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"Trade-off" in Antarctic bacteria: limnetic psychrotrophs concede multiple enzyme expressions for multiple metal resistance

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Abstract The present study examines the metal and antibiotic resistant bacteria in ice and water from lakes east and west of the Indian base camp (Maitri) in Antarctica. The isolates from western and eastern lakes showed distinct geographical differences in properties like metal resistance and enzyme expression. This may be attributed to high organic loading in the lakes on the west of Maitri. However, there was no marked geopraphical distinction in antibiotic resistance between the lakes. Bacteria from the lakes on the eastern side showed resistance to three or more metals including mercury while, those from the western were resistant to only 1–2 metals excluding mercury. Multiple enzyme expression was more pronounced in the lakes on the western side. On the eastern side multiple metal resistance was encountered in bacterial isolates associated with fewer enzyme expressions suggesting a "trade-off". Thus these Antarctic isolates from the east trade their ability to express multiple enzymes for developing resistance to multiple metals including mercury.

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Introduction

Antarctic waters are considered relatively more pristine than the other oceanic waters, experiencing both local and global anthropogenic influences only over larger time scales (Bonner 1984; Evans et al. 2000). This remotest region of the earth is a model system where human assisted biological invasion can be understood (Rudolph and Benninghoff 1977; Vincent 1988). However, it is now being established that microbial diasporas are also reaching Antarctica from land masses (Walton 1990). The krills from these regions harbour heavy metals at varying concentrations (Yamamoto et al. 1987). Petri and Zauke (1993) reported that metal concentrations show considerable interspecific heterogeneity. The cadium (Cd) levels observed in caridean decapods (*Chorismus antarcticus* and *Notocrangon antarcticus*) were highest among marine crustaceans (13 mg/kg dry weight). Yet other crustaceans like amphipod *Maxilliphimedia longipes* and the isopod *Aega antarctica* (6–8 mg/kg) show that they do not have requirements for reduced metals. This led the authors to suggest that in monitoring studies, Antarctic organisms may no longer serve as the basis for global reference levels (Nygaerd et al. 2001). Bioavailability of heavy metals and bio-essential metals by natural leaching from the sediments may also add to the presence of these metals in the Antarctic region (Byerley and Scharer 1992). Marine bacteria are important models for studies of heavy metal toxicity. They not only represent the initial step in most food chains but are also able to adsorb, accumulate and transform heavy metals (Chan and Dean 1988). With the present rate at which some of the heavy metals bioaccumulate, (Krishnamurti and Nair 1999; Guhathakurta and Kaviraj 2000) it is pertinent to understand their effect at the primary microbial level in freshwater environment where there is sparsity of such observations. The present study examines the incidence of multiple metal and antibiotic resistance in psychrotrophic bacteria from the Antarctic lakes.

Material and methods

Site description

The present work is on the freshwater lakes which are situated in the Schirmacher Oasis around the east and west of the Indian Research Station Maitri. Meteorological data shows that the area has a dry polar climate. Environmental parameters from literature (Ingole and Parulekar 1987) of the eastern and western lakes shows that the western lakes harbour twice the organic carbon of the eastern lakes. Also there was a difference in salinity between the east and west lakes. Other environmental parameters of these lakes are described in Table 1.

Table 1 Physicochemical parameters of waters of lakes west and east of Maitri

Parameters*	West	East
Water		
pH	8.4	8.0
Salinity (‰)	0.1	1.1
Oxygen (ml l^{-1})	7.9	7.8
Sediment		
Organic carbon (%)	0.4	0.9

* Values recalculated from Ingole and Parulekar (1987)

Sampling

Water and ice sampling was carried out in Antarctica lakes east and west of Maitri base camp. The details of sampling and analyses are described elsewhere (Loka Bharathi et al. 2001). For sampling lake ice a sterile stainless steel spatula was used. Of the 250 isolates retrieved from nutrient agar medium prepared in freshwater, 209 psychrotrophic isolates could survive repeated sub-culturing. They were successfully maintained for all the experiments and were identified according to Oliver and Smith (1982).

Test for metal and antibiotic resistance

The test has been carried out as outlined in Nair et al. (1992). Briefly, working cultures were maintained in VNSS medium (Hermansson et al. 1987). Metal and antibiotic resistance was examined on VNSS agar medium containing one of the test metals (10 ppm of $HgCl_2$, 100 ppm of $CdCl_2$, $ZnCl_2$ and K_2CrO_4) or antibiotics (50 ppm ampicillin which is a β-lactam antibiotic, 250 ppm streptomycin and 150 ppm kanamycin both aminoglycoside antibiotics, 25 ppm chloramphenicol and 150 ppm tetracycline both are broad spectrum antibiotics) in Muller Hinton agar (Muller and Hinton 1941) which comply with the WHO (1961, 1977) and DIN Norm 58930.

Enzyme expression

The isolates were streaked on nutrient agar medium containing different substrates; for example for amylase activity, 0.2% soluble starch, for gelatinase, 4% gelatin was used as substrate to test the enzymatic activity (Smibert and Krieg 1981). The plates were incubated for a week. All the experiments were carried out at 4°C. The enzyme expression for oxidase, catalase, amylase, nitrate reductase, gelatinase, urease, phosphatase (organic and inorganic) (Kobori and Taga 1978) and proteinase were recorded.

Results

Resistance to 1, 2, 3, 4 and 5 antibiotics was noted in 6, 3, 10, 15 and 28 isolates in the eastern lake waters, and to 1, 5,10, 20 and 22 isolates in the western lake waters respectively. However, the isolates from the eastern lakes showed comparatively higher multiple metal resistance compared to the western lakes. Thirty-seven and 25 isolates from the waters of the eastern lakes which showed resistance to 3–4 metals expressed for only 2–3 enzymes of the nine enzymes tested. The trend was opposite for water isolates from the western lakes where the expression was for 7–8 enzymes by 45 and 13 isolates respectively. However, ice water isolates from eastern and western lakes did not exhibit these trends. (Table 2A, B, C). In general 35% of the isolates were resistant to all the 5 antibiotics tested whereas 12% were resistant to all the metals tested (Fig. 1). Unlike the low percentage (8%) of resistance observed for single antibiotic, about 33% of the isolates could express for single metal resistance (Fig. 1). Taxonomic identification of the isolates revealed 18 groups of bacteria of which 14 were gram-negative, and four were gram-positive. The multiple metal and antibiotic resistant isolates predominantly belonged to *Flavobacterium, Pseudomonas, Alcaligenes, Enterobacteriace* and *Moraxella* . Besides other genera like *Coryneforms, Bacillus, Vibrio, Aeromonas, Xanthomonas, Agrobacterium, Acetinobacter, Micrococcus, Staphylococcus, Flexibacter, Lucibacterium, Photobacterium* and *Spirillum* were also encountered.

Bacteria showing multiple metal resistance inclusive of mercury could elaborate only one or two enzymes. Examples of the most dominant groups are seen in Table 3A and belonged to freshwater lakes east of Maitri. Conversely, bacteria expressing multiple enzymatic activity were resistant to only one or two metals excluding Hg (Table 3A and Fig. 2) and belonged to lakes west of Maitri. Interestingly, bacteria from ice water samples which were able to express multiple enzyme activity and also show resistance to multiple metals were invariably sensitive to mercury (Table 3B). Thus, bacterial propensity to express for multiple enzymes and multiple metal resistance show reverse trends—bacteria showing

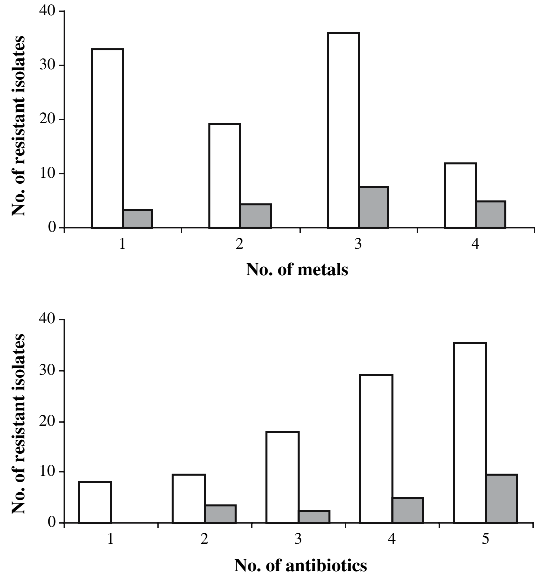

Fig. 1 Resistance of total (□) and pigmented (■) isolates to metals and antibiotics tested. No. = Number

Table 2 Distribution of bacterial isolates showing (a) antibiotic resistance, (b) metal resistance, (c) enzymes expression, in lakes west and east of Maitri

	Western lakes									Eastern lakes								
(a)																		
No. of antibiotics resistant	1	2	3	4	5					1	2	3	4	5				
No. of isolates from water	1	5	10	20	22					6	3	10	15	28				
No. of isolates from ice	9	7	11	9	11					1	5	6	17	13				
(b)																		
No. of metals resistant	1	2	3	4						1	2	3	4					
No. of isolates from water	58	–	–	–						–	–	37	25					
No. of isolates from ice	8	31	8	–						3	9	30	–					
(c)																		
No. of enzymes expressed	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
No. of isolates from water	–	–	–	–	–	–	45	13	–	–	14	48	–	–	–	–	–	–
No. of isolates from ice	–	2	5	13	16	5	5	2	–	–	2	5	13	16	5	5	2	1

Table 3 Enzyme expression in antibiotic and metal resistant bacteria from, (a) waters of lakes, (b) ice of lakes west and east of Maitri

Genera	Lakes											
	Resistance (≥3)				Expression (2–3)		Resistance (<3)				Expression (>3)	
	Metal*		Antibiotic		Enzyme		Metal@		Antibiotic		Enzyme	
	West	East	West	East	West	East	West	East	West	East	West	East
(a)												
Flavobacterium spp.	–	15	3	12	–	15	4	–	1	1	4	–
Pseudomonas spp.	–	14	12	13	–	14	14	–	2	1	14	–
Alcaligens spp.	–	9	7	7	–	9	9	–	2	1	9	–
Enterobacteriacea spp.	–	6	8	4	–	6	8	–	–	2	8	–
Moraxella spp.	–	6	5	5	–	6	5	–	–	1	5	–
(b)												
Flavobacterium spp.	–	4	–	5	–	–	–	4	–	3	–	2
Pseudomonas spp.	7	–	6	5	–	–	3	8	3	3	3	8
Alcaligens spp.	2	1	3	4	–	–	1	3	–	–	1	3
Enterobacteriacea spp.	2	1	4	4	–	–	4	5	2	2	2	5
Moraxella spp.	2	1	4	2	–	–	4	1	3	–	5	1

* including mercury

@ excluding mercury

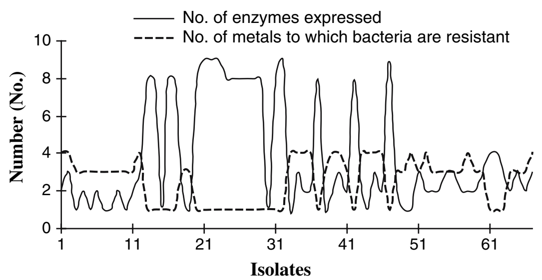

Fig. 2 Graph showing reverse trend in isolates having metal resistance and enzymatic expression

multiple metal resistance expressed for fewer enzymes and those expressing for more enzymes were resistant to fewer metals.

Of the 209 bacterial isolates from Antarctic freshwater lakes, 20% were pigmented, of which half were associated with multiple metal and antibiotic resistance. Fourteen percent of the pigmented bacteria showed multiple resistance to all the metal and antibiotics tested (Fig. 1).

Discussion

Prokaryotes dominate and play a major role in food chains in the energy transfer within the southern oceanic ecosystem (Alam and Singh 2002). Depending on the food web structure, bacteria may be either a link in food webs, supporting metazoan production, or largely a sink, where bacterial production is respired by microorganisms (Pomeroy and Deibel 1986; Wylie and Currie 1991; Vaque et al. 1992). These microorganisms undergo selection pressures in the presence of toxic compounds and develop resistance (Hideomi et al. 1977). The most common resistance is to metal and antibiotics, which can be a result of bio-essentiality or of abuse of the metal, and/or antibiotics. Enumeration of this resistant group from different geographical locations (Mudryk et al. 2000; De Souza et al. 2006) has shown that these groups are ubiquitous. Bacteria isolated from natural habitats may show ecologically important capabilities, such as metal and antibiotic resistance, which provide them with selective advantages. This resistance to heavy metals is developed mainly in response to the stress associated with heavy metals in the environment (Nair et al. 1992). In this study, bacterial isolates showed interesting trends in phenotypic expressions. Where there was a decline in the number of enzymes elaborated the bacteria were resistant to multiple metals (3–4) inclusive of Hg in the eastern lakes.

This resistance to heavy metals is developed mainly in response to the stress associated with heavy metals in the environment (Nair et al. 1992). The western lakes are known to have twice as much organic carbon as that observed in the eastern lakes (Ingole and Parulekar 1987). Organic carbon is known to bind metal forming an organo-metallic complex and make the metal less bioavailable. In the eastern lakes the organic carbon was half that found in the western lakes. Thus the metals would be more bioavailable in the eastern lake perhaps inducing higher adaptability. However, in the lakes west of Maitri where the bioavailability of metal is reduced due to organo-metal binding isolates were mercury sensitive and expressed multiple enzymes. Kim et al (1999) also found that metal toxicity reduced in the presence of natural organic matter and was largely ascribed to the presence of organic ligands that bind metals and reduce the concentration of free ionic metals in the aquatic environment. Salinity also affects metal bioavailability. In the present study the western lakes had an average salinity of 0.1% while the eastern lakes averaged 1.1%. There have been reports on increased solubility of mercury by the presence of chloride (Stolzenberg et al. 1986; Olson et al. 1991). Barkay et al. 1997 also observed a reduction in metal bioavailability in freshwater as compared to saline environments. Thus the bioavailability of the metals would be comparatively more in the eastern than the western lakes. Accordingly, we have also encountered higher number of mercury and multiple metal resistant bacteria in the east than the west.

Residual effects of heavy metals like cadmium, and mercury on aquatic biota are long lasting and highly deleterious as they are not easily or rapidly eliminated from these ecosystems by natural degradative processes. These metals tend to move up the aquatic food chain ultimately reaching human being causing chronic and acute ailments (Forstner and Wittmann 1979) including a number of DNA mutations (De Flora et al. 1994). In the Antarctic environment the low growth rates which are due to the temperature regime may promote high concentrations of some metals in certain organisms (Petri and Zauke 1993). Plasmid-mediated resistance to Hg has been linked to resistance to some antibiotics (Ka et al. 1994) in agricultural land. Thus the eastern lakes of Antarctica are not different from the coastal environment of India (Ramaiah and De 2003) where there is a sharp rise in mercury resistant bacteria. However, in this study resistance to lower concentration of Hg was observed in the Antarctic freshwaters compared to the coastal waters suggesting that the contamination of this metal in these waters could be low. Many earlier studies observed that mercury resistant bacteria are also resistant to many antibiotics and other toxic chemicals (Barbieri et al. 1989; 1996; Canstein et al. 1999) by virtue of carrying plasmids and or transposons encoding genetically linked metal and antibiotic resistance.

Besides Hg resistance, the incidence of multiple resistance either to metal or antibiotics was also observed in the Antarctic freshwater strains. Prevalence of such resistance in bacteria to multiple heavy metals has been reported from Providence River, the Narragansett Bay and in Antarctic marine waters (Traxler and Wood 1981; De Souza et al. 2006). Sabry et al. (1997) showed that the response of the isolates to 11 tested antibiotics ranged from complete resistance to total sensitivity. Besides, their study showed multiple antibiotic resistance in 70% of the total isolates. This was in agreement with our findings where, multiple resistance was exhibited by 67% of the total isolates. However, the response of the isolates to the five antibiotics tested ranged from complete resistance to single antibiotic resistance.

Mudryk et al. (2000) demonstrated that the toxic effect of different concentrations of heavy metal on growth and respiratory activity of neustonic and planktonic bacteria, depended on the metal uptake in these bacteria and the kind and its concentration. Our studies showed that there was variation in the enzyme profile of the resistant isolates. Single-metal-resistant isolates had wide range of enzyme activity compared to isolates with multiple resistance. Differences in enzymatic profile also have been observed in areas which are highly eutrophic compared to less eutrophic areas (Hoppe et al. 1998). As reported by Alam and Singh (2002) in this study too, all the isolates were catalase and oxidase positive. While monitoring the Arabian Gulf, Chandy (1999) found heavy metal resistance in chromogenic and non-chromogenic marine bacteria. Similarly, differential sensitivity to both metals and antibiotics were observed among pigmented and non-pigmented bacteria isolated from the coastal waters (Nair et al. 1992). Accordingly, resistance to metal/antibiotics could also be linked to chromogenesis in freshwater isolates in the present study. However, the pigmented bacteria in the marine waters showed more resistance to antibiotic and metal than in freshwater forms (De Souza et al. 2006). In the present study too, *Flavobacterium* spp. from the eastern lakes exhibited multiple metal resistance. Fourteen isolates of *Pseudomonas* spp from the eastern lakes also showed multiple metal resistance while those from the western lakes showed single metal resistance. Resistance to heavy metals was also reported to be pronounced in gram-negative bacteria (Nair et al. 1993; Duxbury 1986) and most of the resistant bacteria were mainly gram negative in this study. All the strains of *Aeromonas* showed resistance to mercury and chromium while there was difference in their resistance to antibiotics. A similar observation was made in *Pseudomonas* which showed difference in resistance to metals. This may be due to the difference in the strains. Beja et al. (2002) suggested that considerable functional diversity might exist even in bacteria having similar genotype. Low levels of enzyme expression in isolates showing multiple metal resistance suggesting a trade-off i.e. a disadvantage for performing one function is compromised for the advantage for performing another function (Bohannan et al. 2002). Species are know to assume trade-offs among the abilities of organisms to respond to the different factors that constrain their fitness and abundance (Tilman 2000). Such a trade-off could allow the coexistence of different types of bacteria, each specialized in the use of a particular energy source (Bohannan et al. 2002) as in this case of metal resistant bacteria. Ecological implication of resistant assemblages of Antarctic bacteria would mean better ability to adapt to changing systems. Extended studies with other isolates from freshwater samples would confirm the possibilities of intrinsic influences due to natural lithology or antibiotic production from autochthonous microbes.

Our results suggest that the Antarctic waters from the Indian side are not exempt to the spread of metal and antibiotic resistant bacteria and the enzymatic profiles of the isolates were apparently controlled to a certain extent by their resistance to metals especially mercury. These Antarctic isolates from the eastern lakes trade off their ability to express multiple enzymes for developing mercury resistance.

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