) calcium impregnated in the thallus. For macroinvertebrates, samples of tissue or entire individuals in the case of some species (e.g. *Corynactis californica*, *Diopatra ornata*) were analyzed (Table 1). Tissues were excised, submerged in 10% HCl until bubbles stopped forming, rinsed with deionized water, and dried at 60°C. Organisms that were analyzed whole were held in seawater overnight to allow gut evacuation prior to processing. Dried samples of macroalgal and animal material were ground to a fine powder with a ceramic

mortar and pestle and stored in a desiccator until analysis.

**Isotopic analysis.**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of POM, macroalgae, and invertebrate consumers were determined using a Europa Tracermass isotope mass spectrometer coupled with a Europa Roboprep elemental analyzer unit for samples collected in 2001–2002 or a Thermo Finnigan Delta-Plus Advantage isotope mass spectrometer with a Costech EAS elemental analyzer for samples collected in 2003–2005. Instrument precision, determined from replicate analyses of the same standard (NBS 1572, citrus leaf) run on both machines was  $\pm 0.3\text{‰}$  for C and  $\pm 0.5\text{‰}$  for N for the Europa Tracermass and  $\pm 0.2\text{‰}$  for C and N for the Thermo Finnigan Delta-Plus Advantage. The natural abundances of  $^{13}\text{C}$  and  $^{15}\text{N}$  are expressed in standard  $\delta$  notation and calculated as follows for element X:

$$\delta X_n = 1000 \times [(R_{\text{sample}} - R_{\text{standard}})/R],$$

where  $R = X_n/X_{n-1}$  and expressed per mil (‰) relative to the PDB standard for carbon and atmospheric  $\text{N}_2$  for nitrogen. Variation between replicate portions of the same ground sample was generally less than  $0.3\text{‰}$  for C and  $0.5\text{‰}$  for N.

**Data analysis.** We used correlation analysis to examine covariation in the stable isotope values of suspended POM among reefs over time, and to explore relationships between the isotope values of suspended POM and the abundance of 2 potential sources of organic matter on the reefs: phytoplankton as chl *a* concentration, and giant kelp. Samples of suspended POM and chl *a* concentration were taken on the same day, whereas estimates of giant kelp biomass were within 7 d of collection of the POM samples. We used ANOVA followed by *post hoc* Tukey tests, if necessary, to test for differences in the isotopic composition of suspended POM and giant kelp among reefs, and of selected reef consumers among reefs and times (Underwood 1997). Reef was treated as a fixed factor since the study reefs were chosen *a priori* based on anticipated differences in exposure to freshwater runoff and in biomass of giant kelp. Time was treated as a fixed factor in the analysis of consumer isotope data since the same time-of-year was sampled each of 4 years and we were testing for an isotopic response in consumers to freshwater runoff. All statistical analyses were done using Systat 9.0 (SPSS).

A simple 2-source mixing model (Eddins 2001) was used to estimate the proportion of terrestrial POM in the reef POM pool on 3 occasions:

$$F_T = (\delta^{13}\text{C}_{\text{POM}} - \delta^{13}\text{C}_M) / (\delta^{13}\text{C}_T - \delta^{13}\text{C}_M),$$

where  $\delta^{13}\text{C}_{\text{POM}}$  is the C isotope value of the reef POM,  $\delta^{13}\text{C}_T$  is the mean value of the terrestrial end-member,

$\delta^{13}\text{C}_M$  is the value of the marine end-member, and  $F_T$  is the proportional contribution of terrestrial particulates to the reef POM pool.

## RESULTS

### Rainfall, salinity, biomass of giant kelp, chl *a* concentration

Rainfall during the study occurred primarily during December through March, exceeding the historical annual mean prior to our study of 46 cm (calculated from September through August,  $n = 129$  yr) during 2000–2001 (65.6 cm), 2002–2003 (63.4 cm), and 2004–2005 (93.8 cm) and falling below the mean in 2001–2002 (22.9 cm) and 2003–2004 (27.2 cm) (Fig. 2a). Rainfall during 2004–2005 was exceptionally high and was exceeded in only 5 of the previous 133 yr.

Carpinteria Reef experienced the lowest daily mean salinity values of the study reefs (e.g. 29.2 to 31.1 psu in January and February 2005; Fig. 2b). In general, salinity data indicated that the amount of time that reefs were exposed to substantial freshwater was brief even following major storm events. For example, during the 4 yr period from 15 February 2001 through 30 April 2005, daily mean salinity values fell below 32 psu for only 14 d at Carpinteria Reef and only 3 and 2 d at Naples Reef and Arroyo Quemado Reef, respectively (Fig. 2). However, some freshwater influence was detectable at all reefs over the longer term during the winter storms of 2005 when salinity values remained below 33 psu on a scale of weeks at all sites (Fig. 2).

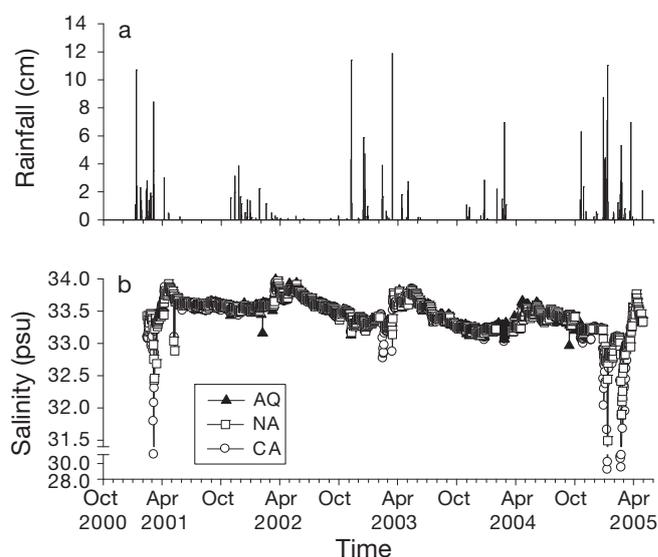


Fig. 2. Pattern of daily rainfall measured in Santa Barbara, California, and salinity measured at the study reefs. Site abbreviations as in Fig. 1

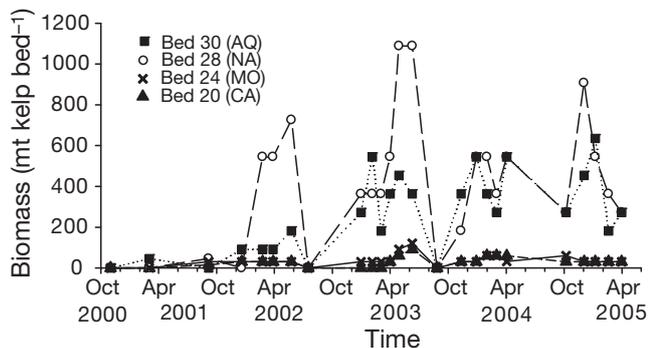


Fig. 3. *Macrocyctis pyrifera*. Total biomass (metric tons, mt) per kelp bed estimated from aerial survey along sections of coastline that include AQ, NA, MO, and CA reefs from 2002 to 2005

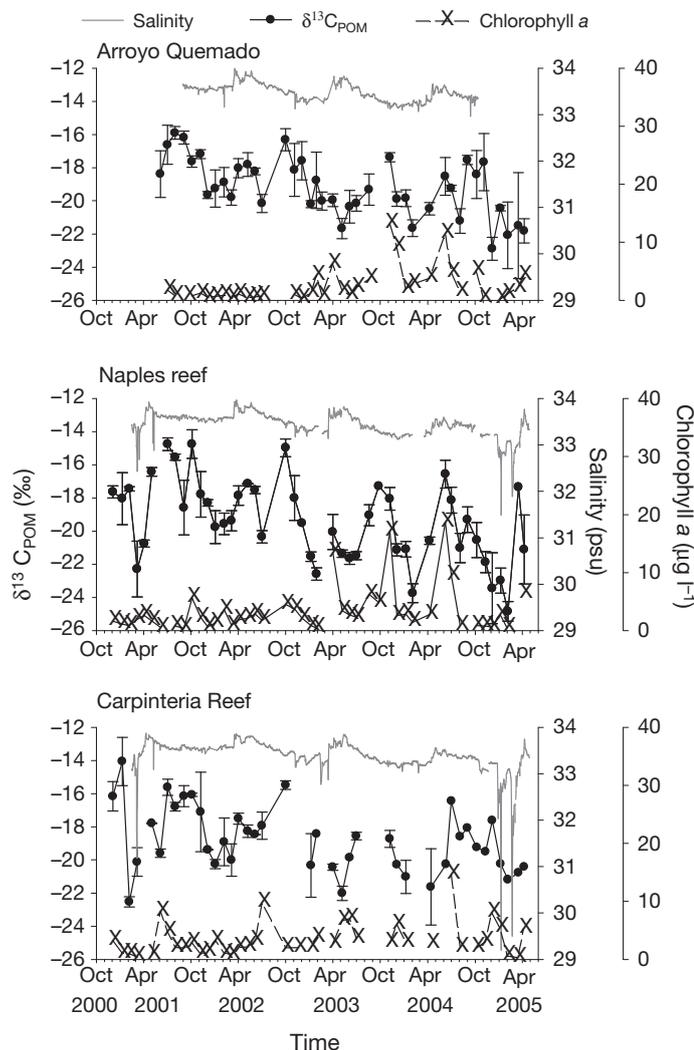


Fig. 4.  $\delta^{13}\text{C}_{\text{POM}}$  values and chl *a* concentration, from AQ, NA, and CA reefs. Values for  $\delta^{13}\text{C}_{\text{POM}}$  and chl *a* concentration connected by lines collected 1 mo apart. Time series data for these variables are not available from MO

The biomass of giant kelp varied among reefs and over time (Fig. 3). Generally, kelp biomass was low at CA throughout the entire study and regionally low in 2001 and 2002. Total kelp biomass was highest at NA and AQ in 2003 through 2005. Kelp plants grow year round with fastest growth in the winter (D.C. Reed unpubl. data). Abrupt decreases in kelp biomass (e.g. Fall 2002, 2003) occurred as a result of disturbance from swell that removed entire plants from the reef.

Chl *a* concentrations were quite variable over time at all reefs, ranging from  $<0.5$  to  $20 \mu\text{g l}^{-1}$  during bloom events (Fig. 4).

### Isotope values of primary production

#### Offshore, terrestrial POM and reef macroalgae

The mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values ( $\pm 1\text{SD}$ ) for offshore suspended POM computed across sampling dates were  $-21.0 \pm 1.2\text{‰}$  and  $6.8 \pm 0.8\text{‰}$ , respectively (Table 2). Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for POM in terrestrial runoff were  $-24.6 \pm 0.9\text{‰}$  and  $2.9 \pm 1.5\text{‰}$ , respectively ( $n = 8$  streams).

Mean values of new and old growth giant kelp computed across sampling dates ranged from  $-13.8 \pm 1.9\text{‰}$  to  $-12.2 \pm 1.0\text{‰}$  (Table 3). There were significant effects of month (ANOVA:  $p = 0.020$ ,  $F_{11,85} = 2.230$ ) and age of blade ( $p = 0.045$ ,  $F_{1,85} = 4.140$ ), but not reef ( $p = 0.142$ ,  $F_{2,85} = 1.996$ ) on the  $\delta^{13}\text{C}$  values. However, the difference in mean  $\delta^{13}\text{C}$  values among months ( $\leq 1.6\text{‰}$ ) or between ages ( $\leq 0.8\text{‰}$ ) was small.

Mean  $\delta^{15}\text{N}$  values of new and old growth kelp computed across sampling dates ranged from  $8.5 \pm 1.1\text{‰}$  to  $9.7 \pm 2.1\text{‰}$  (Table 3). There were significant interaction effects between age of blade and month (ANOVA:  $p = 0.013$ ,  $F_{11,85} = 2.384$ ) and age of blade and reef ( $p = 0.027$ ,  $F_{2,85} = 3.766$ ) on  $\delta^{15}\text{N}$  values, but again the differences in mean values among months ( $\leq 1.7\text{‰}$ ), among reefs ( $\leq 0.7\text{‰}$ ), and between ages ( $\leq 1.2\text{‰}$ ) were small.

$\delta^{13}\text{C}$  values of individual understory species generally ranged between  $-23$  and  $-18\text{‰}$  and were  $^{13}\text{C}$ -

Table 2. Mean stable C and N isotope values ( $\pm 1\text{SD}$ ) of suspended POM sampled in the Santa Barbara Channel 8 to 20 km offshore of the study reefs.  $n =$  number of samples

Date	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n
8 Sep 2002	$-22.4 \pm 1.0$	$6.2 \pm 1.3$	6
12 Oct 2003	$-19.6 \pm 1.4$	$7.3 \pm 1.1$	5
26 Feb 2004	$-20.9 \pm 1.1$	$7.5 \pm 0.4$	12
10 May 2004	$-20.0 \pm 0.3$	$5.7 \pm 0.4$	3
13 Sep 2004	$-21.9 \pm 0.4$	$7.3 \pm 0.9$	5
Mean	$-21.0 \pm 1.2$	$6.8 \pm 0.8$	

Table 3. *Macrocystis pyrifera*. Mean stable C and N isotope values ( $\pm 1$  SD) for new and old growth blades sampled from December 2000 to January 2005. Mean values calculated over time. Number of samples from each reef in parentheses

Reef	New growth		Old growth	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Arroyo Quemado	$-12.2 \pm 1.0$ (27)	$9.7 \pm 1.4$ (27)	$-12.7 \pm 1.3$ (27)	$8.6 \pm 1.2$ (27)
Naples	$-13.0 \pm 2.0$ (31)	$9.5 \pm 1.6$ (31)	$-13.8 \pm 1.9$ (30)	$8.5 \pm 1.1$ (30)
Carpinteria	$-12.4 \pm 1.0$ (18)	$9.7 \pm 0.9$ (18)	$-13.2 \pm 1.4$ (16)	$9.7 \pm 2.1$ (16)

depleted relative to values of giant kelp (Table 4). There were significant interaction effects among reef, year, and species on  $\delta^{13}\text{C}$  values of understory macroalgae (ANOVA:  $p < 0.01$ ).  $\delta^{13}\text{C}$  values of 2 species (*Chondracanthus corymbiferus*, *Corallina officinalis*) from CA were noticeably  $^{13}\text{C}$ -enriched relative to understory macroalgae from other reefs and other species from the same reef.  $\delta^{13}\text{C}$  values of the red alga *Rhodymenia californica* were distinctively more  $^{13}\text{C}$ -depleted ( $\leq -30\%$ ) than other understory species or giant kelp.  $\delta^{15}\text{N}$  values of understory macroalgae, generally 6 to 9‰, overlapped values for giant kelp (Table 4). There were significant interactions among reef, year, and species on  $\delta^{15}\text{N}$  values of understory macroalgae (ANOVA:  $p < 0.01$ ).

### Isotope values of reef suspended POM

Monthly  $\delta^{13}\text{C}$  values of reef suspended POM ranged from  $-23.7$  to  $-14.1\%$  (Fig. 4).  $\delta^{13}\text{C}$  values of POM at AQ, NA, and CA were significantly correlated with

one another in time (AQ vs. NA:  $p = 0.002$ ,  $r^2 = 0.226$ ,  $n = 40$ ; AQ vs. CA:  $p = 0.001$ ,  $r^2 = 0.444$ ,  $n = 36$ ; NA vs. CA:  $p = 0.001$ ,  $r^2 = 0.254$ ,  $n = 41$ ) and the mean values ( $\pm 1$  SD) for each reef averaged over time (AQ:  $-19.2 \pm 1.7$ ; NA:  $-19.4 \pm 2.4$ ; CA:  $-18.8 \pm 2.0$ ) were not significantly different from each other (ANOVA:  $p = 0.319$ ,  $F_{2,128} = 1.154$ ).

$\delta^{13}\text{C}$  values of reef POM tended to decrease following periods of significant rainfall (as indicated by a drop in salinity), increase during phytoplankton blooms (as measured by chl *a* concentration), and generally decline in late fall through early winter at all reefs in the absence of any obvious drivers (Fig. 4). Abrupt declines in  $\delta^{13}\text{C}_{\text{POM}}$  (ranging from 2.6 to 8.4‰) following significant rainfall events were most evident at CA (e.g. 5 February 2001, 7 January 2003, 7 January 2005), which experiences the greatest amount of freshwater runoff. However, this pattern did not necessarily occur at the other reefs, which were less influenced by freshwater runoff. For example, the appreciable change in  $\delta^{13}\text{C}_{\text{POM}}$  values evident at CA in early February 2001 was not evident at NA.

If one assumes that abrupt decreases in  $\delta^{13}\text{C}_{\text{POM}}$  values at CA following storm events were due to inputs of land-derived POM, then a 2-source mixing model can be used to estimate the proportion of these particles in the reef POM pool (Eddins 2001). Using a value of  $-24.6\%$  as the terrestrial end-member ( $\delta^{13}\text{C}_T$ ) and values of  $-14.1$ ,  $-17.6$ , and  $-17.2\%$  as the marine end-members ( $\delta^{13}\text{C}_M$ ) prior to the storms of January 2001, December 2002, and December 2004, respectively, we

Table 4. Mean C and N isotope values ( $\pm 1$  SD) for 5 species of understory algae sampled annually from 2002 to 2005. Mean value for all taxa, excluding *Rhodymenia californica*, averaged across years. Values are averages of 4 yr unless indicated otherwise in parentheses

Taxon	Arroyo Quemado	Naples	Mohawk	Carpinteria
<b><math>\delta^{13}\text{C}</math></b>				
<i>Chondracanthus corymbiferus</i>	$-24.3 \pm 2.2$	$-21.1 \pm 3.8$	$-21.6 \pm 3.4$	$-15.5$ (2)
<i>Corallina officinalis</i>	$-22.3 \pm 0.3$	$-18.6 \pm 3.0$	$-19.8 \pm 0.9$	$-15.4 \pm 0.8$
<i>Cystoseira osmundacea</i>	$-21.8 \pm 3.0$	$-22.1 \pm 0.9$	$-21.2 \pm 1.0$	$-18.6$ (2)
<i>Gelidium robustum</i>	$-22.2$ (2)	$-20.2 \pm 1.3$	$-21.0 \pm 1.3$	$-17.4 \pm 2.3$
<i>Rhodymenia californica</i>	$-31.7$ (2)	$-31.5$ (2)	$-31.0$ (2)	$-30.3$ (2)
Mean value	$-22.8 \pm 1.3$	$-20.6 \pm 1.8$	$-20.9 \pm 0.9$	$-16.8 \pm 2.4$
<b><math>\delta^{15}\text{N}</math></b>				
<i>Chondracanthus corymbiferus</i>	$7.3 \pm 1.1$	$6.9 \pm 0.9$	$7.1 \pm 0.8$	$8.3 \pm 1.0$
<i>Corallina officinalis</i>	$8.2 \pm 0.6$	$8.0 \pm 0.5$	$8.2 \pm 0.4$	$9.7 \pm 0.7$
<i>Cystoseira osmundacea</i>	$8.2 \pm 1.0$	$6.3 \pm 0.5$	$8.1 \pm 1.3$	$5.9 \pm 2.9$
<i>Gelidium robustum</i>	$9.4$ (2)	$7.3 \pm 1.2$	$4.9 \pm 0.1$	$7.5 \pm 1.3$
<i>Rhodymenia californica</i>	$7.8$ (2)	$7.8$ (2)	$8.0$ (2)	$7.9$ (2)
Mean value	$7.9 \pm 0.5$	$7.1 \pm 0.9$	$7.8 \pm 0.6$	$8.0 \pm 1.9$

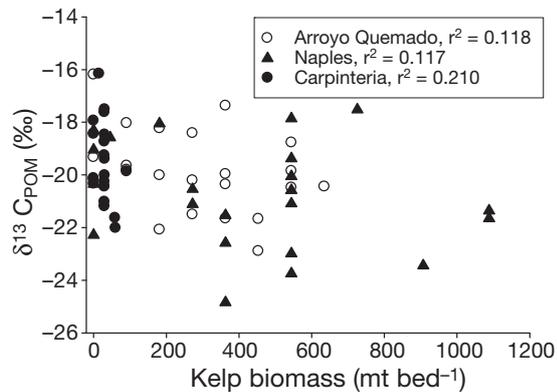


Fig. 5. Relationship between the biomass of giant kelp and the  $\delta^{13}\text{C}$  value of suspended POM

estimated that ~80, 39, and 37% of the suspended POM was of terrestrial origin in the samples collected following these storm events.

We explored the potential importance of temporal and spatial variation in the biomass of giant kelp in influencing reef  $\delta^{13}\text{C}_{\text{POM}}$  values (Fig. 5). We expected that  $\delta^{13}\text{C}_{\text{POM}}$  values would be more positive on reefs and in years of greater kelp biomass, reflecting kelp detrital inputs to the POM pool. However,  $\delta^{13}\text{C}_{\text{POM}}$  values were not correlated with the biomass of giant kelp at AQ ( $p = 0.138$ ,  $r^2 = 0.118$ ,  $n = 23$ ) or NA ( $p = 0.110$ ,  $r^2 = 0.117$ ,  $n = 23$ );  $\delta^{13}\text{C}_{\text{POM}}$  values were unexpectedly negatively correlated with kelp biomass at CA ( $p = 0.043$ ,  $r^2 = 0.210$ ,  $n = 22$ ).

We also examined the potential importance of phytoplankton abundance in influencing  $\delta^{13}\text{C}_{\text{POM}}$  values. Our expectation here was that reef  $\delta^{13}\text{C}_{\text{POM}}$  values would more closely resemble  $\delta^{13}\text{C}$  values of ocean phytoplankton (i.e. become more negative) during periods of high chl *a* concentration. Overall, there was no correlation between reef  $\delta^{13}\text{C}_{\text{POM}}$  values and chl *a* concentration ( $p > 0.05$ ). However, chl *a* concentrations were higher and more variable from January 2003 through April 2005 than in the preceding months (Fig. 4). In contrast to expectations,  $\delta^{13}\text{C}_{\text{POM}}$  values were positively correlated with chl *a* concentration at all reefs during this period (AQ:  $p = 0.018$ ,  $r^2 = 0.237$ ,  $n = 20$ ; NA:  $p = 0.001$ ,  $r^2 = 0.563$ ,  $n = 22$ ; CA:  $p = 0.020$ ,  $r^2 = 0.267$ ,  $n = 20$ ).

Monthly  $\delta^{15}\text{N}_{\text{POM}}$  values ranged from 2.7 to 14.5‰ across the reefs (Fig. 6). There was a significant correlation in values among reefs over time (AQ vs. NA:  $p = 0.005$ ,  $r^2 = 0.192$ ,  $n = 39$ ; AQ vs. CA:  $p = 0.001$ ,  $r^2 = 0.291$ ,  $n = 37$ ; NA vs. CA:  $p = 0.001$ ,  $r^2 = 0.412$ ,  $n = 42$ ), and mean values for each reef averaged over time (AQ:  $8.9 \pm 2.3\%$ ; NA:  $8.3 \pm 1.8\%$ ; CA:  $8.7 \pm 2.6\%$ ) were not significantly different ( $p = 0.310$ ,  $F_{2, 128} = 1.181$ , ANOVA).  $\delta^{15}\text{N}_{\text{POM}}$  values were variable, but there was a general pattern of more  $^{15}\text{N}$ -enriched values during the late summer and fall at all reefs (Fig. 6). A consistent pattern of change in  $\delta^{15}\text{N}_{\text{POM}}$  values associated with rainfall events (as indicated by a drop in salinity) was absent. There was no correlation between  $\delta^{15}\text{N}_{\text{POM}}$  values and chl *a* concentration overall or for the period from January 2003 through April 2005 (AQ:  $p = 0.922$ ; NA:  $p = 0.371$ ; CA:  $p = 0.742$ ).

### Isotope values of reef consumers

#### Patterns among taxa and functional groups

$\delta^{13}\text{C}$  values for reef suspension-feeders tended to be  $^{13}\text{C}$ -depleted relative to values of benthic herbivores and predators; however, substantial variability among

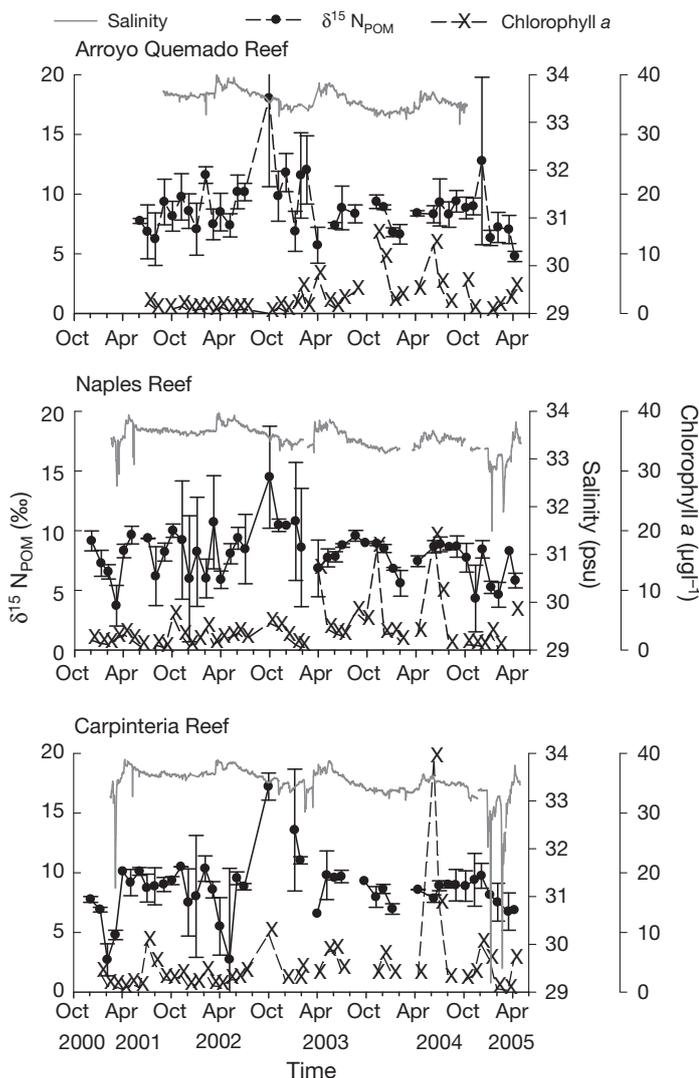


Fig. 6.  $\delta^{15}\text{N}_{\text{POM}}$  values and chl *a* concentration, and salinity from AQ, NA, and CA. Values for  $\delta^{15}\text{N}_{\text{POM}}$  and chl *a* concentration connected by lines collected 1 mo apart

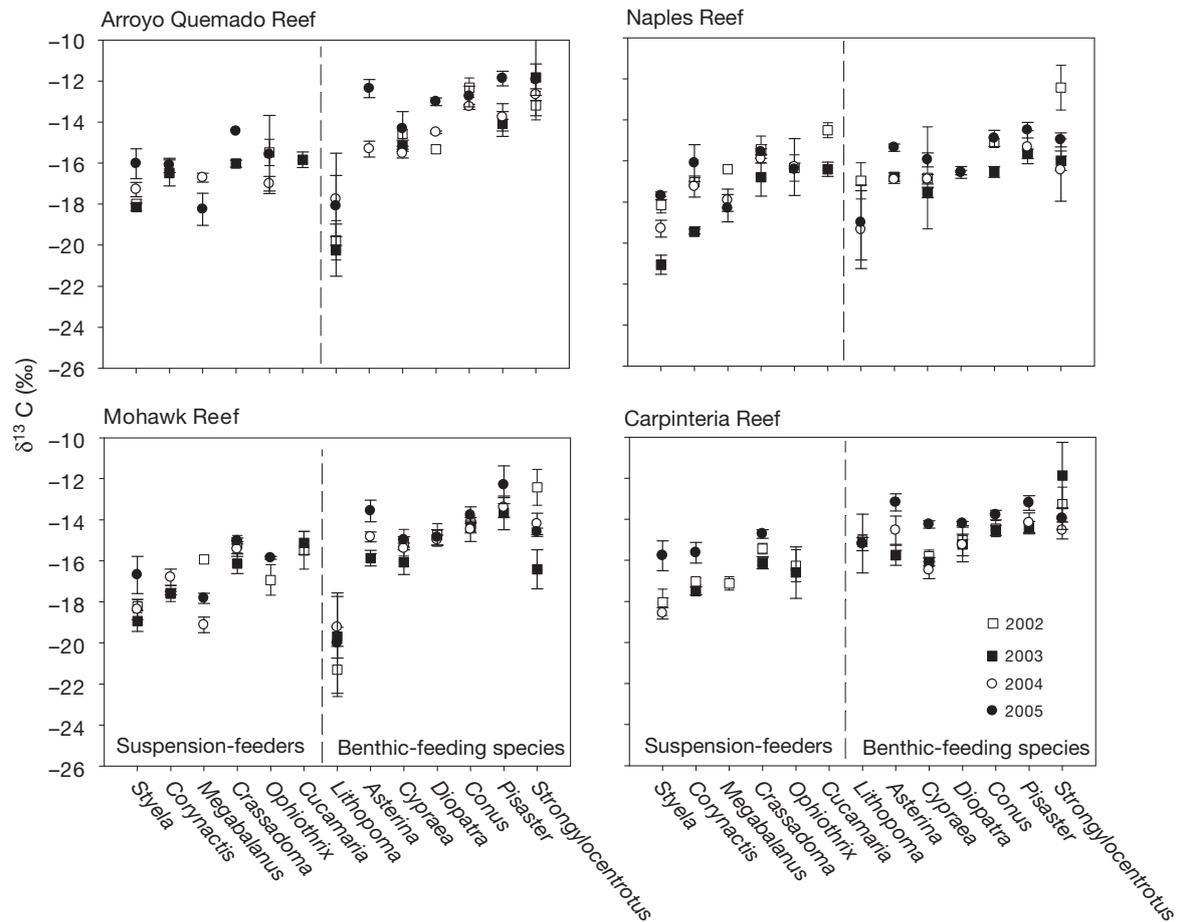


Fig. 7.  $\delta^{13}\text{C}$  values for common invertebrate consumers collected annually in March to April 2002 through 2005 at CA, MO, NA, and AQ reefs. Species were not always available from every reef each year

sites and years was observed for some species (Fig. 7).  $\delta^{13}\text{C}$  values of the stalked tunicate *Styela montereyensis* were consistently the most  $^{13}\text{C}$ -depleted of suspension-feeding taxa within a given year at Naples Reef ( $-21.1$  to  $-17.7\text{‰}$ ), but this pattern was less evident at the other reefs. In general, values of the scallop *Craspedomena gigantea*, sea cucumber *Cucumaria salma*, and brittle star *Ophiothrix spiculata* were enriched ( $-16.8$  to  $-14.5\text{‰}$ ) relative to other suspension-feeding taxa within a given reef and year (Fig. 7).

$\delta^{13}\text{C}$  values for the sea urchin *Strongylocentrotus purpuratus* and the seastar *Pisaster ochreus* were generally among the most  $^{13}\text{C}$ -enriched for herbivores and predators, respectively ( $-16.4$  to  $-11.9\text{‰}$ ), whereas  $\delta^{13}\text{C}$  values of the snail *Lithopoma gibberosum* were generally the most  $^{13}\text{C}$ -depleted of this group of consumers ( $-21.3$  to  $-17.8\text{‰}$ ) except at CA where values of this snail were approximately  $-15.0\text{‰}$ .

$\delta^{15}\text{N}$  values for predators tended to be  $^{15}\text{N}$ -enriched relative to those of deposit feeders and herbivores for both suspension-feeding and benthic-feeding taxa

(Fig. 8). For suspension-feeding taxa, the anemone *Corynactis californica* generally had the most enriched values ( $13.2$  to  $14.6\text{‰}$ );  $\delta^{15}\text{N}$  values of other suspension-feeding taxa were more variable, generally ranging between  $11$  and  $13\text{‰}$ .  $\delta^{15}\text{N}$  values of benthic-feeding predators (*Cypraea spadicea*, *Pisaster giganteus*, *Conus californica*, *Asterina miniata*) generally ranged between  $12$  and  $15\text{‰}$ , whereas values of benthic-feeding herbivores (*Strongylocentrotus purpuratus*, *Diopatra ornata*, *Lithopoma gibberosum*) were more  $^{15}\text{N}$ -depleted, ranging between  $10$  and  $12\text{‰}$  (Fig. 8).

#### Spatial and temporal variability

We tested for differences in the C and N isotope values of selected consumers among reefs (sites) and years that might reflect spatial or temporal influences of freshwater runoff or other factors on material inputs into reef food webs. To facilitate comparisons across

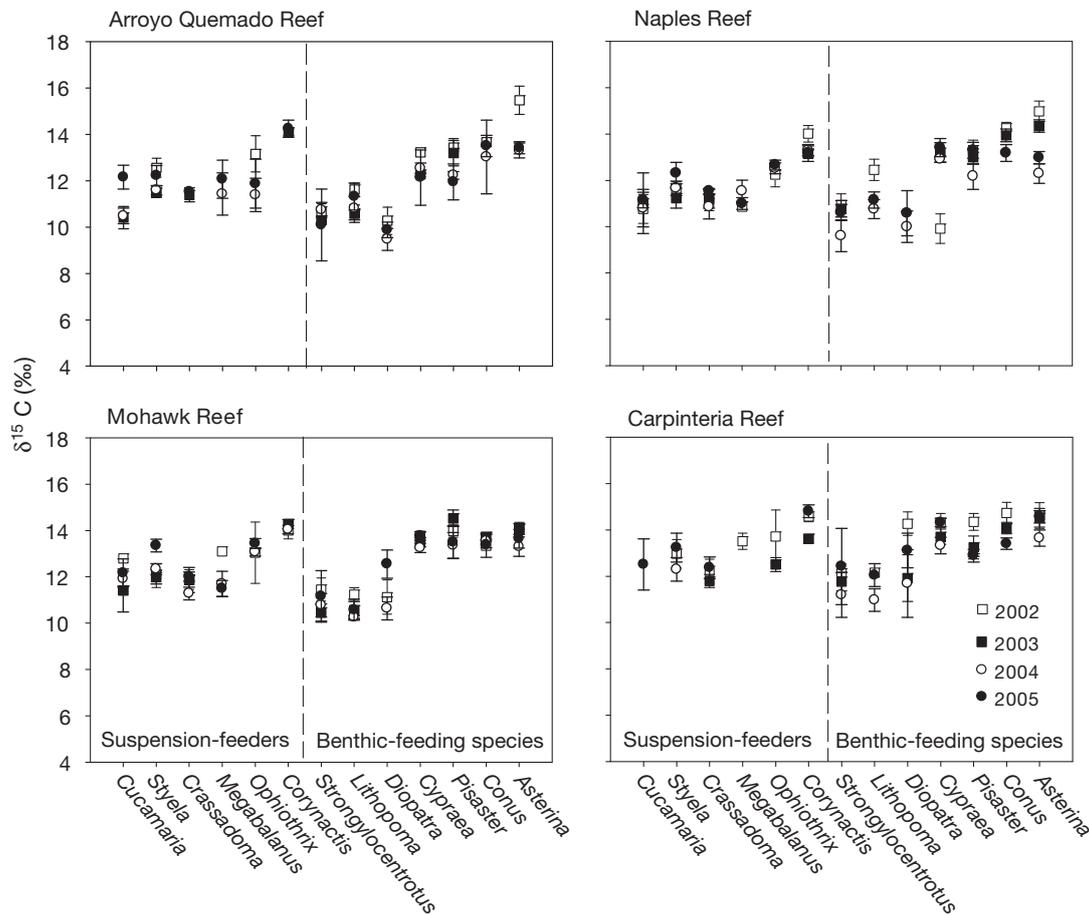


Fig. 8.  $\delta^{15}\text{N}$  values for common invertebrate consumers for the years 2002 through 2005. Sample sites and collection time as in Fig. 7

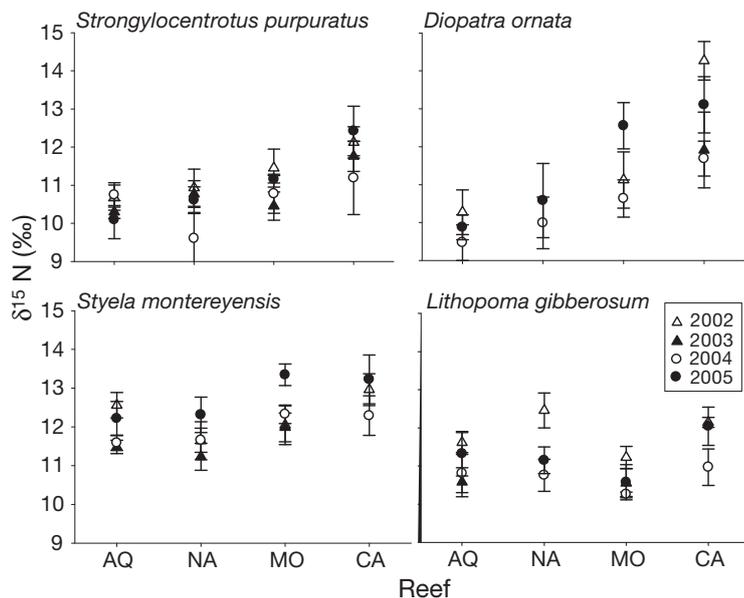


Fig. 9. Variation in the  $\delta^{15}\text{N}$  values of selected consumers among reefs. Reefs are arranged from left to right relative to increasing influence of freshwater runoff as measured by variation in salinity

reefs and reduce variability associated with trophic enrichment effects (DeNiro & Epstein 1978, 1981, Minagawa & Wada 1984, Peterson & Fry 1987), this analysis focused on the 4 lower trophic level taxa that were sampled on all reefs in at least 2 years (the stalked tunicate *Styela montereyensis*, the purple sea urchin *Strongylocentrotus purpuratus*, the ornate tube worm *Diopatra ornata*, and the turban snail *Lithopoma gibberosum*).

For  $\delta^{13}\text{C}$  values, there was a significant reef  $\times$  year interaction for all 4 consumers (ANOVA:  $p < 0.001$ ). Differences in mean  $\delta^{13}\text{C}$  values among reefs and years were generally small ( $\leq 1.5\%$ ) and consistent patterns that might suggest an influence of reef location or of 'wet' or 'dry' year on consumer  $\delta^{13}\text{C}$  values were absent (Fig. 7). Noteworthy exceptions include the consistently  $^{13}\text{C}$ -enriched values of *Lithopoma gibberosum* across all years at CA ( $-15.1 \pm 0.8$ ) compared with the other reefs ( $-19.9 \pm 1.6$  to  $-18.2 \pm$

1.9‰).  $\delta^{13}\text{C}$  values of *Strongylocentrotus purpuratus* and *Diopatra ornata* were also consistently most  $^{13}\text{C}$ -enriched at AQ, whereas values for *Styela montereyensis* were most  $^{13}\text{C}$ -depleted at NA.

There was a significant reef effect on the  $\delta^{15}\text{N}$  values for 3 of 4 species, *Diopatra ornata* (ANOVA:  $p < 0.001$ ,  $F_{3,25} = 26.225$ ), *Strongylocentrotus purpuratus* ( $p < 0.001$ ,  $F_{3,60} = 15.098$ ), and *Lithopoma gibberosum* ( $p < 0.001$ ,  $F_{3,54} = 10.719$ ), in the absence of a reef  $\times$  year interaction. Overall,  $\delta^{15}\text{N}$  values for *S. purpuratus* and *D. ornata* were significantly  $^{15}\text{N}$ -enriched at CA compared with the other reefs (Tukey test:  $p < 0.01$ ) (Fig. 9).

A similar, though less pronounced, pattern was found for *Styela montereyensis*, but the significant effect of reef was confounded by a reef  $\times$  year interac-

tion (ANOVA:  $p = 0.007$ ,  $F_{8,57} = 3.026$ ). Although there were significant effects of reef and year ( $p < 0.001$ ,  $F_{3,54} = 20.897$ ) on the  $\delta^{15}\text{N}$  values of *Lithopoma gibberosum*, differences in mean values across reefs and among years were small ( $\leq 1\%$ ) and no patterns were evident (Fig. 9).

#### Sources of production used by reef consumers

When averaged across years, plots of  $\delta^{15}\text{N}$  versus  $\delta^{13}\text{C}$  values (Fig. 10) provide a qualitative depiction of potential sources of organic matter used by consumers at each reef; however, these plots do not consider inter-annual variability in sources of production that include

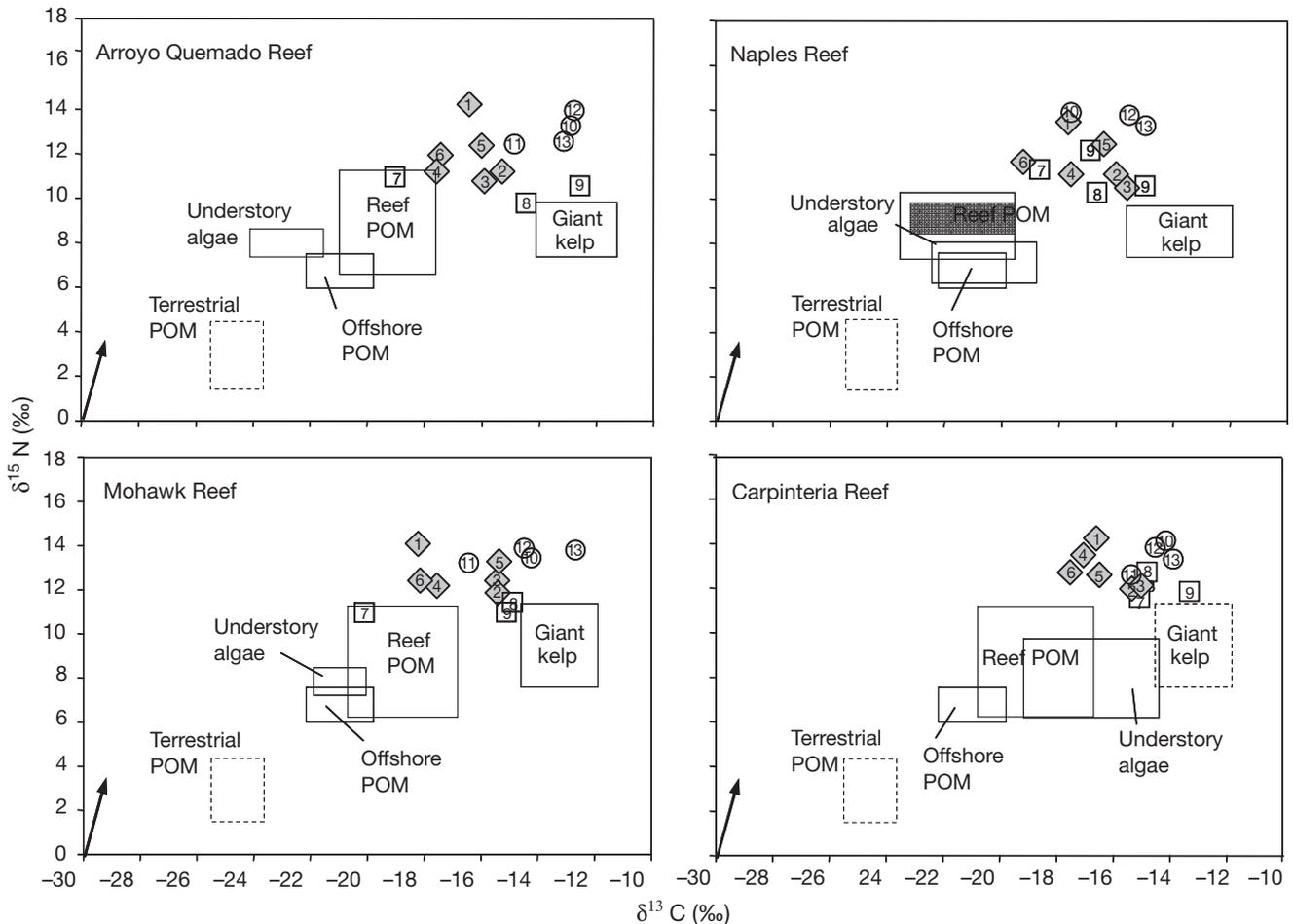


Fig. 10.  $\delta^{15}\text{N}$  versus  $\delta^{13}\text{C}$  values averaged across years for common invertebrate consumers from AQ, NA, MO and CA reefs together with mean values ( $\pm 1$  SD) enclosed by rectangles for the giant kelp *Macrocystis pyrifera*, and suspended reef POM, understory macroalgae, offshore POM, and terrestrial POM (values from text and Tables 2 to 4). Giant kelp was not abundant at Carpinteria Reef during this study. Consumer values are from Figs. 7 & 8. Arrow: predicted trophic enrichment in isotope values for C (+1‰) and N (+3.5‰); ( $\diamond$ ): suspension-feeders, (1) *Corynactis californica*, (2) *Crassadoma gigantea*, (3) *Cucumaria salma*, (4) *Megabalanus californicus*, (5) *Ophiothrix spiculata*, and (6) *Styela montereyensis*; ( $\square$ ): benthic-feeding herbivores, (7) *Lithopoma gibberosum*, (8) *Diopatra ornata*, (9) *Strongylocentrotus purpuratus*; ( $\circ$ ): benthic-feeding predators/scavengers, (10) *Conus californicus*, (11) *Cypraea spadicea*, (12) *Asterina miniata*, (13) *Pisaster ochraceus*. Taxonomic category and common names are provided in Table 1

regionally low biomass of giant kelp the first 2 years of the study (Fig. 3). The isotope values of common reef consumers were enriched (by at least +5‰ for C and +7‰ for N) relative to terrestrial POM and, taking into consideration trophic enrichment effects for C and N that would increase this difference (Fry & Sherr 1984, Minagawa & Wada 1984, Peterson & Fry 1987), there was no suggestion that marine consumers were incorporating significant amounts of terrestrially-derived particulate C and N at any of the reefs (Fig. 10).

$\delta^{13}\text{C}$  values of some suspension-feeders (i.e. *Styela montereyensis*, *Corynactis californica*, *Megabalanus californicus*) agreed more closely with values for reef POM than others (i.e. *Crassadoma gigantea*, *Cucumaria salma*, *Ophiothrix spiculata*). For the latter species,  $\delta^{13}\text{C}$  values were more  $^{13}\text{C}$ -enriched relative to reef POM than would be predicted by a trophic enrichment factor for C of +1‰.

The plots suggest an important contribution of  $^{13}\text{C}$ -enriched carbon to the diet of *Diopatra ornata* and *Strongylocentrotus purpuratus*, which could originate from giant kelp, or at CA, from  $^{13}\text{C}$ -enriched coralline or other benthic algae in the absence of giant kelp. The benthic-feeding herbivorous gastropod *Lithopoma gibberosum*, which had a  $^{13}\text{C}$ -depleted signature at AQ and MO, was one exception. Isotope values for this species suggested grazing on  $^{13}\text{C}$ -depleted understory algae at these reefs. However,  $^{13}\text{C}$ -enriched values of this snail at CA, which lacked appreciable giant kelp during this study, suggested the use of the  $^{13}\text{C}$ -enriched coralline or other macroalgae present at this location.

## DISCUSSION

### Source of reef suspended POM

A major goal of this study was to explore the contributions of land- and marine-derived sources of organic matter to the reef POM pool and their potential use by reef consumers. Since land-derived POM is typically  $^{13}\text{C}$ -depleted relative to marine POM (Fry & Sherr 1984, Canuel et al. 1995, this study), we predicted that reef  $\delta^{13}\text{C}_{\text{POM}}$  values would decrease with inputs of land-derived POM during significant rainfall events. Some of the variability in reef  $\delta^{13}\text{C}_{\text{POM}}$  values could be directly attributed to inputs of land-derived POM. Notably, the abrupt decreases in  $\delta^{13}\text{C}_{\text{POM}}$  values that occurred at CA in January to February 2001 and December 2004 to January 2005 were associated with the first significant storms of the rainy season and depressed salinities on the reef.

However, abrupt decreases in  $\delta^{13}\text{C}_{\text{POM}}$  values associated with storm events were superimposed on a tem-

poral pattern of  $^{13}\text{C}$ -enrichment in reef POM in mid-fall (October), followed by a gradual decrease in  $\delta^{13}\text{C}_{\text{POM}}$  values through the winter that occurred at all reefs in both wet and dry years. This pattern occurred, for example, in 2002, a drought year without major storms, when annual runoff was approximately 20% of that in 2001. This pattern also occurred at AQ despite little obvious influence of storm runoff on surface salinity.

The general pattern of  $^{13}\text{C}$ -enrichment of the reef POM during mid-fall (October 2002, 2003, 2004) and mid to late summer (2005) often coincided with elevated chl *a* concentrations, and a significant correlation existed between chl *a* concentration and  $\delta^{13}\text{C}_{\text{POM}}$  values for monthly samples taken in January 2003 through April 2005. If peaks in chl *a* concentration represented bloom events and elevated rates of production, then  $^{13}\text{C}$ -enriched  $\delta^{13}\text{C}_{\text{POM}}$  values may reflect a decrease in  $^{13}\text{C}/^{12}\text{C}$  fractionation by phytoplankton under conditions of rapid cell growth. Isotopic fractionation occurs during photosynthesis leading to higher rates of fixation of the lighter C isotope ( $^{12}\text{C}$ ) compared with  $^{13}\text{C}$  (Fry 1996). However, as phytoplankton growth rates increase, diffusion of  $\text{CO}_2$  across the cell membrane becomes the rate-limiting step in photosynthesis leading to a decrease in isotopic fractionation and greater fixation of  $^{13}\text{C}$ . A positive relationship has been found between  $\delta^{13}\text{C}_{\text{POM}}$  values and rate of primary production (Cifuentes et al. 1988).

In general, suspended POM over the study reefs was more  $^{13}\text{C}$ -enriched than offshore POM. This pattern of  $^{13}\text{C}$ -enrichment in  $\delta^{13}\text{C}_{\text{POM}}$  values in the nearshore was similar to that found by Kaehler et al. (2000) and Fredriksen (2003) in comparisons of POM sampled offshore and in forests of the kelps *Laminaria hyperborea* on the Norwegian coast, and *Durvillaea antarctica* and *Macrocystis laevis* in the Prince Edward Islands (Southern Ocean), respectively. In these studies, the authors attributed  $^{13}\text{C}$ -enrichment of nearshore POM relative to offshore POM to a mixing of phytoplankton with more  $^{13}\text{C}$ -enriched material that included kelp detritus. However, these authors acknowledged the possibility that reef phytoplankton may have a different isotopic signature than offshore phytoplankton. Such a pattern could occur, for example, due to differences in the growth rate and/or species composition of inshore and offshore phytoplankton assemblages (Gearing et al. 1984, Kaehler et al. 2000), but data are needed to evaluate these possibilities at our study reefs.

The lack of correlation between kelp biomass and  $\delta^{13}\text{C}_{\text{POM}}$  values (Fig. 5) and the overall similarity of  $\delta^{13}\text{C}_{\text{POM}}$  values among our reefs, irrespective of large differences in kelp biomass, indicates that kelp-derived detritus did not constitute an appreciable frac-

tion of the reef suspended POM during our study. The contribution of kelp-derived detritus to the reef POM pool can not be confidently quantified with a mixing model that uses kelp and offshore phytoplankton C isotope values as end-members if the  $\delta^{13}\text{C}$  value for reef phytoplankton differs from that of offshore phytoplankton, as suggested by the positive relationship between  $\delta^{13}\text{C}_{\text{POM}}$  values and phytoplankton standing crop (chl *a* concentration) in 2003–2005. In this regard, our analyses benefited from the multi-year dataset, which showed the temporal variability in isotopic composition of reef  $\delta^{13}\text{C}_{\text{POM}}$  and its relationship with chl *a* concentration and giant kelp biomass. Our study suggests that caution be used in drawing conclusions from data with little temporal replication and illustrates the importance of possessing ancillary data on producer abundance. More detailed studies comparing the productivity and composition of inshore and offshore phytoplankton assemblages are needed to evaluate sources of variation in the isotope values of these sources.

### Isotopic composition of reef macroalgae

Mean  $\delta^{13}\text{C}$  values of giant kelp were distinctly enriched (+6 to +8‰) relative to values of suspended reef POM. This phenomenon, also reported for other geographic locations (Dunton & Schell 1987, Duggins et al. 1989, Kaehler et al. 2000, Fredriksen 2003), is generally attributed to  $\text{CO}_2$  limitation at the blade–water boundary in rapidly growing kelp plants, which reduces isotopic discrimination between  $^{12}\text{C}$  and  $^{13}\text{C}$  during carbon fixation (Simenstad et al. 1993). This situation may occur at our study sites since the growth rate of *Macrocystis pyrifera* is rapid (up to ~3% per day, Coon 1982). An alternative hypothesis, proposed to explain  $^{13}\text{C}$ -enrichment in *Alaria fistulosa* in subarctic Alaskan waters, places more emphasis on the role of high kelp standing crop and its interaction with local hydrodynamic conditions to reduce  $[\text{CO}_2]_{\text{aq}}$ , which leads to  $\text{CO}_2$  limitation during carbon fixation and subsequent  $^{13}\text{C}$ -enrichment of kelp plants (Simenstad et al. 1993). This mechanism of interaction between kelp standing crop and the hydrodynamic environment in affecting  $^{13}\text{C}/^{12}\text{C}$  fractionation was proposed to explain some of the among site variation observed in kelp  $\delta^{13}\text{C}$  values in that study. However, we found little evidence supporting this hypothesis in our study as we observed little variation among reefs in  $\delta^{13}\text{C}$  values of giant kelp despite large differences in kelp standing crop. Other mechanisms proposed to explain  $^{13}\text{C}$ -enrichment of macroalgae include the differential storage and translocation of biochemical components of different isotopic composition (Fredriksen 2003) and increased

uptake of  $\text{HCO}_3^-$  under conditions of  $\text{CO}_2$  limitation (Maberly et al. 1992).

In contrast to the  $^{13}\text{C}$ -enriched values of giant kelp,  $\delta^{13}\text{C}$  values of understory macroalgae were within the range of values reported for macroalgae in other studies (e.g. Simenstad & Wissmar 1985, Duggins et al. 1989). Of interest,  $\delta^{13}\text{C}$  values of the red alga *Rhodomenia californica* were quite  $^{13}\text{C}$ -depleted relative to values for *Macrocystis pyrifera* and understory brown macroalgae.  $^{13}\text{C}$ -depleted values (<–30‰) of some red algal taxa have also been noted by others and may relate to the inability of these algae to use  $\text{HCO}_3^-$ , which has a more positive  $\delta^{13}\text{C}$  signature than  $\text{CO}_2$  in seawater, as a photosynthetic carbon source (reviewed in Raven et al. 2002). The standing crop of *R. californica* was low at our study sites and its contribution to the reef POM pool would probably be small relative to the total amount of C produced by phytoplankton, other understory algae, and giant kelp.

### Sources of production used by reef consumers

The absence of a consistent directional shift in consumer isotope values towards the isotope values of terrestrial organic matter in ‘wet’ years, or with greater influence of freshwater runoff at CA (Figs. 7, 8 & 9), allows us to conclude that reef consumers were not directly incorporating significant amounts of land-derived production in this open coast ecosystem. To date, reports of the use of terrestrial or freshwater-derived production by consumers in the coastal zone have largely been restricted to estuarine systems that receive significant riverine inputs (Canuel et al. 1995, Riera & Richard 1997, Chanton & Lewis 2002). In these systems, consumer  $\delta^{13}\text{C}$  values are most negative in closest proximity to the river mouth and increase with distance from the influence of river inputs; a pattern that reflects the use of terrestrial (riverine) organic matter and/or estuarine production that has assimilated terrestrially-derived  $^{13}\text{C}$ -depleted dissolved inorganic carbon (DIC).

The absence of a pattern indicative of the incorporation of terrestrially-derived POM by reef consumers suggests 2 possible explanations. First, the exposure time of reef organisms to terrestrial inputs may not be long enough, relative to carbon turnover time in organism tissues, to detect the incorporation of this carbon source in  $\delta^{13}\text{C}$  values. Unlike estuarine systems that receive and retain more riverine inputs of organic matter, our study reefs experience runoff events that are highly seasonal and episodic. Reef consumers are probably exposed to suspended terrestrial inputs on the order of days to perhaps weeks, depending on rates of deposition, retention, resuspension and advective

tion from the reef by ocean physical processes (e.g. swell, currents) following storm events.

Second, terrestrial POM may be a poor food source for reef consumers. The streams inshore of the study reefs are relatively small, lacking the extensive *in situ* phytoplankton production of larger riverine systems that could be utilized directly by reef consumers. Other studies have noted that terrestrial POM is largely refractory, high in lignin and other difficult to digest components (Williams 1981), although microbial processing of terrestrial POM on the reef could improve its quality as a food source (Mann 1988).

$\delta^{13}\text{C}$  values suggest that the diets of suspension-feeders were similar among reefs, and we propose that it consists largely of nearshore phytoplankton rather than kelp detritus or offshore phytoplankton transported to the reef. This supposition is based on the similarity in isotope values of these consumers among reefs during the first 2 yr of sampling when kelp biomass was regionally low, and on the absence of a directional shift that would indicate the use of more  $^{13}\text{C}$ -enriched production during the last 2 yr of the study when kelp biomass was considerably higher on 2 of the reefs. It is interesting to note that the  $\delta^{13}\text{C}$  value of the tunicate *Styela montereyensis* was most negative at the offshore reef (NA), suggesting a greater contribution of offshore phytoplankton to the food web of this reef. Small but consistent differences in  $\delta^{15}\text{N}$  values for this tunicate among reefs also suggest the use of locally-produced POM.

Our conclusion that kelp-derived material is not an important component of the diet of reef suspension-feeders differs from those of other studies in regions with less variable kelp abundance, where kelp-derived material was estimated to comprise from ~20 to 80% of the diet of some suspension-feeding species (e.g. bivalves, sponges, bryozoans, ascidians, barnacles) (Dunton & Schell 1987, Duggins et al. 1989, Kaehler et al. 2000, Fredriksen 2003). However, the isotope values for benthic herbivores on our reefs were generally  $^{13}\text{C}$ -enriched relative to understory algae (Fig. 10), suggesting the use of local sources of giant kelp or other  $^{13}\text{C}$ -enriched benthic algal production, such as coralline algae at CA.

There were some discrepancies between the predicted trophic enrichment factors and the actual isotopic composition of consumers and their presumed diet (Fig. 10). Notably,  $\delta^{13}\text{C}$  values of 3 suspension-feeding taxa (the bivalve *Crassadoma gigantea*, and 2 echinoderms, *Cucumaria salma* and *Ophiothrix spiculata*) were more  $^{13}\text{C}$ -enriched than predicted by a trophic enrichment factor of +1‰ relative to the reef POM. Isotopic enrichment of stomach contents and tissues of bivalves relative to isotope values for bulk POM is a well-documented phenomenon (Riera &

Richard 1997, Hsieh et al. 2000, Page & Lastra 2003) and generally attributed to selective feeding on isotopically enriched components of the POM pool. In addition, although average trophic enrichment factors of +1‰ for C and +3.5‰ for N are generally accepted, the actual values may deviate considerably from these predicted values (Stephenson et al. 1986, Vanderklift & Ponsard 2003, Crawley et al. 2007) and no data are available on the trophic enrichment factors for the species in our study. Because of uncertainty regarding the isotopic signature of reef phytoplankton in this system, the possibility of selective feeding on components of the reef POM that were not identified as isotopic end-members in this study, and the lack of information on trophic enrichment factors for reef consumers, we are not comfortable in using multi-source mixing models (e.g. Philips & Gregg 2003) to assess specific contributions of organic matter sources to reef consumers.

While we found no direct evidence that terrestrial POM plays a major role in the reef food web, we did find evidence of terrestrial influence in the form of increasing  $^{15}\text{N}$ -enrichment in  $\delta^{15}\text{N}$  values in some taxa associated with exposure of the reef to freshwater runoff:  $\delta^{15}\text{N}$  values were most enriched at CA and most depleted at AQ (Fig. 8). This pattern was most pronounced in 2 benthic-feeding species (*Strongylocentrotus purpuratus* and *Diopatra ornata*) and was also apparent, but less pronounced, in the suspension-feeding *Styela montereyensis*.

We hypothesize that variation in  $\delta^{15}\text{N}$  values across reefs reflected different exposures of the reef assemblages to anthropogenic N. Carpinteria Reef is located directly offshore of a coastal plain that is highly developed for agriculture. The streams draining the coastal plain contain exceptionally high concentrations of dissolved and particulate N, which is discharged to the coastal ocean (Page et al. 1995, Robinson 2006). Dissolved inorganic N may be taken up by algae directly, whereas particulate bound N species may be deposited on the benthos and become available for assimilation through remineralization to inorganic N over time. Similar  $^{15}\text{N}$ -enrichment of consumers associated with anthropogenic N inputs has been observed in other coastal habitats (Page 1997, McClelland & Valiela 1998, Riera et al. 2000).

In conclusion, our data suggest that the consumer base of the study reefs is supported primarily by locally produced phytoplankton and benthic macroalgae with little direct contribution from terrestrial POM. However, nutrients of terrestrial origin may enter the food web of these reefs indirectly through pathways that involve a trophic intermediate (e.g. microbes, algae). We have no convincing evidence that reef suspension-feeders are using appreciable amounts of giant kelp-

derived POM, but consumption of kelp by benthic herbivores was evident. Thus, spatial and temporal fluctuations in the biomass of giant kelp in this system will likely have disproportionately larger effects on consumers that feed on the bottom compared to those that feed on particles suspended in the water column.

*Acknowledgements.* We thank M. Anghera, B. Evans, J. Hoesterey, B. Mardian, C. Nelson, J. Jones, and S. Harrer for collecting and processing marine samples, S. Coombs and F. Setaro for collecting and processing stream samples, and R. Petty for conducting the isotope analyses. This research was supported by the National Science Foundation (Award Nos. OCE-9982105 and OCE-0620276).

#### LITERATURE CITED

- Beighley E, Melack JM, Dunne T (2003) Impacts of California's climatic regimes and coastal development patterns on streamflow characteristics. *J Am Water Resour Assoc* 39:1419–1433
- Bishop JKB, Davis RE, Sherman JT (2002) Robotic observations of dust storm enhancement of carbon biomass in the North Pacific. *Science* 298:817–821
- Bouchard SS, Bjorndal KA (2000) Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology* 81:2305–2313
- Canuel EA, Cloern JE, Ringelberg DB, Guckert JB, Rau GH (1995) Molecular and isotopic tracers used to examine sources of organic matter and its incorporation into the food webs of San Francisco Bay. *Limnol Oceanogr* 40:67–81
- Chanton J, Lewis FG (2002) Examination of coupling between primary and secondary production in a river-dominated estuary. *Limnol Oceanogr* 47:683–697
- Cifuentes LA, Sharp JH, Fogel ML (1988) Stable carbon and nitrogen isotope biogeochemistry in the Delaware estuary. *Limnol Oceanogr* 33:1102–1115
- Coon D (1982) Primary productivity of macroalgae in North Pacific America. In: Zaborsky OR (ed) *CRC handbook of biosolar resources*. CRC Press, Boca Raton, FL, p 447–454
- Crawley KR, Hyndes GA, Vanderliff MA (2007) Variation among diets in discrimination of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in the amphipod *Allorchesthes compressa*. *J Exp Mar Biol Ecol* 349:370–377
- Deegan LA, Garritt RH (1997) Evidence for spatial variability in estuarine food webs. *Mar Ecol Prog Ser* 147:31–47
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–506
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351
- Duggins DO, Eckman JE (1997) Is kelp detritus a good food for suspension feeders? Effects of kelp species, age and secondary metabolites. *Mar Biol* 128:489–495
- Duggins DO, Simenstad CA, Estes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245:170–173
- Dunton KH, Schell DM (1987) Dependence of consumers on macroalgal (*Laminaria solidungula*) carbon in an arctic kelp community:  $\delta^{13}\text{C}$  evidence. *Mar Biol* 93:615–625
- Eddins SGN (2001) Calculation of terrestrial inputs to particulate organic carbon in an anthropogenically impacted estuary in the southeastern United States. *Water Air Soil Pollut* 127:227–241
- Fredriksen S (2003) Food web studies in a Norwegian kelp forest based on stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) analysis. *Mar Ecol Prog Ser* 260:71–81
- Fry B (1996)  $^{13}\text{C}/^{12}\text{C}$  fractionation by marine diatoms. *Mar Ecol Prog Ser* 134:283–294
- Fry B (2002) Conservative mixing of stable isotopes across estuarine salinity gradients: a conceptual framework for monitoring watershed influences on downstream fisheries production. *Estuaries* 25:264–271
- Fry B, Sherr EB (1984)  $\delta^{13}\text{C}$  measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contrib Mar Sci* 27:13–47
- Gearing JN, Gearing PJ, Rudnick DT, Rejujo AG, Huchins MJ (1984) Isotopic variability of organic carbon in a phytoplankton-based temperate estuary. *Geochim Cosmochim Acta* 48:1089–1098
- Hsieh HL, Kao WY, Chen CP, Liu PJ (2000) Detrital flows through the feeding pathway of the oyster (*Crassostrea gigas*) in a tropical shallow lagoon:  $\delta^{13}\text{C}$  signals. *Mar Biol* 136:677–684
- Kaehler S, Pakhomov EA, McQuaid CD (2000) Trophic structure of the marine food web at the Prince Edward Islands (Southern Ocean) determined by  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. *Mar Ecol Prog Ser* 208:13–20
- Maberly SC, Raven JA, Johnston AM (1992) Discrimination between  $^{12}\text{C}$  and  $^{13}\text{C}$  by marine plants. *Oecologia* 91:481–492
- Mann KH (1988) Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. *Limnol Oceanogr* 33:910–930
- Mann KH (2000) *Ecology of coastal waters*. Blackwell Science, Malden, MA
- McClelland JW, Valiela I (1998) Linking nitrogen in estuarine producers to land-derived sources. *Limnol Oceanogr* 43:577–585
- Minagawa M, Wada E (1984) Stepwise enrichment of  $^{15}\text{N}$  along food chains: further evidence and the relation between  $\delta^{15}\text{N}$  and animal age. *Geochim Cosmochim Acta* 48:1135–1140
- Norderhaug KM, Fredriksen S, Nygaard K (2003) Trophic importance of *Laminaria hyperborea* to kelp forest consumers and the importance of bacterial degradation to food quality. *Mar Ecol Prog Ser* 255:135–144
- Otero MP, Siegel DA (2004) Spatial and temporal characteristics of sediment plumes and phytoplankton blooms in the Santa Barbara Channel. *Deep-Sea Res II* 51:1129–1149
- Page HM (1997) Importance of vascular plant and algal production to macro-invertebrate consumers in a southern California salt marsh. *Estuar Coast Shelf Sci* 45:823–834
- Page HM, Lastra M (2003) Diet of intertidal bivalves in the Ria de Arosa (NW Spain): evidence from stable C and N isotope analysis. *Mar Biol* 143:519–532
- Page HM, Petty RL, Meade DE (1995) Influence of watershed runoff on nutrient dynamics in a southern California salt marsh. *Estuar Coast Shelf Sci* 41:163–180
- Parsons TR, Maita Y, Lalli CM (1984) *A manual of chemical and biological methods for seawater analysis*. Pergamon Press, New York
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320
- Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. *Oecologia* 136:261–269

- Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28: 289–316
- Raven JA, Johnston AM, Kubler, JE, Korb R and others (2002) Mechanistic interpretation of carbon isotope discrimination by marine macroalgae and seagrasses. *Funct Plant Biol* 29:355–378
- Reed DC, Kinlan BP, Raimondi P, Washburn L, Gaylord B, Drake P (2006) A metapopulation perspective on the patch dynamics of giant kelp in southern California. In: Kritznner JP, Sale PF (eds) *Marine metapopulations*, Elsevier Academic Press, San Diego, CA, p 353–386
- Riera P, Richard P (1997) Temporal variation of  $\delta^{13}\text{C}$  in particulate organic matter and oyster *Crassostrea gigas* in Marennes-Oleron Bay (France): effect of freshwater inflow. *Mar Ecol Prog Ser* 147:105–115
- Riera P, Stal LJ, Nieuwenhuize J (2000) Heavy  $\delta^{15}\text{N}$  in intertidal benthic algae and invertebrates in the Scheldt Estuary (The Netherlands): effect of river nitrogen inputs. *Estuar Coast Shelf Sci* 51:365–372
- Roberts C, Andelman S, Branch G, Bustamante RH and others (2003) Ecological criteria for evaluating candidate sites for marine reserves. *Ecol Appl* 13(Suppl):S199–S214
- Robinson T (2006) Catchment and subcatchment scale linkages between land use and nutrient concentrations and fluxes in coastal California streams. PhD dissertation, University of California, Santa Barbara, CA
- Simenstad CA, Wissmar RC (1985)  $\delta^{13}\text{C}$  evidence of the origins and fates of organic carbon in estuarine and near-shore food webs. *Mar Ecol Prog Ser* 22:141–152
- Simenstad CA, Duggins DO, Quay PD (1993) High turnover of inorganic carbon in kelp habitats as a cause of  $\delta^{13}\text{C}$  variability in marine food webs. *Mar Biol* 116:147–160
- Stephenson RL, Tan FC, Mann KH (1984) Stable isotope variability in marine macrophytes and its implications for food web studies. *Mar Biol* 81:223–230
- Stephenson RL, Tan FC, Mann KH (1986) Use of stable carbon isotope ratios to compare plant material and potential consumers in a seagrass bed and a kelp bed in Nova Scotia, Canada. *Mar Ecol Prog Ser* 30:1–7
- Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge
- Valiela I, Bowen JL, Cole ML, Kroeger KD and others (2001) Following up on a Margalevian concept: interactions and exchanges among adjacent parcels of coastal landscapes. *Sci Mar* 65:215–229 Suppl
- Vanderklift MA, Ponsard S (2003) Sources of variation in consumer-diet  $\delta^{15}\text{N}$  enrichment: a meta-analysis. *Oecologia* 136:169–182
- Williams P (1981) Detritus utilization by *Mytilus edulis*. *Estuar Coast Shelf Sci* 12:739–746
- Womersley HBS (1954) The species of *Macrocystis* with special reference to those on southern Australia coasts. *Univ Calif Publ Bot* 27:109–132

*Editorial responsibility: Otto Kinne, Oldendorf/Luhe, Germany*

*Submitted: May 10, 2007; Accepted: December 19, 2007  
Proofs received from author(s): May 12, 2008*