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The microbial loop concept: A history, 1930–1974

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ABSTRACT

The microbial loop as a leading concept in marine microbiology gained wide recognition in the 1980s, but it has roots extending back to the 1930s when microbiologists first began to take a more dynamic approach to investigating the roles of bacteria in ocean food webs and biogeochemical cycles. Here we present a history of the microbial loop concept with emphasis on the period starting in 1930, when marine bacteriologists in Russia and the West began to study explicitly the roles of marine bacteria in the sea. Selman Waksman at Woods Hole and Claude ZoBell at La Jolla relied on colony counts on agar plates as the basis of their work. We suggest that failure to accept direct microscopic evidence of high numbers of bacteria in seawater retarded conceptual development in the West well into the 1970s. Easterners pioneered direct count and radioisotopic techniques and created a dynamic marine microbiology integrating bacteria as important components of marine food webs by the 1960s. Yurii Sorokin and colleagues carried out extensive experimental studies of bacteria as food for marine grazers and provided data for Mikhail Vinogradov and his group to write the first numerical simulation models of ocean ecosystems incorporating microbial components. It had little impact on the Western modeling community, as other Russian work of the times. In spite of continuing technical shortcomings in the field, Lawrence Pomeroy constructed a new conceptual model, providing a synthesis pointing the way toward a modern view of marine microbial ecology that finally matured technically and conceptually in the West in the early 1980s.

Keywords: Bacteria, colony count, direct count, fluorescence microscopy, marine microbiology, microbial ecology, microbial loop, history of science, Russian science

Nature does not deem it her business to make the discovery of her laws easy for us.

—Albert Einstein, *The Collected Papers of Albert Einstein* (1987, vol. 5, p. 202)

1. Introduction and background

We live in a microbial world. About half of the number of cells in the human body are bacterial (nonhuman) cells. This is probably true of most higher organisms: each individual accommodates a microbiome, or assemblage of microbial species that influences the

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interactions between the host and its internal and external environments. Even microbes have microbiomes (Frischkorn, Haley, and Dyhrman 2018). Bacteria likewise dominate the ocean. Each cubic meter of seawater contains about 10^{11} cells; the volume of the ocean is about 10^{18} m^3 giving a total of 10^{29} cells, a billion times more than Carl Sagan's billions and billions of stars in the universe ($\sim 10^{20}$). Bacteria are the engines driving the massive elemental cycles of the planet (Falkowski, Fenchel, and Delong 2008). This is achieved as a consequence of their small size, giving potentially high metabolic rates, combined with their great physiological diversity: there are aerobic and anaerobic, photo- and chemoautotrophic, and photoheterotrophic and chemoheterotrophic modes of nutrition. Some bacteria prey on other bacteria. By serving as sources and sinks of greenhouse gases, they regulate the climate of the planet over geological timescales. In this article, we are concerned with one aspect of the ocean microbiome: the roles of aerobic, heterotrophic bacteria and archaea as integral members of marine planktonic food webs in the upper few hundred meters of the ocean. They consume preformed organic matter and oxidize it to harvest energy needed to survive and grow. Bacterial biomass likely exceeds the rest of the ocean's total living mass, and marine bacteria daily respire about half the total amount of carbon synthesized by photosynthesis (Bowman and Ducklow 2018). It follows that bacteria must be important parts of the ocean plankton system.

Marine microbiology as a recognized field of science extends back to the late 19th century, when scientists, originally trained as soil or medical microbiologists, or perhaps as botanists or zoologists, began to gain access to oceanographic expeditions to document the abundance, distribution, and identity of bacteria in the world ocean (ZoBell 1946). This descriptive, "natural history" period lasted into the 1930s. In the West, marine bacteriologists lacked a firm quantitative and mechanistic understanding of the conditions of bacterial existence and were far from recognizing their dominance in the sea; the focus of the Western work was on the taxonomic and nutritional capabilities. In contrast, there is evidence that the Eastern[4] marine microbiological and oceanographic community as a whole had a better general grasp of the relative scale of marine bacterial activity than their Western counterparts until the mid- to late 1970s, when Lawrence Pomeroy (1974b) published his farsighted synthesis. In this article, we trace some of the conceptual and technical evolution of scientific understanding of marine microbial food webs. Several reviews, prior to this one, document the major developments (Pomeroy 1974b; Sorokin 1978; Williams 1981, 1984; Azam et al. 1983; Ducklow 1983; Sherr and Sherr 2000; Karl and Proctor 2006; Pomeroy et al. 2006; Fenchel 2008). Our interest is primarily in the earlier period leading up to the better-known developments of the mid-1960s onward.

It would be easy to infer from papers on the subject of the contribution of microbial processes to overall planktonic organic flux that the contemporary paradigm derived from

4. The terms "Russia," "Eastern," and "Soviet," as well as "Soviet Union," "Soviet bloc," and "Eastern bloc," have different meanings and connotations to European and American readers and also to Eastern and other citizens of the former Soviet Union. In an attempt to minimize confusion and use politically neutral terms, where appropriate we refer to the two groups as "Western" and "Eastern," respectively, in the body of the text.

relatively few, well-cited papers. So why bother about the history of its development? One reason is to bring home that it was in fact the product of a large community. We attempted to estimate the scale of the number of individuals involved in the development and revision of the earlier concept. To do so, we have taken the reference lists from three reviews (Williams 1981; Azam et al. 1983; Ducklow 1983), extracted the individual authors and coauthors, and removed duplicate names to obtain 224 individuals, of whom some 50 are included more than once. A further reason is to gain some understanding of the track (as it turns out, two parallel tracks) that led to the development of the current paradigm. We were motivated in part by Pomeroy (1974b) explicitly identifying his influential paper with paradigm change. Was there a preceding paradigm? Did it truly change? It is no surprise that it is not a simple trail, and, at times, although the truth was there in the observations, fashion overrode fact, and it was missed.

a. Overview: The concept of bacteria in plankton food webs

The principal role we ascribe to the aerobic heterotrophic bacteria in the upper, productive layer (0–200 m) of the ocean is metabolizing and transforming the particulate and dissolved organic matter (DOM) in a microbial food web called the microbial loop. Hereafter, for simplicity, we use the term "bacteria" for the vastly diverse group including marine bacteria and archaea. The latter group may mostly be chemoautotrophic, but they are usually included in estimates of total "bacterial" abundance, and they are consumed by bacteriovores, lysed by viruses, and cycle nitrogen and other elements; thus they are functioning members of marine plankton food webs (Kirchman 2008). We use the term "microbes" to refer to an organism requiring a microscope for visualization, including unicellular phytoplankton and other protists. A vague concept of bacteria in marine food webs extends back at least to the 1930s, but any estimate of its magnitude and governing mechanisms is much more recent.

The microbial loop, a shorthand term for the integrated processes of DOM and inorganic nutrient consumption and production initiated by bacteria in the plankton, was formalized in an influential, widely cited article (Azam et al. 1983). Free-living bacterial cells (bacterioplankton) consume DOM released by all other organisms (Fig. 1). Because they are the only organisms capable of using DOM at in situ nanomolar concentrations, they effectively "recover" excreted DOM that would otherwise be lost from the trophic system. Protozoans efficiently graze individual, free-living bacteria and in turn are consumed by zooplankton. Thus, some fraction of the carbon and other nutrients that were originally captured in dissolved form by bacteria move up the food chain toward fish and larger consumers. The "loop" is completed when bacteria take up the "lost" DOM. The Azam paper, as others of its time, did not consider the role of bacteria in the decomposition of particulate detritus—the Pomeroy (1974b) paper being something of an exception.

b. The magnitude and scale of bacterial processes in the sea

There are two general matters that we would like to introduce first as they help with understanding the development of methods and ideas. First, it is clear from the writings

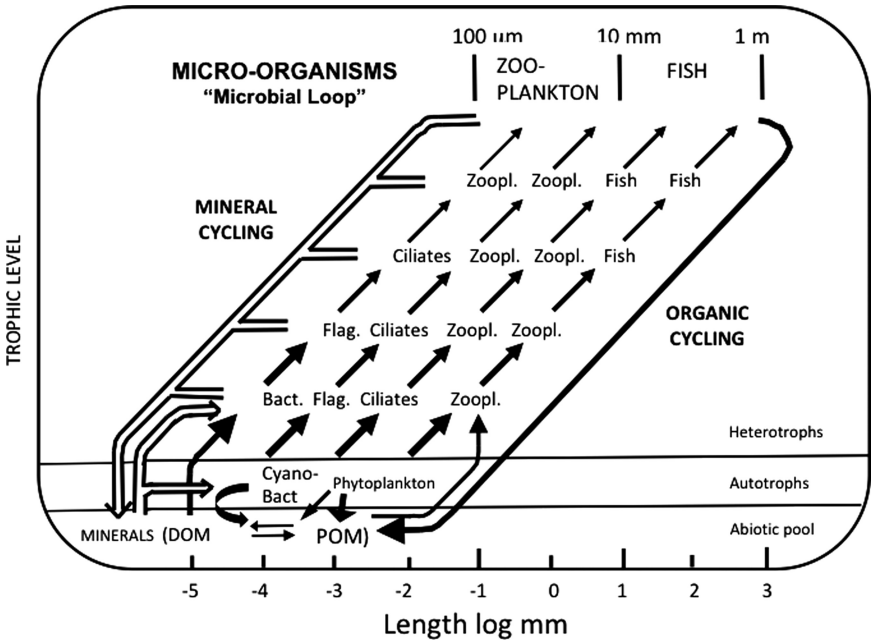

Figure 1. The microbial loop, "semiquantitative model of planktonic food chains" organized by cell size and trophic level. The downward return flow of dissolved organic cycling completes the microbial loop. Reproduced from Azam et al. (1983, The ecological role of water-column microbes in the sea, Mar. Ecol. Prog. Ser., *10*, 257–263, fig. 3, p. 260).

of the early workers that when assessing the scale of bacterial activity vis-à-vis overall plankton activity, they took guidance from the implications of their assessment of bacterial biomass. Early studies of phytoplankton production made by Gaarder and Gran (1927) and Marshall and Orr (1930) gave rates measured in micrograms of carbon per liter per day; these may have provided some insight of the scale of planktonic carbon flux in the euphotic zone. Prior to the development of biochemical indicators of bacterial biomass, it had to be estimated from measurements of bacterial numbers. Two techniques were used—the plate count technique and direct microscopic counts of bacteria collected on filters. In the euphotic zone, the former gave numbers generally in the range of 10–1,000 cells mL^{-1}, and the latter some 1,000-fold greater. It was not uncommon to find no colony-forming cells below the upper 200 m (ZoBell and Anderson 1936). The estimation of rates from bacterial numbers calls for assumptions about a number of features of the dynamics of bacterial growth about which there are uncertainties; however, from Table 1 we can infer that such uncertainties would have little effect on the conclusion that the rates of carbon flux estimated from plate counts would only give rates in the nanograms of carbon per liter per day, whereas the direct counts projected rates of micrograms of carbon per liter per

Table 1. Scaling calculations to estimate the order of carbon flux by varying bacterial population densities. Mass of a bacterial cell: 10 fg (Ducklow 2000, p. 94). BGT (bacteria generation time): 1 and 10 days (Kirchman 2000, p. 108, fig. 6.8). BGY (bacterial growth yield): 10% and 25%. Kirchman 2000. Processes in Microbial Ecology. Oxford University Press, Oxford p. 312. Ducklow 2000. Bacterial Production and Biomass in the Oceans. p. 85–120 In: Kirchman (Ed.). Microbial Ecology of the Oceans. New York: Wiley-Liss, p. 542.

	BGT	1 Day		10 Days	
Parameter	BGY	10%	25%	10%	25%
Plate counts	Cells mL^{-1}	Carbon utilization as ng C L^{-1} per day			
	10	10^0	4×10^{-1}	10^{-1}	4×10^{-2}
	100	10^1	4×10^0	10^0	4×10^{-1}
	1,000	10^2	4×10^1	10^1	4×10^0
Direct counts	Cells mL^{-1}	Carbon utilization as μg C L^{-1} per day			
	10,000	10^0	4×10^{-1}	10^{-1}	4×10^{-2}
	100,000	10^1	4×10^0	10^0	4×10^{-1}
	1,000,000	10^2	4×10^1	10^1	4×10^0

Table 2. Timeline of the development of fine-porosity filters.

Decade	Event	Location
1920s	1927: Zsigmondy developed membrane filters.	Germany
	1929: Cholodny developed collodion filters.	Russia
1950s	1952: Rukina and Biriuzova described method for producing membrane filters free from contamination.	Russia
	1954: Jack Bush started Millipore.	United States
	1959: Millipore filters came into production.	United States
1960s	1964: General Electric began commercial production of Nuclepore filters (source: Karl 2007).	United States

day. Thus, the plate counts would imply a small to insignificant contribution by bacteria to the overall turnover of organic material; the direct counts, conversely, implied a possibly significant contribution.

All the different versions of direct microscopic counts set requirements on the optical and other physical properties of the filters used to collect bacteria in seawater samples. For a number of reasons, the traditional paper and glass fiber filters were not suitable for visualizing bacterial cells. To some extent, the progress in determining bacterial numbers in the sea was dependent on what and when particular types of filters were available to researchers. The development of the filters is summarized in Table 2.

The Eastern researcher Nicolai Cholodny (1882–1953) developed filters from collodion (nitrocellulose) used them from the 1930s onward. Although so called "membrane filters" (also nitrocellulose) were produced in Germany by Sartorius since the 1930s, the first use we

can locate for the Western bloc as a whole was in an exploratory paper by Holger Jannasch (1958). He and Ferguson Wood earlier proposed the use of membrane filters stained with acridine orange for fluorescence microscopy (Jannasch 1954), but neither, as far as we have been able to determine, published findings using this technique. Western bloc scientists were generally wary of the results of direct counts of erythrosine-stained bacteria on membrane filters; as a result, little progress was made until the mid-1970s, when Nuclepore filters came into common use (Karl 2007). Then followed rapid development in methodology and field studies, notably in Germany and the United States (Hoppe 1976; Meyer-Reil 1977). Hobbie, Daley, and Jasper (1977) and Watson et al. (1977) demonstrated using the newly available Nuclepore filters that there were about 10^8–10^9 bacterial (plus archaeal) cells with intact nucleic acids (i.e., potentially viable) in a liter of seawater, much higher than even the highest prior estimates.

Like most scientific advances, these discoveries did not happen in a vacuum. The idea that abundant, free-living bacteria formed the base of a marine food web had anything but a straightforward history, as we discuss subsequently. In Section 2, we address the role of upper ocean bacteria, as it was understood in the West between the 1930s and 1960s. In Section 3, we consider the understanding in Russia in the same general period. In Section 4, we sketch the warning signs encountered by some Western oceanographers that prevailing models of microbial existence gave an insufficient account of the role of bacteria in the modern synthesis leading to the microbial loop. Finally, we conclude (Section 6) by discussing several questions raised during our study: Was the Eastern understanding in advance of that in the West and, if so, why? What, if anything, held back developments in the West? Why did the Eastern ideas not take root and grow in the West?

We choose to end our story in 1974 with the publication of Pomeroy's (1974b) seminal paper, "The Ocean's Food Web, a Changing Paradigm."

2. The historical development of marine microbiology in the West, 1933–1974

a. Bacterial autecology in the West, 1930–1974

The estimation of bacterial numbers and biomass in surface waters has a long history. The plate count technique was used as early as 1889 by Bernhard Fischer (1894) as part of the German Plankton Expedition (Mills 1989). As noted in the previous section, direct microscopic counting was pioneered by Eastern scientists was used in their field studies from the 1930s onward (see Section 3a). Marine bacterial research in the 1930s to 1960s among Western marine microbiologists was focused mostly on studies of bacteria capable of growing in the lab, in amended seawater, or on solid media such as agar in glass Petri dishes, containing high added concentrations of organic matter—grams per liter in many cases. This practice goes back to the earliest days of modern bacteriology as practiced by Louis Pasteur and Robert Koch. Many microbiologists had large collections of purified bacterial cultures and devoted their efforts to studying their physiology, growth, and survival

under various conditions in the laboratory. Colony count estimates of bacterial abundance are based on the idea that one viable bacterial cell would grow into a visible colony on a suitable solid medium, from which it could be purified and grown in culture. Then the properties and biochemical capabilities of the organism could be determined in the lab. In addition, if the colonies were sufficiently distinct, the cellular abundance in nature could be determined. Often the estimates were as low as zero to perhaps a few hundred cells per milliliter of seawater. It slowly became obvious that there was no universally "suitable" medium, so in essence, as a means of estimating the total number of bacteria in a sample of water, the approach was flawed. The key observation influencing most thinking among Western marine microbiologists in this era about the ecology of bacteria in the sea was that very few bacteria were reported to be living in the water column (Krogh 1934a; Waksman 1934a; ZoBell 1946).

The use of solid surfaces and enhanced concentrations of organic matter was highly selective for species adapted to those specialized conditions. The results caused marine bacteriologists to question the potential roles of bacteria in the sea, and this puzzle forms a major theme of our history of the subsequent development of the field. In retrospect, we know that comparatively few marine species can grow in such conditions; hence, the very low estimates of bacterial abundance that characterized the early era until the 1970s (although not in Russia; Section 3). Such apparently low estimates of bacterial abundance were in contrast to what bacteriologists knew about soils and marine sediments (which had 10^5–10^6 cells per gram; Waksman 1922) and greatly influenced most views of microbial ecology in the ocean water column.

In some specialized cases, bacterial roles were evident, even if numbers were low. For example, it was well established that a specialized group of bacteria was responsible for nitrification, the oxidation of ammonium to nitrite and nitrate, a major biogeochemical pathway (Carey and Waksman 1934).[5] In contrast to bacteria catalyzing nitrogen transformations, the Western perspective of the roles of bacteria in decomposing the organic matter synthesized by primary producers (phytoplankton and seaweeds) was less clear, as was their role in marine food webs, if any. In the following section, we focus on two prominent American microbial ecologists—Selman Waksman and Claude ZoBell—and the Danish physiologist and chemist August Krogh and assess their impact on the understanding of the roles of bacteria in the plankton ecosystem.

b. August Krogh: Studies on organic metabolism

In the 1930s, two prominent scientists from other fields, Selman Waksman (soil microbiology) and August Krogh (animal physiology), undertook studies at the newly formed

5. Cornelia Carey was one of the first women to conduct research at Woods Hole Oceanographic Institution and was a professor of biology at Barnard College in New York City. Woods Hole residents might recognize her name as the conservator of "The Knob" in Quissett Harbor (http://saltpondsanctuaries.org/the-knob/).

Woods Hole Oceanographic Institution (WHOI). They directed their attention to the problems of organic matter and marine bacteria and their roles in the life cycle of the sea. Both were awarded Nobel Prizes for research in their home fields—Krogh in 1920 for the functioning of capillaries and Waksman for the discovery of streptomycin in 1952.

Krogh made a short sojourn at WHOI in the summer of 1933. His coworkers Ancel Keys and Erik Christensen continued the research in 1934; thereafter, Keys worked with Redfield on ammonium distributions. Krogh had come to marine science via studies of the flux of DOM in fresh water. In a review, published in 1931, he addressed and dismissed the claims of August Pütter (1909) that DOM was a major food source for aquatic animals. Using very precise measurements and an innovative line of argument, Krogh, Lange, and Smith (1930) showed that the purported source of DOM—high levels of phytoplankton organic exudation—did not stand up to close examination. They concluded, "We think it most probable that the organic substances directly lost during assimilation are wholly negligible" (Krogh, Lange, and Smith 1930, p. 1671). A major part of the work undertaken at WHOI that summer (Keys, Christensen, and Krogh 1935) was motivated by the following question: "There remains the question to what extent bacteria may utilize the dissolved organic matter in sea-water. This is of considerable importance because of the undoubted fact that bacteria may serve as food for larger organisms such as protozoa" (p. 181). Presumably, this would have enabled Krogh to hammer the final nail into the coffin of Pütter's hypothesis. The approach they used was to split a water sample in to two parts; one part was passed through a paper filter (Whatman No. 44 or 50) that was presumed to remove all plankton save the bacteria, and they compared the oxygen consumption curve of the filtered samples against that of the unfiltered water (Fig. 2).

The outcome of the study could have been read that in relation to the whole community respiration, there was a significant amount of respiration in the filtrate that contained only bacteria. The initial rates in the filtrates were 37% and 42% of the unfiltered rates. The authors were well aware that such high rates (fitted initial rates equivalent to 70 and 234 $\mu g\ C\ L^{-1}$ per day) were far beyond the capability of the bacterial populations derived from plate counts obtained by Waksman and his group who occupied the same building at WHOI as the Krogh group. Keys, Christensen, and Krogh's (1935) accommodation is insightful: "respiration, though small in total, was always very large per unit of viable cells. Unless the plating methods give a grossly erroneous picture, the results seem to indicate that bacterial respiration proper can be responsible only for a fraction of the oxygen used up, while the rest which disappears fairly rapidly, even at low temperature, must be accounted for in some other way" (p. 189; the underlining is ours). They placed their faith in the plate count technique and its implications, concluding that the high oxygen consumption rates they observed must derive from some artifact of the experimental procedure. It is important to note that at that point in time there were no published data on bacterial numbers in the Western sector other than plate counts, so there was no compelling reason to anticipate that the plate count could be giving numbers three orders of magnitude too low (cf. Table 1). The Eastern microbiologist A. S. Razumov (1932) had published a paper reporting direct

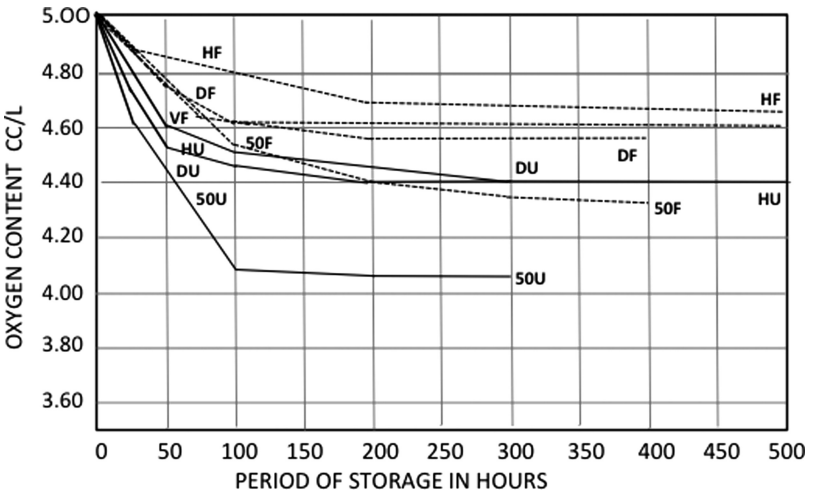

Figure 2. Keys, Christensen, and Krogh's (1935) plot of oxygen depletion (i.e., respiration) in various seawater samples stored in the dark at 21°C to 23°C. HF, filtered Woods Hole Harbour water; UF, the same unfiltered; VF, filtered water from Vineyard Sound; 50F, sea-water from the open sea; 50 metres depth, filtered; 50U, the same unfiltered. DF, water from the same station as 50 F but from a depth of 1800 metres, filtered; DU, the same unfiltered. Reproduced from Keys, Christensen, and Krogh (1935, The organic metabolism of sea-water with special reference to the ultimate food cycle in the sea, J. Mar. Biol. Assoc. U. K., *20*, 181–196, fig. 3, p. 185) with permission from Cambridge University Press.

microscopic counts 10^4 times greater than the plate counts. Waksman was familiar with the discrepancy, but noted: "A direct microscopic examination gave about 200 times as many organisms, the ratio becoming narrower upon addition of fresh organic matter. With due recognition of the limitations involved in the use of the plate method for measuring the abundance of bacteria in a natural substrate such as sea water, it was felt that this method is still most reliable for comparative purposes" (Waksman and Carey 1935a, p. 3). Thus, there were no grounds for Krogh's group to reject the numbers given by the plate counts. Keys, Christensen, and Krogh considered how the high rates associated with the bacteria may have come about. Krogh and his colleagues were well-suited to consider these questions as a result of Krogh's research on animal metabolism from insects (Krogh 1914) to blue whales (Krogh 1934c). They regarded their high rates to be a consequence of some undefined artifact associated with sampling, arguing:

> Thus much of the total dissolved organic matter, then, is readily susceptible to biological degradation, provided the stimulus of handling of the sea-water in the laboratory is supplied. That such a "stimulus" is necessary is shown by the fact that, in the sea, neither the bacterial multiplication nor oxygen consumption can be observed to take place. It may be possible, of course, that in the sea protozoan populations keep pace

> and by feeding on the bacteria restrict them to small numbers. More likely would it be that there is always only a very small bacterial activity in pure sea-water owing to the extreme stability of the ocean as a chemical and physical environment. (Keys, Christensen, and Krogh 1935, p. 193)

That is, the observed high rates of oxygen consumption were some artifact associated with the collection and containment of the sample—some "bottling effect." This implied "stimulus" that gave rise to the artifact of high rates was in effect pure invention based on no more than the need to square the observed rates with the expectation from the bacterial abundances derived from plate counts.

The reasoning used by Keys and coworkers brings out a significant but commonly overlooked hindrance toward understanding the scale of in situ metabolism of marine microorganisms—the so-called bottle effect. It had been long known (Whipple 1901) that a sector of the bacterial population, principally that revealed by the viable plate count approach, underwent a significant increase in numbers on containment—characteristically after a lag period of a day or so. This topic was later developed by ZoBell (1943) in an extensively cited paper (1,052 citations in Google Scholar). The bottle effect put a major question mark over the results of in vitro incubation studies, which had the potential to falsify the bottle effect concept; thus, in this respect the hypothesis of the bottle effect was self-preserving (Andrews and Williams 1971).

Krogh (1934a, 1934b) presented two reviews on conditions supporting life in the oceans. The main topic, relevant to the present narrative, is his discussion of the lability of DOM in the second of these papers. In conjunction with Keys, Krogh had spent 2 years developing methods for dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) analyses of seawater (Krogh and Keys 1934). In his review, Krogh reported a profile from the Sargasso Sea (WHOI *Atlantis* cruise 15, station 1467, 14 February 1933; 30.5° N, 68.5° W) from the surface down to 4,750 m. There is a significant difference both in scale and form between Krogh and Key's DOC profiles and contemporary ones. However, it is the form of the depth profile that is most significant to the present discussion and the conclusion they draw from it. In the case of both the DON and DOC, Krogh and Keys note that the profiles are homogeneous within the analytical limits of the error of the method. They acknowledge that there will be systematic error "which is not, however, likely to be large (Krogh 1934b, p. 436)."

The lack of difference between the surface and deep samples was in line with their view of the low importance of DOM in the organic cycle in the seas, noting that: "It follows therefore that changes in the quantity of dissolved material brought about by organisms must be extremely slow and gradual and that local differences, if any, must fall within the limits of error of the rather crude analytical methods" (Krogh 1934a, p. 436).

Why there is such a difference between the form and scale of their results and contemporary ones is still a puzzle. Krogh had put considerable effort into developing these methods and was confident in their performance even though at that point in time there was nothing

to compare their results against. There is, however, a statement in this second paper that sums up his conclusions of the work he and his group undertook on marine microorganisms:

> In the ocean water the number of bacteria appears to be small only, and according to the recent very interesting studies by Waksman and his collaborators from the Gulf of Maine the bacteria seem to be closely associated with the phytoplankton organisms. To my mind this furnishes rather a strong argument against the nutritive value of the organic material present in solution.
>
> Beyond the bacteria the protozoa and especially the naked forms should be able to utilize dilute solutions of organic material, but if they really do so is an open question. Many at least do not thrive in cultures without solid food in the shape of bacteria and other microorganisms. (Krogh 1934b, p. 437)

Later, Krogh's findings on the longevity of the deep-water DOM were confirmed by ^{14}C measurements of DOM (Williams and Druffel 1987), which showed that the organic material in the sea has a turnover rate of several thousand years. However, the lack of elevated levels at the sea surface, which was essentially unique to Krogh's work, extended this conclusion to the whole water column, the euphotic zone included. This served to confirm Krogh's hypothesis that DOM was generally not part of the biological cycle and thus there was little scope for bacteria to flourish. This conclusion substantially, but not entirely (see Skopintsev's work; Section 3a), shut down the interest in the biological dynamics of DOM for a number of decades as was noted by Barker Jørgensen, quoted by Bodil Schmidt-Nielsen (Krogh's daughter) in her biography of Krogh and his wife Marie: "The main results and conclusion of Krogh's investigation were so convincing that research in the field almost stopped for about 30 years. Only when radioactively labeled molecules, especially amino acids, became available was the problem again taken up for further research" (Schmidt-Nielsen 1995, p. 169). Indeed, in the Western bloc, except for a small number of papers (Seiwell 1937; Rakestraw, 1947; Plunkett and Rakestraw 1955), there was no work on the concentration and distribution of DOM until the work of Duursma (1961, 1963) and Menzel and Vaccaro (1964) more than a quarter of a century later.

The lack of citation of Krogh's marine papers might be considered as evidence of Krogh's negative impact on the field. Krogh's seven marine papers have together a total of 485 citations since their publication in 1931–1935, an average of 0.5 citations per year (Google Scholar, 27 August 2018). This seems astounding for a Nobel Prize winner, in whatever field. However, if his impact was to shut down research, there would have been little reason to cite his work. Krogh had planned to do further work on the distribution of DOM, but nothing further was ever published beyond the brief note of it in his paper in *Ecological Monographs*, which we discussed previously.

c. Selman Waksman: Pioneering the study of microbial rate processes

Selman A. Waksman was born on 22 July 1888 in Nova Pryluka (now Vinnytsia Oblast) in what is presently the Ukraine. After completing his early studies, he immigrated to the

United States in 1910 and became a naturalized American citizen 6 years later. Waksman received his PhD in biochemistry from Rutgers in 1918 and joined the faculty of the Rutgers Department of Agriculture soon thereafter. He remained at Rutgers for his entire career.

In 1930, Henry Bigelow, secretary of the founding committee of WHOI, invited Waksman to join the new institution and establish a program in marine bacteriology. Waksman accepted, and from 1931 to 1942, he and his students and colleagues spent their summers in Woods Hole, conducting research on marine bacteria from the new WHOI research vessel, R/V *Atlantis*.[6] When he started working on marine bacteria, for more than a decade he had been conducting research on soil actinomycetes that led to the discovery of streptomycin (Schatz, Bugie, and Waksman 1944) and his Nobel Prize in 1952. His first research paper in marine microbiology was published in 1933 (Waksman and Carey 1933), and he went on to author a total of 18 publications in marine bacteriology, the last appearing in 1943 (Waksman, Johnstone, and Carey 1943). During his decade in the marine field, he continued to conduct research in soil science back at Rutgers. He maintained a home in Woods Hole, dying there in 1973.

On arrival at WHOI, he set about laying down the basic foundations of the role of bacteria in the sea both in the water column and the sediments. In doing this, his presumed familiarity with the Russian language suggests that he could take advantage of Eastern work in the field. One important aspect of Waksman's approach was that he, or more particularly his colleagues, conducted experimental research on the research vessel using samples taken and processed at sea. He commented that other workers had often worked with seawater that had been stored for days to weeks (Waksman 1934b). His focus was on two major aspects of the ecology of bacteria: the process of organic decomposition and the nitrogen cycle. The former attracted most of his attention. We focus on his research on decomposition because it also contains his discoveries and speculations on the roles of marine bacteria in the plankton, as we describe subsequently.

The initial work was directed toward determining the physiological scope of bacterial decomposition. They (Waksman et al. 1933) examined the basic biochemical components of zooplankton and algae and followed their decomposition by measuring CO_2 and NH_3 release. In these experiments, Waksman made early contributions to the stoichiometry of bacterial growth and decomposition activity. About decomposition of zooplankton, he wrote: "Their decomposition of these substances that are low in nitrogen or are totally free from nitrogen will not only not result in any ammonia liberation but may actually result in ammonia consumption by bacteria for cell synthesis" (Waksman et al. 1933, pp. 57–79). Further on, he observed: "The same law seems to hold true also for the decomposition of algal residues in the sea" (p. 66).

These relationships were already well known in soil ecology (Waksman 1916a, 1925); however, Waksman may have also been influenced by Alfred Redfield, another of the original

6. Waksman suffered terribly from sea sickness, and after his second—and last—expedition, Bigelow excused him from the otherwise mandatory summer cruises.

Bigelow appointees to WHOI. Redfield cites work from *Atlantis* cruise 15 (one of the early cruises that Waksman suffered through) as the basis for his famous paper on the fixed ratios of carbon, nitrogen, phosphorus, and oxygen (Redfield 1934).

Waksman's group isolated bacteria capable of degrading the plant constituents—cellulose and hemicellulose—from seawater organisms and sediments. They returned to this general theme in a later paper (Waksman et al. 1938) directing their attention to nitrogen-containing organics and also bacterial relationships with diatoms (Waksman, Stokes, and Butler 1937). In Waksman and Carey (1933), they noted Krogh's (1931) finding that "the organic matter in solution is greatly in excess over that present as plankton; this organic matter… which is not readily available for animal nutrition, and only to a limited extent to bacterial development." They reaffirmed this: "Sea water is a rather poor medium for the growth of bacteria, while the marine bottom is comparatively richer in the total number of bacteria capable of developing on the plate and in solution media" (Waksman et al. 1934b, p. 524).

They were later (Waksman and Carey 1935b) to depart from this unqualified view of the water phase being a poor environment for bacterial growth.

This, and other early work, is summarized in two reviews where Waksman (1934a, p. 528) noted: "The distribution of bacteria in the sea is thus found to be controlled by a number of factors, which are of primary importance in the cycle of life in the sea. In their turn, the marine bacteria contribute an important share to the plant and animal life in the sea, through their activities in the processes of mineralization of organic residues, and in the transformation of various elements and compounds." He also makes the point very strongly that "it is not merely sufficient to isolate an organism, cultivate it and determine what it does in pure culture; it is far more important to determine what it does in its natural substrate and how these activities dove-tail with the activities of other bacteria, as well as with the whole complex mass of higher plants and animals" (Waksman 1934b, p. 38). This principle directed his subsequent work. In his review, Waksman (1934b) illustrates his current understanding of the flows within the marine system. Figure 3(a) shows bacteria as a biological dead end for organic flux in the water column—implying their role was to contribute to the marine humus in the sediments. However, in the accompanying Figure 3(b), we are given a very much more modern view where bacteria are shown redirecting organic detritus back into the food web.

In the papers subsequent to these reviews (Waksman and Carey 1935a, 1935b; Waksman and Renn 1936), they directed their attention more to rate processes. Like Keys, Christensen, and Krogh (1935), Waksman and Carey examined the rates of oxygen consumption and ammonia production in whole and fine-filtered water—they noted the close parallelism between oxygen uptake and ammonia release. The oxygen consumption of the filtered sample (presumably mainly bacteria) accounted for 60% or so of that of the unfiltered sample—broadly similar the findings of Keys, Christensen, and Krogh (1935) and the later work of Pomeroy and Johannes (1966, 1968).

In a paper published in 1935, Waksman and Carey (1935b) address a number of matters. The most significant, in the present context, is that they used the oxygen consumption rates

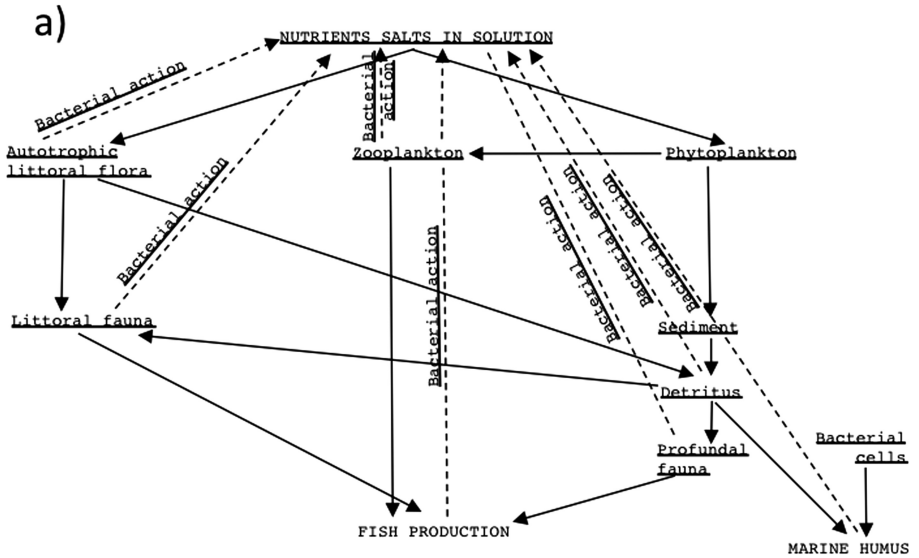

CHART I. PLANT, ANIMAL, AND BACTERIAL RELATIONSHIPS IN THE SEA

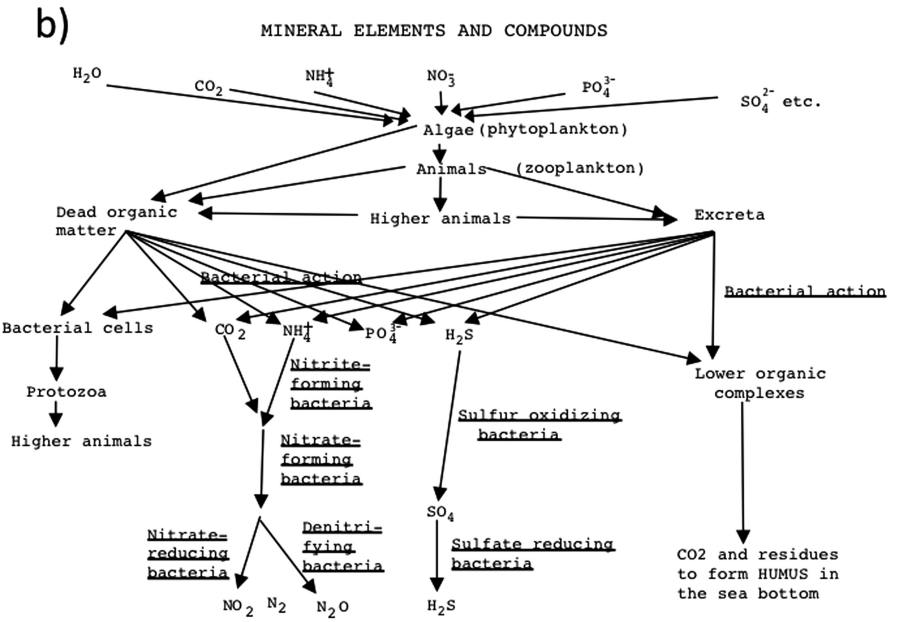

CHART II. RÔLE OF BACTERIA IN THE CYCLE OF LIFE IN THE SEA

Figure 3. Waksman's conceptual models of bacteria in the sea. (a) The general relation of the bacterial activities to the interrelationships of plants and animals in the sea and to the various degradation products. (b) A more detailed analysis of the specific marine processes in which bacteria are chiefly concerned. Reproduced from Waksman (1934b, The role of bacteria in the cycle of life in the sea, Sci. Mon., *38*, 35–49, Charts I and II, p. 37) with permission from American Association for the Advancement of Science.

to obtain an estimate of the labile DOM in the sea of about 0.5 to 1 mg C L^{-1}, at least 25% of the total DOM by their estimate. This left them (as others of the time) in something of a quandary—how to square this with the apparently low abundance of bacteria in seawater given by the methods they used, coupled with the very reproducible rise in bacterial numbers returned by plate counts. Their explanation is interesting; they proposed the following:

> The most important and crucial question may now be raised. Since extensive bacterial multiplication can take place in sea water, when some of it is enclosed in a glass vessel and allowed to remain undisturbed, why does the same process not occur in the sea itself, under natural conditions? No definite answer can as yet be given to this question until more is known of the factors controlling and favoring bacterial development in the sea …
>
> Under natural conditions, the organic matter in the water is in a state of equilibrium between formation and decomposition … [by the] consumption of the bacteria by protozoa, copepods and other marine animals … When sea water is placed in a glass container, the animals rapidly die out; … These modifications, however, are sufficient to enable the bacteria to begin to multiply rapidly and utilize the organic substances present in the water both in suspension and in solution. The relatively large amount of organic matter found in solution in sea water may, therefore, not be due merely to its absolute stability, but to the fact that the specific conditions are not favorable for rapid bacterial multiplication. (Waksman and Carey 1935b, p. 558)

They did not test the suggestion that the increase in bacteria abundance was a result of the reduction of protozoan grazing pressure, a consequence of damage of these organisms during the handling of the sample.

The paper published in the following year (Waksman and Renn 1936) is a remarkably modern piece of work. In it they determine oxygen production and consumption rates in order to address a complex set of issues surrounding respiration and also its links with photosynthesis. Unfortunately, they used incubation times of five or more days, so there is a degree of uncertainty over the exact interpretation of the observations. The point, however, is that it reveals the move of Waksman and his group's interest to environmental rates and demonstrates their adherence to his insistence that the bacteriological studies need to lead to an understanding of in situ circumstances and processes. In a multifactorial study, they investigated the nitrogen requirement of decomposition, finding that the decomposition of the in situ DOM was not limited by nitrogen, but if glucose was added at concentrations of 1.5–6 mg L^{-1}, then a nitrogen supplement was needed—another observation well known in soil work. They also reaffirmed that nitrate was as suitable an N-source as ammonia for the bacteria.[7]

In another elegant study they determined the changes in respiration rate as photosynthesis progressed. They then turned to measuring the changes in the rates of respiration with depth

7. This was rediscovered 50 years later by Wheeler and Kirchman (1986) in a highly cited paper (353 citations).

and season in samples from shelf-sea waters (the Gulf of Maine and the Georges Bank), showing a summertime (August) maximum in respiration rates and a decline in autumn (November). Finally, they report the changes in surface (5 m) respiration rates along a transect from Cape Cod to Bermuda, noting the significant fall in the oxygen consumption rate as Bermuda was approached.

It is unfortunate that Waksman made no summary of this later work. Mills (1989) in his history of biological oceanography only gives Waksman brief mention. Waksman and his group addressed marine bacterial processes in nearly 20 papers on water column and sediment processes studied at sea and in the lab in just a single decade of study. However, they left the puzzle unfinished—they did not follow up on their suggestion that removal of grazing pressure was the basis for the increase in bacterial numbers upon collecting and containing samples. This seems surprising as Waksman was surely aware of the importance of bacterivory in soil (Waksman 1916b). If they had, one might speculate that they would have laid the foundation for a comprehensive theory of microbial oceanography. As it was, they studied marine bacteria from a mostly biogeochemical perspective, 30–40 years or so before this approach was commonly adopted, with measurements of oxygen consumption, carbon dioxide, and ammonium production rather than focusing on the biological dynamics of bacteria and their predators. As we discussed previously, they were hampered by refusing to accept the evidence that bacterial populations in seawater were orders of magnitude greater than indicated by plate counts. Hotchkiss and Waksman (1936) provided a rigorous comparison of direct counts and plate counts, but it is not clear from the description of methods what techniques (e.g., filtration, staining) they used for direct enumeration. As far as we are aware, commercially manufactured membrane filters were not available in the United States at that time. Waksman's contribution was moving the field from defining states (static representations of microbial populations) toward measurements of key rates of marine microbial processes.

Waksman left surprisingly little lasting influence on the field, at least as indicated by citation analysis (Fig. 4). His 18 marine papers (both Waksman and ZoBell published in other fields throughout their careers) published during his brief stay in Woods Hole have accumulated just 404 citations since 1933, an average of fewer than 5 citations per year. Currently, his marine papers are cited just two or three times each year. The reasons for his weak citation support are not obvious. Possibly, it is a consequence of leaving the marine field and returning to soil microbiology; as a result, he had no more publications to draw attention toward his early work. His citations are far outshined by ZoBell's publications in the same period. We next turn to considering ZoBell's research.

d. The ZoBell era: Return to the study of bacterial states

Whereas one might be inclined to regard Waksman as the father of marine microbiology, Claude ZoBell (1904–1989) was undoubtedly the most influential marine microbiologist of his time, at least in the West. ZoBell joined Scripps Institution of Oceanography as its

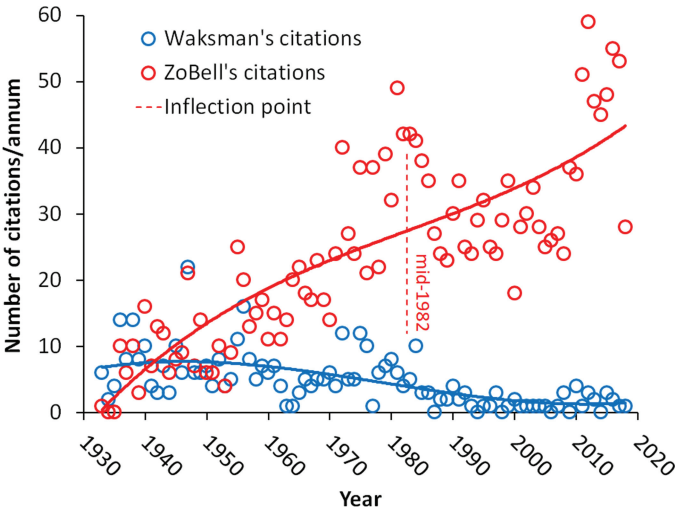

Figure 4. Analysis of citations of Waksman's 18 marine papers (1933–1943) and ZoBell's 30 marine papers for the same period (data from Web of Science). The lines are a third-order polynomial fit (Waksman, $R^2 = 0.36$; ZoBell, $R^2 = 0.66$).

marine bacteriologist in 1932. He wrote a highly cited monograph, *Marine Microbiology: A Monograph on Hydrobacteriology* (ZoBell 1946). His influence today, as judged by citations of his work, is greater than it has ever been (Fig. 4). He investigated the physiological requirements of bacteria for the major ions present in seawater, nitrogen cycle transformations, and chemolithotrophic bacteria. In his book, ZoBell (1946, p. 137) provided a diagram of the carbon cycle in the sea (Fig. 5) in which the bacteria connect with more or less everything else but with no indication of even the relative scale of the various processes.

Earlier, in the 1930s, ZoBell and Anderson (1936) cited recent work by Waksman (described previously) and other earlier papers on the growth of bacteria in contained samples (Whipple 1901; Foyn and Gran 1928). ZoBell's model was based on the results of experiments in which bacterial abundance was measured daily over time in containers of various sizes, with correspondingly different surface to volume ratios (Fig. 6). They found that bacteria grew to higher densities in the smallest volumes, with the highest surface to volume ratios, as had also been observed in the earlier studies. Combing these results with observations of the apparent paucity of bacterial cells in the water column, they concluded that concentrations of DOM in the water were too low for bacterial cells to access. Certainly, they were significantly lower than what was formulated in laboratory media. In this view, free-living cells in the water column could not realize sufficient growth to attain the high abundances observed in soils and marine sediments. ZoBell regarded the dominant fraction of bacteria instead to flourish on surfaces, hypothetically exploiting enhanced concentrations of organic matter adsorbed there, where it accumulates to (unspecified) levels at

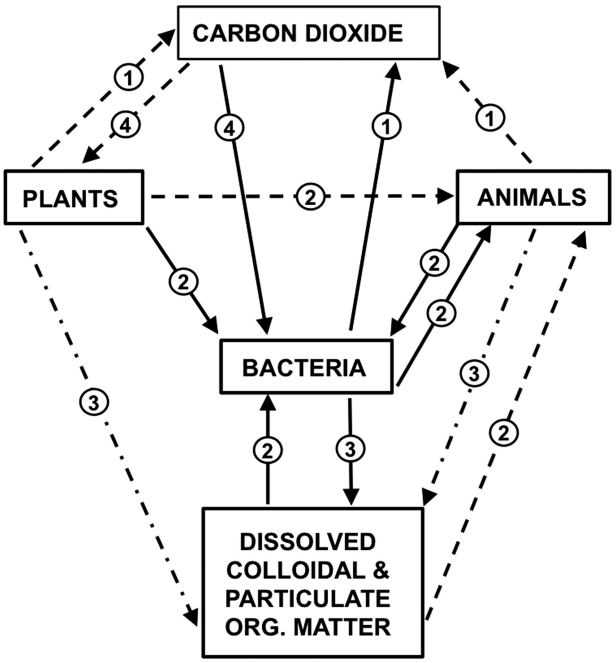

Figure 5. Zobell's diagram of the carbon cycle in the sea, from his *Marine Microbiology* treatise. Solid lines represent processes in which bacteria exclusively participate, dot-dashed lines represent processes in which bacteria may participate, and dashed lines represent processes in which bacteria do not participate. Respiration (1), nutrition (2), decomposition (3), and CO_2 fixation (4). Reproduced from ZoBell (1946, Marine Microbiology, Waltham MA: Chronica Botanica, fig. 10, p. 137). Chronica Botanica publishers no longer exists and no Rights outlet could be found.

which it becomes accessible for bacterial uptake. He asserts in the introduction of his 1943 paper that "it follows that any factor which tends to concentrate the organic matter would promote bacterial activity" (ZoBell 1943, p. 39). From his hypothesis, it follows that most marine bacterial activity would be found on surfaces, and little, if any, in the surrounding seawater. The ZoBell model was consistent with the reports of very low numbers of bacteria in seawater, obtained from agar plate colony counts (often on organically rich ZoBell 2216E medium) ranging from less than 10 to thousands of colony forming units (CFUs) per milliliter (Sverdrup, Johnson, and Fleming 1942; ZoBell 1946). In contrast, there were 10,000–100,000 CFUs g^{-1} in sediments, consistent with the large particle surface areas and high amounts of organic matter in sediments. ZoBell's surface model (Fig. 7) was depicted in his most highly cited review paper (ZoBell 1943; 625 citations). ZoBell's model was essentially qualitative, and, to our knowledge, its physico-chemical validity has never been examined.[8]

8. We note the comment in Purcell's (1977, p. 3) famous essay "Life at Low Reynolds Numbers" that "this world (i.e. the bacterial world) is quite different from the one we have developed our intuitions in."

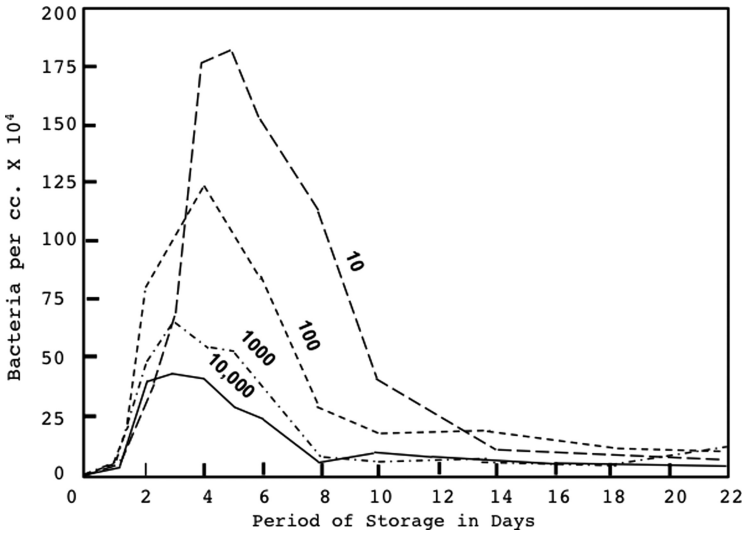

Figure 6. The influence of incubation volume on the multiplication of bacteria in stored seawater. The numbers on the lines are the volume of the incubation vessels in milliliters. Reproduced from Zobell and Anderson (1936, Observations on the multiplication of bacteria in different volumes of stored sea water and the influence of oxygen tension and solid surfaces, Biol. Bull., *71*, 324–342, fig. 1, p. 326) with permission from The Lancaster Press.

Already in the late 1940s there were suggestions of inconsistencies in what one might term the "ZoBell's model." As outlined previously, the model derived extensively from the study of ZoBell and Anderson (1936). Taylor and Collins (1949) found the matter to be more complex than ZoBell's description, in that that the nature of the glass of the bottle used for the experiments was critical. They observed increases in bacterial numbers in bottles manufactured from older forms of glass—Bohemian glass (potash was used in its manufacture) and soda glass (soda ash was used in its manufacture). These additions, part of the manufacturing process, brought along contaminants. By contrast, water samples incubated in purer, more modern forms of glass—borosilicate glass (e.g., Pyrex) and fused silica—showed no increase in numbers. ZoBell and Anderson referred to using Pyrex glassware; thus the nature of the glass could not be the cause of the difference, and so we are left with a fundamental and unresolved difference between ZoBell's findings and those of Taylor and Collins. The latter additionally reported that the rates of oxygen consumption (presumably in borosilicate bottles) showed no dependence on the size of the container, which is not consistent with the effect of container size on the growth of a bacterial population on containment—a central part of ZoBell's concepts. Similar observations of the lack of influence of the surface to volume ratio of the container on oxygen consumption of water samples were made in an elegant study by Romanenko (1969).

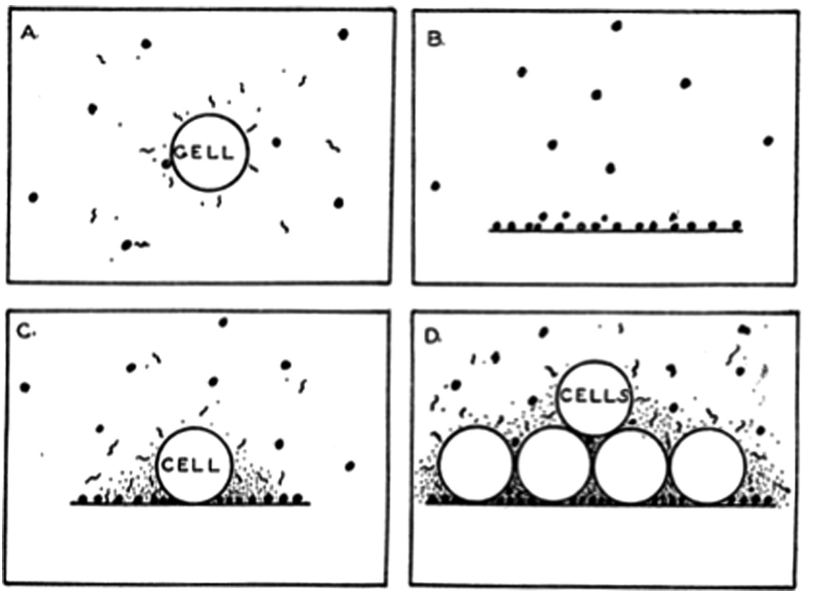

Figure 7. ZoBell's conceptual model of the growth of bacteria attached to a surface. (a) A free-floating bacterial cell surrounded by a few suspended particles of food (dark circles) that must be hydrolyzed by the exoenzyme (helicoidal lines) before the resulting hydrolyzates (dots) can be ingested and assimilated. (b) Particles of food concentrated in a monomolecular layer on a solid surface. (c) Food particles are more available to the cell on the solid surface where the interstices at the tangent of the bacterial cell and the solid surface retard the diffusion of exoenzymes and hydrolyzates away from the cell. (d) Multiple cells form additional interstitial spaces. Reproduced from Zobell (1943, The effect of solid surfaces upon bacterial activity, J. Bacteriol., *46*, 39–56) with permission from the American Society of Microbiology.

In their carefully couched summary, Taylor and Collins (1949, p. 33) noted that ZoBell's arguments were "not wholly consistent" and that "we have no evidence that an increase in surface area in relation to the volume of the container increases the amount of organic matter decomposed, as would be expected if ZoBell's theory were correct." They they cautiously concluded that "ZoBell's hypothesis of the adsorption of organic matter on the walls of the container has not been confirmed; and it cannot be entirely refuted" (p. 41).

The Taylor and Collins paper, although being published in a major bacteriological journal, had little to no influence on the thinking of Western marine microbiologists (13 citations since 1949). Thus, despite questions about ZoBell's proposal, the hypothesis of the so-called bottle effect (i.e., explosive growth of bacteria on containment, related to surface area) was widely accepted and gave rise to a disinclination within the community to accept the outcome of studies of in vitro measurements of oxygen consumption rates (see Williams 1970, p. 869; see quotation in Section 4d).

ZoBell's conceptual model of the ecology of bacteria in the seas dominated Western marine microbiology until well into the 1960s. ZoBell's influence reached well beyond marine microbial ecology. His work virtually created the now enormous field of bacterial biofilm research on surfaces (Bertoglio et al. 2018), including, for example, studies of marine biofouling (Moser et al. 2017), dental microbiology (Wirthlin, Marshall, and Rowland 2003), and the global plague of plastics pollution (Oberbeckmann, Kreikemeyer, and Labrenz 2018).

However, his immediate influence on the field of ocean bacterial ecology was to stifle consideration of the scale of bacterial activity in relation to other components of the plankton because of the great attention directed to bacterial proliferation in bottles and on other surfaces. There is a revealing transcript of a discussion that followed a paper presented by Crawford at the 1971 Belle W. Baruch Coastal Research Institute's Symposium on Estuarine Microbial Ecology. To a question about comparing phytoplankton and bacterial production rates, influential microbiologists and biological oceanographers of the time (notably ZoBell and Stanley Watson, Waksman's successor at WHOI) were clearly disinclined to regard bacteria as being important:

> WATSON: "I have always assumed that the bacteria were not responsible for recycling more than 1–10% of the total organic carbon produced by plants … It is very difficult to believe bacteria could be responsible for recycling 50% of the organic matter, at least in the oceans as a whole. Dr. ZoBell, you must have thought about this for a long time. How important are bacteria in the ocean?"
>
> ZOBELL: "I have spent a few minutes thinking about this and working on it … Annual production of bacterial biomass is of the order of 10^6–10^7 tons per year in the oceans at large. This is a lot of bacterial biomass. Ten million tons is quite a bit of animal food. However, when compared with a primary production of the order of 10^{10} tons per year, it is only a small fraction. These data are for the oceans as a whole …"
>
> WATSON: "What percent of the energy captured by the plants is being utilized by the bacteria? Is it more than 1%?"
>
> ZOBELL: "I do not think so because there are so many predators, so many kinds of animal that are eating plant material. I do not think it is anything like 1%." (Stevenson and Colwell 1973, p. 173)

Besides revealing that ZoBell and others had no clear concept of the cycling and reuse of organic carbon in food webs, the aforementioned views are in sharp contrast with those of contemporary Western marine chemists and ecologists (e.g., Richard Dugdale, Lawrence Pomeroy, John Strickland, and Tim Parsons, among others) who were quite prepared to accept bacteria making a major contribution to overall organic flux and nutrient regeneration. They were also at variance with a contemporary statement by the Eastern scientist Yurii Sorokin (1971a, p. 101), who in the opening sentence of a paper published in an English language journal, wrote: "It is clear at present that bacterial biosynthesis is one of the

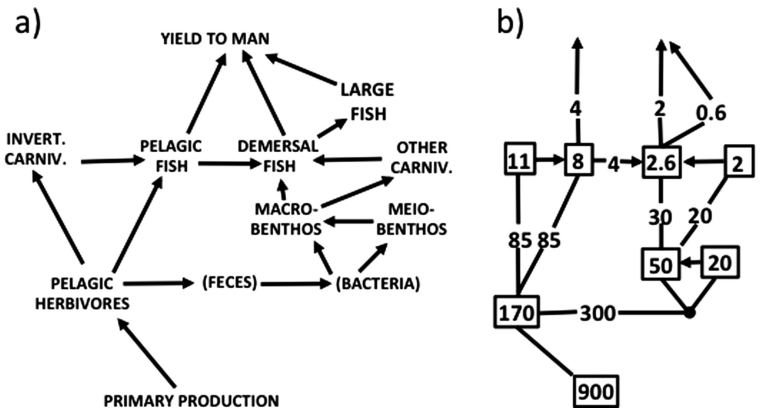

Figure 8. John Steele's conceptual models of planktonic and benthic fisheries. (a) North Sea food web based on the main groups of organisms. (b) Values for yearly production (kcal m^{-2} per year). Reproduced from Steele (1974, The Structure of Marine Ecosystems, Cambridge, MA: Harvard University Press, fig. 2.7, p. 20): Copyright © 1974 by the President and Fellows of Harvard College.

most important large scale processes in the transformation of organic matter in aquatic ecosystems."

ZoBell's view of the (lack of) importance of bacteria at the global scale derived from his understanding that there was very little surface area in the ocean remote from the coasts and sediments, as in the deep, central ocean basins. This model of the role of water column bacteria, or lack of it, was included in the classic monograph in oceanography, *The Oceans* (Sverdrup, Johnson, and Fleming 1942), showing its wide acceptance beyond the immediate field of microbiology. Interestingly however, Sverdrup, Johnson, and Fleming (probably Fleming, a physiologist) also presented a primitive concept of a microbial food web in the plankton. They postulated that grazers possibly constituted a check on the bacterial accumulations that would follow from exponential growth. This concept was well established in soil microbiology (Waksman 1916b). Sverdrup, Johnson, and Fleming also stated explicitly that bacteria were likely key agents of the decomposition of the large amount of total primary production by phytoplankton, seaweeds, and green plants in the world ocean. However, they failed to resolve this idea with the almost infinitesimally low abundance of bacteria in the open sea. They knew that the primary production did not accumulate over annual timescales. This small bacterial population would have to be growing at extraordinarily rapid rates to maintain a balance between phytoplankton production and heterotrophic respiration. Sverdrup, Johnson, and Fleming included a planktonic bacterial component in their conceptual model of plankton carbon cycling in the sea, but its role was left unspecified. As a consequence, all the decomposition needed to occur at the seafloor, mostly in the deep ocean, despite the constraints set by high pressure and low temperature.

In summary, ZoBell's influence was twofold. On one hand, his studies on bacterial relationships to surfaces created a new major field of study ranging from ship hulls to teeth.

This influence is still being felt in marine ecology. On the other hand, the success of the surface model, along with ZoBell's (and for that matter Waksman's and Krogh's) resistance to embrace the higher bacterial abundances indicated by the Eastern direct counts, served as a serious obstacle to recognizing the importance of bacteria in the economy of the sea. Significant bacterial activity was relegated to the sediments as late as 1974, when John Steele's *The Structure of Marine Ecosystems* did exactly that (Fig. 8).

3. Marine microbiology in the East

a. Early eastern work on bacterial abundance—1930s to 1950s

As we have shown, the American and much of the Western European communities of marine microbiologists were strongly influenced by the techniques and procedures employed in clinical bacteriology, notably the plate count technique and Robert Koch's postulates—that is, emphasis was placed on the isolation and identification of the bacteria (ZoBell 1946). The Eastern community—and to an extent some parts of the European community (notably the Netherlands)—adopted a more holistic approach. A number of the great names in geomicrobiology—Vasily Dokuchaev (1846–1903), Martinus Beijerinck (1851–1931), Sergei Winogradsky (1856–1953), Vladimir Vernadsky (1863–1945), and Cornelius van Niel (1897–1985)—all originated from east of Greenwich. Vernadsky's epochal book *The Biosphere*, published in Moscow in 1926, was translated into French and published in Paris in 1929, but it was not until some 70 years later that the full text was published in English (Vernadsky 1998). Eastern marine scientists seemed to have adopted systems thinking well before their Western counterparts. Thus, perhaps Eastern research in marine microbiology followed a very different route from the studies in the West. In the late 1940s–1950s, as the emphasis in ecology shifted from autecology to synecology (Odum 1953), the Eastern work and perspective became very relevant. However, probably because of a combination of a language barrier and lack of ready availability of Eastern journals, this work was missed by all but a few Western (mostly German and Dutch) scientists.

Unlike their Western counterparts, the Eastern marine microbiologists largely discounted the numbers derived from plate counts and placed greater credence in those derived from direct microscopic counts. In his early review of the role of bacteria in the sea, Waksman (1934a) refers to Cholodny's (1928, p. 43) work: "The plate method may thus give an unbalanced picture of the bacterial population of the sea. To meet these objections, Cholodny and others suggested the use of a direct microscopic method. This method has certain advantages, since it gives a more correct picture of the abundance of bacteria in the sea; however, it does not enable one to distinguish the living from the dead bacteria or to separate the various types of organisms for further study of their physiological characteristics." Waksman nonetheless stayed firmly in the agar plate count camp. The reason, at least in his case, clearly was not because of ignorance of the other methods. A major factor could have been that the marine microbial research of his group up to that time was centered on

autecological questions that did not call for information on bacterial abundance, so there was no need to invest time and resources developing the method.

It was Cholodny's (1928) development of membrane filters that enabled the Eastern work on direct counts of bacteria in aquatic systems. His filters were made from nitrocellulose (colloidion), as are Millipore, Sartorius, and like filters today—reputedly in the Eastern case from movie film stock. In Cholodny's initial procedure, the sample above the filter was stirred during filtration producing a concentrate that was then deposited on a slide and counted. Jannasch and Jones (1959) give an illustration of the setup used. By the time of Razumov's work in the early 1930s, the early Eastern microbiologists shifted from Cholodny's original procedure of working on concentrates to staining and viewing the organisms directly on the filters. Developmental work on the filters was undertaken by Razumov (1932) and Dianova and Vorosshilova (1932). In his paper, Razumov additionally made comparisons of numbers from plate and direct counts and found that whereas the former gave numbers of typically 10–100 cells mL^{-1}, direct counts gave number abundances of 10^5–10^6 cells mL^{-1}. He further noted that the ratio of the counts given by the two different methods was neither constant nor showed any systematic variations with place and time.

The first measurements by the Eastern aquatic microbiologists we are aware of that used direct microscopic counts in offshore waters come from studies in the Caspian Sea and the Sea of Azov by Butkevitch (1938). Using "homemade" colloidion filters, he obtained 150–350 $\times$ 10^3 cells mL^{-1} for the Sea of Azov and 100–500 $\times$ 10^3 cells mL^{-1} for the Caspian. In the case of the latter location, he converted the numbers to wet biomasses obtaining values of 50–250 μg cells L^{-1}. He noted that the bacterial biomass on average did not differ considerably from that of the planktonic algae. All of this is broadly in accord with modern estimates.

Following World War II, there was a significant step-up in the scale of the Soviet work, which was maintained, indeed intensified, through the period considered by this review. There is a sense in these reports of a new young generation heading off in ships armed with new methods and concepts to explore the microbial world of the oceans. Starting in 1946, there was a series of studies of the large inland seas—the Black and the Caspian Seas. This was an era when academician Kriss, author of the book *Marine Microbiology—Deep Sea* (1959, English translation published in 1963), was influential in the Eastern community. Kriss's quantitative work, which naturally formed a substantial part of the book's content, was principally based on the immersed slide technique introduced by Henrici (1938) that gave bacterial numbers per unit area on an immersed microscope slide. These data cannot be transformed into numbers or biomasses per unit volume and so have little relevance to the present review. However, in chapter 5 of his book, which deals with the abundance of microbial populations and their biomass, Kriss reports in some detail the results of Lebedeva's (1953) studies in the Black Sea, Osnitskaya's (1954) work in the Caspian Sea, and Limberg-Ruban's (1952) work in the northwest Pacific. Additionally, in his first chapter (pp. 9–14), he explains the problem they faced with bacterial contamination of commercial filters and its resolution by the work of Rukina and Biriuzova (1952).

Table 3. Estimates of bacterial numbers and projected biomasses obtain by a number of Russian researchers reported in Kriss (1963).

Originator of data	Location of information in *Marine Microbiology*	Geographic location	Numbers as 1,000 cells mL^{-1}	Biomass (wet) as $\mu g\ L^{-1}$
Lebdeva (1953)	Table 79, p. 79	Black Sea	100–500	20–100
Osnitskaya (1954)	Table 88, Fig 83; pp. 321, 322	Caspian Sea	100–400	16–40
Limberg-Ruban (1952)	p. 331	Northwest Pacific	10–40	
Undeclared	Tables 89, 90; pp. 332, 337	Northwest Pacific	16–406	19–33

The results of the studies by the aforementioned workers are summarized in the Table 3. To our knowledge, the data reported by Limberg-Ruban (1952) for the northwest Pacific are the first data for bacterial numbers and biomasses using microscope counts for an oceanic area. The numbers of cells from Limberg-Ruban's study as reported by Kriss appear to be somewhat low—we have been unable to verify whether or not this is a transcription error.

Thus, in summary, the various studies by the Eastern marine microbiologists provided a range of 10–500 $\times$ 10^3 bacterial cells mL^{-1}, with estimated wet biomasses of 16–100 $\mu g\ L^{-1}$, which (taking dry weight as 25% wet weight, and carbon content as 40% of dry weight) transforms to 1.6–10 $\mu g\ C\ L^{-1}$. The data in Table 1 imply that, with two qualifications, they would make a significant contribution to the turnover of organic material in the planktonic system, and this is consistent with the calculations made by Kriss (1963, pp. 412–414).

The first qualification is that the calculation has to assume a growth rate. Although Kriss has a chapter on reproduction rates, they are derived from the rate of changes in numbers of cells attached to glass slides, and we have no idea how this relates to organisms freely distributed in the water. The second caveat surrounds the uncertainty over the fraction of the counted cells that are active, which had been a long-standing uncertainty. The stain normally used—the dye erythrosine—stains both living and dead cells. This was apparently addressed in the paper of Alfimov (1954), and Jannasch and Jones (1959, p. 128) commented: "After comparing the bacterial numbers and the oxygen demand of corresponding water samples, Butkevich and Butkevich (1936) concluded that a considerable portion of the bacteria must be present in the resting stage. However, Alfimov (1954) doubted the occurrence of many 'dead' bacteria in sea water and sediments." In 1958, the Eastern freshwater scientist Sergey Kuznetsov (1958) reported a dual staining technique that he claimed could distinguish living from dead cells and estimated that 10% of the counted cells were not living. His technique, as far as we are aware, was not extensively used or independently tested. The debate over what proportion of the total count was living cells did not start to be resolved until the introduction of microautoradiography and fluorescent vital stains (Francisco, Mah, and Rabin 1973; Hoppe 1976; Zimmermann, Iturriaga, and Becker-Birck 1978).

This closes one chapter of the Eastern work. In this period, Eastern microbiologists established themselves as integral members of ocean-going science teams. They also solidified the practice of relying on direct counts to define levels of bacterial abundance and began converting those measurements into estimates of biomass. In this way, they could start to

consider bacteria in marine food webs. In the 1960s, the main thrust of work shifted from the Institute of Microbiology at the Academy of Sciences in Moscow to the Shirshov Institute of Oceanography, also in the Academy of Sciences in Moscow, where the prime mover was Mikhail Vinogradov. Critically, this shift matched the general shift in ecological research from autecology to synecology, which looked for processes and quantitative rate estimates over description of species occurrence.

The work and writings of the leading Eastern marine organic chemist Boris Aleksandrovich Skopintsev (1902–1983) may be seen as a bridge between the two lines of study. Skopintsev commenced his work on the organic chemistry of marine ecosystems in the late 1930s and returned to it in the 1950s, publishing a series of papers on DOC distribution in the oceans (see reviews referring to his work in Skopintsev [1962b] and Skopintsev, Romenska, and Sokolova [1968]). Early in this period, Skopintsev (1962a) published a paper examining the long-term in vitro consumption of oxygen in seawater (biochemical oxygen demand)—studies of the type had been made earlier by Seiwell (1937) and Rakestraw (1947). Skopintsev (1966) took his observed rates of oxygen consumption further and apportioned them between the bacterial and zooplankton populations based on their relative biomasses reported by Sorokin (1962) and Yashnov (1962). The rates attributed to these two groups were comparable, although there were subtle differences in the depth distribution. The calculation was taken further in Skopintsev's (1972) review where he reports rates as average annual rates for the oceans—the water column total for bacterial respiration being 110 g C m^{-2} y^{-1}. ZoBell's contemporary estimate of the scale of annual production of bacterial biomass is of the order of 10^6–10^7 tons per year (see Section 2d); this converts to 4–44 mg C m^{-2} y^{-1}, more than a thousand-fold smaller. There are question marks over some steps in Skopintsev's calculation, and clearly it would be all too easy to dismiss the result as artifact of long incubation in glass bottles and, as such, worthless. However, in a very thorough analysis of short-term measurements of respiration, not subject to this criticism, Robinson (2008) estimated bacterial whole water column respiration ranging from 16 to 27 mmol C m^{-2} d^{-1}; using a mean of 20 mmol C m^{-2} d^{-1}; this converts to 88 g C m^{-2} y^{-1}. One of course may argue that closeness is merely fortuitous. Right or wrong, Skopintsev's analysis provided the Eastern oceanographic community with the justification and need to incorporate bacterial processes in their understanding and models of the marine food chain and so in principle gave direction for their work in the late 1960s, which we consider next.

b. Founding of dynamic marine microbiology in the East, 1960 to early 1970s

Trophodynamics, as a way of viewing ecosystems, grew in influence in the early 1950s through to its establishment as the primary approach by the 1960s (Cook 1977). In this section, we focus on Eastern efforts to model the trophodynamic system of the oceanic plankton, as a leading example of their growing mechanistic conception of the microbial food web, and on their efforts to produce data to help build the models.

The key figure in the development of Eastern marine microbial food web research was Yurii Sorokin (1927–2013). Sorokin suffered a childhood that one should be glad not to have experienced, although it was probably not wholly unusual for the times in Soviet society. The following has been extracted, with light edits, from a memorial written and kindly provided by his son Dmitrii:

> Sorokin's parents were Soviet civil servants who were placed relatively high in bureaucratic level when they moved to Urals. In 1937, when Yurii Sorokin would have been 10 years old, both parents were arrested at the peak of Stalin's repressive campaign. His father was consigned to infamous Kolyma GULAG camp in northern Siberia for 12 years. […] His mother, with her two children, was also placed in a concentration camp. It was poorly guarded and they managed to escape one night and hid during the war in a small village near Voronezh, illegally, as refugees hiding their identity. (D. Sorokin, "Memorial to Yurii Sorokin," unpublished manuscript, 2013)

In 1945 Yurii, who somehow managed to get through schooling, went to Moscow where he commenced his education as a biologist. Dmitrii writes: "He did not like to speak about that part of his life; I understood that it was extremely difficult in comparison with our modern standards. For example, he was nearly starving as a student, had to hide his real origin as a son of repressed parents, lived in a shower closet in a flat of remote relatives."

At that time, Moscow University's Department of Microbiology had just started to bloom. After finishing there in 1951, Yurii Sorokin became a PhD student at the Institute of Microbiology of the Russian Academy of Sciences, which was headed by one of Russia's foremost aquatic microbiologists—Sergey Ivanovich Kuznetsov, a founder of the field of geomicrobiology and author of *Introduction to Geological Microbiology* (Kuznetsov, Ivanov, and Lyalikova 1963). Kuznetsov provided him with a hydrobiology background and encouraged him to adapt and to modify the Steeman Nielsen ^{14}C method of measuring phytoplankton productivity. During that time, Sorokin started to develop a variant of the ^{14}C technique to determine in situ bacterial activity. After finishing his PhD in 1953, he was invited to head a laboratory of aquatic microbiology at the newly founded Institute of Biology of Inland Waters, located 350 km north of the Volga River, on the shore of the massive Rybinsk freshwater reservoir.

There he continued to explore the use of ^{14}C tracers to investigate planktonic processes and published a paper in 1958 in which he described a protocol for the ^{14}C measurement of phytoplankton productivity that circumvented excessive ship time being taken up on stations undertaking long in situ incubations of productivity rigs (Sorokin 1958). In the same paper, there is a brief report of the use of ^{14}C-labeled bacteria to determine their assimilation by invertebrates (*Daphnia* in this case). Sorokin's move to Rybinsk was fortunate for the development of his research: freshwater crustacean zooplankton are better suited for measurement of small, naturally occurring bacteria than many of their marine counterparts (Pace, McManus, and Findlay 1990). Sorokin further refined his method and described it

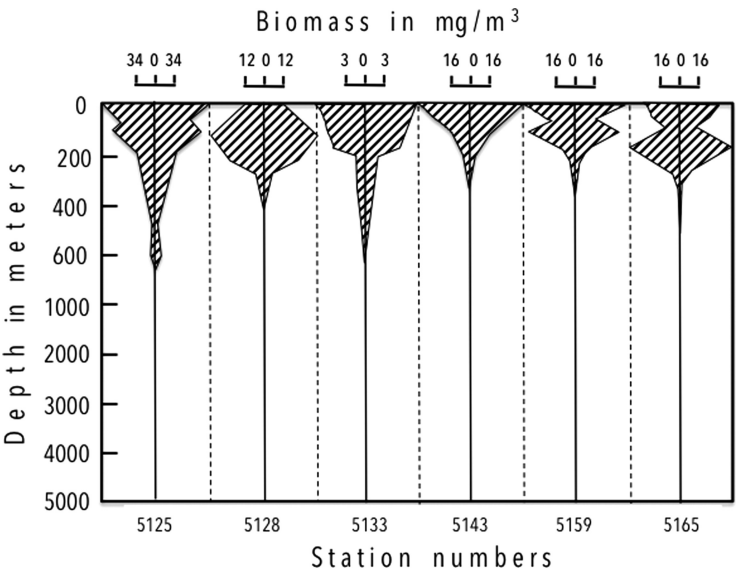

Figure 9. Distribution of wet biomass of bacteria in vertical sections from the water column of the central Pacific Ocean. Reproduced from Sorokin (1964b, A quantitative study of the microflora in the central Pacific Ocean. ICES J. Mar. Sci., *29*, 25-40, fig. 7, p. 32) with permission from Oxford University Press.

more fully in a later paper (Sorokin 1968). With this work, he entered a period of extraordinary scientific productivity (Sorokin 1960, 1962, 1963, 1964a, 1964b, 1967), extending his work on primary production and microbiology from freshwater to the offshore waters of the Pacific and Atlantic Oceans and the Black Sea. It is also notable that many of these early papers were published in Western journals, although frequently German-language journals.

In 1961, he participated in a 5-month study aboard the R/V *Vitjaz*, when he undertook a wide ranging quantitative study of the microflora in the central Pacific Ocean—both in the sediments and the water column as a whole. A summary of the work was published in the *ICES Journal of Marine Science* (Sorokin 1964b). The bacterial component of the study represented a transition from the classical plate count procedure to the direct count on membrane filters assessment and their projection to biomass (shown in Fig. 9). He discussed the microbiology of the whole water column and the sediments and concluded that "the greater part of the easily assimilated substance of the dead phytoplankton is oxidized by bacteria and eaten by zooplankton in the upper part of the water column. […] Only an insignificant part of the primary organic matter consisting of its most stable components reaches the deep water and participate there in the forming of the water humus" (Sorokin 1964a, p. 39).

Later, in an extensive paper, Sorokin (1968) gave a very detailed account of radiotracer (^{14}C) techniques he had evolved to determine the significance of zooplankton grazing on

bacteria, algae, and small animals, as well as the partitioning of the acquired food into growth, feces, respiration, and excreted DOC. The methodology had to take account of a number of complications—for example, the significant time offsets between linked processes such as between acquisition of the labeled food and its respiration and excretion. It was pioneering work well ahead of its times, sufficiently so that the late R. G. Wetzel took it upon himself to revise and rewrite the text for him. This work almost certainly led to the collaboration with biologists Petipa and Pavlova during the *Vityaz* cruise 44.

There was a further item in Sorokin's 1968 paper that has to be part of any consideration of his work and of its acceptance by Western researchers. He adopted a procedure devised by Romanenko (1965) that used the rate of dark $^{14}CO_2$ fixation (a component of the ^{14}C measurement of planktonic photosynthesis) to estimate bacterial respiration and growth. The Romanenko technique is based on the bacterial incorporation of CO_2 during anapleurotic metabolism. Romanenko (1965) and Sorokin (1966) had undertaken studies on $^{14}CO_2$ uptake and associated O_2 consumption with pure cultures of bacteria to obtain ^{14}C incorporated/oxygen consumption conversion factors. The two workers obtained broadly similar values. Sorokin adopted a factor of 150 (O_2 consumption as mass O_2 per unit of dark CO_2 fixation as mass) for his work. At that point in time, there was no available direct method for the determination of metabolic rates of natural bacterioplankton; thus how representative the conversion factor was for natural communities could not be ascertained.

In 1968/1969, Sorokin was involved in back-to-back cruises of the R/V *Vityaz* (cruise numbers 43 and 44) leading to an initial descriptive paper (Vinogradov, Gitelzon, and Sorokin 1970) that provided the biological calibration data for the model in Vinogradov, Menshutkin, and Shushkina (1972). From this extensive work, Sorokin (1971b) examined a number of aspects of microbial abundance and overall metabolism, the latter derived from the dark $^{14}CO_2$ fixation approach described previously. He found that in the open areas of the tropical Pacific Ocean, his estimate of overall bacterial carbon flux (respiration plus growth; the latter it would appear calculated from the respiration estimates using a C-based bacterial growth yield of 30%) was 2 to 10 times greater than the ^{14}C-determined photosynthetic production (Sorokin 1971b, pp. 10–11). Curiously, although the same dark fixation data were apparently incorporated into Vinogradov and Menshutkin (1977a), this feature is not seen in Vinogradov, Menshutkin, and Shushkina (1972) and Vinogradov (1973a, 1973b). The basis for the difference between the two findings is not clear, although there appear to have been additional constraints imposed on bacterial production in the models (see Vinogradov, Menshutkin, and Shushkina 1972, p. 263). Sorokin in his analysis argued that the shortfall between the measurements of phytoplankton production and bacterial consumption was because of an underestimation of photosynthetic rates by the ^{14}C technique. This would have ruffled some feathers; however, similar claims were made by a number of Western workers in that era and subsequently (Peterson 1980). For example, Gieskes, Kraay, and Baars (1979) argued at length for errors in the ^{14}C estimates of photosynthesis of a similar scale to those reported by Sorokin. Thus, although Sorokin's claims were contentious, they would not have been rejected out of hand at the time.

However, Sorokin chose to take the argument regarding the discrepancy to another level. He claimed that the difference in part resulted from a significant subsidy of in situ bacterial production by allochthonous organic material imported from underlying waters. Sorokin's argument was based on the proposition that at high latitudes, because of low temperatures, a significant proportion of labile organic production was not decomposed and was subducted and advected to lower latitudes, where it upwelled and supplemented the in situ productivity, thus enabling the community metabolism to exceed the input associated with local primary production. The concept was strongly criticized in a paper by Banse (1974). Banse argued that Sorokin's estimates could not be supported by observed local sources of DOM nor by remote (e.g., deep-sea) sources, because the necessary physical transport mechanisms do not deliver labile deep-water DOC in sufficient quantities. It is very likely that Sorokin's paper and his scientific standing may have suffered from this exchange, but it should be remembered that although he was wrong on this specific point, he was posing trophodynamic questions about bacteria in an oceanographic context.

In summary, although some aspects of Sorokin's work have been questioned, the more important point is that in an era when few in the West were even asking questions about the existence and importance of bacteria in marine food webs, Sorokin was actively borrowing and adapting existing methods and inventing new ones in an attempt to answer them.

There was a growing interest in Russia in the dynamics of the ocean and freshwater biology in the early 1960s (Sieburth 1960). A major stimulus to Soviet open-ocean biology came from a directive on 8 September 1967 from the Eastern Academy of Sciences that "rational utilization of the food resources of seas and oceans must be based on in-depth studies of the biological productivity of marine communities and recommends elaboration of methods for improving the ocean's biological productivity by controlling the transformation of matter and energy in the communities of marine organisms in the World Ocean" (Vinogradov 1973b, p. 2.). This directive gave rise to a major research expedition from December 1968 through March 1969 led by the late Mikhail Evgen'evich Vinogradov (1927–2007). Vinogradov was born in Moscow to a family of academics. He studied at the Institute of Energy and joined the Institute of Oceanology in 1952. Vinogradov devoted about 60 years to the science of the world ocean. For many decades, he headed Eastern biological oceanography being a recognized international authority among researchers of marine and oceanic ecosystems. In 1990, he was elected as a member of the Russian Academy of Sciences, and in 1998, as a full member of the Russian Academy of Natural Sciences. Much of his time was given over to scientific organizational activity. He was secretary general of the International Oceanographic Congress and a UNESCO expert on plankton.[9]

The research ship *Vityaz* was converted to an open-ocean experimental biology research platform specifically for the study. Vinogradov (1973a, p. 3) sketches the context of the research as "studies of the trophic relationships within a community, of the flow of energy through the biological system and its utilization on the different trophic levels … should

9. Biography extracted from the 2007 obituary in the journal *Oceanology* (*47*, 449–451).

run along two related lines: development of a theory and methods of controlling the terminal product yield in biological systems of coastal waters and development of a theory for controlling biological systems of the open ocean." In accordance with the general project, a detailed series of investigations of primary production and zooplankton physiology and ecology were undertaken during the cruise, notably including "studies of the trophic structure of plankton communities; determination of the production intensity of zooplankton; evaluation of the efficiency of utilization of energy flowing from the first trophic level; quantitative evaluation of metabolic processes in planktonic organisms" and "studies of the abundance and production of the microbial population and its role in zooplankton alimentation; studies of the ways of incorporating dissolved organic matter in the production process by bacteria (Vinogradov 1937, p. 3)." It was deemed that the nearest accessible region for their research was the tropical part of the Pacific Ocean south of the equator and west of 180° E; the Eastern researchers had earlier worked on the physics of the area.

In order to design and parameterize new food web models, Vinogradov brought together specialists from a number of Soviet institutes, in addition to colleagues from his own group. Alexey Andreevich Lyapunov, from Institute of Hydrodynamics of the Siberian branch of the Academy of Sciences, designed the primary computational structure. Vladimir Vasil'evich Menshutkin from the Sechenov Institute of Evolutionary Physiology and Biochemistry, Academy of Sciences of the USSR, Moscow, along with Vinogradov and Shushkina, put together the eventual model. Tamara Sergeevna Petipa and E. V. Pavlova, from Institute of Biology of the Southern Seas of the Academy of Sciences of the Ukraine SSR, Sevastopol, in conjunction with Yurii Sorokin, from the Institute of Biology of Inland Waters of the Academy of Sciences, were engaged in empirically determining the parameters for the biological model.

The *Vityaz* cruise was a major and diverse undertaking. Only a small fraction of the work (e.g., Vinogradov, Gitelzon, and Sorokin 1970; Sorokin 1971b; Vinogradov, Menshutkin, and Shushkina 1972) appeared in Western journals. We are fortunate that since the mid-1960s the Eastern journal *Okeanologija* has been routinely translated into English in the journal *Oceanology*, though inevitably with some delay. Even more valuable is that the original cruise report edited by Vinogradov was translated in its entirety under the title *Life Activity of Pelagic Communities in the Ocean Tropics* (Vinogradov 1973a). In his papers, Vinogradov gives the English version of the title as *Functioning of Pelagic Communities in the Tropical Regions of the Ocean*. This version features more highly in online searches.[10]

The study spawned a number of pertinent papers, notably those of Vinogradov, Petipa and Pavlova, and Sorokin. Whereas from our vantage point, we may see the concepts in these papers and their content as very modern for the times, their impact on the Western bloc

10. As the original Russian version and the translation were published on different dates (1971 and 1973), we refer to just the English translation in both the text and the references as we lack the page numbers for the original 1971 Russian language version. Much of what we discuss subsequently is abstracted from this latter publication, with additions from two later publications (Vinogradov and Menshutkin 1977a, 1977b), which describe and illustrate the work in greater detail and clarity.

oceanographic community (as judged from citations) and on Western biological modelers in particular was weak to nonexistent. We return to this point later in the article.

i. Parameterization of the models. Intensive and painstaking shipboard experimental studies were performed by the Eastern researchers to obtain data for model parameterization. Petipa, Pavlova, and Sorokin (1973) had produced a steady-state model for the epipelagic and bathypelagic zones of the Black Sea. In parameterizing their model, they undertook studies of the physiological and feeding properties of the zooplankton—for this they would have presumably used conventional chemical measurements (O_2 consumption, dry weight, and carbon mass). The analyses would have been time consuming and not ideally suited for the onboard work planned for the *Vityaz* expedition. Since the early 1960s in his studies of the dynamics of freshwater systems, Sorokin had been developing techniques, based on ^{14}C-labeled organisms and preparations, to measure a number of these properties. The techniques (described in detail in Sorokin [1968]) were applicable to marine systems and, although complex, when set up were feasible to undertake onboard a research ship. It would appear that the two groups pooled their skills in order to provide the necessary parameterization for the planned model. During the research cruise, the group undertook a major study of a number of aspects of the physiology of zooplankton feeding. The work included studies of the food spectrum of zooplankton species, the effects of concentration of food on intensity of feeding, and determination of the principal elements of the food energy balance.

ii. Parameterizing of bacteria as food for the zooplankton. Bacteria labeled with ^{14}C were supplied to various groups of zooplankton, and the daily rate of uptake was expressed as a percentage of the organism's biomass (C_{assim}/C % in their text). Altogether, some 26 different zooplankton animals were used; they were grouped by feeding mechanisms: filter feeders, mixed feeders, and what the authors termed "graspers." The utilization of bacteria as food was generally low: the range, expressed as C_{assim}/C %, was 0.01%–3%. However, in the case of the appendicularians, the contribution to the daily diet was very significant—the average uptake being 34%. The values for the mixed feeders ranged from 0.18% to 3.2%, and the uptake by the "graspers" was lower, ranging from 0.003% to 0.6%, with mean of 0.16%.

They made a short comparison of the rates of uptake by small calanoid copepods on free bacteria and bacteria aggregated on small particles—the rate of uptake of the latter was 10 times greater than the free-living cells. Sorokin (1973b) had demonstrated that some 20%–40% of the bacteria were in aggregates; thus 70%–85% of the assimilation of bacteria was associated with aggregates. They concluded: "Planktonic crustaceans which are mixed feeders cannot satisfy their food requirements (energy losses in respiration) by consuming only natural bacterioplankton at the optimum concentration of 0.1–2.0 g/m^3. Bacterial food alone is not sufficient for the normal functioning of these animals. Bacteria can satisfy the food requirements of only fine filter feeders" (Pavlova, Petipa, and Sorokin 1973, p. 3).

iii. Parameterization of the physiological features and outcomes of feeding. Pavlova, Petipa, and Sorokin (1973) and Petipa, Pavlova, and Sorokin (1973) made a detailed analysis of the fate of the food intake, separating out the various loss terms: respiration, production of feces, and excretion of soluble organic material (DOM). In this case, although the variability was considerable, the quantity of the data was such that the errors were comparatively small: DOM production, 4 ± 0.49%; growth, 15 ± 2.6%; respiration, 27 ± 3.3%; and fecal production, 54 ± 4.6%.

In Petipa, Pavlova, and Sorokin (1973, p. 153) the authors give an insightful summary of their studies:

> In the tropical regions of the ocean, with their relatively stable water masses, small biomass and large specific variety of the plankton, planktonic animals have a broad food spectrum and prefer relatively large forms, irrespective of their morphological adaptation to any specific kind of food and the mode of its capture. Animal food is obligatory for most zooplanktonic organisms. In its absence, their energy requirements are not satisfied even at high assimilation rates for plants and bacteria. The food spectrum of planktonic animals is usually narrower in the temperate regions, with their high plankton biomass, low specific variety and dominance of a single or a few kinds of food. Their energy requirements can be satisfied by plant and/or bacterial food alone.
>
> Therefore, the choice and consumption of specific kinds of food by planktonic animals in both the tropical and the temperate regions of the ocean depend significantly on the ratio between the concentration, variety, and partly the size of food items and consumers. Zooplankton consistently tends to be more omnivorous and predatory the higher the specific variety of the phytoplankton and zooplankton and the lower the total biomass.

This is a justification for the simple biological structure of temperate coastal plankton of the sort that Steele was soon to publish but also suggested that the same results could not be simply transposed to oligotrophic areas—not that it is at all likely that Steele would have contemplated this.

c. Evolution of the models

Vinogradov and colleagues sought to simulate the development and changes within the upper layer of the equatorial upwelling region with time and the resultant intensification of activity at particular depths through the water column. The conceptual model they used for the work is illustrated in Figure 10. Lyapunov (1973) developed a prototype model and reported on it in the cruise report. We find the later reports by Vinogradov and Menshutkin (1977a, 1977b) easier to follow. We have been unable to resolve some of the minor apparent differences in detail between the three accounts. Where there is an uncertainty we have used the Vinogradov and Menshutkin (1977a, 1977b) papers as our preferred sources.

The ecosystem is presented as an assemblage of interacting elements connected by trophodynamic fluxes or exchanges. Lyapunov's prototype is a classical depth- and time-resolved

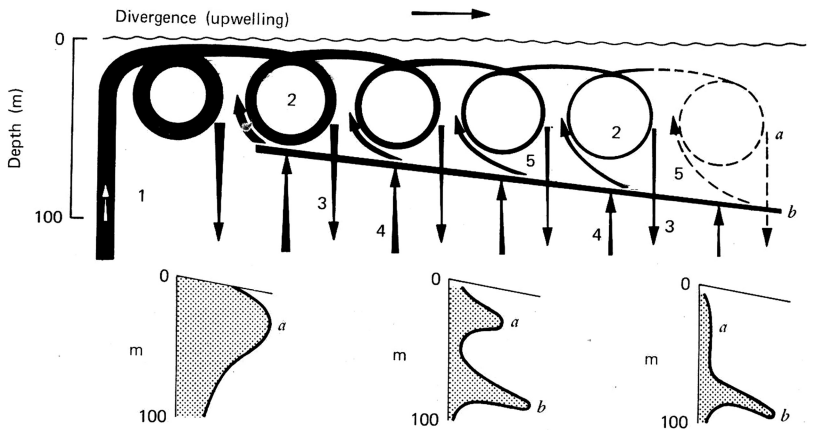

Figure 10. Vinogradov's schematic of physical and biological processes in an upwelling zone. (1) Ascent of nutrients and DOM in upwelling; (2) repeated use of nutrients and dissolved organic matter in the production-"destruction" cycle of a surface community; (3) loss of nutrients with sinking organic remains and migrating organisms; (4) turbulent diffusion ascent of nutrients with deep water and their retention in the layer of the maximum; (5) incorporation of nutrients carried up from layer of lower maximum by migrating organisms into the production cycle of a surface community. Bottom: changes in the vertical distribution of relative phytoplankton concentrations with distance from the zone of upwelling (*a*, upper maximum; *b*, lower maximum). Reproduced from Vinogradov, Gitelzon, and Sorokin (1970, The vertical structure of a pelagic community in the tropical ocean, Mar. Biol., *6*, 187–194, fig. 5, p. 193) with permission from Nature/Springer/Palgrave.

nutrient/phytoplankton/zooplankton/detritus model, similar to that of Steele (1974). Lyapunov's model, described in detail in Lyapunov (1973) and Vinogradov and Menshutkin (1977a), comprises six compartments: light, nitrogen in utilizable inorganic form, utilizable phosphorus, the biomass of phytoplankton, the biomass of zooplankton, and the concentration of detritus. The depth resolution was essential to reproduce the observed intermediate peaks in the depth profile of plankton biomass; time resolution was imposed by the time development of the upwelled water shown in their conceptual diagram (Fig. 10). It was assumed that detritus was formed from dying zooplankton and excreta with the quantity being proportional to the quantity of food ingested. The detritus was mineralized to inorganic nitrogen and phosphate with simple first-order decay functions. In the prototype model, there was no agent (i.e., a bacterial component) in the model to enable this process. However, Lyapunov cited Sorokin's (1973b) measurements of considerable bacterial production and concluded the following:

> Production of bacteria in the surface pelagic layers of tropical oligotrophic region is comparable to, and possibly even exceeds, the phytoplankton production. In this case, development of zooplankton is no longer entirely (or chiefly) limited by development of phytoplankton, as was assumed in the first variant of the model…How this limiting

> takes place, to what extent it depends on the composition of organic matter, and which of the latter components are critical, is obscure and calls for special investigation. Nevertheless it is obvious that an ecosystem model cannot be complete if it ignores the activity of the microflora and its role in the food chains. (Lyapunov 1973, p. 20–21.)

There were two further elaborations of the original Lyapunov formulation. The first (Vinogradov, Menshutkin, and Shushkina 1972) was derived from studies during the 1968/1969 *Vityaz* research cruise 44, and the second (Vinogradov et al. 1973) was based on data from the *Vityaz* expedition 50 in April to July 1971. The first of the two revised models was published in English in *Marine Biology* (Vinogradov, Menshutkin, and Shushkina 1972), and the second was translated from the Russian and published in the English version of the Russian journal, *Oceanology* (Vinogradov et al. 1973). The whole development of the three models is discussed in depth in a chapter of *The Sea*, volume 6 (Vinogradov and Menshutkin 1977a).

The two evolved models (a flow diagram redrawn from the 1972 paper is given in Fig. 11), as far as one can determine, differ only in small detail. The first (Vinogradov, Menshutkin, and Shushkina 1972) model incorporated the work of Petipa, Pavlova, and Sorokin (1973) and Sorokin (1973b), adding a bacterial component to mineralize the dissolved and particulate detritus. Vinogradov and coworkers subdivided the zooplankton into four components, based on size and feeding mechanism: (i) small "zooplankton" (protozoa, microzooplankton and small herbivores), (ii) large herbivorous zooplankton, and (iii) small omnivores and large carnivores. The later (Vinogradov et al. 1973) model further subdivided the zooplankton. The models were time- and depth-resolved to allow the development of the vertical profiles (Fig. 10). The models incorporated exchanges between vertically adjacent cell by turbulent diffusion, cannibalism within zooplankton categories, and also vertical migration in the case of the larger zooplankton. There was exchange between the bottom cell and the underlying water, but no lateral exchange in these two-dimensional (Z-T) models.

d. Output of the model

Figure 12 contains a comparison of the vertical distributions of biomass in the field observations and the model output. The general expectations of their conceptual model (Fig. 9) are realized—that is, (i) after the initial bloom, a progressive decrease in the total biomass occurs because of sinking loss to the deeper water, and (ii) there is the formation of one or two pronounced intermediate peaks in the vertical profile.

Despite the limitations on exact comparison between the model and field observations, general comparisons can be made. There are further cautions when comparing the biomasses of bacteria from cell counts and phytoplankton biomass from cell counts or chlorophyll. The conversion factors incur a high degree of uncertainty. (In the case of bacteria, the size of the organism is close to the limits of the light microscope, and in the case of a 0.5 μm diameter bacterium, an error on 0.2 μm would give a 300% error in the estimate of biovolume.) Given these cautions, the correspondence between the modeled and field observations within the

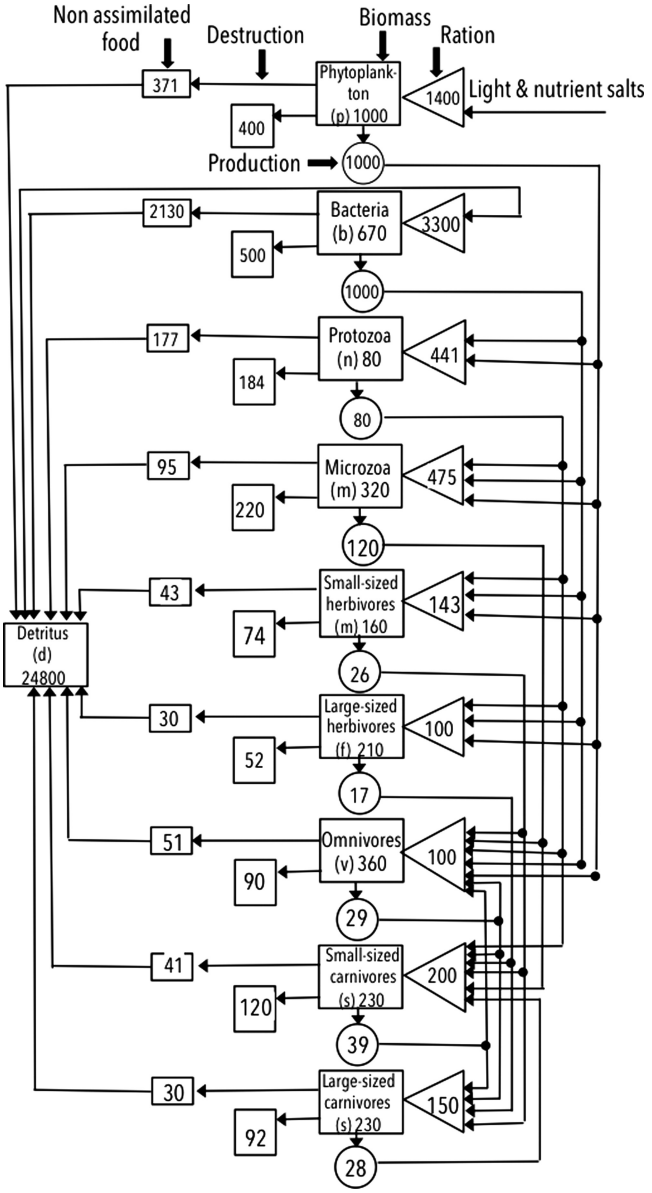

Figure 11. Block-diagram of energy flow (cal m^{-2} per day) through the community inhabiting the upper 0 to 200 m layer of the mesotrophic tropical areas of the ocean. Concentration magnitudes of each element listed were obtained at R/V "*Vityaz*" Station 6033 (04° S, 168° E; December 1969). Magnitudes of the rates of food consumption, production, exchange, and assimilation were determined from direct measurements made on the 44th and 50th R/V "*Vityaz*" cruises. More elements and relations are indicated than were incorporated into the model. Trophic relations within integrated elements (*m* and *s*) are considered as inessential. Microzoa on this diagram unite nauplii and copepodite stages of copepods. Reproduced from Vinogrado, Menshutkin, and Shushkina (1972, On mathematical simulation of a pelagic ecosystem in tropical waters of the ocean, Mar. Biol., *16*, 261–268, fig. 1, p. 262) with permission from Nature/Springer/Palgrave.

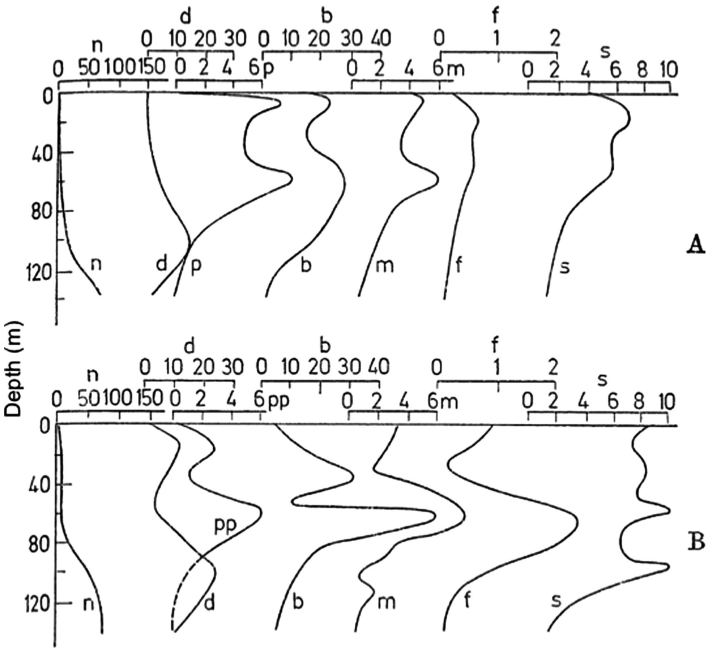

Figure 12. Comparison of the depth profile of field observations of biomass with the output of the Vinogradov et al. (1972) model at day 40. Note panel (a) (model data) reports the biomass of phytoplankton (p), whereas panel (b) reports phytoplankton production (pp). The letters accompanying the individual profiles refer to the biological groups in Figure 11. Biomass is expressed as cal m^{-3}; productivity, as cal m^{-3} per day; nutrients (n); and inorganic nitrogen, as mg N m^{-3}. Reproduced from Vinogradov, Menshutkin, and Shushkina (1972, On mathematical simulation of a pelagic ecosystem in tropical waters of the ocean, Mar. Biol., *16*, 261–268, fig. 4, p. 267) with permission from Nature/Springer/Palgrave.

major groupings shows no marked discrepancies. The biomass of the bacteria is comparable to the metazoan groups. With their smaller size, and potentially higher metabolic rate, the flux of organic material through to bacterial component probably far exceeds that of the other heterotroph groupings.

e. Conclusion

Vinogradov (1973a, 1973b, pp. 7–8) lists the main results of the study, which include the following: "The rate of consumption and assimilation of bacterioplankton … was shown (Sorokin, Petipa, and Pavlova) to be commensurate with the rate of its consumption of algae.

The use of radioisotopic techniques elucidated the quantitative characteristics of the energy balance of mass zooplankton species (phytophages, euryphages, predators) and permitted determination of not only the production of organic matter by algae (Koblents-Mishke et al.,), but also the production of phytophagous animals (Shushkina) and bacteria

(Sorokin)." He goes on (p. 8) to make the claim that "the investigations for the first time furnished a quantitative evaluation of the consumption and production of the principal trophic levels of the oceanic pelagic ecosystem and offered a novel view of certain crucial aspects of its functioning."

We have gone to some lengths to describe the Soviet models to make the point that they had fully conceived the microbial food web concept and represented it in numerical simulations starting some years prior to Pomeroy's seminal paper, accounting for lags between the original publications in Russian and eventual translations. Nonetheless, Vinogradov's most prominent paper published in the West (Vinogradov, Menshutkin, and Shushkina 1972) had seemingly little influence. To date, it has been cited just 35 times in 46 years. Nearly all the citations are to papers about zooplankton processes or primary production. Only six (including his own) are about microbes (Vinogradov 1973a; Williams 1984; Ducklow 1991; Legendre and Rivkin 2002, 2008, 2015). It is cited by neither Pomeroy (1974b) nor Azam et al. (1983). Azam et al. do cite three papers by Sorokin (Sorokin and Lyutsarev 1978; Sorokin 1979, 1981). Both of the Vinogradov et al. models incorporated essentially all the elements, published more than a decade later as the microbial loop (Azam et al. 1983); further, they demonstrated that collectively it was an operational and apparently essential system. Microbial processes were not addressed numerically by Western modelers until the continental shelf model by Pomeroy's colleague Mike Pace (Pace, Glasser, and Pomeroy 1984). Without explanation, John Walsh apparently saw little need to add a microbial component to his models of diverse continental shelf systems (Walsh and Dieterle 1986; Walsh 1988).

4. Challenges to the prevailing Western concepts and models, 1960–1970

We can look back from our vantage point and easily identify inaccuracies and shortcomings. However, the historical question is, when did contemporary scientists see evidence that the existing conceptual models were inadequate, and what were the barriers preventing adoption of new ones? Were there methodological limitations, or were there conceptual blocks, or both? How did they combine to retard development of a new concept?

There was evidence, starting in the 1960s, of clear deficiencies in the Western models that made it impossible to account for a number of key aspects of material flux within the oceanic plankton community. The growing recognition of these contradictions starting in the1960s with studies using radioactive tracers of organic compounds (Parsons and Strickland 1962) coincided with the transition toward synecological approaches in terrestrial and aquatic food webs started by the Odums at the University of Georgia in the 1950s (Odum and Odum 1955; Odum 1956, 1957). In the following sections, we outline some of the observations that led to questioning the conceptual model ("paradigm") held by the influential Western biological oceanographers at the time.

a. Evidence for lability of oceanic DOM

The early 1960s saw a revival of interest in the West about the concentration and dynamics of DOM in the oceans—the papers of Duursma (1961, 1963) and Menzel (1964) are the most significant. Both authors noted the constancy of DOC in deeper waters, below the euphotic zone. This essentially confirmed the earlier contention of Krogh (1934b) that the DOC in the oceans was turning over very slowly. Menzel (1964) very elegantly showed that the variability of DOC along isopycnals in the deep water of the western Indian Ocean was tightly correlated with salinity changes. The DOC concentrations for the deeper ocean water reported by Krogh (essentially 200 μM C L^{-1}) were substantially greater than those obtained by Menzel and Duursma; contemporary observations for deep water are in the range of 40–50 μM C L^{-1} (Hansell 2002, fig. 4, p. 714–715). The difference is a puzzle; if the problem lay with one of the two analytical techniques (DOC or DON), there would be a comparable difference between the DOC/DON ratio for Krogh's analyses and contemporary ones. However, this is not the case. The DOC/DON ratio of Krogh's data was 9.9 ± 0.55, and the ratio reported in the review by Bronk (2002) is 14.7 ± 2.8—the difference is far smaller than that between the concentrations (a ratio of 1.5 vs. 4).

However, matters are quite different in the euphotic zone. In the data reported by Duursma and Menzel, there is a distinct variability in DOM concentrations in the surface waters. Duursma (1961) had obtained DOC sections in the North Atlantic in the spring and autumn—the elevated levels and variability are very evident in the profiles shown; they are also present in his profiles of DON. He estimated a difference in concentration of about 0.6 mg C L^{-1} between April and September in the Gulf Stream region south of Greenland on top of a baseline the order of 0.8 mg C L^{-1}. Additionally, in a subsequent study, Duursma (1963) analyzed the seasonal changes for a station in the English Channel. He noted a distinct increase in DOC concentration in the summer period of about 1.3 mg C L^{-1} on top of a baseline of 0.8 mg C L^{-1}. His analysis of the seasonal profile suggested a flux of DOC of 2.6 mg C L^{-1} through the year. He assumed that if this occurred over a depth range of 20 m, it would give an annual DOC flux within that ecosystem of 52 g C m^{-2}. He noted Steemann Nielsen's estimate for the annual productivity of the oceans generally of 55–70 g C m^{-2}, although 100–150 g C m^{-2} y^{-1} would be a more appropriate range for the English Channel (Boalch, Harbour, and Butler 1978), not that it would change Duursma's argument materially.

These studies showed that there was significant and active flux of dissolved organic material in the euphotic zone of marine ecosystem in contrast to the views put forward by Krogh (1934b) and ZoBell (1943).

b. Significant rates of respiration by the microbial plankton

Another line of conflicting observations came from the two papers of Pomeroy and Johannes (1966, 1968). These researchers undertook an extensive set of measurements to

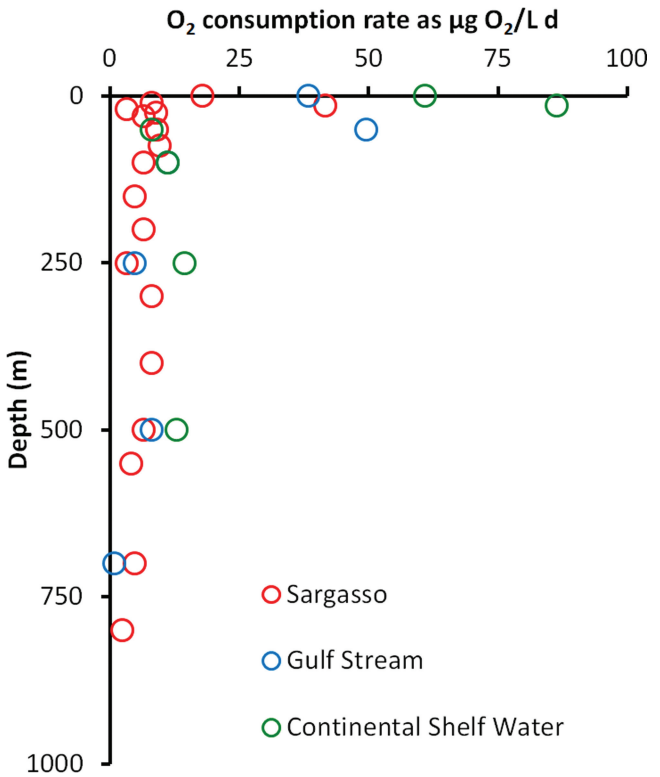

Figure 13. Measured ultraplankton (<60 µm) respiration at stations in the western North Atlantic. One value of 248 µg O_2 at 5 m for the slope water has been omitted as it overextends the x-axis. Drawn from data in Pomeroy and Johannes (1968, table 1).

determine the scale of what they termed "ultraplankton" respiration. They defined ultraplankton as the component of the plankton community that passed through a 366 µm mesh net but was retained by a 0.8 µm membrane filter. In order to obtain rates of oxygen consumption of the scale they could measure with a respirometer based on an oxygen probe system (Carritt and Kanwisher 1959), they concentrated the sample some 1,000- to 5,000-fold using the system described by Dodson and Thomas (1964). Using this procedure in a set of stations off the east coast of the United States, they obtained respiration rates for the zooplankton collected by a 366 µm net and the ultraplankton. They concluded: "Organisms too small to be retained in the net (300 µm) accounted for 94–99% of the total respiration. In the Gulf Stream and Sargasso Sea flagellates usually appeared to be the most important metabolic component of the plankton" (Pomeroy and Johannes 1966, Abstract, p. 971).

In a follow-up paper in 1968, Pomeroy and Johannes made sections at a number of oceanic sites (Fig. 13). They reported three profiles of oxygen consumption of ultraplankton respi-

ration in the Sargasso Sea; a plot of the depth distribution of the mean rates was shown in the accompanying figure. From a very extensive study in the Southeast Pacific off the coast of Peru, they presented rates integrated over the entire water column and estimated the photosynthesis to respiration ratio of the depth integrated values to have a range from 0.7 to 5.3, with a geometric mean of 1.3. This implies that ultraplankton respiration accounted for just short of 80% of the primary production; they conclude in the abstract of the paper that "evidence is presented that much of the energy fixed by photosynthesis is utilized by Protista" (Pomeroy and Johannes 1968, p. 381). In neither of the two papers do they make reference to Duursma's work, which would have provided supporting evidence for their fluxes.

c. Insufficient regeneration of nutrients

Dugdale and Goering (1967), in a seminal paper, used ^{15}N-labeled tracers to determine the rates of photosynthetic uptake of ammonium and nitrate. Ammonium uptake was some 55-fold greater than that of nitrate. As ammonium is predominantly a recycled form of nitrogen, it must derive from the plankton metabolism. From the available data, they made a careful analysis of the scale of the zooplankton contribution to the ammonium flux concluding that "the role of zooplankton in regenerating nitrogen as ammonia in the Sargasso Sea is examined theoretically. Probably only about 10% of the daily ammonia uptake by phytoplankton is contributed by the zooplankton living in the upper 100m" (Dugdale and Goering 1967, Abstract, p. 196).

This left the remaining 90% of the supply of ammonium unaccounted for. They undertook no discussion of the alternatives sources other than rain, which they estimated made an insignificant contribution (0.25%). The paper that could have supplied the answer (Pomeroy and Johannes 1968) had yet to be published. Dugdale and Goering's analysis for the Sargasso Sea, whether this small contribution to inorganic nitrogen recycling by the net zooplankton could be regarded as a general model or just specific for that particular ecosystem, was an obvious point of contention.

d. Lack of an identified sink in the water column for detritus

In Steele's (1974) organic energy flux model of the North Sea, the pelagic herbivores generated a significant amount of detritus—some 64% of their throughput. In the model, the recycling of this material was attributed, with limited evidence, to the bacteria in the sediments. Steele however gave careful thought to the possibility of decomposition by microorganisms in the water column but rejected it as he felt the evidence available was not strong enough.

e. Direct demonstration of the uptake and metabolism of DOM constituents by the microplankton

Parsons and Strickland (1962) introduced a technique using tracer amounts of ^{14}C-labeled organic substrates (glucose and acetate) to measure the uptake kinetics of low-molecular-weight dissolved organic substrates. This stimulated a number of lines of work. One such,

by Williams (1970), employed membrane filters to examine the size distribution of the organisms taking up these substrates. He concluded: "In surface waters the heterotrophic population usually appears to be predominantly bacterial, as judged by size analysis. … The results also suggest that the population is either free, or loosely attached to particles or is attached to friable particles. Occasionally this pattern is broken and the organic compounds are broken up extensively by large organisms or associates" (Williams 1970, p. 869). Williams and Askew (1968) used a modification of the original Parsons and Strickland technique, which involved measuring the $^{14}CO_2$ released, thus enabling the respiration of the substrates to be determined. In a follow-up paper, Andrews and Williams (1971) used this technique with ^{14}C glucose and a ^{14}C amino acid mixture with the proportions of the individual amino acids adjusted to that observed for seawater. With this approach, coupled with direct measurements of the glucose and amino acid concentrations in seawater, they were able to obtain an estimate of the scale of the flux of low-molecular-weight organic compounds in seawater. They concluded that "heterotrophic processes resulting in the uptake of dissolved organic compounds may consume organic material equivalent to 50% of the measured phytoplankton production" (Andrews and Williams 1971, Abstract, p. 111).

In summary, although we are able to focus on the aforementioned publications as pointing to a need to revise the then-prevailing view of the scale of bacterial processes in plankton organic flux, they were embedded in a mass of other publications, in some cases with conflicting views. Whereas collectively they can be seen to make a strong case, none of the papers by themselves would. None of the authors attempted to put forward a full picture. Each of the various pieces of work had weak points: they could be dismissed as special cases or that they involved techniques that contained potential flaws—indeed this was recognized by the authors. Williams (1970), for example, was well aware of the doubts that were raised over the reliability of bottle incubations he used in his work: "It has been long known that sea water samples will show considerable increases in bacterial numbers when placed in glass vessels. Thus, at first sight one might conclude that any approach which relies upon work with water samples incubated in bottles will yield only artefacts and thus the validity of the present and similar type of work must be questioned" (Andrews and Williams, 1971, p. 123). Pomeroy (1974b) likewise had reservations over his fractionation studies. Additionally, in the background was the specter of the bacterial numbers from plate counts.

5. Denouement and synthesis, 1970–1974

The years between 1970 and 1974 are an informative period to take stock of the Western and Eastern views of the diverse understandings of the role microorganisms play in planktonic food webs. We set the earlier date as prior to the publication of Lawrence Pomeroy's (1974b) paper "The Ocean's Food Web, A Changing Paradigm." We explain why subsequently. Before embarking on a detailed comparison of the different understandings of Western and Soviet biological oceanographers, it is worth giving some consideration to the differences in the structure of research in the two sectors.

In the Eastern sector, the research we describe came almost entirely from the large national institutes—the Shirshov Institute of Oceanology in Moscow being preeminent for the research we consider. We encountered no publications from academic sources. In the West, the major oceanographic research institutions included the federally operated National Institute of Oceanography in the United Kingdom and the Bedford Institute in Canada; the Planktologie Department of the University of Kiel in Germany; and Scripps Institution of Oceanography and WHOI in the United States. The latter two institutes were privately operated, though heavily funded by federal sources. They both later became affiliated with degree-granting university programs at the University of California, San Diego and Massachusetts Institute of Technology, respectively. Last, though hardly least, there were a host of university departments throughout the West that made highly significant contributions to the development of our topic. Among the notable university research programs was the Institute of Ecology at the University of Georgia, to which we return subsequently.

The significance of this is that individual institutions are inclined to have their own research legacies and tend to develop their own perspectives. In Russia, where the lines of research we have been considering were restricted to single government-operated institutions, scientific views would tend to be dominated over time by one or a few leading scientists. By contrast, in the West, where there are many independent research institutions and universities, there was inevitably a greater diversity of views—indeed there was no shortage of differing views. As a consequence, we choose to refer to an "Eastern view" of matters, whereas in the case of the West, especially in the case we are exploring, and particularly at the point in time we are considering, no such consensus existed.

We have demonstrated from publications and reports from the Eastern community we have been able to access that they had settled on the view that direct microscopic counts of stained bacteria on membrane filters (Section 3) predicted biomasses of bacteria on a scale that could enable them to make a major contribution to the flux of organic material in planktonic ecosystems. With this as a conceptual starting point, as we described in Section 3b, Vinogradov and his coworkers were able to design and undertake an extensive field study to parameterize and run ambitious time- and depth-resolved models of the plankton that incorporated discrete trophic levels from bacteria to the higher zooplankton carnivores. The models also incorporated the internal recycling of detritus through the bacteria, a process not seen in the few Western models of the time (e.g., Steele 1974). In Vinogradov's models, dissolved and particulate detritus were a major (50%–75%) carbon and energy supply for the bacteria. It was a decade before such ambitious models were produced by a Western group—the model (Fig. 14) by Pace, Glasser, and Pomeroy (1984), which we believe to be the first of its type from a group in the Western bloc, had most of the elements present in the Vinogradov models and also the microbial loop.

In Section 4, we discussed the gathering of storm clouds in the West, in the era from roughly 1960 to 1970. Collectively, these lines of evidence put together would argue for a major role played by the bacteria in carbon flux within the plankton. At the same time (1971) in a discussion reported in Stevenson and Colwell (1973), reproduced in Section 2d,

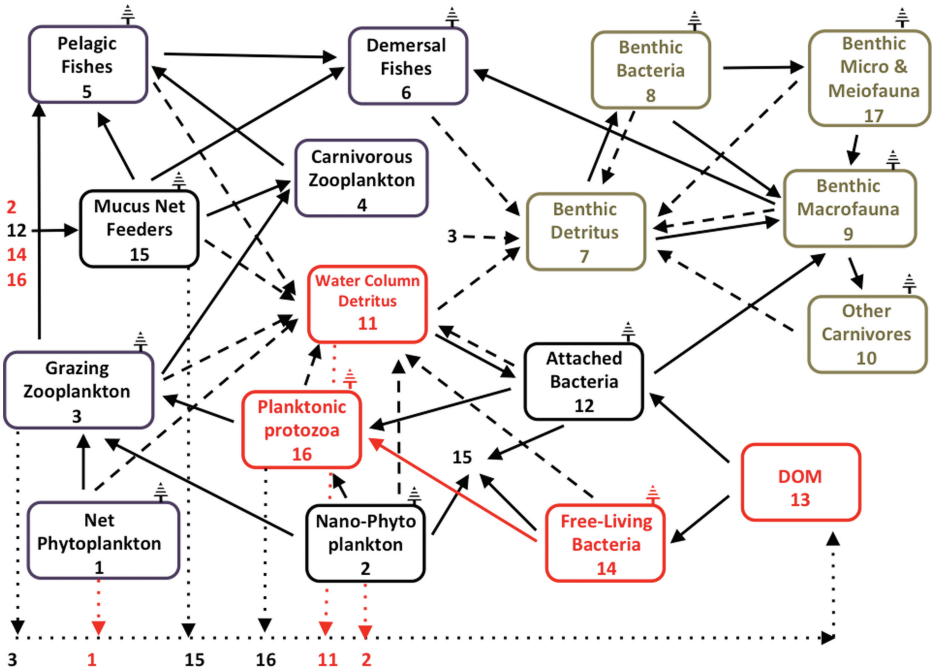

Figure 14. Continental food web model. Notation: net phytoplankton—all algal cells, colonies, and chains greater than 60 μm in maximum dimension. The composition of the collective groups in the flow chart are as follows: nanoplankton, algae less than 60 μm in maximum dimension; benthic detritus, organic matter on or in the sediment layer inhabited by benthos; benthic bacteria, bacteria associated with benthic detritus; water column detritus, nonliving particulate organic matter greater than 0.45 μm in the water; attached bacteria, bacteria attached to particles in the water column; dissolved organic matter, organic matter that passes through a 0.45 μm filter; free bacteria, bacteria that are not associated with particles in the water column; and planktonic protozoa, zooplankton less than 200 μm in maximum dimension, primarily protozoa. The highlighted compartments are outside the circle in Figure 15. Reproduced from Pace, Glasser, and Pomeroy (1984, A simulation analysis of continental shelf food webs, Mar. Biol., *82*, 47–63, fig. 1, p. 49) with permission from Nature/Springer/Palgrave.

influential marine microbiologists such as ZoBell and Watson were inclined to the totally contrary view that the bacteria played a very minor role—not "anything like 1%" was ZoBell's view.

In 1972, the results of a highly focused study by a group of "new wave" biological oceanographers was published (Hobbie et al. 1972) in an attempt to pin down the problems of accessing biomass and respiration and the distribution of respiration within the planktonic community. The correspondence they obtained between the results of various approaches, then available, to estimating biomass and respiration was found to be good—giving credibility to their observations. However, the authors were led to the conclusion that the bacteria

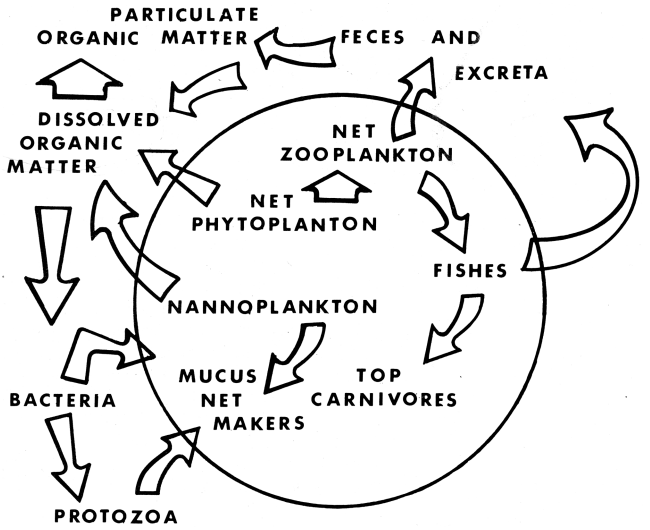

Figure 15. The representation of the classical paradigm of the ocean's food web in simplified form is enclosed within the circle (Pomeroy 1974b). More recently (i.e., in 1974) conceived pathways are-outside the circle. Reproduced from Pomeroy (1974b. The ocean's food web, a changing paradigm. BioScience, *24*, 499–504, fig. 1, p. 502) with permission from the American Institute of Biological Sciences.

were "not present in sufficient numbers to constitute a significant fraction of living biomass or to contribute significantly to the respiration processes we measured" (Hobbie et al. 1972, p. 552).

In 1974, in the midst of this dissent, came a review paper by Lawrence Pomeroy. Pomeroy was an invertebrate zoologist who joined the staff of Eugene Odum's great Institute of Ecology at the University of Georgia in 1953 (Barrett and Barrett 2001). Pomeroy worked with fellow institute researcher Robert Johannes trying to measure ocean respiration in the 1960s. In the 1970s he continued a career-long investigation of nutrient cycling and regeneration with several synthesis papers and edited volumes (Pomeroy 1970, 1974a, 1979). The 1974 review paper (Pomeroy 1974b) was remarkable on a number of accounts: its publication history was unique, as was its clarity about the importance of small organisms in the plankton, and its immediate impact, or lack of it, was nonetheless remarkable. We also encountered a similar lack of impact in the case of Waksman's work. The somewhat checkered history of its publication is related in the review by Sherr and Sherr (2000). In brief, Pomeroy submitted his manuscript to *BioScience*, and the editor sent it out to two referees. One gathers from the Sherr and Sherr review that one referee did not respond, and apparently the other replied that the paper was nonsense and should be rejected. However, the editor in chief—John Bardach—liked the paper and, thankfully, published it.

The clarity of Pomeroy's conceptual model (Fig. 15) is more than remarkable, as we discussed earlier in this section, in that this clarity did not prevail in the published Western science of the time. Pomeroy summarized the growing evidence for the importance of nanoplankton (<60 μm) productivity over that of the larger net plankton and for the release of photosynthetic products by both groups of phytoplankton to nurture bacteria. The evidence (Pomeroy and Johannes 1966; Williams 1970; Andrews and Williams 1971) was not as concrete for other plankton processes. Supporting papers were strongly dependent on the size fractionation capability of membrane filters. As Pomeroy (1974b, p. 500) further noted, "These separations, which were made with membrane filters of different porosities, have been criticized because of the possibility of fragmentation of fragile nannoplankton [*sic*]. Verification of the results by microscopic methods such as Watt's autoradiography is needed." Pomeroy (he was a coauthor of the Hobbie et al. [1972] paper) mentioned "bacteria" 13 times in his paper, more than any other related term, yet he avoids any debate over bacterial abundance and their contribution to overall planktonic carbon flux, noting that "both Strickland (1971) and Raymont (1971) suggest that micro-organisms are a major metabolic component of the oceanic ecosystem, but they do not attempt to quantify their importance" (Pomeroy 1974b, p. 502). In using the term "micro-organisms" rather than the more specific "bacteria," Pomeroy might have been hedging his bets. Even today, it is seldom clear what different microbiologists mean when they use the term microorganisms. It can mean any microscopic organism, or it can refer to bacteria alone.

Thus, a major part of the vision Pomeroy presented was, at the time, supposition. The work in the following 6 years proved his suppositions to be prophetic. The group at Kiel (Hoppe 1976; Meyer-Reil 1978; Zimmermann, Iturriaga, and Becker-Birck 1978) used microautoradiography techniques to establish the scale of the abundance of metabolically active bacteria. The introduction of Nuclepore filters into the study of the microbial biomass (Salonen 1974) and metabolism (Azam and Hodson 1977), along with the development of epifluorescence microscopy, initially employing acridine orange stain (Jones and Simon 1975; Ferguson and Rublee 1976; Hoppe 1976; Hobbie, Daley, and Jasper 1977; Watson et al. 1977) and subsequently DAPI (Coleman 1980; Porter and Feig 1980), gave a much firmer basis to estimating bacterial numbers and their biomass. In addition to the aforementioned developments in the research areas Pomeroy considered, there were major developments in the kindred areas of bacterial growth and estimation of growth rates (Sieburth et al. 1977; Sheldon and Sutcliffe 1978; Hagstrom et al. 1979; Fuhrman and Azam 1980) and bacterial production rates (Karl 1979; Fuhrman and Azam 1982) that collectively supported Pomeroy's vision. This, and further supportive work, gave rise to the burst of reviews in the early 1980s (Williams 1981, 1984; Joint and Morris 1982; Azam et al. 1983; Ducklow 1983), and it was the Azam et al. paper that most successfully broadcast the developments to the wider community.

To return to Pomeroy's 1974 paper: the success of the paper judged by the criterion of citation history presents a puzzle as illustrated in Figure 16. Over the first 7 years until 1981, it received an average of a mere 4 citations per annum, then over about 10–20 years

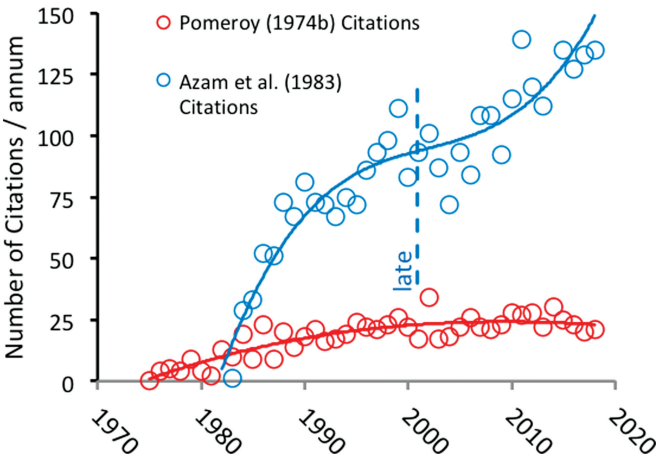

Figure 16. Analysis of citations of Pomeroy (1974) and Azam et al. (1983); data from the Web of Science. The lines are a third-order polynomial fit of the data, ($R^2 = 0.76$; Azam et al. [1983], $R^2 = 0.89$).

its citation rate increased to about 15–20 citations per annum reaching a steady rate, up to the present, of 20–25 citations per annum, for a total of 802. This pattern seems surprising for a paper most scientists in the field consider important, even seminal. For example, the citation rate for ZoBell's 30 marine papers (1933–1945) continues to increase (Fig. 4). His most cited paper, ZoBell (1943), has had periods of increasing and decreasing rates and is currently cited at a rate of about 15 per annum, for a total of 636. The 1983 paper by Azam et al. also exhibits a pattern of still-increasing citations, currently at about 140 citations per annum and a grand total of 3,234 (on 22 January 2019).

The reasons for the modest citation rate of Pomeroy's paper are not clear. One possibility is that the slow start reflected the small size of the scientific community at the time, which was predisposed to understand and profit from Pomeroy's model. By the time the community came of age, in the 1975–1980 period we just described, Pomeroy's article was possibly superseded by the spectacular performance of the Azam et al. (1983) paper. However before the publication of Azam et al., there were suggestions that Pomeroy (1974b) had not yet taken off. For example, in neither of two NATO Symposium volumes focusing on planktonic processes (Hobbie and Williams 1981; Fasham 1984) was Pomeroy (1974b) cited, including the introductory chapter by Pomeroy in the 1981 book. The 1981 publication dealt specifically with microbial processes.

Pomeroy (1974b, p. 499) himself emphasized the caution to be observed when adopting new scientific ideas: "Marine scientists have been approaching this view of the food web cautiously for decades, and caution is to be expected whenever an established paradigm is questioned (Kuhn 1962). Now there are many lines of evidence, which suggest that a new paradigm of the ocean's food web is indeed emerging." By invoking Thomas Kuhn's (1962) epochal *The Structure of Scientific Revolutions*, and the paradigm meme, used to

denote both a central organizing idea and the scientific community sharing that idea and agreeing on the approved methods and approaches to be followed, Pomeroy clearly thought of the intellectual developments he described as revolutionary. In the same year, he wrote the following in the preface of a book he edited, *Cycles of Essential Elements* (Pomeroy 1974a, p. ix): "The task of presenting a generally acceptable history of one of the specialized fields of ecology is especially difficult in this regard. Ecology is a very young science. In fact, it is really just beginning to be science. Perhaps because ecology is in a state of growth and metamorphosis, its paradigms are not yet well fixed. There is substantial disagreement about what is true and what is important."

6. Summary and conclusions

Our account of the processes in creating a new field of research in marine microbial ecology does indeed embody a number of the stages identified by Kuhn as characterizing a prerevolutionary period: a range of contending ideas (East vs. West), a focus on details and minor problem solving, disagreement over the correct methods to use to estimate bacterial abundance, and a cautious approach to upsetting the established order.

Science progresses by the interplay of conceptual, social, and technological developments. Early practitioners in the West, including Waksman, Krogh, and ZoBell, were unwilling or unable to accept evidence that abundance estimates derived from CFUs were underestimates by as much as three or four orders of magnitude. If bacterial abundance were so low, their activity would be similarly unimportant. Indeed, ZoBell, still active and influential in the early 1970s, stated that bacterial activity could not amount to more than 1% of the primary production. At about the same time as Waksman and ZoBell were starting to work at the two great American oceanographic centers, Eastern microbiologists were beginning to examine marine bacteria using direct microscopic techniques. While most microbiologists in the West were still wedded to plate counts and would not, or could not, conceive of bacteria as being important in the oceanic pelagic, the Eastern scientists had formed a mechanistic theory of marine bacteria and encoded it in numerical simulation models.

We conclude by addressing the questions raised at the end of our introduction: Was the Eastern understanding in advance of that in the West and, if so, why? What, if anything, held back developments in the West? Why did the Eastern ideas not take root and grow in the West?

We consider the question, was the Eastern understanding in advance of that in the West? for the era up to 1960. We take the context to be the development of the microbial loop paradigm. Eastern scientists had developed the method of direct bacterial counts in the early 1930s. As judged by chapters 5 and 7 in Kriss's (1963) book, by the late 1950s Eastern marine microbiologists had compiled a substantial body of data on the abundance of bacteria. Some of these data were converted to biomass, and Kriss undertook tentative calculations of the implied organic flux for the Caspian and Black Seas—thus these researchers were

making small encroachments into the microbial loop model. The early work of Western scientists Krogh and Waksman, in the 1930s, was a mixture of the study of states and rates. Waksman's early work (Waksman and Carey 1933a, 1935a, 1935b; Waksman et al. 1933) was substantially autecological, and so he had no need to draw on in situ measurements of total bacterial abundance. Krogh, during his short sojourn at Woods Hole, made measurements of oxygen flux of size-fractionated coastal and ocean water samples and posed the question of whether the results indicated a major role for bacteria. However, based on the information on bacterial abundance from plate counts, he concluded this could not be so. Waksman's later work (Waksman and Renn 1936) moved also to in situ rate measurements. His group also undertook comparative studies of direct and plate counts (Hotchkiss and Waksman 1936), but the work centered on correlations and was not fed into their work on rates. The work of these two groups was followed by that of ZoBell, who was a major influence up to the late 1950s. ZoBell reverted to autecological studies.

Thus, if we take 1960 as a time point, we can conclude that the Eastern marine microbiologists had made further progress toward the microbial loop concept than their Western counterparts. If we take the period from 1960 to the end of the time we are considering (1974), the matter is more complex. Both sectors were advancing on quite broad fronts. We may conclude that the models of Vinogradov, Menshutkin, and Shushkina (1972) and Vinogradov et al. (1973) were distinctly ahead of those of Western food web models, but we would be wary of generalizing this further to other aspects of the quantitative role of microorganisms in the planktonic food web.

We can answer the second and third questions (and, if so, why? What, if anything held back developments in the West?) together. From the previous discussion, we would conclude that the primary reason why the Eastern microbiologists were further ahead in the study of bacterial dynamics in the period up to 1960 stemmed from the questions posed: autecological or synecological. This choice led to the enumeration methods they adopted and in turn to the perception of the scale of bacterial activity in the marine food web. Western marine microbiologists adopted the plate count approach as it satisfied the requirements of the autecological questions they asked. There was, however, no sign that they were unable to adopt the direct count method. Indeed, it appears that Waksman's group had used it in the Hotchkiss and Waksman (1936) study, although no details are given in the paper. Thus, in principle there was no methodological block.

We now turn to the last question: Why did the Eastern ideas not take root and grow in the West? Language and the lack of easy access to journals published in the East are obvious answers, but they cannot be the complete explanation. A number of Sorokin's and Vinogradov's significant papers in the mid-1960s to early 1970s (Sorokin 1960, 1962, 1964a, 1964b, 1968, 1971a, 1971b, 1973a; Vinogradov, Gitelzon, and Sorokin 1970; Vinogradov, Menshutkin, and Shushkina, 1972) appeared in English in Western journals, yet as judged by citations, they had little impact. However, a great deal of the Eastern work would have been missed. There are at least two other possible factors. First, 1960 was the peak of the Cold War, which gave rise to major political tensions between East and West. To some extent, the

scientific community overrode this—we note in our review the gesture Robert Wetzel made by working on the 1968 paper by Sorokin. However, despite this, the participation of Eastern scientists in conferences held in the West would have been severely controlled by their governments; this would have limited interaction and exchange of ideas between Eastern and Western scientists and the informal recognition of one another's accomplishments. A further factor very likely would be the context and conclusion of a given paper in relation to the prevailing thinking. That is, papers distinctly ahead of contemporary thinking may be put aside until a new idea takes hold. Overall, our story can be summarized as a long evolution toward a more realistic and quantitative understanding of the scale of marine bacterial activity.

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