

# 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)

<b>1985</b>	Rivier et al.—Growth of microzooplankton: a comparative study of bacterivorous zooflagellates and ciliates
<b>1986</b>	Sherr et al.—Phagotrophic Protozoa as food for metazoans: a 'missing' trophic link in marine pelagic food webs?
<b>1987</b>	Berman et al.—Nutrient flux between bacteria, bacterivorous nanoplanktonic protists and algae
<b>1988</b>	Raimbault et al.—Size fraction of phytoplankton in the Ligurian Sea and the Algerian Basin (Mediterranean Sea): size distribution versus total concentration
<b>1989</b>	Claustre et al.—Fatty acid dynamics in phytoplankton and microzooplankton communities during a spring bloom in the coastal Ligurian Sea: ecological implications
<b>1990</b>	Williams—The importance of losses during microbial growth: commentary on the physiology, measurement and ecology of the release of dissolved organic material
<b>1991</b>	Lessard—The trophic role of heterotrophic dinoflagellates in diverse marine environments
<b>1992</b>	Smith & Azam—A simple, economical method for measuring bacterial protein synthesis rates in seawater using <sup>3</sup> H-leucine
<b>1993</b>	Sanders & Wickham—Planktonic Protozoa and Metazoa: predation, food quality and population control
<b>1994</b>	Jürgens—Impact of <i>Daphnia</i> on planktonic microbial food webs: a review

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Table 2. The 2 most cited articles for each year in *Aquatic Microbial Ecology* (AME)

1995	Cooksey & Wigglesworth-Cooksey — Adhesion of bacteria and diatoms to surfaces in the sea: a review Legendre & Le Fèvre — Microbial food webs and the export of biogenic carbon in oceans
1996	Carlson & Ducklow — Growth of bacterioplankton and consumption of dissolved organic carbon in the Sargasso Sea Fagerbakke et al. — Content of carbon, nitrogen, oxygen, sulfur and phosphorus in native aquatic and cultured bacteria
1997	Cotner et al. — Phosphorus-limited bacterioplankton growth in the Sargasso Sea Reckermann & Veldhuis — Trophic interactions between picophytoplankton and micro- and nanozooplankton in the western Arabian Sea during the NE Monsoon 1993
1998	Noble & Fuhrman — Use of SYBR Green I for rapid epifluorescence counts of marine viruses and bacteria Kühl et al. — A H <sub>2</sub> S microsensor for profiling biofilms and sediments: application in an acidic lake sediment
1999	Sherr et al. — Estimating abundance and single-cell characteristics of respiring bacteria via the redox dye CTC Pinhassi et al. — Coupling between bacterioplankton species composition, population dynamics, and organic matter degradation
2000	Hagström et al. — Biogeographical diversity among marine bacterioplankton Pinhassi & Hagström — Seasonal succession in marine bacterioplankton
2001	Pomeroy & Wiebe — Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria Fandino et al. — Variations in bacterial community structure during a dinoflagellate bloom analyzed by DGGE and 16S rDNA sequencing
2002	Zwart et al. — Typical freshwater bacteria: an analysis of available 16S rRNA gene sequences from plankton of lakes and rivers Simon et al. — Microbial ecology of organic aggregates in aquatic ecosystems
2003	Selje & Simon — Composition and dynamics of particle-associated and free-living bacterial communities in the Weser estuary, Germany Stepanuskas et al. — Covariance of bacterioplankton composition and environmental variables in a temperate delta system
2004	Engel et al. — Transparent exopolymer particles and dissolved organic carbon production by <i>Emiliania huxleyi</i> exposed to different CO <sub>2</sub> concentrations: a mesocosm experiment Berman et al. — Planktonic community production and respiration and the impact of bacteria on carbon cycling in the photic zone of Lake Kinneret

The hot subjects of the period 1995 to 2005 are reflected in the titles of the most popular articles. The 2 most highly cited papers from each year of AME (AME has published many more papers than MMFW) are

listed in Table 2. The past decade has been characterised 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 protists) 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 inappropriately 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

- Azam F, Smith DC (1991) Bacterial influence on the variability in the ocean's biogeochemical state: a mechanistic view. In: Demers S (ed) Particle analysis in oceanography. Springer-Verlag, Berlin, p 213–257
- Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. *Mar Ecol Prog Ser* 10:257–263
- Beers JF (1982) An introduction and historical overview. *Ann Inst Oceanogr Paris* 58:5–14
- Berman T, Nawrocki M, Taylor GT, Karl DM (1987) Nutrient flux between bacteria, bacterivorous nanoplanktonic protists and algae. *Mar Microb Food Webs* 2:69–82
- Berman T, Parparov A, Yacobi YZ (2004) Planktonic community production and respiration and the impact of bacteria on carbon cycling in the photic zone of Lake Kinneret. *Aquat Microb Ecol* 34:43–55
- Carlson CA, Ducklow HW (1996) Growth of bacterioplankton and consumption of dissolved organic carbon in the Sargasso Sea. *Aquat Microb Ecol* 10:69–85
- Christaki U, Jacquet S, Dolan, JR, Vaulot, D, Rassoulzadegan F (1999) Growth and grazing on *Prochlorococcus* and *Synechococcus* by two marine ciliates. *Limnol Oceanogr* 44:52–61
- Claustre H, Marty JC, Cassiana L, Dagaut J (1989) Fatty acid dynamics in phytoplankton and microzooplankton communities during a spring bloom in the coastal Ligurian Sea: ecological implications. *Mar Microb Food Webs* 3:51–66
- Cooksey KE, Wigglesworth-Cooksey B (1995) Adhesion of bacteria and diatoms to surfaces in the sea: a review. *Aquat Microb Ecol* 9:87–96
- Cotner JB, Ammerman JW, Peele ER, Bentzen E (1997) Phosphorus-limited bacterioplankton growth in the Sargasso Sea. *Aquat Microb Ecol* 13:141–149
- Dufresne A, Salanoubat M, Partensky F, Artiguenave F and 17 others (2003) Genome sequence of the cyanobacterium *Prochlorococcus marinus* SS120, a nearly minimal oxygenotrophic genome. *Proc Natl Acad Sci USA* 100:10020–10025
- Eldredge N, Gould SJ (1972) Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf TJM (ed) Models in paleobiology. Freeman Cooper, San Francisco, CA, p 82–115
- Engel A, Delille B, Jacquet S, Riebesell U, Rochelle-Newall E, Terbrüggen A, Zondervan I (2004) Transparent exopolymer particles and dissolved organic carbon production by *Emiliania huxleyi* exposed to different CO<sub>2</sub> concentrations: a mesocosm experiment. *Aquat Microb Ecol* 34:93–104
- Fagerbakke KM, Heldal, M, Norland S (1996) Content of carbon, nitrogen, oxygen, sulfur and phosphorus in native aquatic and cultured bacteria. *Aquat Microb Ecol* 10:15–27
- Fandino LB, Riemann L, Steward GF, Long RA, Azam F (2001) Variations in bacterial community structure during a dinoflagellate bloom analyzed by DGGE and 16S rDNA sequencing. *Aquat Microb Ecol* 23:119–130
- Fenchel T (2002) Microbial behavior in a heterogeneous world. *Science* 1068–1071
- Fuhrman JA, Azam F (1980) Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica, and California. *Appl Environ Microbiol* 39:1085–1095
- Hagström Å, Pinhassi J, Zweifel UL (2000) Biogeographical diversity among marine bacterioplankton. *Aquat Microb Ecol* 21:231–244
- Heinbokel JF, Beers JR (1979) Studies on the functional role of tintinnids in the Southern California Bight. III. Grazing impact of natural assemblages. *Mar Biol* 52:23–32
- Hobbie JE, Daley RJ, Jasper S (1977) Use of nucleopore filters for counting bacteria by fluorescence microscopy. *Appl Environ Microbiol* 33:1225–1228
- Jürgens K (1994) Impact of *Daphnia* on planktonic microbial food webs—a review. *Mar Microb Food Webs* 8:295–324
- Kühl M, Steuckart C, Eickert G, Jeroschewski P (1998) A H<sub>2</sub>S microsensor for profiling biofilms and sediments: application in an acidic lake sediment. *Aquat Microb Ecol* 15:201–209
- Legendre L, Le Fèvre J (1995) Microbial food webs and the export of biogenic carbon in oceans. *Aquat Microb Ecol* 9:69–77
- Lessard EJ (1991) The trophic role of heterotrophic dinoflagellates in diverse marine environments. *Mar Microb Food Webs* 5:49–58
- Malone TC (1980) Size fractionated primary productivity of marine phytoplankton. In: Falkowski P (ed) Primary productivity in the sea. Plenum Press, New York, p 301–319
- Noble RT, Fuhrman JA (1998) Use of SYBR Green I for rapid epifluorescence counts of marine viruses and bacteria. *Aquat Microb Ecol* 14:113–118
- Partensky F, Hess WR, Vaulot D (1999) *Prochlorococcus*, a marine photosynthetic prokaryote of global significance. *Microbiol Mol Biol Rev* 63:106–127
- Pinhassi J, Hagström Å (2000) Seasonal succession in marine bacterioplankton. *Aquat Microb Ecol* 21:245–256
- Pinhassi J, Azam F, Hemphälä J, Long RA, Martinez J, Zweifel UL, Hagström Å (1999) Coupling between bacterioplankton species composition, population dynamics, and organic matter degradation. *Aquat Microb Ecol* 17:13–26
- Pomeroy LR (1974) The ocean's food web, a changing paradigm. *Bioscience* 24:499–504
- Pomeroy LR, Wiebe WJ (2001) Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. *Aquat Microb Ecol* 23:187–204
- Raimbault P, Rodier M, Taupier-Letage I (1988) Size fraction of phytoplankton in the Ligurian Sea and the Algerian Basin (Mediterranean Sea): size distribution versus total concentration. *Mar Microb Food Webs* 3:1–8
- Rassoulzadegan F (1978) Dimensions et taux d'ingestion des particules consommées par un tintinnide: *Favella ehrenbergii* (Clap. & Lachm.) Jörg., cilié pélagique marin. *Ann Inst Océanogr Paris* 54:17–24
- Reckermann M, Veldhuis MJW (1997) Trophic interactions between picophytoplankton and micro- and nanozooplankton in the Western Arabian Sea during the NE monsoon 1993. *Aquat Microb Ecol* 12:263–273
- Rivier A, Brownlee DC, Sheldon RW, Rassoulzadegan F (1985) Growth of microzooplankton: a comparative study of bacterivorous zooflagellates and ciliates. *Mar Microb*

- Food Webs 1:51–60
- Sanders RW, Wickham SA (1993) Planktonic protozoa and metazoa: predation, food quality and population control. *Mar Microb Food Webs* 7:197–224
- Selje N, Simon M (2003) Composition and dynamics of particle-associated and free-living bacterial communities in the Weser estuary, Germany. *Aquat Microb Ecol* 30: 221–237
- Sharp JH (1977) Excretion of organic matter by marine phytoplankton: do healthy cells do it? *Limnol Oceanogr* 22:381–391
- Sherr BF, del Giorgio P, Sherr EB (1999) Estimating abundance and single-cell characteristics of respiring bacteria via the redox dye CTC. *Aquat Microb Ecol* 18:117–131
- Sherr EB, Sherr BF, Paffenhöfer GA (1986) Phagotrophic protozoa as food for metazoans: a 'missing' trophic link in marine pelagic food webs? *Mar Microb Food Webs* 1: 61–80
- Simon M, Grossart HP, Schweitzer B, Ploug H (2002) Microbial ecology of organic aggregates in aquatic ecosystems. *Aquat Microb Ecol* 28:175–211
- Smith DC, Azam F (1992) A simple, economical method for measuring bacterial protein synthesis rates in seawater using <sup>3</sup>H-leucine. *Mar Microb Food Webs* 6:107–114
- Stepanauskas R, Moran MA, Bergamaschi BA, Hollibaugh JT (2003) Covariance of bacterioplankton composition and environmental variables in a temperate delta system. *Aquat Microb Ecol* 31:85–98
- Williams PJleB (1990) The importance of losses during microbial growth: commentary on the physiology, measurement and ecology of the release of dissolved organic material. *Mar Microb Food Webs* 4:175–206
- Zwart G, Crump BC, Kamst-van Agterveld MP, Hagen F, Han SK (2002) Typical freshwater bacteria: an analysis of available 16S rRNA gene sequences from plankton of lakes and rivers. *Aquat Microb Ecol* 28:141–155