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The role of pelagic-benthic coupling in structuring littoral benthic communities at Terra Nova Bay (Ross Sea) and in the Straits of Magellan*

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SUMMARY: In Antarctic and peri-Antarctic regions, benthic communities are persistent in time and show high biomass and large numbers of individuals, mainly consisting of suspension and deposit feeders. In fact, apart from recruitment, the major factor structuring these communities is the high flow of organic matter from the pelagic domain to the bottom, representing an important energy source for the benthic organisms. The aim of this paper is to review, compile and compare the data from earlier investigations in Terra Nova Bay (Ross Sea) and the Straits of Magellan, in order to come to a more general conclusion about the role of the pelagic-benthic coupling in structuring littoral benthic communities in southern coastal areas. Few measurements of flux rates and the biochemical composition of the sinking particles occurring in Antarctic and peri-Antarctic shallow waters are available, but a compilation of our own data and others allows a comparison of these two systems. The different environmental conditions between Antarctica and the Straits of Magellan lead to differences in the origin of the particulate organic matter and in its biochemical composition, and consequently in the coupling between pelagic and benthic domains. At Terra Nova Bay the summer particulate matter shows a high labile fraction of a good food value: its flux has been evaluated at about 0.67 g $m^{-2}d^{-1}$. Conversely, the Straits of Magellan show multi-structured ecosystems where the quality and quantity of the organic matter flux towards the bottom change according to the local geomorphology and current dynamics. Moreover, the three-dimensional assemblages of suspension-feeders, so common in Antarctic shallow waters, seem to be absent in the Magellan area. In particular sponges, gorgonarians and bryozoans play a secondary role inside the Straits of Magellan, where polychaetes (60%) and molluscs (9-10%) are dominant on soft bottoms, and where they reach high values in density and biomass. Bivalves seem to play an important role in both regions: for instance, at Terra Nova Bay, the scallop *Adamussium colbecki* processes about 14 % of the total carbon flux, with an assimilation efficiency of 36 %. This scallop seems to be able to adapt its reproductive period and its trophic behaviour to the changes in the quality and quantity of the pelagic events. The pulsing trend of the vertical flux, which in a few weeks can reach the total annual input, produces significant changes in the physiology (growth, reproduction, spawning) and trophic behaviour of many benthic species, such as sponges and polychaetes. The study of the pelagic-benthic coupling could be essential in the evaluation of the trophic capacity and the environmental response around sites of sea-farming, which are an ever-growing activity in the Magellan area.

Key words: Antarctica, Straits of Magellan, pelagic-benthic coupling.

RESUMEN: EL PAPEL DEL ACOPLAMIENTO PELÁGICO-BENTÓNICO EN LA ESTRUCTURACIÓN DE LAS COMUNIDADES LITORALES BENTÓNICAS EN LA BAHÍA DE TERRA NOVA (MAR DE ROSS) Y EN EL ESTRECHO DE MAGALLANES. – En las regiones Antártica y periantártica, las comunidades bentónicas son persistentes en el tiempo y muestran altos valores de biomasa y número de individuos. Estas comunidades están constituídas, principalmente, por organismos suspensívoros y detritívoros. Aparte del reclutamiento, el factor más importante en estructurar estas comunidades es el flujo de materia orgánica desde la zona pelágica al bentos, lo que representa una importante fuente de energía para los organismos del fondo. No obstante la gran importancia de la producción primaria como suministro de alimento para las comunidades béntonicas litorales, la información sobre la tasa de flujo y la composición bioquímica del material que sedimenta es reducida. Muestreos rea-

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lizados con trampas de sedimento han mostrado altos valores de flujo de materia orgánica caracterizado por una elevada presencia de paquetes fecales, particularmente importantes en el transporte de materia orgánica desde la zona fótica a las aguas profundas. En Bahía Terra Nova (Mar de Ross) la materia orgánica estival presenta una fracción lábil importante, un alto valor alimentario y un flujo que se evaluó en aproximadamente 0.67 g m^{-2} d^{-1}. Las diferentes condiciones ambientales de la Antártida y el Estrecho de Magallanes ocasionan diferencias en el origen y en la composición bioquímica de la materia orgánica particulada y, consecuentemente, en el acoplamiento entre los dominios pelágico y bentónico. El Estrecho de Magallanes, contrariamente a las observaciones hechas en la Antártida, muestra un sistema de flujo de materia orgánica hacia el fondo , debido a su geomorfología peculiar y a la dinámica de las corrientes. Por otra parte, los agrupamientos tridimensionales de suspensívoros, comunes en las aguas someras antárticas, parecen estar ausentes en el área del Estrecho de Magallanes. Particularmente esponjas, gorgonias y briozoos desempeñan un papel secundario en el interior del Estrecho de Magallanes, donde poliquetos (60%) y moluscos (9-10%) dominan en los fondos blandos, alcanzando altos valores de densidad y biomasa. Los bivalvos desempeñan un papel importante en ambas regiones: en la Bahía de Terra Nova, el pectínido *Adamussium colbecki* procesa aproximadamente el 14% del flujo total de carbono, con una eficiencia de asimilación del 36%. Este pectínido sería capaz de adaptar su periodo reproductivo y su estrategia trófica a los cambios en la calidad y la cantidad de materia orgánica. Los pulsos del flujo vertical, que en pocas semanas puede alcanzar el suministro total anual, producen cambios significativos en la fisiología (crecimiento, reproducción, freza) y en el comportamiento trófico de algunas especies bentónicas, como esponjas y poliquetos. Finalmente, el estudio del acoplamiento bentos-pélagos puede ser esencial en la evaluación de la capacidad trófica y la respuesta ambiental para la ubicación de zonas de cultivos marinos, actividad en continuo crecimiento en el área de Magallanes.

Palabras clave: Antártica, Estrecho de Magallanes, acoplamiento pelágico-bentónico.

INTRODUCTION

In high productive marine areas, the major biological factor structuring benthic communities, excluding recruitment, is the flow of organic matter from the pelagic domain to the bottom. It may represent the main energy source for the heterotrophic benthic organisms (Graf, 1992). This is particularly true in Antarctica (Grebmeier and Barry, 1991), as well as in the Arctic, where the primary production, higher in coastal waters (83-170 g C m^{-2} y^{-1}) and over continental shelves than in oceanic waters (26 g C m^{-2} y^{-1}; Wefer *et al.*, 1988), occurs in a short summer time, with blooms of *Phaeocystis* (Palmisano *et al.,* 1985; SooHoo *et al.*, 1987) and/or diatoms (Krebs, 1983).

The influence of the organic matter in the water column on the benthos has been evidenced at McMurdo Sound: Dayton and Oliver (1977) observed strong quantitative and qualitative differences in the soft-bottom communities living in areas influenced by oligotrophic currents flowing from beneath the Ross Ice Shelf and those influenced by more eutrophic waters, flowing southward.

Several studies have been carried out on particle flux and sedimentation in Antarctica (Wefer *et al.,* 1988; Peinert *et al.*, 1989; Smetacek *et al.*, 1990; Grebmeier and Barry, 1991; Knox, 1994). However, despite the great importance of the primary production as food supply in littoral and ice-covered waters, few measurements of the flux rate and the biochemical composition of the sinking particles are available from Antarctic and peri-Antarctic littoral areas.

In the shallow waters of Terra Nova Bay (Ross Sea), Fabiano *et al.* (1996; 1997) found that the amount of total suspended matter (TSM) reaching the bottom during the summer (generally 30-40 days) can rise to 14 g m^{-2} d^{-1}, practically 97% of the total flux as, during all other months, it is about 10-100 times lower. This pulsing input supports numerous littoral benthic communities which are persistent in time, showing high biomass and large numbers of individuals. They are mainly constituted by deposit- and active and passive suspension feeders (sponges, bivalves, polychaetes, echinoderms), whose trophic strategies are strongly related to the flux occurring in the water column.

The aim of this paper is to compare the different environmental conditions occurring at a shallow water site in Antarctica (Terra Nova Bay, Ross Sea) and in the Straits of Magellan, paying particular attention to possible adaptations of suspension-feeders to face changes in the flux rates. Moreover, the Straits of Magellan, a peri-Antarctic area, show environmental conditions so different from those generally found along the Antarctic coasts, to be a significant place to study these phenomena under completely different hydrodynamic forces.

PELAGIC-BENTHIC COUPLING IN TERRA NOVA BAY

In Terra Nova Bay phytoplankton blooms occur during and immediately after the pack-ice melting (Fabiano *et al.*, 1997). Significant differences can arise, linked to the annual sea-ice cover variation and upper layer stratification, e.g., if the pack-ice melting starts early in the season, and a second bloom occurs at the beginning of February. During the summer, inshore primary production at Terra Nova Bay can be evaluated as an average value of about 2-3 mg C m^{-3} h^{-1}, but it is also important to take into account that, for a few days, the sympagic algae can reach the impressive primary production of about 500 mg C m^{-3} h^{-1} with biomass values ranging about 1-7 g Chl-*a* m^{-3} and making a heavy contribution to the final flux (Lazzara *et al*., 1995).

Another organic source comes from the benthic algae. Between 3 and 10 m depth, *Iridaea cordata* reaches a density of 4,336 plants m^{-2} in January, but the highest biomass value (about 3.5 kg m^{-2} WW), at the beginning of summer, suggests that it also grows, although at a low rate, during the Antarctic winter. Deeper, from 10 to 25 m, *Phyllophora antarctica* forms dense and expansive beds, reaching its highest density and biomass values (about 10,000 plants m^{-2}, 1.5 kg m^{-2} WW, respectively) at the end of January (Cormaci *et al*., 1996).

Moreover, all the bottoms, down to 150-200 m depth, show a patchy distribution of highly dense seasonal populations of benthic diatoms, revealed by greenish layers seen using a ROV. Their biomass ranges from 4 to 80 μg Chl-*a* g^{-1}, with an average value of around 10 μg Chl-*a* g^{-1} (A. Pusceddu, pers. comm.).

In January the intense flux of living diatoms, organic matter and fecal pellets can reach 0.69 g POC m^{-2} d^{-1}. The high values of TSM/POC sometimes recorded in the same period (Fabiano *et al.,* 1997) depend on the large amount of inorganic matter due to eolic input, which varies greatly (3-300 g m^{-2} y^{-1}) according to the distance from the rocky outcrop.

The organic flux (Fig. 1) from the water column supports large littoral zoobenthic communities dominated by suspension- and deposit feeders (scallops, sponges and polychaetes). At Terra Nova Bay, the soft bottoms, between 20-30 and 60-70 m depth, are completely covered by the large scallop *Adamussium colbecki,* which reaches high biomass (100-120 g m^{-2} DW soft tissues) and density (60-80 ind. m^{-2}) values (Cattaneo-Vietti *et al*., 1997). Between 80 and 120 m depth, hard bottoms are dominated by filter-feeding assemblages, mainly characterized by sponges which can reach very high biomass values (over 2-3 kg m^{-2} WW; Cattaneo-Vietti, unpublished data). Polychaetes (mainly *Spiophanes tcherniai*) are dominant below 100 m depth, reaching abundance values of 3,000 ind. m^{-2}, exceeding 20 g m^{-2} WW of biomass (Gambi *et al*., 1997).

All these species play a key role in transferring energy from the water column to the benthos, a behaviour that allows them to reach high biomass values. For example, considering the average filter-

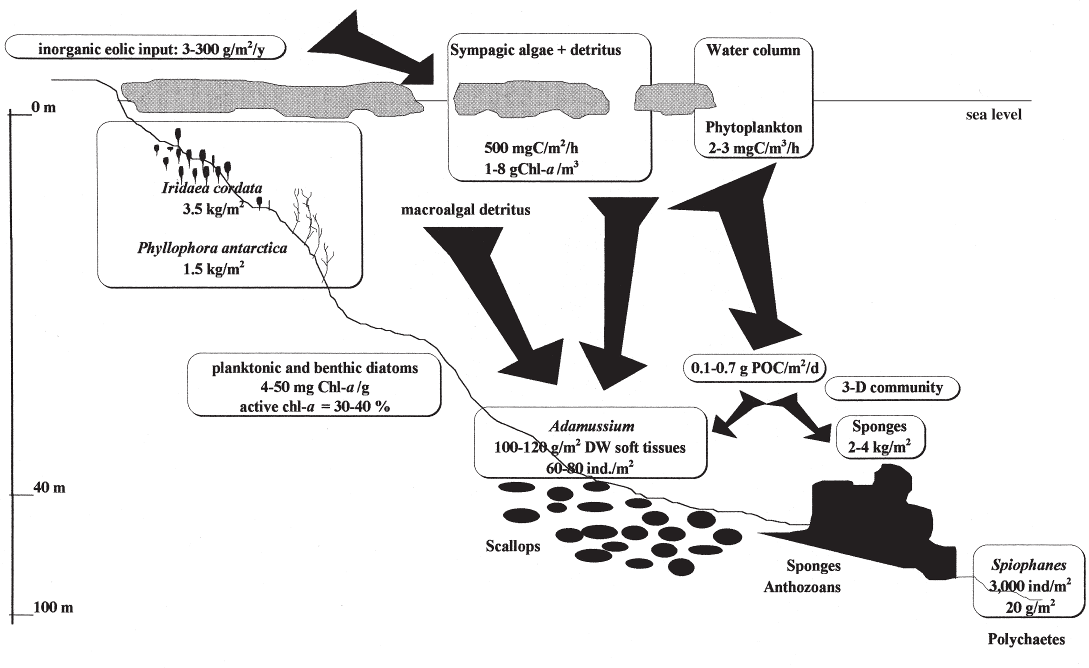

FIG. 1. – Scheme showing the main pathways of the organic flux at a littoral site in Terra Nova Bay (Ross Sea).

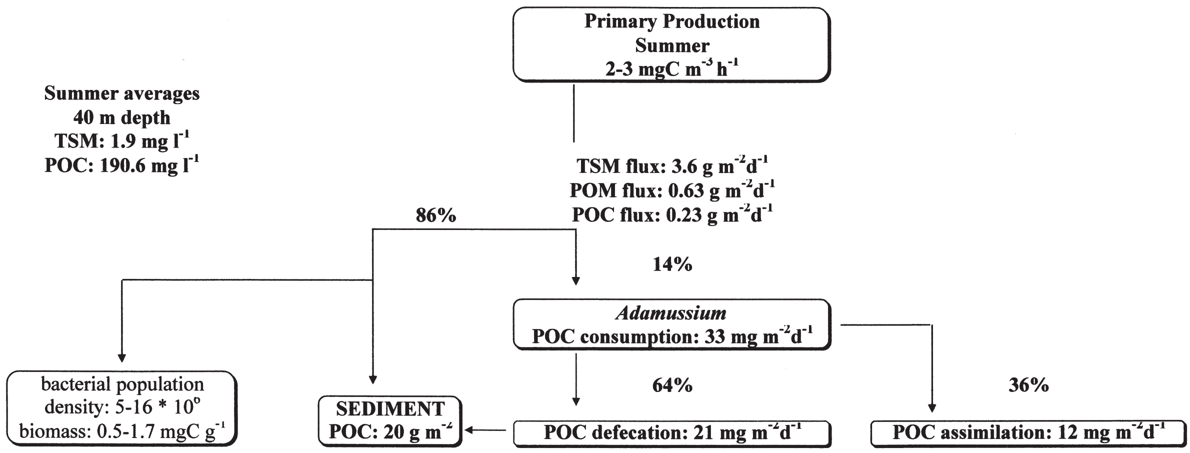

FIG. 2. – Scheme showing the pelagic-benthic coupling, measured as flux of POC, through the littoral scallop *Adamussium colbecki* at 40 m depth (Terra Nova Bay, Ross Sea). Summer primary production, measured total suspended matter (TSM), organic matter (POM) and organic carbon (POC) fluxes, TSM and POC concentration at 40 m depth and utilisation by *Adamussium colbecki* are reported. The POC assimilation of this scallop reaches about 4-5% of the summer primary production (from Chiantore *et al*., 1998, modified).

ing rate of *Adamussium colbecki*, of about 1 l $h^{-1}g^{-1}$ DW soft tissues, and the biodeposition rate, measured as faecal pellet production, of about 5-6 mg DW g^{-1} DW soft tissues d^{-1} (Chiantore *et al*., 1998), it is possible to estimate that the C_{org} flux, through *A. colbecki* towards the bottom, is about 21 mg C m^{-2} d^{-1}. Locally this scallop may process about 14 % of total carbon flux from the water column to the sediments, with an assimilation efficiency of 36 % (Fig. 2). A large part of the flux is also utilized by bacterial communities, with densities (n g^{-1}) varying between 8.7 * 10^5 and 1.56 * 10^8 with an average biomass of 8.3 μg C g^{-1} (A. Pusceddu, unpublished data; Fabiano *et al*., 1995).

The summer food supply increase may influence the life cycle of many benthic species: the comparison between the gonado-somatic indices in *Adamussium colbecki* populations in December and in January shows, in fact, that sexual maturity is reached late in summer, closely linked to the phytoplankton bloom (Chiantore *et al.,* 1998).

The flux of organic matter, being quantitatively variable during the year, could represent a metabolic constraint for suspension feeders when the winter oligotrophic condition occurs (Matsuda *et al*., 1987). But suspension-feeding communities are persistent in time and they do not seem to show significant differences between summer and winter, when the maximum oligotrophy is reached. All this could be faced and overcome thanks to different adaptations with a change of the trophic behaviour during the year (Barnes and Clarke, 1994).

Suspension-feeding polychaetes could easily become deposit feeders, while the large bivalve *Adamussium*, using clapping activities, seems to be able to resuspend the sunken organic matter (Chiantore *et al*., 1998). In this species, it is also possible to note a change in its behaviour: the juveniles are bissally attached on the free adults and use the organic matter resuspended by the clapping of the adults (Ansell *et al*., 1998). Other forms of epibiosis, adopted by serpuloids, bryozoans, holothurians and ophiuroids, are frequent in well structured communities and could be considered an adaptation to find better feeding conditions above the seafloor (Arntz *et al*., 1994).

Another example of change in the trophic strategy to overcome the oligotrophic period and to face the severe fluctuations in food availability in the environment has been described in sponges. Many demosponges take up and store planktonic and benthic diatoms by phagocytic activity (Gaino *et al*., 1994). This new functional adaptation is confirmed by the high Chl-*a* and Chl-*c* values extracted from several sponges collected from Terra Nova Bay at 80-120 m depth (Cattaneo-Vietti *et al*., 2000).

Particularly rich and 3-dimensionally structured communities (Fig. 3) develop in areas characterized by the presence of sponge spicule mats (Dearborn, 1967; Koltun, 1968; Dayton *et al*., 1974; Barthel, 1992): the amount of Chl-*a*, biomass and species richness increase in comparison with spicule-free sediments. A possible explanation is the fact that sponge spicules, creating a 3-D substratum, favour diatom population development, probably supported by the capacity of the opale spicules to channel light as natural optical fibres (Cattaneo-Vietti *et al*., 1996).

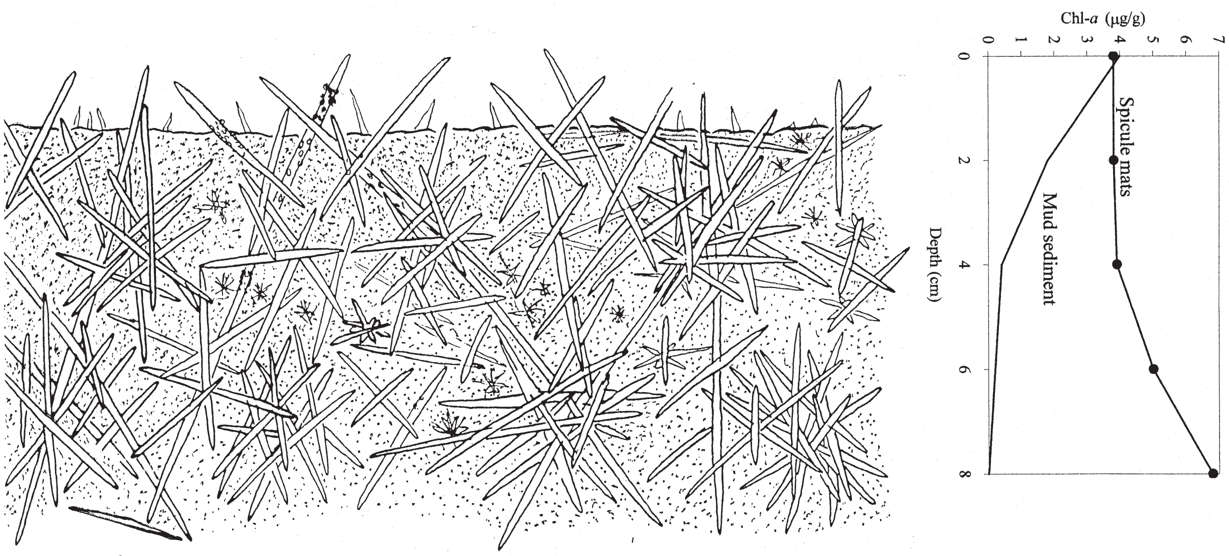

FIG. 3. – Scheme of the superficial texture of a spicule mat in a soft-bottom at Terra Nova Bay (Ross Sea), showing sponge spicules in the sediments. The amount of Chl-*a* inside the sediments rich in spicules does not change in the first 5 cm depth.

PELAGIC-BENTHIC COUPLING IN THE STRAITS OF MAGELLAN

In contrast to the rather uniform environment at Terra Nova Bay, the Straits of Magellan, a 570 km long V-shaped channel between Southern Patagonia and Tierra del Fuego, show a complex geomorphology, turbulent tidal currents, different precipitation rates and fresh water inputs. No studies on the pelagic-benthic coupling in this area have been made, but available data regarding some water column parameters (TSM, Chl-*a*, POC, C:N) suggest that it may be considered as a multi-structured system with strong spatial differences in the composition and origin of the particulate organic matter. Thanks to the rich variety of sills and shelves, it is possible to distinguish at least three well defined sectors (Fig. 4): the Angosturas connect the Straits with the Atlantic and are characterized by a series of narrows and bays in which tidal amplitudes vary from 8 to 1.5 m and the shallow bottoms (30-50 m) are mainly constituted by gravel; Paso Ancho represents the wider part of the channel, characterized by mud and sandy mud bottoms and a maximum depth of 400 m; and the Pacific section, from Cabo Froward to the Pacific, shows depths down to 1100 m and is characterized by important glacio-fluvial runoff constituting coarse sediments.

These sectors have different hydrological and trophic characteristics. The Angosturas are dominated by resuspension processes due to the strong currents (4.5 m sec^{-1}), consequently TSM is high (> 2mg l^{-1}), TSM/POC high (16.36) and the quality of the organic matter is generally poor, as suggested by the high ratio between C and N (C:N > 7; Carrada *et al*., 1994).

Paso Ancho shows a well stratified system, characterized by feeble currents near the bottom (up to 35 cm sec^{-1}; Budillon *et al*., 1997), autotrophic conditions (1-2 Chl-*a* µg l^{-1} up to 7 Chl-*a* µg l^{-1} in November; Panella *et al*., 1991; Antezana *et al*., 1996), evidencing a high primary production (0.5-1 mg C m^{-3} h^{-1}; Saggiomo *et al*., 1994; Saggiomo and Mangoni, 1997). Nanoplankton density reaches 10^5-10^7 cells l^{-1} (Vannucci and Bruni, 1997), while phytoplankton density is about 10,000 cells l^{-1} (Iriarte *et al*., 1997). The biochemical composition of the suspended particulate matter is rich in proteins (C:N < 6), suggesting a high food value.

In the third area, towards the Pacific Ocean, the particulate matter is characterized by large amounts of heterotrophic detritus (0.36 Chl-*a* µg l^{-1}) of quite low energetic value (C:N = 6.07; Carrada *et al*., 1994).

Considering the different hydrodynamic conditions, the quantity and the biochemical composition of the organic particulate matter of the considered sectors, it is reasonable to suppose that important biological coupling processes may occur mainly in Paso Ancho.

In the Magellan Region, many data are available regarding the structure and distribution of species of economic interest, such as the kelp *Macrocystis pyrifera* (Vasquez *et al*., 1984; Santelices, 1989), the mussels or choritos *Aulacomya ater, Choromytilus chorus*, *Mytilus chilensis* (Miranda and Acuña, 1979;

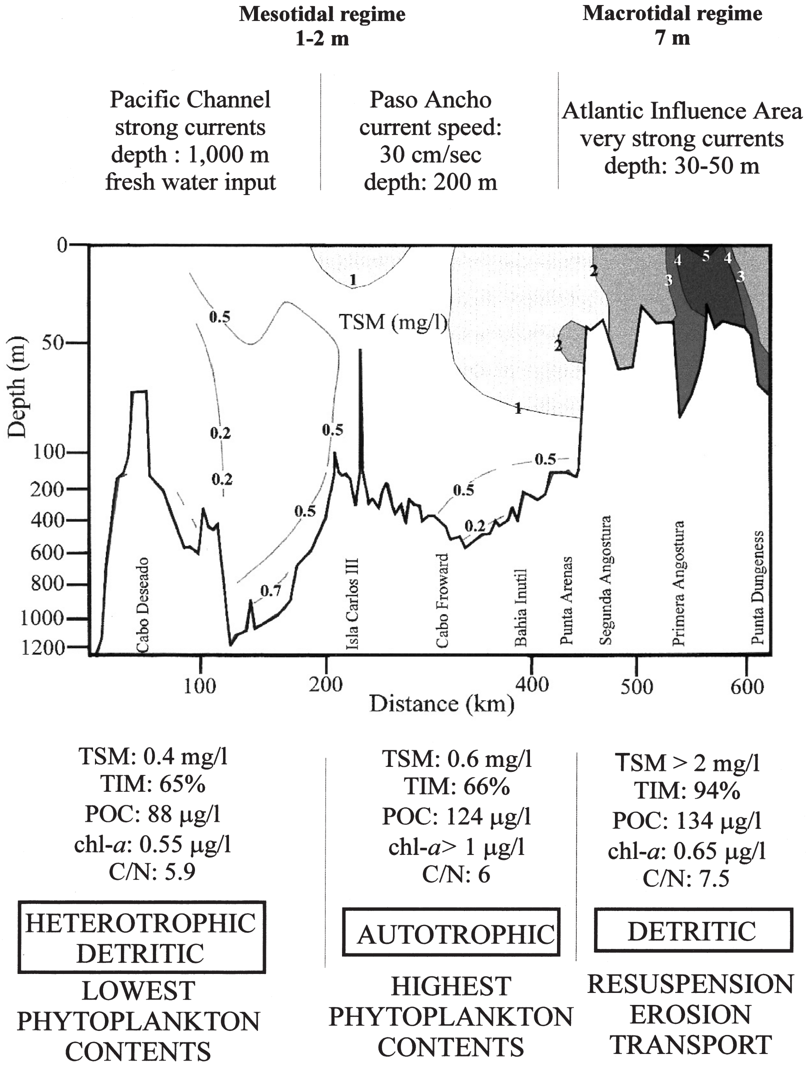

FIG. 4. – Scheme showing the different sectors into which the Straits of Magellan can be classified according to different trophic parameters (TSM = Total Suspended Matter; TIM = Total Inorganic Matter; POC = Particulate Organic Carbon; chl-*a* = chlorophyll-*a*; C/N = Particulate Organic Carbon/Particulate Organic Nitrogen ratio). The isolines indicate water masses of different contents of TSM (from Fontolan and Panella, 1991, modified).

Langley *et al.*, 1980) the scallop or ostión *Chlamys (Zygochlamys) patagonica*, the loco *Concholepas concholepas* (Guzmán *et al.*, 1987a;b), the crabs or centolla *Lithodes santolla* (Campodónico and Oyarzún, 1991; Vinuesa, 1991; Oyarzún, 1992) and centollón *Paralomis granulosa* (Campodónico, 1977), the langostino *Munida subrugosa* (Rodríguez and Bahamonde, 1986), and the erizo *Loxechinus albus*, but little information is available as regards the structure and composition of the benthic communities. This does not show evidence of possible relationships between the different trophic conditions and community distributions, but some considerations can be made. In the Angosturas (Langley *et al.*, 1980) and in Paso Ancho (Miranda and Acuña, 1979), the intertidal and subtidal rocky zones are dominated by mussels which can reach high covering values (90%) and densities (up to 120-150 ind. m^{-2}), together with the limpet *Nacella magellanica* (up to 8 ind. m^{-2}; Guzmán, 1978; Guzmán and Ríos, 1987). Kelp (*Macrocystis pyrifera)* forests (Ojeda and Santelices, 1984; Santelices, 1989) are present in the sheltered areas of the channel, reaching high biomass values. Their densities are controlled by sea star and sea urchin activities (Castilla, 1985). The intertidal soft-bottom communities are very poor, dominated by filamentous green algae (*Enteromorpha* spp., *Ulothrix flacca*) and large populations of the deposit-feeding amphipod *Paramoera fissicauda* (Langley and Lembeye, 1977).

The sublittoral benthos reaches high values, in terms of abundance and biomass, in shallow water (15-130 m) and is characterized by bivalves (*Chlamys patagonica*), decapods (*Munida subrugosa*), asteroids and echinoids, with large populations of deposit feeders and scavenging crustaceans (Arntz *et al*., 1996; Gorny *et al*., 1996) and, where strong floor currents are missing, brachiopods (Gutt and Schickan, 1996). The infauna is dominated by polychaetes (60 %) and molluscs (9-10 %), reaching high values in density and biomass (Gerdes, 1996). The hard bottoms, so common in Antarctic shallow waters, are rare here and no 3-D communities of suspension feeders, comparable to those present in Antarctica, have been found. In particular, sponges, gorgonarians, bryozoans and crinoids seem to play a secondary role.

CONCLUSIONS

In the shallow waters of Terra Nova Bay, the lack of physical disturbance (excluding occasional events such as anchor ice and scouring) favours the development of well-structured benthic communities which depend mainly on the pulse-like particulate organic matter flux. If the environmental conditions are favourable, it supports a strong development of suspension-feeding communities, dominated at different depths by sponges, bivalves, brachiopods, polychaetes and echinoderms. This vertical flux (Fig. 1), which in a few weeks can reach the total annual input, produces significant changes in the physiology (growth, reproduction, spawning) and in the trophic behaviour of many benthic species. Finally, seasonally restricted availability of food may force organisms to save energy by adopting low metabolic rates and slow growth, while many suspension-feeding species seem to be able to take advantage of smaller size particles or to shift to deposit-feeding behaviour with surprising facility.

Conversely, the Straits of Magellan (Fig. 4) are generally dominated by strong currents and the organic input controlled by turbulent diffusion which brings large amounts of detritus. Intense processes of inorganic matter resuspension, occurring mainly in the Angosturas and in the Pacific Channel, reduce the trophic value of the flux, and consequently the benthic communities are poor and less structured. The sessile taxa that are so dominant in Antarctic waters, such as sponges, gorgonarians, and bryozoans, are not so common inside the Straits of Magellan probably because the elevated inorganic component (TIM) can impede and even damage their filtering structures. Accordingly, the communities are dominated by deposit feeders, scavengers and omnivores, such as crustacean decapods. Anyway, bivalves, reaching high values of biomass and density, play an important role in the coupling processes in both areas.

Food input from the water column may sometimes be insufficient to cover the requirements of some communities which reach high values of biomass and density (Arntz *et al*., 1994) suggesting a lateral advection of suspended matter as an additional resource. At Terra Nova Bay and at Paso Ancho, large macroalgal communities can certainly support this secondary input, which is used by large deposit-feeding populations of crustaceans.

Finally, it is import to underline that studies on the pelagic-benthic coupling also have an applied significance and could be essential in the evaluation of the trophic capacity and the environmental response in the location of sea-farming sites, which is an ever-growing activity in the Magellan region. These activities will in fact play an important role in changing the pristine features of the Magellan environment, determining more or less heavy phenomena of dystrophy, through the input of high amounts of catabolites and particulate organic matter.

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