

## $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ Measurements of Antarctic Peninsula Fauna: Trophic Relationships and Assimilation of Benthic Seaweeds<sup>1</sup>

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**SYNOPSIS.** Measurements of  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and C/N for a variety of Antarctic peninsula fauna and flora were used to quantify the importance of benthic brown algae to resident organisms and determine food web relationships among this diverse littoral fauna.  $\delta^{13}\text{C}$  values ranged from  $-16.8\text{‰}$  for benthic algal herbivores (limpets) to  $-29.8\text{‰}$  for the krill, *Euphausia superba*; the average pooled value for brown macroalgae, including their attached filamentous diatoms, was  $-20.6\text{‰}$ . There was no correlation between biomass  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  with C/N content, and consequently both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were useful in evaluating trophic relationships.  $\delta^{15}\text{N}$  values of the fauna ranged from 3.1 to 12.5‰, with lowest values recorded in suspension feeders (e.g., bryozoans) and highest values in Adelie penguins (12.5‰) collected in 1989. The comparatively lower  $\delta^{15}\text{N}$  value for a Chinstrap penguin (6.9‰) collected in 1997 is attributed to the different dietary food sources consumed by these species as reflected in their respective  $\delta^{13}\text{C}$  values. Significant amounts of benthic macroalgal carbon is incorporated into the tissues of invertebrates and fishes that occupy up to four trophic levels. For many benthic and epibenthic species, including various crustaceans and molluscs, assimilation of benthic algal carbon through detrital pathways ranges from 30 to 100%. Consequently, the trophic importance of benthic brown algae may well extend to many pelagic organisms that are key prey species for birds, fishes, and marine mammals. These data support the hypothesis that benthic seaweeds, together with their associated epiphytic diatoms, provide an important carbon source that is readily incorporated into Antarctic peninsula food webs.

### INTRODUCTION

Along the rocky shores of the Antarctic peninsula, marine macroalgae form extensive and luxuriant submerged forests that extend from the shallow subtidal to depths of 30 m (Neushul, 1965, 1968; Delépine *et al.*, 1966; Moe and DeLaca, 1976; Lamb and Zimmerman, 1977; Zielinski, 1990; Amsler *et al.*, 1995). These erect macroalgal beds provide a three dimensional structural habitat for diverse assemblages of marine invertebrates and fish, many of which are known to be key prey species for larger pelagic organisms (Iken *et al.*, 1998). The direct consumption of some macroalgae by various fish and invertebrates (Iken *et al.*, 1997; Iken, 1999; Iken *et al.*, 1999) and the

assimilation of benthic macroalgal carbon through detrital food webs (Dayton, 1990), links the high productivity of the shallow antarctic benthos with the pelagic food web. The assimilation of carbon derived from large brown algae by consumers has been demonstrated in Alaskan coastal food webs and reflects the importance of this process in providing a continuous supply of organic material that is passed on to higher trophic levels (Dunton and Schell, 1987; Duggins *et al.*, 1989).

On the Antarctic peninsula, quantitative studies conducted on Signy Island (Richardson, 1979), King George Island (Chung *et al.*, 1994), and Anvers Island (DeLaca and Lipps, 1976; Amsler *et al.*, 1995), revealed that macroalgal biomass, which consists mainly of large overstory brown algae, ranges from 3 to 8 kg m<sup>-2</sup>. Near Anvers Island, four species of large brown algae (*Desmarestia antarctica*, *D. menziesii*, *D. anceps*, and *Himantothallus grandifolius*)

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can constitute up to 75% of the overall percent cover and biomass (Amsler *et al.*, 1995). Another species, *Ascoseira mirabilis*, has also been known to occur in great abundance on the Peninsula (Chung *et al.*, 1994). There is considerable evidence, based on the occurrence of algal fragments in samples collected in the water column and sediments, that this huge source of organic material is advected onto the adjacent shelf and into deeper waters, especially in Bransfield Strait (Liebezeit and von Bodungen, 1987). Reichardt (1987) found algal fragments on both sides of the Peninsula and suggested that algal material provided an additional carbon source to deep water benthic infauna.

Aside from feeding studies on specific organisms, there is relatively little information on trophic relationships among nearshore Antarctic peninsula organisms that inhabit the most productive areas in the Antarctic. A combination of observational techniques and stable isotope measurements have confirmed, in a variety of other ecosystems, the incorporation of macroalgae in consumer diets, either directly or indirectly (Kitting *et al.*, 1984; Sullivan and Montcreiff, 1990). In addition, isotopic measurements have confirmed that many consumers possess opportunistic feeding strategies over both temporal and spatial scales (Dunton *et al.*, 1989; Rau *et al.*, 1992; Iken *et al.*, 2001). Measurement of  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  in consumer tissues has provided extremely useful information on organism feeding relationships and food web structure when the ultimate sources of carbon and nitrogen are well elucidated and defined isotopically (reviewed by Lajtha and Michener, 1994).

The objective of this study was to (1) quantify, using  $^{13}\text{C}/^{12}\text{C}$ , the incorporation of benthic macroalgal carbon into the diet of invertebrate and vertebrate consumers, and (2) assess, using  $^{15}\text{N}/^{14}\text{N}$ , trophic relationships among the diverse fauna that inhabit the nearshore zone of the Antarctic peninsula. My approach is based on the knowledge that  $^{13}\text{C}/^{12}\text{C}$  will best reflect ultimate carbon sources since trophic enrichments between a consumer and its diet are small (*ca.* 1‰) and the isotopic values for the two

major carbon sources in this area, macroalgae and phytoplankton are relatively well defined (*e.g.*, Dunton and Schell, 1987). In contrast,  $^{15}\text{N}/^{14}\text{N}$  abundances are best suited for elucidating trophic relationships based on the relatively large (*ca.* 3‰)  $^{15}\text{N}$  enrichment that occurs with each trophic step. The previous work by Rau *et al.* (1991a,b, 1992), who used carbon and nitrogen stable isotope ratios to examine feeding diversity and trophic structure in the Weddell Sea, provides an excellent comparison to an adjacent ecosystem whose primary source of carbon originates from phytoplankton.

## MATERIALS AND METHODS

### Field collections

Samples of macroalgae, invertebrates, and fish were collected near Palmer Station on several different islands (Cormorant, DeLaca, Dream, Limotrophe, Hermit) between 64°43'S and 64°48'S on the southwest side of Anvers Island on the Antarctic peninsula (Fig. 1). All samples were collected between the intertidal zone and a depth of 30 m by hand on rocky shores using small nets in March and April 1989 and again in March 1996 and 1997. SCUBA was employed for sampling at subtidal depths. In 1989, samples of *Euphausia superba* (krill) were collected by net tows in the area immediately southwest of DeLaca Island. In addition, breast muscle tissue from Adelie penguins (*Pygoscelis adeliae*) were removed from birds collected as part of another study from Comorant and Limotrophe Islands in 1989, and from a Chinstrap penguin (*Pygoscelis antarctica*) caught near Palmer Station in 1997. Deep water trawl samples in Dallmann Bay (located between Anvers and Brabant Islands) in March 1997 provided benthic fish from an area devoid of attached macroalgae for comparison.

In the field, invertebrates were washed of debris and generally held alive for several hours to clear their guts. All samples (plant and animal) were dried in aluminum dishes at 60°C following removal of extraneous organic matter. When possible, soft tissues were removed from shelled organisms, but all invertebrate samples were subsequently

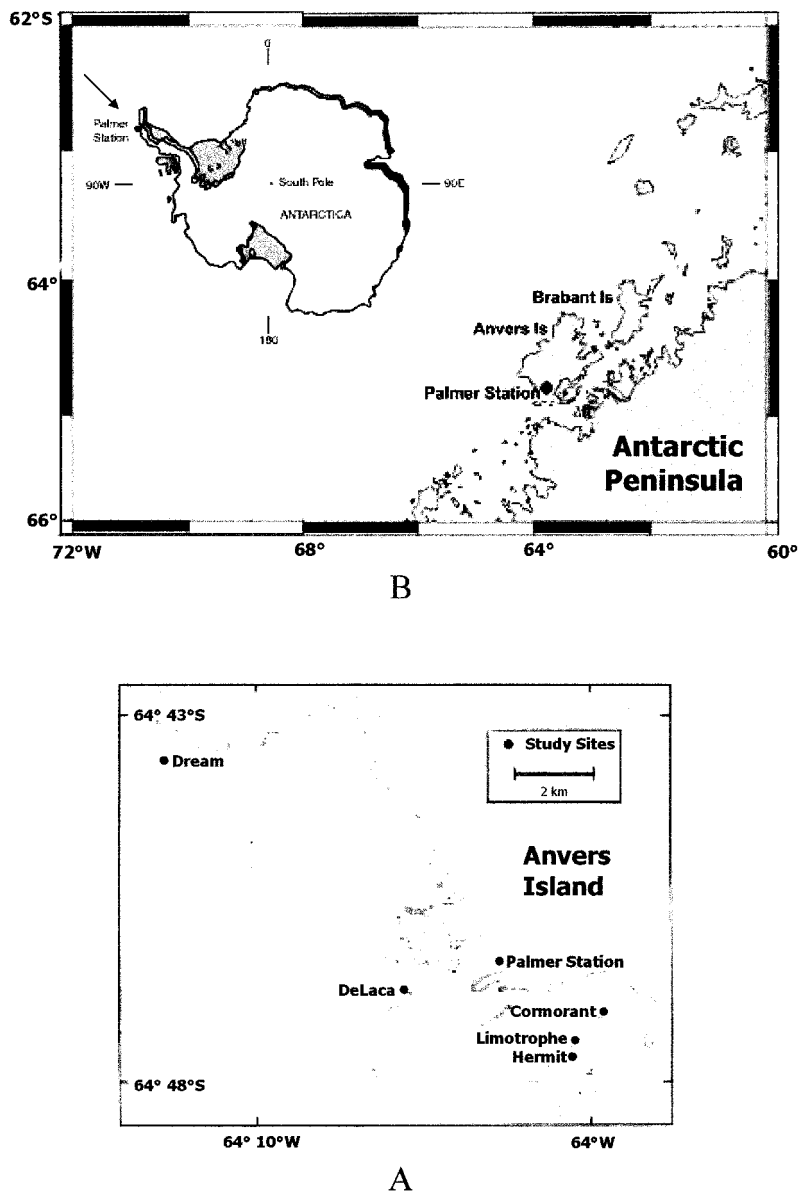


FIG. 1. Location of nearshore sampling sites in macroalgal beds near Palmer station (A). Additional samples were collected in Dallmann Bay, located between Anvers and Brabant Islands (B).

soaked in 1 N HCl for several hours (or until bubbling stopped) to remove carbonates, rinsed in distilled water, and then dried at 60°C. Disks 2.0-cm in diameter were punched 10 to 150 cm from the holdfast in the fronds of *Himantothallus grandifolius* and *Ascoseira mirabilis* to examine variability in carbon isotopic ratios. For all other algal species, they were either analyzed

whole as a composite (e.g., *Navicula schef-ferae*), or for larger plants, 5-cm disks were excised from the center of the thallus. Only muscle or body wall tissue was analyzed from bivalves, gastropods, brachio-pods, large crustaceans (euphausiids and amphipods), holothurians, birds and fish; all other organisms were analyzed whole (only the digestive tract was analyzed in urchins).

TABLE 1.  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and C/N values of macroalgae collected in the vicinity of Anvers Island on the Antarctic peninsula.\*

Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C/N
	(‰)	(‰)	(atoms/atom)
<b>Chlorophyta</b>			
<i>Enteromorpha</i> sp.	-13.2	6.7	8.1
<i>Monostroma hartiotti</i>	-23.3	9.4	7.4
<i>Ulothrix</i> sp.	-11.5	5.9	7.4
Snow algae	-18.7	13.8	9.9
<b>Rhodophyta</b>			
<i>Georgiella confluens</i>	-35.3	0.6	7.9
<i>Grateloupia</i> sp.	-29.8	3.3	10.2
<i>Iridaea cordata</i>	-19.6 $\pm$ 0.4 (3)	6.0 $\pm$ 0.6 (3)	11.3 $\pm$ 1.0 (3)
<i>Myriogramme manginii</i>	-33.1	3.4	ND
<i>Palmaria decipiens</i>	-19.9 $\pm$ 1.0 (3)	5.5 $\pm$ 0.4 (3)	7.3 $\pm$ 0.6 (3)
<i>Phycodrys antarctica</i>	-33.7 $\pm$ 0.3 (2)	1.4 $\pm$ 0.4 (2)	7.0
<i>Phyllophora antarctica</i>	-35.2	8.8	10.6
<i>Plocamium cartilagineum</i>	-32.3	3.6	
<i>Porphyra endiviifolium</i>	-27.4 $\pm$ 0.1 (3)	5.8 $\pm$ 0.4 (3)	8.3 $\pm$ 0.6 (3)
<i>Trematocarpus antarcticus</i>	-20.7	4.5	8.2
<b>Phaeophyta</b>			
Brown Macroalgae			
<i>Adenocystis utricularis</i>	-13.9	4.8	13.3
<i>Ascoseira mirabilis</i>	-18.7 $\pm$ 0.6 (3)	3.3 $\pm$ 0.3 (3)	19.5 $\pm$ 1.3 (3)
<i>Cystosphaera jacquinotii</i>	-28.4	2.3	24.2
<i>Desmarestia anceps</i>	-25.3	ND	ND
<i>Desmarestia antarctica</i>	-14.0	5.8	ND
<i>Desmarestia menziesii</i>	-25.0 $\pm$ 0.5 (5)	3.7	12.5
<i>Himantothallus grandifolius</i>	-23.3 $\pm$ 0.5 (11)	2.0 $\pm$ 0.3 (11)	ND
Epiphytic Diatoms			
<i>Navicula schefferae</i>	-17.6	5.8	6.9

\* Values are  $\bar{x} \pm \text{SE}$  (n). ND: no data.

Entire organisms or tissues (e.g., excised pieces of macroalgae) were then manually ground for isotopic analysis. In all cases, replicate analyses reflect the analysis of individual organisms, not composite samples.

All samples were analyzed on an automated system for coupled  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  measurements using a Finnegan MAT Delta Plus mass spectrometer that was coupled to an elemental analyzer (CE Instruments, NC 2500). Samples were combusted at 1,020°C and then injected into the mass spectrometer with continuous flow. Results are expressed in standard  $\delta$  notation relative to carbonate PeeDeeBelemnite and atmospheric nitrogen where:

$$\delta^{13}\text{C} \quad \text{or} \quad \delta^{15}\text{N} (\text{‰})$$

$$= [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

and  $R = (^{13}\text{C}/^{12}\text{C} \text{ or } ^{15}\text{N}/^{14}\text{N})$ , respectively. By definition then, as  $\delta$  values increase (or decrease), the relative abundances of the

heavier isotopes,  $^{13}\text{C}$  or  $^{15}\text{N}$ , increase (or decrease). Secondary standards were used routinely for cross-calibration checks of tank reference gases, against which all samples were run. Our data were reproducible to within  $\pm 0.2\text{‰}$ . Machine analytical error was  $\pm 0.15\text{‰}$ .

## RESULTS

### Isotopic composition of the macroalgae

In contrast to  $\delta^{15}\text{N}$  values (range 0.6 to 9.4‰), the  $\delta^{13}\text{C}$  values of 22 species of macroalgae collected near Anvers Island ranged considerably, from -11.5‰ for the green alga *Ulothrix* to less than -35‰ for the red algae *Phyllophora antarctica* and *Georgiella confluens*. (Table 1). The  $\delta^{13}\text{C}$  values of five common species of large brown algae (*Ascoseira mirabilis*, *Desmarestia antarctica*, *D. menziesii*, *D. anceps*, and *Himantothallus grandifolius*) ranged from -14 to -25‰. For both *H. grandifol-*

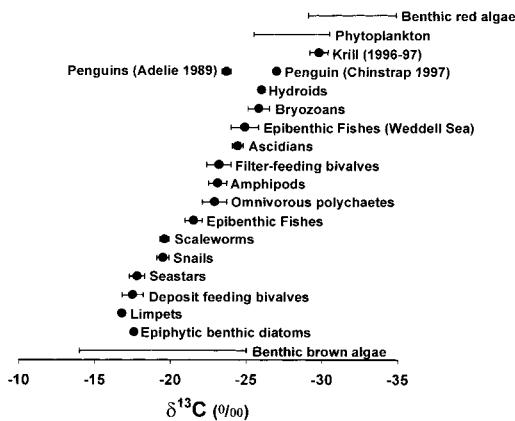


FIG. 2.  $\delta^{13}\text{C}$  values of the fauna ( $\bar{x} \pm \text{SE}$ ) and flora (range in mean values for common species) collected in nearshore habitats in the vicinity of Palmer Station. Data summarized from Tables 1 and 2 (range in phytoplankton  $\delta^{13}\text{C}$  compiled from Wada *et al.*, 1987; Rau *et al.*, 1991a; and Fischer and Wiencke, 1992).

*ius* and *A. mirabilis*, disks punched at various distances up to 1.5 m from the holdfast in 14 different plants rarely revealed a total range of more than 2.5‰ within any one individual. There was no consistent trend in  $\delta^{13}\text{C}$  values with increasing distance from the holdfast in *H. grandifolius*, although there was evidence for some increase in  $^{13}\text{C}$  with blade length in *A. mirabilis*. Epiphytic diatoms (*e.g.*, *Navicula*) which were common on these large perennials had a  $\delta^{13}\text{C}$  value of  $-17.6\text{‰}$ . The pooled carbon isotopic value for epiphytic diatoms and the five predominant brown algae,  $-20.6\text{‰}$ , was used in subsequent calculations to estimate the dependence of consumers on benthic brown algae. With the exception of the brown alga *Cystosphaera jacquinotii* and a few species of red algae that were distinctly depleted in  $^{13}\text{C}$ , the average  $\delta^{13}\text{C}$  value of the remaining macroalgae was about  $-18.5\text{‰}$ . The extremely  $^{13}\text{C}$  depleted values for many red algal species, especially in comparison to faunal  $\delta^{13}\text{C}$  values (Fig. 2), did not indicate that this group represented a significant source of carbon to the nearshore food web. The composite mean  $\delta^{15}\text{N}$  value for brown algae (including epiphytic diatoms) was  $4.0\text{‰}$ . For contrast, the  $\delta^{15}\text{N}$  for snow algae collected on Hermit Island was very high ( $13.8\text{‰}$ ) and likely reflects a terrestrial source of nitrogen.

### $\delta^{13}\text{C}$ measurements of fauna

The distribution of mean  $\delta^{13}\text{C}$  values of various fauna ranged from  $-16.8\text{‰}$  for the benthic herbivorous limpet, *Nacella concinna*, to  $-29.8\text{‰}$  for the krill, *Euphausia superba*, a pelagic suspension feeder (Fig. 2). These  $\delta^{13}\text{C}$  values closely approximate the isotopic composition of their respective diets. Limpets are almost exclusively epilithic, and were frequently found attached to both rocks and large brown seaweeds in intertidal and shallow subtidal areas. They possess specialized structures for scraping and consuming attached diatoms (Barnes, 1980) which is reflected in the  $0.8\text{‰}$   $\delta^{13}\text{C}$  trophic enrichment from their diatom food source ( $-17.6\text{‰}$ ). Similarly, the carbon isotopic signature of euphausiids ( $-29.8\text{‰}$ ), which feed exclusively on phytoplankton, corresponds to the range of particulate organic matter that is derived from phytoplankton ( $-28.0$  to  $-30.4\text{‰}$ ; Fisher, 1991; Rau *et al.*, 1991a; Fisher and Wiencke, 1992). The higher scatter of  $\delta^{13}\text{C}$  values among some species (*e.g.*, omnivorous polychaetes) indicates a diet of higher diversity; in contrast, little scatter in  $\delta^{13}\text{C}$  values (*e.g.*, limpets or hydroids) indicates an isotopic similarity of diet among the individuals sampled. The mean  $\delta^{13}\text{C}$  values of all animal species collected in the vicinity of Anvers Island are shown in Table 2.

To confirm the validity of using faunal  $\delta^{13}\text{C}$  values as evidence of dietary and trophic differences among species, I examined the relationship between biomass  $\delta^{13}\text{C}$  and biomass C/N (Fig. 3) using the data derived from Table 2. Previous studies (Rau *et al.*, 1991b) have documented significant negative correlations between consumer  $\delta^{13}\text{C}$  and C/N because of the effect of high lipid concentrations (depleted in  $^{13}\text{C}$ ) on the  $\delta^{13}\text{C}$  values of invertebrate biomass. Such a relationship, which compromises the application of stable carbon isotope measurements for feeding studies, was not found in our data. Only one species, *Euphausia superba*, was characterized by a distinctly high C/N (7.6) that was correlated with a low  $\delta^{13}\text{C}$  value.

In nearly all cases, we found that our observations and existing knowledge on the



TABLE 2.  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and C/N values of fauna collected in the vicinity of Anvers Island on the Antarctic peninsula.\*

Species	$\delta^{13}\text{C}_{\text{PDB}}$	$\delta^{15}\text{N}_{\text{air}}$	C/N
	(‰)	(‰)	(atoms/atom)
<b>Porifera</b> (sponges)	$-27.1 \pm 0.7$ (5)	$5.1 \pm 0.6$ (5)	$5.9 \pm 0.5$ (3)
<b>Cnidaria</b>			
Hydrozoa	$-26.0 \pm 0.2$ (3)	$4.0 \pm 0.0$ (3)	$4.6 \pm 0.5$ (2)
Anthozoa (soft corals)	$-24.5 \pm 0.3$ (2)	$6.0 \pm 0.1$ (2)	5.8 (1)
<b>Nemertea</b>			
<i>Parborlasia corrugatus</i>	$-20.1 \pm 1.3$ (3)	$9.6 \pm 0.0$ (2)	4.8 (1)
Other unidentified	$-19.6 \pm 0.1$ (4)	$9.6 \pm 0.5$ (4)	$4.9 \pm 0.2$ (4)
<b>Annelida</b> (polychaetes)			
<i>Harmothoe spinosa</i>	$-19.6 \pm 0.3$ (12)	$9.8 \pm 0.2$ (12)	$4.9 \pm 0.2$ (11)
<i>Neanthes kerguelensis</i>	$-22.9 \pm 0.8$ (2)	$7.7 \pm 0.3$ (2)	$5.0 \pm 0.0$ (2)
<i>Terebella ehlersi</i>	$-19.0$ (1)	7.2 (1)	NA
Tubicolous-unident.	$-23.5 \pm 0.5$ (5)	$6.3 \pm 0.3$ (5)	$6.0 \pm 0.2$ (3)
<b>Mollusca</b>			
Gastropoda			
Snails			
<i>Neobuccinum eatoni</i>	$-19.6 \pm 1.0$ (3)	$10.2 \pm 0.4$ (3)	$5.7 \pm 0.2$ (2)
<i>Margarella</i> sp.	$-19.3$ (1)	7.7 (1)	ND
Other unidentified	$-19.6 \pm 0.4$ (5)	$7.5 \pm 0.7$ (5)	$5.8 \pm 0.4$ (5)
Nudibranchs			
<i>Austrodoris</i> sp.	$-19.9 \pm 0.3$ (3)	$9.6 \pm 0.1$ (3)	$5.9 \pm 0.3$ (3)
Other unidentified	$-22.9 \pm 0.7$ (6)	$7.5 \pm 0.4$ (4)	$6.0 \pm 0.5$ (4)
Limpets			
<i>Nacella concinna</i>	$-16.8 \pm 0.2$ (35)	$6.2 \pm 0.3$ (33)	$5.8 \pm 0.1$ (30)
Pelecypoda (bivalves)			
<i>Laternula elliptica</i>	$-23.2 \pm 0.8$ (6)	$5.7 \pm 0.6$ (6)	$5.6 \pm 0.4$ (3)
<i>Yoldia eightsi</i>	$-17.5 \pm 0.7$ (3)	$6.5 \pm 0.2$ (3)	4.6 (1)
<b>Arthropoda</b>			
Pycnogonida (sea spider)			
<i>Colossendeis scotti</i>	$-24.3$ (1)	9.6 (1)	4.8 (1)
Other unidentified	$-24.0 \pm 0.9$ (2)	$6.9 \pm 1.4$ (2)	ND
Crustacea			
Amphipods	$-23.1 \pm 0.6$ (15)	$5.6 \pm 0.4$ (15)	$6.5 \pm 0.2$ (10)
Euphausiids			
<i>Euphausia superba</i>	$-29.8 \pm 0.6$ (12)	$3.6 \pm 0.2$ (12)	$7.6 \pm 0.7$ (14)
Isopods			
<i>Glyptonotus antarcticus</i>	$-24.7 \pm 0.9$ (4)	$7.3 \pm 0.8$ (4)	$5.6 \pm 0.3$ (3)
<b>Bryozoa</b>			
<i>Flustra antarctica</i>	$-26.6 \pm 0.4$ (5)	$3.1 \pm 0.2$ (5)	$4.6 \pm 0.1$ (2)
Other unidentified	$-25.1 \pm 1.3$ (5)	$4.1 \pm 0.1$ (5)	$5.0 \pm 0.4$ (4)
<b>Brachiopoda</b>			
<i>Liothyrella uva</i>	$-22.3 \pm 3.0$ (6)	$6.4 \pm 0.1$ (6)	$5.8 \pm 0.1$ (3)
<b>Echinodermata</b>			
Asteroids	$-17.2 \pm 0.5$ (11)	$8.9 \pm 0.1$ (11)	$6.3 \pm 0.2$ (8)
Echinoids	$-20.9 \pm 0.7$ (10)	$6.1 \pm 0.2$ (10)	$6.9 \pm 0.3$ (8)
Holothuroids	$-24.8 \pm 0.7$ (11)	$7.4 \pm 0.2$ (11)	$6.1 \pm 0.2$ (9)
<b>Urochordata</b>			
<i>Cnemidocarpa verrucosa</i>	$-23.7 \pm 0.3$ (6)	$6.6 \pm 0.1$ (6)	$6.1 \pm 0.2$ (6)
Other unidentified	$-24.8 \pm 0.5$ (11)	$5.2 \pm 0.4$ (10)	$5.9 \pm 0.2$ (7)
<b>Chordata</b>			
Osteichthyes			
* <i>Chaenocephalus aceratus</i>	$-24.9 \pm 0.1$ (4)	$11.0 \pm 0.6$ (4)	$4.3 \pm 0.0$ (3)
* <i>Gobionotothen gibberifrons</i>	$-24.9 \pm 0.9$ (3)	$10.1 \pm 0.7$ (3)	$4.5 \pm 0.0$ (3)
<i>Harpagifer antarcticus</i>	$-20.7 \pm 0.5$ (5)	$11.8 \pm 0.2$ (5)	$4.5 \pm 0.2$ (3)
<i>Notothenia coriiceps</i>	$-20.4 \pm 0.5$ (5)	$12.0 \pm 0.3$ (3)	$4.7 \pm 0.3$ (2)
<b>Aves</b> (Penguins)			
<i>Pygoscelis adeliae</i>	$-23.7 \pm 0.3$ (6)	$12.5 \pm 1.6$ (6)	$4.8 \pm 0.3$ (3)
<i>Pygoscelis antarctica</i>	$-27.0$ (1)	6.9 (1)	4.8 (1)

\* Samples collected in Dallmann Bay.

\*\* Values are  $\bar{x} \pm \text{SE}$  (n). ND: no data.

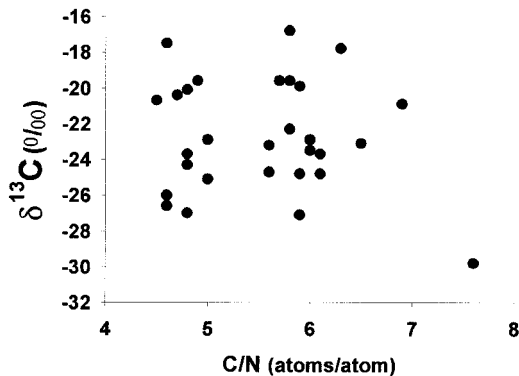


FIG. 3. Average  $\delta^{13}\text{C}$  vs. mean C/N for invertebrate and fish groups listed in Table 2.

feeding habits of various animals were supported by the isotope data. For example, the bivalve *Yoldia eightsi*, a benthic deposit feeder (Davenport, 1988) had a mean  $\delta^{13}\text{C}$  value of  $-17.5\text{‰}$ , close to benthic brown algae (Fig. 2), compared to the mean value of  $-23.2\text{‰}$  for *Laternula elliptica*, a suspension feeding bivalve (Ahn, 1993). In general, benthic suspension feeders (e.g., sponges, hydroids, soft corals, bryozoans, holothurids, and ascidians) were markedly depleted in  $^{13}\text{C}$  as reflected in average  $\delta^{13}\text{C}$  values that were less than  $-24.5\text{‰}$ . In contrast, omnivorous benthic invertebrates, including many predatory species (nemerteans, polychaetes, gastropods, sea urchins, and sea stars) had  $\delta^{13}\text{C}$  values that averaged between  $-17.2$  and  $-23\text{‰}$ .

Epibenthic fish collected near Palmer (*Harpagifer antarcticus* and *Notothenia coriiceps*) had mean  $\delta^{13}\text{C}$  values of about  $-20.5\text{‰}$ . *H. antarcticus* feeds primarily on amphipods or krill (Casaux, 1998) while *N. coriiceps* exhibits a great variety in diet (Kock, 1992), and is known to directly consume benthic algae (Iken *et al.*, 1997; Iken *et al.*, 1999). In contrast, *Chaenoccephalus aceratus* and *Gobionotothen gibberifrons* from Dallmann Bay, both bottom feeders on polychaetes and fish (Kock, 1992), were considerably more depleted in  $^{13}\text{C}$  ( $\delta^{13}\text{C} = -24.9\text{‰}$ ). Large differences in  $\delta^{13}\text{C}$  values for Adelie (*Pygoscelis adeliae*) and Chinstrap (*Pygoscelis antarctica*) penguins, which feed predominantly on euphausiids (Williams, 1995), were noted be-

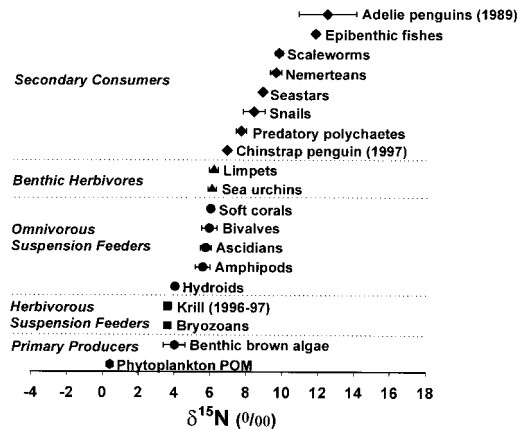


FIG. 4.  $\delta^{15}\text{N}$  values of the fauna and flora collected near Palmer Station. The value for benthic brown algae includes epiphytic diatoms; the mean phytoplankton POM value is from Wada *et al.* (1987). Data are  $\bar{x} \pm \text{SE}$ .

tween 1989 ( $-23.7\text{‰}$  for six Adelies) and 1997 ( $-27.0\text{‰}$ , one Chinstrap). The  $\delta^{13}\text{C}$  value of the Chinstrap penguin captured in 1997 is close to the isotopic composition of euphausiids collected in March 1996 and 1997 ( $-29.8\text{‰}$ ). No euphausiids could be found in March 1989 despite numerous attempts.

#### $\delta^{15}\text{N}$ measurements of fauna

Tissue  $\delta^{15}\text{N}$  values of the fauna ranged from  $3.1\text{‰}$  for the bryozoan *Flustra antarctica* to  $12.5\text{‰}$  for several individuals of *Pygoscelis adeliae*, the Adelie penguin (Fig. 4; Table 2). As in the case with  $\delta^{13}\text{C}$ , I found no apparent relationship between  $\delta^{15}\text{N}$  and C/N. Consequently, changes in  $^{15}\text{N}$ , which average 3–4‰ per trophic level in marine environments (Rau *et al.*, 1992; Minagawa and Wada, 1984; Fry, 1988), can be valuable indicators of feeding strategies among marine invertebrate and vertebrate consumers.

The  $\delta^{15}\text{N}$  analyses of a variety of organisms collected near Palmer Station were used to separate organisms into groups that corresponded to their known feeding behavior (Fig. 4). A mean value of  $0.4\text{‰}$  was used for antarctic phytoplankton POM (average of two replicate analyses, Wada *et al.*, 1987) which is known to vary from about  $-5$  to  $6\text{‰}$  (Rau, 1991b; Frazer, 1996).

TABLE 3. *Trophic levels of organisms common to coastal areas of the Antarctic peninsula ecosystem.\**

Trophic level	Organisms
1. Marine algae	POM and benthic brown macroalgae
2. Herbivores-pelagic	<i>Euphausia superba</i> : 2.0
Herbivores-epibenthic	Amphipoda: 2.2
Herbivores-benthic	Bryozoa: 2.0
Suspension feeders	Hydrozoa: 2.1
	Pelecypoda ( <i>Laternula</i> ): 2.1
	Brachiopoda: 2.3
	Porifera: 2.5
	Urochordata: 2.7
	Anthozoa (soft corals): 2.8
Herbivores-benthic	Limpets ( <i>N. concinna</i> ): 2.2
	Echinoids: 2.2
	Pelecypoda ( <i>Y. eightsi</i> ): 2.3
3. Omnivores-benthic predators	Polychaeta: 2.6–3.4
	Gastropoda: 2.9
	Asteroids: 3.1
	Holothuroids: 3.2
	Nudibranchs: 3.3
	Nemertea: 3.3
Carnivores-nekton	Chinstrap Penguin ( <i>P. antarctica</i> ): 3.0
4. Omnivores-nekton	Epibenthic fish ( <i>H. antarcticus</i> and <i>G. gibberifrons</i> ): 4.0
	Adelie Penguins ( <i>P. adeliae</i> ): 4.2

\* Calculations are based on a mean  $\delta^{15}\text{N}$  value of 0.4‰ for organisms that are clearly dependent on phytoplankton POC (e.g.,  $\delta^{13}\text{C} = < -24.0\text{‰}$ ) and 2.25‰ for organisms that assimilate a mixture of POM and benthic brown algae (e.g.,  $\delta^{13}\text{C} = > -24.0\text{‰}$ ).

The  $\delta^{15}\text{N}$  values of two herbivorous suspension feeders, euphausiids and bryozoans (Winston, 1977; Frazer, 1996), averaged 3.6‰, indicating a 3.2‰ increase per trophic level, nearly identical to that found by Wada *et al.* (1987) in the Ross Sea.

Benthic herbivores (limpets and sea urchins) which graze on benthic brown algae (mean  $\delta^{15}\text{N}$  of 4.0‰), averaged 6.2‰, a trophic enrichment of only 2.2‰. However, both organisms are not known as strict herbivores and may also consume bryozoans and hydrozoans (Dearborn, 1965), some of which are relatively  $^{15}\text{N}$  depleted in comparison to benthic algae.

With the exception of hydroids, the  $\delta^{15}\text{N}$  values of omnivorous suspension feeders (e.g., amphipods, ascidians, bivalves, and soft corals), ranged from 5.2 to 6.6‰. An even mix of phytoplankton and benthic algae ( $\delta^{15}\text{N} = 2.2\text{‰}$ ) would result in  $\delta^{15}\text{N}$  values at a first order trophic step of about 5.4‰, within the range of measurements reported for species within this group. Based on the distribution of  $\delta^{15}\text{N}$  values exhibited by fauna from the Palmer area, there exist about four trophic levels, including the ul-

timate plant food base.  $\delta^{15}\text{N}$  values of secondary consumers, including the nemertean *Parborlasia corrugatus*, a known scavenger and predator with a voracious appetite (Dearborn, 1965), ranged to 9.6‰. Other predators with high  $\delta^{15}\text{N}$  values included the nudibranch *Austrodoris* (9.6‰) and seastars (8.9‰). Epibenthic fishes and Adelie penguins from Palmer were near the top of the food web based on  $\delta^{15}\text{N}$  values of 11.9 and 12.5‰ respectively.

## DISCUSSION

### Food web structure

The range in  $\delta^{15}\text{N}$  values in Antarctic peninsula fauna reflects a food web characterized by four trophic levels, similar to that observed by Wada *et al.* (1987) in the Ross Sea and Rau *et al.* (1991b, 1992) in the Weddell Sea. Unlike the Ross and Weddell Sea systems however, the Antarctic peninsula system is more complex with respect to the contribution of additional carbon from benthic primary producers.

To calculate trophic levels (T.L.) for Peninsula fauna (Table 3), I used their respec-



tive  $\delta^{13}\text{C}$  values to determine relative dependency on benthic macroalgae. I also assumed, based on a mean  $\delta^{15}\text{N}$  value for phytoplankton POM (0.4‰) from Wada *et al.* (1987) and the average isotopic value (3.6‰) for three herbivorous suspension feeders analyzed in this study (hydroids, euphausiids, and bryozoans), that  $\delta^{15}\text{N}$  increased 3.2‰ per trophic level for Peninsula fauna. Wada *et al.* (1987) calculated nearly an identical trophic level enrichment (3.3‰) which was subsequently applied by Rau *et al.* (1992) to examine the Weddell Sea food web.

Previous studies have demonstrated that  $\delta^{13}\text{C}$  values of invertebrates and fish from the Ross and Weddell Seas (Wada *et al.*, 1987; Rau *et al.*, 1991b) were uniformly less than  $-24.0$ ‰, reflective of phytoplankton-dominated POC. Therefore calculations of trophic level utilized a  $\delta^{15}\text{N}$  value for POM of 0.4‰ for organisms with respective  $\delta^{13}\text{C}$  values less than  $-24.0$ ‰ (e.g., sponges, hydrozoans, krill, bryozoans). For all other consumers, I applied a  $\delta^{15}\text{N}$  value of 2.2‰, which represents an even mix of phytoplankton POM and benthic brown algae. Herbivores and suspension feeders were clearly identified as first level consumers (T.L. = 2.0–2.8), with second level consumers (polychaetes, nudibranchs, gastropods, seastars) falling between T.L. 2.6 and 3.4. Chinstrap penguins (T.L. = 3.0) were exactly one step above krill (T.L. = 2.0), their primary food source. Top level consumers included epibenthic fish (T.L. = 4.0) and Adelie penguins (T.L. = 4.2). Values intermediate between integers likely reflect organisms whose diet overlaps more than one trophic level.

The results of this analysis confirmed known trophic relationships among Peninsula organisms and revealed their position in the food web (Table 3). The analysis also demonstrated that many consumers occupy similar trophic levels, but derive their carbon from different sources. For example, as first level consumers, both limpets and ascidians have similar  $\delta^{15}\text{N}$  values (6.2‰–6.6‰), but their  $\delta^{13}\text{C}$  values differ by 7‰ since they derive their carbon from two entirely different sources.

One interesting finding of this study is

the large range in both carbon and nitrogen isotopic composition of penguins collected near Palmer Station. It is unfortunate that this variability is based on the collection of six Adelies in 1989 and only one Chinstrap penguin in 1997. However, the range in isotopic values for Adelies ( $\delta^{13}\text{C}$ :  $-24.9$  to  $-22.8$ ‰;  $\delta^{15}\text{N}$  = 7.8 to 19.4‰) were by themselves noteworthy. They were very different than values reported for Adelies collected in the Weddell Sea ( $\delta^{13}\text{C}$  =  $-26.8$  to  $-24.5$ ‰;  $\delta^{15}\text{N}$  = 5 to 7‰) by Rau *et al.* (1991a). The addition of a Chinstrap penguin in 1997 ( $\delta^{13}\text{C}$  =  $-27$ ‰;  $\delta^{15}\text{N}$  = 6.9‰) only served to accentuate the distinct isotopic values of Adelie penguins collected in 1989. The relatively higher  $\delta^{13}\text{C}$  values of Adelies may be explained by the incorporation of benthic algal carbon into their diets when they may become more omnivorous and depend on other food sources when krill are scarce. Although the carbon isotopic composition of krill can exhibit large spatial and temporal variations (Frazer *et al.*, 1997), the less negative  $\delta^{13}\text{C}$  value ( $-23.7$ ‰) of Adelie penguins collected in 1989, when we were unable to find krill, was associated with higher  $\delta^{15}\text{N}$  values. The much higher  $\delta^{15}\text{N}$  values for Adelie penguins indicate that these animals were probably feeding at a higher trophic level in 1989 than Chinstrap penguins collected in the same area in 1997. The apparent shift in diet implied by the difference in  $\delta^{15}\text{N}$  values may not be unusual; although Adelie penguins eat mainly euphausiids, they are known to consume fish and squid (Williams, 1995). The  $\delta^{15}\text{N}$  values of krill generally range from 1 to 5‰ (this study; Wada *et al.*, 1987; Rau *et al.*, 1991b; Frazer, 1996), compared to 7–12‰ for Antarctic squid and fishes (this study; Wada *et al.*, 1987; Rau *et al.*, 1992).

#### *Consumer diets and dependence on benthic brown algae*

The large range in invertebrate consumer  $\delta^{13}\text{C}$  values, from  $-17$ ‰ to nearly  $-30$ ‰, compared to  $-24$ ‰ to  $-34$ ‰ reported for Ross and Weddell Sea invertebrates (Wada *et al.*, 1987; Rau, 1991b), support the hypothesis that many of the organisms that inhabit the nearshore Antarctic peninsula as-

TABLE 4. Comparison of  $\delta^{13}\text{C}$  values (‰) of organisms collected within and outside benthic macroalgal beds near Palmer Station and in Antarctic oceanic waters.\*

Group	Palmer Station (this study)	Weddel Sea <sup>1</sup>	Ross Sea <sup>2</sup>	Dallmann Bay (this study)
Hydrozoa	$-26.0 \pm 0.2$ (3)	$-26.1 \pm 1.5$ (2)	—	—
Polychaeta	$-20.9 \pm 0.4$ (23)	$-30.0$ (1)	$-26.9 \pm 0.2$ (2)	—
Amphipoda	$-23.1 \pm 0.6$ (15)	$-30.8 \pm 0.3$ (4)	$-27.1$ (1)	—
Epibenthic Fish	$-20.6 \pm 0.5$ (10)	—	—	$-24.9 \pm 0.5$ (7)

\* Values are  $\bar{x} \pm \text{SE}$  (n).<sup>1</sup> Rau *et al.*, 1991b.<sup>2</sup> Wada *et al.*, 1987.

similate carbon derived from benthic seaweeds. Additional evidence for the incorporation of macroalgae into the Peninsula food web is based on the difference in  $\delta^{13}\text{C}$  values of omnivorous animals collected in macroalgal beds near Palmer compared to those collected either in Dallmann Bay or the Weddel or Ross Seas (Table 4).

Omnivorous epibenthic fish, amphipods and polychaetes from Palmer ranged from  $-20.6\text{‰}$  to  $-23.1\text{‰}$  compared to  $-24.9\text{‰}$  to  $-30.8\text{‰}$  for organisms collected outside benthic macroalgal beds, a difference of 4–6‰. The  $\delta^{13}\text{C}$  value of hydrozoans, which are filter feeders, was the same for both areas ( $-26.0\text{‰}$ ), indicative of an isotopically similar source of phytoplankton carbon. Because many of these suspension feeders are sessile and long-lived, they can be excellent long-term integrators of phytoplankton isotopic composition (Dunton and Schell, 1987). Several other invertebrates from Palmer exhibited strong selectivity for food that resulted in little or no incorporation of benthic macroalgae.

Sponges and bryozoans are particularly good examples of selective suspension feeders that consume particles generally less than 50  $\mu\text{m}$  in size, which includes small phytoplankton, bacteria, and unresolvable particulate organic matter (Reiswig, 1971; Winston, 1977; Kowalke, 2000). The mean  $\delta^{13}\text{C}$  value of sponges ( $-27.1\text{‰}$ ) and the bryozoan *Flustra antarctica*,  $-26.8\text{‰}$ , was used to estimate a phytoplankton  $\delta^{13}\text{C}$  value of  $-27.7\text{‰}$  using a fractionation of 0.8‰ per trophic level (DeNiro and Epstein, 1978). The isotopic value of limpets also reflected a 0.8‰ enrichment from their benthic diatom food

source (see Tables 1 and 2). Other invertebrates that demonstrated a clear dependence on phytoplankton (based on  $\delta^{13}\text{C}$  values ranging from  $-25\text{‰}$  to  $-30\text{‰}$ ) included euphausiids, holothurians, and urochordates (ascidians), all of which are suspension feeders (Gutt, 1991; Frazer, 1996; Kowalke, 1999).

In contrast, the  $\delta^{13}\text{C}$  value of other organisms clearly indicate some diversity of feeding and assimilation of  $^{13}\text{C}$  enriched benthic algal detritus. For example, the  $\delta^{13}\text{C}$  values of two polychaetes, *Neanthes kerguelensis* and *Terebella ehlersi*, ranges from  $-19$  to  $-23\text{‰}$ . Since the  $\delta^{15}\text{N}$  values of both species are similar ( $7.2$ – $7.7\text{‰}$ ), the difference in  $\delta^{13}\text{C}$  values can be attributed to the utilization of different carbon sources by these two species. The large difference in the  $^{13}\text{C}$ :  $^{12}\text{C}$  ratios of two bivalves, *Laternula elliptica*, a filter feeder ( $-23.2\text{‰}$ ) and *Yoldia eightsi*, a deposit feeder ( $-17.5\text{‰}$ ), is indicative of the distinct difference in feeding strategies employed by these two species (Davenport, 1988; Ahn, 1993). The greater dependence on benthic algae by *Y. eightsi* reflects the utilization of the large amounts of detached macroalgae that accumulates and decomposes on the seabed.

Since benthic brown seaweeds clearly contribute the greatest biomass of material to the nearshore environment (Amsler *et al.*, 1995) and their carbon isotopic values overlap with that of the endemic fauna (Fig. 2), I attempted to estimate their relative carbon contribution to the Peninsula food web. A simple mixing equation was employed to interpret the  $\delta^{13}\text{C}$  values of the fauna (McConnaughey and McRoy, 1979, Dunton

and Schell, 1987). This equation accounts for the isotopic fractionation that results from  $^{13}\text{C}$  enrichment at successive trophic levels, providing a more conservative estimate of consumer dependence on benthic algae, which are  $^{13}\text{C}$  enriched relative to phytoplankton. In this study, a fractionation factor of 0.8‰ per trophic level was used to account for progressive enrichment of animal  $^{13}\text{C}$ , which can vary between 0.5 and 1.5‰ (Fry and Sherr, 1984). This value is based on the 0.8‰  $^{13}\text{C}$  enrichment shown by limpets relative to benthic diatoms from this study and is in agreement with a dietary study using stable carbon isotopes by DeNiro and Epstein (1978).

The  $\delta^{13}\text{C}$  measurements of animals collected both within and outside macroalgal beds near Palmer Station and in Antarctic oceanic waters also provide a means to estimate the relative importance of benthic brown algae to Peninsula food webs (Table 4). Post-photosynthetic isotope fractionation can be accounted for through comparison of  $\delta^{13}\text{C}$  values of similar organisms collected both within benthic algal dominated areas and outside these areas. Calculations are based on the proportional incorporation of benthic brown algal carbon (−20.6‰) and phytoplankton carbon (−27.7‰) into animal tissue, where:

% benthic algal C

$$= \{[\delta^{13}\text{C}(\text{animal}) - \delta^{13}\text{C}(\text{phytoplankton}) - I] / [\delta^{13}\text{C}(\text{benthic algae}) - \delta^{13}\text{C}(\text{phytoplankton})]\} \times 100$$

The additional term  $I$  accounts for post photosynthetic fractionation and is estimated for the animals as ( $I$ ) =  $\delta^{13}\text{C}$  (animal) −  $\delta^{13}\text{C}$  (phytoplankton) for specimens collected outside benthic macroalgal beds and in oceanic waters (Table 4). For all other species,  $I$  was calculated by multiplying 0.8‰ by the organism's trophic level. Trophic levels were calculated from organism  $\delta^{15}\text{N}$  values (Table 3). To provide a more conservative estimate for the incorporation of benthic algal carbon into consumer tissues, the calculations were also performed using the  $\delta^{13}\text{C}$  value for benthic diatoms (−17.6‰). This provided a range in dependence for

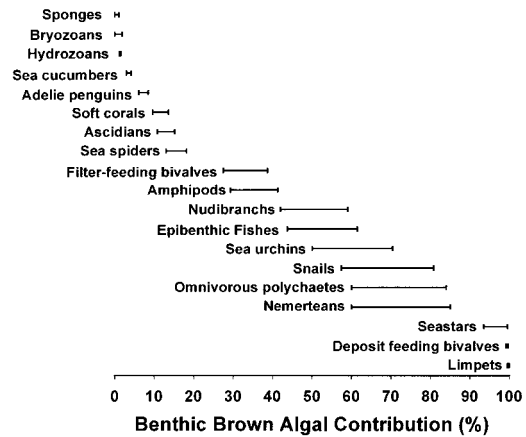


FIG. 5. Consumer assimilation of carbon from benthic brown algae. The range in dependence for various Peninsula fauna near Palmer reflects the pooled  $\delta^{13}\text{C}$  value for a mixture of benthic brown seaweeds with their associated diatom epiphytes and filamentous benthic diatoms alone. Calculations are based on a simple mixing equation that accounts for post-photosynthetic fractionation (see "Discussion—Consumer diets and dependence on benthic brown algae").

peninsula fauna based on a mixture of benthic brown seaweeds with their associated diatom epiphytes and filamentous benthic diatoms alone.

The significant fraction of benthic brown algal carbon incorporated into the tissues of a variety of organisms collected on the Antarctic peninsula confirms their opportunistic feeding behavior as omnivorous scavengers (Fig. 5). The fraction of benthic algae was greatest (over 90%) in limpets and deposit feeding bivalves which feed directly on a mixture of epiphytic diatoms and macroalgae, but also very high in seastars which are a major predator of these consumers. Other clearly benthic organisms, including snails, polychaetes and nemerteans, showed a high but variable (60–85%) assimilation of benthic algae that reflected the diversity in omnivorous feeding behavior. Epibenthic organisms (filter feeding bivalves, amphipods, nudibranchs, fishes) fell into a third group whose dependence on benthic algae was lower but also variable (30 to 60%). Suspension feeders clearly showed the least dependence for benthic algal carbon (0 to 14%). These results are very consistent with that of previous studies that have examined the role of kelp in arctic (Dunton

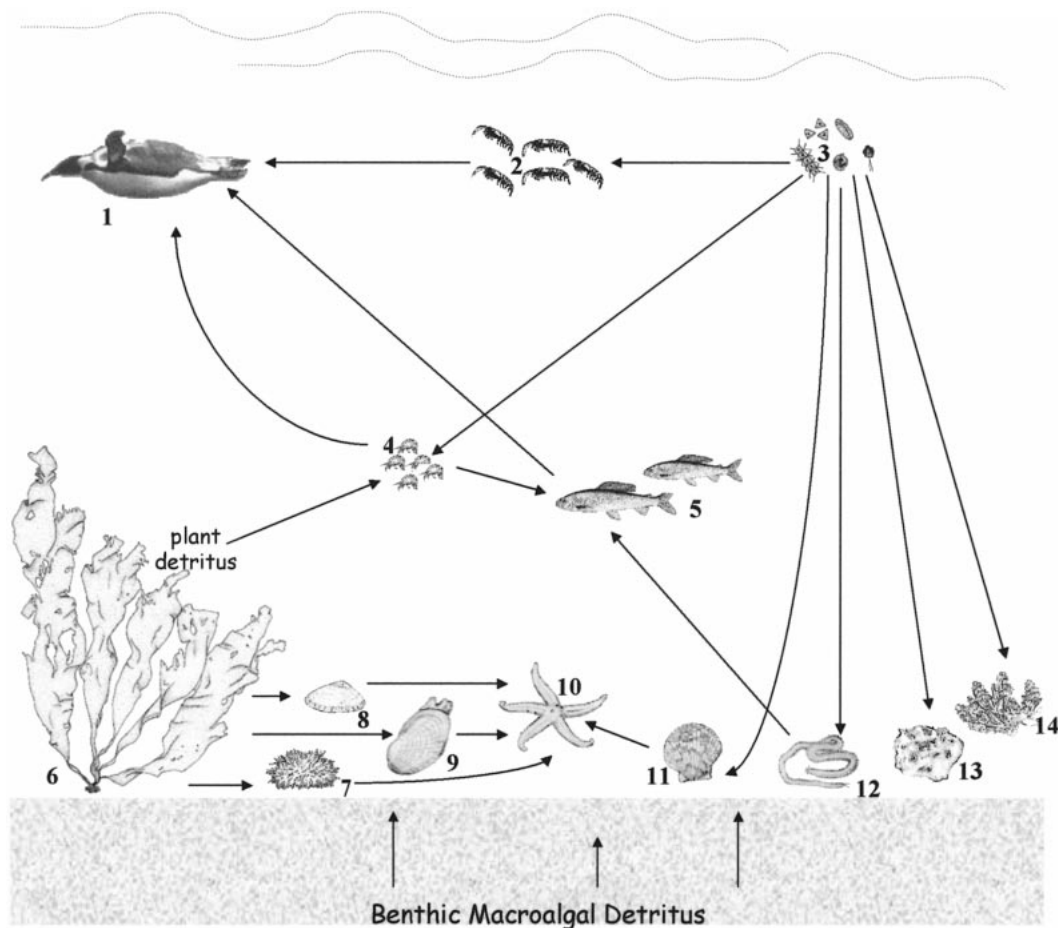


FIG. 6. Simplified representation of an Antarctic peninsula food web. Arrows point from prey to consumer. Organisms most dependent on benthic algae are closest to their ultimate carbon source. Organisms depicted are as follows: 1: Adelie penguins; 2: krill; 3: phytoplankton; 4: amphipods; 5: epibenthic fishes; 6: benthic macroalgae; 7: urchins; 8: limpets; 9: deposit-feeding bivalves; 10: seastars; 11: filter-feeding bivalves; 12: omnivorous polychaetes; 13: sponges; 14: bryozoans.

and Schell, 1987) and sub-arctic (Duggins *et al.*, 1989) food webs.

In addition to the clear dependence on benthic algal carbon by a variety of organisms in Antarctic peninsula food webs, 25 to 40% of the carbon assimilated by benthic and epibenthic molluscs and crustaceans may be derived from benthic algae. The fraction of tissue carbon derived from a mixture of benthic algae for amphipods, an important prey item for many second level consumers, ranged from 30 to 40%. The incorporation of benthic algal carbon into the tissues of these animals may at least partially explain the large range in  $\delta^{13}\text{C}$  values

of penguins ( $-23.7$  to  $-27\text{‰}$ ) who may depend on other food sources when krill are scarce.

Consequently, the trophic importance of benthic brown algae may well extend into the pelagic food web (Fig. 6). Evidence for this nearshore coupling appears in the small but distinguishable benthic algal fraction in soft corals and ascidians, which primarily feed on drifting plankton and particulate matter. In contrast, the high fraction of benthic algal carbon in deposit feeding bivalves and their associated seastar predators (Fig. 5) indicate that most of this carbon is channeled through the detrital food web and is



transferred to higher trophic levels. The presence of multiple carbon sources on the Antarctic peninsula results in complex food webs in which consumers that occupy similar trophic levels may depend on completely different carbon sources. As a result, the benthic macroalgal populations on the Antarctic peninsula not only serve as valuable habitat (DeLaca and Lipps, 1976; Richardson, 1979), but provide a dynamic substrate for epiphytic diatoms which together with the seaweeds provide an important carbon source that is readily assimilated by Antarctic peninsula fauna.

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