Vol. 41: 39–48, 2005 | AQUATIC MICROBIAL ECOLOGY
Aquat Microb Ecol | Published November 11

THEME SECTION

Biogeography of aquatic microbes

Coordination: **John R. Dolan**

Contributors to Theme Section: **A. J. Baldwin, P. Catala, B. Costas, J. R. Dolan, T. Fenchel, W. Foissner, A. Griffin, Å. Hagström, W. H. Jeffrey, F. Joux, L. A. Katz, S. J. Kemp, C. D. Lowe, G. B. McManus, D. J. S. Montagnes, J. A. Moss, J. D. Pakulski, J. Pinhassi, K. Pirog, T. Pommier, O. L. O. Snoeyenbos-West**

An introduction to the biogeography of aquatic microbes

John R. Dolan*

Marine Microbial Ecology Group, Laboratoire d'Océanographie de Villefranche, CNRS Université Paris VI UMR 7093, Station Zoologique, BP 28, 06230 Villefranche-sur-Mer, France

ABSTRACT: Aquatic microbes, like all organisms, have biogeographies, but this subject has attracted relatively little attention. In this review, recent results exploiting techniques of molecular biology are summarized to place in perspective the studies of this Theme Section. The studies considered concern large-scale patterns of spatial distribution among heterotrophic planktonic prokaryotic and eukaryotic microbes. For freshwater bacterioplankton communities, reported patterns are inconsistent. Taxonomic richness may increase with system size, and composition may be related among neighboring bodies of water. However, inconsistencies in patterns may be due to differences in the temporal and spatial scales considered. Among planktonic marine prokaryotes, biogeographic patterns are known only in terms of high level groups, e.g. Archea are perhaps dominant in deep oceanic waters. However, studies of large-scale patterns have just begun and they suggest that some ribotypes or species may be restricted to certain oceanic areas. Eukaryotic microbes appear to characterised by high capacities for both dispersal and gene flow. Recent studies appear to conclude that we can form morphological, genetic and physiological groupings but their inter-relationships are obscure at this point in time.

KEY WORDS: Bacteria · Protists · Latitudinal diversity gradient · Island biogeography · Biodiversity

INTRODUCTION

Biogeography is the observation, recording, and explanation of the geographic ranges of organisms (Pielou 1979). Although microbes have biogeographies, this subject has received very little attention: biogeography is generally absent from recent books on microbial diversity (e.g. Bull 2004, Ogunsseitan 2005) as are microbes from discussions on biogeography (e.g. Pielou 1979, Lomolino & Heaney 2004) or ecological geography (Longhurst 1998). To some extent this is probably because of a perception that there is no interesting microbial biogeography — all microbes are potentially everywhere. This is a long-standing assertion. The idea

*Email: dolan@obs-vlfr.fr

that everything is everywhere is generally attributed to Beijerinck (1913). Indeed, most geographic barriers are theoretically irrelevant (extreme environments such as hot springs, deep-sea vents and sea ice may be exceptions). Nonetheless, not all taxa are everywhere in significant quantities. Where a microbe is found with reasonable ease is where it is able to reproduce. This will depend upon a balance between the presence and quantities of resources it requires and the mortality it suffers from biological or physical interactions. Thus, the environment selects — the addendum to 'everything is everywhere', which is usually credited to Baas-Becking (1934).

Microbial biogeography differs from traditional biogeography as historical factors are much less important (and often of no importance) than biological and physical factors. Leaving aside the question of a 'species' for microbes, 3 major characteristics distinguish microbes from most multicellular organisms: large absolute population sizes, short generation times, and of course, high dispersal capabilities. These differences are fundamental. Consider the temporal scale of microbial life compared to other organisms. A bloom of an autotrophic microbe can develop and disappear in a matter of days compared to the decades needed for the dominance of a terrestrial autotroph in the form of a woody plant. Thus microbes are unlikely to provide clues as to the geological history of an area, compared to vascular plants (e.g. Humphries & Parenti 1999).

The interest of studying the biogeography of aquatic microbes is the elucidation of biological and physical factors controlling the presence or absence of microorganisms. However, this field is in its infancy and contrasting patterns and trends are being described. We are not yet at the stage of proposing testable hypotheses to explain agreed upon patterns of distribution. However, there are some hints of generalities. In this paper, I describe recent results concerning patterns of different spatial scales; prokaryotes are considered separately from eukaryotes with the emphasis being on heterotrophic forms. In order to avoid what has been identified as a flaw of macroecology — the uncritical acceptance of data and mixing of scales of analysis (i.e. Rahbek 2005) — attempts have been made throughout the paper to note the scale of analysis relative to the data employed and the generality of the pattern described.

Two very interesting and promising fields (extreme environments and symbionts/parasites) are not reviewed herein: readers interested in these topics are referred to reviews and reports on microbes from extreme environments (Fenchel 2003, Staley & Gosnik 1999, Whitaker et al. 2003, Papke & Ward 2004) and recent reports on symbiotic bacteria (e.g. Bright & Giero 2005, Taylor et al. 2005). Likewise, with regard to viruses, see Breitbart & Rohwer (2005), who recently reviewed biogeographic patterns.

HETEROTROPHIC BACTERIOPLANKTON IN LAKES

Some of the first attempts to apply the new molecular approaches to bacterial biogeography in freshwaters found, not surprisingly, that bacterial communities like phytoplankton and zooplankton change with the season and nearby lakes can differ in bacterial community composition (Konopka et al. 1999, Lindström 2000). Thus it appeared that there need not be a clear relationship between lake location and bacterial community composition.

For example, Lindström (2000) compared communities of 5 small lakes (0.04 to 6.2 ha), all within 75 km of each other in southern Sweden, using denaturing gradient gel electrophoresis (DGGE). The technique allows separation of 16S rDNA sequences, representing different taxa, which appear as bands on a gel. Large volume samples (50 l) were collected in May, July, October and February. DNA was extracted from 0.5 to 9.5 l subsamples. The number of taxa detected per sample using DGGE ranged from 6 to 17. Community composition differed with season as much as it varied between lakes. Statistical analysis suggested that the strongest relationships were between the variability of bacterial community composition and variability in the biomass of microzooplankton, cryptophytes and chrysophytes rather than between lake location or size. A subsequent study of lakes in northern Sweden yielded very similar results (Lindström 2001).

Enlarging the spatial scale, comparison of bacterial communities in sets of lakes in different climatic zones (southern Sweden, northern Sweden, Norwegian Arctic) showed little evidence to support the view that neighboring lakes share bacterioplankton communities (Lindström & Leskinen 2002). The results supported the view that biological interactions, and/or physio-chemical conditions within a given lake, are more important in determining bacterial community composition than lake location.

A lack of community relatedness among neighboring lakes can be an artifact of sampling scales — both spatial and temporal. The problem of spatial variability was considered by Yannarell & Triplett (2004) in a study of the variability both between zones within a lake and between lakes. They investigated 13 northern temperate lakes (Wisconsin, USA) in July using a tube sampler to obtain samples from the entire surface layer. A 250 to 500 ml subsample was analyzed using another 16S rDNA community fingerprinting technique: automated ribosomal intergenic spacer analysis (ARISA). The scales of spatial variability considered were 10s of meters, 100s of meters–lake basin level, and between lakes. They found that the bacterial communities differed less within a lake than between lakes. At the

basin level within a lake, the average dissimilarity was 17%, while between lakes it was 75%. However, they found no evidence of regional patterns or trends of taxonomic richness with lake size (range 1 to 4000 ha in surface area). Within the set of lakes, with a chlorophyll concentration range from 1.8 to 26 µg l^{-1}, bacterial diversity was positively related to lake productivity.

Short-term temporal variability in bacterial community composition was evaluated in a multi-lake study. Three Wisconsin lakes were sampled every 2 wk for 2 yr during the ice-free period by Yannarell et al. (2003). The lakes all showed stable community composition in the fall and spring but quite variable community composition during the summer. The database was expanded to include a third year and analysis suggested very little similarity in bacterial community composition from year to year (Kent et al. 2004).

On a larger spatial scale, 2 sets of Wisconsin lakes (separated by about 300 km) were sampled during the spring, summer and fall of 2002 by Yannarell & Triplett (2005). They found that bacterial community composition was related to both location and lake type (seepage lakes compared to drainage lakes) as communities varied with lake pH and Secchi disk depth.

The relationships between water characteristics, bacterial community composition and physiological rates (respiration, growth rates and growth efficiency) were examined experimentally in communities from 4 Swedish lakes by Langenheder et al. (2005). Bacterial communities from distinct lakes (dissolved organic carbon [DOC] = 6 to 41 mg l^{-1}, phosphorus = 8 to 41 µg l^{-1}) were inoculated into filtered water from their own and all the other lakes. Changes in bacterial biomass were monitored over 11 d and oxygen consumption, DOC consumption and bacterial community composition were examined at the end of the experiment. Extracted 16S rRNA sequences were PCR amplified for another fingerprinting method: terminal restriction fragment length polymorphism (T-RFLP). This method relies on separation through electrophoresis of DNA sequences recognized by restriction enzymes. After 11 d, the genetic structure of the bacterial community had been influenced by the origins of both the inoculum and the water. Interestingly, the physiological rates of the bacterial community were related only to the origin of the water, not to the inoculum.

Overall, studies carried out thus far on northern temperate lakes, both Scandinavian and North American, suggest that lake location is a poor predictor of bacterial community composition and taxonomic richness is not closely related to lake size. These findings are in conflict with basic predictions from the theory of Island Biogeography (MacArthur & Wilson 1967): (1) neighboring lakes (aquatic islands) should resemble one another in taxonomic composition more than distant lakes; and (2) system size (island size) should be related to taxonomic richness. High dispersal capacity, making location and system size simply irrelevant to the presence or absence of taxa, is a possible explanation. However, 2 recent studies (Bell et al. 2005, Reche et al. 2005), carried out specifically to test predictions of Island Biogeography, came to the conclusion that freshwater bacterioplankton communities do conform to the theory of Island Biogeography.

The effect of lake location on taxonomic composition was addressed in a study of 11 small lakes in the Sierra Nevada of Spain using DGGE (Reche et al. 2005). The lakes ranged in surface area from 0.4 to 2 ha and chlorophyll concentration from 0.2 to 4 µg l^{-1}. A single sample (sampling depth unspecified) was taken from the center of each lake during the ice-free period (date not specified). Variable volumes, ranging from 200 to 2500 ml, from each lake were analyzed. Per sample, 4 to 9 taxa were detected. In contrast to previous studies, Reche et al. (2005) reported that nearby lakes contained similar taxa. Furthermore, they found a positive relationship of the taxonomic richness of a bacterial community and lake surface area — a relationship found among many lake taxa, ranging from micro-crustaceans to insects.

The other attempt to apply the theory of Island Biogeography to freshwater bacteria was a study of tree hole communities in a British forest (Bell et al. 2005). The tree holes, ranging in volume from about 50 ml to 20 l, were considered to represent islands of various sizes. For each of ca. 30 tree holes, the entire volume was removed, homogenized and material from a 50 ml sample analyzed using DGGE. A plot of the logarithm of tree hole volume versus the logarithm of the number of DGGE bands resulted in a linear relationship across the entire range of tree holes sampled and was taken as evidence that 'larger islands house more bacteria' in the same manner that larger islands contain more species of plants and animals than smaller islands (Bell et al. 2005). Critics pointed out that ephemeral tree holes of small volumes are likely to differ fundamentally from large volume communities in ways very distinct from simply size (Fenchel & Finlay 2005, Mitchell 2005). Indeed, plotting the data presented on linear scales suggests similar but different relationships for small, medium and large volume communities (Fig. 1). Thus, it would appear unwise to extrapolate trends across systems varying orders of magnitude in size.

Overall, support for the existence of biogeographic patterns in lake or freshwater bacteria, in terms of 'species' as ribotypes, seems to depend on the time and space scales examined. If the lakes are somewhat homogenous in terms of size, water chemistry and primary production, some patterns may emerge. On very large spatial scales, which likely increases 'lake diversity', patterns may emerge only through integrating seasonal and inter-annual variability.

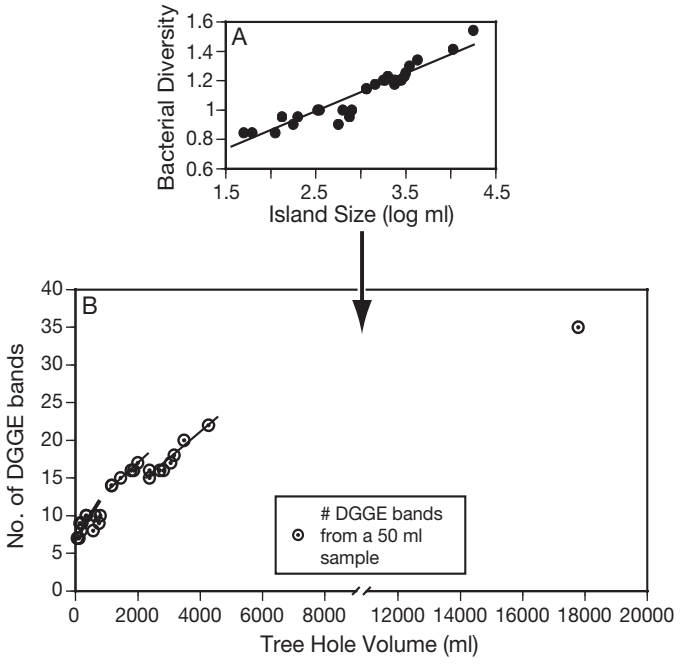

Fig. 1. (A) Relationship between bacterial taxonomic richness and system size (re-drawn from Bell et al. 2005). (B) Same relationship but for un-transformed data (extracted from an enlarged version of the published figure); suggests that small, medium and large tree holes show similar but distinct patterns

HETEROTROPHIC PROKARYOTES IN THE SEA

In the marine sciences, large-scale patterns often have a longer history of investigation than small-scale patterns and bacterial biogeography is no exception. Thus, one of the first attempts to use molecular techniques to compare bacterial communities concerned a study of the central Pacific, the Caribbean Sea and the Long Island Sound (NW Coastal Atlantic). Lee & Fuhrman (1991) used a DNA cross-hybridization technique and concluded that total community DNA varies significantly over time (2 wk periods) and space (basin-scale, euphotic zone vs. deep water).

Interestingly, these early indications of distinct communities and their temporal variability became lost as 16S rDNA became a focus around the same time (e.g. Giovannoni et al. 1990). Surveys of bacterial community composition employing rRNA gene cloning and sequencing reported the presence of similar sequences in diverse systems. The archetypal example is SAR11. Although later clearly identified as a clade rather than a single 'species' (e.g. Rappé et al. 2002), it has entered the popular imagination as a ubiquitous organism. In a recent comic novel (Moore 2004), SAR11 plays a role as a trans-oceanic transmitter of the needs and desires of whales; its ubiquity is an important characteristic as it represents the remnant of the fictional era when the planet earth was a single organism.

Early molecular studies reinforced the view that perhaps prokaryotic communities were the same in different areas of the world ocean (e.g. Mullins et al. 1995). This view has slowly shifted over the past decade. Firstly, the apparently ubiquitous forms such as SAR11 bacteria are now known to be a taxonomically, physiologically and morphologically diverse group of bacteria (e.g. Malmstrom et al. 2005). Secondly, there is at least 1 example of a group of prokaryotes characteristic of particular water masses: oceanic Archea, discovered using molecular approaches (Fuhrman et al. 1992), appear to be an especially important part of the prokaryotic community in deep ocean waters. Interestingly, the metabolism of Archea is obscure but we know they dominate the prokaryote community at depths below 100 m in the Pacific (Karner et al. 2001) as well as in the Atlantic (Herndl et al. 2005).

Archea provide an example of the few distributional patterns known among planktonic heterotrophic prokaryotes. Other examples include the finding that 2 proteobacterial groups (alpha- and beta-proteobacteria) differ markedly in their relative abundances in marine water compared to lakes (Glöckner et al. 1999). Members of other groups such as Cytophaga-Flavobacteria are abundant in both freshwater and marine systems (Kirchman 2002). Thus, there are some biogeographical patterns of high-level groupings but the underlying mechanisms are unclear (Kirchman et al. 2005). One hypothesis is that bacterial groups which appear to be more widespread are more diverse, i.e. they are composed of a higher number of low-level taxa or low-level taxa which are distinct from one another (Kirchman et al. 2005). This was examined with regard to the bacteria found in the Delaware River Estuary with the result that indeed the 16S rRNA sequences of the widespread Cytophaga-Flavobacteria group were more 'dissimilar' than the sequences of the alpha- or beta-proteobacteria (Kirchman et al. 2005).

Among individual taxa there is an apparent lack of large-scale distributional patterns; however, there have been few geographic surveys, and 2 studies in this Theme Section (Balwdin et al. 2005, Pommier et al. 2005) go a long way towards filling this void.

The distribution of bacterial groups across large spatial scales was examined in 2 distinct fashions: data mining by Pommier et al. (2005, this issue) and a field study by Baldwin et al. (2005, this issue). Pommier et al. (2005) conducted a detailed analysis of data submitted to GenBank, a follow-up study to Hagström et al. (2002). The authors retrieved about 3000 DNA sequences that included data on the geographic origin of the sample. Based on a 97% similarity level, 1336 bacterial ribotypes were distinguished in samples orig-

inating from 41 polar sites, 90 temperate sites and 17 tropical sites. Ribotypes were then designated as either cosmopolitan (occurring in all 3 regions) or restricted to 1 or 2 areas. It was found that 41% were reported from both temperate and polar sites, 24% from temperate sites only, 23% from both temperate and tropical sites, 11% were found in all 3 regions, 8% were restricted to polar areas and none were found to be reported from tropical areas only. Thus, 'restricted ribotypes' found only in a single geographic zone were apparent.

Pommier et al. (2005) point out that the finding of no 'tropical-only ribotypes' was likely an artifact of the relatively few tropical sites sampled. Indeed, this conclusion is supported by plotting the number of sequences found to be restricted to one of the 3 climatic zones versus the number of sites sampled in the given zone (Fig. 2). The linear relationship suggests that the number of 'endemic taxa' in a climate zone, as indicated by the GenBank database, is more a function of sampling intensity than any particular characteristic of any climate zone.

A completely different approach was taken by Baldwin et al. (2005). They collected 1 l samples of surface water at 40 stations along a transect from 70° N to 68° S latitude in the Pacific Ocean. Extracted 16S rRNA and 18S rRNA sequences were PCR amplified for analysis of prokaryotes and eukaryotes, respectively, using T-RFLP. Only the results concerning prokaryotes will be considered herein as 1 l sample volumes are inadequate for a robust analysis of eukaryotic community composition (e.g. Dolan 2005). The prokaryotic communities showed high similarity across the nearly pole

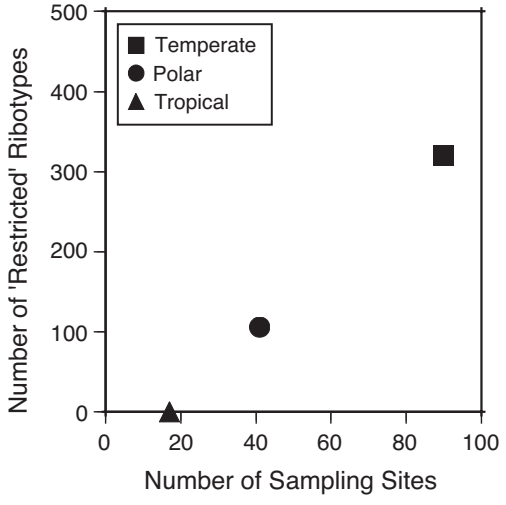

Fig. 2. Relationship between the number of prokaryotic ribotypes found only in a climate zone and the number of sites sampled within that same climate zone. Data from the report of Pommier et al. (2005) on sequences and sample sites extracted from GenBank

to pole Pacific transect, perhaps in part because few ribotypes were detected per station (8 to 14). Cosmopolitan ribotypes were detected as several were present at all or most of the stations. The tropical communities were distinguished by the presence of a unique ribotype, possibly that of *Prochlorococcus* the common warm water bacterial autotroph.

The apparent consistency of the Pacific prokaryotic community composition from Arctic to Antarctic waters may correspond with relative consistency throughout all seasons and in their ecological role. Distinct seasonal shifts in community composition have been reported from the Bermuda time-series study site (Morris et al. 2005). The seasonal shifts may be related to DOC dynamics at the site as changes occur with water column mixing.

As Delong & Karl (2005) stated, a major challenge is determining the influence of diversity (as well as physiology and ecology) on the biogeochemical role of prokaryotic communities. In this regard it should be noted that, thus far, attempts to determine a relationship between bacterial community composition and basic community metabolic functions, such as remineralization of dissolved organic matter, have proven unsuccessful for marine (e.g. Reinthaler et al. 2005) and lake bacterioplankton (Langenheder et al. 2005).

On the positive side, community composition of bacterioplankton has been reasonably tied to physical mixing where one would expect it to be important, i.e. in an estuary (Crump et al. 2004). The Parker River estuary (NE USA) was sampled along the salinity gradient during July, August and September, seasons of different flow regimes. DNA was extracted from surface layer samples (volumes unspecified) and processed using DGGE. Crump et al.'s (2004) study of estuarine bacterioplankton found that the development of a true estuarine community (distinct from a the freshwater or fully marine community) depended upon bacterial growth exceeding the flushing rate of the system.

HETEROTROPHIC EUKARYOTES

With regard to protists, discussions on whether all species are everywhere (Finlay et al. 1996, Fenchel et al. 1997, Fenchel & Finlay 2004) or not (Foissner 1999, Foissner et al. 2003) have given way to the realization that indeed many, if not most, morphological forms appear to be very widely distributed, while cryptic species (forms genetically distinct but morphologically similar) may be common. Two important questions remain: (1) Are there biogeographic patterns among 'morphological forms'? and (2) Do genetically distinct groups show biogeographic patterns?

First, we consider patterns among taxa distinguished via morphology. It may be worth recalling that some researchers have attributed apparent cosmopolitanism among protists to 'force-fitting' taxa — attributing names based on monographs of European taxa (e.g. Tyler 1996). Regardless, it is clear that not all species are everywhere at the same concentrations. Large-scale patterns do appear to exist. There are, for example, latitudinal gradients of species richness. The patterns among eukaryotic microbes, such as foraminifera (Rutherford et al. 1999) and tintintinnid ciliates (Dolan & Gallegos 2001), closely resemble those of multi-cellular organisms in that distinct peaks are often evident at about 25° N and 25° S latitude. However, once again microbes differ from multi-cellular organisms. While tropical systems are indeed species-rich, the composition of tropical communities differs from that of multi-cellular organisms in that they contain many widely distributed taxa as well as some endemic or specialized forms.

For example, protist taxa encountered at a station in the tropical South Central Pacific (Fig. 3) included some typically tropical forms. These forms are often characterized by morphologies that appear to be elaborate relative to taxa found at mid-latitudes. The morphological features of tropical forms such as marked asymmetry, keels, etc. have been explained as adaptations serving to lessen sinking rates as tropical water has half the viscosity of polar water (Tappan & Loeblich 1973). However, protists without elaborate morphological features, forms found widely distributed, were equally abundant (Fig. 3).

The co-occurrence of tropical forms and widely distributed taxa suggests that the explanation for the apparent peak in species-richness found at low latitudes is possibly a simple temperature range effect (e.g. Bra-

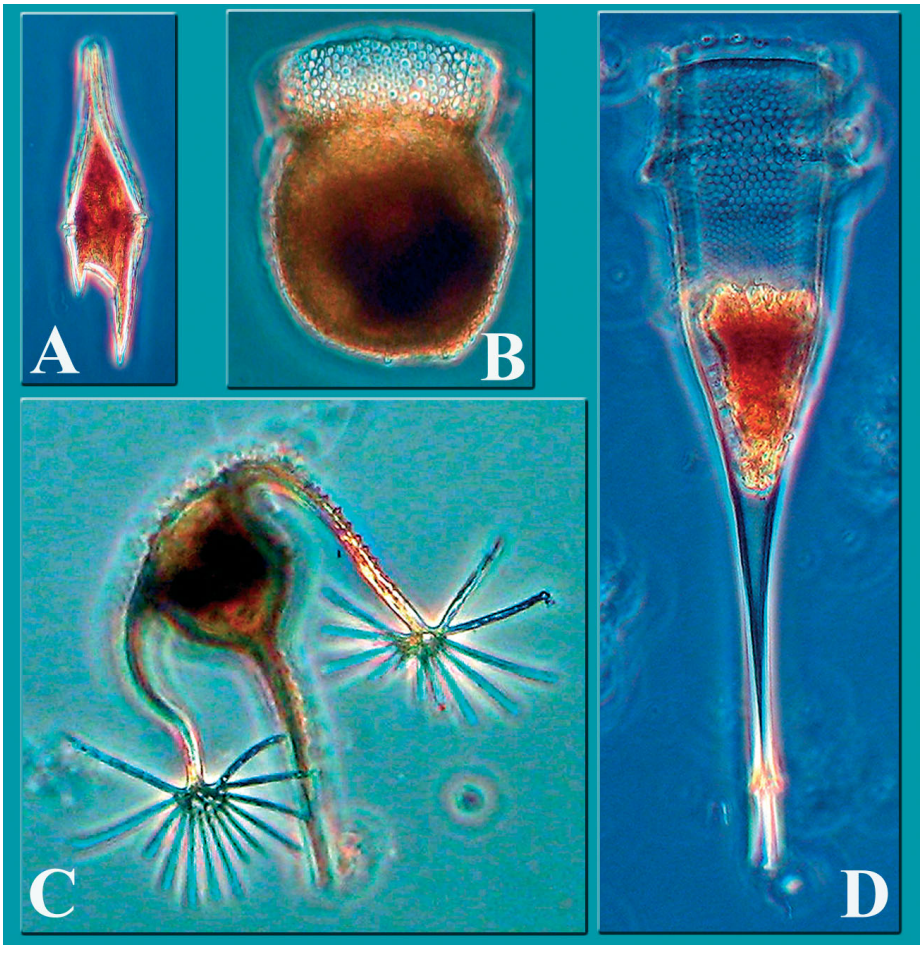

Fig. 3. Examples of the planktonic protist community found at a station in the Southwest Pacific (15° 30′ S, 132° W) during the BIOSOPE cruise of the French oceanographic program PROOF. Dinoflagellates of the genus *Ceratium* included typical tropical forms with elaborate morphologies such as *C. ranipipes* (C) and widespread taxa like *C. furca* (A). Likewise, tintinnids included widespread taxa such as *Codonella nationalis* (B) and tropical forms with elaborate lorica architecture like *Xystonellopsis dicymatica* (D)

yard et al. 2005), rather than one of the many interesting mechanisms suggested to explain the gradients found in both plants and animals (e.g. Rohde 1999, Macpherson 2002, Hillebrand 2004). A similar phenomenon, but on a temporal rather than a spatial scale, would be that of species richness appearing to be highest between seasons because in the autumn, for example, summer and winter taxa as well as autumn taxa are present.

Biogeographic patterns do exist among 'morphological' species of aquatic microbes. The patterns may or may not result from the same mechanism driving patterns among multi-cellular organisms. The temperature range effect described could be a variant of Rapoport's rule: within a group of organisms, the average geographic range of species increases with latitude. This phenomenon has been proposed as one explanation (among many) of latitudinal diversity gradients known in multi-cellular organisms (Kolasa et al. 1998, Gaston 1999).

Interestingly, cryptic species, in the guise of mating types, have been recognized for decades among protists (e.g. Sonneborn 1957), and with the advent of DNA sequencing appear to have been re-discovered (Saez & Lozano 2005). Some investigators have suggested the existence of geographic species which appear intuitively reasonable. For example, Arctic and Antarctic populations of a species of foraminifer appear to be genetically distinct (Darling et al. 2004). Nonetheless SSU rDNA sequences appear identical in other bipolar species (Darling et al. 2000).

In yet other foraminifera species genetic distance exists with little geographic isolation. Overlapping distributions of 3 cryptic species of another foraminifer, *Orbulina universa*, have been reported (De Vargas et al. 1999). Genetically distinct populations occur among more or less continuously distributed species, such as the dinoflagellate 'species complex' of *Alexandrium tamarense* (Uwe et al. 2003). The opposite situation of near genetic identity in separated populations also exists. Populations of the dinoflagellate *Polarella glacialis* in Arctic waters differ by only 6 base pairs in the sequence of their SSU rDNA from those found in Anarctica (Montressor et al. 2003).

Protists can at this point in time be characterized as displaying both high genetic diversity and high gene flow. Thus one might conclude that genetic shifts in a population can occur fairly rapidly and are perhaps dynamic. A precise example of genetic and physiological divergence was recently reported by Kim et al. (2004), who found that different culture media were needed to culture the same dinoflagellate (*Peridinium limbatum*) found in 2 neighboring lakes (separated by 400 m) of different chemical and biological characteristics. They tested the possibilty that the 2 lake populations were genetically distinct by culturing 5 strains from each lake and examining ITS sequences. Nuclear DNA was sequenced at the ITS region of the rDNA locus (ITS1, 5.8S rDNA, ITS2). ITS analysis showed that the 2 *P. limbatum* populations, with distinct culture requirements, were indeed genetically distinct. Sequence differences between strains from the same lake were less than 0.5% while between lake populations differed by nearly 9%. In comparison, differences of 2% have been identified as distinguishing species of ciliates (e.g. Shin et al. 2000). However, some hybrid sequences were found, suggesting that the 2 populations may still experience genetic exchange. Although the authors made no attempt to date the divergence, it would seem reasonable to assume the separation to be no older than the last glacial period as one lake was a bog lake.

The daphnid *Eubosmina* provides a further example of genetic divergence in a lake organism. Although muticellular, *Eubosmina* is capable of asexual reproduction and is presumed to be unaffected by geographic barriers to dispersal. Haney & Taylor (2003) examined nuclear and mitochondria DNA sequences of *Eubosmina* in widely separated Holarctic sites in North America and Europe. Morphological similarity was inversely linked to genetic similarity. Thus, existing morphologically defined species appear to be the result of strong selection pressure maintaining morphological differences despite high gene flow between populations.

Evidence of genetic diversity and high gene flow was found in oligotrich ciliates by Katz et al. (2005, this issue). They examined variation in the ITS locus and found a multitude of distinct haplotypes for the freshwater species *Halteria grandinella* and the marine tide pool species *Strombidium oculatum*, but the haplotypes were not coherent geographically. Genetic diversity was quite high for some areas (15.7% sequence divergence for Irish Sea poulations). Thus, despite apparently high gene flow, genetic diversity exists for ciliates found in marine and freshwaters. Interestingly, some marine planktonic ciliates, in comparison, seem genetically homogenous (Snoeyenbos-West et al. 2002).

The results of high genetic diversity in the tide pool ciliate resemble those reported by Lowe et al. (2005a) concerning the marine would-be dinoflagellate *Oxyrrhis marina*. Using ITS data and 5.8 SSU rDNA they found high divergences between strains unrelated to geographic origin. Lowe et al. (2005a) furthermore found no clear relation between genetic and physiological groups (defined by salinity-growth response).

Lowe et al. (2005b, this issue) subsequently examined the relationship between genetic and physiological groups in the rotifer *Brachionus plicatilis*. An enzyme important in osmo-regulation was employed. Genetic

groups were defined via similarity of sequences coding for the enzyme, and physiological groups were defined according to growth rates at various salinities. The authors discovered that the physiological groups bore no relation to the genetic groups because sequence similarity was not linked to rates of gene expression. Physiological groups were poor indicators of genetic similarity.

Fenchel (2005, this issue) ascribes part of the problem of attempting to relate geography to genetic groups to the phenomenon of neutral mutations. According to this explanation, random, neutral mutations can accumulate in the sequences commonly employed to define genetic groups. However, these differences bear no relationships to geographical isolation or physiological specialization. Overall, it is difficult to avoid the conclusion that genetic, physiological and morphological divergence are, at this time, quite difficult to relate to one another, at least with regard to eukaryotic aquatic microbes.

Against this background of complexity, the existence of simple relationships has been asserted, e.g. 'phytoplankton species richness scales consistently from laboratory microcosms to the world's oceans' (Smith et al. 2005). Thus, it would appear that from benchtop aquaria to the Central Pacific, the number of eukaryotic and prokayotic autotroph species is a predictable function of surface area. Such assertions should, however, be carefully examined, as sampling efforts, taxonomic expertise and temporal scales are rarely similar across studies of systems of different size and complexity.

CONCLUSION

Progress in the biogeography of aquatic microbes will likely depend on both conceptual as well as technical advances. Conceptually, we may have to accept the possibility that different groups may experience change at different rates — molecular yardsticks developed for one group simply may not apply to another group. It should be recognized that molecular 'yardsticks' are not infallible. For example, in the intensively studied *Helicobacter*, discovered by the Nobel Prize team of Marshall & Warren (1983), 16S rRNA sequences now appear much less reliable than 23S rRNA due to horizontal gene transfer; this has led to a plea for a greater reliance on phenotypic characteristics for identification (Dewhirst et al. 2005). Furthermore, we perhaps need to accept that reproductive isolation need not require geographic isolation, and vice versa — everything depends on the scales of time and space under consideration. Sorting out group-specific relationships may be contingent on the investigation of molecules of direct ecological significance to the organisms (Lowe et al. 2005b).

Acknowledgements. This Theme Section is a set of papers derived from solicited presentations given in the session 'Diversity among Components of the Microbial Loop' at the June 2005 ASLO meeting in Santiago de Compostela, Spain. The session was conceived in the framework of the MARBEF Network of Excellence 'Marine Biodiversity and Ecosystem Functioning', funded in the EEC Sixth Framework Programme (contract no. GOCE-CT-2003-505446). This paper is contribution number MPS-05018 of MarBEF. Financial support was also provided by the CNRS and the Université Pierre et Marie Curie, Paris VI. The images in Fig. 3 are from samples obtained through the BIOSOPE cruise, organized by H. Claustre, as part of the French oceanographic program PROOF. D. Vaulot and coworkers did the actual sampling. The constructive remarks of T. Fenchel and G. McManus on previous versions of this paper are gratefully acknowledged, but all errors of fact and interpretation are mine alone.

LITERATURE CITED

Baas-Becking LGM (1934) Geobiologie of Inleiding Tot de Milieukunde. Van Stockum & Zoon, The Hague

Baldwin AJ, Moss JA, Pakulski JD, Catala P, Joux F, Jeffrey WH (2005) Microbial diversity in a Pacific Ocean transect from the Arctic to Anarctic Circles. Aquat Microb Ecol 41:91–102

Beijerinck MW (1913) De infusies en de ontdekking der backteriën. In Jaarboek van de Koninklijke Akademie v Wetenschappen. Müller, Amsterdam

Bell T, Ager D, Song J-I, Newman JA, Thompson IP, Lilley AK, vander Gast CJ (2005) Larger islands house more bacterial taxa. Science 308:1884

Brayard A, Escarguel G, Bucher H (2005) Latitudinal gradient of taxonomic richness: combined outcome of temperature and geographic mid-domaine effects? J Zool Syst Evol Res 43:178–188

Breitbart M, Rohwer F (2005) Here a virus, there a virus, everywhere the same virus? Trends Microbiol 13:278–284

Bright M, Giero 0 (2005) Microbial symbiosis in annelida. Symbiosis 38:1–45

Bull AT (2004) Microbial prospecting. ASM Press, American Society for Microbiology, Washington, DC

Crump BC, Hopkinson CS, Sogin ML, Hobbie JE (2004) Microbial biogeography along an estuarine salinity gradient: combined influence of bacterial growth and residence time. Appl Environ Microbiol 70:1494–1505

Darling KF, Wade CM, Stewart IA, Kroon D, Dingle R, Leigh Brown AJ (2000) Molecular evidence for genetic mixing of Arctic and Antarctic subpolar populations of planktonic foraminifers. Nature 405:42–47

Darling KF, Kucera MC, Pudsey J, Wade CM (2004) Molecular evidence links cryptic diversification in polar planktonic protists to Quaternary climate dynamics. Proc Natl Acad Sci USA 101:7657–7662

Delong EF, Karl DM (2005) Genomic perspectives in microbial oceanography. Nature 437:336–342

Dewhirst FE, Shen Z, Scimeca MS, Stokes LN, Boumenna T, Chen T, Paster BJ, Fox JG (2005) Discordant 16S and 23S rRNA gene phylogenies for the genus *Helicobacter*: implications for phylogenetics inference and systematics. J Bacteriol 187:6106–6118

De Vargas C, Norris R, Zaninetti L, Gibb SW, Pawlowski J (1999) Molecular evidence of cryptic speciation in planktonic foraminifers and their relation to oceanic provinces. Proc Natl Acad Sci USA 96:2864–2868

Dolan JR (2005) Marine ecology — different measures of bio-

diversity. Nature 433:E9
Dolan JR, Gallegos CS (2001) Estuarine diversity of tintinnids (planktonic ciliates). J Plankton Res 23:1009–1027
Fenchel T (2003) Biogeography for bacteria. Science 301: 925–926
Fenchel T (2005) Cosmopolitan microbes and their 'cryptic' species. Aquat Microb Ecol 41:49–54
Fenchel T, Finlay BF (2004) The ubiquity of small species: patterns of local and global diversity. BioScience 54:777–784
Fenchel T, Finlay BF (2005) Bacteria and island biogeography. Science 309:1995
Fenchel T, Esteban GF, Finlay BF (1997) Local versus global diversity of microorganisms: cryptic diversity of ciliated protozoa. Oikos 80:220–225
Finlay BF, Corliss JO, Esteban GF, Fenchel T (1996) Biodiversity at the microbial level: the number of free-living ciliates in the biosphere. Q Rev Biol 71:221–237
Foissner W (1999) Protist diversity: estimates of the near imponderable. Protist 150:363–368
Foissner W, Strüder-Kypke M, van der Staay GW, Moon-van der Staay SY, Hackstein JH (2003) Endemic ciliates (Protozoa, Ciliophora) from tank bromeliads (Bromeliaceae): a combined morphological, molecular, and ecological study. Eur J Protistol 39:365–372
Fuhrman JA, McCallum K, Davis AA (1992) Novel major archaebacterial group from marine plankton. Nature 356: 148–149
Gaston KJ (1999) Why Rapoport's rule does not generalize. Oikos 84:309–312
Giovannoni SJ, Britschgi TB, Moyer CL, Field KG (1990) Genetic diversity in Sargaso Sea bacterioplankton. Nature 345:60–63
Glöckner FO, Fuchs MB, Amann R (1999) Bacterioplankton-compositions of lakes and oceans: a first comparison based on fluorescence in situ hybridization. Appl Environ Microbiol 65:3721–3726
Hagström Å, Pommier T, Rohwer F, Simu K, Stolte W, Svensson D, Zweifel UL (2002) Use of 16S ribosomal DNA for delineation of marine bacterioplankton species. Appl Environ Microbiol 68:3628–3633
Haney RA, Taylor DJ (2003) Testing paleolimnological predictions with molecular data: the origins of Holarctic *Eubosmina*. J Evol Biol 16:871–882
Herndl GJ, Reinthaler T, Teira E, van Aken H, Veth C, Pernthaler A, Pernthaler J (2005) Contribution of Archea to total prokaryotic production in the deep Atlantic Ocean. Appl Environ Microbiol 71:2303–2309
Hillebrand H (2004) Strength, slope and variability of marine latitudinal gradients. Mar Ecol Prog Ser 273:251–267
Humphries CJ, Parenti LR (1999) Cladistic biogeography, interpreting patterns of plant and animal distributions, 2nd edn. Oxford University Press, Oxford
Karner MB, Delong EF, Karl DM (2001) Archael dominance in the mesopelagic zone of the Pacific Ocean. Nature 409: 507–510
Katz LA, McManus GB, Snoeyenbos-West OLO, Griffin A, Pirog K, Costas B, Foissner W (2005) Reframing the 'everything is everywhere' debate: evidence for high gene flow and diversity in ciliate morphospecies. Aquat Microb Ecol 41:55–65
Kent AD, Jones SE, Yanarell AC, Graham JM, Lauster GH, Kratz TK, Triplett EW (2004) Annual patterns in bacterioplankton community variability in a humic lake. Microb Ecol 48:550–560
Kim E, Wilcox L, Graham L, Graham J (2004) Genetically distinct populations of the dinoflagellate *Peridinium limbatum* in neighboring Northern Wisconsin lakes. Microb Ecol 48:521–527
Kirchman DL (2002) The ecology of Cytophaga-Flavobacteria in aquatic environments. FEMS Microbiol Ecol 39:91–100
Kirchman DL, Dittel AI, Malmstrom RR, Cottrell MT (2005) Biogeography of major groups in the Delaware Estuary. Limnol Oceanogr 50:1697–1706
Kolasa J, Hewitt CL, Drake JA (1998) Rapoport's rule: an explanation or a byproduct of the latitudinal gradient in species richness? Biodivers Conserv 7:1447–1455
Konopka A, Bercot T, Nakatsu C (1999) Bacterioplankton community diversity in a series of thermally stratified lakes. Microb Ecol 38:126–135
Langenheder S, Lindström ES, Tranvik LJ (2005) Weak coupling between community composition and functioning og aquatic bacteria. Limnol Oceanogr 50:957–967
Lee S, Fuhrman JA (1991) Spatial and temporal variation of natural bacterioplankton assemblages studied by total genomic DNA cross-hybrdization. Limnol Oceanogr 36: 1277–12187
Lindström ES (2000) Bacterioplankton community composition in five lakes differing in trophic status and humic content. Microb Ecol 40:104–113
Lindström ES (2001) Invesitigating influential factors on bacterioplankton community composition: results from a field study of five mesotrophic lakes. Microb Ecol 42:598–605
Lindström ES, Leskinen E (2002) Do neighboring lakes share common taxa of bacterioplankton? Comparison of 16S rDNA fingerprints and sequences from three geographic regions. Microb Ecol 44:1–9
Lomolino MV, Heaney LR (2004) Frontiers of biogeography: new directions in the geography of nature. Sinauer, Sunderland, MA
Longhurst A (1998) Ecological geography of the sea. Academic Press, New York
Lowe CD, Day, A, Kemp SJ, Montagnes DJS (2005a) There are high levels of functional and genetic diversity in *Oxyrrhis marina*. J Eukaryot Microbiol 52:250–257
Lowe CD, Kemp SJ, Montagnes DJS (2005b) An interdisciplinary approach to assess the functional diversity of free-living microscopic eukaryotes. Aquat Microb Ecol 41:67–77
MacArthur R, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ
Macpherson E (2002) Large-scale species richness gradients in the Atlantic Ocean. Proc R Soc Lond B 269:1715–1720
Malmstrom RR, Cotrell MT, Elifantz H, Kirchman DL (2005) Biomass production and assimilation of dissolved organic matter by SAR11 bacteria in the Northwest Atlantic Ocean. Appl Environ Microbiol 71:2979–2986
Marshall BJ, Warren JR (1983) Unidentified curved bacilli on gastric epithelium in active chronic gastritis. Lancet 1: 1273–1275
Mitchell EAD (2005) Bacteria and island biogeography. Science 309:1995
Montressor M, Lovejoy C, Orsini L, Procaccini G, Roy S (2003) Bipolar distribution of the cyst-forming dinoflagellate *Polarella glacialis*. Polar Biol 26:186–194
Moore C (2004) Fluke or I know why the winged whale sings. Perennial, Harper Collins, New York
Morris RM, Vergin KL, Cho JC, Rappé MS, Carlson CA, Giovannoni SJ (2005) Temporal and spatial response of bacterioplankton lineages to annual convective overturn at the Bermuda Atlantic Time-series Study site. Limnol Oceanogr 50:1687–1696
Mullins TD, Britschgi TB, Krest RL, Giovannoni SJ (1995) Genetic comparisons reveal the same unknown bacterial lineages in Atlantic Pacific communities. Limnol Oceanogr 40:148–158

Ogunsseitan O (2005) Microbial diversity. Blackwell Publishing, Maden, MA

Papke RT, Ward DM (2004) The importance of physical isolation to microbial diversification. FEMS Microbiol Ecol 48:293–303

Pielou EC (1979) Biogeography. Wiley-Interscience, New York

Pommier T, Pinhassi J, Hagström Å (2005) Biogeographic analysis of ribosomal RNA clusters from marine bacterioplankton. Aquat Microb Ecol 41:79–89

Rahbek C (2005) The role of spatial scale and the perception of large-scale species-richness patterns. Ecol Lett 8: 224–239

Rappé MS, Connon SA, Vergin KL, Giovannoni SJ (2002) Cultivation of the ubiquitous SAR11 marine bacterioplankton clade. Nature 418:630–633

Reche I, Pulido-Villena E, Morales-Baquero R, Casamayor EO (2005) Does ecosystem size determine aquatic bacterial richness? Ecology 86:1715–1722

Reinthaler T, Winter C, Herndl GJ (2005) Relationship between bacterioplankton richness, respiration, and production in the Southern North Sea. Appl Environ Microbiol 71:2260–2266

Rohde K (1999) Latitudinal gradients in species diversity and rapoport's rule revisited: a review of recent work and what can parasites teach us about the causes of the gradients. Ecography 22:593–613

Rutherford S, D'Hondt S, Prell W (1999) Environmental controls on the geographic distribution of zooplankton diversity. Nature 400:750–753

Saez AG, Lozano E (2005) Body doubles. Nature 433:111

Shin MK, Hwang UW, Kim W, Wright ADG, Krawczyk C, Lynn DH (2000) Phylogenetic position of the ciliates *Phacodinium* (order Phacodiniida) and *Protocruzia* (subclass Protocruziidia) and systematics of the spirotrich ciliates examined by small subunit ribosomal RNA gene sequences. Eur J Protistol 36:293–302

Smith VH, Foster BL, Grover JP, Holt RD, Leibold MA, deNoyelles F Jr (2005) Phytoplankton species richness scales consistently from laboratory microcosms to the world's oceans. Proc Natl Acad Sci USA 102:4393–4396

Snoeyenbos-West OLO, Salcedo T, McManus GB, Katz LA (2002) Insights into the diversity of choreotrich and oligotrich ciliates (class Spirotrichea) based on genealogical analysis of multiple loci. Int J Syst Evol Microbiol 52:1901–1913

Sonneborn TM (1957) Breeding systems, reproductive methods and species problems in Protozoa. In: Mayr E (ed) The species problem. American Association for the Advancement of Science, Washington, DC, p 155–324

Staley JT, Gosnik JJ (1999) Poles apart: biodiversity and biogeography of sea ice bacteria. Annu Rev Microbiol 53: 189–215

Tappan H, Loeblich AR (1973) Evolution of the oceanic plankton. Earth-Sci Rev 9:207–240

Taylor MW, Schupp PJ, de Nys R, Kjelleberg S, Steinberg PD (2005) Biogeography of bacteria associated with the marine sponge *Cymbastela concentrica*. Environ Microbiol 7:419–433

Tyler PA (1996) Endemism in freshwater algae with special reference to the Australian region. Hydrobiologia 336: 127–135

Uwe J, Fensome RA, Medlin LK (2003) The application of a molecular clock based on molecular sequences and the fossil record to explain biogeographic distributions within the *Alexandrium tamarense* 'species complex' (Dinophyceae). Mol Biol Evol 20:1015–1027

Whitaker RJ, Grogan DW, Taylor JW (2003) Geographic barriers isolate endemic populations of hyperthermophilic archea. Science 301:976–978

Yannarell AC, Triplett EW (2004) Within- and between-lake variability in the composition of bacterioplankton communities: investigations using multiple spatial scales. Appl Environ Microbiol 70:214–223

Yannarell AC, Triplett EW (2005) Geographic and environmental sources of variation in lake bacterial community composition. Appl Environ Microbiol 71:227–239

Yannarell AC, Kent AD, Lauster GH, Kratz TK, Triplett EW (2003) Temporal patterns in bacterial communities in three temperate lakes of different trophic status. Microb Ecol 46:391–405