Integrating classical and microbial food web concepts: evolving views from the open-ocean tropical Pacific

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Abstract

Over the past half-century, and particularly the last two decades, new paradigms, perspectives and technological capabilities have greatly advanced our understanding of open-ocean pelagic ecosystems. Major new insights have come from the microbial loop concept and related discoveries, the iron limitation hypothesis and ocean time series. Focusing mainly on the tropical and subtropical Pacific Ocean, I review the influences of these new perspectives on classical views of food web complexity, phytoplankton regulation and diversity, and temporal dynamics.

"Microorganisms (bacteria, fungi, protozoa) are responsible for about 95% of the CO_2 evolved into the atmosphere, while animals contribute about 5%. These estimates are based on figures from terrestrial environments, but there is every reason to believe that microorganisms are relatively as important in the oceans".

(Lecture Note Handouts, OCN 434, Winter, 1971)

Introduction

Present-day students of biological oceanography will find the above quote remarkable only to the extent that it suggests an open issue. Such has been the influence of the 'microbial loop' paradigm (Williams, 1981; Azam et al., 1983) and the research that it has inspired over the past two decades that we accept microbial dominance of the ocean's metabolism as a well established fact. So completely have bacteria, protists and their interactions been woven into our modern understanding of the pelagic food web that, to many, 'classical' plankton community concepts exist only as a caricature, the linear chain from diatoms to copepods to fish. Thus, it is of some interest that the above quote was taken not from a modern oceanographic textbook or from a pioneering marine microbiologist. It comes from the Lecture Notes of an introductory graduate course on biological oceanography taught by 'classical' plankton ecologists, J.C. Lewin and B.W. Frost, at the University of Washington in early 1971. Influenced perhaps by the small but growing body of work on microbial processes, but preceding by several years the first call for a changing paradigm (Pomeroy, 1974), the message reflects an awareness of microbial potential that is little appreciated among those who have critiqued the classical mindset. Nonetheless, even the most open minds of that era could not have anticipated the extent to which our present perception of open-ocean food webs would reflect the dominance of bacteria and protozoa in community structure as well as carbon, energy and nutrient cycling. As in terrestrial systems, however, this backdrop of microbially mediated processes is compatible with and in no way diminishes our interest in the life and death dramas of classical plants and animals.

In the three decades since my introduction to oceanography in Professor Frost's classroom, our comprehension and ability to study the functioning of ocean ecosystems have advanced enormously. By the 1960s, the relatively new techniques of ^{14}C-bicarbonate uptake and chlorophyll analysis were facilitating quantitative, process-oriented studies of phytoplankton. At the same time, however, tax-

onomy and adequate sampling strategies (who and how many?) were issues of great activity in zooplankton ecology, and the field was only beginning to address the challenges of conducting and interpreting experimental studies under controlled laboratory conditions. Now, field and modeling studies routinely target processes and interactions at the ecosystem level, and the ultimate aims, e.g. global predictive models, are even higher. In reflecting on these advances on the occasion of my mentor's 60th birthday, and wishing him many more, I offer a few brief perspectives on the ecology of the open oceans. I emphasize, though not exclusively, the vast regions of tropical and subtropical Pacific Ocean where the integration of classical and microbial community concepts has come far but continues to evolve as we add new information.

Classical webs and microbial chains

It is not clear from where we first derived the notion of a simple trophic hierarchy for marine plankton. Nonetheless, in setting the stage for the new microbial paradigm, Pomeroy (1974) invoked the image of "the classical textbook description of a chain from diatoms through copepods and krill to fishes and whales", and it has defined the pre-microbial viewpoint ever since. While simplified representations of plankton trophic interactions have certainly been used to highlight energy flows and facilitate modeling over the years (e.g. Ryther, 1969; Steele, 1974), most textbooks, past and present, illustrate the principles with some version of Hardy's (1924) herring food web (e.g. Hardy, 1959; Raymont, 1963; Gross, 1972; Sumich, 1976; Garrison, 1993; Duxbury & Duxbury, 1996; Pinet, 1998). The relationships portrayed are neither simple nor linear (Fig. 1). Nanoflagellates and dinoflagellates complement diatoms at the base of this food web. Invertebrate predators are the intermediate consumers of copepods, the predators of herring larvae and the prey of adult fish. We see that the diet of herring varies with size and development, from dinoflagellates, ciliates and small metazoans for larvae to a diverse suite of predatory and suspension feeding invertebrates and smaller fish for adults. Behind the scenes, and the primary focus on herring diet, is a secondary network of interactions involving individual developmental stages of each animal represented. Since juveniles are typically 2–4 orders of magnitude smaller than adults in terms of biomass, each species exploits varied sources of food during its development and runs a

gauntlet of diverse predators, including its direct competitors and prey when adult. Within such a network, it is a daunting challenge to follow energy and material flows, to predict outcomes, or even to define explicit trophic levels beyond the primary producers (Isaacs, 1972, 1973; Banse, 1995). We should, therefore, recognize this classic textbook illustration for what it truly depicts – a complex web. With more plant and animals species, the tropical ocean food web would be even more so. The relatively recent arrival of microbial concepts has added important new dimensions and insights to food web organization, but the foundations of such networks were well established by classical pelagic ecologists (e.g. reviewed by Landry, 1977).

As we have come to learn, protists can also be complicated, particularly if we consider their mixotrophic strategies and multi-faceted life histories (Estep & MacIntyre, 1989; Stoecker, 1998). Aspects of the feeding behaviors and selectivities of heterotrophic protists rival those of the metazooplankton (e.g. Strom & Buskey, 1993). At least in some respects, however, our current understanding of microbial trophic interactions is simpler than that of the classical web. Since most phagotrophic protists reproduce by simple fission, for example, multiple developmental stages and sizes do not confound predator–prey relationships within the microbial assemblage. Even allowing for some size variation due to nutritional status, the prey consumed by a specific taxon or consumer type (e.g. <5-μm nanoflagellates) remain reasonably fixed through life. Our present understanding of microbial networks is also limited by inadequate taxonomic knowledge, particularly among the smallest size components. Interactions among bacteria and flagellates comprise the dominant pathways of total energy flux (autotrophic and heterotrophic) in extensive regions of the tropical and subtropical oceans (Landry & Kirchman, 2002). Yet with regard to the details of trophic linkages at this level of the open-ocean food web, we have not advanced much further than the initial description of the 'microbial loop'; bacteria are consumed by small flagellates, and they, in turn, by larger protists.

In some respects, this simplification may be a reasonable representation of reality, or at least work to our advantage in studying natural processes and relationships. When size fractionation is used to remove successive layers of consumers, for instance, this part of the food web does, indeed, appear to function as a predatory chain (Fig. 2). The filters first strip away the predators of bacterivores, and net growth rates of bac-
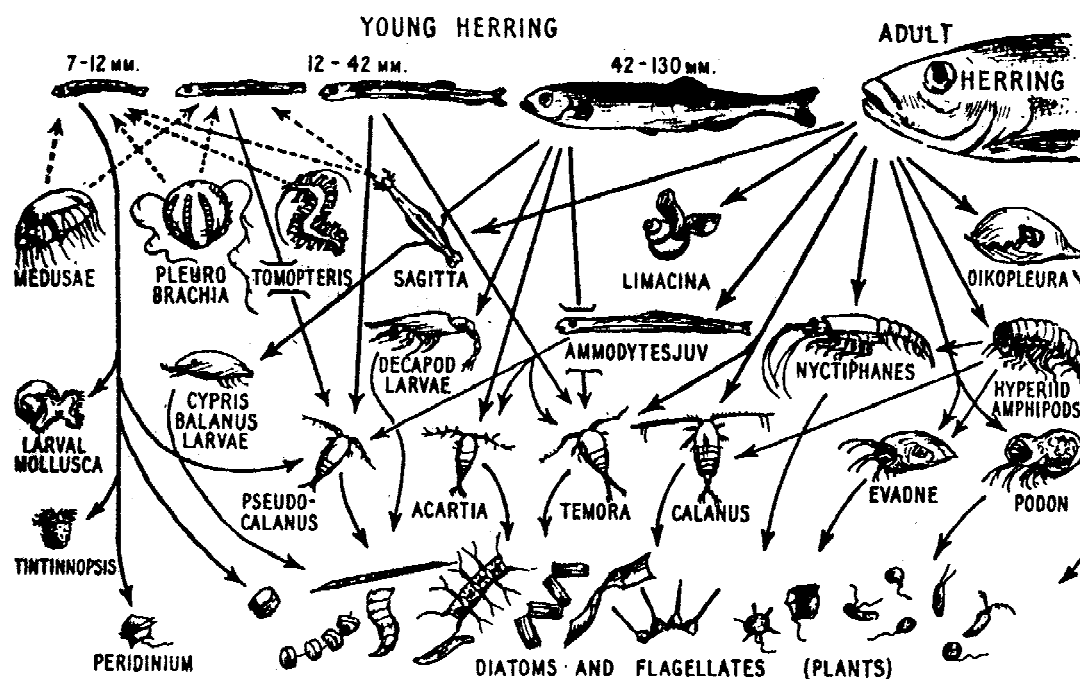
Figure 1. Classical textbook representation of the pelagic marine food web based on the plankton and feeding habits of herring in the North Sea (from Hardy, 1959; courtesy of Harper Collins, London).

teria decline with the resulting trophic cascade. The trend is reversed as the primary grazers of bacteria are removed with even smaller filters. More detailed study has shown unexpected variability in the number and relative strengths of the grazing chain linkages, with cascades strongest at intermediate to high levels of bacterial biomass (Calbet et al., 2001). This variability may be due to the oscillating importance of substrate availability and protistan predation in regulating the relative constancy of bacterial standing stocks. It could also reflect as yet unknown complexity in trophic interactions within the protist assemblage. The promising first applications of molecular approaches to pico-eukaryotic taxa in the tropical oceans have revealed numerous taxa (e.g. Guillou et al., 1999; Moon-van der Staay et al., 2001). Given the paucity of information about specific functions, however, we cannot really say how, or even whether, taxonomic diversity, time-varying behaviors or selective pressures contribute to regulatory processes within the microbial assemblage. This is an area where the combination of experimental manipulations and molecular techniques to distinguish population responses might be put to good advantage.

Phytoplankton balance and community structure

From the relative constancy of phytoplankton stocks and production in the subtropical oceans and their implications for nutrient requirements, Steemann Nielsen (1958) reasoned that plant growth must be balanced by losses to zooplankton grazers, with the substantial daily turnover in cell nutrient content replenished by regeneration within the surface layer. Many details of the arguments laid out in this early synthesis, including the magnitude of production rates, have been refined by almost half a century of research. However, the essential features of a growth and grazing balance with remineralized nutrient feedbacks remain central to our understanding of tropical ocean systems.

The modern view has been profoundly influenced by the microbial paradigm and related discoveries and by the iron limitation hypothesis (Martin & Fitzwater, 1988). From the former came the discovery of *Prochlorococcus* spp. (Chisholm et al., 1988), bacteria with global significance as primary producers and ecosystem dominants. *Prochlorococcus* established a major link among warm-water, oceanic ecosystems with respect to their common base of community structure. It also made us consider the implications of systems in
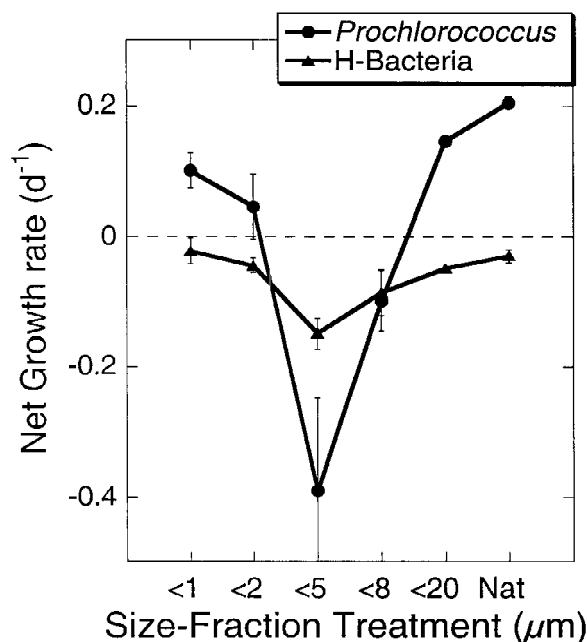
Figure 2. Effects of size-fraction removal of protistan consumers on the net growth rate of heterotrophic bacteria and *Prochlorococcus*. Seawater was collected from 110 m in the subtropical Pacific (Stn. ALOHA). Net population changes were determined from flow cytometric analyses on initial and final samples incubated at 1% surface light for 24 h after filtration through polycarbonate membrane filters of 1–20 μm pore size (Nat=natural sample control with no filtration). Vertical bars show standard errors of 4 replicates (modified from Calbet & Landry, 1999).

which prokaryotes were central to autotrophic as well as heterotrophic pathways. With respect to the iron hypothesis, high-nutrient, low-chlorophyll (HNLC) waters of the eastern equatorial Pacific were the testing ground for mesoscale iron fertilization experiments, with IronEx II providing the first unequivocal evidence that iron limited phytoplankton growth rates and biomass accumulation in this region (Coale et al., 1996; Landry et al., 2000b). These results established a common thread between adjacent HNLC and classical low-nutrient, oligotrophic regions with respect to basic processes regulating growth rates and standing stocks.

In both systems, primary producers are resource-limited, and therefore dominated by small cells, capable of competing most efficiently for the limiting substrate (Morel et al., 1991). They grow at rapid, but usually less than physiologically maximal rates (Laws et al., 1987; Mann & Chisholm, 2000). These superior competitors are maintained at relatively constant and low biomass by microzooplankton (protistan) grazers, and their sustained growth is largely dependent on the remineralized by-products of grazing (Frost & Franzen, 1992; Landry et al., 1997). As suggested theoretically by Thingstad (1998), successively larger phytoplankton (and their consumers) can become more important in such systems as the total pool of limiting resource increases and if protistan grazers continue to suppress the smaller phytoplankton components.

The general principles of a size-based competitive hierarchy among primary producers and strong grazer (top-down) regulation of the smallest size fractions are well illustrated in natural observations. For example, mean concentrations of the smallest phytoplankter, *Prochlorococcus* spp., are remarkably similar throughout the tropical open-ocean Pacific, from severely oligotrophic regions of the central subtropical gyres and the western Warm Pool to high-nutrient, low chlorophyll (HNLC) waters of the equatorial upwelling zone (Landry & Kirchman, 2002). Over multiple years and cruises, 0–50 m mean concentrations of *Prochlorococcus* were, in fact, slightly less abundant in the HNLC upwelling zone than at subtropical Stn. ALOHA (1.45 vs 1.83 10^5 cells ml^{-1}) (Fig. 3). Both also display comparable levels of variability (coefficient of variation=9–10% for different depths, sampled from the upper 50 m at a given station and 25–26% between mean concentrations of stations sampled at different times). The higher total biomass of phytoplankton in the HNLC region principally reflects the added contributions of other small forms; for example, *Synechococcus* spp. and pico-eukaryotic algae are enhanced by 5- and 8-fold, respectively, compared to Stn. ALOHA (Landry & Kirchman, 2002). Phytoplankton biomass is further increased in this food web by adding more limiting nutrient, as was done during the IronEx II fertilization (Fig. 4). The result was a >40-fold increase in the biomass of microphytoplankton (>20-μm size fraction), with a largely negligible effect on smaller cells (Landry et al., 2000a). Such observations define the order in which successively larger phytoplankton are added to the food web by 'overprinting' its relatively stable base of small cells (e.g. Chisholm 1992; Landry et al., 1997).

Diversity

Well-stratified, oligotrophic waters of subtropical oceans have long been known to contain a great diversity of planktonic plants and animals compared to more nutrient-rich coastal and boreal environments
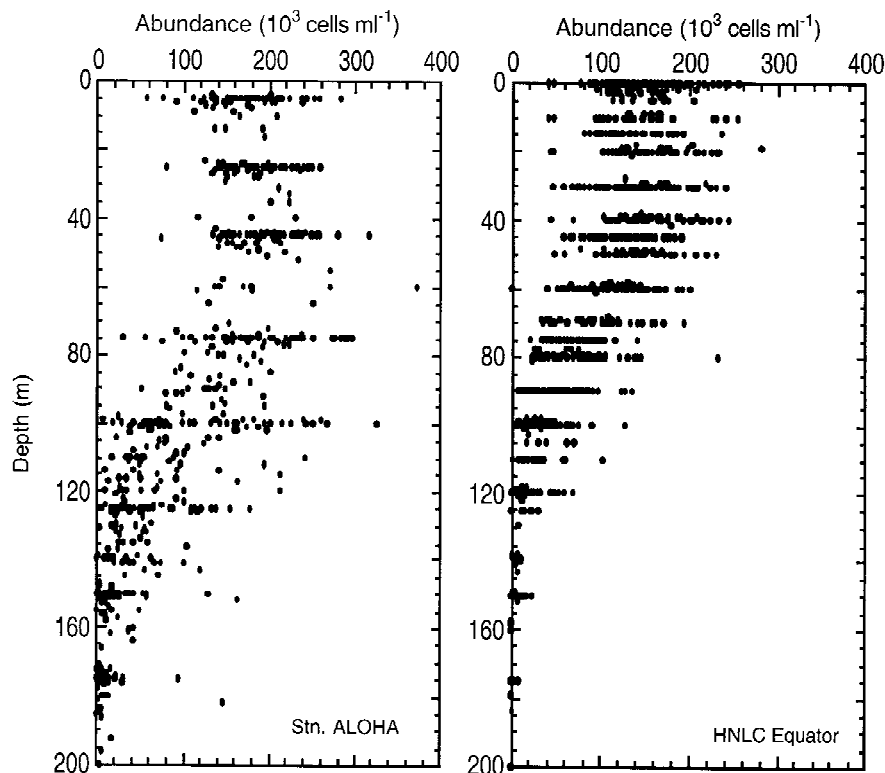
Figure 3. Variability in the depth distributions of *Prochlorococcus* abundance from the equatorial HNLC (2° S to 2° N) and subtropical oligotrophic (Stn. ALOHA) regions of the central Pacific. HNLC data are flow cytometric analyses from all US and French cruises in the region (EqPac, OLIPAC, FLUPAC, EBENE and IronEx II) between 1992 and 1996. ALOHA data are approximately monthly depth profiles at 22.4° N, 158° W from 1991 to 1998 from the Hawaii Ocean Time-series (HOT) Program (modified from Landry & Kirchman, 2002).

with strong seasonal forcing (e.g. Grice & Hart, 1962; Hulburt, 1963; Longhurst, 1967; McGowan & Walker, 1979, 1985). From this association with environmental stability, it has been natural to seek the explanation for enhanced diversity among the factors internal to equilibrium food webs, such as niche differentiation, selective removal processes and co-evolved strategies, that might mitigate competitive exclusions (e.g. Longhurst, 1967; Mullin, 1967; Timonin, 1969). As a counter to equilibrium theories, it has also been suggested that disturbances, caused by the non-uniform distributions and impacts of the biota or by external physical processes, could further diversity by resetting successional processes that would ultimately lead to the exclusion of opportunists (Richerson et al., 1970). Among terrestrial ecologists, similar considerations have lead to the Intermediate Disturbance Hypothesis (IDH), which was initially advanced to explain the stunning diversity of tropical rain forests and coral reefs (Connell, 1978). In the first test of this concept for plankton, Flöder & Sommer (1999)

found, as predicted, that freshwater phytoplankton in experimental mesocosms achieved maximal diversity at an intermediate level of mixing, hence intermediate nutrient and light regimes (see also Sommer et al., 1993).

Similar lines of experimentation and hypothesis testing have not been undertaken in the open-ocean marine plankton, but presumably could be pursued by combining old-fashioned taxonomy and quantitative new molecular techniques with manipulations of open-ocean mesocosms or direct, *in situ* fertilizations. From the discussion in the previous section, the microbial components ignored in classical studies offer a new perspective about diversity of tropical phytoplankton. For instance, the extraordinary abundance of *Prochlorococcus* spp. throughout the tropical and subtropical Pacific (>98% of total phototrophs; Landry & Kirchman, 2002) is currently recognized to comprise two distinct genotypes, dividing the upper and lower euphotic zones (Moore & Chisholm, 1999; Partensky et al., 1999). Since diversity is typically quantified

by indices that account for the relative abundances of species (i.e. *eveness*) as well as the total species present (Washington, 1984), such metrics would be strongly skewed by the pronounced dominance of this one genus. This would, of course be reduced, but still substantial, if our diversity index was based on biomass rather than abundance of individual genotypes. Either way, *Prochlorococcus* spp. dominance of the phytoplankon community is clearly strongest in stable subtropical regions, where severe oligotrophy depresses other populations. Since *Prochlorococcus* is present throughout the central Pacific at relatively constant levels, its dominance is reduced by the increased importance of *Synechococcus* and pico-eukaryotic algae in the more physically disturbed and nutrient-rich equatorial upwelling zone, thereby enhancing evenness and likely local diversity. The IronEx II results (Fig. 4) further suggest that there should be some intermediate level of limiting nutrient addition where the biomass distribution among all species, including larger taxa, like diatoms and dinoflagellates, would show a maximum. There is little doubt that we currently underestimate the true species richness of open-ocean phytoplankton, particularly in the smaller size classes. Even without this critical information, however, we might reasonably speculate that diversity of the open-ocean plankton will conform to predictions of the IDH.

Seasonal dynamics of a 'stable' oligotrophic ocean

Few concepts of plankton dynamics have provided more insight or been more durable than Sverdrup's (1953) 'critical depth' explanation for the initiation of the temperate phytoplankton bloom. From this cornerstone of conventional understanding, we can readily appreciate how mixing processes, stratification and light penetration drive regional and interannual variability in seasonal production cycles. Compared to higher latitudes, for instance, subtropical waters are expected to experience blooms relatively early in the year, when winter storms mix nutrients into well-illuminated and stratified euphotic zones. Conversely, plankton standing stocks and production rates should be lowest during the summer period of intense stratification and nutrient deprivation. Classical studies of seasonal plankton cycles in the subtropical North Atlantic conform well to these expectations and have illustrated the principles in countless classroom lectures (Menzel & Ryther, 1961; Deevey, 1971).

While the implications of physical forcing were not ignored in early studies of the subtropical North Pacific (e.g. McGowan & Hayward, 1978), these studies largely advanced the notion of a relatively stable physical system and a diverse, but monotonously uniform, plankton community (e.g. McGowan, 1977; McGowan & Walker, 1985). This may reflect, in some measure, the system's *a priori* selection as an old, stable and isolated habitat in which successional processes could reach their ultimate result in a 'climax' community (Venrick, 1995). With sampling heavily biased during mostly summer months, the CLIMAX studies resolved no clear patterns in seasonal variability (Hayward et al., 1983).

In contrast to this relatively static historical perspective of the subtropical central Pacific, time-series sampling at Stn. ALOHA since 1988 has revealed a vibrant and dynamic ecosystem at many scales (Karl, 1999). One indication of this is a clear seasonal cycle of mesozooplankton biomass (Fig. 5). As either abundance or biomass, the zooplankton maximum occurs during summer months when the stratified water column is most isolated from nutrient inputs from mixing (Landry et al., 2001). The biomass amplitude is about 400 mg DW m^{-2}, a factor of two for permanent (daytime) residents of the euphotic zone, with a comparable amount added approximately uniformly throughout the year by nighttime migrants. Coincidentally, summer is also broadly the time of the seasonal maxima in phytoplankton standing stock, primary production and carbon export from the euphotic zone (Letelier & Karl, 1996; Karl, 1999; Scharek et al., 1999). Thus, the timing of this phytoplankton increase defies conventional explanation from physically driven nutrient fluxes.

Where this system differs from convention is in the seasonal occurrence of large nitrogen-fixing phytoplankton, which thrive under highly stratified oligotrophic conditions, particularly when the sea surface is calm. In June–July 2000, for example, an extensive bloom area visible from SeaWiFS color imagery was dominated by diatom species (*Rhizosolenia*, *Hemiaulus* and *Mastogloia* spp.) containing the diazotrophic endosymbiont, *Richelia intracellularis*. In September 2001, filamentous cyanophytes, *Trichodesmium* spp., were the dominant N$_2$-fixers in sampled bloom waters. These taxa, all previously noted in CLIMAX studies (Venrick, 1974; Heinbokel, 1986), provide a biologically derived 'new' nitrogen source to stimulate development of the seasonal biomass accumulation. In addition, they may also provide, by
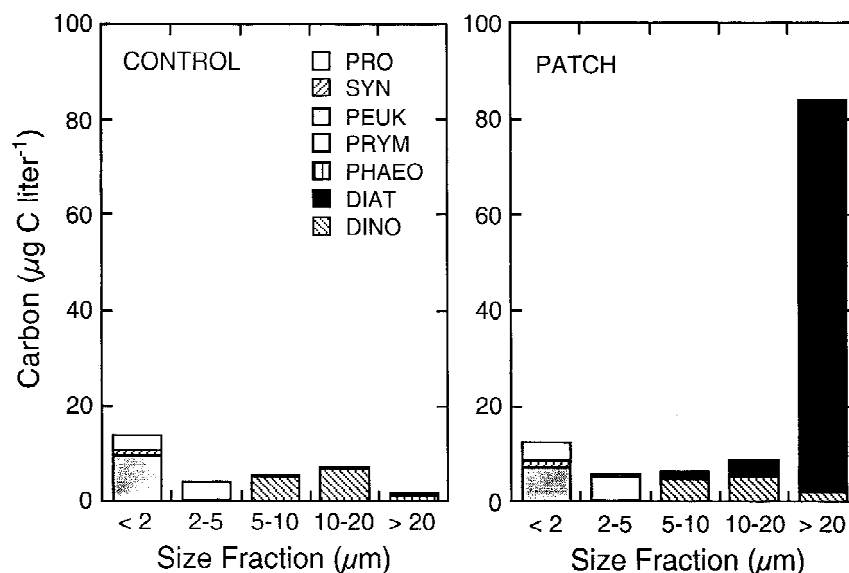
Figure 4. Phytoplankton community size structure in the ambient environment (CONTROL) and the iron-fertilized PATCH during the IronEx II study (eastern equatorial Pacific, May–June 1995). Carbon estimates are based on flow cytometric analyses of picophytoplankton (PRO=*Prochlorococcus*, SYN=*Synechococcus*, and PEUK=picoeukaryotic algae) and biovolume-based microscopical assessments of prymnesiophytes (PRYM), *Phaeocystis* (PHAEO), diatoms (DIAT) and dinoflagellates (DINO). Distributions are the means of three sampling dates in ambient and four days of sampling during the peak of the patch bloom (modified from Landry et al., 2000a).

buoyancy regulated migrations (Villareal et al., 1993), a source of other minerals such as phosphate (Karl, 1999). Recently discovered coccoid cyanobacteria (3–10 μm) have also been suggested to contribute to nitrogen fixation in the subtropical Pacific (Zehr et al., 2001), but their seasonal cycles of abundance and activity have yet to be determined.

One of the important biogeochemical functions of N_2-fixing phytoplankton is their disproportionate contribution to export fluxes and carbon sequestration by the biological pump. Physical mixing of NO_3^- into the euphotic zone, for example, also injects previously remineralized carbon in the approximate molar ratio of 6:1. This largely offsets the carbon ultimately exported in sedimenting material. In contrast, 'new' nitrogen from the reduction of gaseous N_2 to NH_4^+ within the euphotic zone is unencumbered by a deep-ocean carbon complement, and the full value of its carbon export must be replaced by carbon absorbed from the atmosphere. In addition to this larger multipling factor for net carbon export, the large size of the classical N_2-fixing phytoplankton (*Trichodesmium* and diatoms) facilitates export efficiency and deeper depth penetration by mass aggregate settling (e.g. Scharek et al., 1999) or the fecal pellets of large consumers. Both production and export pathways are thus sensitive to seasonal or long-term changes in community compos-
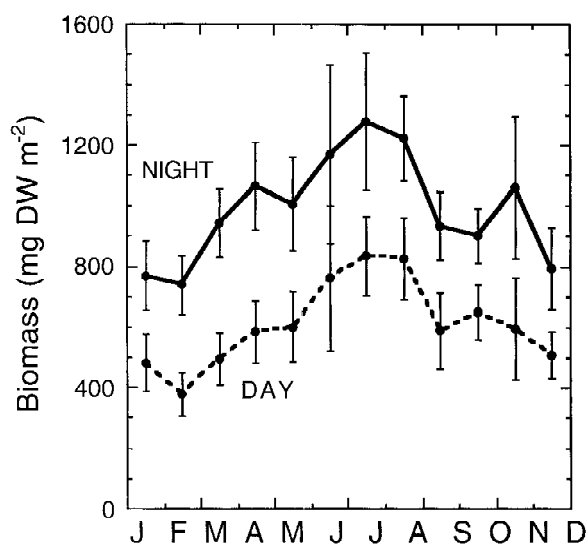

Figure 5. Seasonal variation of mesozooplankton biomass in daytime (1000–1400) and nighttime (2200–0200) net collections at Stn. ALOHA, subtropical North Pacific. Dry weight samples were taken from integrated oblique hauls over the euphotic zone (mean tow depth=155 m) with a 1-m^2 net and 200-μm mesh (Landry et al., 2001). Error bars are 95% confidence intervals for the means of all samples collected within each month from 1994 through 2000.

ition that involve shifts in the relative importance of large, N_2-fixing phytoplankton.

Long-term trends

Planktologists and fisheries biologists have historically noted periods of increase or decrease in the organisms of their specialties, but long-term data sets have only recently revealed coherent patterns among different components of communities, functionally comparable organisms separated by long distances, and physical indices of potential forcing mechanisms. In the Pacific, interacting cycles of the El Nino-Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO) and the North Pacific Mode (NPM) appear to link the dynamics of adjacent ocean regimes in complex ways (Hare & Mantua, 2000; Barlow et al., 2001). This new awareness of long-term and large-scale climatic linkages and the desire to understand and predict future trends is stimulating fresh insights about the functional interrelationships and ecology of open-ocean ecosystems.

In the subtropical North Pacific, for example, the ecological importance of nitrogen fixation appears to be part of a recent, possibly cyclical, regime shift which Karl (1999) attributes to decreased trade wind forcing and altered gyre circulation, and ultimately to ENSO and PDO variations. Increased stratification and decreased nutrient fluxes from below the euphotic zone enhance oligotrophy and select for nitrogen fixers. These, in turn, alter nutrient balances, driving the system to phosphorus limitation. Over the 18 years of CLIMAX studies, total phytoplankton standing stock, as inferred from standard chlorophyll measurements, increased by about a factor of two (Venrick et al., 1987). Over the same time, species dominance structure among classical eukaryotic phytoplankton (diatoms, dinoflagellates and coccolithophores) changed significantly (Venrick, 1995).

Comparing phytoplankton pigment trends in recent collections at Stn. ALOHA (22° 45′ N, 158° W) to those at the CLIMAX site (28° N, 155° W), Karl et al. (2001) have further speculated that *Prochlorococcus* spp. are now more abundant than they were previously, before their discovery. At least according to the current thinking described above, *Prochlorococcus* should always be able to compete efficiently for limiting nutrients and only enhanced and sustained levels of direct grazing pressure from bacterivores could keep them consistently below present abundances. Thus, such a change would need to be driven by a realignment of top-down predatory pressures within the microbial grazing chain. Some alteration of consumer networks are suggested by two-fold higher levels of mesozooplankton biomass at Stn. ALOHA today than those in historical CLIMAX collections (Landry et al., 2001), but there is no way to assess how intermediate levels of protistan consumers may have changed.

As implied above, we are increasingly aware of how the interpretations of long-term and large-scale changes in the open ocean both influence and involve organism interactions at all levels. With the articulation of explicit working hypotheses (e.g. Karl et al., 2001) comes the challenge to make the necessary measurements and experimental tests for resolving mechanisms.

Summary

It is not the intent of these brief comments to disassemble the components of open-ocean food webs and argue their relative merits. This would only undo advances over the past two decades that have brought disparate concepts and paradigms into a more satisfying and integrated whole. Upon reflection, however, it does seem that certain ironies have emerged from the integration of these ideas. For one, the concept of a simple linear food chain applies rather poorly to the classical views of plankton trophic complexity to which it is ascribed. However, it aptly describes our present understanding of the dominant energy pathway from bacteria through protists, although this is likely to change with additional focused research. Similarly, the hypothetical balance between phytoplankton growth, grazing and remineralization processes was proposed at a time when we knew only classical planktonic plants and animals. It now represents the accepted mechanistic explanation for microbial community stability, against which the imbalances and dynamics of larger plankton are seen to occur. Further, the discoveries of major groups of photosynthetic microbes (*Prochlorococcus*, *Synechococcus* and pico-eukaryotic algae) may make the 'climax' phytoplankton communities of the oligotrophic central gyres somewhat less, not more, diverse than previously thought. This might nonetheless help to bring our mechanistic understanding of marine plankton diversity in line with current ecological theory. Lastly, in an oligotropic ocean system indisputably dominated by microbes, new importance is ascribed to classical planktonic taxa (e.g. *Trichodesmium* and symbiont-containing diatoms) which now seem to hold the answers to unconventional seasonal blooms, carbon

sequestration potential and climate-driven community responses.

Facilitated by time-series observations, new perspectives and paradigms, and advancing technologies, research to date has given us tangible evidence of long-term and large-scale patterns and trends in open-ocean ecology. Our evolving understanding emphasizes the interconnections among climate-driving forces, oceanic physical, chemical and biological responses, and particularly the interactions and feedbacks among organisms in an integrated food web. Many open issues and challenges remain. In particular, we need to define better the diversity in taxa and function at lower levels of the food web. We can hopefully look forward to many more years of progress in developing a mechanistic understanding of these complex systems.

Acknowledgements

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