The biodiversity and ecology of Antarctic lakes: models for evolution

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Antarctic lakes are characterised by simplified, truncated food webs. The lakes range from freshwater to hypersaline with a continuum of physical and chemical conditions that offer a natural laboratory in which to study evolution. Molecular studies on Antarctic lake communities are still in their infancy, but there is clear evidence from some taxonomic groups, for example the Cyanobacteria, that there is endemism. Moreover, many of the bacteria have considerable potential as sources of novel biochemicals such as low temperature enzymes and anti-freeze proteins. Among the eukaryotic organisms survival strategies have evolved, among which dependence on mixotrophy in phytoflagellates and some ciliates is common. There is also some evidence of evolution of new species of flagellate in the marine derived saline lakes of the Vestfold Hills. Recent work on viruses in polar lakes demonstrates high abundance and high rates of infection, implying that they may play an important role in genetic exchange in these extreme environments.

Keywords: lakes; bacteria; flagellates; cyanobacteria; ciliates

1. INTRODUCTION

Lake systems in Antarctica provide a natural laboratory for studying evolution in micro-organisms. A number of key studies are emerging that suggest a degree of endemism, which may be attributable to a unique combination of selection pressures that prevail in these polar lacustrine ecosystems (Franzmann & Dobson 1993; Taton *et al.* 2006). Unlike the majority of lower latitude lakes, Antarctic lakes are removed from the direct effects of human impact, with the few exceptions of lakes close to research stations that may be used as water supplies (Ellis-Evans *et al.* 1998). Wherever the human species has colonized and embarked on a settled agricultural mode of life, changes have occurred in catchment hydrology and inputs of nutrients to lakes. While most Antarctic lakes escape direct human impact, they are subject to the indirect effects of man's activities. The effects of ozone depletion and elevated ultraviolet radiation are impacting on Antarctic aquatic systems, as are the effects of climate warming (Quayle *et al.* 2002). What is becoming evident is that Antarctic lakes are delicate ecosystems that respond rapidly to local climatic perturbations (Lyons *et al.* 2007).

Despite the fact that nature offers us an exciting natural laboratory for investigating the evolution of mostly microbial organisms, there is, as yet, only a small pool of molecular data and a paucity of systematic studies on Antarctic lakes. What follows is a synthesis of the present knowledge on the biodiversity and

evolution of bacteria and protists in Antarctic freshwater and saline lakes.

(a) *Antarctic lake types*

The Antarctic continent is almost entirely covered by a vast icecap that reaches 4 km in thickness. Despite this, the continent possesses a remarkable array of lake ecosystems, many of them located in the small ice-free coastal areas or Antarctic oases—so-called because in this continental polar desert they are areas supporting life, albeit sparse. There are some inland ice-free areas that have also lake ecosystems, notably the largest ice-free expanse of the Dry Valleys in Southern Victoria Land (figure 1). The lakes of the ice-free regions range from freshwater to hypersaline (almost seven times seawater). Some abut onto glaciers, for example, Cheltnock Lake (Vestfold Hills) and maintain thick ice-covers that may be up to 3–5 m in thickness (J. Laybourn-Parry 2000, unpublished data), while neighbouring lakes may lose their ice for a few weeks in summer, for example, Crooked Lake and Lake Druzhby (Laybourn-Parry *et al.* 1992; Bayliss *et al.* 1997). The lakes of the Dry Valleys lie far south (77° S) and are among the most extreme Antarctic lacustrine ecosystems. They are covered by debris containing thick ice (up to 4.3 m; Howard-Williams *et al.* 1998; Spigel & Priscu 1998).

Epishelf lakes are a lake type virtually unique to Antarctica. Only one or two such lakes have been noted in the Arctic (Vincent *et al.* 2001; Mueller *et al.* 2003). These are unusual freshwater lakes that lie between ice shelves and the land mass (figure 2). The freshwater overlies denser, colder seawater creating a tidal freshwater lake. Typically, they have rafted ice around their shorelines created by the daily tidal cycle. Some epishelf lakes are thought to be very old, for example,

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Figure 1. Map of Antarctica to show the sites of suites of lakes referred to in the text. Places: 1, Byers Peninsula; 2, Potter Peninsula, King George Island; 3, Hope Bay—Boeckella Lake, Chico Lake; 4, Signy Island—Heywood Lake, Sombre Lake, Tranquil Lake; 5, Lake Ellsworth; 6, Shirmacher Oasis; 7, Showa Oasis; 8, Heard Island; 9, Larsemann Hills; 10, Vestfold Hills—Ace Lake, Biseroye Lake, Burton Lake, Cat Lake, Crooked Lake, Depot Lake, Lake Druzhyby, Highway Lake, Organic Lake, Pauk Lake, Pendant Lake, Rookery Lake, Watts Lake; 11, Bunge Hills; 12, Lake Vostok; 13, Dry Valleys—Lake Bonney, Lake Fryxell, Lake Hoare, Lake Vanda; 14, Amery Oasis—Beaver Lake, Radok Lake, Terrasovoje Lake.

Beaver Lake in eastern Antarctica which is also the largest of these lakes on the continent (Wand *et al.* 1987; Adamson & Darragh 1991; figure 1), while others are very young, only a few thousand years (Doran *et al.* 2000). Knowledge of the biology of these lakes is sparse, but there are some intriguing questions, for example, how did a dwarf form of the copepod *Boeckella poppei* colonize Beaver Lake? It has not been recorded elsewhere in eastern Antarctica apart from other lakes in the Amery Oasis, but does occur on the Antarctic Peninsula (western Antarctica) and Signy Island (Laybourn-Parry *et al.* 2001a; Bayly *et al.* 2003). Palaeolimnological evidence indicates that it has been in Beaver Lake for a long time (Bayly *et al.* 2003).

Temporary lakes often form on glacier surfaces. Although they have not been investigated from a biological perspective, it is probable that their communities closely resemble those of cryoconite holes which are a common feature of glacier surfaces in summer. Such communities are ephemeral. Airborne radio-echo sounding (RES) in the Seventies revealed subglacial lakes below the polar icecap (Oswald & Robin 1973). Later work using an extensive analogue database of 60 MHz RES covering 50% of the continent revealed a vast array of subglacial lakes (Siebert *et al.* 1986) and has identified further potential target lakes for investigation, such as Lake Ellsworth (www.geos.ed.ac.uk/research/ellsworth/). The largest, Lake Vostok, has been most extensively surveyed using both satellite remote sensing and RES (Kapitsa *et al.* 1996). Lake Vostok has an area equivalent to Lake Ontario and a maximum depth of 500 m. The biology of these extraordinary lakes awaits investigation, but offers the exciting prospect of micro-organisms that have been isolated for at least 420 000 years (Christner *et al.*

Figure 2. Diagrammatic section of an epishelf lake.

2001). Analysis of material from an ice core that extended into ice accreted below glacial ice by freezing of Lake Vostok water, showed that at least four bacterial lineages are likely to be present in the lake: *Brachybacteria*; *Methylobacteria*; *Paenibacillus*; and *Sphingomonas*. A number of these are related in terms of their 16S rDNA sequences to bacteria found in other extreme cold environments (Christner *et al.* 2001). However, when control for contamination was conducted rigorously, a 3607 m sample yield only one extant thermophilic facultative chemolithoautotroph *Hydrogenophilus thermoluteolus* (Bulat *et al.* 2004) and this might increase speculation that Lake Vostok could harbour novel lineages.

The majority of the coastal oases lakes were formed by glacial processes and isostatic uplift. Some of these suites of lakes have been subject to detailed long-term study, because permanent research stations are located in the vicinity. Examples are the Vestfold and Larsemann Hills in eastern Antarctica and the Dry Valleys of Southern Victoria Land (figure 1). The Vestfold Hills and many of its lakes were formed by isostatic rebound after the last major glaciation (Adamson & Pickard 1986). More recently, models have been developed relating sea level changes to ice-sheet history (Zwart *et al.* 1998). A review of a range of published palaeolimnological data indicates that eustatic sea level changes occurred more rapidly than isostatic rebound (Hodson *et al.* 2004). As a consequence, there were marine incursions. There is good evidence of marine incursions and successive periods of meromixis in the sedimentary history of one of the most studied lakes in the Vestfold Hills, Ace Lake (Roberts & McMinn 1999; Cromer *et al.* 2005). Evidence suggests that the Larsemann Hills were largely ice-free during the Wisconsin glaciation (Burgess *et al.* 1994). More recent work demonstrated that part of the Larsemann Hills (Broknes Peninsula) has been ice-free for at least 45 000 years (Hodson *et al.* 2001). Data on the history of other coastal oases, such as the Bunge Hills, Shirmacher Oasis and Syowa, are limited.

(b) *The physical/chemical environment and food webs*

As indicated earlier, there are unique selection pressures related to the extreme environmental conditions. Antarctic lakes are characterized by continuous low temperatures (figure 3), low annual levels of photosynthetically active radiation (PAR) and low

Figure 3. Typical temperatures for large freshwater Antarctic lakes over an annual cycle at different depths in the water column. Crooked Lake—filled circles, 0 m immediately under ice cover; filled squares, 5 m; filled triangles, 20 m. Lake Druzhby—open circles, 0 m immediately under ice cover; open squares, 5 m; open triangles, 20 m.

concentrations of inorganic nutrients (nitrogen and phosphorus). While there may be 24 h daylight in summer, there is a long winter phase when the Sun does not rise above the horizon. The lake ice-covers attenuate light, often very significantly, as is the case in the perennially ice-covered Dry Valley lakes. For example, in Lake Bonney under ice PAR was 1.8–3.3% of downwelling irradiance at the lake surface (Lizotte & Priscu 1992) and in Lake Hoare 0.5–2.8% of surface PAR (Howard-Williams *et al.* 1998). Thus, the phytoplankton are confronted by a poor light climate and have evolved joint photo systems adapted to the shade as well as other survival mechanisms such as a heavy dependence on mixotrophy (Morgan *et al.* 1998; Neale & Priscu 1998; Marshall & Laybourn-Parry 2002). Unless the waters are enriched by seal or avian faeces, the lakes are nutrient poor, as there are no significant allochthonous inputs. Overall, the majority of Antarctic lakes are ultra-oligotrophic to oligotrophic. Only a few species are adapted to survive in the extreme conditions of these lakes resulting in truncated simplified food webs (figure 4).

Typically, continental Antarctic lakes and cryoconites are dominated by plankton composed of photosynthetic and heterotrophic protozoa, a few algae, fungi, bacteria and viruses (figure 4). In the coastal oasis lakes, there may be a single crustacean, for example, the cladoceran *Daphniopsis studei* in the freshwater lakes or a marine copepod in the saline lakes, and a few rotifers (Laybourn-Parry *et al.* 1991; Bell & Laybourn-Parry 1999a). In the more extreme Dry Valley lakes, there are usually no crustaceans, but only a few rotifers belonging to the genus *Philodina* (Laybourn-Parry *et al.* 1997). Crustacea have been recorded from only one Dry Valley lake, Lake Joyce (Roberts *et al.* 2004a,b). The lakes of the sub-Antarctic Islands, such as Signy Island (60° S), have more diverse communities, but even here metazoan diversity is sparse (Heywood 1972).

Many of the saline lakes of coastal oases such as the Vestfold Hills are marine derived, formed from pockets of seawater trapped in closed basins when the land rose during isostatic rebound following the last glaciation. The original eukaryotic marine communities became progressively simplified leaving a few dominant nanoflagellates and dinoflagellates, ciliates and diatoms. This

Figure 4. Typical food web structure of an Antarctic lake. The example shown is a freshwater or brackish lake in the Vestfold Hills.

suite of lakes ranges from slightly brackish (approx. 4–5‰) to hypersaline (240‰). They offer a continuum of salinity and physical conditions in which to study the allopatric evolution of marine-derived organisms.

The freshwater lakes were formed when fjords were truncated or behind ice dams. New lakes are also forming at the edge of the icecap as it recedes. These lakes have probably been colonized by propagules brought to Antarctica on air masses (Marshall 1996; Muñoz *et al.* 2004) and by birds such as Skuas that are frequently seen bathing in the moats around the lake edges in summer.

(c) The application of molecular techniques to the study of biodiversity, biogeography and evolution

Traditionally, the microbial community structure in Antarctic freshwater lakes has been regarded as a black box, the similarity in morphological characteristics making species distinctions extremely difficult. However, the advent of molecular techniques has allowed the study of community structure and stability within the bacterioplankton and increasingly the virioplankton and phytoplankton (Pearce & Butler 2002; Pearce 2003, 2005; Pearce *et al.* 2003, 2005; Unrein *et al.* 2005), and as techniques become more sophisticated, taxonomic studies are now attempting to identify associated functional relationships and distribution biogeography (Purdy *et al.* 2003; Moosvi *et al.* 2005).

Over recent years, an increasing variety of molecular techniques has been applied to the study of Antarctic lake systems. In particular, the potential of direct sequencing of the PCR-amplified 16S rRNA gene for phylogenetic comparison is well documented, and has been applied to the identification of new species from Antarctic lakes for over a decade (Dobson *et al.* 1993). However, the successful application of PCR to the identification of non-indigenous micro-organisms has limitations; non-indigenous micro-organisms in Antarctic lake systems may be transported to and distributed within the Antarctic continent by natural processes, and specific 16S rRNA gene sequences may be present, but beyond the limits of detection due to their low concentrations and heterogeneous distribution (Baker *et al.* 2003). It has also been suggested that the conserved nature of the 16S rRNA molecule means that it may not be as useful for detecting evolutionary change in Antarctic prokaryotes

when compared with non-Antarctic prokaryotes (Franzmann & Dobson 1993). However, the enormous strength of PCR detection lies in accessing microbial taxonomy without the need to culture the organisms (Baker *et al.* 2003), and as a result, much use is currently made of 16S rRNA clone library construction and screening in Antarctic biodiversity studies (Bowman *et al.* 2000).

The PCR-based detection technique has been further developed to use a denaturing gradient gel to separate PCR-amplified DNA fragments based on their denaturing (strand separation) characteristics and hence their DNA sequence (Muyzer *et al.* 1993; Nübel *et al.* 1997; Stakebrandt *et al.* 2004). The particular power of this technological development in community studies is that it selectively amplifies predominant members of the community (Chan *et al.* 2002; Koizumi *et al.* 2003), as 5000 cells per ml⁻¹ are necessary to generate a denaturing gradient gel electrophoresis fragment (Kan *et al.* 2004). By sequencing individual fragments, it is now possible to identify the dominant members of the community.

An alternative DNA sequence-based detection technique, which does not rely on the need for PCR amplification, and thus avoids potential bias inherent in the PCR itself, is fluorescence *in situ* hybridization (Adamson & Darragh 1991). In this technique, an oligonucleotide (a short sequence of DNA nucleotides) is chemically attached to a fluorescent dye. This molecule recognizes and binds to specific DNA sequences in the target population, to show the presence or absence of that sequence. This powerful technique has been applied successfully to a number of Antarctic lake systems (Pearce 2003; Pearce *et al.* 2003, 2005) and has the potential for further development using catalysed reporter deposition CARD-FISH (Pernthaler *et al.* 2002), as this technique is particularly powerful in low biomass systems.

When such DNA-based techniques are combined with an alternative technology, such as immunobiology (James *et al.* 1994), spectrophotometry, isotope chemistry, radioactive isotope incorporation, thymidine incorporation for ultraviolet B radiation (Chantila *et al.* 2001), stable isotopes (Noon *et al.* 2002) and microautoradiography (Pearl & Priscu 1998), it is possible not only to study what function micro-organisms have within the environment, but also to attribute the function to a particular species or group.

Following the genomic revolution, it has now become possible to apply whole genome methodologies to Antarctic limnetic systems (Clark *et al.* 2004; Peck *et al.* 2005). Environmental metagenomics involves the genomic analysis of micro-organisms by direct extraction and cloning of DNA from a whole assemblage of organisms (Handelsman 2004), and this allows questions to be asked about the physiological potential or function of the community as a whole. Specific gene targeting allows genes of interest, perhaps for a specific function such as cellulose degradation to be cloned and sequenced or expressed in a vector in the laboratory (Cowan *et al.* 2005). Proteomic approaches target the products of gene transcription, and as such, provide a more detailed insight into what cells are actually doing, rather than the potential they have (Goodchild *et al.*

2004). Furthermore, we are now entering a new era in Antarctic research as the first whole genome sequence for a marine psychrophilic bacterium *Colwellia psychrerythraea* 34H, a model for the study of life in permanently cold environments, has revealed capabilities important to carbon and nutrient cycling, bioremediation, production of secondary metabolites and cold-adapted enzymes (Methé *et al.* 2002, 2005). As more of this type of information becomes available, it will enable comparative genomics among Antarctic lake species (Saunders *et al.* 2003) and the subsequent analysis of differential gene expression in the laboratory using microarray technology (Weber & Jung 2002).

(d) *Antarctic lake systems and the study of evolution*

The potential of Antarctic lake systems for the study of evolutionary biology lies in the fact that they are discreet systems for colonization and that biodiversity among dominant microbial groups is relatively low. For example, two water bodies Chico and Boeckella Lakes near Hope Bay showed periods when a maximum of only three species comprised more than 80% of the organisms present. Low biodiversity is particularly important, as it makes it possible to identify a high proportion of the diversity present. In more diverse communities, microbial ecologists must rely on statistics to estimate coverage of diversity. However, when statistics are used, it is impossible to show that any particular sequence is definitely not present, making the study of endemism difficult. This is illustrated through the comparison of closely analogous psychrophilic environments. When the diversity and community structure of anoxic sediment from marine salinity meromictic lakes and a coastal meromictic marine basin were compared, little similarity was found to exist between the phylotypes detected and other clone libraries based on marine sediment, suggesting that an enormous prokaryotic diversity occurs within marine and marine-derived sediments (Bowman 2004). This observation suggests a high degree of niche separation in this type of system, where selection pressures related to the psychrophilic nature of the environment do not predominate.

Antarctic lake systems also provide ideal systems in which to test the 'everything is everywhere' hypothesis (Beijerinck 1913; Baas-Becking 1934; Fenchel & Finlay 2003) through the study of comparative phylogenies based upon a number of different conserved genes (e.g. 16S, 18S, *gyrB*, *ectBC*), and where the Antarctic might be just one sample in a geographical transect. For example, the lake ice microbial community appears to be dominated by organisms that are not uniquely adapted to the lake ice system, but originate elsewhere in the surrounding region and may colonize the habitat provided by the sediments suspended in lake ice opportunistically (Gordon *et al.* 2000). Other key habitats in which such studies might be undertaken include cryoconite holes (Mueller *et al.* 2001). Christner *et al.* (2003) demonstrated that DNA preparations from cryoconite holes had sequences similar to rDNA molecules of species present in adjacent lake ice and microbial mat environments. The cryoconite hole community was therefore most probably seeded by

propagules from these local environments. Thus, cryoconite holes may serve as biological refuges that, on glacial melting, can repopulate local environments. Sealed cryoconite holes in the McMurdo Dry Valleys have ice lids which may be sealed for decades. Photoautotrophs and heterotrophs grow within this closed environment, and as such they might also act as refugia (Tranter *et al.* 2004). In addition, permanent lake ice (Gordon *et al.* 2000), the phase change of water to ice, in brine pockets (Deming 2002), the marine/freshwater interface and freshwater streams each merit further attention as potentially novel environments in which candidate endemics could exist. To this end, much work has already been done on the microbial biodiversity and function of bacteria in the Southern Ocean (Delille 1996), on Arctic ecosystems (Cottrell *et al.* 2005; Kastovska *et al.* 2005; Leck & Bigg 2005; Yu *et al.* 2005; Connelly *et al.* 2006; Garneau *et al.* 2006) and on Antarctic soils (Sjoling & Cowan 2000; Ruberto *et al.* 2005; Powell *et al.* 2006).

2. BACTERIA

To date, much research effort has been devoted to the study of bacterial biodiversity in Antarctic lake systems, and a number of new Antarctic lake bacterial species are published on an annual basis (Bowman *et al.* 2003; Busse *et al.* 2003; Reddy *et al.* 2003a,b; Sheridan *et al.* 2003; Spring *et al.* 2003; Van Trappen *et al.* 2003, 2004a–c, 2005; Donachie *et al.* 2004; Hirsch *et al.* 2004a,b; Jung *et al.* 2004; Montes *et al.* 2004; Pocock *et al.* 2004; Chen *et al.* 2005; Yi *et al.* 2005a,b). Using this information, patterns are beginning to emerge in this biodiversity, for example, it is now known that there are common groups of freshwater bacteria (Glockner *et al.* 2000; Zwart *et al.* 2002), and molecular methods applied to the bacteria are starting to suggest a restricted distribution of certain taxa.

Bacteria and Archaea that grow in the oceans and freshwater, respectively, frequently show a clear evolutionary separation—this is apparent from the identification of the phylogenetic clusters that are restricted to either freshwater or marine habitats (Tindall *et al.* 2000). However, sequence dissimilarity between the rRNA sequences of Antarctic strains and their nearest known relatives suggests that they diverged from each other much earlier than the establishment of their modern Antarctic habitat (Franzmann & Dobson 1993). For example, the Vestfold Hills and the refugia that appear within them have only appeared in the last 8000 years (Adamson & Pickard 1986). Franzmann & Dobson (1993), applying the calibration of Ochman & Wilson (1987) equated this period to a change of 0.25 of a nucleotide for a gene of 1600 bp.

Elsewhere, work on Antarctic strains of *Janthinobacterium* (Tindall *et al.* 2000) has shown that the Antarctic strains are virtually identical at the 16S rDNA level to the two known species of the genus: *Janthinobacterium lividum* and *Janthinobacterium agaricidamnosum*. However, Tindall (2004) cited subsequent unpublished data which indicated that the Antarctic isolates were distinct and formed two separate subgroups. The implication is that the

Antarctic strains have evolved independently from populations in other parts of the globe (allopatric evolution). However, Tindall (2004) also suggested that there may be potential for speciation within the local Antarctic population (sympatric evolution), as there were two distinct Antarctic subgroups, which may have arisen from the same initial Antarctic strain.

There is gathering evidence, which shows that similar effects are to be seen in other groups of strains, which would indicate some interaction between the strains and the local environment. In such cases, the relatively small degree of 16S rDNA sequence divergence clearly indicates that the Antarctic isolates have not separated from their 'parent populations' hundreds of millions of years ago, but rather that a time-scale of thousands of years may be more appropriate. However, there is currently no consensus regarding the degree of endemism in Antarctic bacteria, largely due to the difficulty in proving that all of the bacteria from a given system have been identified.

As a result of novel selection pressures in Antarctic lake systems, there is a potential for the discovery of novel biochemical pathways and physiological adaptations, although most Antarctic bioprospecting, to date, has been with soil isolates. The mere existence of novel biochemical pathways in particular ecosystems suggests potential evolutionary separation. Extremophiles are a potential source for novel enzymes, extremozymes, which have a great economic potential in many industrial processes, including agricultural, chemical and pharmaceutical applications (Van den Burg 2003). A particular interest is for low-temperature enzyme activity, cold shock induction and ice-active substances. Biochemicals with a specific type of activity are being sought in a range of Antarctic systems. A β -galactosidase with a low-temperature optimum has been obtained from an Antarctic soil *Arthrobacter* isolate (Coker *et al.* 2003), a cold-active alkaline phosphatase has been isolated (Dhaked *et al.* 2005), and high levels of proteolytic activity found at 20°C (Vazquez *et al.* 1995). Elsewhere, and of importance for industrial exploitation, a low-temperature lipase was obtained from the Antarctic marine system (Yang *et al.* 2004) and Antarctic bacteria, which inhibit the growth of food-borne micro-organisms at low temperatures, have been isolated from Antarctic soil (O'Brien *et al.* 2004).

Ice-active substances have been discovered associated with Antarctic freshwater and terrestrial photosynthetic organisms (Raymond & Fritsen 2000). For example, Ideno *et al.* (2001) describe a cold shock inducible peptidyl-prolyl *cis*-transferase. Anti-freeze proteins (AFPs) have been demonstrated in planktonic bacteria from a diverse range of saline lakes in the Vestfold Hills (Gilbert *et al.* 2004). Among these, a hyperactive Ca^{2+} -dependent AFP was demonstrated in *Marinomonas primoryensis* isolated from Ace Lake (Gilbert *et al.* 2005). AFP-producing plants and bacteria, so far reported, show substantially lower thermal hysteresis than do AFPs from animals, consistent with a freeze-tolerant strategy where the organisms readily freeze but use the recrystallization inhibition activity of AFPs to control the size of the ice crystals (Xu *et al.* 1998; Griffith & Yaish 2004)—previously,

Ca²⁺-dependent AFP activity had only been reported from fish AFP activity (Ewart *et al.* 1996).

Biochemical investigations have also helped understanding of how Antarctic lake ecosystems function, such as estimates of sulphate reduction rates in Lake Vanda (Purdy *et al.* 2001). Depth profiles of metals in Lake Vanda, a permanently ice-covered, stratified Antarctic lake, suggested the importance of particulate manganese oxides in the scavenging, transport and release of metals. The release of adsorbed trace metals accompanying the solubilization of manganese oxides may provide populations of *Carnobacterium* with a source of nutrients in this extremely oligotrophic environment (Bratina *et al.* 1998). Anoxygenic photosynthesis is thought to play an important role in the primary productivity of permanently frozen lakes in the Antarctic Dry Valleys and a remarkable diversity of phototrophic purple bacteria in permanently frozen Antarctic lakes has been described using *pufM* sequences which generate a product involved in photosynthesis (Kerr *et al.* 2003).

Novel physiological adaptations could also suggest evolutionary separation—biofilm formation and synergy may be two physiological strategies for nutrient acquisition in these systems. Data indicate that nitrifying bacteria have an important role to play in the vertical distribution of nitrogen compounds in Antarctic lake systems (Voytek *et al.* 1999), and nitrogen budgets show that nitrogen fixation is responsible for up to one-third of demand in Antarctic pond benthic communities (Fernández-Valiente *et al.* 2001). The low concentration of nutrient has led to nitrogen fixation levels of 1 g m⁻² y⁻¹ in cyanobacterial mats, so nitrogen availability is a key nutritional factor controlling microbial production in Antarctic freshwater habitats (Olson *et al.* 1998). Physical and chemical changes have been shown to influence anaerobic function such as acetate-driven sulphate reduction and H₂-driven methanogenesis (Mountfort *et al.* 2003) and the balance between anaerobiosis and aerobiosis in Antarctic lacustrine bacteria (Bharathi *et al.* 1999). Low temperatures might induce the viable but non-culturable (VBNC) state in Antarctic lake micro-organisms and the VBNC state of some bacteria, collected from Antarctic lakes, has been reported (Chattopadhyay 2000). This work also cites examples of the demonstration of transcription and translation at low temperature (Chattopadhyay *et al.* 1995), production of cold-active enzymes (Chattopadhyay *et al.* 1997) and temperature-dependent synthesis of pigments in some Antarctic phototrophs (Ray *et al.* 1998).

3. CYANOBACTERIA

Evidence for potential endemism among the cyanobacteria appears to be growing and it is perhaps, among this group that we will eventually be able to establish the degree of endemism in Antarctic microbiota. Benthic cyanobacterial mats are a major feature of the Dry Valley lakes, as well as lakes elsewhere in Antarctica, and make a significant contribution to carbon fixation (Hawes & Schwartz 1999). Based on morphological analysis, the species found in the littoral mats of Lake Fryxell appeared to be of cosmopolitan

distribution with the exception of *Oscillatoria* cf. *subproboscidea*, which is endemic to Antarctica (Taton *et al.* 2003). Molecular analysis has revealed a very different picture. 16S rRNA sequences were distributed in 11 phylogenetic lineages, three of which were exclusively Antarctic and two of which were novel. These Antarctic sequences together with all other polar sequences were distributed into 22 lineages. Nine of these were exclusively Antarctic including the two novel lineages (Taton *et al.* 2003). In contrast, the genus *Nostoc* apparently has a cosmopolitan distribution. The cluster to which the Lake Fryxell sequences belonged has both a polar and non-polar distribution. More recent work that compared samples from the Dry Valley lakes in western Antarctica with material from lakes in the Larsemann and Vestfold Hills in eastern Antarctica identified 17 morphospecies and 28 16S rRNA gene-based operational taxonomic units belonging to the Oscillatoriales, Nostocales and Chroococcales (Taton *et al.* 2006). The molecular data suggested that endemic Antarctic species are more abundant than suggested by traditional morphological investigations. Elsewhere, Jungblut *et al.* (2005) investigated the diversity of cyanobacterial mat communities of three meltwater ponds—Fresh, Orange and Salt Ponds, south of Bratina Island, McMurdo Ice Shelf, Antarctica. Although morphological studies had concluded that cyanobacteria had originated in temperate climates and hence polar cyanobacteria were assumed not to be endemic in Antarctica (Vincent 2000), they also found phylotypes of the order Oscillatoriales which have, to date, only been identified in Antarctic environments. For other groups, Vincent *et al.* (2000) investigated the phylogenetic diversity of picocyanobacteria in Arctic and Antarctic ecosystems. Analysis of 16S rRNA genes from Antarctic isolates showed that they were 96–97% similar to *Prochlorococcus marinus*, but that they formed a distinct cluster relative to all other picocyanobacteria. Powell *et al.* (2005) used a combination of molecular and physiological techniques to study *Synechococcus* strains in saline Antarctic lakes. They concluded that Antarctic lake *Synechococcus* populations were similar to other polar picocyanobacteria in terms of cardinal growth temperatures and slow growth, and were related only peripherally to marine strains and that the Antarctic strain represented a unique and highly adapted clade in the stable water columns of some saline Antarctic lakes. Even within lake systems, microenvironments exist with the opportunity for enhanced niche differentiation and novel selection pressure—there is evidence for the long-term isolation of the lake bottom of Lake Vida (Hall & Henderson 2001), and frozen microbial mats within the ice cover which are still viable on thawing have a history that extends to at least 2800 C-14 years BP (Doran *et al.* 2003).

4. VIRUSES

It is now well established that viruses are ubiquitous in aquatic ecosystems worldwide (Wilson *et al.* 2000), and given that Antarctic lakes have a plankton almost entirely made up of bacteria and protists, and that virus-like particle (VLP) abundances are particularly

Table 1. VLP abundances and virus-to-bacteria ratios (VBRs) in Antarctic and Arctic lakes and freshwater and marine systems for comparisons.

site	VLP (ml ⁻¹)	VBR
Pendant Lake (Madan <i>et al.</i> 2005)	1.2–12.0 × 10 ⁷	30.4–96.7
Ace Lake (Madan <i>et al.</i> 2005)	0.9–6.1 × 10 ⁷	30.6–80.0
Crooked Lake (Säwström <i>et al.</i> 2007)	0.16–0.91 × 10 ⁶	1.9–6.9
Lake Fryxell (Kepner <i>et al.</i> 1998)	max 3.35 × 10 ⁷	1.7–141
Sombre Lake (Wilson <i>et al.</i> 2000)	1.2 × 10 ⁷	2.4
Heywood Lake (Wilson <i>et al.</i> 2000)	2.74 × 10 ⁷	3.6
Tranquil Lake (Wilson <i>et al.</i> 2000)	0.76 × 10 ⁷	2.8
Svalbard Lakes (Anesio <i>et al.</i> in press)	0.43–2.89 × 10 ⁷	11.3–25.2
freshwater systems (Maranger & Bird 1995)	0.41–2.5 × 10 ⁸	4.9–77.5
marine systems (Maranger & Bird 1995)	0.0067–7.1 × 10 ⁷	0.38–53.8

high (table 1), it is probable that viruses play a pivotal role in carbon cycling in these extreme ecosystems (Laybourn-Parry *et al.* 2001b; Madan *et al.* 2005). Indeed, previous studies have indicated that the importance of viruses in polar aquatic ecosystems might be greater than in lower latitude systems (Kepner *et al.* 1998). Viral numbers exceed bacterial numbers by an order of magnitude, and represent a significant carbon pool (Priscu *et al.* 1999). Viruses can influence bacterial evolution through the acquisition of new phenotypic characteristics through gene exchange (transduction), confer immunity from infection by other viruses and through enhanced reproductive fitness of the host (Wommack & Colwell 2000), influence genomic structure through lysogeny, which can account for up to 63.2% of the bacterial population (Lisle & Priscu 2004), they can affect community succession and influence biodiversity through selective host mortality (Madan *et al.* 2005) and they can also alter pathways of nutrient and energy flow (Wilson *et al.* 2000). At present, we have only a broad brush picture of viral activity in Antarctic lakes, but given their apparent abundance, they may be contributing significantly to genetic exchange in these extreme lakes. This offers an exciting avenue for future research.

5. PROTISTS

(a) *Flagellated protozoa*

The saline lakes of the Vestfold Hills are many and varied and range widely in salinity. The least saline are unstratified, while others have undergone phases of meromixis resulting in permanent stratification with strong physical and chemical gradients in their water columns (Burton 1981). The most saline lakes show summer stratification and winter mixis. Their salinity prevents the development of ice-cover and, consequently, they experience extremely wide temperature fluctuations plummeting to –17°C in winter and rising to +11°C in summer (Burke & Burton 1988; Ferris & Burton 1988) imposing extreme physiological challenge. As indicated earlier, the biota of these lakes were derived from marine communities, which underwent subsequent simplification leaving a small number of apparently highly adapted protists and bacteria. Molecular analysis of Antarctic bacteria is still relatively sparse and extremely limited for the protists. Thus, we have little data on which to base speculation. The

Vestfold Hills possesses a suite of marine-derived lakes that have developed distinct physical and chemical variations presenting us with a natural laboratory in which to study the potential evolution of new genotypes and the environmental selection of specific strains and ecotypes.

The limited evidence suggests that new species of protist are evolving in response to the extreme physical and chemical environments prevalent in these saline environments. A new species of amoeba flagellate *Tetramitus* (*Tetramitus vestfoldii*) has been described from Pendant Lake (16‰) based on SSU rDNA and microscopic analysis (Murtagh *et al.* 2001). It was not seen in detailed studies of the neighbouring lakes (Ace Lake and Pendant Lake; Laybourn-Parry *et al.* 2005; Madan *et al.* 2005) and appears unable to survive in salinities above 30‰. However, *Tetramitus* was observed in the plankton of an adjacent marine basin (Murtagh *et al.* 2001). Other distinct morphological forms of protists have been observed in the hypersaline lakes. A loricate choanoflagellate which resembled *Acanthocorbis unguiculata* (Thomsen) was described in Organic Lake (176‰). It occurs in the sea off the Vestfold Hills (Marchant 1982), and while it resembles the marine form, there were distinct differences. Notable dissimilarities were a lower number of transverse costae and a much smaller protoplast size (Van den Hoff & Franzmann 1986).

The evolution of physiological strategies, which permit survival under extreme conditions and enable exploitation of the short summer for growth, is clearly apparent in these lakes. One of the dominant phytoflagellates in lakes with salinities approximately 15–20‰ is the prasinophyte *Pyramimonas gelidicola* McFadden. In meromictic Ace Lake, it is mixotrophic feeding on bacteria, while it has not been reported as mixotrophic elsewhere (Bell & Laybourn-Parry 2003). Moreover, while its numbers declined in winter, it started building up its biomass in spring (Bell & Laybourn-Parry 1999a). *Pyramimonas* also produces cysts allowing the growing population to be augmented in spring by excysting individuals. More recent work has indicated considerable nutritional versatility in *Pyramimonas*. While it ingests bacteria in meromictic Ace Lake, in neighbouring brackish Highway Lake, it does not ingest bacteria but instead takes up dissolved organic carbon across a range of molecular weights from 4 to 500 kDa (Laybourn-Parry *et al.* 2005).

Figure 5. Grazing impact of cryptophytes in Ace Lake (solid columns) and Highway Lake (hatched columns) during 2001/2002. The data were derived from Laybourn-Parry *et al.* (2005).

Cryptophytes are a conspicuous component of the phytoflagellate community of Ace and Highway Lakes where they graze on bacteria throughout the year (figure 5), enabling them to maintain a population during the winter (Laybourn-Parry *et al.* 2005). At times, their grazing impact on the bacterioplankton equals that of the heterotrophic flagellates. These physiological differences between what appears to be the morphologically the same species of phytoflagellates across lakes may indicate differing genotypes. A molecular approach to speciation in phytoflagellates in the saline lakes of the Vestfold Hills offers an exciting avenue for studying allopatry.

The Dry Valleys of Southern Victoria Land represent the largest ice-free area in Antarctica and have been investigated more or less continuously since 1957–1958. The Taylor Valley is the most intensively studied region and contains a number of lakes, including Lake Bonney, Lake Hoare and Lake Fryxell that are the sites of detailed investigation as part of the Long-Term Ecosystem Research Programme which commenced in 1993. Stable chlorine isotope analysis of the lake water profiles suggests that these lakes have differing geomorphological histories. Meromictic Lake Bonney experienced marine incursions during its history evidenced today in the deeper waters, which might be very old (10^5 – 10^6 years; Hendy *et al.* 1977; Lyons *et al.* 1999). Lake Fryxell underwent a draw-down during a cooler period prior to 1000 years BP, while Lake Hoare is a young lake probably originating in the last 1000 years (Lyons *et al.* 1999).

Both Lakes Fryxell and Hoare have similar phytoplankton communities dominated by three species of cryptophyte and lesser numbers of other phytoflagellates like *Pyramimonas* sp. and *Chlamydomonas* sp. (Spaulding *et al.* 1994; Roberts *et al.* 2000, 2004a,b). Cryptophytes are a group common in many polar lakes both in the Arctic and in the saline lakes of the Vestfold Hills (Laybourn-Parry & Marshall 2003; Laybourn-Parry *et al.* 2005) as indicated earlier. In all of these locations, cryptophytes have been seen to practise mixotrophy. In lower latitudes where cryptophytes form deep chlorophyll maxima, they are entirely dependent on photosynthesis (Gasol *et al.* 1992, 1993; Gervais 1998). There are only a few reports of cryptophytes being mixotrophic (Sanders & Porter 1988; Tranvik *et al.* 1989). The dependence on

mixotrophy in the Dry Valley lakes is high. Studies which have considered the balance of carbon acquisition from photosynthesis and ingestion of bacteria have shown that even at mid-summer cryptophytes did not become independent of the need to feed on bacteria (Marshall & Laybourn-Parry 2002). The dependence on grazing at mid-summer was most marked on the deep chlorophyll maximum of Lake Fryxell, where 24% of carbon acquisition was derived from ingesting bacteria.

The evidence suggests that the dependence on heterotrophic carbon acquisition is likely to increase in autumn and winter. While we have no physiological measurements from the Dry Valleys in winter, a remotely operated plankton sampling device that took samples throughout the winter in Lake Fryxell showed cryptophyte numbers increasing before the light returned, suggesting that heterotrophy was being employed as a mechanism to support growth (McKnight *et al.* 2000). As indicated earlier, mixotrophy among some cryptophytes also occurs in the saline lakes of more northerly Vestfold Hills, but here the dependence on mixotrophy is less strong.

The success of cryptophytes in the extreme polar lakes of the Vestfold Hills and the Dry Valleys is undoubtedly related to their physiological plasticity and pre-adaptation. They clearly possess the ability to adopt a mixotrophic nutritional strategy, although this is apparently not exploited to any degree at lower latitudes. In Antarctic systems, mixotrophy has become an important survival mechanism allowing populations to build-up numbers in late winter/early spring and enter the short austral summer with rapidly increasing biomass. As yet, we have no molecular data on these phytoflagellates. It is possible that these phytoflagellates are distinct endemic species. Some preliminary molecular analysis of cultures of the dinoflagellate *Polarcella* sp. isolated from a range of differing saline lakes in the Vestfold Hills indicates that while they are morphologically similar, there are distinct differences between lakes but not within lakes (K. Rengefors *et al.* 2005, unpublished data).

The lakes of the Dry Valleys are covered by perennial debris containing ice that reduces light penetration by between 78 and 99% (Howard-Williams *et al.* 1998). Consequently, the phytoplankton has to function in a severely shaded environment. As one might anticipate, there have been evolutionary changes among the phytoplankton to accommodate life in these extreme environmental conditions. *Chlamydomonas subcaudata* is a common species in the plankton of Lake Bonney. The strain isolated from Lake Bonney is a psychrophile growing only at 16°C and below. *Chlamydomonas subcaudata* possessed higher levels of the xanthophylls lutein, neoxanthin and violaxanthin in comparison with mesophilic species (*Chlamydomonas reinhardtii*; Neale & Prisco 1995; Morgan *et al.* 1998). Based on this observation, it has been suggested that the phytoplankton of Lake Bonney have traded off photo-protection mechanisms against an enhanced ability for efficient light harvesting and energy usage. However, when *C. subcaudata* is grown under relatively high light conditions ($150 \mu\text{mol m}^{-2} \text{s}^{-1}$), the species retained its ability to adjust the xanthophyll cycle and the capacity for

dissipating excess energy as heat (Morgan *et al.* 1998). Immunoblotting investigations indicated that the stoichiometry of photosystem II : photosystem I : coupling factor is significantly altered when compared with *C. reinhardtii*, which suggests that *C. subcaudata* is adapted to grow at the low irradiances found in the water column of Lake Bonney (Morgan *et al.* 1998).

(b) Ciliated protozoa

The ability to evolve successful populations in extreme Antarctic lakes, as they have undergone progressive change, undoubtedly requires some pre-adaptation. An excellent example, observed in the saline lakes of Vestfold Hills, is the marine autotrophic ciliate *Mesodinium rubrum*. This is a species complex that was believed to contain an endosymbiotic cryptophycean (Lindholm 1985). However, recent work suggests that at least some members of this species complex sequester plastids from cryptophyte prey (Gustafson *et al.* 2000). *Mesodinium rubrum* dominates the ciliate communities of many of the lakes reaching concentrations in excess of $100\,000\text{ l}^{-1}$ (Perriss *et al.* 1995; Laybourn-Parry *et al.* 2002). This ciliate can form red tides in the sea and estuaries, but is usually present in low densities (Crawford 1989). It occurs in brackish lakes (4‰) and survives in lakes with salinities up to 62‰ (27% higher than seawater). When the lakes were formed, the stranded seawater would have contained the ancestors of the current populations. Today, *M. rubrum* dominates the ciliate communities of many of the saline lakes of Vestfold Hills. Its success is attributable to its high motility, enabling it to position itself in an ideal light climate in the upper water and to move to deeper waters to gain inorganic nutrients in an ice-covered water column lacking turbulence. Its winter survival strategy involves both encystment and survival in the vegetative stage (Bell & Laybourn-Parry 1999a). Electron microscopy analysis of the active stages revealed large numbers of starch bodies that probably enabled survival while light levels precluded photosynthesis.

The process of isostatic uplift is still continuing and consequently lakes are still forming and evolving. Some, such as Burton Lake, have occasional contact with the sea. One of the more recently formed lakes lying close to the sea is Rookery Lake, which possesses a plankton that still contains many more marine ciliate species than the older lakes (Bell & Laybourn-Parry 1999b). The greater diversity can be attributed to its youth and geologically recent separation from the sea, but may in part be due to its relatively eutrophic status resulting from avian faecal enrichment from a nearby penguin rookery.

Despite the marked differences in the ages the lakes of the Dry Valley and their complex evolution, they have many biological characteristics in common, which suggests that Lake Hoare was colonized relatively quickly by propagules from neighbouring lakes after its formation in the last 1000 years. Observations on freshwater lakes in the Vestfold Hills also indicate that newly formed lakes close to the receding icecap quickly develop identical communities to the older lakes (J. Laybourn-Parry, unpublished data). Lakes Hoare and Fryxell are separated by the Canada Glacier, and

Table 2. The ciliate communities of the Taylor Valley lakes. (Adapted from Kepner *et al.* 1999; Roberts *et al.* 2004a,b.)

species	Lake Bonney	Lake Fryxell	Lake Hoare
<i>Plagiocampa</i> sp.		●	●
<i>Urotricha</i> sp.		●	●
<i>Halteria</i> sp.	●	●	●
<i>Srrombidium</i> sp.	●	●	
<i>Pelagiosrrombidium</i> sp.			●
<i>Didinium</i> sp.	●	●	●
<i>Monodinium</i> sp.	●	●	●
<i>Mesodinium</i> spp.		●	●
<i>Askenasia</i> sp.	●	●	●
<i>Lacrymaria</i> sp.		●	
<i>Spathidium</i> sp.			●
<i>Nassula</i> sp.		●	●
<i>Frontonia</i> sp.		●	
<i>Blepharisma</i> sp.		●	●
<i>Euplotes</i> sps.	●	●	●
<i>Sphaerophrya</i> sp.	●	●	●
<i>Vorticella mayeri</i>		●	●
<i>Vorticella</i> sps.		●	●
<i>Bursaria</i> sp	●	●	●

possess an almost identical ciliate community, while the much more saline waters of Lake Bonney have fewer species in common (table 2).

6. CRUSTACEA

While crustacean zooplankton are not an abundant component of continental Antarctic lakes, they do occur in low numbers, often as single species. Some, such as the cladoceran *D. studei* Rhe, are endemic to Antarctica, specifically eastern Antarctica and its sub-Antarctic islands (Akatova 1966). Increasing salinity and the resultant reduced productivity as the Vestfold Hills lakes developed after their isolation from the sea, had the effect of eliminating most of the metazoans. In lakes above 50‰, the marine copepod *Paralabidocera antarctica* I.C. Thompson disappears, while it has established populations in lakes down to around 16‰ (Perriss & Laybourn-Parry 1997). Burton Lake, that still has a marine contact, has a much more diverse zooplankton community (Bayly 1986). At the other end of the salinity spectrum in slightly brackish lakes, *P. antarctica* has been replaced by the indigenous freshwater cladoceran *D. studei* Rhe. Essentially, *D. studei* is a freshwater species, but it has successfully invaded the brackish lakes of the Vestfold Hills, for example, Highway Lake (Laybourn-Parry & Marchant 1992) and Watts Lake (Hann 1986; Gibson *et al.* 1998).

Overwintering in the active form is the norm, unlike the strategy adopted by cladocerans in lower latitude cold-temperate lakes, where populations largely overwinter as resting eggs. In the Arctic and sub-Antarctic islands, such as Signy Island, crustaceans also overwinter as adults, though often resting or ephippial eggs are produced (Edmondson 1955; McClaren 1964; Heywood 1972). The life-cycle stage that *D. studei* overwinters apparently varies between lakes. In ultra-oligotrophic Crooked Lake juveniles undergo gradual development over the winter, while in slightly more

Table 3. Dry weights and fecundity of *D. studei* in lakes of the Vestfold Hills and Heard Island. (Data from Laybourn-Parry & Marchant (1992).)

lake	dry weight (μg)	mean no. of eggs/juveniles per brood	salinity (‰)
Crooked	50.3 $\pm$ 4.1	2.8 $\pm$ 1.2	0.02
Highway	101.1 $\pm$ 8.2	7.7 $\pm$ 3.0	4.58
Pauk	42.5 $\pm$ 6.1	1.9 $\pm$ 1.0	0.01
Cat	53.0 $\pm$ 5.7	2.7 $\pm$ 1.1	1.20
Depot	50.0 $\pm$ 6.5	2.7 $\pm$ 0.2	1.30
Bisernoye	60.0 $\pm$ 5.9	2.9 $\pm$ 1.2	0.05
Heard Island	234.5 $\pm$ 21.6	16.7 $\pm$ 5.2	not known

productive Lake Druzhby *D. studei* overwinters as adult females (Bayliss & Laybourn-Parry 1995). There are also distinct variations in the size and weights of populations in different lakes of the Vestfold Hills (table 3). As one might expect individuals in the extremely oligotrophic freshwater lakes are smaller and have low fecundity, while the brackish lakes support larger specimens that achieve higher fecundity. Populations in the lakes of Heard Island (an eastern sub-Antarctic island) are large in comparison with their continental cousins, and possess very much higher fecundity (table 3).

All the eggs noted in table 3 appeared to be subitaneous eggs produced by parthenogenesis. The production of ephippial eggs by Arctic and high alpine cladoceran populations does not require the presence of males. For example *Daphnia middendorffiana*, a common species in the Arctic, is an obligate parthenogen. Both subitaneous and ephippial eggs are produced asexually (Hebert 1981). Hebert (1981) has suggested that the transition from cyclical to obligate parthenogenesis does not require major genetic change. The suppression of meiosis during ephippial egg formation may be achieved by a single gene mutation. The single mutant clone might subsequently displace the parent population or coexist with it. Males and ephippial eggs have been observed in some of the lakes in the Vestfold Hills (Gibson *et al.* 1998). However, the ephippial eggs may not have been produced sexually, as non-functional males do occur in Arctic populations (Hebert 1981). In the sparse populations of Antarctic lakes, sexual reproduction is a difficult option, as the chances of finding a mate in large water body where the density of cladocerans is around 1 m^{-3} are limited, suggesting obligate parthenogenesis.

There are no DNA-based molecular studies on *D. studei*, but it is quite evident from work on allozyme differentiation among *Daphnia* species that morphological likeness hides significant genetic divergence and that geographical isolation minimizes gene flow to levels that may lead to the development of distinct new species (Cerny & Hebert 1999). *Daphniopsis studei* also occurs in the Larsemann Hills some 50 miles distant from the Vestfold Hills. It is highly probable that distinct genotypic populations have developed within the various coastal oasis and sub-Antarctic island populations.

Daphniopsis studei possesses a pink pigmentation that may protect it against UV-B radiation. Copepods

use the red carotenoid astaxanthin as an antioxidant, which is able to neutralize free radicals formed when oxygen is exposed to ultraviolet radiation (Hairston 1979; Miki 1991). Studies in the Arctic have shown that crustaceans have to effect a trade-off between possessing protection pigmentation and being conspicuous and liable to predation (Hansson 2000, 2004). In lakes lacking fish, copepod pigmentation was seven times higher than in those lakes with fish. Antarctic lakes lack fish and consequently high pigmentation is an option that *D. studei* can exploit as a protective mechanism against the high levels of UV radiation that prevail in Antarctica. UV-B radiation penetrates through lake ice to around 4 m in the lakes of the Vestfold Hills (M. Foster & J. Laybourn-Parry 2000, unpublished data).

One of the most intriguing species of copepod found in Antarctic lakes is *B. poppei* Mrázek. It occurs in the lakes of the Antarctic Peninsula, Signy Island (western Antarctica) and South America and in lakes in the Amery Oasis in eastern Antarctica (Heywood 1977; Bayly & Burton 1993; Laybourn-Parry *et al.* 2002; Bayly *et al.* 2003). It has not been recorded in any other coastal oasis in eastern Antarctica. The populations that occur in Radok Lake, Terrasovoje Lake and the large epishelf Beaver Lake in the Amery Oasis differ significantly in their morphology from those of found in western Antarctica and South America. They are dwarf forms and there has been a significant modification of the endopod of the fifth leg (Bayly *et al.* 2003). The dwarfism can be attributed to the extremely oligotrophic nature of the lakes where chlorophyll *a* concentrations are below $1 \mu\text{g l}^{-1}$ (Laybourn-Parry *et al.* 2002). The other morphological modifications are undoubtedly related to the long isolation of the Amery populations from the western Antarctic populations. The evidence suggests that the population in eastern Antarctica has been isolated from a time predating the current interglacial (Bayly *et al.* 2003).

7. PALAEO LIMNOLOGY

Palaolimnology includes the study of changes in species composition and abundance over time (Roberts *et al.* 2000) and as such it is a science more traditionally associated with evolution in Antarctic lake systems. Studies of fossils in Ace Lake sediment have shown a diverse assemblage of organisms at an early stage in the evolution of the lake, suggesting either that they were part of an endemic Antarctic flora and fauna, which pre-dated the last glacial maximum and survived in glacial refugia or that efficient intercontinental dispersal had occurred (Swadling *et al.* 2001). Lake-sediment cores from Heywood and Sombre Lakes on Signy Island provide a high-resolution record of climate change (Jones *et al.* 2000; Roberts *et al.* 2004a,b) and offer the potential to study DNA profiles. Preserved ribosomal DNA of planktonic phototrophic algae has been recovered from Holocene anoxic sediments of Ace Lake (Antarctica), and the ancient community members were identified by comparative sequence analysis. Combining lipid biomarkers and preserved DNA, the post-glacial development of Ace Lake from freshwater basin to marine inlet and the present-day

lacustrine saline system was shown to cause major qualitative and quantitative changes in the biodiversity of the planktonic populations over time (Coolen *et al.* 2004).

8. CONCLUSIONS AND FUTURE DIRECTIONS

Advances in molecular biology now offer us the opportunity to unravel how the communities of Antarctic lakes have evolved and will greatly enhance our ability to understand the biogeography of the lake ecosystems. Some suites of lakes offer continuums of salinity and age (e.g. the Vestfold Hills and the Dry Valley lakes) providing natural laboratories in which to study evolution in relation to physical and chemical pressures. These microbially dominated pristine ecosystems with their simple food webs and apparently low species diversity are relatively easy to study compared with much more complex lower latitude lakes. At present, we are only beginning to scratch the surface of the exiting biological potential these systems offer us. There are intriguing data that suggest the evolution of distinct ecotypes and endemic species. The application of functional genomics is a particularly exciting prospect. In summary, based on traditional and molecular approaches, it is evident that Antarctic saline and freshwater lakes are unique systems for studying the evolution of both eukaryotic and prokaryotic microorganisms, as well as the few metazoans that are able to function in their extreme conditions.

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