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Diet components in the food of Antarctic ascidians living at low levels of primary production

MARCOS TATIÁN[1]*, RICARDO SAHADE[1] and GRACIELA B. ESNAL[2]

[1]*Ecología Marina, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Avenida Vélez Sársfield 299, 5000 Córdoba, Argentina*

[2]*Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, 1428 Buenos Aires, Argentina*

**mtatian@com.uncor.edu*

Abstract: Coupling between pelagic and benthic systems has been described in numerous shallow water communities. In Potter Cove, where pelagic primary production is low (not only during the Antarctic winter but also during the summer), the rich benthic community present there must depend on other food sources than phytoplankton. Over a year-round period we determined the abundance of the different seston particles which constituted the stomach contents of the Antarctic ascidian *Cnemidocarpa verrucosa* (Lesson, 1830) at Potter Cove. Stomach repletion was highest in November and lowest in June. Ascidians took in a wide range of particles from large detritus (macroalgal debris and faecal pellets) to minute particles < 5 µm. Large detritus and minute particles together represent the main percentage of contents throughout the year (mean 91%). Diatoms were a low percentage (mean 4.5%). Unidentified flagellates, dinoflagellates and coccolithophorids were scarce, with mean values lower than 4%. Among diatoms benthic species were more abundant in summer and pelagic ones prevailed from March to November. Resuspension of benthic material due to wind mixing and the input of allochthonous particles by currents are important mechanisms that ensure food for ascidians and the community of suspension feeders in Potter Cove.

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Key words: benthos, seston, Southern Ocean, South Shetland Islands, stomach contents

Introduction

Benthic biomass is usually related to productivity in the water column, since phytoplankton, and especially diatoms, constitute an important food source for benthic organisms such as suspension feeders (Fisher 1977, Goddard & Hoggett 1982). In Antarctica, primary production is reduced to a few months during spring and summer, a period of high irradiance, when phytoplankton biomass increases considerably. The low availability of food during winter, determines a degree of seasonality in the biology of polar marine organisms. This seasonality varies with their position in the food web, with the herbivores being most seasonaly affected (Clarke 1988). There is not a complete famine during the Antarctic winter since nanoplankton and organic particles appear to provide some energy, reducing the negative effect produced by the fall of the overall primary production. The levels of nanoplankton that remain in winter were stated to be enough to support the metabolism of suspension feeders (Clarke 1985, Barnes & Clarke 1994). Similarly, benthic diatoms could survive the winter season in shallow water (Dayton *et al.* 1986, Gilbert 1991), constituting an alternative food source for these animals. The retention efficiency of different particle-size determines the use of these particles as food. Colonial ascidians can filter particles as small as 1 µm and particles 2–3 µm are retained with high efficiency (Randløv & Riisgård 1979).

Other factors affecting phytoplankton production in near-shore Antarctic environments are the presence of pack-ice and sedimentation processes. In Potter Cove, while formation of pack-ice is highly variable, large amounts of terrigenous particles are carried into the Cove by melt water streams during summer, which makes the euphotic zone very shallow (Schloss & Ferreyra 2002). The combination of physical factors affecting both the radiation penetrating the water column and the depth of vertical turbulent mixing are responsible for the low phytoplankton concentration in Potter Cove, compared with other localities (Schloss *et al.* 1998). In spite of these conditions, ascidians are one of the most abundant mega-epibenthic animals in Potter Cove from a depth of 20 m onwards (Sahade *et al.* 1998), where up to 17 different species have been found (Tatián *et al.* 1998). In a previous study, based on chemical analysis carried out on gut contents of the ascidian *Cnemidocarpa verrucosa*, year-round intake and absorption of organic matter was detected (Tatián *et al.* 2002). This means that ascidians can handle large amounts of terrigenous material (which does not affect the absorption of organic seston) and can survive in a habitat with low phytoplankton throughout the whole year, and especially in winter. We hypothesize that the origin of the organic seston that reaches the benthic environment is not only the sinking of particles from the water column, but also the resuspension and the input of allochthonous material. Although ascidians appear to be

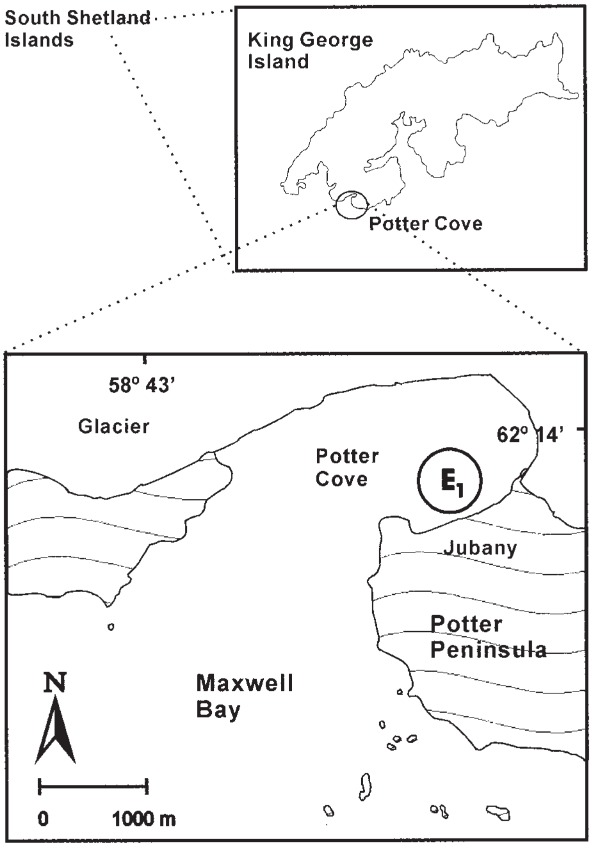

Fig. 1. Map of Potter Cove showing the location of the sampling area (E1).

feeding on other particles besides microalgae, these seston particles and their relative contribution to the diet of ascidians are still unknown. In the present study we microscopically analysed the stomach contents of the ascidian *Cnemidocarpa verrucosa* (Lesson) over a year to identify the diet components on a seasonal basis.

Materials and methods

Study area

Potter Cove, where the Argentinean station Jubany and the Argentinean-German Dallmann laboratory are situated, is an inlet of the larger Maxwell Bay system, King George Island, South Shetland Islands (62°14'S, 58°38'W) (Fig. 1). The inner cove is characterized by soft bottoms of fine sediments, whereas the glacier front consists of moraine deposits. Ascidians are the dominant macrobenthic fauna from 20 m deep, while pennatulids and the bivalve *Laternula elliptica* (King & Broderip) are the most abundant macrobenthic fauna at shallower depths (Sahade *et al.* 1998). A dense macroalgae community attached to the hard substrate dominates the mouth of the cove and the glacier front. The total area of the cove is over 4.5 km^2 with a maximum depth of 100 m.

Sampling

Five specimens of the ascidian *Cnemidocarpa verrucosa* (9–11 cm long) were collected monthly between March 1996 and February 1997 by SCUBA diving, at 30 m depth at E_1. Immediately after sampling, the whole gut was removed, fixed and stored in 2.5% formaldehyde in filtered seawater. The stomach repletion percentage was calculated as:

$$R = (\text{volume of stomach contents}/\text{length of stomach})*100$$

Determination of volume of the stomach contents was made by the displacement of a known volume of formaldehyde in a graduated test tube.

Microscopic observations

Samples were stained with Lugol's solution and stirred. Quantitative analysis were performed under microscope (up to 1600x magnification), using a Neubauer counting chamber (haematocytometer, 0.1 mm deep). Observations were done in the central grid of the chamber (1 mm^2 area), counting the particles under each crossing of the grid (a total of 441 points). These counts gave information about the relative abundance of the different particles found in the stomach at the moment that the animals were caught. Relating the relative abundance of each component to the stomach repletion, we estimated the absolute amount of components per stomach, which help distinguish real from apparent seasonality. The origin of particles filtered by ascidians (from the pelagic or benthic systems) during the year-round period was determined using only diatoms and discriminating between pelagic and benthic species (Frenguelli & Orlando 1958, Medlin & Priddle 1990, Klöser *et al.* 1994, Klöser 1998, Ahn *et al.* 1997). Samples of gut contents were placed in a Neubauer chamber and ten fields were scored (6.75 mm^2 total area).

The microscope had an ocular micrometer to measure the size of particles.

Data analysis

Counts are expressed as estimated amounts of each component per stomach. The differences throughout the period for each kind of particles were assessed by one-way analyses of variance (ANOVA) at a significance level of 5% with an *a posteriori* least-significant-difference (LSD) test. When necessary and prior to statistical analyses, data were log-transformed ($\log_{10}$ (0.1+x)) to homogenize the variances, which were tested using Cochran's C test.

Results

The highest repletion percentage was measured in November 1996 (mean 51%), whereas June 1996 was the

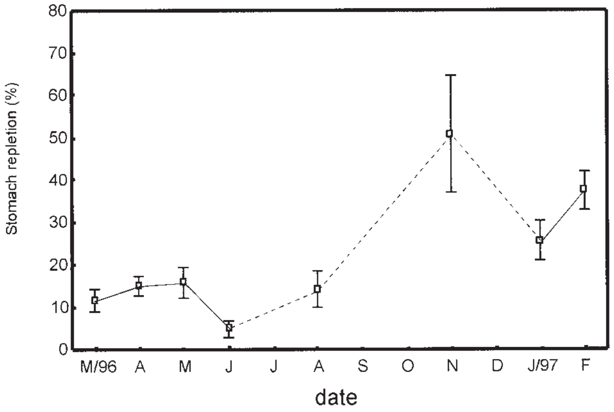

Fig. 2. *Cnemidocarpa verrucosa.* Stomach repletion percentage measured over the year (mean ± s.e.).

lowest (mean 5%) (Fig. 2). A wide range of particle size was observed in stomach contents. Among the largest there were from dense aggregations of particles (up to 1.3 mm long), brown in colour, made up of both organic and inorganic material (faecal pellets), as well as recognizable macroalgal debris, green in colour, up to 0.5 mm long. On the other hand, a background of minute particles, < 5 µm size was observed. Large detritus and particles < 5 µm size were present throughout the year, and together constituted the main percentage of particles counted (up to 98%). Diatoms reached the highest density in November, (20.4% of the total of items counted) which was determined by the abundance of the large pelagic species *Corethron criophilum* Castracane. In winter, diatom frustules were very scarce (0.8%). Unidentified flagellates, dinoflagellates and coccolithophorids were scarce, with maximum monthly values of 7.7%, 4% and 2.5% respectively. Silicoflagellates represented by the genus *Dictiocha,* were observed occasionally during winter. For the large detritus and particles < 5 µm, estimated absolute amounts per stomach showed very low values in winter (June), while maximum values were registered in November and February (Fig. 3a).

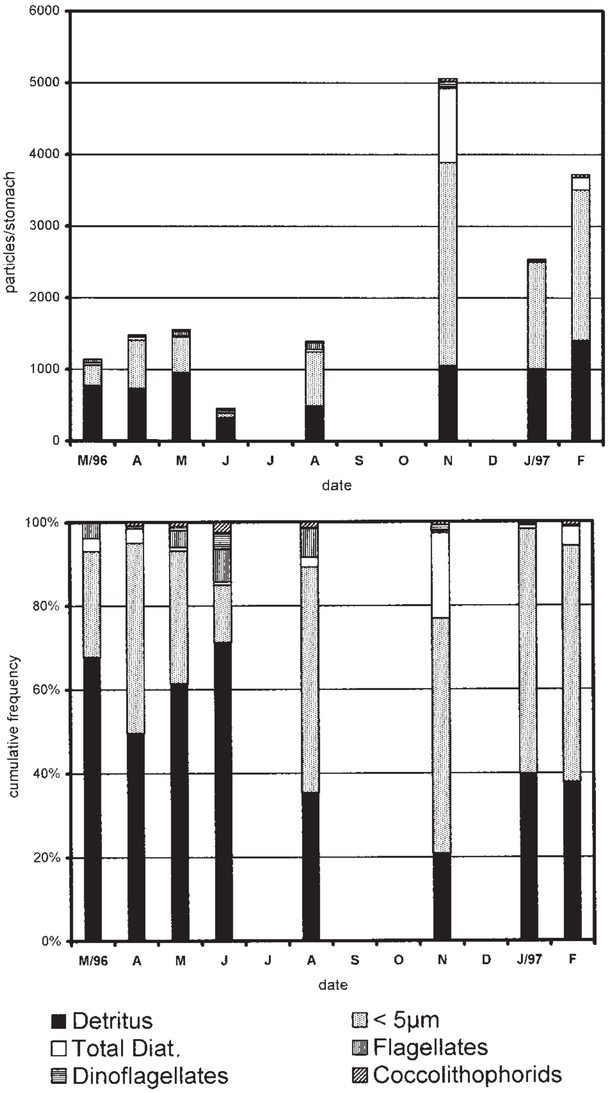

Fig. 3. *Cnemidocarpa verrucosa.* **a.** Estimated absolute amounts of components in the stomach contents. **b.** Relative abundance of components in the stomach contents (cumulative frequencies).

Table I. Abundance of the main particles counted in the stomach contents of *Cnemidocarpa verrucosa* over the year (estimated amounts per stomach).

	Detritus	Particles < 5µm *	Flagellates*	Total Diatoms*	Dinoflagellates*	Coccolithophorids*
Mean ± s.e.	826 ± 86	1094 ± 175	34 ± 10	183 ± 77	17 ± 8	16 ± 5
P-value	0.011	0	0.125	0	0.43	0.313
F-ratio	3.17	10.87	1.78	8.03	1.03	1.24
LSD**						
March 1996	a b c	b		b c		
April	a b c	c d		c d		
May	b c d	b c		a b		
June	a	a		a		
August	a b	b c		c d		
November	c d	e		e		
January 1997	b c d	c d e		c d		
February	d	d e		d e		

*ANOVAS and LSD-test were performed with data log-transformed.

**Significant differences at 5% significance level among the different months, indicated with different letters.

It contrasts with the values of relative abundance, being lowest for detritus in November (Fig. 3b).

Variation of the estimated absolute amounts of components is showed in Table I. Only large detritus, particles < 5 µm and total diatoms varied significantly throughout the year.

Comparing benthic and pelagic diatoms present in stomach contents, benthic were more abundant in January and February, while pelagic dominated from March to November (Fig. 4). Benthic diatoms were more abundant in May, due to an increase of the genus *Licmophora.* Individual diatoms prevailed over those grouped in chains: only the genus *Fragilariopsis* showed a typical ribbon formation. The species, *C. criophilum and Thalassiossira* spp. (pelagic), *Licmophora* spp., *Gyrosigma* spp. and *Cocconeis* spp. (benthic) were the most frequent diatoms observed in the guts during the studied period.

Discussion

The traditional point of view has been that Antarctic benthic organisms must actively feed to store reserves during spring-summer season, in order to survive a period of starvation in winter**.** Recent studies stressed the importance of the finest seston fraction as food source for animals like suspension feeders (Clarke 1985, Clarke & Leakey 1996). The nanoflagellate bloom, although reaching peak concentrations an order of magnitude lower than those of diatom, lasts much longer (Clarke & Leakey 1996), representing a greater contribution to diets than previously suspected. This study shows that *Cnemidocarpa verrucosa* makes use of a wide range of particles, including faecal pellets, macroalgal debris (transported by currents from rocky areas present in other parts of the cove) and minute particles < 5 µm. These small particles were probably bacteriae, protozoans, nanoplankton, minute organic and inorganic seston and internal secretions (mucus). Large detritus and minute particles < 5 µm were the principal components of the stomach contents during the whole year. It is difficult to define a marked seasonality in terms of the presence of these main components in the stomach contents, the estimated absolute amounts gave a better approach than the value of their relative abundance. Although their representation in the total stomach contents but differed significantly throughout the year, these particles can be an alternative source of organic matter for suspension feeders. Studies performed in the water column at 30 m depth showed non-significant differences in the amounts of particulate organic matter throughout the year (Schloss *et al.* 1999, Tatián *et al.* 2002), revealing that the availability of organic seston is not directly linked to the seasonal pulses of primary production in Potter Cove. Summer pelagic primary production in Potter Cove is lower than in other locations, ranging from 91–478 mg C m^{-2} d^{-1}, whereas data from other Antarctic shallow areas reach 4800 mg C m^{-2} d^{-1} (Schloss *et al.* 1998). Microalgae were not the main components found in stomach contents in terms of relative abundance, even during November and late summer, when large diatoms like *Corethron criophilum* or *Gyrosygma* spp. were abundant. This agrees with a study previously performed in *C. verrucosa* where chemical composition of gut contents was not related, as expected, to the increase of pigment concentration both in the water column and sediments in spring and summer (these data were taken during the same period of this study) (Tatián *et al.* 2002). Although the nutritive value of diatoms is higher than those of non-living particles, such as detritus, especially in terms of its C/N ratio (Paine & Vadas 1969, Fisher 1977, Cammen 1980), suspension feeders can use plant detritus as a carbon resource (Newell *et al.* 1982, Stuart *et al.* 1982, Seiderer & Newell 1985, Alber & Valiela 1996, Charles *et al.* 1996). In the same way, they may consume faecal pellets from macroconsumers, which may have a relatively high organic content. Depending on source and state of decomposition, the components of the detritus pool can be "nutritionally available", i.e. directly assimilable by macroconsumers (e.g. sugars, nonstructural carbohydrates, proteins) or "nutritionally unavailable" (e.g. cellulose, lignine). Nutritionally not available detritus can be converted by microbial activity into material available to macroconsumers or these associated microbes can themselves serve as food (Tenore *et al.* 1982). Bacteria represent an important food source to those organisms which are capable of exploiting particles in the bacterial size range, like ascidians (Randløv & Riisgård 1979, Stuart & Klumpp 1984, Seiderer & Newell 1985). Studies on *C. verrucosa* revealed that this species starts filtering from

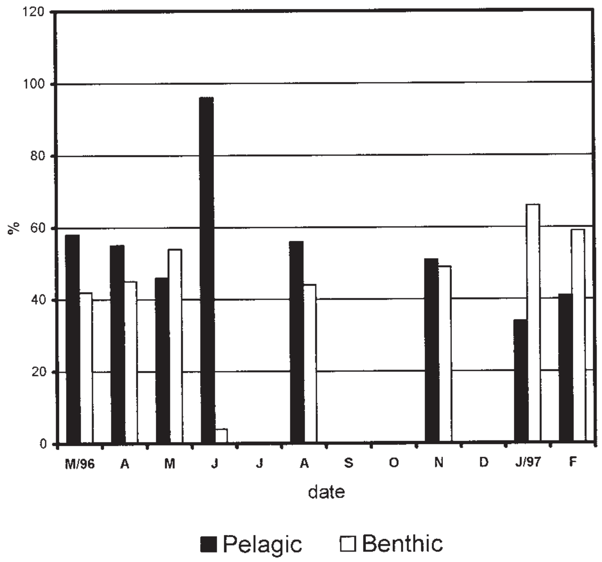

Fig. 4. *Cnemidocarpa verrucosa.* Relative abundance of pelagic and benthic diatoms in the stomach contents through the studied period.

1.3 µm particle size (Kowalke 1999). Thus, the wide range of particle sizes on which ascidians are capable of feeding, make the intake of detritus and the related microbial communities possible. These seston particles support the rich ascidian biomass found in this area, which is characterized by low pelagic primary production.

Availability of seston in Potter Cove is higher in summer than in winter but is principally inorganic material, owing to the abundant sedimentation. These fine sediments (which turns the water brown), stem from riverine input of glacial melt water, and are then dispersed through the water column by winds. Characteristic of the inner Cove is the resuspension, also caused by winds, of the fine bottom material. The frequent eastern gales create an upwelling effect which drags the bottom material into the water column. Thus, sediment in the water column persists throughout the ice free months. Ascidians could be better adapted than other suspensivores (such as sponges or bivalves) to sort the abundant inorganic material (by means of "squirting" or expulsion of particles at high seston concentrations), and to filter and entrap the organic particles. In the case of Potter Cove, the load of inorganic material does not affect the absorption efficiency of *Cnemidocarpa verrucosa* which was above 70% throughout the year (Tatián *et al.* 2002). As Schloss *et al.* (1999) pointed out, total organic content is higher 20 cm above the bottom (where the ascidian *C. verrucosa* filters) than close to the bottom, where other species like the bivalve *Laternula elliptica* takes up particles. Filtering effort for the bivalve is probably higher and consequently ascidians probably have a better energy balance, the bivalve is also capable of maintaining a stable biomass despite the fluctuation of its energy sources (Momo *et al*. 2002). Winter is characterized by sea ice formation and the lack of mixing of the water column and resuspension which should produce low availability of both organic and inorganic seston. However, only specimens from June showed empty stomachs, while gut contents corresponding to summer months, such as March 1996, were similar to those from May and August 1996 (Fig. 2). During winter 1996, the pack ice was not consolidated and this should facilitated bottom resuspension and mixing of the different layers in the water column, reducing the "stress period" to ascidians. Analysing the relation between benthic and pelagic diatoms, it is clear that during summer, benthic species prevailed. These diatoms seem to be available for suspension feeders once they were brought back into the water column by resuspension. Benthic diatoms predominated in bottom, trap sediment, gut contents and faecal material of *L. elliptica* during a summer in Marian Cove, a close locality (Ahn 1997). Benthic diatoms constituted the most abundant prey found in the gastric cavity of a hydroid from intertidal communities of Potter Cove (Gili *et al.* 1996). Diatoms of benthic origin were detected in different Antarctic areas, even during winter (Dayton *et al.* 1986, Gilbert 1991). In Potter Cove, diatom films (which were observed in summer by divers) characterize brown coloured soft bottom areas. Measurements on photosynthetic pigments in benthic sediments revealed higher values of these pigments in summer than in winter (Tatián *et al.* 2002). In winter, stomach contents showed a predominance of pelagic diatoms over benthic ones, but the frustules (markedly scarce in comparison with spring and summer) were probably sunk material, resuspended and entrapped by ascidians. The pelagic origin of some diatom genera found such as *Corethron, Thalassiosira, Coscinodiscus* or *Fragilariopsis* (this latter could be from the pelagic or pack-ice according to Medlin & Priddle 1990), and also the benthic origin of some others like *Cocconeis, Licmophora, Melosira* or *Gyrosygma* is important in characterizing the mechanism that provides food for ascidians. Although the role of ice diatoms is not defined in the present work, and must be important, our goal is to know if ascidians feed on sunken particles or resuspended ones. Although we cannot confirm the presence of living benthic diatoms in the sediments during winter, especially in June, it seems that, since pack-ice was not consolidated, resuspension of particles from the bottom was an important process during the studied period. This phenomenon and the horizontal flux of allochthonous material by currents (from the presence in the gut contents of macroalgal debris) appear to be the main processes that ensure availability of organic matter to ascidians and the suspension feeder community in Potter Cove.

Conclusions

Cnemidocarpa verrucosa at Potter Cove does not depend exclusively on the characteristic summer primary production pulses in Antarctica, since ascidians feed on other sources than phytoplankton. A wide range of particle size was found in stomach contents. Among these particles, large detritus and minute particles < 5 µm were the most abundant items during the year: this material should provide enough energy to ascidians. Ingestion of a wide range of particle sizes at different concentrations, together with the ability to exclude high amounts of inorganic material, could be important factors in explaining the abundance of ascidians in Potter Cove. Bottom resuspension and advection of allochtonous particles are important mechanisms which provide food to benthic suspension feeders year-round.

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References

Ahn, I.Y. 1997. Feeding ecology of the Antarctic lamellibranch *Laternula elliptica* (Laternulidae) in Marian Cove and vicinity, King George Island, during one austral summer. *In* Battaglia, B., Valencia, J. & Walton, D.H.W., *eds. Antarctic communities: species, structure and survival.* Cambridge: Cambridge University Press, 142–151.

Ahn, I.Y., Chung, H., Kang, J.S. & Kang, S.H. 1997. Diatom composition and biomass variability in nearshore waters of Maxwell Bay, Antarctica, during the 1992/1993 austral summer. *Polar Biology,* **17**, 123–130.

Alber, M. & Valiela, I. 1996. Utilization of microbial organic aggregates by bay scallops, *Argopecten irradians* (Lamarck). *Journal of Experimental Marine Biology and Ecology,* **195**, 71–89.

Barnes, D.K.A. & Clarke, A. 1994. Seasonal variation in the feeding activity of four species of Antarctic bryozoan in relation to environmental factors. *Journal of Experimental Marine Biology and Ecology,* **181**, 117–133.

Cammen, L.M. 1980. The significance of microbial carbon in the nutrition of the deposit feeding polychaete *Nereis succinea*. *Marine Biology,* **61**, 9–20.

Clarke, A. 1985. Energy flow in the Southern Ocean food web. *In* Siegfried, W., Condy, P. & Laws, R., *eds. Antarctic nutrient cycles and food webs*. Berlín: Springer, 573–580.

Clarke, A. 1988. Seasonality in the Antarctic marine environment. *Comparative Biochemistry and Physiology,* **90B**, 461–473.

Clarke, A. & Leakey, R.J.G. 1996. The seasonal cycle of phytoplankton, macronutrients and the microbial community in a nearshore Antarctic marine ecosystem. *Limnology and Oceanography,* **41**, 1281–1294.

Charles, F., Grèmare, A. & Amouroux, J.M. 1996. Ingestion rates and absorption efficiencies of *Abra ovata* (Mollusca: Bivalvia) fed on macrophytobenthic detritus. *Estuarine Coastal and Shelf Science,* **42**, 83–102.

Dayton, P.K., Watson, D., Palmisano, A., Barry, J.P., Oliver, J.S. & Rivera, D. 1986. Distribution patterns of benthic microalgal standing stock at McMurdo Sound, Antarctica. *Polar Biology,* **6**, 207–213.

Fisher, T.R. 1977. Metabolic maintenance costs of the suspension feeder *Styela plicata*. *Marine Biology,* **41**, 361–369.

Frenguelli, J. & Orlando, H.A. 1958. Diatomeas y Silicoflagelados del Sector Antártico Sudamericano. *Contribuciones del Instituto Antártico Argentino,* **5**, 15–191.

Gili, J.M., Alvà, V., Pagès, F., Klöser, H. & Arntz, W.E. 1996. Benthic diatoms as the major food source in the sub-Antarctic marine hydroid *Silicularia rosea*. *Polar Biology,* **16**, 507–512.

Gilbert, N.S. 1991. Primary production by benthic microalgae in nearshore marine sediments of Signy Island, Antarctica. *Polar Biology,* **11**, 339–346.

Goddard, C.K. & Hoggett, A.K. 1982. Gut contents of the ascidian *Pyura praeputialis*: endogenous and exogenous components. *Journal of Zoology London,* **196**, 489–497.

Klöser, H. 1998. Habitats and distribution patterns of benthic diatoms in Potter Cove (King George Island, Antarctica) and its vicinity. *In* Wiencke, C., Ferreyra, G., Arntz, W. & Rinaldi, C., *eds*. The Potter Cove coastal ecosystem, Antarctica. *Reports on Polar Research,* **299**, 95–105.

Klöser, H., Ferreyra, G., Schloss, I., Mercuri, G., Laturnus, F. & Curtosi, A. 1994. Hydrography of Potter Cove, a small, fjord-like inlet on King George Island (South Shetlands). *Estuarine Coastal and Shelf Science,* **38**, 523–537.

Kowalke, J. 1999. Filtration in Antarctic ascidians - striking a balance. *Journal of Experimental Marine Biology and Ecology,* **242**, 233–244.

Medlin, L.K. & Priddle, J. 1990. *Polar marine diatoms*. Cambridge: British Antarctic Survey, 216 pp.

Momo, F., Kowalke, J., Schloss, I., Mercuri, G. & Ferreyra, G. 2002. The role of *Laternula elliptica* in the energy budget of Potter Cove (King George Island, Antarctica). *Ecological Modelling,* **155**, 43–51.

Newell, R.C., Field, J.G. & Griffiths, C.L. 1982. Energy balance and significance of micro-organisms in a kelp bed community. *Marine Ecology Progress Series,* **8**, 103–113.

Paine, R.T. & Vadas, R.L. 1969. Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. *Marine Biology,* **4**, 79–86.

Randløv, A. & Riisgård, H.U. 1979. Efficiency of particle retention and filtaration rate in four species of ascidians. *Marine Ecology Progress Series,* **1**, 55–59.

Sahade, R., Tatián, M., Kowalke, J., Kühne, S. & Esnal, G.B. 1998. Benthic faunal associations on soft substrates at Potter Cove, King George Island, Antarctica. *Polar Biology,* **19**, 85–91.

Schloss, I. & Ferreyra, G.A. 2002. Primary production, light and vertical mixing in Potter Cove, a shallow bay in the maritime Antarctic. *Polar Biology,* **25**, 41–48.

Schloss, I., Ferreyra, G.A. & Curtosi, A. 1998. Phytoplankton primary production in Potter Cove, King George Island. *In* Wiencke, C., Ferreyra, G., Arntz, W. & Rinaldi, C., *eds*. The Potter Cove coastal ecosystem, Antarctica. *Reports on Polar Research,* **299**, 67–73.

Schloss, I., Ferreyra, G., Mercuri, G. & Kowalke, J. 1999. Potential food availability for benthic filter feeders in an Antarctic coastal shallow environment: a sediment trap study. *In* Arntz, W.E. & Rios, C., *eds*. Magellan-Antarctic: ecosystems that drifted appart. *Scientia Marina,* **63**, 99–111.

Seiderer, L.J. & Newell, R.C. 1985. Relative significance of phytoplankton, bacteria and plant detritus as carbon and nitrogen resources for the kelp bed filter-feeder *Choromytilus meridionalis*. *Marine Ecology Progress Series,* **22**, 127–139.

Stuart, V., Field, J.G. & Newell, R.C. 1982. Evidence for the absorption of kelp detritus by the ribbed mussel *Aulacomia ater* (Molina) using a new 51 Cr-labelled microsphere technique. *Marine Ecology Progress Series,* **9**, 263–271.

Stuart, V. & Klumpp, D.W. 1984. Evidence for food-resource partitioning by kelp-bed filter-feeders. *Marine Ecology Progress Series,* **16**, 27–37.

Tatián, M., Sahade, R.J., Doucet, M.E. & Esnal, G.B. 1998. Ascidians (Tunicata, Ascidiacea) of Potter Cove, South Shetland Islands, Antarctica. *Antarctic Science,* **10**, 147–152.

Tatián, M., Sahade, R.J., Kivatinitz, S.K. & Esnal, G.B. 2002. Food availability and gut contents in the ascidian *Cnemidocarpa verrucosa* at Potter Cove, Antarctica. *Polar Biology,* **25**, 58–64.

Tenore, K.R., Cammen, L., Findlay, S.E.G. & Phillips, N. 1982. Perspectives of research on detritus: do factors controlling the availability of detritus to macroconsumers depend on its source? *Journal of Marine Research,* **40**, 473–490.