COMPARATIVE STUDY OF EFFECTS OF ORGANIC MATERIALS FROM TERRESTRIAL AND MARINE SOURCES ON THE GROWTH OF SUBANTARCTIC MARINE PELAGIC BACTERIA

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COMPARATIVE STUDY OF EFFECTS OF ORGANIC MATERIALS FROM TERRESTRIAL AND MARINE SOURCES ON THE GROWTH OF SUBANTARCTIC MARINE PELAGIC BACTERIA

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ANTARCTIQUE
BACTÉRIOPLANCTON
ZOOPLANCTON
GOÉMON GÉANT
MATIÈRE ORGANIQUE TERRESTRE

RÉSUMÉ – Les effets de divers matériaux organiques d'origine marine et terrestre sur les microflores bactériennes pélagiques subantarctiques ont été comparés dans des bacs expérimentaux de 3 m^3 remplis d'eau de mer. Le matériel terrestre est composé essentiellement de débris de la Rosacée *Acaena magellanica* (lam.) Vahl qui est dominante dans la zone subantarctique étudiée. Les sources marines correspondent d'une part au goémon géant *Macrocystis pyrifera* (C.A. Agardh) et au Copépode *Drepanopus pectinatus* (Brady, 1887). Le suivi bactériologique comprend une analyse quantitative des microflores totale et hétérotrophe ainsi qu'une estimation de la production bactérienne par incorporation de Thymidine tritiée. La plus forte stimulation de la croissance bactérienne est obtenue après addition de zooplancton fraichement tué, mais l'influence positive de l'ajout de goémon géant est toujours significative. L'absence totale d'effet induit par l'addition de matériel terrestre suggère que ce type de matériel pourrait n'avoir, au moins dans la zone côtière subantarctique étudiée, qu'un impact relativement limité sur les flux biogéniques.

ANTARCTICA
BACTERIOPLANKTON
ZOOPLANKTON
GIANT KELP
TERRESTRIAL ORGANIC MATTER

ABSTRACT – The effects of organic material from terrestrial and marine sources on the growth of subantarctic marine pelagic bacteria was compared in 3 m^3 batch experiments. The terrestrial source was mainly made up of the subantarctic dominating rosaceous suffruticose herb *Acaena magellanica* (Lam.) Vahl. The marine sources included giant kelp (*Macrocystis pyrifera* C.A. Agardh) and zooplankton (*Drepanopus pectinatus* Brady, 1887). The bacteriological survey included total and heterotrophic counts and estimation of bacterial production by the ^3H thymidine method. The main enhancement of bacterial growth was observed after addition of dead zooplankton, but the influence of giant kelp was always significant. The absence of any measurable effect of terrestrial material suggest that, in this particular subantarctic coastal area, terrestrial inputs may have a rather limited influence on the biogenic fluxes.

INTRODUCTION

Bacteria are capable of metabolising dissolved organic compounds released from living and detrital organic materials (Robertson *et al.* 1982, Kirchman *et al.* 1984). Bacteria also have enzymes for degrading particulate organic compounds and are capable of altering the physical composition of detritus (Rieper-Kirchner 1989, Hoppe *et al.* 1993). Recent reviews on marine microbes (Meyer-Reil 1984, Moriarty 1986, Cho & Azam 1988) have acknowledged that detrital decomposition is a microbially mediated process, but that surprisingly little is known about controls of microbial assemblages in nature. The aim of the present paper is to compare the effect of different sources of terrestrial and marine organic matter on natural subantarctic seawater microbial assemblages.

Reviewing recent reports of phytoplankton and bacterial abundance and production, Bird & Kalff (1984) and Cole *et al.* (1988) found significant correlations between bacterial and phytoplankton parameters suggesting the ubiquity of a functional relationship between bacteria and phytoplankton. Since the latter excrete the organic substrates essential for bacterial metabolism, it can be assumed that bacterial dynamics are essentially controlled

by phytoplankton dynamics. This model is probably valid in the oceans, however, in coastal areas, the situation is likely to be more complex due to the existence of important sources of non-phytoplanktonic substrates (Albrigh 1983, Ducklow & Kirchman 1983, Wright & Coffin 1983, Painchaud & Therriault 1989).

In the subantarctic marine environment the main non-phytoplanktonic sources of organic matter are relatively limited.

Drepanopus pectinatus Brady, specifically localised in the southern Indian Ocean (Hülsemann 1985), is the predominant herbivorous copepod species in the Morbihan Bay and represents more than 99 % of the zooplankton population in the summer period (Razouls & Razouls 1990). Thus this single copepod species makes up the bulk of the mesozooplankton biomass.

Penguins and other birds transfer nutritive materials from a large zone of the Southern ocean to some restricted terrestrial area. Consequently, large rookeries of seabirds produce substantial amounts of organic matter (Myrcha *et al.* 1985). Previous studies have demonstrated the impact of Antarctic ornithogenic soils on the surrounding seawater bacterioplankton (Delille 1987, 1990a, Fiala & Delille 1992).

A substantial proportion of the coastlines are occupied by highly productive giant kelp *Macrocystis pyrifera* C.A. Agardh forests (Belsher & Mouchot 1992). Both living and stranded macrophytes support a large part of the subantarctic coastal food webs (Bouvy *et al.* 1986, Bouvy & Delille 1988, Delille & Perret 1991).

Terrestrial coastal environment is dominated by the rosaceous suffruticose herb *Acaena magellanica* (Lam.) Vahl. Leaf senescence can begin early in summer (Walton 1976). All leaves die before winter and considerable decay occur (Hurst *et al.* 1985). Although leached materials accumulate in the litter layer, considerable amount of organic material reach the marine area (Platt 1979).

The present study was designed to compare the enhancing effects of organic material coming from different sources on marine pelagic bacterial abundance.

MATERIALS AND METHODS

Study area

The study was carried out between January and July 1988 using water collected from Morbihan Bay, Kerguelen Archipelago (49° 20'S ; 70° 10'E). Located in the south-east of the Archipelago, the Bay (about 30 × 20 km), which is always free of ice, opens to the Indian Ocean through Royal Pass (12 km wide and 40 m deep). Batch experiments were carried out on-shore near the "Port aux Français" marine laboratory.

Experimental studies

Fresh kelp were always harvested in the same surface station located in a giant kelp *Macrocystis pyrifera* (L.) C.A. Agardh forest growing in front of the laboratory.

Zooplankton was collected at a depth of 50 m using a WP2 net (0.1 mm mesh size) which was vertically hauled from bottom to surface. Animals were killed by freezing.

For the January 1987 experiment, detritic terrestrial material was collected using a 0.1 mm mesh size net in a small stream flowing through a large *Acaena magellanica* field located approximately two kilometres to the west of the laboratory ("Anse du Pacha"). For the second terrestrial enrichment experiment (June 1987), living and senescent leaves of *Acaena magellanica* were harvested in the same location.

Batch experiments were carried out in 3 m^3 tanks (4 cylinders of 150 cm diameter and 170 cm depth) exposed to natural environmental conditions. The tanks (experiments and one control without artificial addition) were filled simultaneously with coastal seawater and incubated for 5 to 10 days at ambient temperature (ranging from 2°C in winter to 13°C in summer). Experiments commenced with an addition of a given quantity of organic nutrients (3 or 30 mg C l^{-1}) in the enriched tanks. Estimations of natural concentrations of the added nutrients are extremely difficult. Their distributions are very patchy and very strong gradients occur between coastal and offshore areas (Bouvy *et al.* 1986). The concentration generally used (3 mg C l^{-1}) try to simulate the enrichment in *Macrocystis* leaves visually observed in coastal area after a moderate storm. A stronger concentration (30 mg C l^{-1}) was chosen for the second terrestrial input experiment after the first tests showing that the used concentration had no measurable effects on seawater bacterial microflora.

Daily sampling allowed a regular survey of the bacterial microflora (3 replicate subsamples from each tank, taken 2 cm under the surface with a sterile glass pipette).

Determination of bacterial parameters

Total bacteria were determined by acridine orange direct counts (Hobbie *et al.* 1977). A minimum of 300 fluorescing cells with a clear outline and definite cell shape were counted as bacterial cells in ten randomly selected microscope fields.

After tenfold dilutions in sterile aged seawater, viable heterotrophic platable bacteria were counted using the spread plate method with 2216 E medium (Oppenheimer & ZoBell, 1952, Marine Agar DIFCO). Each dilution were plated in triplicate. After inoculation (0.2 ml) the plates were incubated at 12°C for 10 days. A large majority of the bacteria isolated from subantarctic seawater must be considered psychrotrophic and not truly psychrophilic strains (Delille & Perret 1989) ; in Antarctic and subantarctic seawater samples there was no significant difference between viable counts obtained after incubation at 4°C and 20°C (Delille *et al.* 1988, Delille 1992, Fiala & Delille 1992). Thus, the relatively high incubation temperature used in the present study had no significant effect on the data and allowed a substantial reduction of the incubation time.

The precision of the bacterial counts, based on ten replicates during two periods of the year (winter and summer), was 10 % for AODC and 15 % for viable heterotrophic platable bacteria.

The rate of uptake of tritiated thymidine was measured over the course of the experiments according to the procedure of Fuhrman and Azam (1982). The rate of uptake was determined in one hour incubations in the dark of triplicate aliquots at a final concentration of 10 nM methyl ^{3}H-thymidine. The one hour period was within the linear portion of the thymidine incorporation curve (unpublished data).

Estimation of organic carbon content

Organic content of the added material was evaluated on aliquots of terrestrial herbs, kelp and zooplankton. Carbon was oxidised (1 200°C) in an induction furnace equipped with an infra-red detector (LECO IR 212). The total organic carbon was estimated without washing on separate aliquots of dry material decalcified by a 12 hours treatment with 1M H_3PO_4 at 60 °C.

RESULTS

No lag times were observed in the increase in heterotrophic bacterial populations (Fig. 1 and 2). Increases in total bacteria appeared later and were always much smaller than viable count increases. The bacterial increase could be divided in two distinct phases. The first one showed a stimulation of the heterotrophic viable community while the total microflora showed little change. The second phase indicated a concomitant change of total and heterotrophic bacteria (this fast growth of bacterial microflora gave a direct counts/viable counts ratio close to 1). Similar patterns were observed in every experiment.

Effect of addition of marine materials

Strong enhancement of bacterial abundance (Fig. 1) and production (Table I) was observed after addition of giant kelp and dead zooplanktonic cells (*Drepanopus pectinatus*). Added zooplanktonic material could no longer be seen after the second day of incubation of the summer experiment (February 1987).

Effect of terrestrial macrophytes addition

Both detrital (first experiment, January 1987) and fresh (second experiment, June 1987) materials originating from *Acaena magellanica* had no significant effects on bacterial microflora during both the summer (January 1987) and fall (June 1987) experiments (Fig. 2, Table I). The early peak (first hours) of bacterial abundance observed during each experiment might be attributed to the survivance of bacteria originally present in the added material.

DISCUSSION

It has been demonstrated that the uptake of ^{3}H-thymidine is relatively specific for the bacterial assemblage (Davis, 1989). Its rate of incorporation is now employed routinely as an index of bacterial productivity (Fuhrman & Azam, 1982). However, the appropriate factor for converting moles of thymidine taken up by bacterial cells to the production of bacterial cells has been increasingly questioned in recent years (Moriarty 1984, Scavia & Laird 1987, Smits & Riemann 1988, Karl *et al.* 1991). For this reason our conclusions concerning bacterial productivity are based only on relative differences in the rate of uptake of ^{3}H-

Table I. – Changes in bacterial production during the first 72 hours for each experiment.

	Zooplk.	Kelp	*Acaena*
	June	*September*	*June*
	10^{-3} nmol ^{3}H thymidine $l^{-1} h^{-1}$		
To	1	2	1
To+72h	58	53	7

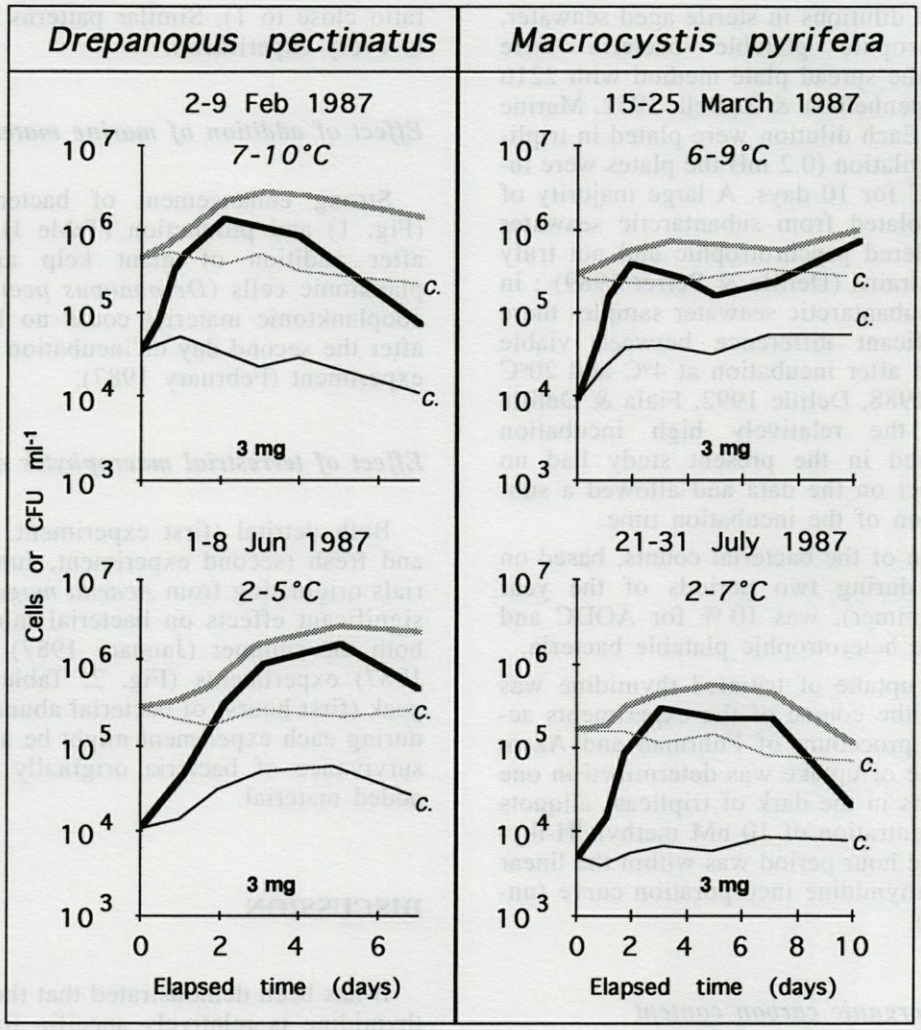

Fig. 1. – Comparison of time course of changes in total (dotted lines) and heterotrophic bacterial microflora (solid lines) after addition of zooplankton or kelp materials (c. = control, concentration of added material is expressed in mg organic C l^{-1}).

thymidine between bacterial microflora of each kind of enrichment.

Total direct counts reflect the actual bacterial abundance but their variations in time are less pronounced than the changes observed with heterotrophic bacteria. During growth periods the quantitative difference between direct and viable counts showed a marked decline. Similar findings related to the decreasing number of metabolically inactive cells present in the total bacterial microflora have been previously reported even in natural conditions (Bouvy *et al.* 1986, Delille *et al.* 1988) and are discussed elsewhere (Delille 1987, Delille & Bouvy 1989).

A definite seasonality in the species composition and abundance has been described for the bacterial microflora of coastal subantarctic seawater (Delille 1990b). The stucture of the seawater bacterial communities encountered at the beginning of each experiment may thus largely determine the nature of the microflora which develops following the addition of organic material (Delille & Vaillant 1990). Further, the presence of possible different starting levels of bacterivorous protozoa in the different treatments could have masked some short term responses in bacterioplankton abundances to enrichment. Nevertheless, even in winter, giant kelp and zooplankton additions always induced rapid and substantial bacterial increases. The observed absence of marked seasonality suggest that, as earlier reported (Delille *et al.* 1988, Delille & Perret 1989), temperature has only a slight influence on bacterial growth in subantarctic seawater.

It is generally assumed that most of the primary production in pelagic ecosystems is sustained by a continuous and rapid recycling of the growth-limiting inorganic nutrients and that bacteria are the major agents effecting the rapid remineralisa-

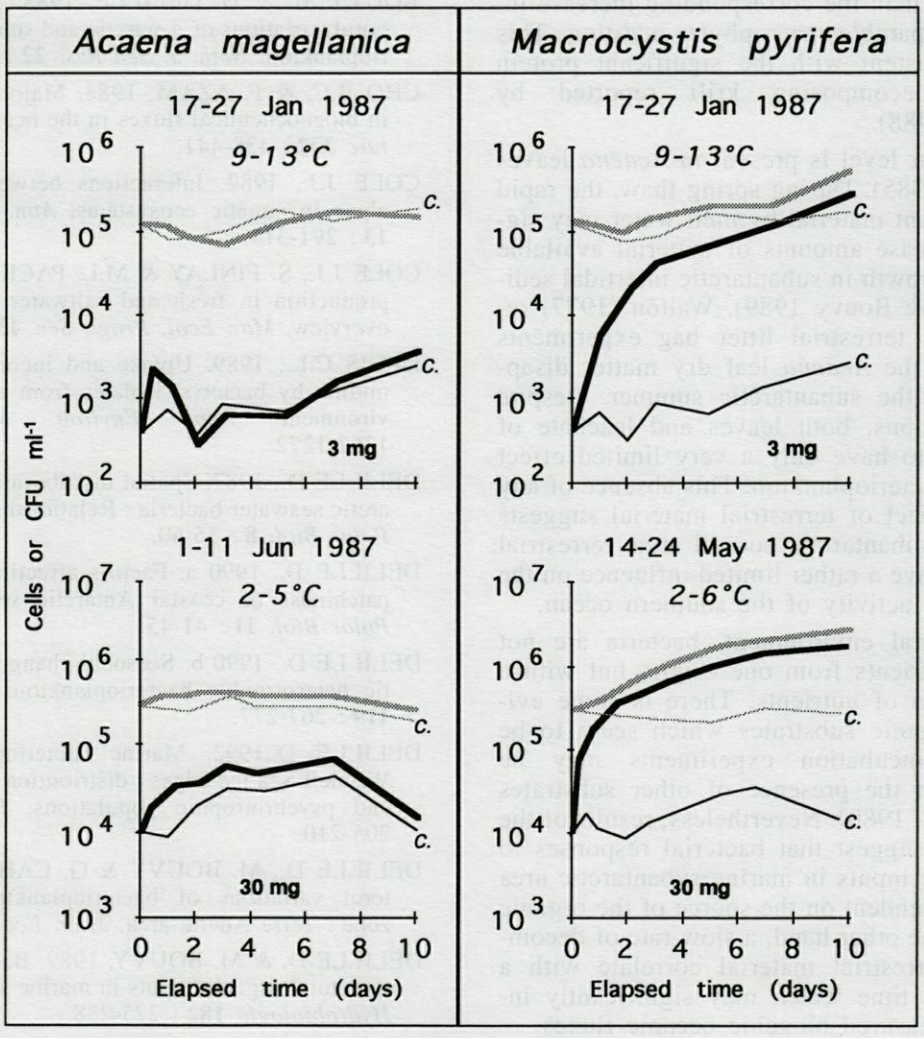

Fig. 2. – Comparison of time course of changes in total (dotted lines) and heterotrophic bacterial microflora (solid lines) after addition of detritic (January) or freshly harvested (June) terrestrial plant materials or marine kelp materials (c. = control, concentration of added material is expressed in mg organic C l^{-1}).

tion of nutrients (Lancelot & Billen 1984, Cole *et al.* 1988, Glibert *et al.* 1991, Fiala & Delille 1992). On the other hand, heterotrophic bacteria in the euphotic zone are largely reliant on phytoplankton for their energy supply, either through excretion of dissolved organic matter (Kuosa & Kivi 1989, Suttle *et al.* 1991) or by decomposition of dead phytoplankton cells (Riemann & Sondergaard 1986, Jumars *et al.* 1989, Van Boekel *et al.* 1992). However, it is likely that living phytoplanktonic cells may be resistant to microbial invasion and then to further decomposition (Cole 1982, Vaqué *et al.* 1989). The present investigation clearly reveals that natural bacterioplanktonic assemblages are able to utilise other sources of organic matter than phytoplanktonic materials.

Since the methods used were not suited to assessing the effects of grazing on the abundance of bacteria in the batches, the estimates probably underestimate growth rates. However, the study of Linley & Newell (1981) which examined the growth of bacterial microflora and microheterotrophic grazers on kelp debris in South Africa showed a lag time of 8 days before the effects of microheterotrophic grazing were detectable. The fact that logarithmic growths of bacteria were observed throughout the initial three day periods suggests that grazing may have been relatively low during these initial period and confirm the obvious activity of southern polar bacterial microflora previously reported (Delille *et al.* 1988, Delille & Vaillant 1990).

Although a low bacterial activity in fresh Antarctic krill tissue has been observed (Kelly *et al.* 1978, Turkiewicz *et al.* 1982) and that additionally, a very low concentration of chitinolytic bacteria ($\simeq$ 1 cell ml^{-1}) has been reported in the water column in the Southern Ocean (Herwig *et al.* 1988) addition of dead zooplankton induced an enhancement of bacterial abundance and pro-

duction larger than the corresponding increase induced by comparable macrophytes addition. This result is consistent with the significant protein loss from decomposing krill reported by Zdanowski (1988).

A high sugar level is present in *Acaena* leaves (Hurst *et al.* 1985). During spring thaw, the rapid leaching of plant material by melt water may significantly increase amounts of material available for bacterial growth in subantarctic intertidal sediment (Delille & Bouvy 1989). Walton (1977) reported that in terrestrial litter bag experiments over 90 % of the *Acaena* leaf dry matter disappeared during the subantarctic summer. Despite these observations, both leaves and leachate of *Acaena* seem to have only a very limited effect on seawater bacterioplankton. This absence of any measurable effect of terrestrial material suggests that, even in subantarctic coastal area, terrestrial inputs could have a rather limited influence on the bacteriological activity of the southern ocean.

In the natural environment, bacteria are not faced with nutrients from one origin, but with a broad spectrum of nutrients. There is some evidence that organic substrates which seem to be resistant in incubation experiments may be decomposed in the presence of other substrates (Jacobson *et al.* 1980). Nevertheless, results of the present study suggest that bacterial responses to natural organic inputs in marine subantarctic area are greatly dependent on the source of the organic material. On the other hand, a slow rate of decomposition of terrestrial material correlate with a long residence time which may significantly influence the measured biogenic oceanic fluxes.

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REFERENCES

ALBRIGHT L.J., 1983. Influence of river-ocean plumes upon bacterioplankton production of the Strait of Georgia, B.C. *Mar. Ecol. Progr. Ser.* **12** : 107-113.

BELSHER T. & M.C. MOUCHOT, 1992. Use of Satellite Imagery in Management of Giant Kelp Resources, Morbihan Gulf, Kerguelen Archipelago. *Oceanologica Acta* **15** : 297-307.

BIRD D.F. & J. KALFF, 1984. Empirical relationships between bacterial abundance and chlorophyll concentration in fresh and marine waters. *Canad. J. Fish. Aqu. Sci.* **41** : 1015-1023.

BOUVY M., M. LE ROMANCER & D. DELILLE, 1986. Significance of microheterotrophs in relation to the degradation process of sub-Antarctic kelp beds (*Macrocystis pyrifera*). *Polar Biol.* **5** : 249-253.

BOUVY M. & D. DELILLE, 1988. Spatial and temporal variations of Antarctic and sub-Antarctic bacterioplankton. *Neth. J. Sea Res.* **22** : 139-147.

CHO B.C. & F. AZAM, 1988. Major role of bacteria in biogeochemical fluxes in the ocean's interior. *Nature* **332** : 438-441.

COLE J.J., 1982. Interactions between bacteria and algae in aquatic ecosystems. *Ann. Rev. Ecol. Syst.* **13** : 291-314.

COLE J.J., S. FINLAY & M.L. PACE, 1988. Bacterial production in fresh and saltwater : a cross-system overview. *Mar. Ecol. Progr. Ser.* **43** : 1-10.

DAVIS C.L., 1989. Uptake and incorporation of thymidine by bacterial isolates from an upwelling environment. *Appl. Environ. Microbiol.* **55** : 1267-1272.

DELILLE D., 1987. Spatial distribution of coastal Antarctic seawater bacteria : Relationship with avifauna. *Polar Biol.* **8** : 55-60.

DELILLE D., 1990 a. Factors affecting the horizontal patchiness of coastal Antarctic seawater bacteria. *Polar Biol.* **11** : 41-45.

DELILLE D., 1990 b. Seasonal changes of sub-Antarctic heterotrophic bacterioplankton. *Archiv Hydrob.* **119** : 267-277.

DELILLE D.,1992. Marine bacterioplankton at the Weddell Sea ice edges : distribution of psychrophilic and psychrotrophic populations. *Polar Biol.* **12** : 205-210.

DELILLE D., M. BOUVY & G. CAHET, 1988. Short term variations of bacterioplankton in Antarctic zone : Terre Adélie area. *Micr. Ecol.* **15** : 293-309.

DELILLE D. & M. BOUVY, 1989. Bacterial responses to natural organic inputs in marine subantarctic area. *Hydrobiologia* **182** : 225-238.

DELILLE D. & E. PERRET, 1989. Influence of temperature on the growth potential of Southern Polar marine bacteria. *Micr. Ecol.* **18** : 117-123.

DELILLE D. & N. VAILLANT, 1990. The Influence of crude oil on the growth of sub-Antarctic marine bacteria. *Antarc. Sci.* **2** : 123-127.

DELILLE D. & E. PERRET, 1991. The influence of giant kelp *Macrocystis pyrifera*, on the growth of subaAntarctic marine bacteria. *J. Exp. Mar. Biol. Ecol.* **153** : 227-239.

DUCKLOW H.W. & D.L. KIRCHMAN, 1983. Bacterial dynamics and distribution during a spring diatom bloom in the Hudson River plume, USA. *J. Plankt. Res.* **5** : 333-356.

FIALA M. & D. DELILLE, 1992. Variability and interactions of phytoplankton and bacterioplankton in the Antarctic neritic area. *Mar. Ecol. Progr. Ser.* **89** : 135-146.

FUHRMAN J.A. & F. AZAM, 1982. Thymidine incorporation as a measure of heterotrophic bacterioplankton in marine surface waters : evaluation and field results. *Mar. Biol.* **66** : 109-120.

GLIBERT P.M., C. GARSIDE, J.A. FUHRMAN & M.R. ROMAN, 1991. Time-dependent coupling of inorganic and organic nitrogen uptake and regeneration in the plume of the Chesapeake Bay estuary and

its regulation by large heterotrophs. *Limnol. Oceanogr.* **36** : 895-909.

HERWIG R.P., N.P. PELLERIN, R.L. IRGENS, J.S. MAKI & T.J. STALEY, 1988. Chitinolytic bacteria and chitin mineralization in the marine waters and sediments along the Antarctic Peninsula. *FEMS Microb. Ecol.* **53** : 101-112.

HOBBIE J.E., R.J. DALEY & S. JASPER, 1977. Use of nuclepore filters for counting bacteria by fluorescence microscopy. *Appl. Environ. Microbiol.* **33** : 1225-1228.

HOPPE H.G., H. DUCKLOW & B. KARRASCH, 1993. Evidence for dependency of bacterial growth on enzymatic hydrolysis of particulate organic matter in the mesopelagic ocean. *Mar. Ecol. Progr. Ser.* **93** : 277-283.

HULSEMANN K., 1985. Two species of *Drepanopus* Brady (Copepoda, Calanoida) with discrete ranges in the southern hemisphere. *J. Plankt. Res.* **7** : 909-925.

HURST J.L., G.J.F. PUGH & D.W.H. WALTON, 1985. The effects of freeze-thaw cycles and leaching on the loss of soluble carbohydtrates from leaf material of two sub-Antarctic plants. *Polar Biol.* **4** : 27-31.

JACOBSON S.N., N.L. O'MARA, M. ALEXANDER, 1980. Evidence for cometabolism in sewage. *Appl. Environ. Microbiol.* **40** : 917-921.

JUMARS P.A., D.L. PERRY, J.A. BAROSS, M.J. PERRY & B.W. FROST, 1989. Closing the microbial loop : dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. *Deep-Sea Res.* **36** : 483-495.

KARL D.M., O. HOLM-HANSEN, G.T. TAYLOR, G. TIEN & D.F. BIRD, 1991. Microbial biomass and productivity in the western Bransfield Strait, Antarctica during the 1986-87 summer. *Deep-Sea Res.* **89** : 1029-1055.

KELLY M.D., S. LUKASCHEWSKI & C.G. ANDERSON, 1978. Bacterial flora of Antarctic krill (*Euphausia superba)* and some of their enzymatic properties. *J. Food Sci.* **43** : 1196-1197.

KIRCHMAN D.L., L. MAZZELLA, R.S. ALBERTE & R. MITCHELL, 1984. Epiphytic bacterial production on *Zostera marina*. *Mar. Ecol. Progr. Ser.* **15** : 117-123.

KUOSA H. & K. KIVI, 1989. Bacteria and heterotrophic flagellates in the pelagic carbon cycle in the northern Baltic Sea. *Mar. Ecol. Progr. Ser.* **53** : 93-100.

LANCELOT C. & G. BILLEN, 1984. Activity of heterotrophic bacteria and its coupling to primary production during the spring phytoplankton bloom in the southern bight of the north sea. *Limn. Oceanogr.* **29** : 721-730.

LINLEY E.A.S. & R.C. NEWELL, 1981. Microheterotrophic communities associated with the degradation of kelp debris. *Kieler Meeresf.* **5** : 345-355.

MEYER-REIL L.A., 1984. Bacterial biomass and heterotrophic activity in sediments and overlying waters. *In*, Hobbie J.E. & Williams P.J. Le B., eds. Heterotrophic activity in the sea., 523-546.

MORIARTY D.J.W., 1984. Measurements of bacterial growth rates in some marine systems using the incorporation of tritiated thymidine into DNA. *In*, Hobbie J.E. & Williams P.J.Le B., eds. Heterotrophic Activity in the Sea. Plenum Press, New York, 231-271.

MORIARTY D.J.W., 1986. Measurement of bacterial growth rates in aquatic systems from rates of nucleic acid synthesis. *Adv. Micr. Ecol.* **9** : 245-292.

MYRCHA A., S.J. PIETR & A. TATUR, 1985. The role of Pygoscelid penguin rookeries in nutrient cycles at Admiralty Bay, King George Island. *In*, Siegfried W.R., Condy P.R. & Laws R.M., eds. Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin, 156-162.

OPPENHEIMER C.H. & C.E. ZOBELL, 1952. The growth and viability of sixty three species of marine bacteria as influenced by hydrostatic pressure. *J. Mar. Res.* **11** : 10-18.

PAINCHAUD J. & J.-C. THERRIAULT, 1989. Relationships between bacteria, phytoplankton and particulate organic carbon in the upper St.Lawrence estuary. *Mar. Ecol. Progr. Ser.* **56** : 301-311.

PLATT H.M., 1979. Sedimentation and the distribution of organic matter in a subantarctic marine bay. *Estuar. Coast. Mar. Sci.* **9** : 51-63.

RAZOULS C. & Z. RAZOULS, 1990. Biological cycle of a population of sub-Antarctic copepod, *Drepanopus pectinatus* (Pseudocalanidae), Kerguelen Archipelago. *Polar Biol.* **10** 541-543.

RIEMANN B. & G.A. SONDERGAARD, 1986. Regulation of bacterial secondary production in two eutrophic lakes and in experimental enclosures. *J. Plankt. Res.* **8** : 519-536.

RIEPER-KIRCHNER M., 1989. Microbial degradation of North Sea macroalgae : field and laboratory studies. *Bot. Mar.* **32** : 241-252.

ROBERTSON A.I., A.L. MILLS & J.C. ZIEMAN, 1982. Microbial synthesis of detritus-like particles from dissolved organic carbon released by tropical seagrasses. *Mar. Ecol. Progr. Ser.* **7** : 279-285.

SCAVIA D. & G.A. LAIRD, 1987. Bacterioplankton in lake Michigan : Dynamics, controls, and significance to carbon flux. *Limnol. Oceanogr.* **32** : 1017-1033.

SMITS J.D. & B. RIEMANN, 1986. Calculation of cell production from ^{3}H thymidine incorporation with freshwater bacteria. *Appl. Environm. Microbiol.* **54** : 2213-2219.

SUTTLE C.A., A.M. CHAN & J.A. FUHRMAN, 1991. Dissolved free amino acids in the Sargasso Sea : uptake and respiration rates, turnover times, and concentrations. *Mar. Ecol. Progr. Ser.* **70** : 189-199.

TURKIEWICZ M., E. GALAS & H. KALINOWSKA, 1982. Microflora of Antarctic krill (*Euphausia superba). Acta Microbiol. Polonica* **31** : 175-184.

VAN BOEKEL V.H.M., F.C. HANSEN, R. RIEGMAN & R.P.M. BAK, 1992. Lysis-induced decline of a *Phaeocystis* spring bloom and coupling with the microbial foodweb. *Mar. Ecol. Progr. Ser.* **81** : 269-276.

VAQUÉ D., C.M. DUARTE & C. MARASSÉ, 1989. Phytoplankton colonization by bacteria : encounter probability as a limiting factor. *Mar. Ecol. Progr. Ser.* **54** : 137-140.

WALTON D.W.H., 1976. Dry matter production in *Aceana* (Rosaceae) on a sub-Antarctic island. *J. Ecol.* **64** : 399-415.

WALTON D.W.H., 1977. Studies on *Acaena* (Rosaceae). 2. Leaf production and senescence. *British Antarc. Surv. Bull.* **45** : 93-100.

WRIGHT R.T. & R.B. COFFIN, 1983. Planktonic bacteria in estuaries and coastal waters of northern Massachussets : spatial and temporal distribution. *Mar. Ecol. Progr. ser.* **11** : 205-216.

ZDANOWSKI M.K., 1988. Matter conversion in the course of krill (*Euphausia superba* Dana) decomposition in the Antarctic ecosystem. *Polsk. Arch. Hydrob.* **35** : 65-96.

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