

Survival mechanisms in Antarctic lakes

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In Antarctic lakes, organisms are confronted by continuous low temperatures as well as a poor light climate and nutrient limitation. Such extreme environments support truncated food webs with no fish, few metazoans and a dominance of microbial plankton. The key to success lies in entering the short Antarctic summer with actively growing populations. In many cases, the most successful organisms continue to function throughout the year. The few crustacean zooplankton remain active in the winter months, surviving on endogenous energy reserves and, in some cases, continuing development. Among the Protozoa, mixotrophy is an important nutritional strategy. In the extreme lakes of the McMurdo Dry Valleys, planktonic cryptophytes are forced to sustain a mixotrophic strategy and cannot survive by photosynthesis alone. The dependence on ingesting bacteria varies seasonally and with depth in the water column. In the Vestfold Hills, *Pyramimonas*, which dominates the plankton of some of the saline lakes, also resorts to mixotrophy, but does become entirely photosynthetic at mid-summer. Mixotrophic ciliates are also common and the entirely photosynthetic ciliate *Mesodinium rubrum* has a widespread distribution in the saline lakes of the Vestfold Hills, where it attains high concentrations. Bacteria continue to grow all year, showing cycles that appear to be related to the availability of dissolved organic carbon. In saline lakes, bacteria experience sub-zero temperatures for long periods of the year and have developed biochemical adaptations that include anti-freeze proteins, changes in the concentrations of polyunsaturated fatty acids in their membranes and suites of low-temperature enzymes.

Keywords: mixotrophy; phytoflagellates; ciliates; bacteria

1. INTRODUCTION

Antarctica is a large ice-covered continent. It is a polar desert where most life is found in the so-called polar oases, or ice-free regions that are located at the continent's margins or in the extensive, ice-free Dry Valleys of Southern Victoria Land. While there are sparse communities of lichens, mosses and soil micro-organisms, the limited availability of liquid water curtails biological activity for most of the year. It is in the lakes where liquid water is continuously available that most life on the continent is concentrated. The typical avian and mammalian Antarctic fauna (e.g. penguins, seals) are marine, deriving their food resources from the sea.

Antarctica has a remarkable diversity of lake types, ranging from freshwater, brackish, saline meromictic, hypersaline (up to 10 times the conductivity of seawater), epishelf lakes and subglacial lakes. Epishelf lakes are freshwater lakes situated adjacent to ice-shelves. Their basins continue below the ice-shelf so that the freshwater overlies colder, denser seawater. Consequently, epishelf lakes are tidal freshwater systems that rise and fall in the tidal cycle. There is no appreciable mixing of the freshwater and seawater. These lakes are relatively common in Antarctica, while only a few have been described in the Arctic. Subglacial lakes lie below the continental ice-cap and were revealed by airborne RES in the Seventies (Oswald &

Robin 1973). Later work using an extensive analogue database of 60 MHz RES covering 50% of the continent revealed a vast array of some 77 sub-glacial lakes (Siegert *et al.* 1986). The largest of these lakes has been well surveyed and has been named after the Russian Station Vostock that is situated above it (Kapitsa *et al.* 1996).

Antarctic lakes are unproductive, with typical levels of photosynthesis in the region of $0.5\text{--}30\ \mu\text{g l}^{-1}\ \text{day}^{-1}$ (Vincent 1981; Lizotte *et al.* 1996; Bayliss *et al.* 1997; Laybourn-Parry *et al.* 2001a). This results from low annual levels of photosynthetically active radiation and ice-covers that attenuate light to the water column, continuous low temperatures and the lack of any significant input of inorganic nutrients and organic carbon. The lakes have truncated food chains with no fish, few invertebrates and a dominance of protozoa, bacteria and algae. They are systems dominated by the microbial loop (Laybourn-Parry *et al.* 1992, 2001a; Laybourn-Parry 1997; James *et al.* 1998). Recently, viruses have been reported from a range of Antarctic lakes in the Vestfold Hills and the Dry Valleys at concentrations ranging between 1.0 and $36.5 \times 10^6\ \text{ml}^{-1}$ (Kepner & Wharton 1998; Laybourn-Parry *et al.* 2001b). Viruses are now recognized as potentially important components of the plankton that may impose a very significant effect on carbon cycling (Fuhrman 1999).

Contrary to what one might suppose, many of the planktonic organisms of Antarctic lakes do not cease to function in the winter months (Heath 1988; Laybourn-Parry *et al.* 1992, 1995; Laybourn-Parry & Bayliss 1996;

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Bell & Laybourn-Parry 1999). In order to maintain activity in winter, organisms adopt one or more of a variety of strategies that enable them to enter the short austral summer with actively growing populations.

2. SURVIVAL STRATEGIES IN ZOOPLANKTON

Metazoan zooplankton are sparse in continental Antarctic lakes and are represented by single species of either a cladoceran or a copepod (Bayly & Burton 1987; Bayliss & Laybourn-Parry 1995; Bell & Laybourn-Parry 1999). In some lakes, rotifers are also found and in the lakes of the Dry Valleys they are the only metazoans in the plankton (Laybourn-Parry *et al.* 1997a; James *et al.* 1998). We have only limited data on the winter occurrence of these organisms; however, the crustaceans are found in an active state throughout the winter months. *Daphniopsis studei* (Cladocera) is endemic to eastern Antarctica and its sub-Antarctic islands. In Crooked Lake, it survived the winter by using endogenous fat reserves and presumably also feeding on microbial plankton (Bayliss & Laybourn-Parry 1995). As soon as the summer arrived, it commenced parthenogenic egg production. In the saline lakes of the Vestfolds Hills, the zooplankton consists of a calanoid copepod *Paralabodocera antarctica* that occurs throughout the winter. Naupliar stages were most abundant in winter, indicating that this species continues its development throughout the year as copepodid stages and adults peak in the summer months (Bell & Laybourn-Parry 1999). The data suggest an annual life cycle.

Epishelf lakes are the most extreme of polar lakes, ranking as ultra-oligotrophic, yet they, too, support a zooplankton species. In Beaver Lake, there is a dwarf form of the calanoid copepod *Boeckella poppei* (Bayly & Burton 1993; Laybourn-Parry *et al.* 2001a). Summer sampling revealed animals in a range of development stages from nauplii to gravid females. In the extremely cold (less than 2.0 °C), unproductive waters of Beaver Lake it is probable that *Boeckella* takes several years to complete its development.

Unlike their lower latitude and Arctic relatives, the crustacean zooplankton of Antarctic lakes cannot exploit the strategy of over-wintering as resting eggs or entering a diapause. The austral summer is too short to permit development and reproduction to be completed. Consequently, in a predator-free environment they have opted for slow development, dwarfism and low fecundity.

3. MICROBIAL SURVIVAL STRATEGIES

(a) Protozoa

Mixotrophy is a well-documented phenomenon among planktonic protozoa in the sea and in lakes. It involves a combination of autotrophy and heterotrophy in varying degrees. At one end of the spectrum are photosynthetic phytoflagellates that ingest bacteria, including members of the genera *Dinobryon*, *Ochromonas*, *Poterioochromonas*, *Chrysochromulina* and some cryptophytes (Porter 1988; Sanders 1991). At the other end of the spectrum are heterotrophic ciliates and sarcodines that either harbour endosymbiotic zoochlorellae and zooxanthellae (Anderson 1983; Dolan 1992; Laybourn-Parry *et al.* 1997b), or sequester the plastids of their algal and phytoflagellate

prey (Laval-Peuto & Febvre 1986; Patterson & Dürrschmidt 1987; Rogerson *et al.* 1989). While mixotrophy is common, it is not usually of major importance and only rarely does it make a significant contribution to carbon cycling.

In Antarctic lakes, mixotrophy has been exploited as a crucial component of survival by a number of the most abundant and successful organisms. In the Lakes Hoare and Fryxell in the McMurdo Dry Valleys, a number of cryptophyte species are the dominant planktonic phytoflagellates (Roberts & Laybourn-Parry 1999; Roberts *et al.* 2000). Lake Fryxell is a meromictic lake and is consequently permanently stratified with an aerated upper mixolimnion under 4 m thick, perennial ice. The bottom waters (the monimolimnion) are anoxic and the domain of methanogenic and sulphur-reducing bacteria. The light climate in the mixolimnion is very poor, with only 1.3% of incident irradiance reaching the water column through opaque debris containing ice (Howard-Williams *et al.* 1998). Thus the phytoplankton exists in a severely shaded environment. Water temperatures were very low, ranging from 0.3 °C immediately under the ice to 2.7 °C at 13 m depth (Roberts *et al.* 2000).

The cryptophytes reached their highest concentrations just above the chemocline separating the upper mixolimnion and lower monimolimnion (figure 1). They were effecting a trade-off between being under the ice in the best light environment, where inorganic nutrients (phosphorus and nitrogen) were severely limited, and a poorer light climate but greater access to inorganic nutrients that were diffusing upwards over the chemocline from the nutrient-rich monimolimnion. The cryptophytes of both Lakes Hoare and Fryxell have been shown to ingest bacteria at rates up to 3.6 bacteria cell⁻¹ h⁻¹. Moreover, the grazing rates varied with depth in the water column and at different times during the summer (Roberts & Laybourn-Parry 1999). More recently, photosynthetic and grazing rates have been measured simultaneously with the aim of quantifying the contribution of each nutritional mode to the carbon budget of the cryptophyte community (Marshall & Laybourn-Parry 2002) (figure 2a,b). In Lake Fryxell, the contribution of grazing to the carbon budget ranged from 8–31% in November and 2–24% in December (figure 3). There was a much greater dependence on carbon derived from grazing in early summer compared with mid-summer. However, the cryptophytes never became independent of the need to obtain part of their carbon budget through mixotrophy. We only have direct data for the summer months, as the United States Antarctic programme has not yet mounted a wintering expedition to the Dry Valleys. However, a remote sampling device that took samples throughout the winter in Lake Fryxell showed a decline in cryptophytes in winter, but in August numbers started to increase before the sun returned, indicating that they were probably supporting growth by heterotrophy (D. M. McKnight, personal communication).

Meromictic lakes also occur in the Vestfold Hills and one of them, Ace Lake, has been the subject of several long-term investigations covering an annual cycle (Burch 1988; Bell & Laybourn-Parry 1999). Ace lake has annual ice that is much more transparent than the perennial ice of the Dry Valley lakes, thereby providing a much more

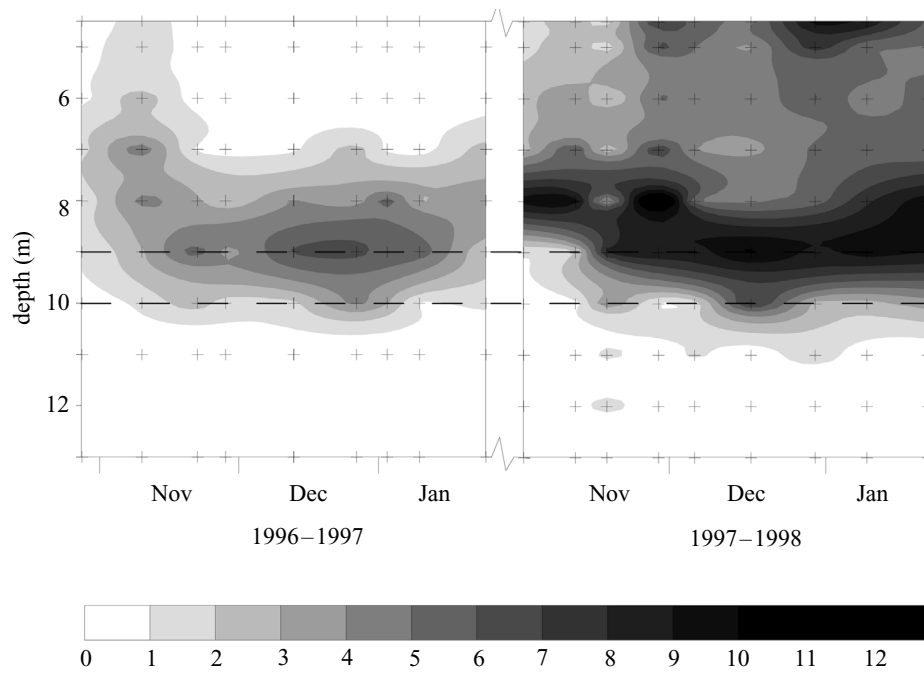


Figure 1. Cryptophyte distribution and abundance ($\times 10^3$ cells ml^{-1}) in the water column of Lake Fryxell during the summers of 1996–1997 and 1997–1998. Crosses indicate sampling dates. (Data from Roberts *et al.* (2000).)

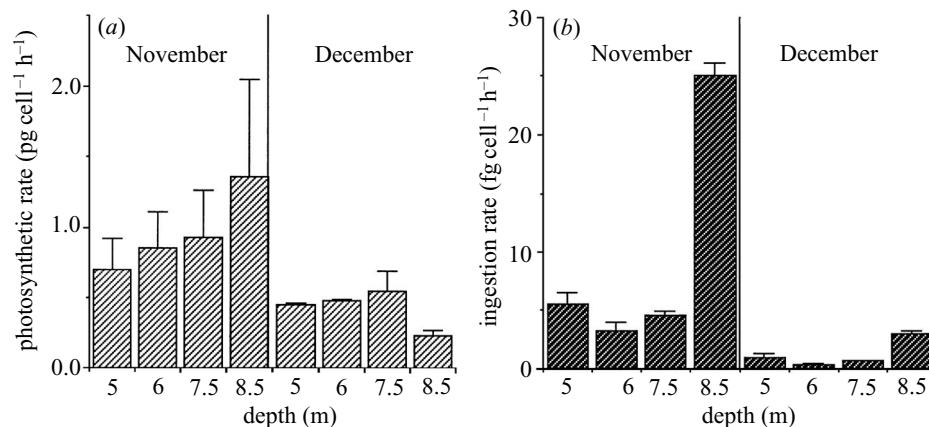


Figure 2. (a) Individual photosynthetic rates and (b) grazing rates in cryptophytes in Lake Fryxell during the summer of 2000 in relation to depth in the water column (with standard errors, $n = 5$). (Data from Marshall & Laybourn-Parry (2002).)

favourable light climate. In this lake, the dominant phytoflagellate is *Pyramimonas gelidicola* (Chlorophyta: Prasinophyceae). It has not been reported as being mixotrophic; however, in Ace Lake it does ingest bacteria and bacteria-sized fluorescently labelled microspheres (Laybourn-Parry *et al.* 2000; J. Laybourn-Parry and W. Marshall, unpublished data). During winter, the numbers of *Pyramimonas* do decline, but they never disappeared completely and they started increasing in abundance in August (Bell & Laybourn-Parry 1999). Cysts were also observed and must also play a role in winter survival. Current work, which is measuring both photosynthesis and grazing, indicates that mixotrophy is not exploited during mid-summer when *Pyramimonas* becomes entirely autotrophic (J. Laybourn-Parry and W. Marshall, unpublished data). Thus, unlike their counterparts in the much more severe Dry Valley lakes, the phytoflagellates of Ace Lake are not entirely dependent on mixotrophy for survival, but they do exploit it as a means of surviving winter and entering the summer as an actively growing population.

Like the cryptophytes of Lake Fryxell, *Pyramimonas* in Ace Lake was found at the highest concentrations just above the chemocline (Bell & Laybourn-Parry 1999). Deep chlorophyll maxima of phytoflagellates, particularly cryptophytes, have been reported from lower-latitude lakes (Gasol *et al.* 1993; Pedrós-Alió *et al.* 1995; Gervais 1998). However, in these lakes the cryptophytes were not mixotrophic, but survived by efficient photosynthesis. Cryptophytes only resort to mixotrophy under extreme circumstances (Sanders & Porter 1988; Tranvik *et al.* 1989). Clearly, in Antarctic lakes mixotrophy has become a crucial survival mechanism in the cold, dark waters of both freshwater and saline lakes. There is debate as to why phytoflagellates resort to mixotrophy. One argument suggests that it is a means of acquiring inorganic nutrients for photosynthesis during phases of limitation (Nygard & Tobiesen 1993). Other researchers contend that it is a means of supplementing the carbon budget (Bird & Kalf 1986; Caron *et al.* 1990; Jones *et al.* 1993). In Antarctic lakes, it is primarily a mechanism for supplementing the

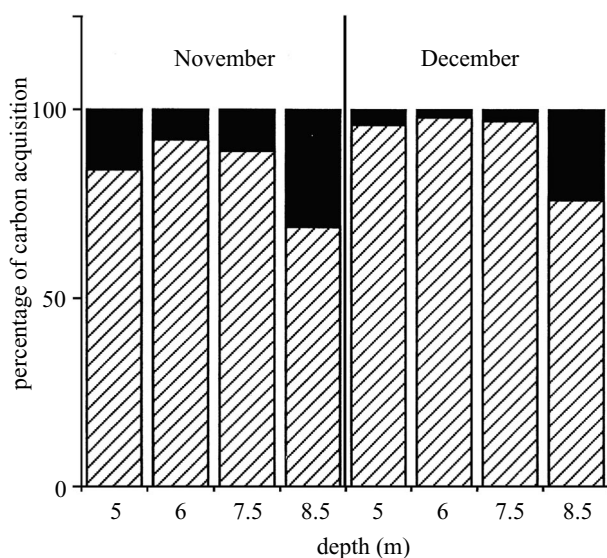


Figure 3. Proportion of carbon acquisition from photosynthesis and grazing in the cryptophyte community of Lake Fryxell in relation to depth during the summer of 2000. Hatched area, photosynthesis; solid area, grazing. (Data from Marshall & Laybourn-Parry 2002.)

carbon budget, though it may also provide nitrogen and phosphorus for photosynthesis in waters that suffer from inorganic nutrient limitation.

Among the ciliated protozoa living in Antarctic lakes, mixotrophy is also common. The plastid-sequestering oligotrich *Strombidium viride* has been reported from lakes in the Vestfold Hills and the nearby Larsemann Hills, as well as the Dry Valleys (Laybourn-Parry *et al.* 1992, 1995; Ellis-Evans *et al.* 1998; James *et al.* 1998; Roberts *et al.* 2000). *Strombidium viride* is a cosmopolitan species found in freshwater lakes from the tropics to the poles (Laybourn-Parry 1994). In the saline and brackish lakes, the species diversity of ciliates can be higher than in freshwater lakes (James *et al.* 1998); however, one species often dominates the community (Perriss *et al.* 1995; Bell & Laybourn-Parry 1999; Roberts *et al.* 2000; Laybourn-Parry *et al.* 2002). These dominant species are successful in the extreme lakes of Antarctica because they have nutritional physiological adaptations that enable them to outcompete the other species.

Mesodinium rubrum is found widely in the plankton of lakes in the Vestfold Hills that have salinities ranging from around 4‰ to around 60‰ (Perriss *et al.* 1995; Laybourn-Parry *et al.* 2002). It is a ubiquitous marine species found in sea and estuaries and is sometimes responsible for red tides (Lindholm 1985; Crawford 1989). It is unique in being the only entirely photosynthetic ciliate. It harbours a cryptophycean endosymbiont with which it has evolved such a close association that it has abandoned feeding and relies entirely on translocated photosynthate from its endosymbiont. *Mesodinium* is highly motile (Lindholm 1985) and can migrate up and down in the water column, positioning itself in the ideal light climate for photosynthesis or in nutrient-rich strata close to the chemocline. Thus it facilitates the photosynthetic activity of its endosymbiont.

The lakes of the Vestfold Hills were formed as a result of isostatic rebound, which started after the last major

glaciation some 10 000 years ago (Adamson & Pickard 1986). As the land rose, it cut off fjords and trapped pockets of seawater in hollows. Some of the lakes were flushed by glacial melt and evolved into freshwater systems, while others with closed basins developed into saline lakes, some of which underwent meromixis. The trapped marine communities lost the majority of their metazoans and many of their algal and protozoan species, leaving simplified communities of highly adapted species able to cope with the extreme conditions prevailing in the lake environments. *Mesodinium* populations trapped in the newly formed lakes held the competitive edge and are found in concentrations as high as tens of thousands per litre (Perriss *et al.* 1995; Bell & Laybourn-Parry 1999; Laybourn-Parry *et al.* 2002) and they make a significant contribution to photosynthesis in a number of the saline lakes (Laybourn-Parry & Perriss 1995).

During the winter, the *Mesodinium* population of Ace Lake showed a decline in numbers towards mid-winter, but it did not entirely disappear and its numbers started to increase in late August. Electron microscopy has revealed significant starch reserves that probably sustained the ciliate during the phase of total winter darkness. *Mesodinium* also encysts, so the actively growing population that entered the spring was likely to be augmented by excysting individuals (Laybourn-Bell & Laybourn-Parry 1999).

In Lake Fryxell, a wider range of ciliate species was found, but one species, *Plagiocampa*, accounted for 80% of the ciliate community (Roberts *et al.* 2000). This ciliate is found in the highest concentrations around the chemocline, where its prey, cryptophyte phytoflagellates, were most abundant (see figure 1). *Plagiocampa* apparently did not digest ingested cryptophytes immediately. They remained intact, showing strong chlorophyll autofluorescence for several weeks (Roberts & Laybourn-Parry 1999). The evidence suggested that *Plagiocampa* is sequestering ingested cryptophytes that continue to undertake photosynthesis within the protozoan cell, which presumably gains some nutritional advantage. *Plagiocampa* grazed at rates of from 0.13 to 0.19 cryptophytes cell⁻¹ day⁻¹, imposing an insignificant predation pressure of less than 3% day⁻¹. As yet, we have no idea what happens to *Plagiocampa* during the austral winter, but it is likely that its abundance pattern follows that of its prey. The apparent mixotrophy exhibited by *Plagiocampa* prevents over-exploitation of its food resources and is probably a recently developed nutritional strategy, in evolutionary terms.

(b) Bacteria

Despite low temperatures of 1–2 °C in freshwater lakes and sub-zero temperatures in the saline lakes, bacterial production continues throughout the year (Laybourn-Parry *et al.* 1995; Bell 1998). We know relatively little about the species composition of the bacteria communities, but the species found in the saline lakes appear to be marine, or of marine origin (Franzmann & Dobson 1993; Mills 1999). The patterns of bacterial growth, measured by the incorporation of tritiated thymidine into DNA and ¹⁴C leucine into protein, tended to follow the concentrations of DOC in the lake waters (figure 4), provided that inorganic nutrients were not limiting. In lower-latitude temperate lakes, the importance of the microbial loop varies seasonally and there is an assumption that low

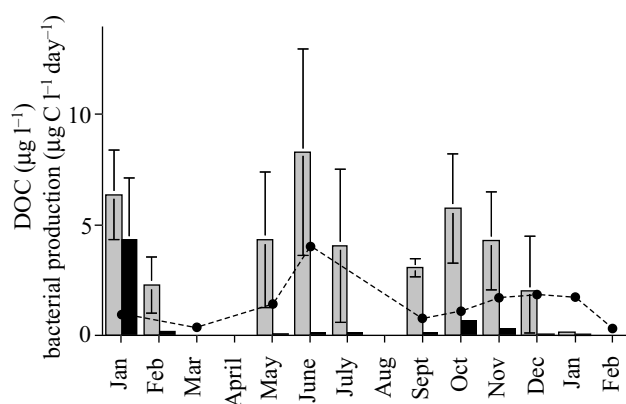


Figure 4. Bacterial production measured from the uptake of ^3H -thymidine into DNA (grey columns) and ^{14}C -leucine into protein (solid columns) in relation to DOC (dashed line) in Lake Druzhy (Vestfold Hills) during 1999–2000 (with standard errors, $n = 3$). (Data from J. Laybourn-Parry and T. Henshaw, unpublished data.)

winter temperatures curtail bacterial growth (Porter *et al.* 1988). In Antarctic lakes, low temperatures prevail throughout the year and while bacterial growth is depressed compared with rates at lower latitudes (Scavia *et al.* 1986; Riemann & Bell 1990; Laybourn-Parry & Walton 1998), it nonetheless provides potential energy for a spectrum of heterotrophic and mixotrophic protozoans.

Functioning at sub-zero temperatures requires very considerable biochemical adaptation. As temperature decreases, organisms must be able to maintain the fluidity of their membranes by increasing the proportions of unsaturated fatty acids and/or decreasing the length of the fatty acid components of the lipids, and this phenomenon has been observed in Antarctic bacteria (Nichols *et al.* 1993; Rotert *et al.* 1993). Indeed, it has been suggested that Antarctic bacteria might have industrial potential for the production of polyunsaturated fatty acids (Nichols *et al.* 1993). Recently, antifreeze proteins have been identified in bacteria from a number of saline lakes in the Vestfold Hills (Mills 1999). To function at low temperatures, organisms must have low-temperature enzyme systems and such enzymes have been identified in bacteria isolated from benthic algal mats collected from Ace Lake and Lakes Hoare and Fryxell (B. Jones, personal communication). These novel biochemicals derived from extremophile organisms have very considerable biotechnological potential in a range of industries. Interestingly, most of the bacteria so far isolated from Antarctic lakes are not psychrophiles, but psychrotrophs able to grow best at temperatures above $15\text{ }^\circ\text{C}$ (Mills 1999).

4. CONCLUSIONS

Among the organisms that have successfully colonized the extreme lake environments of Antarctica, a variety of survival mechanisms have been exploited. Many of the most successful species survive the winter in an active state by using endogenous energy reserves or employing nutritional versatility. Mixotrophy is a particularly common strategy among autotrophic flagellates and in ciliates. In the Dry Valley lakes, cryptophytes, a group in which mixotrophy is seldom exploited, are mixotrophic even at

mid-summer. Clearly it is obligatory and limited evidence indicates that, in winter, they become heterotrophic. The key to success is to be able to hit the deck running in the short austral summer.

There are still many unanswered questions relating to the physiology and biochemistry of Antarctic protozoans that beg to be addressed. The same is true of bacteria. We need information on the species diversity and the degree of endemism, as well as much more data on biochemistry of surviving the cold, particularly as there is a huge biotechnological potential for the novel biochemicals found in such extremophiles.

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Discussion

M. A. Marahiel (*Department of Chemistry, Philipps-Universität Marburg, Marburg, Germany*). What is the mechanism of sensing for the growth of these bacteria?

J. Laybourn-Parry. You are talking about the mixotrophic organisms?

M. A. Marahiel. Yes. How they switch.

J. Laybourn-Parry. I think probably it is a photosynthetic response. They must be sensing in some way the carbon that they are acquiring, and if there is not enough and there are bacteria there, they will respond to the bacteria. There is a change with depth in the water column and with time of the year. So I think it is a response to light rather than anything else, but it is quite evident that many of them in severe systems cannot meet their carbon requirements by photosynthesis alone, so they have to continue feeding. There is a change from high levels of photosynthesis in November to much lower levels of grazing in December and an increase in photosynthesis.

M. A. Marahiel. Can you enforce these conditions?

J. Laybourn-Parry. We have never done it in the laboratory. We have always conducted our experiments *in situ*. This is relatively new data. The next step will be to try and manipulate it and see what the responses are. We are trying to find out what stimuli force it, but we think probably its almost certainly light, but possibly also inorganic nutrients because they do this. There is a good deal of debate as to why organisms are mixotrophic. There is one school of thought that it is entirely to do with the need to acquire extra carbon in poor light conditions, another that it is to obtain inorganic nutrients and photosynthesis when those nutrients are limited in the water, because if you feed on bacteria you have access to inorganic nutrients. So it may be that inorganic nutrient concentration also plays a role together with light.

T. Haymet (*Department of Chemistry, University of Houston, Houston, TX, USA*). I have a question about the response of invertebrates to the environment. You mentioned that, if I understood correctly, small size is an advantage for some of the crustaceans you mentioned, but a few kilometres away in the marine environment when I look in the water I see gigantic tunicates and gigantic starfish and so on. Is that just because the carbon flux is so different in those two environments?

J. Laybourn-Parry. Yes. As you know, the ocean around

Antarctica is a rich environment, but it is a light-limited environment. It is not nutrient-limited like most marine environments. These lakes are very what we call oligotrophic or unproductive, and so it is really the limitation of carbon availability or energy availability that drives this dwarfism.

T. Haymet. Rather than a low temperature?

J. Laybourn-Parry. Well, low temperature obviously affects the scope for growth as well, because the life cycle is very long. These things would go through about five or six generations a year at normal temperatures. They go through perhaps one and a half generations a year at these low temperatures. But if you look at lakes on the sub-Antarctic islands where some of these Crustacea also occur, they do have winter resting eggs and they do actually have higher fecundity, because the lakes are richer. They are more eutrophic. I think the difference between the marine environment and the fresh-water environment is entirely to do with food resource availability.

P. Quick (*Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK*). Presumably then, within this system there must be some form of organism which is completely autotrophic and contributing to the food chain. Presumably the bacteria.

J. Laybourn-Parry. Yes. We get a lot of photosynthetic bacteria sitting on the chemocline and indeed in those anoxic waters in the Meromictic Lakes. You do not tend to find photosynthetic bacteria apart from cyanobacteria, particularly picocyanobacteria in the freshwater lakes. So picocyanos are obviously there, but not in large numbers and they do not contribute an awful lot. Most of the larger photosynthetic elements are actually motile organisms like phytoflagellates. But certainly in some situations photosynthetic bacteria obviously are entirely photosynthetic and they do contribute particularly on the chemocline and in the lower waters.

E. Benson (*Division of Molecular and Life Sciences, University of Abertay, Dundee, UK*). Your photosynthetic phytoflagellates, do they have any CO₂-concentrating mechanisms to help them acquire the carbon which obviously seems to be a problem?

J. Laybourn-Parry. We do not know because we have not really looked at their biochemistry in detail, but they do live in the Dry Valley lakes. One of my colleagues who is a geochemist thinks these systems are actually dissolved inorganic carbon-limited. So not only are you confronted with the problem of photosynthesing in a low-light environment, normally carbon dioxide is not a limiting factor to photosynthesis in most aquatic environments but sometimes is in these environments. Indeed, that is the question one often gets asked, 'Are these inorganic carbon-limited as well as organic carbon-limited?'

E. Benson. So what type of carbon metabolism would there be performing photosynthesis?

J. Laybourn-Parry. I do not know the answer to that question. We have only just started looking at these things and we really need to get to know the biochemistry of photosynthesis as well.

GLOSSARY

RES: radio echo sounding

DOC: dissolved organic carbon