Polar Biol (2001) 24: 473–485
DOI 10.1007/s003000100257

REVIEW

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Are Antarctic suspension-feeding communities different from those elsewhere in the world?

Accepted: 19 March 2001 / Published online: 11 May 2001

Abstract This paper reviews the trophic ecology of benthic suspension feeders in Antarctic shelf communities, studied within SCAR's EASIZ Programme, in comparison with published information from other seas. Dense benthic suspension-feeder communities capture large quantities of particles and may directly regulate primary, and indirectly, secondary production in littoral food chains. Most work has been performed in temperate and tropical seas; however, little is known about suspension feeders in cold environments. Recent studies on Antarctic littoral benthic suspension feeders suggest the period of winter inactivity may last only a few weeks. This contrasts with the hypothesis that in Antarctic communities there is a prolonged period of minimal activity lasting at least 6 months during the austral winter. Results from other oceans may explain how dense benthic communities could develop under such conditions. Alternative food sources, i.e. the "fine fraction", sediment resuspension, lateral advection and efficient food assimilation may play a significant role in the development of suspension-feeder dominated, very diversified, high biomass and three-dimensionally structured communities on the Antarctic shelf.

Introduction

What are we talking about?

Primary producers, together with the products of their biological activity, generate the most abundant available food for heterotrophic organisms in the oceans: the seston. Small particles and cells predominate in such suspended communities (Wottom 1994), providing food for primary consumers and substrata for bacteria. The physical properties of seawater allow living creatures and particulate matter to remain in suspension, thereby creating a niche for a trophic strategy that does not occur on land: suspension feeding (Jørgensen 1990). Suspension feeders are common on all sea-bottom types, and are the main animal component in hard-bottom communities (Gili and Coma 1998).

Filtration rates of benthic suspension feeders are typically between 1 and 10 $m^3 m^{-2} day^{-1}$ (Riisgård et al. 1996a) and dense assemblages of benthic suspension feeders may thus have a pronounced grazing effect (Kimmerer et al. 1994; Riisgård 1998). Large parts of Antarctic benthic communities consist of sessile suspension feeders such as sponges, cnidarians, bryozoans, ascidians and certain echinoderms (Dayton et al. 1986). Fully developed epifaunal assemblages in Antarctica may not be quite as diverse as some tropical reefs, but between 10 and 1,000 m water depth benthic biomass in the Antarctic is higher than in temperate and subtropical communities (Brey and Gerdes 1997). Antarctic benthic communities are highly structured, with a complex functional diversity and a considerable degree of patchiness in species composition at small or intermediate spatial scales (Gutt and Starmans 1998).

The ecological role of suspension feeders in Antarctica is related to the trophic ecology and environmental

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This paper presents results of the Midterm Symposium of the SCAR programme "Ecology of the Antarctic Sea Ice Zone" (EASIZ). The manuscript was edited by W. Arntz and A. Clarke.

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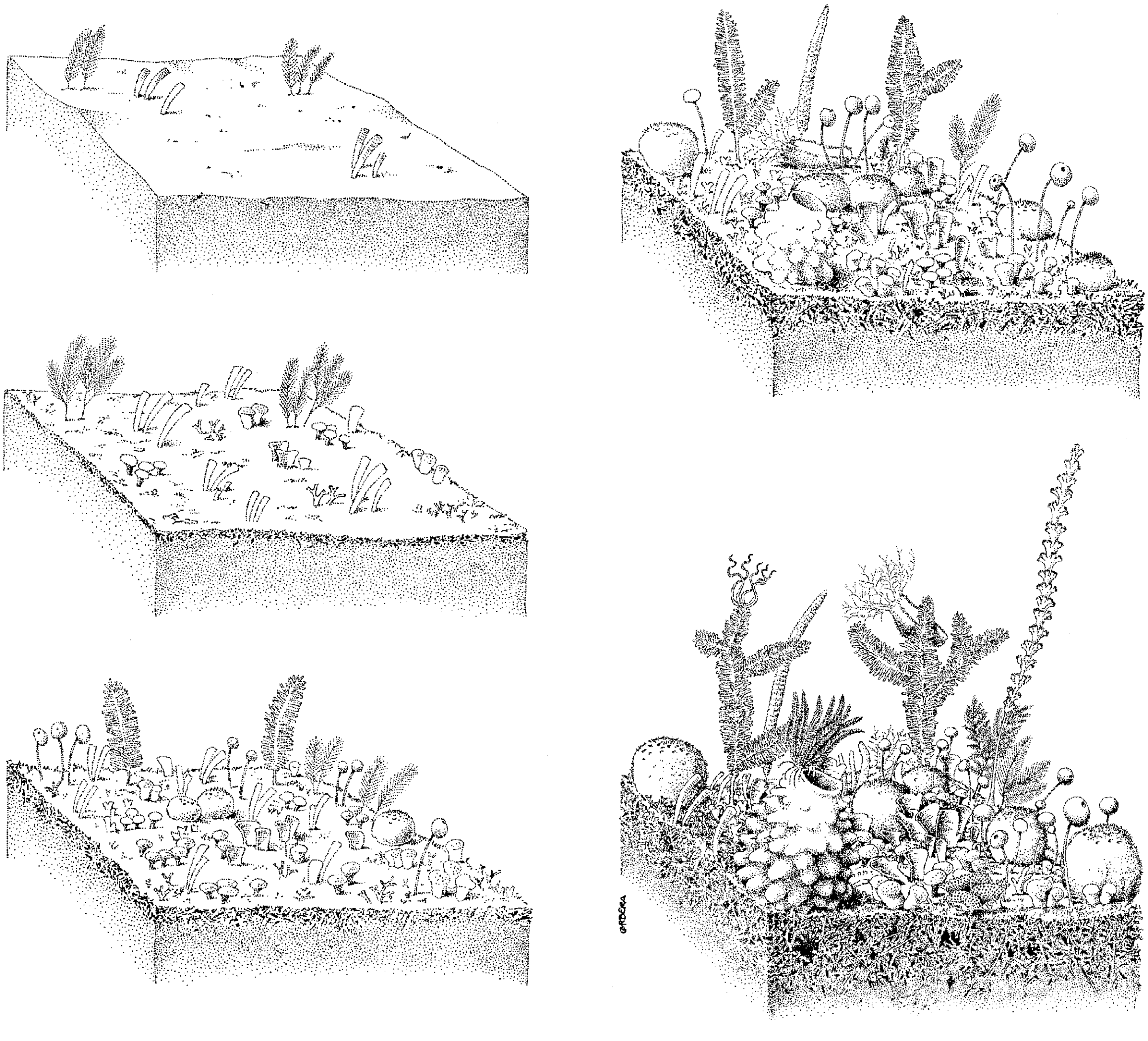
conditions that facilitate the processes of energy transfer between benthic and water-column systems. In this review we focus in particular on: (1) the trophic adaptations of suspension feeders that make them successful foragers worldwide, and (2) the processes responsible for the availability of food to suspension feeders, such as vertical transport, resuspension and lateral advection.

Exploitation of food resources: suspension feeding as an ecologically efficient strategy

Life in patches: a food capture strategy at individual, colony, population and community level

Suspension-feeding colonies or individuals interfere with current flow and they have evolved a multitude of adaptations designed to attract and trap particles in suspension (Gili and Coma 1998). Downstream of those structures that are exposed to the flow, such as the axis of a pennatulacean, viscosity increases and turbulence also increases slightly, generating small eddies (Vogel 1994). This hydrodynamic effect may help not only to increase the residence time of particles on the downstream side of the colony in times of heavy flow, but also to enhance settling of particles in the area adjacent to such structures. This phenomenon is of great importance when different species of suspension feeders aggregate in the same community (Fig. 1).

Fig. 1 Idealized diagram of Antarctic shelf suspension-feeder communities considering the patch theory explained in the text. The development of dense, three-dimensional communities involves a continuous process of patch spreading and aggregation during slow succession



Pliancy of colonies is one of the most widespread adaptations employed to meet the conflicting demands of minimum drag and maximum flux of capturable particles through the feeding structures (Harvell and LaBarbera 1985). As an adaptation to slow flow rates, the colonies of certain species of ascidians and bryozoans have evolved systems for circulating water through their feeding structures and refreshing the colony boundary layer (Vogel 1994). Such conditions are not a problem in active suspension feeders or in filter feeders that pump water through an internal exchange circuit (such as sponges, ascidians, etc.), which is more efficient at moderate flow rates (Shimeta and Jumars 1991) though considerably less efficient at higher flow rates (Wildish and Miyares 1990).

The formation of monospecific patches not only lowers competition (Best and Thorpe 1986) but also improves capture rates among the colonies of the species concerned. Experiments on alcyonarians (MacFadden 1986), actinians and corals (Sebens et al. 1996) have shown that particle capture rates vary among colonies of different size within the population. This, in turn, gives rise to a spatial pattern determined by the optimum distance between colonies or individuals (Eckman and Duggins 1993). Larger colonies have been observed to be more efficient at lower rates of flow, and vice versa. Maximum and mean colony size in each patch are determined by the total food concentration and the intensity of water movement (Anthony 1997). The effect in dense aggregations of barnacles is similar (Pullen and LaBarbera 1991), with larger, asymmetrically shaped aggregates oriented towards the prevailing currents and smaller, more evenly shaped aggregates where current flow is bidirectional. Large assemblages of suspension feeders can deplete food sources under low flow conditions (Best and Thorpe 1986). However, because fast flow is the prevailing condition, enhancement of feeding among neighbours is the more significant interaction (Okamura 1990).

Benthic suspension feeders as optimal foragers

Recent studies of natural feeding show that suspension feeders can feed on a broad spectrum of prey items, which range from bacteria to zooplankton and detrital particulate organic matter (POM). Some taxa exhibit an important diet variability among species (Sorokin 1991), whereas the diet appears to be rather homogeneous in other taxa (Gili et al. 1998). The diet spectrum within most species is rather broad. Examples are octocorals (Fabricius et al. 1995; Ribes et al. 1999a), sponges (Ribes et al. 1999b), ascidians (Klumpp 1984; Ribes et al. 1998) and hydrozoans (Gili et al. 1998). Even species that feed mainly on zooplankton may prefer different prey types and sizes (Sebens and Koehl 1984) (Fig. 2). Certain suspension feeders may change their diet when different food becomes available (e.g. tropical crinoids, Rutman and Fishelson 1969; polar octocorals, Slattery et al. 1997; temperate sponges and ascidians, Ribes et al. 1998, 1999b). Thus, much of the diet variability among species of the same taxa may be due to differences in availability of resources in their environment. Few studies, however, have accounted for seasonal differences in feeding.

The exceptional ecological success of benthic suspension feeders appears to be due to two main features of prey capture mechanisms. First, there is the low cost of prey capture, which is almost nil in passive suspension feeders, while it is below 5% in active ones (Larsen and Riisgård 1996). Second, there is the heterogeneity of their diet, mainly restricted by morphological constraints (Okamura 1990), which agrees with the hypothesis that prey selection cannot be a common phenomenon in organisms that depend on flow to bring resources to their capture structures (Hughes 1980). This trophic plasticity may represent an advantage because it might attenuate the effects of seasonal environmental fluctuations in availability of different resources in the water column.

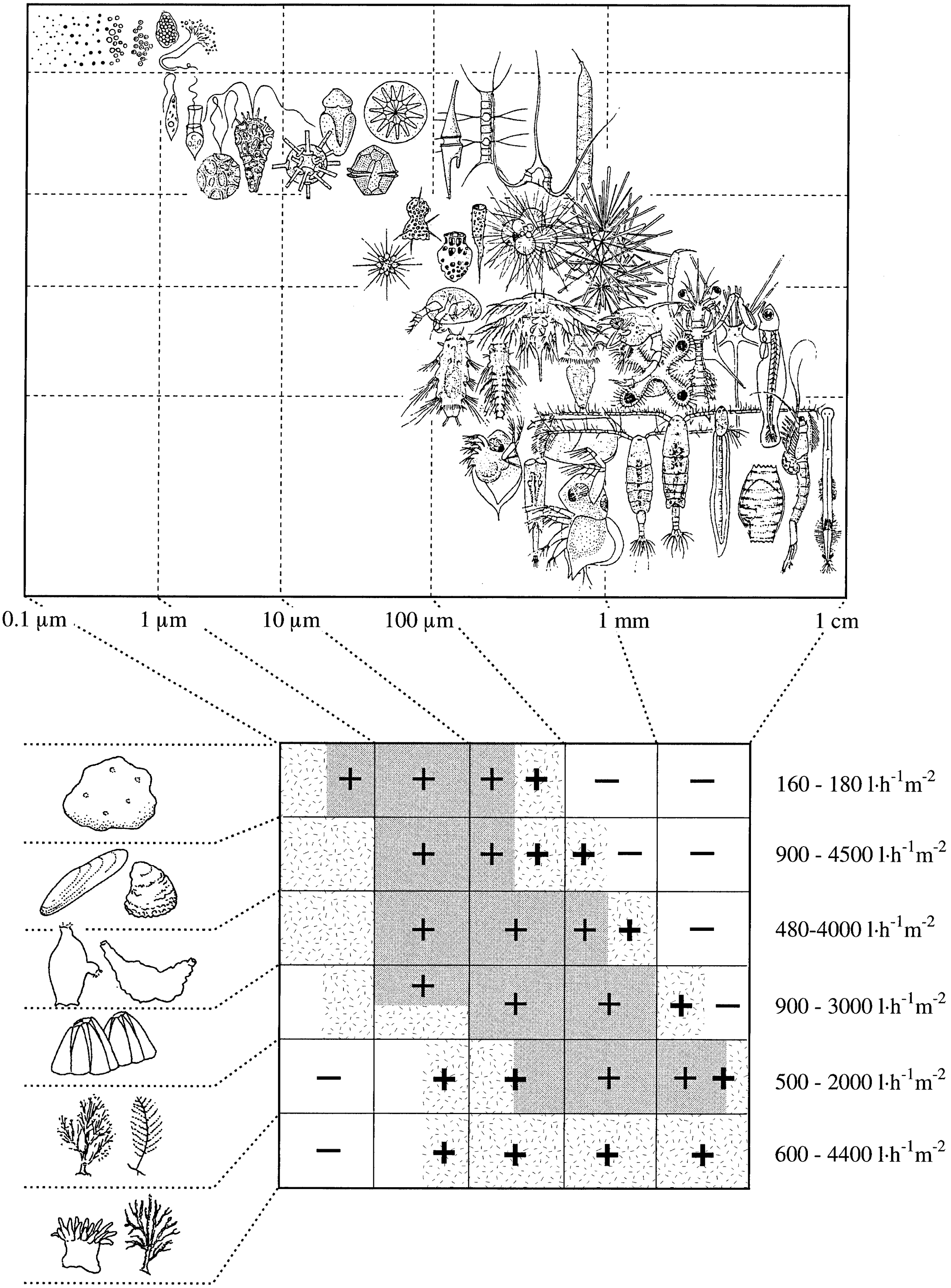
Seston ergo particles: the role of the fine fraction

The major part of marine primary production is not consumed by herbivores (Fenchel 1988) but is mainly transferred to the detrital and microbial food web (Azam et al. 1983), the latter dominating pelagic plankton communities in terms of biomass (Wottom 1994) and production (Burkill et al. 1993). The small particles and cells, which dominate water-column communities, provide surface area for bacterial colonization (Fenchel and Jørgensen 1977), which increases their quality as a feeding resource and favours their utilization (Mann 1988).

Sessile predators must be adapted to capture the most abundant food items, i.e. detrital POC and live carbon in the forms of pico- and nanoplankton. Uptake of Dissolved Organic Matter (DOM) has been reported and discussed for a wide range of invertebrates (Stephens 1982; Frost 1987), but it is generally felt that DOM represents a small source of dietary requirements for marine invertebrates (Valiela 1995).

Live carbon is assimilated to a greater degree than detrital POC but the type of live carbon will affect its assimilation by suspension feeders (Wottom 1994). Plant particles colonized by microorganisms provide a better food value (Mann 1988), besides containing a high concentration of nitrogen. Feeding rates depend on the food quality and quantity; when both are high, lower gut retention time is required to extract nutritive products, and the opposite applies especially when the quality of food is poor (Taghon 1981). Another factor that could modify feeding rates is temperature, but animals that are adapted to very cold temperatures do not show a positive relationship with temperature increase (Anderson and Dyrssen 1989).

Filter feeders can modify the seston composition by several mechanisms: sponges may break up aggregates into small particles and/or introduce other particles and substances generated by their feeding activity into the system (e.g. Witte et al. 1997); other organisms such as gorgonians decrease the velocity of the particle so they become available to other organisms. Many species aggregate small particles in the form of faecal pellets, which are an important food source for deposit feeders (e.g. Amouroux et al. 1990) or for near-bottom microbial production. The bivalve *Laternula elliptica* plays an important role in enhancing particle flux from the water column to the sea bed through biodeposition and may



+	+	+ +	−	−	160 - 180 l·h^{-1}m^{-2}
	+	+ +	+ −	−	900 - 4500 l·h^{-1}m^{-2}
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	+	+	+	+ −	900 - 3000 l·h^{-1}m^{-2}
−	+	+	+	+ +	500 - 2000 l·h^{-1}m^{-2}
−	+	+	+	+	600 - 4400 l·h^{-1}m^{-2}

◄

Fig. 2 Prey type and prey size in different suspension-feeder groups, modified after Riedl (1966), considering the recent findings on suspension feeders' natural diet, which increased the range of quality and quantity of prey both at small size (pico- and nanoplankton, continuous prey) and at large size (zooplankton and microplankton, occasional prey). *Shaded areas* and *black crosses* refer to information that has been added to Riedl's original figure. Potential for filtering water (*right side*) of each group is also shown

thus provide food for other benthic fauna, particularly in phytoplankton-impoverished near-shore waters (Ahn 1993).

Many benthic invertebrates have the capacity to feed on the fine fraction (i.e., pico-, nano-, microplankton and detrital POM) of the water column (Jørgensen et al. 1984). Studies on temperate bivalves (Fréchette et al. 1989; Riisgård 1998), tropical and temperate sponges (Pile et al. 1996) and on temperate and tropical octocorals (Ribes et al. 1999a) have shown, or suggest, a high grazing impact of benthic suspension feeders on near-bottom plankton. A recent study on the Antarctic hydroid *Oswaldella antarctica* shows a diet based on the fine fraction of seston and small zooplankton organisms (Orejas et al., in press). The importance of the fine fraction in the diet of Antarctic suspension feeders is also demonstrated by the hydroid *Silicularia rosea* off King George Island (Gili et al. 1996), other species of sponges (Gaino et al. 1994) and brittle stars (Kellogg et al. 1982), which mainly ingest benthic diatoms and probably other detritus.

The activity of benthic suspension feeders also influences the nutrient concentration near the sea floor. High values of organic nutrients compared with their concentration in the water column are evidence for the role of benthic communities in organic matter remineralization (e.g. Davoult et al. 1990; Orejas et al. 2000).

The importance of large prey: zooplankton as an example

Capture of zooplankton prey items by benthic passive suspension feeders such as hydrozoan and anthozoan species has been demonstrated in many temperate and tropical regions (Sebens et al. 1996; Gili et al. 1998). Its contribution to the requirements of benthic suspension feeders is still a little-studied subject. Recent studies indicate the trophic significance of zooplankton in coral reef metabolism (Sorokin 1995), contributing significantly to the carbon and nutrient budget of some coral species (Dubinsky and Jokiel 1994).

Studies on the diet and feeding rate of reportedly macrophagous (mainly zooplanktivorous) suspension feeders (e.g. the hydrozoan *Campanularia everta* and the gorgonian *Paramuricea clavata*, Coma et al. 1998) have revealed that (1) the amount of zooplanktonic prey items captured could not cover the energy demand of the species, and (2) in terms of ingestion, detrital POM contributed about 50% to the diet. Mixed diets with frequent or occasional zooplankton prey capture are needed to satisfy energy needs of temperate benthic suspension feeders (Coma et al. 1995).

In the Antarctic, many zooplankton species undertake extended vertical migrations (i.e. more than 400 m), with salps, copepods or krill approaching the shelf bottom almost daily (Shulenberger et al. 1984). Moreover, several zooplankton species migrate to deep waters during austral winter to hibernate (Smith and Schnack-Schiel 1990). Recent gastrovascular cavity content analysis of Weddell Sea shelf benthic suspension feeders, such as the hydroid *Tubularia ralphii* and the anthozoans *Clavularia* cf *frankliniana* and *Anthomastus bathyproctus* (Orejas et al., in press), demonstrated significant feeding on zooplankton.

Ecological impact of suspension feeders in coastal and shelf ecosystems: the grazing impact

Benthic filter-feeding populations can have a pronounced grazing impact on the plankton in littoral systems (Kimmerer et al. 1994; Gili and Coma 1998). Without externally generated currents and mixing, however, only a thin layer of near-bottom water will be subject to "biomixing" by the action of inhalant and exhalant currents generated by the filter-feeders themselves. A number of models on the effects of filter feeders on phytoplankton concentration gradients (Nowell and Jumars 1994; Larsen and Riisgård 1996) and empirical evidence (Fréchette et al. 1989; Riisgård et al. 1996b) indicate that usually turbulence and resuspension generated by currents are the primary mixing forces, whereas biological mixing may be dominant under low current conditions.

The distinct trophic plasticity of benthic suspension feeders indicates that in littoral ecosystems their predatory impact should be higher than food selection theories previously assumed. The grazing impact of several species is summarized and compared with data on two Antarctic mollusc species, the bivalves *Adamussium colbecki* (Chiantore et al. 1998) and *L. elliptica* (Ahn 1993). According to Table 1, grazing impact of Antarctic species seems to be of the same order of magnitude as in temperate and tropical seas. Recent observations on littoral ascidians (Kowalke 1999), however, indicate filtration rates 1 order of magnitude less than those of non-Antarctic species.

Seasonality and physiological adaptations of benthic suspension feeders: a time-scale approach

The activity of benthic suspension feeders in temperate and polar seas is strongly seasonal, in contrast to most tropical environments (Harrison and Wallace 1990).

Table 1 Examples of predation impact of different benthic suspension-feeder groups on plankton communities from different ecosystems, which examined the effect of particular species (*Pot. food* potential food; *Cap. food* food captured, *GBR* Great Barrier Reef, Australia) (References: *1* Reiswig 1971; *2* Cloern 1982; *3* Jørgensen 1990; *4* Ahn 1993; *5* Kimmerer et al. 1994; *6* Coma et al. 1994; *7* Coma et al. 1995; *8* Riisgård and Larsen 1995; *9* Pile et al. 1996; *10* Gili et al. 1998; *11* Ribes et al. 1998; *12* Amouroux et al. 1990; *13* Chiantore et al. 1998; *14* Buss and Jackson 1981; *15* Linley and Koop 1986; *16* Yahel et al. 1998; *17* Ribes et al. 1999a)

Site	Level	Ecosystem	Species	Abundance	Current	Pot. Food	Cap. Food	Impact	References
Discovery Bay (Jamaica)	Species	Tropical	Sponges	5–210 cm^{-3} m^{-2}	–	Bacteria, unarmored cells, armored cells, detritus, URPOC	Bacteria, unarmored cells, armored cells, detritus, URPOC	80–1800 mg C m^{-2} day^{-1}	1
San Francisco Bay (USA)	Species	Temperate, estuarine	Bivalves	170–2700 ind. m^{-2}	–	Phytoplankton	Phytoplankton	Daily filtration of 1.2–1.8 times the South Bay volume	2
Different areas	Species	–	Bivalves	–	–	Phytoplankton	Phytoplankton	> 100 m^{-3} m^{-2} day^{-1}	3
Maxwell Bay (Antarctica)	Species	Antarctic	Bivalves	36–76 ind. m^{-2}	–	Seston, Chlorophyll a	Seston, Chlorophyll a	Biodeposition of 95 mg C m^{-2} day^{-1}	4
SanFrancisco Bay (USA)	Species	Temperate	Bivalves	3500 ind. m^{-2}	–	Chorophyll, nauplii	Chorophyll, nauplii	Chorophyll: 62% daily depletion, nauplii: 8.5% daily depletion	5
Medes Islands (NW Mediterranean)	Species	Temperate	Gorgonian	32 col. m^{-2}	–	Zooplankton	Zooplankton	12.2–85.2 mg C m^{-2} day^{-1}	6
Medes Islands (NW Mediterranean)	Species	Temperate	Hydroid	21235 polyps m^{-2}	–	Zooplankton, detrital POC	Zooplankton, detrital POC	Zooplankton: 2.2 mg C m^{-2} day^{-1}; detrital POC: 1.9 mg C m^{-2} day^{-1}	7
Kertinge Nor (Denmark)	Species	Temperate, estuarine	Ascidian	20–277 ind. m^{-2}	–	Phytoplankton	Phytoplankton	Daily filtration of 0.2–1.2 times the Kertinge Nor volume	8
Gulf of Maine (USA)	Species	Temperate	Sponge	8.9% of surface, 7.6 oscula m^{-2}	–	Picoplankton, aut. eucaryotes	Picoplankton, aut. eucaryotes	29 mg C m^{-2} day^{-1}	9
Different areas	Species	Temperate, tropical, Antarctic	Hydroids	–	–	Zooplankton, detrital POC	Zooplankton, detrital POC	6–225 mg C m^{-2} day^{-1}	10
San Blas (Panamá)	Species	Tropical	Gorgonian	0.45 col. m^{-2}	1.2 cm s^{-1}	Picoplankton, microplankton, zooplankton	Microplankton, zooplankton	Microplankton: 10% daily depletion; zooplankton: 0.09–0.23 prey polyp day^{-1}	11
Banyuls-sur-mer (France)	Species	Temperate	Polychaete	Up to 3000 ind. m^{-2}	–	Picoucariotes, cyanophytes	Picoucariotes, cyanophytes	0.001–0.06 µg C ind.$^{-1}$ h^{-1}	12
Terranova Bay (Antarctica)	Species	Antarctic	Bivalve	50–60 ind. m^{-2}	–	POC, DOC, chlorophyll a	POC, DOC, chlorophyll a	Biodeposition of 21 mg C m^{-2} day^{-1}	13
Discovery Bay (Jamaica)	Community	Tropical	Bryozoans	6.2% bryozoans, 74.2% sponges	–	Bacteria, naked cells	Bacteria, naked cells	Bacteria: 89.2% depletion, naked cells: 79.4% depletion	14
One tree Island (GBR)	Community	Tropical	Reef	–	0–20 cm s^{-1}	Bacteria	Bacteria	Bacteria: 37.3%	15

Gulf of Aqaba (Red Sea)	Community	Tropical	Reef	40% live cover	–	Ultraphytoplankton, phytoplankton	Ultraphytoplankton, phytoplankton	Chorophyll a: 15–65% depletion	16
Medes Islands (NW Mediterranean)	Species	Temperate	Gorgonian	32 col. m^{-2}	1.2 cm s^{-1}	DOC, detrital POC, picoplankton, nanoplankton, microplankton	Detrital POC, nanoplankton, microplankton	Detrital POC: 2–10% daily depletion, nanoeucaryotes: 1–9% daily depl., dinoflagellates: 1–26% daily depl., diatoms: 1–22% daily depl., ciliates: 2–99% daily depl.	17

Similar seasonal activity patterns, e.g. feeding-related polyp expansion in anthozoans (Robbins and Shick 1980), have been observed in temperate (Coma et al. 2000) and cold-water (Barnes and Clarke 1995) suspension-feeder populations.

Seasonality in activity is either coupled to water temperature (Giese and Pearse 1974) or to trophic constraints (Clarke 1980). There is little direct experimental evidence for temperature control, however there is increasing evidence for trophic control of life-cycles in benthic suspension feeders inhabiting cold (Clarke 1991) and temperate (Hughes 1989; Coma et al. 2000) environments.

Life in a hydrodynamically active environment: hydrodynamics as a stochastic mechanism of food supply

Physical-biological coupling

Prey availability in the water column is dependent largely on hydrographic conditions. For benthic suspension feeders, input of suspended food is closely related to flow intensity and periodicity (Wildish and Kristmanson 1997). Therefore, water movement plays a fundamental role in determining diversity, biomass, structure and distribution of suspension-feeder communities (Fig. 3). Near-bottom currents enhanced by topographic features and internal waves create a hydrodynamical environment which favours particle sedimentation at the slope and near it (Frederiksen et al. 1992). Substratum heterogeneity and biogenic structures interfere with the flow pattern, increasing its turbulence, which enhances particle capture by benthic suspension feeders (Witte et al. 1997). These environmental conditions favour the development of dense populations of suspension feeders (Rice et al. 1990).

There are several examples of a wide distribution and dominance of benthic suspension feeders throughout continental shelves. The pennatulacean *Pennatula aculeata* represents the major component of benthic macrofauna of the Gulf of Maine (Langton et al. 1990). The ophiuroid *Ophiothrix fragilis* dominates the sessile epifaunal pebble community of the English Channel, with patches of over 200 ind. m^{-2} (Davoult et al. 1990). Banks of the coral *Lophelia pertusa* associated mainly with a rich sponge and bryozoan fauna are frequent throughout the continental shelf and slope in the northeastern Atlantic (Jensen and Frederiksen 1992). Other examples of dense benthic suspension-feeder assemblages present in the shelf-slope region, and therefore subject to similar conditions of considerable water motion and abundant suspended material, are the high concentrations of hexactinellid sponges in the North Atlantic (Rice et al. 1990), the coral banks with associated brittle stars and crinoids in Florida (Neumann et al. 1977), and the antipatharians on top of the vertical walls of seamounts (Kaufmann et al. 1989). All these dense assemblages live in areas of considerable water movement and abundant

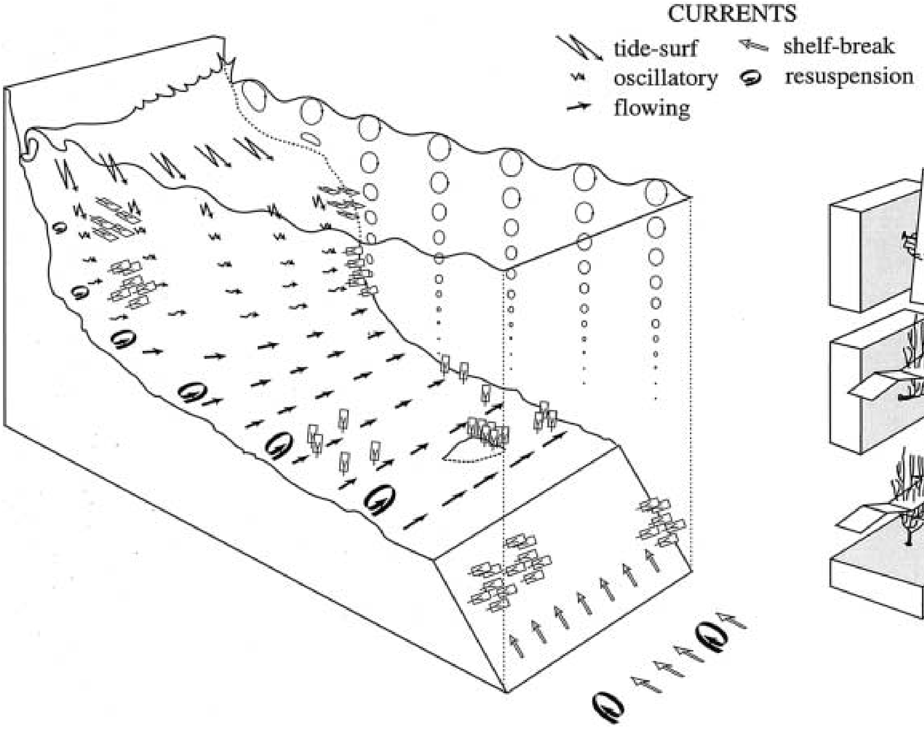

Fig. 3 Bottom-water currents along the continental shelf and slope, composed of oscillatory, longitudinal and lateral coast currents including resuspension processes (*black circular arrows* in the general view, and *white arrows* in the detailed view) (modified from Riedl 1966). Diagrams show the orientation of suspension-feeder colonies and where development of dense suspension feeder-communities is likely

suspended material. We can conclude that small- and medium-scale environmental variability, particularly hydrodynamics, is conducive to the growth of dense populations of benthic suspension feeders (e.g. Eckman and Duggins 1993; Josefson et al. 1993). Accordingly, the diverse and dense benthic suspension-feeder communities found along the eastern Weddell Sea shelf and slope (Gutt and Starmans 1998), where a structure of large sponges and bryozoans enhances the presence of other groups, appear to coincide with the hydrodynamically more active regions of this area.

The Antarctic shelf is unique regarding its depth, averaging about 500 m, with troughs to over 1,000 m (Dayton 1990). High-Antarctic benthic habitats share relatively constant physical parameters such as temperature, salinity and substrata, with few if any important barriers. The major disruptive effects on benthic suspension-feeding communities in Antarctic shallow water are abrasion by ice (Gutt et al. 1996), which replaces the wave and hydrodynamic effects in other areas, and plucking by anchor ice (Dayton 1990). In deeper waters, iceberg scouring has marked effects on the Antarctic shelf benthos (e.g. Gutt et al. 1996). Community destruction is followed by a seemingly long process of recolonization. During the second EASIZ cruise, in iceberg scour marks with early stages of recolonization, two gorgonian species, *Primnoisis antarctica* and *Ainigmaptilon antarcticus*, and bryozoans of the genus *Cellaria* appeared to be the main pioneer species (i.e. species of the first stages of recolonization after a disturbance).

The mesoscale pattern of currents in the eastern Weddell Sea influences the pattern of benthic community distribution on the shelf. Off Kapp Norvegia, diverse and dense communities are dominated by suspension feeders such as sponges and bryozoans. In contrast, in the southern part of the eastern Weddell Sea shelf area, low-biomass and low-diversity benthic communities are present, which are dominated by deposit feeders such as holothurians (Gerdes et al. 1992). Vertical particle flux off Kapp Norvegia is one of the most active in Antarctica (Bathmann et al. 1991); however, no data are available for the southern shelf off Filchner. All information suggests a picture similar to that described for the McMurdo Sound area (Dunbar et al. 1989). Off Kapp Norvegia, high water exchange, partial water mass retention due to the topographic effect of a shelf rise, and strong vertical particle flux may explain the presence of dense and diverse benthic communities dominated by suspension feeders, whereas in the southernmost part, less water renewal, additionally impoverished as it comes from underneath the Filchner Shelf, favours the dominance of deposit feeders.

Life in a boundary system: resuspension as a key process

The importance of near-bottom currents and salinity and/or temperature stratification is of crucial importance for the coupling of benthic suspension feeders to the pelagic system (e.g. Larsen and Riisgård 1996).

Generally, particles and bacteria show high abundance and a distinct small-scale vertical distribution in the benthic boundary layer (Ritzrau et al. 1997). Organic and inorganic particle fractions are sorted by resuspension (Thomsen 1999), because the organic fraction has low settling and high residence times and may form aggregates before settling or biodeposition (Thomsen and van Weering 1998). High microbial activity is associated with these particles and plays a key role in the decomposition of the particulate organic matter (Ritzrau and Thomsen 1997). Enhanced particle residence time in the water column and the formation of aggregates facilitate food availability to benthic filter feeders.

Sediment resuspension is a common phenomenon in near-shore environments surrounding Antarctica (e.g. Klöser et al. 1994), being particularly relevant during the austral winter. In shallow areas, detritus resuspended by wind-generated waves, anchor ice and currents may be a viable food source for benthic invertebrates during this season. In Maxwell Bay and Marion Cove (South Shetland Islands), the most important source of particulate matter in the water column seems to be resuspension of benthic material through a 1-year cycle (Kang et al. 1997). These authors observed two main peaks of chlorophyll, one in summer, dominated by microplankton (mainly large diatoms) and another one later and longer, during autumn and winter, dominated by pico- and nanoplankton (mainly flagellates). Obviously, organic suspended particles, including benthic diatoms resuspended by tidal currents (Ahn et al. 1997), are available practically year round for benthic suspension feeders.

Dunbar et al. (1989) found higher organic flux through the water column in the eastern compared to the western McMurdo Sound, which coincides well with the high biomass of benthic suspension feeders in the former area (Dayton et al. 1986). The high carbon accumulation in McMurdo Sound is enhanced, not only by resuspension, but also by low water temperatures, which reduce rates of organic-matter breakdown by bacteria (Hodson et al. 1981). Both the current view of water circulation and the fact that resuspension events are more common during austral winter support the hypothesis that benthic suspension feeders receive food the year round, especially in areas where they develop dense populations.

The bivalve *L. elliptica* is one of the few examples in the Antarctic where benthic suspension feeders play an important role in enhancing particle flux from the water column to the sea bed through biodeposition and, possibly, providing food for other benthic fauna, particularly in phytoplankton-impoverished near-shore waters (Ahn 1993).

Vertical flux versus horizontal transport: the role of advection

Processes related to organic decomposition in the benthic boundary layer are affected by both resuspension and advection (Jähmlich et al. 1998). Thus particles and aggregates may be transported by near-bottom currents, and recent studies in the Barents Sea (Thomsen and van Weering 1998) indicate that lateral particle fluxes are 2–3.7 times higher than vertical particle fluxes derived from sediment trap data. Vertical flux does not always supply sufficient food to benthic animals, but horizontal advection together with resuspension of material from the bottom can result in higher amounts of benthos-derived material relatively close to the substratum (Johnson 1988).

A close relationship between benthic metabolism and the pulses of vertical flux of organic matter has been observed both in shallow and deep areas (e.g. Witte et al. 1997). Near-bottom currents, however, may resuspend, spread and transport previously settled particles laterally over wide distances. These transport mechanisms enhance particle deposition on continental margins or where topography facilitates current slowdown. Not only light particles may be transported but also organisms such as foraminiferans (Brunner and Biscaye 1997).

In the Antarctic, the high variability of ice cover and its effects on hydrographic processes suggest that other mechanisms besides vertical flux play an important role controlling benthic biomass and diversity (Arntz et al. 1994). Hence, lateral advection may be more relevant than previously thought (Grebmeier and Barry 1991). Benthic organisms living under extended seasonal or even permanent ice cover rely on organic matter transported by resuspension and/or lateral advection (Fig. 4). For example, common littoral benthic diatoms such as *Navicula glaciei* have been observed in sediment traps located near the bottom (1,000 m) during winter in the Bransfield Strait (Palanques et al., in press). Internal waves associated with tidal currents may be able to advect part of the spring bloom, as well as macroalgal detritus, from the shelf areas to surrounding depths.

The role of Antarctic benthic suspension feeders: an efficient system

For Antarctic waters, a poor, flagellate-dominated pelagic community ("regenerating system" according to Eppley and Peterson 1979) is more characteristic than blooms of large phytoplankton species ("upwelling systems" according to Scharek and Nöthig 1995), which only occur in restricted areas during restricted times (Heywood and Priddle 1987). Have Antarctic suspension feeders adapted to the food resources available in a similar way to their temperate counterparts (e.g. Gili and Coma 1998)? Based on the first results obtained during the EASIZ cruises (Orejas et al., in press), we suggest that Antarctic suspension feeders exhibit species with a high renewal rate, a high ingestion rate of microplankton and low maintenance energy requirements and, species with low ingestion, and low renewal and growth rates. The first group of species is associated with the diatom-based plankton blooms occurring in the

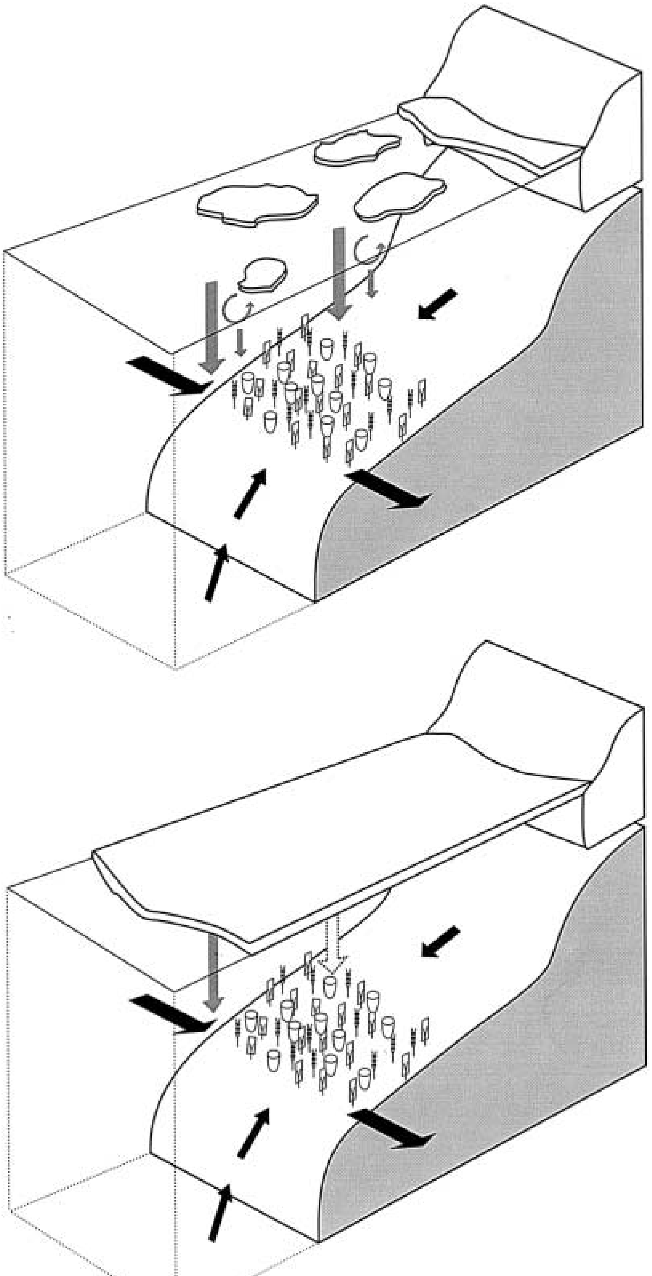

Fig. 4 Idealized diagram of food-supply processes to the Antarctic benthos in summer (*top*) and winter (*bottom*). *Grey arrows* mean microplankton and faecal pellet (summer) and pico- and nanoplankton (winter) vertical flux, *white arrow* zooplankton vertical migration (winter), and *black arrows* lateral (from the shelf, slope and shallow areas) water flow (all year)

upwelling systems. The second group is linked to the regenerating system, which is very stable throughout the whole year. Feeding strategies of sessile species belonging to the latter group will be affected significantly by sediment type and resuspension processes.

At the level of individuals or colonies, Antarctic benthic suspension feeders are efficient in energy recycling. This conclusion may be extended to the community and ecosystem level, thus leading to a new hypothesis regarding the success of these communities in the Southern Ocean: the heterogenous hydrodynamic environment, lateral particle advection and transport over long distances, continuous feeding on organic matter derived from the water column or made available by resuspension, and the ability to feed on almost all potential food lead to high recycling efficiency at the community level.

Are Antarctic benthic suspension feeders different? Conclusions

Despite low primary production, the Southern Ocean does not appear to be a food-limited system for benthic suspension feeders because of the nutritive quality of food, patch feeding (e.g. on zooplankton prey) and the role of lateral advection and resuspension. Studies to date suggest that the feeding strategy of Antarctic benthic suspension feeders does not differ from those of tropical and temperate ecosystems. Suspension feeders are able to feed on a wide range of prey items, in particular on the most abundant items, because of their capability of ingesting prey items of very different kind and size. Being remarkably efficient organisms in terms of energy transfer from the pelagial to the benthic system, benthic suspension feeders build rich but patchy communities under Antarctic conditions. As rich communities of suspension feeders may exert an important predatory impact on plankton populations and on the abundance of suspended organic matter in the water mass adjacent to the bottom, an impact at a similar order of magnitude has to be assumed for Antarctic and temperate regions.

Acknowledgements We would like to especially thank Tom Brey, Andrew Clarke and Jean Bouillon for their constructive comments, which helped to improve the manuscript. We also thank the officers and crew of RV "Polarstern" and many colleagues for their help aboard. The programme related to Ecology of Antarctic Suspension Feeders, a cooperation between the Alfred Wegener Institute and several Spanish research institutions, started in 1998, and forms a contribution to SCAR-EASIZ (Ecology of the Antarctic Sea Ice Zone). Support for this work was provided by CICYT (Spanish Antarctic Research Programme) grants ANT97-1533-E, ANT98-1738-E and by PhD fellowships from DAAD (A/96/13073) and the European Commission (TMR-CT97-2813) to C.O. and a RED contract from the "Generalitat de Catalunya" to R.C.

References

Ahn I-Y(1993) Enhanced particle flux through the biodeposition by the Antarctic suspension-feeding bivalve *Laternula elliptica* in Marian Cove, King George Island. J Exp Mar Biol Ecol 171:75–90

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 Biol 17:123–130

Amouroux JM, Amouroux J, Bastide J, Cahet G (1990) Interrelations in a microcosm with a suspension-feeder and a deposit-feeder. I. Experimental study. Oceanol Acta 13:61–68

Anderson L, Dyrssen D (1989) Chemical oceanography of the Arctic ocean. In: Herman Y (ed) The Arctic seas: climatology, oceanography, geology and biology. Van Nostrand Reinhold, New York, pp 93–114

Anthony KRN (1997) Prey capture by the sea anemone *Metridium senile* (L.): effects of body size, flow regime, and upstream neighbors. Biol Bull 192:73–86

Arntz WE, Brey T, Gallardo VA (1994) Antarctic zoobenthos. Oceanogr Mar Biol Annu Rev 32:241–304

Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad TF (1983) The ecological role of water-column microbes in the sea. Mar Ecol Prog Ser 10:257–263

Barnes DKA, Clarke A (1995) Seasonality of feeding activity in Antarctic suspension feeders. Polar Biol 15:335–340

Bathmann U, Fischer G, Müller PJ, Gerdes D (1991) Short-term variations in particulate matter sedimentation off Kapp Norvegia, Weddell Sea, Antarctica: relation to water mass advection, ice cover, plankton biomass and feeding activity. Polar Biol 11:185–195

Best BA, Thorpe MA (1986) Feeding-current interactions and competition for food among the bryozoan epiphytes of *Fucus serratus*. Mar Biol 93:371–375

Brey T, Gerdes D (1997) Is Antarctic benthic biomass really higher than elsewhere? Antarct Sci 9:266–267

Brunner CA, Biscaye PE (1997) Storm-driven transport of foraminifers from the shelf to the upper slope, southern Middle Atlantic Bight. Cont Shelf Res 17:491–508

Burkill PH, Mantoura RFC, Owens NJP (1993) Biogeochemical cycling in the northwestern Indian Ocean: a brief overview. Deep Sea Res II 40:643–649

Buss LW, Jackson JBC (1981) Planktonic food availability and suspension-feeder abundance: evidence of in situ depletion. J Exp Mar Biol Ecol 49:151–161

Chiantore M, Cattaneo-Vietti R, Albertelli G, Misic C, Fabiano M (1998) Role of *Adamussium colbecki* in circulation of organic matter in Terra Nova Bay (Ross Sea, Antarctica). J Mar Syst 17:411–424

Clarke A (1980) A reappraisal of the concept of metabolic cold adaptation in polar marine invertebrates. Biol J Linn Soc 14:77–92

Clarke A (1991) What is cold adaptation and how should we measure it? Am Zool 31:81–92

Cloern JE (1982) Does the benthos control phytoplankton biomass in south San Francisco Bay? Mar Ecol Prog Ser 9:191–202

Coma R, Gili JM, Zabala M, Riera T (1994) Feeding and prey capture cycles in the aposymbiotic gorgonian *Paramuricea clavata*. Mar Ecol Prog Ser 115:257–270

Coma R, Gili JM, Zabala M (1995) Trophic ecology of a marine benthic hydroid *Campanularia everta*. Mar Ecol Prog Ser 119:211–220

Coma R, Ribes M, Gili JM, Zabala M (1998) An energetic approach to the study of life history traits of two modular colonial benthic invertebrates. Mar Ecol Prog Ser 162:89–103

Coma R, Ribes M, Gili JM, Zabala M (2000) Seasonality in coastal benthic ecosystems. Trends Ecol Evol 15:448–453

Davoult D, Gounin F, Richard A (1990) Dynamique et reproduction de la population d'*Ophiothrix fragilis* (Abildgaard) du détroit du Pas-de Calais (Manche orientale). J Exp Mar Biol Ecol 138:201–216

Dayton PK (1990) Polar benthos. In: Smith WO (ed) Polar oceanography. Part B: chemistry, biology and geology. Academic Press, San Diego, pp 631–685

Dayton PK, Watson D, Palmisano A, Barry JP, Oliver JS, Rivera D (1986) Distribution patterns of benthic standing stock at McMurdo Sound, Antarctica. Polar Biol 6:207–213

Dubinsky Z, Jokiel PL (1994) Ratio of energy and nutrient fluxes regulates symbiosis between zooxanthellae and corals. Pac Sci 48:313–324

Dunbar RB, Leventer AR, Stockton WL (1989) Biogenic sedimentation in McMurdo Sound, Antarctica. Symposium on Glaciomarine Environments, INQUA XII International Congress. Mar Geol 85:155–179

Eckman JE, Duggins DO (1993) Effects of flow speed on growth of benthic suspension feeders. Biol Bull 185:28–41

Epply RW, Peterson BJ (1979) Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282:667–680

Fabricius KE, Genin A, Benayahu Y (1995) Flow-dependent herbivory and growth in zooxanthellae-free soft corals. Limnol Oceanogr 40:1290–1301

Fenchel TM (1988) Marine plankton food chains. Annu Rev Ecol Syst 19:19–38

Fenchel TM, Jørgensen BB (1977) Detritus food chains of aquatic ecosystems: the role of bacteria. In: Alexander M (ed) Advances in microbial ecology. Plenum Press, London, pp 1–58

Fréchette M, Butman CA, Geyer WR (1989) The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. Limnol Oceanogr 34:19–36

Frederiksen R, Jensen A, Westerberg H (1992) The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe Islands and the relation to internal tidal mixing. Sarsia 77:157–171

Frost TM (1987) Porifera. In: Pandian TJ, Vernberg FJ (eds) Animal energetics. Academic Press, San Diego, pp 27–53

Gaino E, Bavestrello G, Cattaneo-Vietti R, Sarà M (1994) Scanning electron microscope evidence for diatom uptake by two Antarctic sponges. Polar Biol 14:55–58

Gerdes D, Klages M, Arntz WE, Herman RL, Galéron J, Hain S (1992) Quantitative investigation on macrobenthos communities of the southern Weddell Sea shelf based on multibox corer samples. Polar Biol 12:291–301

Giese AC, Pearse JS (1974) Reproduction of marine invertebrates: acoelomate and pseudocoelomate metazoans. Academic Press, New York

Gili JM, Coma R (1998) Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol Evol 13:316–321

Gili JM, Alvà V, Pagés F, Kloser H, Arntz WE (1996) Benthic diatoms as the principal food source in the sub-Antarctic marine hydroid *Silicularia rosea*. Polar Biol 16:507–512

Gili JM, Alvà V, Coma R, Orejas C, Pagès F, Ribes M, Zabala M, Arntz W, Bouillon J, Boero F, Hughes RG (1998) The impact of small benthic passive suspension feeders in shallow marine ecosystems: the hydroids as an example. Zool Verh Rijksmus Nat Hist Leiden 323:1–7

Grebmeier JM, Barry JP (1991) The influence of oceanographic processes on pelagic-benthic coupling in polar regions: a benthic perspective. J Mar Syst 2:495–518

Gutt J, Starmans A (1998) Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctic): ecological role of physical parameters and biological interactions. Polar Biol 20:229–247

Gutt J, Starmans A, Dieckmann G (1996) Impact of iceberg scouring on polar benthic habitats. Mar Ecol Prog Ser 137:311–316

Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of sleractinian corals. In: Dubinsky Z (ed) Ecosystems of the world: coral reef. Elsevier Science, New York, pp 133–207

Harvell CD, LaBarbera M (1985) Flexibility: a mechanism for control of local velocities in hydroid colonies. Biol Bull 168:312–320

Heywood RB, Priddle J (1987) Retention of phytoplankton by an eddy. Continental Shelf Res 7:937–955

Hodson RE, Azam F, Carlucci A, Fuhrman JA, Karl DM, Holm-Hansen O (1981) Microbial uptake of dissolved organic matter in McMurdo Sound, Antarctica. Mar Biol 61:185–209

Hughes RN (1980) Optimal foraging theory in the marine context. Oceanogr Mar Biol Annu Rev 18:423–481

Hughes RN (1989) A functional biology of clonal animals. Chapman & Hall, London

Jähmlich S, Thomsen L, Graf G (1998) Factors controlling aggregate formation in the benthic boundary layer of the Mecklenburg Bight (western Baltic Sea). J Sea Res 41:245–254

Jensen A, Frederiksen R (1992) The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (Scleractiniaria) on the Faroe shelf. Sarsia 77:53–69

Johnson AS (1988) Hydrodynamic study of the functional morphology of the benthic suspension feeder *Phoronopsis viridis* (Phoronida). Mar Biol 100:117–126

Jørgensen CB (1990) Bivalve filter feeding: hydrodynamics, bioenergetics, physiology and ecology. Olsen and Olsen, Fredensborg

Jørgensen CB, Kiørboe T, Møhlenberg F, Riisgaard HU (1984) Ciliary and mucus net filter feeding with special reference to fluid mechanical characteristics. Mar Ecol Prog Ser 15:283–292

Josefson AB, Jensen JN, Aertebjerg G (1993) The benthos community structure anomaly in the late 1970s and early 1980s – a result of a major food pulse? J Exp Mar Biol Ecol 172:31–45

Kang J-S, Kang S-H, Lee JH, Chung KH, Lee M-Y (1997) Antarctic micro- and nano-sized phytoplankton assemblages in the surface water of Maxwell Bay during the 1997 Austral summer. Korean J Polar Res 8:35–45

Kaufmann RS, Wakefield WW, Genin A (1989) Distribution of epibenthic megafauna and lebensspuren on two central North Pacific seamounts. Deep Sea Res 36:1863–1896

Kellogg D, Kellog TB, Dearborn JH, Edwards KC, Fratt DB (1982) Diatoms from brittle star stomach contents: implications for sediment reworking. Antarct J US 17:167–169

Kimmerer WJ, Gartside E, Orsi JJ (1994) Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. Mar Ecol Prog Ser 113:81–93

Klöser H, Mercuri G, Laturnus F, Quartino ML, Wiencke C (1994) On the competitive balance of macroalgae at Potter Cove (King George Island, South Shetlands). Polar Biol 14:11–16

Klumpp DW (1984) Nutritional ecology of the ascidian *Pyura stolonifera*: influence of body size, food quantity and quality on filter-feeding, respiration, assimilation efficiency and energetic balance. Mar Ecol Prog Ser 19:269–284

Kowalke J (1999) Filtration in Antartic ascidians – striking a balance. J Exp Mar Biol Ecol 242:233–244

Langton RW, Langton EW, Theroux RB, Uzmann JR (1990) Distribution, behavior and abundance of sea pens, *Pennatula aculeata*, in the Gulf of Maine. Mar Biol 107:463–469

Larsen PS, Riisgård HU (1996) Biomixing generated by benthic filter-feeders: a diffusion model for near-bottom phytoplankton depletion. J Sea Res 37:81–90

Linley LAS, Koop K (1986) Significance of pelagic bacteria as a trophic resource in a coral reef lagoon, One Tree Island, Great Barrier Reef. Mar Biol 92:457–464

MacFadden CS (1986) Colony fission increases particle capture rates of a soft coral: advantages of being a small colony. J Exp Mar Biol Ecol 103:1–20

Mann KH (1988) Production and use of detritus in various freshwater, estuarine and coastal marine ecosystems. Limnol Oceanogr 33:910–930

Neumann AC, Kofoed JW, Keller GH (1977) Lithoherms in the straits of Florida. Geology 5:4–10

Nowell ARM, Jumars PA (1994) Flume experiments on food supply to the blue mussel *Mytilus edulis* L. as a function of boundary-layer flow. Limnol Oceanogr 39:1755–1768

Okamura B (1990) Behavioural plasticity in the suspension feeding of benthic animals, In: Hughes RN (ed) Behavioural mechanisms of food selection. Springer, Berlin Heidelberg New York, pp 637–660

Orejas C, Gili JM, López-González P, Arntz WE (in press) Feeding strategies and diet composition of four species of Antarctic benthic cnidarians. Polar Biol

Orejas C, Gili JM, Arntz WE, Ros JD, López P, Teixidó N, Filipe P (2000) Benthic suspension feeders, key players in Antarctic marine ecosystems. Contrib Sci Barcelona 1:299–311

Palanques A, Isla E, Puig P, Sánchez-Cabeza JA, Masqué P (in press) Annual evolution of settling particle fluxes during the FRUELA experiment (Western Bransfield Strait, Antarctica). Deep Sea Res II

Pile AJ, Patterson MR, Witman JD (1996) In situ grazing on plankton < 10 µm by the boreal sponge *Mycale lingua*. Mar Ecol Prog Ser 141:95–102

Pullen J, LaBarbera M (1991) Modes of feeding in aggregations of barnacles and the shape of aggregations. Biol Bull 181:442–452

Reiswig HM (1971) Particle feeding in natural populations of three marine demosponges. Biol Bull 141:568–591

Ribes M, Coma R, Gili JM (1998) Seasonal variation of in situ feeding rates by the temperate ascidian *Halocynthia papillosa*. Mar Ecol Prog Ser 175:201–213

Ribes M, Coma R, Gili JM (1999a) Heterogeneous feeding in benthic suspension feeders: the natural diet and grazing rate of the temperate gorgonian *Paramuricea clavata* (Cnidaria: Octocorallia) over a year cycle. Mar Ecol Prog Ser 183:125–137

Ribes M, Coma R, Gili JM (1999b) Natural diet and grazing rate of the temperate sponge *Dysidea avara* (Demospongiae, Dendroceratida) throughout an annual cycle. Mar Ecol Prog Ser 176:179–190

Rice AL, Thurston MH, New AL (1990) Dense aggregations of a hexactinellid sponge, *Pheronema carpenteri* in the Porcupine Seabight (Northeast Atlantic Ocean) and possible causes. Progr Oceanogr 24:197–206

Riedl R (1966) Biologie der Meereshöhlen. Parey, Hamburg

Riisgård HU (1998) Filter feeding and plankton dynamics in a Danish fjord: a review of the importance of flow, mixing and density-driven circulation. J Environ Manage 53:195–207

Riisgård HU, Larsen PS (1995) Filter-feeding in marine macro-invertebrates: pump characteristics, modelling and energy cost. Biol Rev 70:67–106

Riisgård HU, Poulsen L, Larsen PS (1996a) Phytoplankton reduction in near-bottom water caused by filter-feeding *Nereis diversicolor* – implications for worm growth and population grazing impact. Mar Ecol Prog Ser 141:47–54

Riisgård HU, Jürgensen C, Clausen T (1996b) Filter-feeding ascidians (*Ciona intestinalis*) in a shallow cove: implications of hydrodynamics for grazing impact. J Sea Res 35:293–300

Ritzrau W, Thomsen L (1997) Spatial distribution of particle composition and microbial activity in the benthic boundary layer (BBL) of the Northeast Water Polynya. J Mar Syst 10:415–428

Ritzrau W, Thomsen L, Lara RJ, Graf G (1997) Enhanced microbial utilisation of dissolved amino acids indicates rapid modification of organic matter in the benthic boundary layer. Mar Ecol Prog Ser 156:43–50

Robbins RE, Shick JM (1980) Expansion-contraction behavior in the sea-anemone *Metridium senile*: environmental cues and energetic consequences. In: Smith DC, Tiffon Y (eds) Nutrition in the lower Metazoa. Pergamon, New York, pp 101–116

Rutman J, Fishelson L (1969) Food composition and feeding behavior of shallow-water crinoids at Eilat (Red Sea). Mar Biol 3:46–57

Scharek R, Nöthig EV (1995) Das einzellige Plankton im Ozean der Arktis und Antarktis. In: Hempel G (ed) Biologie der Polarmeere. Fischer, Jena, pp 116–127

Sebens KP, Koehl MAR (1984) Predation on zooplankton by the benthic anthozoans *Alcyonium siderium* (Alcyonacea) and *Metridium senile* (Actiniaria) in the New England subtidal. Mar Biol 81:255–271

Sebens KP, Vandersall KS, Savina LA, Graham KR (1996) Zooplankton capture by two scleractinian corals, *Madracis mirabilis* and *Monastrea cavernosa*, in a field enclosure. Mar Biol 127:303–317

Shimeta J, Jumars PA (1991) Physical mechanisms and rates of particle capture by suspension feeders. Oceanogr Mar Biol Annu Rev 29:191–257

Shulenberger E, Wormuth JH, Loeb VJ (1984) A large swarm of *Euphausia superba*: overview of patch structure and composition. J Crust Biol 4 (spec 1):75–95

Slattery M, McClintock JB, Bowser SS (1997) Deposit feeding: a novel model of nutrition in the Antarctic colonial soft coral *Germesia antarctica*. Mar Ecol Prog Ser 149:299–304

Smith SL, Schnack-Schiel SB (1990) Polar zooplankton. In: Smith WO Jr (ed) Polar oceanography. Part B: chemistry, biology, and ecology. Academic Press, San Diego, pp 251–263

Sorokin YI (1991) Biomass, metabolic rates and feeding of some common reef zoantharians and octocorals. Aust J Mar Freshwater Res 42:729–741

Sorokin YI (1995) Coral reef ecology, 2nd edn. Springer, Berlin Heidelberg New York

Stephens GC (1982) Recent progress in the study of "Die Ernährung der Wassertiere und der Stoffhaushalt der Gewässer". Am Nat 22:611–619

Taghon GL (1981) Beyond selection: optimal digestion rate as a function of food value. Am Nat 118:202–214

Thomsen L (1999) Processes in the benthic boundary layer at continental margins and their implication for benthic carbon cycle. J Sea Res 41:73–86

Thomsen L, Weering TCE van (1998) Spatial and temporal variability of particulate matter in the benthic boundary layer at the N.W. European Continental Margin (Goban Spur). Progr Oceanogr 42:61–76

Valiela I (1995) Marine ecological processes. Springer, Berlin Heidelberg New York

Vogel S (1994) Life in moving fluids: the physical biology of flow. Princeton University Press, Princeton

Wildish D, Kristmanson D (1997) Benthic suspension feeders and flow. Cambridge University Press, Cambridge

Wildish DJ, Miyares MP (1990) Filtration rate of blue mussels as a function of flow velocity: preliminary experiments. J Exp Mar Biol Ecol 142:213–220

Witte U, Brattegard T, Graf G, Spinger B (1997) Particle capture and deposition by deep-sea sponges from the Norwegian-Greenland Sea. Mar Ecol Prog Ser 154:241–252

Wottom RS (1994) The biology of particles in aquatic systems. Lewis, Boca Raton

Yahel G, Post AF, Fabricius K, Marie D, Vaulot D, Genin A (1998) Phytoplankton distribution and grazing near coral reefs. Limnol Oceanogr 43:551–563