Benthic suspension feeders, key players in Antarctic marine ecosystems?

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Abstract

For quite some time it was generally accepted, from water column and open sea studies, that in Antarctic marine communities there is a prolonged period of minimal winter activity which lasts for at least six months during the Southern winter. However, recent studies on certain littoral benthic suspension feeders have suggested that the period of inactivity may last only a few weeks. This raises the question of what allows these organisms to feed, and hence remain active, for considerably longer periods than previously thought. Special adaptations to feeding at low levels of food concentration, or to using occasional food abundance followed by long periods of starvation have been suggested. Many suspension feeders might use alternative food sources to phyto- and zooplankton, e.g., the «fine fraction» of organic matter, or microplankton (bacteria, ciliates, and flagellates including POC of several origins), which has recently been shown to play a much more significant role than expected in complementing the diet and meeting energy demands in many species of suspension feeders. The possible role of sediment resuspension has also been reported, and given the high food value of the organic component of sediments even on deep bottoms further research would be of interest. Recent observations related to the natural diet (prey capture) of several shallow species lead to the assumption that part of Antarctic suspension feeders have similar growth and reproduction rates to those reported for temperate waters. Efficient food assimilation may contribute to our understanding of the continuous reproduction state observed in octocorals and, also, of the development of tridimensionally structured communities which are suspension-feeder dominated, highly diversified, and have a high biomass. The principal role of Antarctic benthic suspension feeders seems to be related to the efficient recycling of the water column production, which is only partly assimilated by the highly seasonal zooplankton and other secondary consumers during particle sinking. The consideration of the crucial role of benthic suspension feed-

Resum

Ja fa un cert temps que hom accepta, de manera general i a partir d'estudis de la columna d'aigua en mar obert, que en les comunitats marines de l'oceà Antàrtic hi ha un període prolongat d'activitat hivernal mínima que s'estén al llarg de sis mesos com a mínim, que és el temps que dura l'hivern austral. Tanmateix, investigacions recents en algunes espècies d'invertebrats suspensívors (filtradors) bentònics litorals han suggerit que el període d'inactivitat potser dura només unes poques setmanes. Això planteja una interessant qüestió: què és el que permet que aquests organismes antàrtics mengin, i per tant romanguin actius, durant períodes molt més llargs del que fins ara s'havia cregut?

Hom ha suggerit adaptacions especials a menjar en concentracions molt baixes d'aliment, o bé a usar eficientment l'abundància ocasional d'aliment enmig de llargs períodes d'escassedat. Molts animals suspensívors podrien usar fonts alternatives al seu aliment usual, el fito- i el zooplàncton; per exemple, la 'fracció fina' de matèria orgànica, o microplàncton (bacteris, ciliats i flagel·lats, junt amb carboni inorgànic particulat d'orígens diversos), que hom ha demostrat recentment que té un paper molt més significatiu del que hom creia a l'hora de complementar la dieta i de subvenir a les demandes energètiques de moltes espècies de suspensívors. També s'ha esmentat el possible paper de la resuspensió de sediments i, atès l'elevat valor alimentari del component orgànic dels sediments antàrtics, àdhuc de fons pregons, serà interessant investigar més en aquesta línia. Observacions recents relacionades amb la dieta natural (captura de preses) d'algunes espècies d'aigües somes porten a suposar que alguns suspensívors antàrtics, si més no, tenen taxes de creixement i reproducció que són similars a les assenyalades per a espècies d'aigües temperades. L'assimilació eficient de l'aliment pot ajudar a explicar l'estat de reproducció contínua observat en espècies d'octocorals, així com el notable desenvolupament de les comunitats bentòniques litorals antàrtiques, estructurades en tres dimensions, dominades per suspensívors, molt diversificades i amb una biomassa elevada. El principal paper dels suspensívors bentònics antàrtics sembla que està relacionat amb el reciclatge eficient de la producció de la columna d'aigua, que només és parcialment assimilada durant l'en-

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ers suggested in this paper has arisen from preliminary empirical evidence on the RV *Polarstern* cruises ANT XIII/3 and XV/3 (EASIZ I & II) [51] on the southeastern Weddell Sea, and recent literature which is reviewed and commented in this paper.

fonsament de les partícules pel zooplàncton i altres consumidors secundaris, que són molt estacionals.

La consideració del paper crucial que podrien tenir els suspensívors bentònics antàrtics que hom suggereix en aquest article prové d'evidències empíriques preliminars obtingudes de sengles campanyes de recerca del VO *Polarstern*, ANT XIII/3 i XV/3 (EASIZ I i II) [51], realitzades en l'àrea sud-oriental del mar de Weddell, així com de bibliografia diversa que es revisa i comenta en l'article.

Keywords: Suspension feeding, Antarctic marine ecosystems, plankton-benthos coupling, Antarctic benthos

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Many benthic assemblages in Antarctica are abundant and taxonomically diverse. Traditionally densities and biomasses of macrobenthos are considered to be high in the Antarctic on both hard and soft bottoms [25, 30, 73, 79, 117, among others], especially in comparison with the Arctic [29]. Although a fully developed hard substratum epifaunal assemblage in Antarctica may not be comparable with a tropical reef in biodiversity, it is nevertheless rich in species. Average benthic biomass in the Antarctic is higher than in temperate and subtropical communities [2, 18]. However, P/B values of Antarctic benthic invertebrates –for the small number of species which have been studied– are, in general, significantly lower than those of their temperate counterparts [3, 18].

The largest proportion of the Antarctic benthic fauna is made up of sessile suspension feeders, e.g. sponges, bryozoans, ascidians, and certain echinoderms [1, 31] (Fig. 1). Communities of this kind are highly structured, as also observed in temperate waters [46], with a high functional diversity and a considerable degree of patchiness in species composition at small or intermediate spatial scales [57, 85]. Bryozoans, sponges and ascidians have been described to dominate many of the Antarctic shelf benthic communities [45, 113]; cnidarians are another notable component of the suspension feeding community (in many places) and are, perhaps, the group that contributes most to the tridimensional structure of these communities (pers. obs. from ROV images).

Benthic suspension feeders depend on the available food suspended in the water column and on the currents for its renewal. A high degree of seasonality in the supply of fresh food may be a critical factor which conditions the life strategies of benthic organisms, to the point of limiting their growth and reproductive strength. Benthic suspension feeders are highly susceptible to temporal fluctuations in the food supply in other latitudes [27]; they must have adapted their feeding strategies to the features of Southern Ocean: high primary productivity in summer, but almost none in winter. The apparently discontinuous pattern of food availability can be expected to determine their activity rhythms and metabolic

rates [10]. The energy requirements of suspension feeders are expected to be low during periods with no investment in growth and reproduction, while during periods of abundant primary production they are high and used for reproduction and growth. Some species, however, are also able to feed very efficiently on low food concentrations. These organisms must have adapted to feeding on very heterogenous food sources: from the fine fraction of the water (pico- and nanoplankton and particulate and dissolved organic matter) to meso- and macroplanktonic prey.

In this paper we present empirical evidence on the diets of Antarctic benthic suspension feeders, and attempt to relate this to reproduction and growth patterns. We discuss possible sources of food and the mechanisms to obtain it in a highly seasonal environment such as the Antarctic. In light of this study and our knowledge on the benthic Antarctic
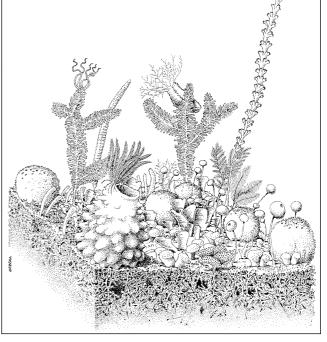

Figure 1. Ideal representation of a benthic community in the Weddell Sea Shelf. (Ca. 0.5 m^2; original by Jordi Corbera.)

ecosystem, we present a new hypothesis on the ecological role of suspension feeders in Antarctica.

Geographic and bathymetric distribution: influence of physical factors

The Antarctic shelf is unique in its great depth, averaging about 500 m with troughs of over 1000 m [29, 84]. High Antarctic benthic habitats share relatively constant physical parameters such as temperature, salinity and substrata, with few, if any, significant barriers. The terrestrial input is negligible with the exception of the runoff from penguin and seal colonies, which can be locally considerable. Most coastal regions exhibit shifts in community composition on small spatial scales, usually in response to differences in wave exposure or substrata. Apart from this, almost identical species assemblages seem to occur around the entire continent. This phenomenon is unique in marine biogeography. In contrast to these relatively stable physical conditions, two relevant sources of disturbance should be mentioned: iceberg scouring and currents.

Iceberg scouring has disruptive effects on the Antarctic shelf benthos [58], with severe disturbance of littoral bottoms followed by a seemingly long process of colonization. Using a ROV, during the second EASIZ cruise [51] early stages of recolonization with the presence of scour marks were found off Kapp Norvegia at a depth of 265 m. Among the pioneer species, two gorgonians, *Primnoisis antarctica* and *Ainigmaptilon antarcticus*, were considered indicator species of the first stages of recolonization after iceberg disturbance.

Currents have great influence on the feeding strategies of passive suspension feeders such as cnidarians. There are strong seasonal variations and interannual differences in the current patterns of the littoral Weddell Sea, which are due to differences in the exchange rate. Taking into account that

the depth of the surface mixed layer is between 50-100 m, increasing to 500 m near the continental shelf edge, the near bottom layers present heterogenous conditions. At present, the current dynamics on the Weddell Sea shelf are still largely unknown [40]. Several authors [42] have provided empirical evidence on significant intrusions of warmer waters onto the shelf from intermediate depths in the Weddell Sea shelf-break region, which may be due to the presence of barotropic shelf waves at diurnal frequencies. The mixing of intermediate warm water with cold shelf water may also be increased by shear instabilities. The result of these phenomena may lead to a continuous semidiurnal movement of deep waters across the Weddell Sea, which may contribute to the resuspension processes which are essential for both the development of benthic suspension feeder communities and for water column production in the area (Fig. 2).

Feeding of suspension feeders in a hydrodynamic environment

For benthic suspension feeders, the probability of inputs of suspended food is closely associated with the dynamics (intensity and periodicity) of the water flow. Prey capture is dependent on the speed, direction and turbulence of the flow [119]. Suspension-feeding colonies or individuals normally interfere with the flow in some way and use one of many strategies to maximize the capture of prey items, thus giving rise to considerable morphological diversity among benthic marine invertebrates. Several groups of suspension feeders have evolved a multitude of adaptations designed to attract and trap particles in suspension. A model of the general operating pattern has been developed from observations of colonies and individuals and predicts a range of ideal flow intensities for optimum prey capture and growth of each species [98]. The components of a single community present varying patterns of prey capture and capture efficiencies according to their spatial distribution [95] and the close proximity of colonies helps to create areas that trap the water flowing around the population, thereby increasing prey residence time adjacent to the colonies [76, 81, 95]. In summary, the diversity of anatomical forms and ecological strategies allows the spatial coexistence of a great number of species (and of dense biomass), which in turn leads to complex tridimensional communities which depend on the local flow regime [46].

Environmental variability, particularly as regards hydrodynamics, is conducive to the growth of dense populations of benthic suspension feeders. Population stability depends on constant hydrodynamic conditions but also on pelagic production in the area [43, 70]. Advection or passive transport mechanisms (such as sedimentation and resuspension) regulate the small and medium-scale availability of food to benthic organisms [41, 53]. Small and medium-scale variations in seston density and quality have been reported to determine the density of suspension-feeding populations [27, 101]. For seston to be continuously available to suspen-
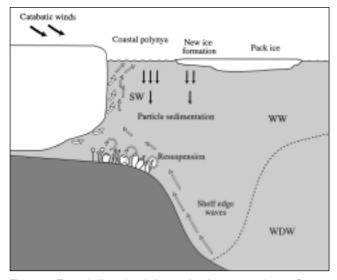

Figure 2. Termohaline circulation under the open polynya. Resuspension processes and their influence on the benthic communities in the Weddell Sea Shelf. (Modified from [94]).

sion feeders, the surrounding water layer must be continuously renewed [35]. Vertical flux and horizontal advection do not always supply sufficient food to benthic animals. Resuspension of material from the bottom can lead to higher amounts of benthos-derived material relatively close to the substratum [68].

In Antarctic communities, a set of hydrodynamic features such as those mentioned previously facilitate continuous water renewal close to the bottom and hence may greatly contribute to explaining the dense benthic suspension feeding communities on the shelf and slope. The water renewal is not necessarily caused by strong bottom currents, but it must be relatively constant. Filter feeding on small particles is not an effective way to obtain sufficient food during short periods of time, but it can be useful if active filtration is facilitated by water circulation. Vogel [112] pointed out that for many sessile suspension feeders, the development of populations in moderately or highly active hydrodynamic environments reduces the cost of filtering because the water layer around the sieving structures is continuously removed. In many sessile active suspension feeders, like ascidians and sponges, ambient currents enhance internal flow and feeding by forcing water into the filtering structures [112]. This induced flow allows low metabolic rates, as it implies low energy demand for food-gathering, and the food energy can be fully used for growth and reproduction [120]. Thus, even if there are no conspicuous events, continuous water renewal and resuspension, as observed in video transects carried out during the RV *Polarstern* cruises, may support the hypothesis that resuspension supplies enough small particles to the water column to compensate for the energy demand of benthic suspension feeders, which do not have to invest major energetic costs to capture prey, thanks to their extraordinary adaptation to environmental hydrodynamic conditions.

Feeding in a particular environment: the Antarctic recycling system

In Antarctica, nutrient concentrations are generally high, with values in upwelled water along the Antarctic Divergence ranging from 27 to 40 µm nitrate, 1.0 µm ammonium, and 2 to 2.4 µm phosphate [54], and values higher than 20 µm nitrate, maximum values of ammonium ranging from 2 to 3 µm and higher than 1.5µm phosphate, for most of the northwestern Weddell Sea [109]. The high rate of grazing and ammonium production in the euphotic zone indicates that much of the primary production is regenerated, thus restricting the export of organic carbon to benthic communities. Although nutrients are typically high in the water column, the average primary production (16-100 gC m^{-2} yr^{-1}) is surprisingly low. Primary production is limited by the deep mixed water layer, because water column stability is the major factor controlling phytoplankton growth and accumulation [36, 103]. In addition, high primary production (41 gC m^{-2}yr^{-1}) and high densities of microalgae at the lower surface of the sea ice indicate

their importance as a source of carbon [56, 104]. In McMurdo Sound, sea ice microbial communities are highly productive [83], and detrital fallout from sea ice may be crucial to benthic communities, as in some Arctic habitats [23]. Recent studies estimate that about 10-76 % of primary production in nearshore and open waters of the Antarctic is cycled through a bacterial loop in the water column [28], resulting in a variable organic carbon input to the underlying benthos.

There appears to be three main processes for vertical flux in the High Antarctic Ocean: (1) mass sedimentation of phytoplankton and ice algae [16], (2) sinking of fecal material of zooplankton feeding on phytoplankton blooms [15], (3) selective sedimentation of small fecal pellets of probably protozoan origin [80]. Resuspension and lateral advection are other significant processes in the benthic environment, transporting biogenic material from shallow sites to deeper basins on the continental shelf [32, 33, 34]. Sediment resuspension during winter has frequently been observed [4, 11, 104]. Although the food value of resuspended material is doubtful, resuspended sediments may contain viable algal material [14]. The high carbon contents and the relatively low opal/Corg ratios, and the very low amounts of non-protein amino acids observed by Bathmann *et al.* [11] in sediment traps deployed during January and February in a shelf area of the Weddell Sea, support the hypothesis that sedimented material does not greatly biodegrade during sinking and remains rather fresh on the surface of the sediment. In the Weddell Sea, the summer flux comprises rapidly sinking particles; a «background flux» of slowly sinking particles is absent as this would have prolonged the sedimentation signal into winter [102]. These observations support our hypothesis that the organic material deposited on the seafloor provides a high nutritive value for benthic animals for a long time due to its low degradation rate, and facilitates the feeding of these animals during winter through resuspension processes [51].

A recently explored aspect of bentho-pelagic coupling is related with the grazing of benthic invertebrates on water column small plankton. Planktonic cells less than 5 µm in size, known as nano- and picoplankton, are the main contributors to marine productivity and biomass [111]. The trophic web they make up has been extensively studied in the water column and has received much attention from planktologists over the last decade. Recently, extensive experimental series of measurements have been carried out in tropical seas and in the Mediterranean that have quantified the diet and the metabolic contribution of all types of plankton for several species of benthic suspension feeders. Many benthic invertebrates from a variety of phyla have the capacity to feed on the pico- and nanoplankton of the water column [69]. However, this has only recently been quantified by the use of flow cytometry. Studies on sponges such as *Mycale lingua* in the Gulf of Maine [86] or the gorgonian *Pseudoplexaura porosa* in the Caribbean [90], as well as on other species in the Mediterranean [89], have shown the high grazing efficiency of these benthic invertebrates on the small-plankton communities in near-bottom waters. This cor-

roborates some previous observations which reported that bacteria, phytoplankton, and suspended organic matter may play an extremely critical role in the feeding of non-molluscan suspension feeders [39, 88, 92]. Suspension feeders capture a broad spectrum of prey ranging from particulate organic matter (often plant detritus) to zooplanktonic organisms; they also have some peculiar feeding behaviours, as found in the hydroid *Silicularia rosea* in King George Island (Antarctica), which mainly ingests benthic diatoms [50]. Even species that feed solely on zooplankton present quite varied diets [7, 96]. Although a single prey type, e.g. particulate organic matter, may cover the demands of certain species [6, 72], non-selective diets appear to be the most suitable strategy for littoral suspension feeders. Okamura [82] pointed out that benthic suspension feeders typically face a heterogenous array of suspended material that varies in quantity, quality and rates of movement in time and space. The filtering effect of the benthic suspension feeding community can significantly reduce nano-, pico- and zooplankton communities from the water that they process. The greatest effect of grazing by benthic invertebrates on water column communities, and hence their impact on the microbial and planktonic food web, is observed in shallow nearshore ecosystems.

Feeding of Antarctic suspension feeders: some empirical results from the EASIZ cruises

Studies with natural and artificially-added prey items have shown that cnidarians, especially gorgonians, are able to ingest particulate matter [105]. Most feeding studies involve mainly the examination of gut contents as during the first EASIZ cruise (RV *Polarstern* ANT XIII/3) [51]. This method is useful in the study of large prey items (usually over 50 µm), but may underestimate the number of small, soft- bodied preys because they leave no recognizable remains. Antarctic pelagic communities are dominated by nano- (< 20 µm) and picoplankton (< 2 µm); most of their components are not recognizable after ingestion. Hence, little is known about the significance of these organisms in the diet of benthic suspension feeders [86, 90]. Therefore, during ANT XV/3 feeding experiments were conducted with octocorals and one hydroid species in order to elucidate the role of the fine fraction of seston in the diet of these animals [51]. The data derived from these experiments are still under analysis.

Gut content analysis of several hydroid species during ANT XIII/3 showed that almost all guts were empty. Either the hydroids were not feeding during the time of study or the prey items were too small or too digested to be recognized by light microscopy. During ANT XV/3, the hydroid *Tubularia ralphii* was collected at a shallow water station (Four Seasons Inlet, at about 70 m of depth). 70% of the specimens studied showed full guts and 90% of the prey items were copepods [51]. Stepanjants [106] reported densities up to 2300 polyps m^{-2} for *T. ralphii* in the Haswell Archipelago (Davis Sea). This species was found with about 113 polyps m^{-2} in our study area. Considering its prey capture efficiency, the predatory impact of *T. ralphii* in the study area can be estimated at 1791 prey items m^{-2} day^{-1}. This is in approximately the same range as the predatory impact of temperate hydrozoans. At present we do not know how *T. ralphii* is able to survive the Antarctic winter on low food concentrations. There are two possible explanations: (i) colonies survive as stolons, as reported for temperate hydroid species [47], or (ii) *T. ralphii* is able to change its diet during winter. This case, together with the study on *Silicularia rosea* [50], are the first empirical results on the diet spectrum of hydroid species in the Antarctic. More information is needed on the processes taking place during the Antarctic winter to answer this question.

Like in hydroids, the stomachs of anthozoan polyps (*Thouarella variabilis, Primnoisis antarctica, Dasystinella* spp., among others) were also empty during the first EASIZ cruise. One of the most common species collected in shallow areas during the second EASIZ cruise was the stoloniferan *Clavularia frankliniana* [51]. This species forms encrusting colonies, which grow in high abundance, in some cases on the same stones as *T. ralphii. C. frankliniana* is a common Antarctic species and seems to grow as fast as hydroids [99]. The gut contents of the stoloniferan polyps were analyzed in order to study the natural diet. 45% of the dissected polyps contained prey. The diet was diverse and composed of benthic organisms such as foraminifera, nematoda and benthic diatoms. This kind of diet is quite frequent in the massive and encrusting anthozoans such as alcyonarians and actiniarians [96]. The polyps of the stoloniferan were very close to the substrate and they probably capture prey from the upper substrate layer. This feeding strategy is an efficient adaptation for prey capture when prey is resuspended by currents and moving around the tentacle crown.

These two examples represent two distinct feeding strategies within the group of cnidarians. The question to be asked is: what happens to the other suspension feeders which have no zooplankters in their guts?

Approach to growth and reproduction patterns and reaction to disturbance: potential pioneer species (slow and fast growth?)

The study of growth layers in skeletal structures has been extensively treated in some organisms, mainly in fish and bivalves, and also in other groups such as gorgonians, corals, echinoderms and bryozoans, and several methodologies have been used [27, 44, 52, 55, 60, among others]. Most of these studies investigate the annual periodicity of growth rings or layers to calculate the growth ratio, and to estimate the age of organisms. This is sometimes done in order to date the community to which they belong; this is especially relevant in Antarctic benthic assemblages owing to the scarcity of available growth and age data [3].

Benthic communities in shallow Antarctic waters are subjected to the disruptive effects of abrasion by ice [58] and plucking by anchor-ice [31, 115]. The dominant taxa in the

zone of persistent scour by icebergs are sessile suspension-feeding organisms.

Many of these organisms are clonal, such as hydrozoans or some soft hexa- and octocorals, and seem to have encountered several ways to increase biomass, e.g. the oldest tissues can degenerate and be reabsorbed depending on the (often unknown) feeding background [47, 63, 71, among others]. Thus, the knowledge of colony growth rates, age or evolution is difficult to assess without monitoring tagged colonies, and it is complicated to separate somatic tissue renewal (for example, after wounding by predators or losing part of colonies broken by currents) from real growth. Total growth rates include partial colony restoration or, in many cases, colony regression [63].

The estimation of the age of benthic communities subjected to periodic disturbances such as iceberg scouring, and the establishment of a successional pattern of recovery from disturbances in these assemblages are two of the open questions in Antarctic marine benthic ecology. One approach is to use structural community parameters such as species diversity. However, the presence or absence of large specimens of species with a long life span (which are good indicators of maximal community age) must also be taken into account. Some gorgonian species (e.g. *Primnoisis antarctica* or *Ainigmaptilon* spp.) are frequently present in the first steps of recolonisation after the impact of icebergs on the sea floor. In these stages, iceberg tracks are sometimes still visible, large individuals of sponges are missing, and the community is of seemingly low diversity [59]. Recognizable ring marks would be a good «chronometer» in this succession phase. Later, other gorgonian species (e.g. *Fannyella* spp.) seem to displace the *Primnoisis* and *Ainigmaptilon* colonies, and the communities undergo further changes. It is necessary to improve the interpretation of rings to date the distinct steps in the successional process. Information about periodicity of growth rings in the axis of gorgonians has often been contradictory. Some authors found an annual periodicity, as in the North Pacific [55], but often a more complex ring structure is recorded, making it difficult to find a clear temporal periodicity [20, 27]. Two species of bryzoans from the Weddell Sea, *Melicerita obliqua* and *Cellaria moniliorata,* have also been studied [9, 19]; the oldest specimens found were 50 years old.

Other anthozoan species such as encrusting stoloniferous octocorals probably grow faster than gorgonians [99]. However, growth ratios of organisms that do not produce growth marks such as these must be interpreted with care [74]. *Clavularia frankliniana* forms stolonate membranous encrusting colonies according to the available space. *C. frankliniana* can develop dense populations such as those described from Explorer's Cove (Ross Sea) with a mean number of 7.3±0.8 colonies and 1337.3±233.1 polyps m^{-2} [99]. During ANT XV/3, we found densities of 30.8 colonies and 2920.9 polyps m^{-2} [51]. The observation of large amounts of *C. frankliniana* during the EASIZ II cruise provided us with an opportunity to study its growth, feeding and reproduction patterns.

For sedentary clonal animals, two opposing life-history strategies have been postulated in the predictive framework of life history theories [65]: (1) species of ephemeral clones follow a life strategy based on maximizing clonal expansion by uninterrupted modular iteration as long as conditions are favourable for growth, holding sexual reproduction in reserve for periods when modular survival or replication is hindered by the environment, and investment in reproduction concentrates in a short period of the year [64 71]; and (2) modules that dwell in persistent habitats may aggregate to form dense colonies, making them more resistant to competition and environmental hazards [22, 66]. This strategy leads to perennation and the defense of the space these colonies have taken over [67], and splits the reproductive effort throughout the year or between consecutive years. In terms of the parameters measured during the EASIZ cruises I and II, the hydroids and the stoloniferans are good representatives of the first group, while the gorgonians belong to the second one. This leads us to hypothesize that not all Antarctic benthic animals grow slowly or take more than one year to produce a new generation of offspring, but a number of species may concentrate their activity during summer, a rich food period, and remain in winter in a hibernation state [64]. For example, the development of resistent stolons is a well-known hibernation mechanism in hydroids [47], as is the formation of resting stages such as cysts in many other organisms [17].

It remains to be determined whether the slow reproduction rates reflect an inherent inability to adapt to low temperatures, or are a response to features of the Antarctic marine environment which are not directly related to low temperatures, such as limited food resources. Reproduction in Antarctica is strongly seasonal for some shallow water species and many authors link reproduction to the summer period of high phytoplankton production [24, 108, 116, 117]. Taking into account the low sea temperatures since the Miocene cooling 14 million years ago [75, 97], well adapted animals with temperature compensation for all life processes may be expected, also in Antarctic marine invertebrates, with physiological processes going on at rates comparable to those typical in temperate, or even tropical, waters. Theoretical models have considered trade-offs between producing (1) many small eggs that develop into feeding larvae and (2) relatively few large eggs that develop without feeding larval stages, and have concluded that when food supplies are low, and development rates slow, as in polar seas, non-feeding modes of development should predominate [107, among others].

Studies on the reproduction of Antarctic Cnidaria are scarce. Some studies on Cnidaria reproduction have been done in the North Atlantic [91, 110]. The high fecundity of some species observed may be a function of the spatial density of these sessile organisms. Other species exhibit very low fecundity, suggesting a two-year reproduction cycle. Although the detailed mechanisms ensuring successful fertilization remain unknown, it is possible that high fecundity contributes to the success of reproduction at the relatively high inter-colony distances which are typical of *Umbellula*.

The Antarctic primnoid gorgonian *Thouarella variabilis* has a low fecundity [21], and the presence of oocytes at different stages of development suggests a two-year cycle of oogenesis or continuous gametogenesis. The lack of continuous sampling prevents us from sorting out some questions. The oocytes grow to a size of 660 μm, and a planula larva of about 860 μm is retained within the polyp. Spawning occurs presumably during the Antarctic summer and the swimming planulae settle soon after release.

Comparing Antarctic gorgonians with the features and reproduction patterns described for species from other geographical areas (e.g. Pacific, Caribbean, Mediterranean), some trends can be observed. The number of offspring per year is generally related to environmental features and tends to be higher in temperate and climatically less stable regions than in the tropics [77, 108]. This places the Antarctic environment in an intermediate position between temperate and tropical areas, with a low number of eggs per polyp, and two clear seasonal periods. Similar gradients, following a latitudinal cline from the Antarctic to the tropics, are common in other groups of invertebrates [3].

Figure 4. Different larval development stages in the same polyp of a colony of *Clavularia frankliniana*.

Colonies of *Clavularia frankliniana* were studied [51] in order to evaluate the sex ratio and the reproductive effort in several parts of their colonies (Fig. 3). According to these preliminary data, the oldest (central) polyps are most involved in the colony reproduction, followed by the intermediate ones, while distal polyps do not participate in reproduction (female colonies) or contribute little (male colonies). Another observation on the reproduction of *C. frankliniana* is that the larvae remain in the polyp cavity until late stages. In some female polyps, several larvae ready for release from the polyp were found together with oocytes in early stages of development (Fig. 4). This suggests a long reproductive period, perhaps from early spring to late austral summer.
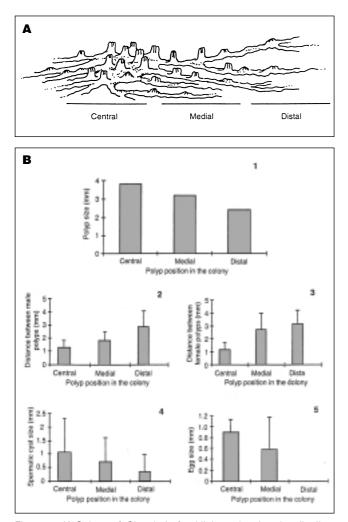

Figure 3. A) Colony of *Clavularia frankliniana* showing the distribution of polyps. B) Distribution of polyps in the colony in relation to polyp size (1); distance between male (2) and female polyps (3) in the colony in relation to their position; size of the spermatic cysts (4) and of the eggs (5) in function of the polyp position in the colony. (From [51]).

Conclusions

It is now accepted that the summer in Antarctica is not characterized by an exceptionally high primary production. The sparse, flagellate-dominated planktonic community is more characteristic than phytoplankton blooms of large species which only occur in restricted areas [37, 61, 93]. The pelagic system in the Weddell Sea has been called a «regenerating» system, which refers to the vertical particle flux, and is an ammonia-based system. The concept of «new» and «regenerated» production in marine ecosystems was proposed by Eppley and Peterson [38] and is now widely regarded as the characteristic system of the Antarctic pelagial with blooms, if they occur, representing a transitory event superimposed on the basal state. Accordingly, interannual variation of the regenerating system is much less than in the case of blooms.

The hard-bottom benthos has usually been regarded as a sink for the remains of the water column production. However in littoral systems, the benthos, and therefore suspension feeding communities, is an extremely active part of the sys-
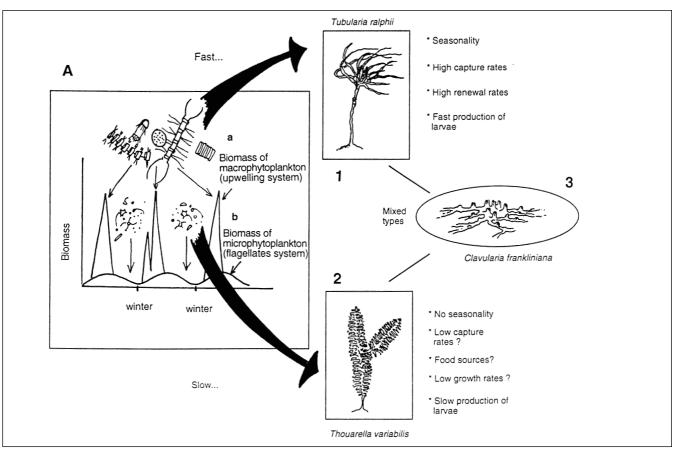
Figure 5. Schematic summary of the hypothesis. A) Pelagic Antarctic recycling system: a) Periodical summer blooms with a representation of a typical phytoplankton community. b) Stable continuous system with a representation of a typical microbial planktonic community. 1) *Tubularia ralphii* as a representative of the first group presented in the text. 2) *Thouarella variabilis* as a representative of the second group presented in the text. 3) Mixed types, with *Clavularia frankliniana* as a representative. (Modified from: [94]).

tem [5]. Not only does the benthos receive food particles that settle out of the water column, but it also actively exploits and temporarily stores particles that are transported by current flows within the water column [46]. Consequently, communities of suspension feeders make up a highly active boundary system. According to Margalef [78], this type of boundary system is more dynamic than those traditionally considered in ecology, i.e., discontinuities and ecotones. This boundary system is so active because, as a system dominated by suspension feeders, it is highly structured and quite efficient in exploiting the less structured system of plankton. From a successional point of view, the ability of suspension feeders to exploit the plankton links the benthic and planktonic systems together. Therefore, the structural and biological complexity of communities of suspension feeders is determined by the structure of the planktonic communities they exploit [46].

Studies of feeding ecology of cnidarians (hydrozoans, sea anemones, jellyfish and corals) on plankton in other latitudes have revealed two distinct life strategies [46], broadly following the already known ones for Cnidarinas as a whole [48]: Anthozoans are characterized by slow growth rates, high longevity and often, by associations with algal symbionts in tropical waters. Predation pressure on the planktonic community by individual colonies is negligible but because they are highly abundant, capture rates for the population as a whole are very high [26]. Hydroids, in contrast, are characterized by rapid growth, short life (ephemeral colonies) and a lower frequency of associations with symbionts. Prey capture rates of hydroid species can be very high [8] and so the role of this taxon in energy transfer is much more significant than expected on the basis of their size and abundance [49].

Have Antarctic suspension feeders adapted to the food resources available in Antarctic waters in a similar way as their temperate counterparts? Based on the preliminary results obtained during the EASIZ cruises ANT XIII/3 and ANT XV/3 [51], we propose the following hypothesis: there are two strategies within the suspension feeders, which are closely related with physical processes: on the one hand species with a high renewal rate, high ingestion rate of zooplankton and low maintenance energy requirements, which are able to invest in growth and reproduction; on the other hand species with low ingestion, and low renewal and growth rates, less able to use seasonal food bounties when (and if) they appear (Fig. 5).

Thus the first group of species would be associated with «superimposed» blooms (occurring in the «upwelling systems» of Scharek and Nöthig [94]). These organisms benefit from the short-term high production level. They reproduce and grow only during this period and may also accumulate lipidic reserves in their stolonial structures to survive the rest

of the year in an «inactive stage». Thus, this group could be categorized as «opportunistic», being adapted to the irregular fluctuation in food availability. *Tubularia ralphii* can be considered a representative organism of this group.

The second group suggested would be related to the «regenerating system» which Eppley and Peterson [38] propose: a very stable system throughout the year, in which the role of sediment and resuspension processes also have a major impact on the feeding strategies of the sessile suspension feeders. *Thouarella variabilis* could be a representative organism of this group.

An intermediate group between the two described above could be represented by the stoloniferan *Clavularia franklini-ana*, which has a mixed diet.

The value of sediments in Antarctica may be greater than suspected, although the carbon accumulation in the sediment is not very high [29]. Recent studies on the gorgonian *Germesia antarctica* show that this species can incline its body to the bottom, to feed in a way that classifies it as a deposit feeder [100]. Similar observations have been reported for *Virgularia mirabilis* (Pennatulacea) in the North Atlantic [62].

The sedimented organic material is believed to play a crucial role in the nutrition of benthic sessile animals during winter [34], although this contradicts recent work carried out in the Mediterranean Sea, which corroborates that suspension feeders are able to feed on the fine live fraction of seston (flagellates, ciliates and bacteria; [90]). In the Antarctic, the organic input that sinks to the bottom is assumed to be strongly seasonal [29]. However, resuspension and transport to the different Antarctic basins may create a tremendous organic influx to benthic communities even though it may be occasional. The availability of this organic input must, in great part, be due to the low microbial decomposition rate, which is itself due to low bacterial growth rates [118]. Bathmann *et al.* [11] showed that sedimented material is not greatly biodegraded during sinking and remains rather fresh on the surface of the sediment. Microbial composition seems to be complex, and biomass may be high in some areas [117]. Thus bacteria may represent a significant food source for benthic suspension feeders, as has recently been demonstrated in other regions [90]. Unfortunately, the trophic potential of sediments is still largely unknown in the Antarctic [29].

The available information, together with our preliminary data, enables us to hypothesize that benthic suspension feeders may feed on very small plankton and resuspended particles during the Antarctic winter, at least to fuel their minimal metabolic costs, or to continue their reproduction by investing in growth during the most favourable food period, the summer.

Acknowledgements

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About the authors

The authors belong to a multicenter Marine Benthic Ecology Group with more than 25 years of experience in the development of research projects, both of national and international scope, having published more than 100 papers in international leading journals during the last 10 years. These cover five main areas: (a) structure and dynamics of littoral benthic communities worldwide, (b) trophic ecology and energetics of benthic invertebrates, (c) biodiversity of benthic and planktonic stages of sessile marine invertebrates, (d) distribution and abundance patterns of zooplankton in relation to mesoscale physical structures, and (e) anthropogenic impact on littoral and shelf marine communities, mainly in marine reserves.Three teams currently make up the Group: the Department of Ecology (University of Barcelona) team with Prof. J. D. Ros as group leader; the Institute of Marine Sciences of Barcelona (CSIC) team with Dr. J. M. Gili as head of the team, and the Laboratory of Marine Biology (University of Seville) team, with Dr. P. López as the head of the team.

The Group has worked mainly in the Mediterranean Sea and in temperate and tropical waters. Lately, in cooperation with the Alfred Wegener Institute for Polar and Marine Research (AWI) of Bremerhaven (Germany), especially with Prof. W. E. Arntz, head of the Department of Marine Biology I, the Group is involved in a joint study of Antarctic benthic communities, in which Ms. C. Orejas, Ms. N. Teixidó and Ms. P. Filipe, all Ph. D. students, also participate. This cooperation started in 1995 as a part of the international research programme on Ecology of the Antarctic Sea Ice Zone (EASIZ) in the framework of the Scientific Committee for Antarctic Research (SCAR). The first part of EASIZ will finish in 2004. Until then, the main goal of both groups will be to study the role of Antarctic benthic suspension feeders, which can be key species in the energy and matter transfer processes in Antarctic marine ecosystems. In this review, the authors summarize the previous relevant information about their joint research topic, they present new data based on results of work done during the first two EASIZ cruises (1996 and 1998), and put forward some new ideas underlining the key role of benthic suspension feeders in polar ecosystems. Joandomènec Ros is a member of the Institut d'Estudis Catalans (1990).