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INTRODUCTION

Rassoulzadegan in Villefranche-sur-Mer and the 'evolution' of marine microbial ecology over the last three decades

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The evolutionary pattern of contemporary marine microbial ecology can be said to resemble that of 'punctuated equilibrium' (Eldredge & Gould 1972), characterised by abrupt shifts in both focal points and methods. Fereidoun Rassoulzadegan's research, spanning the period from the mid-1970s to the 2000s paralleled, and in many cases preceded, the dramatic changes in focus and approaches in the field. In this introduction, we attempt to tell the story of the 'evolution of marine microbial ecology' over the past 3 decades, and the place of the microbial ecology group founded by Rassoulzadegan and now part of the Laboratoire d'Océanographie de Villefranche-sur-Mer.

Despite appearances from literature citations, modern marine microbial ecology was not born in 1983 but much earlier. Indeed, from the early 1900s ciliates and flagellates had been recognized as possibly important members of plankton communities. In modern times, some did postulate that microorganisms likely play a major role in food chains and carbon flow (e.g. Ryther 1969, Pomeroy 1974). However, until the 1970s, marine microbes (protists and prokaryotes) were largely the domain of taxonomists and naturalists. For example, in *The Structure of Marine Ecosystems* bacteria and protists are largely absent (Steele 1974). In the late 1970s, several separate discoveries, collectively, forced a radical re-assessment of the role of marine microbes: an upgrade from 'possibly' to 'quite likely' important. These discoveries were:

(1) A very large portion of primary production is attributable to small algae (e.g. reviewed in Malone

1980) which are not efficiently grazed by copepods (e.g. Nival & Nival 1976).

(2) Phytoplankton excrete a considerable fraction of the carbon fixed (e.g. Sharp 1977).

(3) Direct counting techniques show bacterial concentrations to be orders of magnitude higher than previously thought (e.g. Hobbie et al 1977), and bacterioplankton growth rates suggest that biomass production of bacteria could be comparable to that of phytoplankton (e.g. Fuhrman & Azam 1980).

These findings, which were 'inconvenient' with regard to our image of a food chain resting on herbivorous copepods, focused attention of the oceanographic community on small algae, bacteria, and the presumed consumers of small algae and bacteria, the protists. However, the 'paradigm-shift', as commonly occurs, arose not only from new startling discoveries but also from carefully accumulated observations, difficult to explain in the existing framework, and the new paradigm actually took a bit longer to be generally accepted than commonly thought.

Fereidoun Rassoulzadegan's interest in microzooplankton began with his first investigations near the Caspian Sea, where he observed abundant microzooplankton populations in sturgeon ponds. With some premonition, he concluded that microzooplankton must be of importance in the food web supporting sturgeon. This idea actually turned out to be '*caviar*' as a topic of research.

Arriving in the early 1970s in Villefranche, Rassoulzadegan began his work on ciliate microzooplank-

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ton. His observations (Rassoulzadegan 1977a,b, 1979a,b, Rassoulzadegan & Gostan 1976) and those of others (e.g. Beers & Stewart 1967, 1969, 1970, 1971) clearly showed that protist biomass, even in oligotrophic systems, far exceeded that of metazoan zooplankton. He also found that the diversity was surprising, and rare species could quickly become abundant (Rassoulzadegan 1979b). Clearly protist communities were dynamic. His field and experimental work with ciliates (Ibanez & Rassoulzadegan 1977, Rassoulzadegan 1978), along with that of others such as Heinbokel (1978a,b) and Heinbokel & Beers (1979), suggested that ciliates were major consumers of phytoplankton, both qualitatively and quantitatively. Thus, there were apparently herbivores of some importance other than copepods in the seas. With such findings and the nascent 'paradigm-shift' stemming from the discoveries mentioned above, the stage was set for a key meeting: the NATO ASI and CNRS Workshop, 'Marine Pelagic Protozoa and Microzooplankton Ecology' in Villefranche-sur-Mer in May of 1981. Organized by Fereidoun Rassoulzadegan, Michele Laval-Peuto, Jean and Colette Lefevre, it brought together some top personalities as participants including (among many others), Beers, Conover, Droop, Fenchel, Margalef and Sieburth. The symposium identified trophic interactions as a high priority area for further work. Following the workshop, studies were conducted in the early 1980s describing in detail the feeding of tintinnids (Rassoulzadegan & Etienne 1981) and oligotrichs (Rassoulzadegan 1982). At about the same time, Fenchel was completing his work on flagellates (Fenchel 1982a–d). The ground then was very well prepared for the flowering of the 'microbial loop' concept, which was formally described in 1983 (Azam et al. 1983).

Throughout the 1980s there was an explosion of activity aimed at clarifying the trophic relationships of marine microbes: predator–prey interactions, selective feeding, numerical and functional responses, and studies of trophic modes of protists. Research included considerable efforts devoted to methods development, e.g. fluorochromes for enumerations, protocols to estimate growth and grazing rates. Many of these studies appeared in the journal founded by Fereidoun Rassoulzadegan in 1985, *Marine Microbial Food Webs* (e.g. Sheldon & Rassoulzadegan 1987), the only journal devoted to marine microbial ecology and the direct predecessor of *Aquatic Microbial Ecology*.

Coincidentally or not, at about the same time that microbial ecology was entering an explosive growth phase, biological oceanography was undergoing a clear shift in research priorities, away from food chains leading to exploited species, to a very sharp focus on biogeochemical pathways. The general acceptance of the reality of the greenhouse effect underlined our

need to understand carbon pathways, especially in the world ocean. There was a fair amount of anthropogenic carbon missing from the atmosphere. The era of 'biogeochemical cycles', with an accent on carbon, was ushered in by the Joint Global Oceanic Flux Study, a major international effort which ran from 1987 to 2003.

In Villefranche, as elsewhere, in the microbial ecology group attention was gradually shifted from the phytoplankton–protists link to that of bacteria and protists, especially flagellates (Rivier et al. 1985, Rassoulzadegan & Sheldon 1986, Sheldon et al. 1986). The shift to 'bacteria–flagellates' was driven by the realization that prokaryotes, whether autotrophic (*Synechococcus* or *Prochlorococcus*) or heterotrophic, must play key roles in pelagic food webs given their relative biomasses and growth rates. Furthermore, ciliates were relatively poor candidates for the role of major bacterivores (Rivier et al. 1985, Bernard & Rassoulzadegan 1990). The late 1980s and early 1990s were marked mainly by efforts to clarify the roles of planktonic protists in biogeochemical cycles, as prokaryotes remained largely a 'black box', difficult to address in terms other than bulk rates.

Focusing on planktonic protists, details of the complexities of trophic roles and relationships were revealed. In Villefranche, Rassoulzadegan along with collaborators and students, conducted extensive studies on trophic relationships: mixotrophy (Bernard & Rassoulzadegan 1994), bacterivory (Rassoulzadegan et al. 1988, Sherr et al. 1988, Bernard & Rassoulzadegan 1990, Wikner et al. 1990), and grazing rates on phototrophic pico- and nanoplankton (Hagström et al. 1988, Rassoulzadegan et al. 1988, Sheldon et al. 1992, Bernard & Rassoulzadegan 1993, Christaki et al. 1998, 1999). Biogeochemical cycling was directly addressed through studies of regeneration of nitrogen (Ferrier & Rassoulzadegan 1991, Ferrier-Pagès & Rassoulzadegan 1994a,b, Selmer et al. 1993) phosphorus (Allali et al. 1994, Dolan et al. 1995), and the effects of atmospheric inputs (Klein et al. 1997).

Through the work that continued in the 1990s, the idea that microbes are indeed the key players in pelagic nutrient cycling, and the structuring role of nutrient limitation, slowly gained general recognition and Fereidoun's collaborations played a significant role. For example, the propositions that a continuum of food web structures varying in time and space exists (Legendre & Rassoulzadegan 1995, 1996) and that food web structure could be governed by nutrient limitation (Thingstad & Rassoulzadegan 1995) were launched in part from Villefranche and are now well established.

The era of 'biogeochemical cycles' in the microbial ecology group of Villefranche included key studies detailing the interactions between nutrient limitation

and dissolved organic carbon dynamics (Thingstad et al. 1997, 1998, Thingstad & Rassoulzadegan 1999) and examinations of particulate organic carbon in the sea (Mostajir et al. 1995a,b, Mostajir et al. 1998, Mari & Rassoulzadegan 2004, Mari et al. 2004, 2005), as well as production by protists (Pelegri et al. 1999). For the microbial ecology group in the Laboratoire d'Océanographie de Villefranche, biogeochemical investigations perhaps reached their pinnacle with the 'Cyclops' project and cruise in which a phosphorus addition experiment was performed in the open Eastern Mediterranean (Thingstad et al. 2005).

Another research direction was plainly apparent in the late 1990s and early 2000s, as JGOFS and carbon flux studies began to wind down—the molecular era. In the Villefranche microbial ecology group, new orientations have recently taken root profiting from the capabilities of these new molecular tools: studies of calcifying organisms, marine bacteriophages and protist biodiversity. Fereidoun, for his part, has participated in some of the marine viral research ranging from the theoretical (e.g. Weinbauer & Rassoulzadegan 2004) to the experimental (e.g. Motegi et al. 2009). In addition to new directions or methods (notably of course genomics and metagenomics) changing a field of study, an 'invasion' of a new habitat can mark its history. With regard to marine microbial ecology, the dark ocean appears to be the most active site of colonisation today, and Villefranche has been no exception (Tanaka & Rassoulzadegan 2002, 2004, Tanaka et al. 2005, Winter et al. 2009).

Throughout the past 3 decades, marine microbial ecology has undergone remarkable changes, from a virtually non-existent field of study in the early 1970s to one which now boasts its own journals (e.g. *Aquatic Microbial Ecology*) and meetings. Furthermore, its practitioners nearly dominate many broad-based organisations, such as the American Society of Limnology and Oceanography and populate Academies of Science around the globe. Fereidoun Rassoulzadegan's efforts over the years were an integral part of the establishment of the field and, in one form or another, most every worker can be (or eventually will be) linked to his work in some fashion. The range of authors and subjects in this special issue are good evidence. The paper by Caron & Countway (2009, this Special Issue) on the existence and role of rare protist species, while examining recent data resulting from new molecular approaches, deals with a topic which harks back to some of Fereidoun's earliest work (Rassoulzadegan 1977a) on tintinnid ciliates. Cytometry of the seas, reviewed by Bill Li (2009, this Special Issue) of necessity refers back to particle distribution of Sheldon, Fereidoun's long-time collaborator. The question of the relative importance of protists in grazing phytoplank-

ton, considered by the Sherrs (Sherr & Sherr 2009, this Special Issue), is still a controversial topic. Christaki et al. (2009, this Special Issue) examined the efficiency of transfers of carbon within microbial food webs and the magnitude of temporal and spatial variability, topics which remain very active areas of research. Mixotrophy, the simultaneous use of both heterotrophic and autotrophic nutrition in protists, is reviewed in Stoecker et al. (2009, this Special Issue) and is being re-examined in the light of molecular tools. Nutrient uptake by phytoplankton and bacteria, and possible competition between the two for a limiting nutrient, is addressed in Tambi et al. (2009, this Special Issue). The effects of particles of viral activity is the subject of Weinbauer et al. (2009, this Special Issue) while Motegi & Nagata (2009, this Special Issue) examined the effects of dissolved organic carbon on lytic rates. Perhaps the final geographic frontier of microbial ecology, the deep sea, is the topic of Tanaka's paper (2009, this Special Issue).

As Fereidoun shifts into the emeritus mode we can only speculate as to where his attention will be directed. However, based on past history he will likely be in the forefront of a contingent leading the way of microbial ecology.

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