

## Original Paper

# Food availability and gut contents in the ascidian *Cnemidocarpa verrucosa* at Potter Cove, Antarctica

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**Accepted:** 24 June 2001 / **Published online:**

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**Abstract.** A high seasonality characterizes Antarctic environments, and generates marked differences in availability and composition of food for benthic filter feeders. During a year-round period at Potter Cove, Antarctica, algal pigment concentration (chlorophyll *a*) and organic matter were measured in water column and sediment samples. Chemical composition of gut contents of the ascidian *Cnemidocarpa verrucosa* was also analyzed. Despite the low standing stock, capture and absorption of organic matter were detected year-round, suggesting intake of other particles besides microalgae. The mechanism that provides food to the ascidians and epibenthic communities may be related to the supply of allochthonous particles, bottom resuspension events, and microbial community dynamics. Sea-ice cycles may affect food availability in terms of water-column mixing and benthic resuspension. The scarce primary production and the high amount of sedimented material are not limiting conditions in Potter Cove, which presents a rich ascidian community.

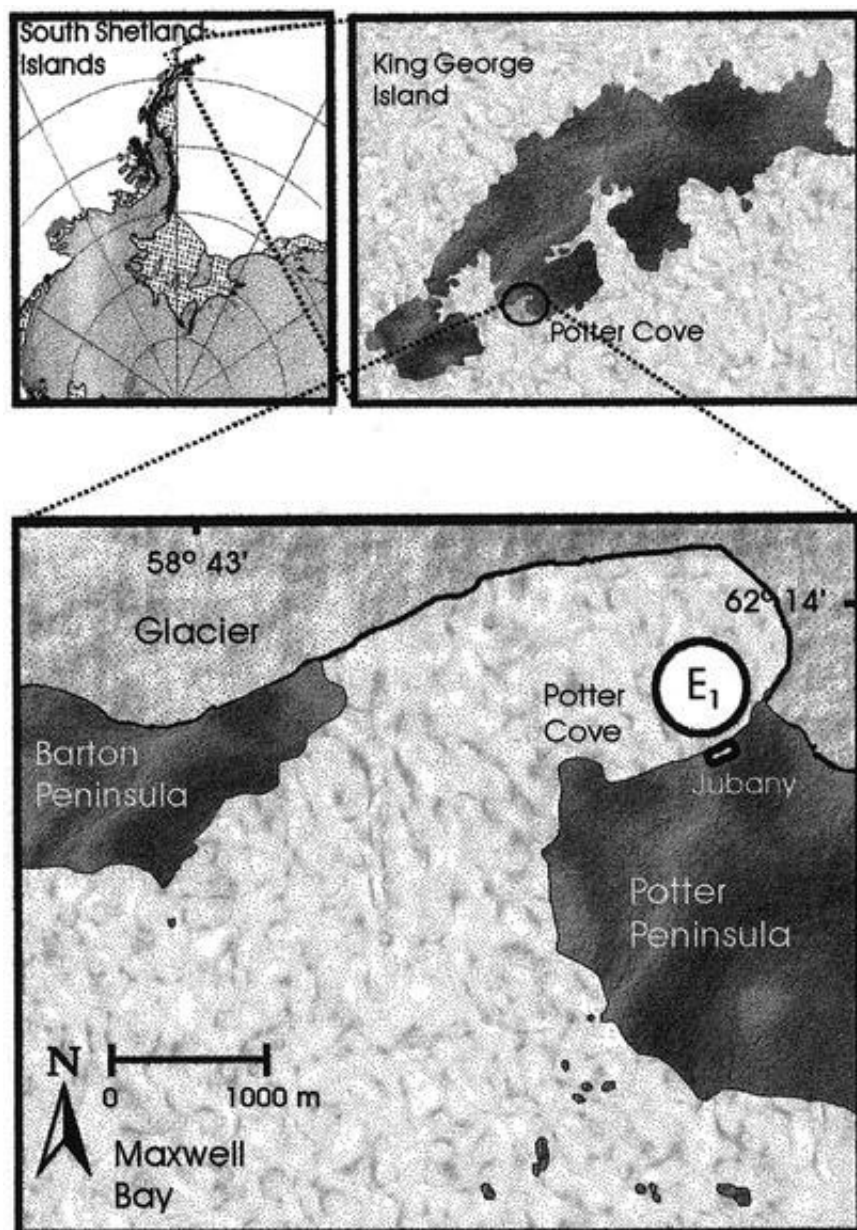
# Introduction

Ascidians are a well-represented benthic group in coastal marine ecosystems. This fauna, which feeds mainly on phytoplankton (Goddard and Hoggett 1982; Seiderer and Newell 1988), can have a significant control of phytoplankton biomass (Riisgård et al. 1995), coupling the pelagic and benthic systems (Gili and Coma 1998; Ribes et al. 1998). Benthic biomass is usually related to productivity in the water column, mainly in Antarctica, where primary production is limited to spring and summer. Also, microalgal growth in Antarctic coastal ecosystems is influenced by other factors that affect light penetration, such as pack-ice formation and sedimentation (Arntz et al. 1994). Low food availability in winter seems to be an important factor which determines non-feeding periods in some benthic suspension feeders (Barnes and Clarke 1995). The summer bloom is composed of a pulse of large diatoms and colonial forms superimposed on a less intense but longer nanoflagellate bloom, whereby suspension-feeding organisms adapted to feed on smaller cells at lower concentrations can experience a much longer annual feeding period than those feeding on larger cells (Clarke and Leakey 1996). Likewise, there is evidence of viable algal material in sediments throughout the period of darkness (Berkman et al. 1986) which rapidly increases in biomass following the influx of light in spring (Gilbert 1991).

Potter Cove, at King George Island, is characterized during summer time by an enormous amount of glacial melt water, which transports terrestrial sediments (Klöser et al. 1994). Although levels of primary production are several times lower than in adjacent areas (Schloss et al. 1998), benthic fauna is abundant. Ascidians are the dominant organisms below 20 m; *Cnemidocarpa verrucosa* is one of the most abundant species, with densities up to 2 ind./m<sup>2</sup> (Sahade et al. 1998a). In order to define the nutrition source necessary to support this biomass, mainly in winter, we studied the food availability and composition, photosynthetic pigments and organic material in water samples and benthic sediments. Gut-content composition and food absorption by ascidians, during a year-round period, were also analyzed.

## Materials and methods

This study was carried out in Potter Cove (Jubany station/Dallmann laboratory), King George, South Shetland Islands, Antarctica (62°14' S-58°38' W). Sampling was performed in an area characterized by soft bottoms (E1) (Fig. 1).



**Fig. 1.** Map of Potter Cove. Sampling area (*E1*) is indicated

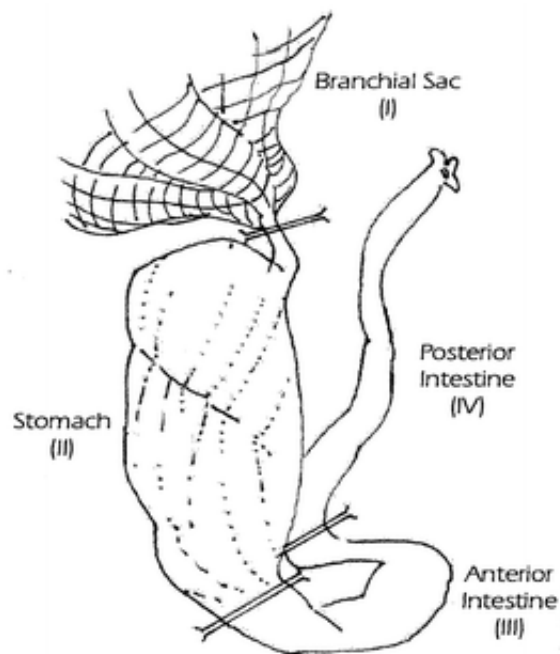
Water samples from 30 m depth were taken by a 4.7-l Niskin bottle at a frequency ranging between 1 and 3 times per month, depending on weather conditions. To avoid contact and resuspension, samples were collected 2 m above the bottom. Different volumes of water were filtered through GF/F filters and the photosynthetic pigment chlorophyll *a* (Chl *a*) was extracted using acetone, and its concentration analyzed according to Strickland and Parsons (1972). Suspended particulate matter (SPM), particulate organic matter (POM), and particulate inorganic matter (PIM) were measured gravimetrically, filtering additional water samples through precombusted and preweighted GF/F filters. POM was calculated after combustion of filters (5 h at 450°C).

Sediment samples were taken monthly at 30 m depth (3 replicates) by corers made with plastic tubes (3.7 cm diameter). In the 1-cm top layer, Chl *a* concentration was calculated according to the Strickland and Parsons (1972) equation modified to a  $\text{m}^2$  basis. Organic matter (OM) was calculated after combustion (5 h at 500°C), and is quantified as  $\text{g/m}^2$ . Data from the water column and sediments were analyzed seasonally (Table 1), due to the lack of data in some months.

**Table 1.** Seasonal data group of water column, benthic sediments and gut-content samples (+ data collected)

		Water column	Benthic sediments	Gut contents
Summer 1996	January	+		+
	February	+		+
	March	+		
Autumn 1996	April	+		
	May	+		
	June	+	+	+
Winter 1996	July	+		
	August	+	+	+
	September	+		
Spring 1996	October	+		
	November	+		+
	December	+	+	+
Summer 1997	January	+	+	+
	February	+	+	+
	March	+	+	+

In order to evaluate the seasonal variations of seston intake and absorption by ascidians in natural conditions, 5 specimens (9-11 cm height) of *C. verrucosa* were collected monthly by scuba diving at 30 m depth. Determinations were done at the level of four different gut sections: branchial sac (I), stomach (II), anterior intestine (III), and posterior intestine (IV). The limit between III and IV sections was arbitrarily defined in the middle of the second intestinal loop (Fig. 2). The gut contents were extracted, homogenized, and lyophilized prior to analysis. Contents of the five specimens were pooled owing to the low dry weight obtained for each, and grouped seasonally (Table 1). The organic matter was determined by combustion (5 h at 500°C). Total lipids were obtained gravimetrically, after 2:1 chloroform-methanol extraction (Folch et al. 1957), and total proteins by the Lowry modified method (Peterson 1977). The remaining organic material was considered to be carbohydrates. Absorption of organic matter was calculated using the ratio of Conover (1966), which assumes that an animal can digest and absorb the organic component of the food, but not the inorganic fraction. This procedure is convenient for determining the absorption efficiency when the food source is natural seston, but variance is greater when the inorganic content of the food is low, as in cultured algae (Navarro and Thompson 1994). Although the original technique of Conover requires determination of the fraction of organic matter in food (seston) and faeces, we did it in material taken from the proximal (I) and distal (IV) end of the gut, according to Fisher (1977).



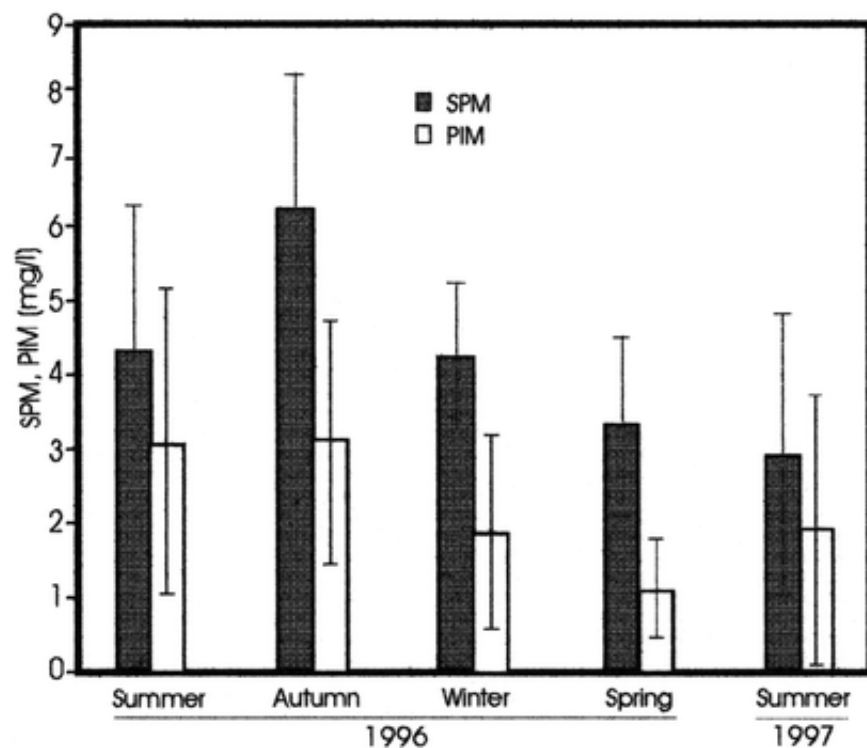
**Fig. 2.** *Cnemidocarpa verrucosa*. Gut sections analyzed

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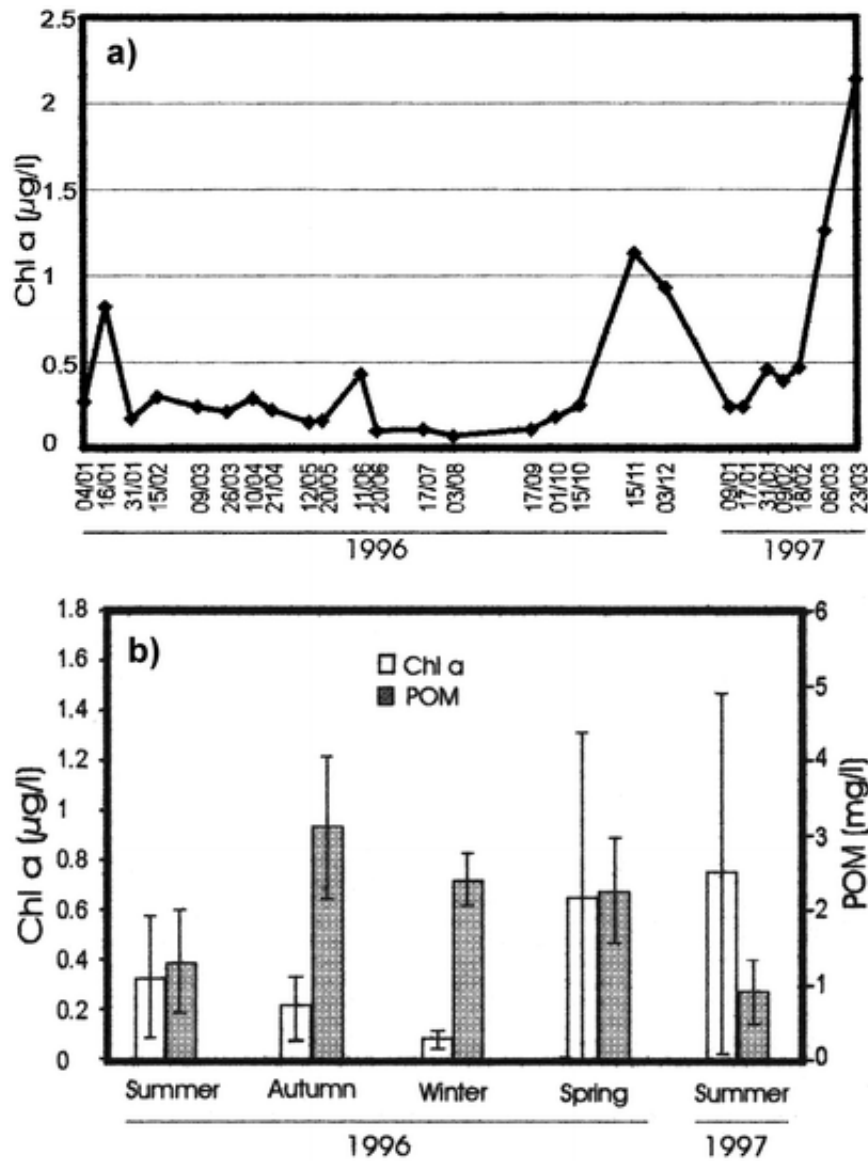
## Results

### Water column and benthic sediments

While SPM and PIM did not show a seasonal pattern (Fig. 3), a high seasonality was detected in water column microalgal standing stock (Fig. 4A). Chlorophyll *a* showed the highest concentration during summer 1997, while the lowest was measured during winter. Levels of Chl *a* also varied greatly in all seasons, with the exception of winter, when values were below 0.2 µg/l. Some interannual differences were detected also, since pigment concentration was lower in summer 1996 than in summer 1997. Surprisingly, POM showed higher values from autumn to spring than in summer periods, and was not related to Chl *a* (linear regression analysis,  $r^2=7.2$ ,  $n=25$ ,  $P=0.19$ ) (Fig. 4B). During winter 1996, the pack ice was not consolidated, allowing the effect of wind on water column, which produces turbulence and bottom resuspension. In this sense, a significant relation was detected between SPM at 30 m and mean wind strength during ice-free months (linear regression analysis,  $r^2=34$ ,  $n=13$ ,  $P=0.004$ ).

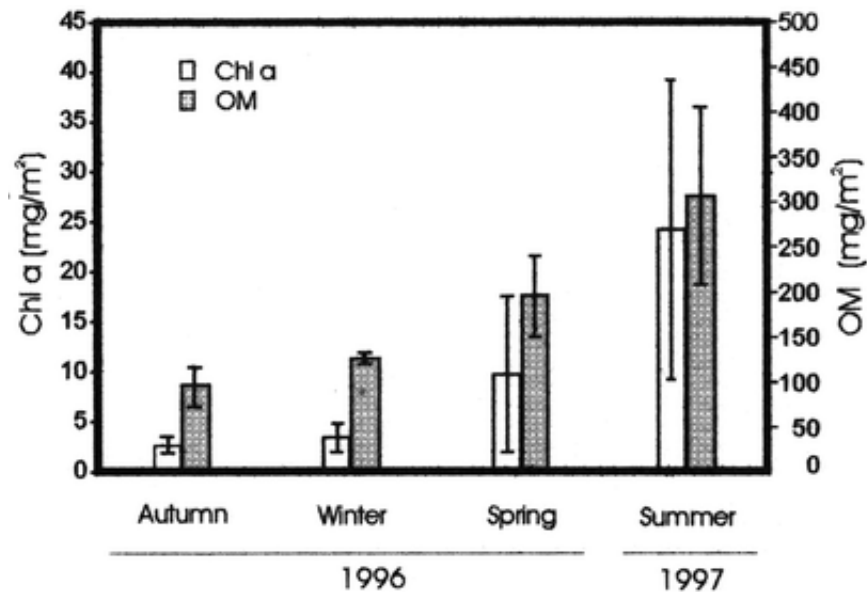


**Fig. 3.** Seasonal variation of suspended particulate matter (*SPM*, grey bars) and particulate inorganic matter (*PIM*, white bars) in water column, 30 m. Values are means $\pm$ SD



**Fig. 4. A** Annual cycle (individual data) of chlorophyll a (*Chl a*) in water column, 30 m. **B** Seasonal variation of chlorophyll a (*Chl a*, white bars) and particulate organic matter (*POM*, light grey bars) in water column, 30 m. Values are means±SD

Clear increases of OM and pigment concentration were detected in sediment samples, both being strongly seasonal, with the highest values in summer (Fig. 5). The OM was related to *Chl a* concentration (linear regression analysis,  $r^2=34$ ,  $n=19$ ,  $P=0.008$ ).



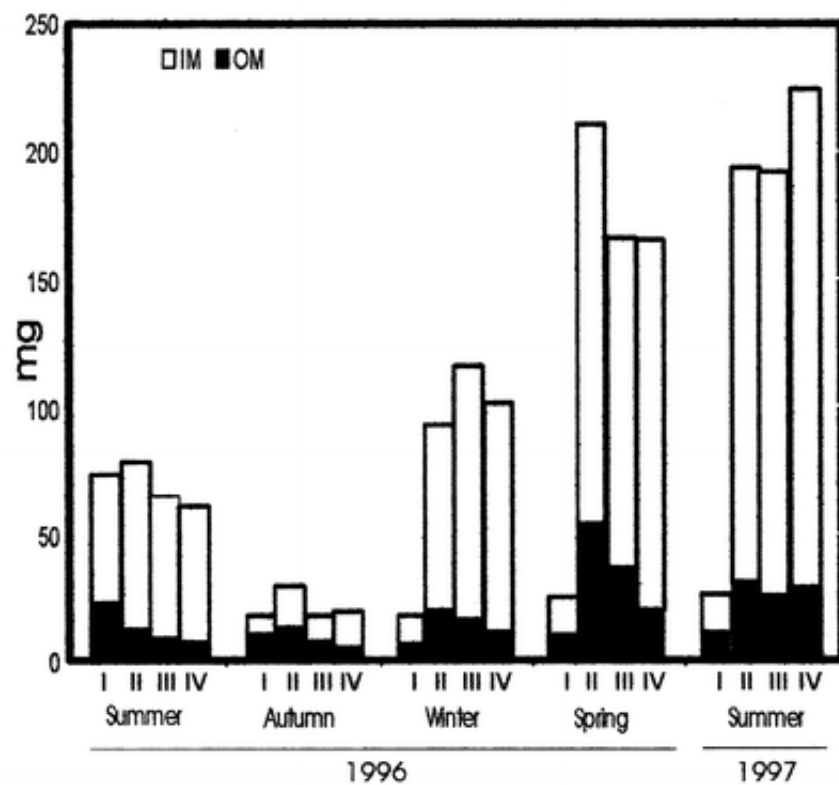
**Fig. 5.** Seasonal variation of chlorophyll *a* (*Chl a*, white bars) and organic matter (*OM*, light grey bars) in sediments, 30 m. Values are means $\pm$ SD

## Gut contents

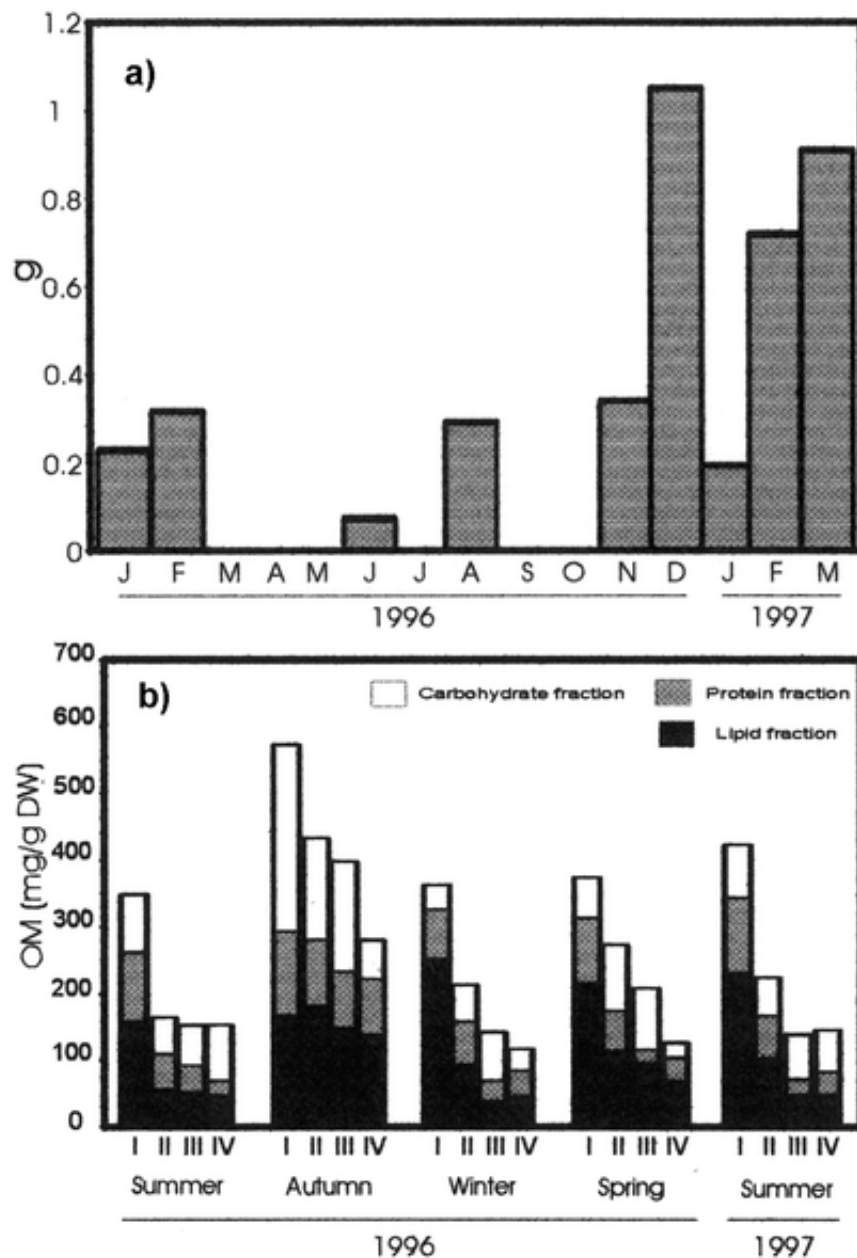
Our results showed, year-round, a clear gradient of organic material, from the input (I, II) to the output (IV) of the gut (Fig. 6). Net absorption of OM was above 70% (mean=73.2%,  $\pm$ 12.5 SD). When data were grouped in different seasons (summer 1996, autumn 1996, winter 1996, spring 1996, and summer 1997), absorption did not vary significantly ( $\chi^2=2.38$ ,  $P<0.66$ ). The OM% between I and II

presented a sharp fall (nearly 40%), while the decrease of OM% after section II was slight, leveling on comparable values in sections III and IV (24% from II to III; 17% from III to IV). This suggests low absorption efficiency throughout the intestine, and that almost all the material is absorbed between sections I and III. The absorption of OM was not related to the inorganic material (IM) present in the input (linear regression analysis:  $r^2=5.4$ ,  $n=9$ ,  $P<0.54$ ). A high OM% was measured in gut contents in autumn, while OM% reached similar values in summer, winter, and spring. Nevertheless, the guts in autumn (June) were nearly empty (Fig. 7A).





**Fig. 6.** Seasonal variation in *IM* (white bars) and *OM* (black bars) in the four ascidian gut sections: branchial sac (*I*), stomach (*II*), anterior intestine (*III*), posterior intestine (*IV*)



**Fig. 7. A** *Cnemidocarpa verrucosa*: total dry weight of gut contents (monthly means, g/specimen). **B** *C. verrucosa*: seasonal variation of organic matter and its lipid (black bars), protein (grey bars), and carbohydrate (white bars) fractions in the four gut sections. Branchial sac (I), stomach (II), anterior intestine (III), posterior intestine (IV)

Chemical composition determination of the OM revealed that the lipid fraction was the main component in the input section, with values higher than 150 mg/gDW during the study period. A decrease of lipids was registered throughout the different sections, but in autumn this decrease was lower than in the other seasons. The analysis of proteins also showed a clear decrease through the four gut sections during the study period (Fig. 7B), while carbohydrates did not fall.

## Discussion

Standing stock showed low values, similar to other Antarctic oligotrophic areas, such as New Harbor West Sound, McMurdo Sound. However, this latter area supports a poor benthic fauna, in terms of biomass and diversity, due to the scarce food availability related to a low primary production (Dayton et al. 1986). In Potter Cove there is a very different situation, since a rich macrofaunal community is present despite the low primary production (Sahade et al. 1998a, b). These considerations indicate that primary production, benthic and pelagic, is not enough to support the benthic faunal communities in Potter Cove.

Standing stock was strongly seasonal as expected: Chl *a* in the water column started to increase in spring, reaching maximum values in summer. This is coincident with the pelagic primary production pattern described for Potter Cove, where two favourable periods were detected for phytoplankton production: one of them starts when the pack ice breaks and glacier melting begins (during spring), and the other one is at the end of summer when melting decreases (Schloss et al. 1998). Despite these favourable periods, a phytoplankton bloom was never detected in Potter Cove, the levels of Chl *a* being lower than in other Antarctic coastal areas.

In Potter Cove, the main source of melt water is Potter Creek, which alone discharged up to 60 kg/s of sediments (Varela 1998). This material reduces light penetration in the water column, affecting photosynthetic activity. The reason for the low primary production during spring/summer is not only light limitation but also the low stability of the water column due to the high frequency of strong winds, which carry algal cells deeper than the critical depth which, in turn, is located at a very shallow depth due to the high load of inorganic material (Schloss et al. 1998). The variation of these conditions may generate the interannual differences found. For example, summer 1996 exhibited much lower levels of Chl *a* than spring 1996/summer 1997. Despite the high turbidity and low stability of the water column, summer conditions are better than winter, allowing more photosynthetic activity.

Winds also determine downwelling and upwelling systems in the inner sector of the cove (Roese and Drabble 1998). This vertical circulation produces vertical mixing and transport of phytoplankton and POM to the bottom. The wind is also important in inducing bottom resuspension, an important phenomenon in near-shore environments surrounding Antarctica, specially during the austral winter (Berkman et al. 1986). The presence of sea ice (which buffers the wind action) affects the magnitude of this resuspension. High interannual differences could be expected, since extension and duration of the sea ice varies greatly. The absence of pack ice (which is usually present in late autumn and winter) during 1996 could explain the high levels of SPM and POM registered during autumn/winter in the water column near the bottom. In a similar period, in Potter Cove, Kowalke (1999) found a seasonal pattern of SPM, with higher amounts of PIM and POM in summer than in winter at 30 m. The period was February 1995/January 1996, when the pack ice was consolidated and lasted until October, preventing water mixture and benthic resuspension.

Benthic microalgal standing stock in Potter Cove was also seasonal with a peak in summer, and the same trend occurred with the benthic OM, although its variations were not completely determined by Chl *a* values. Similarly, in Marian Cove, an area close to Potter Cove, Ahn (1993) found that water column production was not high enough to support the rich bivalve biomass found there. She speculated on the importance of benthic primary production (not measured in her work) and the advection of allochthonous particles as important processes providing organic material to benthic organisms in Antarctic coastal waters.

If the advection of allochthonous material is an important process that provides energy, currents are important, since they allow the transport of this material into the cove. The most frequent west-east winds determine the main current system in Potter Cove, together with the water renewal, which allows the horizontal advection of allochthonous particles into the cove.

Ascidians absorbed organic matter year-round. The lack of seasonal differences in the absorption of organic matter, even during winter, suggests the non-interruption of digestive functions. The highest absorption occurred in the passage through section I to II. Other sections exhibited lower absorption; thus, the contents present in the distal part of the intestine are probably faeces. Absorption and enzyme secretion have previously been described in the first sections of the ascidian postpharyngeal digestive tract (Goddard and Hoggett 1982; Buencuerpo 1991). Data on absorption efficiencies in natural conditions are scarce and highly variable (Tito de Morais and Fiala-Médioni 1985). These differences could be related to seston concentration and/or the position in the gut from which the samples were taken, thus stressing the importance of standardizing the methods to be applied. For example, Fisher (1977) reported absorption efficiencies for *Styela plicata* of ~30% (seston concentration >6 mg/l, input and output not given), while Goddard and Hoggett (1982) measured higher values for *Pyura praeputialis* of ~78% (seston concentration not given; branchial sac as input compartment and terminal section of intestine as output), and Tito de Morais and Fiala-Médioni (1985) reported a maximum organic absorption efficiency of 95% (with 51% of OM in seston, comparing food and faeces).

Ascidians tend to be excluded from areas with high concentrations of inorganic particulate material, and flourish in clearer water, as postulated by Robbins (1985). However, this is not the case in Potter Cove, where the richest ascidian community is present in the inner cove (Sahade et al. 1998b; Tatián et al. 1998) where sedimentation and bottom resuspension processes are more intense than in the outer cove. The lack of correlation between OM absorption and IM% present in the input section of the gut, suggests that while the load of PIM may affect the absorption efficiency of *C. verrucosa* and probably other ascidian species above a clear and sharp limit, below this, absorption is not affected in a proportional way.

A clear decrease of lipids and proteins was observed through the four gut sections, while carbohydrates did not show such a clear decreasing pattern. This could indicate effective lipid and protein absorption and some difficulty in assimilating carbohydrates by *C. verrucosa*. Seiderer and Newell (1988) pointed out that some ascidians are efficient in assimilation of microalgae due to carbohydrase activity in the gut, but polysaccharides are scarcely digested due to low cellulase activity. This suggests the possible lack of specific enzymes to process some complex carbohydrates in *C. verrucosa*.

Microalgae appear to be a weak food source for ascidians, since chemical composition of gut contents did not vary according to the increase of Chl *a* concentration in the water column and sediments during spring and summer. In this sense, lipids were the main components of the organic matter present in the input section year-round, except in autumn, when a sharp increase of carbohydrates was measured. The scarce gut contents found in autumn might be diluted by internal secretions, which in turn could be predominantly carbohydrates. High levels of carbohydrates and lipids were previously found in seston composed mainly of macroalgal debris, an important food source for filter feeders in Antarctica (Albertelli et al. 1998), taking into account that its digestibility is at least as high as that of phytoplankton (Jørgensen 1996). Protein contents in section I were constant through the year; however, it should be taken into account that the gut contents were highest in spring/summer 1997. According to Ribes et al. (1998), the seasonal variation of ingested nitrogen from living particles (phytoplankton) explained 91% of the gonadal development variance for a year in the ascidian *Halocynthia papillosa*, suggesting that living particles are likely to be of more significance in the diet

of this ascidian than particles of detrital origin.

In Potter Cove, the origin of the nitrogen source is still an open question, but probably it is not living algal material. Microscopical analysis of stomach contents of *C. verrucosa* from Potter Cove (M. Tatián, unpublished data) revealed that diatoms only reached 4% of the total items present in stomach contents during a year-round period, while detritus and minute particles <5 µm (probably nanoplankton and bacteria) were the major constituents during the whole year, contributing up to 90% of the particles found. Bacteria represent a nitrogen source of comparable importance to phytoplankton, as postulated by Seiderer and Newell (1985). In Antarctica, bacterial growth does not appear to be limited by in situ substrate concentrations and temperature, since it was reported that during austral winter and spring, bacterial biomass and production can exceed those of phytoplankton (Rivkin et al. 1991) and those of bacteria in ice-free summer seawater (Delille 1993). Bacterioplankton could be important to those filter feeders that are capable of exploiting particles in the bacterial size range, even if their biomass or filtration efficiency is low. *C. verrucosa* starts filtering from 1.3 µm particle size (Kowalke 1999); bacteria (probably related to bacterial films on detritus or large particles) could be an important source of nitrogen, particularly taking into account that the reproductive period of *C. verrucosa* occurs during the austral winter (Sahade et al. 1998c), when phytoplankton production is nearly zero.

The scarce primary production (Schloss et al. 1998) and the high amount of sedimented material (Varela 1998) are not limiting conditions in Potter Cove, where a rich ascidian community has developed (Sahade et al. 1998a, b). All our results are in line with these facts and suggest that ascidians probably obtain energy and nitrogen necessary for metabolism and gonadal development from detritus and from members of the related microbial food web. The physical mechanisms that provide food to the ascidians and epibenthic communities may be related to the advection of allochthonous particles and to bottom resuspension. Sea-ice cycles may affect food availability since the pack ice interferes with wind action, and thus with water mixing and benthic resuspension.

**Acknowledgements.** We are extremely grateful to the members of Jubany Station, specially to the divers Augusto Fernández and Oscar Rillos (Prefectura Naval Argentina) for their field assistance. We would also like to thank Dr. Mariachiara Chiantore, Dr. Andrew Clarke, and an anonymous reviewer, whose valuable suggestions greatly improved the manuscript. This work was possible because of logistic support from Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Instituto Antártico Argentino, Alfred Wegener Institute (Germany), Universidad Nacional de Córdoba and Universidad Nacional de Buenos Aires, Argentina.

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