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Factors regulating bacterial abundance in Antarctic coastal and shelf waters

ABSTRACT: In general, Antarctic marine bacteria are small, with biovolumes ranging from 0.139 to 0.204 μm^3 cell^{-1}, but their total biomass in seawater is considerable due to relatively high numbers that approximate to 10^{20} cells km^{-3}. Bacterial biomass becomes more concentrated closer to land. Our multi-year Antarctic studies demonstrated an average total bacterial biomass of 504 tons in Admirality Bay (24 km^3) or 21 tons per 1 km^3, versus 6.4 tons per per 1 km^3 in the open ocean. Strikingly, bacterial biomass reached 330 tons per 1 km^3 of seawater at the sea-ice edge, as sampled in Goulden Cove in Admiralty Bay. Bacterial biomass in Admirality Bay, which we believe can be enriched by halotolerant and thermotolerant fresh water bacteria from glacial streams, is equal to or even exceeds that of the standing stock of krill (100–630 tons per bay) or other major living components, including phytoplankton (657 tons), flagellates (591 tons), and ciliates (412 tons). However, the bacterial biomass is exceeded by several orders of magnitude by non-living organic matter, which constitutes the basic bacterial carbon source. Factors regulating high bacterial abundance in the vicinity of land are discussed.

K e y   w o r d s : heterotrophic bacteria, protozooplankton, phytoplankton, krill, organic matter, temperature, sea water, freshwater.

Introduction

In his 1969 article "Photosynthesis and fish production in the sea" Ryther remarked that 90% of the world's ocean and nearly three-fourths of the earth's surface is essentially a biological desert. Clearly, this concept cannot be supported as more is learned about the potential role of the "biological pump" (Moore and Bolin 1987), the biological and physical processes in the world's oceans that regulate removal of atmospheric CO_2 (Broecker et al. 1979), organic matter production, and flux and remineralization of particulate matter. There are, however, remarkable differences in micro- and macroorganisms' biomass inshore (high) compared to the open sea (low). Our multi-year studies in Antarctica
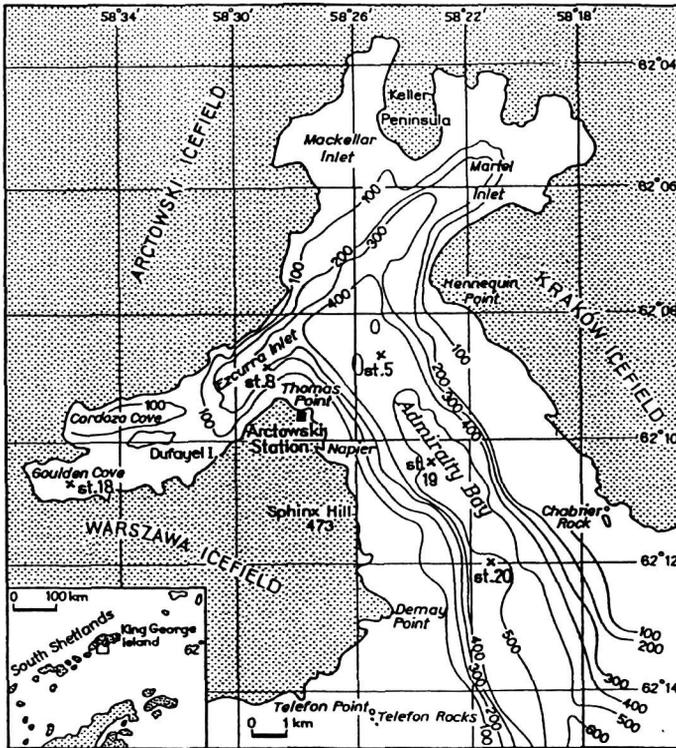
Fig. 1. Bacteriological sampling stations in Admiralty Bay. Map based on Furmańczyk
and Marsz (1980). From Zdanowski (1995).

(Zdanowski 1995), demonstrated that the Antarctic landmass and closely asso-
ciated islands clearly contribute to both the total biomass and metabolic chara-
cteristics of local marine bacteria.

In this paper some suggestions are made as to why bacterial abundance in
nearshore regions is higher, as shown by the example of Admiralty Bay (Fig. 1).
Moreover, relationships between the relative abundance of bacteria and other
biota, and between bacteria and their basic organic source – dissolved organic
carbon (DOC), in the nearshore region and the open sea are evaluated. For this
purpose, many published reports as well as unpublished data are included. In
addition, the halotolerant and thermotolerant properties of freshwater bacteria
that enable survival in other environments are discussed.

Bacteria in Admiralty Bay

Multi-year studies (1979–1988) in Antarctica, across the Drake Passage, the
Bransfield Strait and in Admiralty Bay (Fig. 1), have demonstrated that the
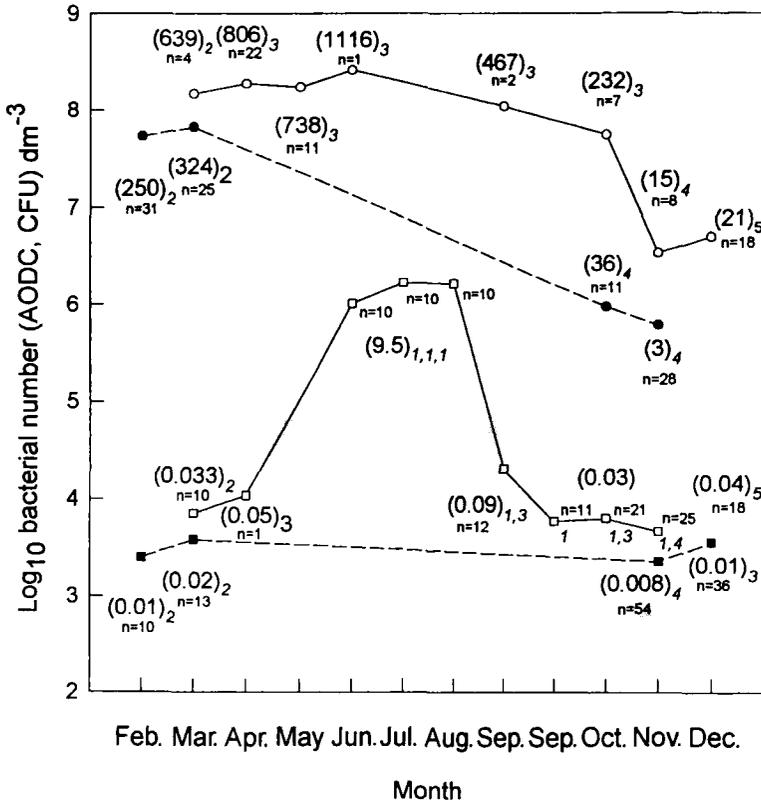
Fig. 2. Seasonal variations of total (AODC) and saprophytic (CFU) bacterial numbers in Admiralty Bay (solid lines), and in open sea (broken lines) based on mean values obtained in 1979 to 1988; 1 – 1979*, 2 – 1981*, 3 – 1983*, 4 – 1986*, 5 – 1988**. In brackets: bacterial biomass in tons per 24 km^3 seawater in Admiralty Bay, and per equivalent volume in the open sea. Symbols: Admiralty Bay: O – AODC, □ – CFU; open sea: ● – AODC, ■ – CFU. *) Zdanowski, 1995; **) Zdanowski and Donachie, 1993b. Note large winter increase in CFU counts in Admiralty Bay, which coincided with episode of June' disappearance of krill' stocks (cf. III-1.2). Note also possibility that this increase would be also due to effect of pack ice drifting (incoming and outcoming) during the whole winter 1979 through Admiralty Bay.

Antarctic continent and associated islands contribute to both total biomass (Fig. 2, Tables 1 and 2), and the metabolic characteristics of local marine bacteria (Zdanowski 1995). In light of these data and other reports in the Antarctic literature (ZoBell 1946, Fuhrman and Azam 1980, Hodson *et al.* 1981, Hanson *et al.* 1983, Karl 1993, White *et al.* 1993), there can be little doubt that the proximity of land in the Southern Ocean enhances the standing stock of bacteria. The same tendency was also observed by Zdanowski and Figueiras (1997, and *in prep.*) in a Spanish-Galician coastal ecosystem, representing a quite distinct geographic region. However, total bacterial biomass in Antarctica is much lower than in Spanish-Galician temperate waters (Tables 1 and 2).

Table 1

Total bacterial biomass (TB) in Admiralty Bay, in one of its inlets – Goulden Cove, in open Antarctic seawater, and for comparison in Galician coastal marine ecosystems. Rough biomasses of krill, phytoplankton (Phy), flagellates (Flag), ciliates (Cil) calculated by author after: Figueiras (*personal commun.*) – [F], Godlewska (1993) – [G], Kalinowski (1988) – [Ka], Kopczyńska (1992) – [K], Rakusa-Suszczewski (1980) – [R], Sorokin (1993) – [S], Zdanowski and Figueiras (1997) – [ZF]. Biomasses expressed in tonnes per 1 km^3 seawater volume. FIBEX – First International BIOMASS Expedition; SIBEX – Second International BIOMASS Expedition; BIOMASS – Biological Investigations of Marine Antarctic Systems and Stocks; SIZE – Sea-Ice Zone Expedition.

Region / season	TB	DOM	Krill	Phy	Flag	Cil
Admiralty Bay			4[R]–26[G]	27[R]	25[K]	17[S]
Mar.–May; 1981, 83	30	7070				
Jun.–Aug.; 1983	46					
Sept.–Oct.; 1983	14	404				
Nov.–Dec.; 1986, 83	0.7					
vicinity of Anvers Island	70					
Admiralty Bay (Goulden Cove)						
Ice edge, Apr. 1983						
surface	330					
bottom 70 m	59					
After melting, May 1983						
surface	56					
bottom	24					
Open seawater						29[S]
Oct.–Nov.; 1986	1		58[Ka]	190[K]	87[K]	
Dec.–Jan. (SIZE); 1988/89	1					
Dec.–Jan. (SIBEX); 1983/84	4	1677	11[Ka]	232[K]	132[K]	
Feb.–Mar. (FIBEX); 1981	20		146[Ka]	29[K]	22[K]	
Ria de Vigo (Spain)	518	2424[F]		626[ZF]		
Glacian coastal waters (Spain)	438	727[F]		229[ZF]		

Table 2

Relationships between total number of bacteria (TC), flagellates (Flag), and ciliates (Cil) in Admiralty Bay and, for comparison, in other geographic regions. nfH – nanoflagellates; other symbols described in Table 1.

Bay	TC $\times 10^5 ml^{-1}$	Flag (cells ml^{-1})	Cil (cells ml^{-1})	TC:Flag	TC:Cil
Admiralty Bay	1.2	59.5 Flag[K]	0.88[S]	2017	136400
Open Antarctic Sea	0.35	321 Flag[K]	0.78[S]	109	44880
(spring to summer transition)					
Ria de Vigo	17.5	920 nfH[ZF]	13.2[ZF]	1902	132580
Galician coastal sea	14.8	2614 nfH[ZF]		566	
(spring to summer transition)					
Los Angeles Harbor					311850
San Pedro Chanell					558860
(grazing experiments; Taylor *et al.* 1985)					

Bacteria are small but very numerous (of the order of 10^{11} cells m^{-3}), and their total biomass compares with that of other biota (Zdanowski 1995); on the other hand their total surface area is much larger than that of other biota. A very high surface/volume ratio is essential in nutrient transport through cellular membranes in low-nutrient environments (Poindexter 1981, Hanson and Lowery 1983). Estimations of total phytoplankton, krill, flagellate and ciliate biomasses in Admiralty Bay, with 24.24 km^3 of water (Rakusa-Suszczewski et al. 1993), calculated by this author (after Rakusa-Suszczewski 1980, Kalinowski 1988, Kopczyńska 1992, Godlewska 1993, Sorokin 1993) gave a similar average order of magnitude as that of bacterial biomass (cf. Table 1). It must be noted, that while phytoplankton and krill essentially inhabit the upper, mainly euphotic layer (ca. 100 m) of the water column (ca. 13.6% of total water wolume), bacteria are ubiquitous, inhabiting all oceanic layers. During seasonal studies of marine bacterial communities (Donachie 1996), neither total bacteria (AODC), nor its saprophytic fraction (CFU) varied significantly over the 400 m water column in Admiralty Bay. The low stability of water column (Lipski 1987, Madejski and Rakusa-Suszczewski 1990), promotes relatively uniform bacterial distribution, contemporaneously providing them with organic matter produced in the euphotic layer. On the other hand, bacterial biomass was exceeded by several orders of magnitude by non-living organic matter (DOM), the basic bacterial carbon source. It should be noted however, that only small fraction of Antarctic DOM is biovailable. The majority of DOM is poorly characterised and the rates at which its various components are utilized by bacteria are not determined (Karl et al. 1996).

The total bacterial surface area in Admiralty Bay (the latter covering 122 km^2) is approximately 4200 km^2 whereas in the open sea, bacterial surface area (per equivalent 24.24 km^3 volume i.e. of Admiralty Bay) was estimated to be 883 km^2. A high bacterial biomass, with an equivalent large surface area and relatively short generation times, which in the case of saprophytic bacteria growth in the course of krill decomposition amounts to 17.5 h (Zdanowski 1981) as well as high turnover and uptake rates, has profound consequences for the cold coastal waters of Antarctica, where according to Hodson et al. (1981) free living bacteria are 50 to 100 times more active than large organisms.

The following assumptions were made for approximate calculation of total bacterial biomass and surface; average bacterial numbers in Admiralty Bay ranged from 2.3×10^6 l^{-1} to 2.5×10^8 l^{-1}, in open waters from 6.2×10^5 l^{-1} to 6.6×10^7 l^{-1} (cf. Fig. 2); average volumes of bacterial cells from 0.139 to 0.204 μm^3 $cell^{-1}$; conversion factor for biomass from biovolume – 220 fg C μm^{-3} (Bratbak and Dundas 1984); carbon content – 20.6% of bacterial wet weight (Bratbak and Dundas 1984, Zdanowski 1995); mean diameter (assuming that all bacteria are coccoid) 0. 7 μm.

Factors regulating bacterial numbers

What might account for the higher bacterial biomass in coastal sea waters? Most important in this author's opinion are environmental factors that drive bacterial biomass towards higher values in inshore areas.

Higher concentration of dissolved organic matter (DOM)

So far, as we are not able to answer the questiones (Karl *et al.* 1996): "what nutrients regulate bacterioplankton growth?" and "can bacterial growth be modelled as a functional response to bulk dissolved organic carbon or dissolved organic nitrogen?", the thesis on controlling function of bacterial growth by DOM will be controversial. Considering, however such thesis we reviewed DOM estimates from Karl *et al.* (1996) who summarized that DOM in the Antarctic Peninsula region ranges from traces to extraordinarily high levels (> 1000μM – > 12mg l^{-1}), and then reviewed estimates from other authors.

In surface waters of the open ocean, dissolved organic carbon (DOC) fluctuates between 0.3 and 1.2 mg C l^{-1} and between 0.35 and 0.7 mg C l^{-1} in water below 200–300 m (Menzel and Ryther 1970). In inshore areas, DOC is 2–4 times greater than in open water (Menzel and Vaccaro 1964, Mann 1985, Zdanowski 1985, 1995); in Admiralty Bay, DOC fluctuates between 1.62 and 3.22 mg C l^{-1}, (Pęcherzewski 1980a), although Dawson *et al.*, (1985) and Zdanowski and Donachie, (1993a) reported even higher values, of 5.76 mg DOC l[-1] during the summer, and of 6.57 mg DOC l[-1] during the autumn, respectively. Assuming that organic carbon can represent on average about 50% of total DOM (carbohydrates 46.2%, lipids and carotenoids 75.7%, aminoacids 44.2%, proteins 48.7%, including related compounds, according to Maciołek, 1962), then mean DOM content in Admiralty Bay, determined by the present author during late summer 1983 (Table 1), exceeds that in open waters (mid summer 1984) by a factor of 4.2. Native bacteria possess substrate transport systems of very high efficiency with high affinities for natural substrates; transport constant values (K_t) were noted even below 10^{-8} C mole l[-1] (Hoppe 1978, Bell 1983). This characteristic may enable uptake and assimilation of extremaly diluted organic nutrients from the environment. Variations in low DOM concentration (below transport system saturation) in coastal or open Antarctic seas can therefore control growth and metabolism of bacterial populations (Hobbie and Rublee 1977, Herbst and Overbeck 1978, Bell 1983).

The concentration of DOM in inshore areas, depends on at least four most important sources: the photosynthesized organic matter released by phytoplankton and macrophytic algae; excretion and secretion from the nekton and benthic fauna, autolytic and/or bacterial decomposition of organic debris; allochthonous drainage, *e.g.* with terrestrial run-off, which can be especially high near penguin and seal rookeries.

Photosynthesized organic matter. As documented or cited by many authors (*e.g.* Hellebust 1965, Bell 1983, Wolter 1982, Huntley *et al.* 1991), 5 to 50%, (attaining 90%) of the total photosynthetically combined carbon is released into the water column by live phytoplankton. However, only a small fraction of this (amino acids, sugars, fatty acids, and other organic compounds) is directly available for bacterial uptake (*cf.* Sieburth 1979). There are indications that photobreakdown by UV-B radiation transforms some of the rest (60 to 90%) of the unidentified humic fractions to substances easily assimilated by bacteria (Laane *et al.* 1985). Due to the unique ability of heterotrophic bacteria to take up soluble compounds present in very low concentrations – in the nanomolar (Hanson and Lowery 1983), or even picomolar range (Morita 1984), they are one of the basic components of the marine food web. Transferring dissolved organic matter (DOM) to their own cells, they initiate energy flow through bacterivores (Berk *et al.* 1976, Rassoulzadegan and Sheldon 1986, Garrison and Gowing 1993) to higher trophic levels (Williams 1981, Joint and Morris 1982, Azam *et al.* 1983, Ducklow 1983). Moreover, by converting particulate organic matter (POM) to both soluble forms and detritus (Soutar *et al.* 1977, Karl and Knauer 1984, Zdanowski 1988) heterotrophic bacteria play an crucial role in the regeneration of many types of organic matter in the pelagic zone of oceanic ecosystems.

As reported by Rakusa-Suszczewski (1980) and El-Sayed (1988), primary production by phytoplankton in the nearshore regions exceeds that in the open ocean. Maximally, summer chlorophyll *a* can attain 100 and 50 mg m^{-2}, respectively (Huntley *et al.* 1991). Holm-Hansen *et al.* (1994) explain the paradox of high macro – nutrient (N, P, Si) concentrations and low phytoplankton biomass in open Antarctic pelagic waters, giving the first *in situ* evidence linking iron limitation to that paradox. These insights support earlier hypotheses of Hart (1934) and Martin *et al.* (1990, 1991) that Fe availability may limit phytoplankton biomass in open Antarctic waters, but not in coastal waters where Fe concentrations are relatively high. Iron atoms which are bound to free sulfur and to ferredoxin protein, play an important role as key elements in the electron transport system during photosynthesis.

On the other hand, in Admiralty Bay, where solar radiation can reach extensive areas of benthic macrophytes nearly year round, photosythesis is probably the most important source of DOM (Dawson *et al.* 1985, Pregnall 1983). Photosynthate exudation by benthic macroalgae can be prolonged beyond summer and the phytoplankton bloom. To 90 m, bottom of Admiralty Bay is overgrown with macrophytes whose total biomass has been estimated at 74000 tonnes (Zieliński 1990). These macrophytes cover an area of 36.9 km^2, which constitute 31% of the total surface area of the bay.

Autolytic and bacterial decomposition of organic debris. During the winter to summer transition, part of the total biota abundance enters the detritus food chain.

Conversely, considerable dissolved organic matter (*cf.* Table 1) is released into the environment during the course of autolysis and bacterial decomposition (*e.g.* matter conversion in the course of krill decomposition, Zdanowski 1988). The high concentration of DOM in Admiralty Bay (Table 1) can be recognized as an effect of natural mortality (of phytoplankton), the effect of grinding forces exerted by pack-ice (on benthic macrophytes) (Reichardt and Dieckmann 1985) or, for example, of infection, disease and parasitism (on krill) (Hamner, *personal commun.*).

One drawback of dense krill aggregations is infection, disease and parasitism. Hamner (1984) found significant numbers of whitish-coloured krill in all the swarms observed at sea. Opaque animals were more abundant near the back of these schools. Interestingly, Hamner observed that 23 of 25 isolates died within 36 h of capture, whereas none of the 25 control animals captured from within schools died during the following 14 days. Microscopic examination showed that the primary causes of mortality were parasites, moult failure, and physical damage by predators, in that order of importance. This observation might be linked to a sudden decrease in the numbers of krill in Admiralty Bay, which occurred during the summer to winter transition 1978/79. During the summer, exceptionally high numbers of krill were noted, with the prevalence of healthy adults of both sexes, of mean wet weight *ca.* 800 mg (Zdanowski 1988). The quantity of krill decreased suddenly during June, and then disappeared entirely. By the end of summer, more of the krill were unhealthy, and could not be maintained in the aquarium. Disappearance of krill coincided with exceptionally high numbers of saprophytic bacteria, $1.6–4.05 \times 10^6$ l^{-1} in the water column, compared to $10^3–10^4$ l^{-1} previously (Fig. 2).
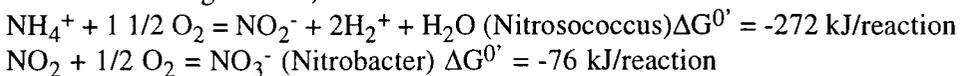
Excretion and secretion from nekton and from benthic fauna. Previously, Jawed, (1969) noted excretion of amino acids and urea by euphausiids. More recently Zdanowski (1985) observed close to Elephant Island, that the highest concentration of DOC occurred in water samples collected from the center of krill, *E. superba* swarms. In Admiralty Bay, however, the benthic fauna, whose total biomass was estimated at 60000 tonnes (wet weight) (Jażdżewski *et al.* 1986), can be considered one of the most productive sources of DOM.

Terrestrial run-off. The importance of terrestrial run-off can be illustrated by enormous quanities of suspended matter flowing into Admiralty Bay. According to Pęcherzewski (1980b) daily inflow to the bay amounts to 2000 tonnes, about five times higher than the average quantities of suspended matter recorded in open Antarctic waters. Allochthonous drainage of DOM from land is concentrated close to areas inhabited by animals, *e.g.* penguin rookeries (Pietr 1993), or where decomposition of macroalgae (Zieliński 1981), or dead krill cast ashore, occurred. It is to be noted, however, that only a small part of the organic matter in terrestrial run-off is directly available for microorganisms. High concentrations of humus (predominantly condensed aromatic products) or sapropel (predominantly n-alkanes) are highly resistant to biochemical degradation. As

a result of consecutive and random repolymerization and polycondensation reactions or selective preservation (Tegelaar *et al.* 1989), they are incorporated into the kerogens – precursors of various types of hydrocarbons. It has been documented, however, that photo-breakdown of humic substances by UV-B radiation from sunlight leads to substances such as pyruvate, acetaldehyde, formaldehyde, and glyoxylate that can be easily broken down or assimilated by bacteria (Mopper and Zhou 1990). The rate of formation of low molecular weight breakdown products is directly proportional to the light intensity at 300 nm, and to the concentration of humus.

Higher concentration of reduced inorganic electron donors (*e.g.* NO_2, NH_3, H_2S) and reduced minerals (*e.g.* Fe, Cu, Mn, Mg) as energy source for chemosynthesis

Chemolithoautotrophic processes in Antarctic are noted (Karl 1993) as important factors in the microbial food web. This bacterial process becomes dominant in the absence of a substantial PAR flux. In winter, chemolithoautotrophs are important in the production of nutrients (*e.g.* nitrates in a two step process; Brock and Madigan 1991):

$NH_4^+ + 1\ 1/2\ O_2 = NO_2^- + 2H_2^+ + H_2O$ (Nitrosococcus)$\Delta G^{0'} = -272$ kJ/reaction
$NO_2 + 1/2\ O_2 = NO_3^-$ (Nitrobacter) $\Delta G^{0'} = -76$ kJ/reaction

This process is characterised by the enormous potential of chemotrophs for producing oxidised nutrients. Reduction of 1 mole of CO_2 requires 100 moles of nitrites. This process is also responsible for rapid O_2 consumption in the sea. As suggested by Horrigan (1981), bacterial chemotrophs under the Ross Ice Shelf provide microfauna with sufficient organic production. We can presume a similar situation in Goulden Cove (Fig. 1), where a large area was covered by ice until the end of summer (1983). This could provide excellent conditions for chemosynthesis based on reduced inorganic detritus exuded during the process of ice melting. Close to the ice edge in April we found an extraordinarily high bacterial biomass, and considerable biomass reduction after ice breakout (Table 1). On the other hand, Goulden Cove is surrounded by glaciers. Glacial meltwater brings into the bay considerable quantities of inorganic supended matter (Pęcherzewski 1980b). It should be noted that this peaks between March and May (Gurgul *et al.* 1995), and coincides with maximal bacterial numbers. Unfortunately, thus far there are few indications concerning the chemical composition of reduced minerals in suspended matter.

Heterotrophic protozoa as an important factor in maintaining the bacterial standing stock in coastal marine ecosystems

Protozooplankton exploit areas of high bacterial numbers. As it is estimated that 30 to 50% of primary production in the marine environment is utilized by heterotrophic bacteria (Williams 1981, Azam *et al.* 1983, Ducklow 1983, Hag-

strom 1984), one can foresee their key role in reintroducing DOM to the food web. The availability of large quantities of bacterial biomass as a source of food in pelagic habitats is restricted, however, above all to other ecologically important and diverse microbial groups, such as protozooplankton. Sieburth (1979) comments on the role of protozoa thus, "by removing the excess populations of the smaller heterotrophs, they help keep them in an actively growing healthy state. The dynamics of any populations depend upon the rate at which it is consumed as well as upon the rate at which it is produced". Curds and Cockburn (1968) stressed the importance of the bacteria-protozoa ratio in attributing feeding rates. According to Berk *et al.* (1976) there is a critical density of bacteria below which the growth of bacterivores is inhibited.

No data are available on heterotrophic flagellata numbers (nfH) in Admiralty Bay. On the basis of Kopczyńska (1992, and *personal commun.*) we calculated total numbers of flagellates in Admiralty Bay during the summer (Table 2). Assuming provisionally that the nano-phytoflagellate to heterotrophic nanoflagellate ratio would be similar to that found by Zdanowski and Figueiras (1997) in Ria de Vigo, *i.e.* 2:1, we would expect 19.8 nfH ml^{-1} in Admiralty Bay. Correspondingly, we could expect 6050 bacteria (AODC) per one heterotrophic nanoflagellate in Admiralty Bay compared to 1902 bacteria per 1 nfH in Ria de Vigo. In open Antarctic and in Galician waters the ratios were much lower and amounted to 330 and 566 respectively. On the other hand the bacteria to ciliate ratio amounted to $1.4 \times 10^5 : 1$. One can see a similar proportion of bacteria : ciliates in Admiralty Bay and in two other bays representing distinct geographic regions (Table 2). Thus we can presume, after the many authors cited by Austin (1988), that there is a similar predation pressure on the bacterial population in Admiralty Bay as in the other coastal waters, where daily grazing amounts to more than one third of the bacterial population. It should be to noted however, that bacterial and protozoan numbers in Antarctica were much less than in temperate zones.

Are nearshore marine bacterial populations supplemented by cells of terrestrial origin?

During bacteriological analyses of the drinking water at *Arctowski* Station in 1983, attention turned to the possibility that the nearshore marine bacterial population was supplemented by cells of terrestrial origin. Mean AODC during July and November 1983 in a nearby glacial stream was on average 2.3×10^3 ml^{-1}, and comprised 25.5 FW-CFU ml^{-1} (total fresh water-saprophytic bacterial fraction) (Table 3). About 12.8% of the latter were halotolerant. This was consistent with Pietr's (1993) characterization of soil microorganisms active in the degradation of ornithogenic soils, including peat. He found that no more than 10–15% of soil bacteria were halotolerant. Similar findings, indicating the importance of terrestrial run-off in supplying bay waters with a significant fraction

Survival abilities of freshwater bacteria, revealed by their thermo- and halo-tolerance, during bacteriological analyses of drinking water at *Arctowski* Station in 1983. FW – total fresh water CFU fraction; SW – halotolerant CFU fraction, able to replicate at sea water salinity.

Sampling points	AODC $\times 10^4 ml^{-1}$	FW-CFU $\times 10 ml^{-1}$	SW-CFU $\times 10 ml^{-1}$	SW/FW %
Nearbly glacial stream before water intake (0.2°C)	2.28	25.6	3.28	12.8
Water intake (gently heated)	3.83	5.75	0.73	12.6
Pump-station (heated to 46°C)	3.52	0.37	0.13	35.1
Tap-water; laboratory (7°C)	5.32	0.56	0.28	50

of halotolerant soil bacteria such as spore formers, were noted by Zdanowski and Figueiras (1997) in the Galician Ria de Vigo.

Recent analysis of soil bacterial communities (Zdanowski and Węgleński, *in prep.*) from the vicinity of *Arctowski* Station revealed high bacterial abundances (AODC) in very different habitats: from extremely nutritionaly poor moraine – 6.6×10^8 cells g^{-1} dry weight of soil to very nutritionaly rich soil, close to sea, below penguin rookery – 1.15×10^9 cells g^{-1} dry weight, and even more abundant – 2.9×10^9 cells g^{-1} dry weight from the bottom of small pond. All this throw the light on the potential of such bacterial source.

Another interesting phenomenon was revealed by CFU analysis of bacteria inside the circulating system of drinking water at *Arctowski* Station. This system included gentle heating (*ca.* 10°C) in the water intake, and hard heating (for short periods to above 40°C) in the pump station (Table 3). Heating eliminated a considerable portion of the CFU but supported an increase in the percentage of the halotolerant fraction (Table 3). AODC analysis did not reveal any reduction in total bacterial numbers in the circulating fresh water system; instead AODC was clearly higher in the plumbing system walls and pipes than it was originally in the glacial stream. Most of bacteria isolated from the glacial stream (Fig. 3) were obligate psychrophiles, according to the definition of Morita (1975), with fewer being recognized as psychrotrophs (Eddy 1960). Only a small fraction of these were able to survive at 30°C, but none were survived at 35°C. On the other hand, most bacteria isolated from the water intake were psychrotrophs and some survived at 35°C. Only small fraction of "tap-water bacteria" were psychrotrophs or psychrophils, most being mesophiles, growing best at 30°C and thermophils (35°C). Note that all these groups originating from natural glacial or soil populations adapted to growth at much higher temperatures. This finding reflects a much higher survivability or "plasticity" of this population at high temperatures, than of the bulk of bacteria isolated from sea water (Zdanowski 1995). On the basis of this broad temperature/salinity adaptive potential, and considering the continuous inflow of terrestrial waters into the bay, we can speculate that autochthonous bacterial populations in Admiralty Bay can be supplemented with an
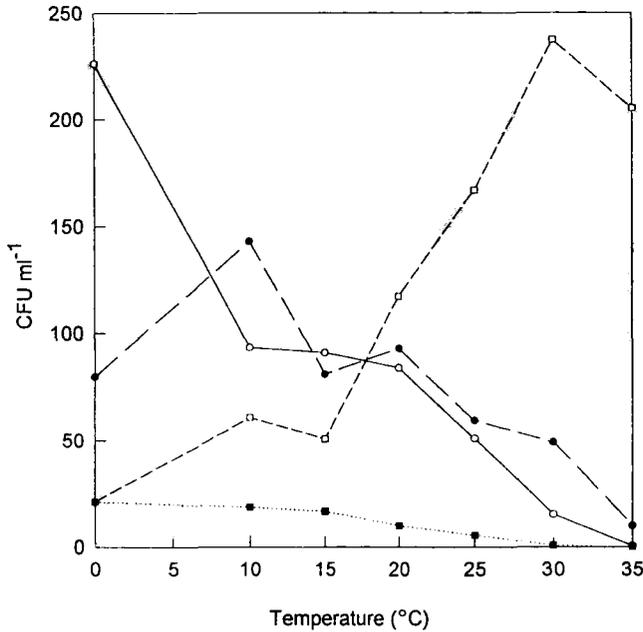
Fig. 3. Relation of bacterial number (CFU) to temperature; revealed by incubation of bacterial isolates from different fresh water sources at *Arctowski* Station (using fresh water nutrient agar – NAFW), and from Admiralty Bay (on sea water nutrient agar – NASW), at various temperatures. Symbols: O – glacial stream, ● – water intake, □ – tapwater, ■ – Admiralty Bay.

allochthonous terrestrial bacterial fraction. It should be noted, however that in addition to the permanently cold waters generally found in Antarctic marine habitats, geothermally heated waters also occur (Karl 1993); the ability of some bacteria to tolerate wide ranges in temperature and/or salinity seems to be an important feature.

Summary and conclusion

In both Antarctic inshore and offshore waters, bacterioplankton numbers and biomass vary greatly. There is no doubt though that proximity to the coast enhances bacterioplankton standing stock in surface water. Reasons for this phenomenon have been investigated in this paper, using Admiralty Bay as an example, and are summarized in Fig. 4. The main factors influencing bacterial productivity in shallow inshore waters include terrestrial run-off of dissolved organic or inorganic nutrients and bacteria, products of photosynthesis, and exudates from benthic communities. The broad diversity within coastal bacterial communities in terms of the origins of their components, and their respective physiology, ensures some species will be found in permanently cold water, whilst