The first decade of ‘Aquatic Microbial Ecology' (1995–2005): evidence for gradualism or punctuated equilibrium?

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Aquatic Microbial Ecology (AME) celebrates its first 10 years of publication. AME began in 1995 and soon became the companion journal to Marine Ecology Progress Series (MEPS). It is the successor to Marine Microbial Food Webs (MMFW), which first appeared in 1985. Between a decade of MMFW and a decade of AME an entire generation of microbial ecologists has come of age. Was the field fundamentally altered by the advent of molecular biology? Have there been sudden shifts or rather gradual changes in focus and methodology? We attempt to answer these questions by looking at the most cited articles published.

MMFW came into existence when the field of microbiology was taking center stage in aquatic ecology. While the existence of large quantities of bacteria, flagellates and ciliates in aquatic systems had been known since the early 1900s (e.g. Beers 1982), their importance was largely ignored until the 1980s. Aquatic microbial ecology became a focal point of research following 5 key discoveries: (1) A large portion of primary production is attributable to small size-classes, too small for typical metazoan grazers (e.g. Malone 1980). (2) Ciliates can attain a considerable biomass and are capable of consuming a large part of the primary production (e.g. Rassoulzadegan 1978, Heinbokel & Beers 1979). (3) Phytoplankton excretes a significant fraction of the carbon fixed as dissolved organic matter (e.g. Sharp 1977). (4) Fluorochrome dyes reveal that bacteria are very abundant, much more so than previously assumed (e.g. Hobbie et al. 1977). (5) Despite relatively constant concentrations, heterotrophic bacteria are continually dividing and producing a considerable biomass (e.g. Fuhrman & Azam 1980). Thus, it became clear that very significant ecological activity occurs among the microbes (Azam et al. 1983).

A review of the most cited articles published in MMFW provides a good idea of the key topics from 1985 to 1994 (Table 1). The most cited titles reflect the importance accorded to trophic relationships: who eats whom or what? A recurring topic (1986, 1993 and 1994) is the relationship between metazoans (copepods and daphnids) and microbial populations. The focus of food web analyses progressed from stock estimates, to qualitative studies of the relationships between the stocks, followed by attempts to quantify these relationships (i.e. to quantify fluxes).

Table 1. The most cited articles for each year in Marine Microbial Food Webs (MMFW)

<table>
<thead>
<tr>
<th>Year</th>
<th>Title</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>1985</td>
<td>Growth of microzooplankton: a comparative study of bactivorous zooflagellates and ciliates</td>
<td>Rivier et al.</td>
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<td>1986</td>
<td>Phagotrophic Protozoa as food for metazoans: a ‘missing’ trophic link in marine pelagic food webs?</td>
<td>Sherr et al.</td>
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<tr>
<td>1987</td>
<td>Nutrient flux between bacteria, bactivorous nanoplanktonic protists and algae</td>
<td>Berman et al.</td>
</tr>
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<td>1988</td>
<td>Size fraction of phytoplankton in the Ligurian Sea and the Algerian Basin (Mediterranean Sea): size distribution versus total concentration</td>
<td>Raimbault et al.</td>
</tr>
<tr>
<td>1989</td>
<td>Fatty acid dynamics in phytoplankton and microzooplankton communities during a spring bloom in the coastal Ligurian Sea: ecological implications</td>
<td>Claustre et al.</td>
</tr>
<tr>
<td>1990</td>
<td>The importance of losses during microbial growth: commentary on the physiology, measurement and ecology of the release of dissolved organic material</td>
<td>Williams</td>
</tr>
<tr>
<td>1991</td>
<td>The trophic role of heterotrophic dinoflagellates in diverse marine environments</td>
<td>Lessard</td>
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<td>1993</td>
<td>Planktonic Protozoa and Metazoa: predation, food quality and population control</td>
<td>Sanders &amp; Wickham</td>
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<td>1994</td>
<td>Impact of Daphnia on planktonic microbial food webs: a review</td>
<td>Jürgens</td>
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Table 2. The 2 most cited articles for each year in *Aquatic Microbial Ecology* (AME)

<table>
<thead>
<tr>
<th>Year</th>
<th>Article Title</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995</td>
<td>Cooksey &amp; Wigglesworth-Cooksey — Adhesion of bacteria and diatoms to surfaces in the sea: a review</td>
</tr>
<tr>
<td>1996</td>
<td>Carlson &amp; Ducklow — Growth of bacterioplankton and consumption of dissolved organic carbon in the Sargasso Sea</td>
</tr>
<tr>
<td>1997</td>
<td>Cotner et al. — Phosphorus-limited bacterioplankton growth in the Sargasso Sea</td>
</tr>
<tr>
<td>1998</td>
<td>Noble &amp; Fuhrman — Use of SYBR Green I for rapid epifluorescence counts of marine viruses and bacteria</td>
</tr>
<tr>
<td>1999</td>
<td>Sherr et al. — Estimating abundance and single-cell characteristics of respiring bacteria via the redox dye CTC</td>
</tr>
<tr>
<td>2000</td>
<td>Hagström et al. — Biogeographical diversity among marine bacterioplankton</td>
</tr>
<tr>
<td>2001</td>
<td>Pomeroy &amp; Wiebe — Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria</td>
</tr>
<tr>
<td>2002</td>
<td>Zwart et al. — Typical freshwater bacteria: an analysis of available 16S rRNA gene sequences from plankton of lakes and rivers</td>
</tr>
<tr>
<td>2003</td>
<td>Selje &amp; Simon — Composition and dynamics of particle-associated and free-living bacterial communities in the Weser estuary, Germany</td>
</tr>
<tr>
<td>2004</td>
<td>Engel et al. — Transparent exopolymer particles and dissolved organic carbon production by <em>Emiliania huxleyi</em> exposed to different CO₂ concentrations: a mesocosm experiment</td>
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</table>

The hot subjects of the period 1995 to 2005 are listed in Table 2. The past decade has been characterized by the widespread adoption of molecular techniques, but the titles of the most cited AME articles give very little evidence of a major shift in focus. The tools of molecular ecology are evident in their use to distinguish taxonomically distinct populations of prokaryotes, i.e. to describe stocks. The new molecular approaches have not yet served to quantify fluxes or explain the control of fluxes. These questions are still important, as papers describing processes and methods for quantifying populations remain among the most popular articles. Therefore, change in the field appears to be an example of ‘gradualism’ rather than of ‘punctuated equilibrium’ (sensu Eldredge & Gould 1972). Perhaps ‘punctuation’ results from changes in the questions asked because, at least in part, the old questions have been answered.

We are still gradually moving along a pathway that has been visible since the aquatic microbial domain came into focus over 30 years ago (Pomeroy 1974). Pomeroy pointed out that ‘We know much less about respiration in the ocean than about photosynthesis’ (p. 500) — this is still the case today. He continued by pointing out that ‘we need to know what kinds [of microbes] are the metabolically important ones and how they fit into the food web’ (p. 501) — this issue may now become approachable with molecular techniques. Interestingly, Pomeroy posed the question of the linkage of microbial populations to higher trophic levels — the topic treated in the top papers of MMFW in 1986, 1993 and 1994. He stated that ‘We have quite limited information on the mean residence time of Protista in the open sea. If it is short (hours) then Protista probably are an active link in a major pathway in the food web. If it is long (days or weeks), the Protista may be consuming most of the energy they capture. In this case they will be a major energy sink.’ (p. 502). Data on the fate of most microbial populations (not only prokaryotes) are still lacking; e.g. for *Prochlorococcus*, the most abundant autotroph on the planet (Partensky et al. 1999), the genome has been sequenced (Dufresne et al. 2003), but the identity of its consumer(s) remains largely unknown (Christaki et al. 1999).

Overall, the field does not appear to have experienced or attained a punctuation point. One possible reason is that a focus has been on appropriately large scales of time and space. We should not forget that the spectacular advances in the biomedical field seen in recent years from molecular techniques were solidly grounded in the ‘bottom-up’ approach of biochemistry. What occurs in a cell was known from working from the simple to the complex. Types of compounds were identified, metabolic pathways defined, molecular structures and their interactions were then determined. However, in microbial ecology the major effort...
over the past 20 years has been on attempting to determine the role of microbes in ecosystems. Microbial communities may be just as complex as coral reef or rainforest communities (Fenchel 2002). Perhaps then we first need to better determine the relationships of microbes among themselves. This may indeed necessitate abandoning the ecosystem scales of meters and days and focusing on scales of microbial significance of microns and hours (e.g. Azam & Smith 1991).

**LITERATURE CITED**


Dufresne A, Salanoubat M, Partensky F, Artiguenave F and 17 others (2003) Genome sequence of the cyanobacterium Prochlorococcus marinus SS120, a nearly minimal oxyzphototrophic genome. Proc Natl Acad Sci USA 100:10020–10025


Food Webs 1:51–60