

Macroscopic Patterns in Marine Plankton

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Glossary

Comparative analysis Pattern-seeking across natural ecosystems based on the premise that existing gradients and variations generate regularities which can be discerned by statistical analysis of the composite aggregate, of component variables, or of mechanistic connections.

Complex adaptive system A system of multiple interconnected diverse elements whose localized interactions are subject to autonomous selection, leading to continual change and hierarchical structure.

Ecological stoichiometry The quantitative relationship between chemical elements (especially carbon, nitrogen, and phosphorus) arising from ecological processes and interactions such as nutrient acquisition, biomass formation, remineralization, trophic transfer, sedimentation, and dilution.

Macroscopic pattern Regularity observed at a scale higher than that of the interacting units, being the statistical or emergent expression of the ensemble arising from the components.

Multiscale analysis A change in the resolution or range of a measurement to evince a change in pattern.

Plankton functional types A classification of plankton according to commonly shared adaptive features such as physiological and morphological traits which lead in

combination to predictable ecosystem or biogeochemical functions.

Plankton size classes A classification of plankton according to size, based on the International System of Units prefixes of the approximate live weight in grams for successive logarithmic intervals of organism width or length: femtoplankton (0.02–0.2 μm), picoplankton (0.2–2 μm), nanoplankton (2–20 μm), microplankton (20–200 μm), mesoplankton (0.2–20 mm), macroplankton (2–20 cm), and megaplankton (20–200 cm).

Plankton trophic types A classification of plankton according to whether they obtain energy from light ("photo") or chemicals ("chemo"), whether they obtain electrons from water ("litho") or organic carbon ("organo"), and whether they obtain carbon from inorganic ("auto") or organic ("hetero") compounds, with the possibility of mixed modes ("mixo"): for example, photolithoautotrophy, chemoorganoheterotrophy, photoorganoautotrophy, photoorganoheterotrophy, and mixotrophy.

Power law A relationship that scales a dependent variable (Y) to an independent variable (X) through a normalization factor (a) and a power exponent (b) in the form $Y = aX^b$.

Scale The distance or time over which a significant change in some quantity of interest can be resolved.

Microscopic Organisms and Macroscopic Patterns

Marine Plankton

Marine plankton are pelagic organisms, motile or nonmotile, that are entrained by the prevailing movement of water. These biological entities range over many orders of magnitude in size from nanometer-scale viruses of the femtoplankton to meter scale gelatinous animals of the megaplankton. By numbers, biomass, and diversity, it is the microscopic forms of plankton that pervade the oceans. The majority of these are prokaryotes and unicellular eukaryotes. Global estimates of prokaryotic marine plankton indicate a stock of 10^{29} cells, a

biomass of over 2 Pg carbon, and a genetic richness of perhaps up to 2 million different kinds of taxonomic units. These bacteria and archaea, together with the smaller pool of eukaryotic algae and protists, constitute the foundation of pelagic food webs. In oxygenated waters, most microbial plankton are photolithoautotrophs, chemoorganoheterotrophs, or mixotrophs, but significant number of them also possess capabilities for photoorganoautotrophy or photoorganoheterotrophy. Thus, not only is there great diversity in size and form amongst the microbes, but also there is a wide range of metabolic functions. All other plankton, being metazoan, are chemoorganotrophs and depend ultimately on the microbes. Individually, plankton live short lives and

interact over short distances. However, they have collectively established the conditions for life over the entire Earth since the beginning of evolutionary time, and continue to maintain biospheric integrity through complex adaptations.

Patterns and Processes

In ecology, a pattern can be described as regularities in what we observe in nature; that is, they are widely observable tendencies (Lawton, 1999). Importantly, patterns can exist at various scales in time and space. A macroscopic pattern is one in which the regularity is observed at a scale higher than that of the interacting units. At each scale, the number of biological units is larger than that at the next higher scale. The expression of the ensemble in terms of the component units results in the pattern, which is called macroscopic. The study of macroscopic patterns in ecology is macroecology, and it can be stated as the enterprise of trying to infer laws of nature from the statistical manifestations of the many interacting biotic units of ecological systems (Brown, 1995).

A bulk effect, which is a statistical resultant of aggregating system components, is no less a macroscopic character than an epiphenomenon that emerges from underlying complexity, or one that appears out of constraints imposed from even larger scales. Thus, macroscopic patterns can arise from large number systems in which many independent, essentially identical components interact randomly to give system averages, which are stated in the formalism of statistical mechanics. Macroscopic patterns can also arise from systems in which intermediate numbers of components interact in structured and complex interrelationships. Plankton might be viewed as complex adaptive systems because the essential elements of such systems are in place: natural selection acting on individual components with diversity sustained through localized interactions yielding a subset for replication or enhancement (Levin, 1998). Indeed, macroecology might be considered a perspective on ecological complexity, whether one believes populations and communities to be complex adaptive systems, or simply to be the convenient assemblages of organisms selected for study (Brown, 1995).

In a strict sense, a macroscopic pattern refers only to that which is observed. It is a separate and much more difficult matter to understand the determinant, which is the process. Pattern seeking is an exercise in empirical observation, and the enterprise of large numbers often requires observation over extensive geographic areas and over prolonged durations. Biogeography and macroevolution are therefore sometimes implicated in macroecology, but macroscopic patterns need not necessarily inform about these disciplines. Understanding process through deduction is a part of the macroecological agenda; but it necessarily follows inductive insight gained from pattern detection.

Comparative Ecology and Macroecology

Comparative Analyses of Plankton Ecosystems

The study of macroscopic patterns is a well-established part of biological oceanography, even though the neologistic origin of macroecology is strongly based in terrestrial and avian eco-

logy. At a symposium held in 1956, Alfred Redfield addressed the imbalance of experiment and observation in marine biology and suggested that "to understand the distribution and abundance of life in the sea, the approach must be primarily statistical through the development of significant relationships between large quantities of observations on biological and physical events, occurring often in widely scattered places" (Redfield, 1960). Essentially, this is a prescription for comparative analyses of ecosystems, an approach that has since been extensively used in the study of plankton.

Some of the most common comparative analyses in aquatic ecology are bivariate relationships between plankton trophic groups (Gasol and Duarte, 2000). Plankton are adaptive and complex, so it becomes a simplification when single variables are chosen as surrogates for entire trophic groups. In principle, this simplification is not necessary for comparative analyses, but the demands for large number analyses require measurements that are operationally well defined and easy. For example, the entire photoautotrophic pelagos is often represented by the concentration of chlorophyll *a*. In many cases, this photopigment is not only an adequate and suitable surrogate for the diversity of unicellular algae and cyanobacteria, but is also a useful predictor variable amenable to widespread application. In other cases, however, the surrogate confounds process and obscures patterns. Generality at a high level of description comes at the expense of a loss in detail at a lower level.

Macroecology in Biological Oceanography

The spatial and temporal structures in plankton ecosystems are a fertile area for macroecological study because some aspects are accessible to easy measurement at many scales. For phytoplankton, if we do not restrict the definition of structure only to ecosystem rate parameters, but also admit state variables, then either the surrogate of chlorophyll *a* (and its many proxies such as fluorescence and ocean color) or direct counts of individual cells can provide useful information across many scales. In this way, horizontal distributions of phytoplankton can be studied from turbulent regimes of local environments (Platt, 1972) to biogeochemical regimes of the global ocean (Platt and Sathyendranath, 1999). The premise that phytoplankton distributions are under the broad control of abiotic forcing at regional and global scales allows the pelagos to be viewed in an ecological geography rather than in a traditional biogeography (Longhurst, 1998). In other words, areas of the ocean with common abiotic forcing might be expected to have similar ecologies (Platt *et al.*, 2005). Testing this premise with other plankton is more difficult because of limited data, but some progress can be seen in studies of heterotrophic bacterioplankton, which show marked contrasts at the largest scale of ecological domains (Ducklow, 2003). In the ocean, variations in physical forcing tend to increase with spatial and temporal scales. Red noise, so called, makes a dominant difference in the variance structure between marine and terrestrial systems, and is associated with stronger adaptive responses to long-term change in the ocean (Steele, 1985). Spectral analysis, as a statistical mechanical representation of ecological systems, has deep roots in phytoplankton studies

(Platt and Denman, 1975). Macroecology, it seems, has always been a part of biological oceanography.

Scales of Variability

Multiscale Analysis

The linkage of spatial and temporal variability is a long-standing concept in oceanography. Graphical representations of the variability in a measured quantity in the space–time domain are familiar to physical oceanographers, for example, the Stommel diagram, and to biological oceanographers, for example, the Haury–McGowan–Wiebe diagram (Haury *et al.*, 1978). In logarithmic fashion, time ranges from minutes to hundreds of thousands of years on one axis, space ranges from centimeters to tens of thousands of kilometers on a second axis, and biological variability is indicated on a third axis. These diagrams portray the overlapping hierarchy of patterns along the diagonal, stretching from small space–time scales to large space–time scales. They also convey the reality that what can be perceived is limited by the narrow space–time window through which observations are made. The search for macroscopic patterns is an exercise of increasing the scale of analysis.

In multiscale analysis, a systematic change is made to the scope of a quantity. Scope, which is the dimensionless ratio of extent to grain, expresses space or time as the number of

measured units adding up to the length of the investigation. For example, if plankton is collected from a site once every week (the grain) for a total duration of 14 years (the extent), the scope is 728 ($52 \times 14/1$). Various scaling methods exist to change the scope (Schneider, 2001).

Coarse Graining

The method of coarse graining takes the full extent of the weekly measurements and averages them within increasingly larger grain sizes, such as a month, a year, a quadrennial, and so on. An example is shown for time series of bacterioplankton and phytoplankton sampled weekly for 14 and 13 years, respectively (Figure 1). Averaging of raw measurements into increasingly larger grains reduces variance. In the example, at the largest grain of a year, all the weekly heterogeneity becomes unresolved, and the between-year heterogeneity decreases (Figure 1(d)). It then becomes meaningful to seek a long-term (macroscopic) signal from the annual averages unencumbered by the weekly noise. For the phytoplankton in this example, cell abundance has increased at a rate of 4% per year from 1993 to 2005. As the time series lengthens into the future, it should not be a surprise if annual variance were to increase since a larger extent encompasses more realized situations. Emphatically, this multiscale analysis demonstrates the difficulty of empirically detecting a

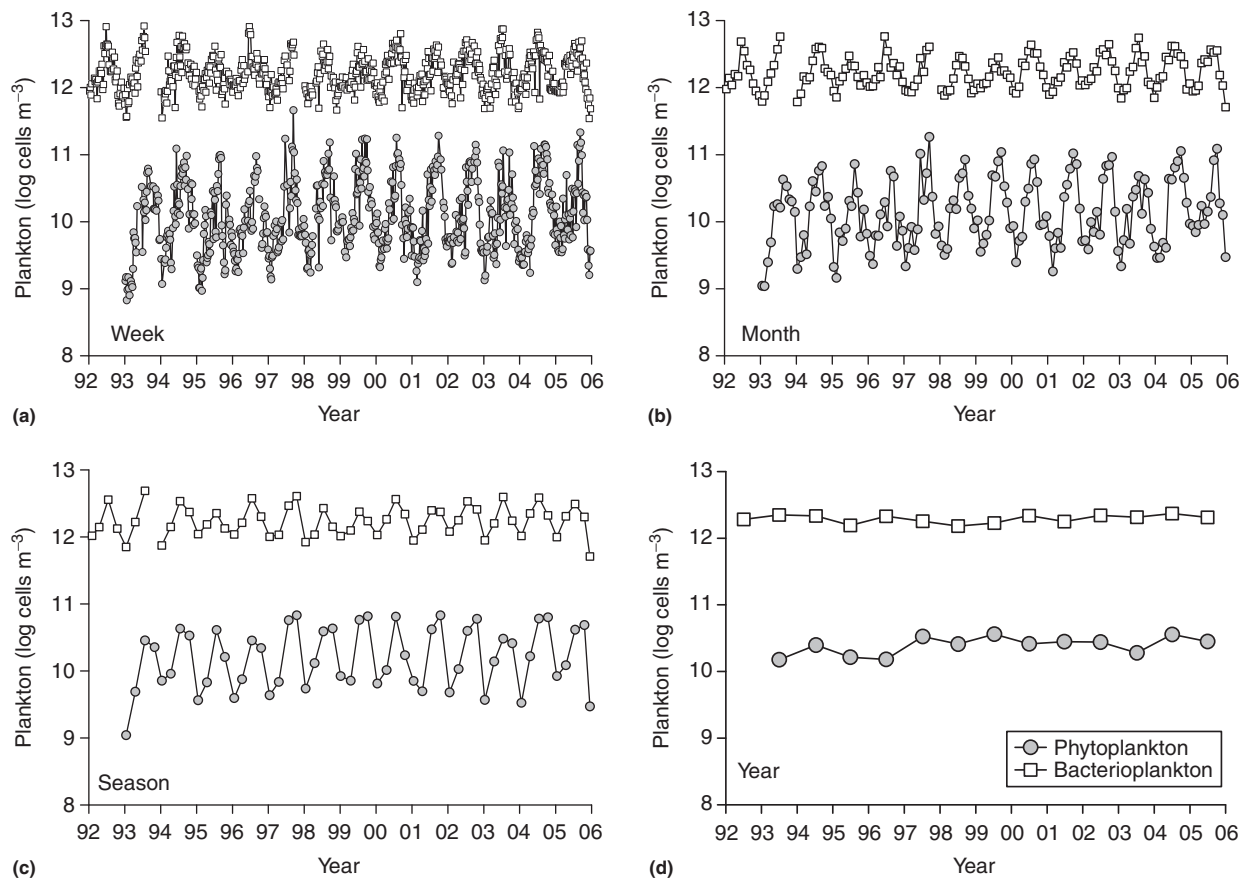


Figure 1 Multiscale analysis by coarse graining. Time series of phytoplankton and heterotrophic bacterioplankton abundance in Bedford Basin, Canada from 1992 to 2005. (a) Weekly measurements, (b) monthly averages, (c) seasonal averages, and (d) annual averages.

multiyear trend if either the grain size of raw observation is not small enough, or if the extent is not large enough.

Accumulating

Another method of changing the scale of analysis is to accumulate an increasing collection of samples. By always using the same operational procedure for collection, each sample may be considered an element in the set of all possible configurations. The more samples accrued, the higher the degree of aggregation. A herculean human endeavor of counting and identifying all 195,983 microphytoplankton cells in 1388 Mediterranean Sea samples, and all 1,111,859 such cells in 1144 Caribbean Sea samples by Margalef (1994) and his colleagues is a majestic exemplar. From these ensembles emerge an elegantly succinct pattern: $S(n) \propto n^{-1}$, which is to say that there is a simple power-law relationship between the number of individuals, n , and the number of species, S , represented by that particular number of individuals (Solé *et al.*, 2002). In other words, only a few species have large populations of individuals, but many species have small populations.

With electronic technology, it is possible to count picophytoplankton and nanophytoplankton with considerable ease. The detection of these cells is based on biooptical characteristics such as light scatter and photopigment autofluorescence. Bivariate diagrams plot each cell as a single dot on an $m \times m$ grid (where m is usually 256 or 1024) representing the position of the cell on the coordinate space of light scatter and pigment fluorescence. A subsequent cell that occupies the same coordinates makes the display dot darker in appearance. The result of analyzing a single water sample is a cytometric diagram showing the density of occupancy of the coordinate space. One such realization taken on a single day in 1996 detected several thousand cells (Figure 2(a)). Samples measured week after week (Figure 1) accrued over an entire year greatly increase the number of cells. A larger portion of the coordinate space is occupied by the yearly accumulation, and the cell abundance at occupied positions increases. At this annual level, there is an accrual of a few hundred thousand cells (Figure 2(b)). The procedure can be carried further to show accumulation of greater than a million cells at the quadrennial scale (Figure 2(c)), and finally to the extent of the entire 676-week time series (Figure 2(d)) during which 5 million cells have been counted. By pooling all fluorescence measurements at a given light scatter value into a single bin, the cytometric data can be displayed as univariate frequency histograms resembling cell-size spectra. Increasing the scale by accumulation transforms the heterogeneous single-week spectra (Figure 3(a)) to more homogeneous annual (Figure 3(b)) and quadrennial spectra (Figure 3(c)), and finally to the unitary 13-year spectrum (Figure 3(d)). As with coarse graining, accrual smooths out variance.

Macroscopic Assembly

Trophic Classification

One of the most enduring constructs in ecology is the trophic pyramid. Organisms are assigned to one, and only one, of a

small number of feeding categories, which are then arranged in food chain sequence, showing the importance of each trophic level in relation to those below and above it. Traditionally, the categories are primary producers (autotrophs), decomposers (bacteria), primary consumers (herbivores), secondary consumers (carnivores), and tertiary consumers (apex predator). Importance can be indicated by the number of individuals, by total biomass, or by energy flux. Trophic diagrams of energy are constrained by thermodynamics to have an upward pyramidal shape, but diagrams of numbers and biomass are free to assume other appearances, even inverted pyramid. Plankton biomass pyramids built of autotrophs (phytoplankton) and heterotrophs (bacterioplankton, microzooplankton, and mesozooplankton) have a tendency to be inverted in open ocean waters. This implicates both a fast turnover of phytoplankton and a tight consumer control of primary production (Gasol *et al.*, 1997).

A trophic pyramid might be considered a nonnested hierarchy. In other words, the apex predator in a marine food chain does not nest within it (as reducible components) all the carnivorous zooplankton, the herbivorous zooplankton, and the phytoplankton. Yet, the system is a hierarchy as defined by a system of communication where entities with slow behavior are at the top, while successively faster behaving entities occur lower in the hierarchy (Allen and Starr, 1982). In principle, the behavior of some nested hierarchies may be determinable if observations are sufficiently complete so that the parts can be added up. There are other properties of nested systems that could prevent this realization; but in any case, actual determinability in real ecosystems is likely unachievable. However, nonnested hierarchies are truly indeterminable because the entities are themselves quasi-independent wholes, with nested hierarchies within each (Allen and Starr, 1982).

For several reasons, the pyramid as described is less useful as a construct for plankton ecosystems than it once may have appeared to be. As a system that transfers mass and energy in a linear route from plants to herbivores to carnivores, the traditional pyramid fails to give explicit account to the microbial loop, which diverts primary production to heterotrophic prokaryotes (bacteria and archaea) and thence to phagotrophic protistan eukaryotes (microzooplankton). Microzooplankton is an important prey for mesozooplankton, so trophic linkage remains; but the microbes as a whole are a large respiratory sink, which greatly alters the dynamic functioning of the system. The pyramid also fails to recognize the viral shunt, which by recycling energy within the microbial loop becomes a futile path for any transfer to metazoans. Finally, the idea that an organism must be of a singular trophic type is too restrictive since mixotrophs are common.

Nevertheless, the partition of plankton into nominal trophic groups offers ecological insight that can be particularly robust in statistical terms. The structural relationship between trophic groups is most often represented by a linear model. As more ecosystems are progressively sampled, a greater degree of natural variability is encountered. Patterns formed by a large number of observations have more freedom to reveal nonlinear structures such as thresholds, boundaries, and inflections (Duarte, 1991). For example, the relationship between oceanic bacterioplankton and phytoplankton appears linear in regional ecosystems, and this is consistent

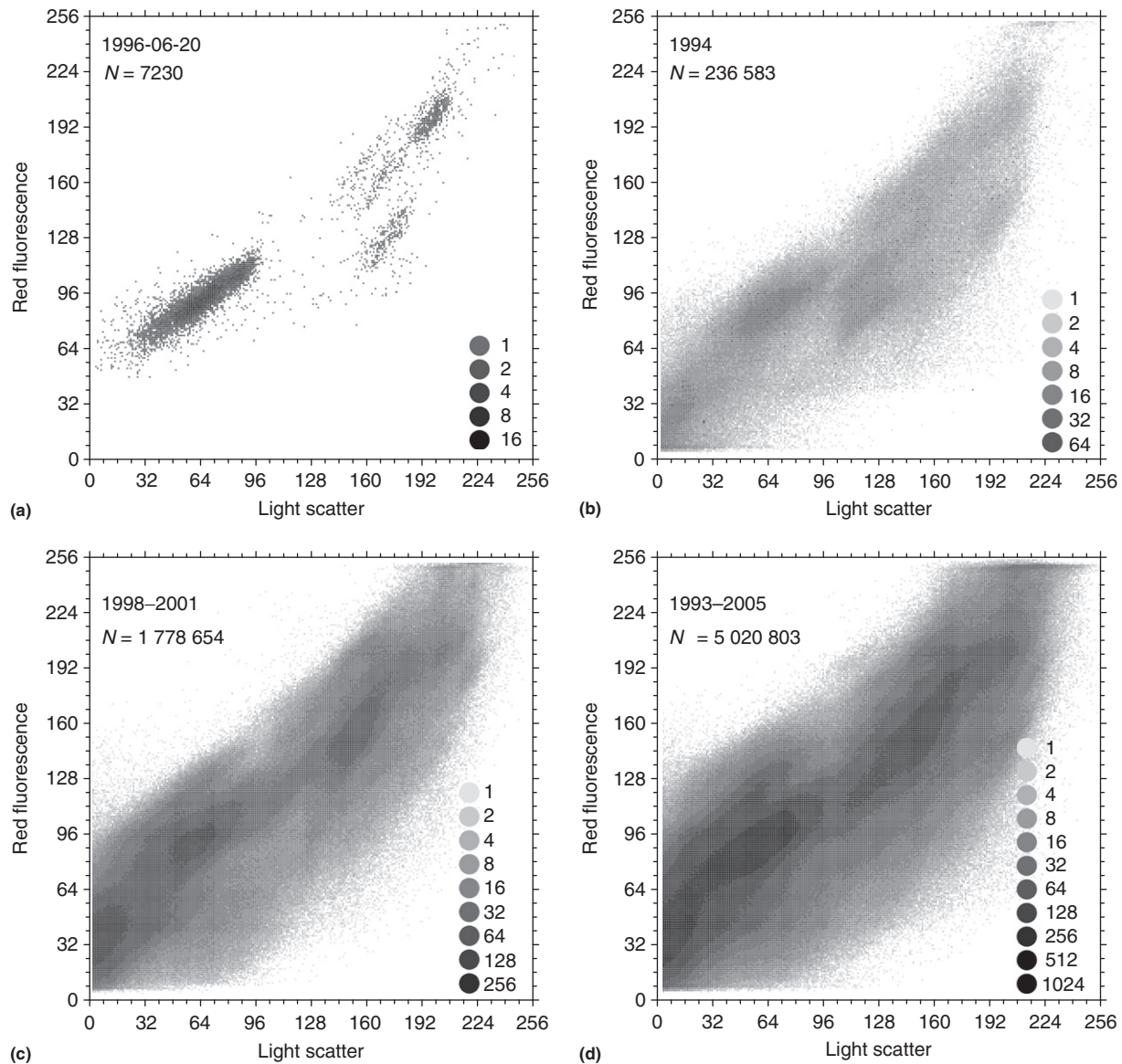


Figure 2 Multiscale analysis by accumulation. Bivariate plots of phytoplankton in Bedford Basin showing the density of particle occurrence in the coordinate space of cellular light scatter (cell size proxy) and cellular red fluorescence (chlorophyll *a* proxy). (a) Measurement on a single day, (b) annual accumulation, (c) quadrennial accumulation, and (d) 13-year accumulation.

with known mechanisms of carbon flux between the interacting trophic groups. However, a global aggregation of these observations reveals a nonlinear constraint on the actualized expression, indicating a need for more descriptive details of other interacting components (Li *et al.*, 2004). Interestingly, with appropriate attention to statistical nuances, it may be possible to invert the problem and use cross-system information to investigate the structural relationship between variables within a single system (Prairie and Marshall, 1995).

Size Classification

Organism size has been a fundamental organizing attribute in plankton ecology since the early days of oceanography when

nets of different mesh size were used to selectively retain plankton. The fact that named plankton size classes (see Glossary) are arrayed in logarithmic series is tacit recognition of the importance of power-law scaling. As a means to manage complexity, power-law scaling of plankton size has much appeal because it portends consilience with many other natural systems. Metabolic rate is related to body size of organisms ranging from microbes to the largest vertebrates through a common power exponent whose value is generally (but not universally) taken to be < 1 . Although new evidence suggests that even suborganismal entities (mitochondria and respiratory complexes) may share the same exponent (West *et al.*, 2002), considerations of nonscalable components within a cell such as a minimum genome and biological membranes of constant thickness may imply a different power exponent for the

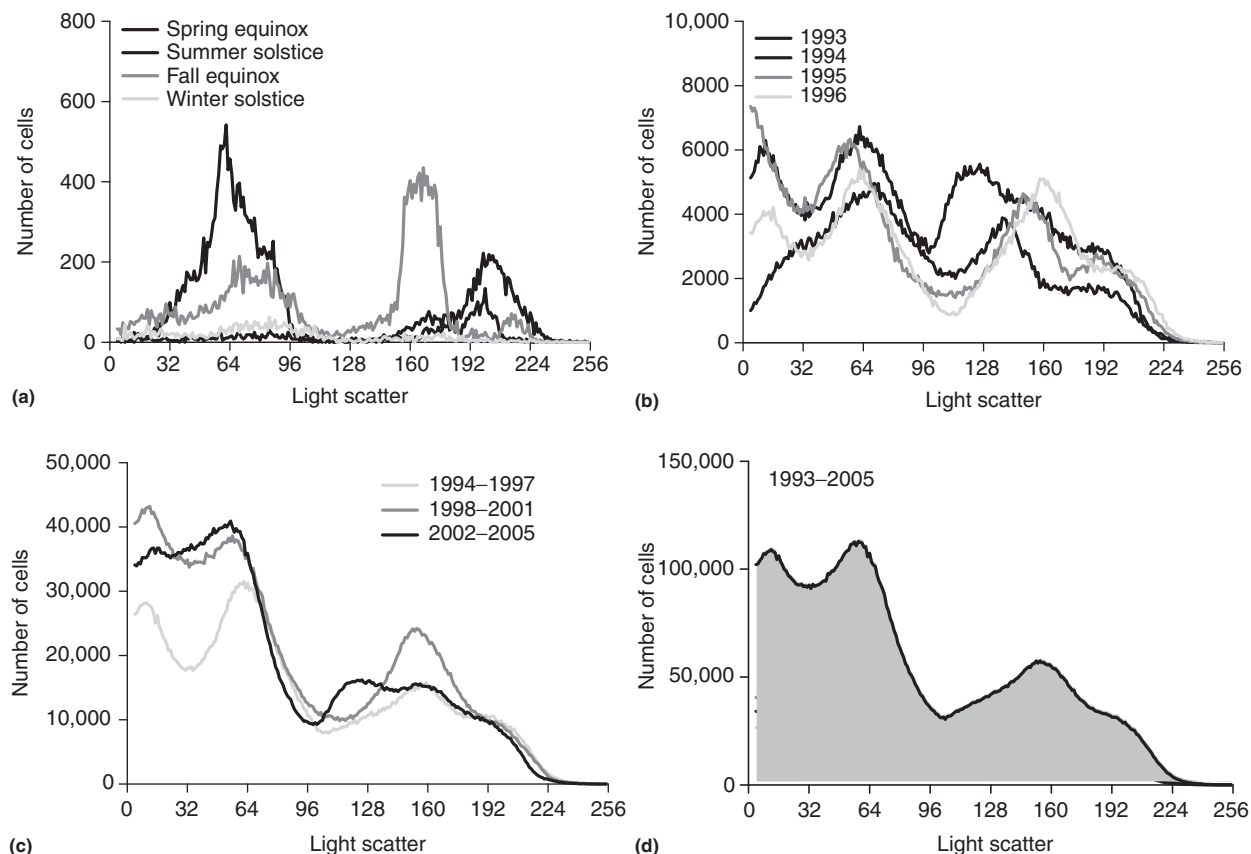


Figure 3 Multiscale analysis by accumulation. Size-frequency histograms of phytoplankton in Bedford Basin. (a) Four weekly measurements, (b) four annual accumulations, (c) three quadrennial accumulations, and (d) 13-year accumulation.

smallest picoplankters (Raven *et al.*, 2005). Notwithstanding the exact value of the exponent, metabolic scaling has given rise to various theoretical models deriving the distribution of organism abundance and biomass according to body size. All such models, implicitly or explicitly, address one of the most striking macroscopic patterns in pelagic ecology. This pattern, first anticipated by pioneering ecologists Charles Elton and Howard Odum, was demonstrated by observations made by Sheldon *et al.* (1972) showing that in the euphotic zone of oceanic regions, “to a first approximation, roughly equal concentrations of material occur at all particle sizes within the range from 1 to 10^6 μm , i.e., from bacteria to whales.”

Trophic models of plankton size spectra take apparent universal metabolic scaling within each trophic level, assign a large difference to the body size of predator and prey, and dissipate energy at each feeding step (Kerr, 1974). Biomass invariance across logarithmic size classes can indeed be an outcome of these models (Brown *et al.*, 2004). Microbial ecologists who view the plankton system at a lower hierarchical level may find the simplifications to be unjustified. They see primary producers virtually span the entire size range from picoplanktonic *Prochlorococcus* to macroplanktonic *Trichodesmium*; they see a considerable number of unicells functioning at more than one trophic level; and they see a majority of protistan grazers only slightly larger than their prey, and therefore in a closely adjacent logarithmic size class.

An alternative model of unidirectional biomass flow from small to large organisms (Platt and Denman, 1978), inspired by the cascade of turbulent energy from small to large wave numbers, replaces discrete trophic levels with a size continuum. The model predicts a slight decrease of biomass with size. This has been confirmed in both the North Pacific (Rodríguez and Mullin, 1986) and the North Atlantic (Quiñones *et al.*, 2003) by high-resolution spectra carefully constructed by merging windows of observation derived by different plankton measurement technologies. A strength of this model is that it can be integrated analytically to yield metabolic information for the community as a whole, therefore providing constraints on function based on structure. A difficulty, pointed out by Platt himself, is the need to reconcile the microbial loop, which is a counterflow of material against the general direction.

At an adequately high level of aggregation, such as achieved by accumulating inventories from many different habitats acquired over many years into a “superspectrum,” a similitude appears toward a system in which biomass is shared randomly among size classes without preference (Rodríguez, 1994). This type of power-law distribution suggests another way to regard plankton size spectra, namely as a case of scale invariance or self-similarity. In other words, plankton systems may not have any characteristic scale and the components may be organized according to dynamics that cross scales.

Self-similarity thus provides a means to extrapolate between scales.

A notable example of power-law phenomena in plankton can be found in the microbes where, coincidentally, trophic and biomass flow concepts are least clear-cut. In this limited range at the low end of the size spectrum, not only does a power law describe the community (Li, 2002), but also a related power law with the same scaling exponent also describes the relationship between abundance and size for the components: heterotrophic bacteria, *Prochlorococcus*, *Synechococcus*, other picophytoplankton and nanophytoplankton (Rinaldo *et al.*, 2002). The individual distributions are strongly peaked, but partial overlap in size from one to another results in smoothed ensembles. Where one group (e.g., *Prochlorococcus*) might be missing, there might be more of another (e.g., heterotrophic bacteria) or a broadening of the distribution of another (e.g., *Synechococcus*) to fill the gap (Cavender-Bares *et al.*, 2001). Individuals interact with each other locally but become organized into aggregates that appear regular. The size structure of the phytoplankton community may at times be strongly regulated by factors such as competition, grazing, infection, sinking, and physical aggregation, but it also seems that size scaling of cellular nutrient requirements and growth alone can suffice to produce widely observed features such as the power-law relationship, the dominance of small phytoplankton cells in oligotrophic oceans, and the relative increase in large phytoplankton cells under eutrophic conditions (Irwin *et al.*, 2006).

Functional Classification

In terrestrial ecology, plant functional types are sets of species with similar responses to the environment and with similar effects on ecosystem functioning. In essence, this classification seeks functional commonalities in life forms that cut across phylogenetic, autecological, and allometric diversities. Extending this concept to phytoplankton has resulted in detailed assembly rules for freshwater assemblages (Reynolds *et al.*, 2002) and marine dinoflagellates (Smayda and Reynolds, 2001). In these works, the primary emphasis has been on recognizing shared adaptive features that favor a close association of certain organisms well disposed toward certain habitats. These organism associations are mapped against a matrix of habitat gradients (nutrients, irradiance, and water turbulence) to reveal a pattern at a macroscopic level. Functional classification is a polyphyletic approach that arranges organisms according to their biological attributes and sensitivities, which are associated with particular habitat conditions. But even so, proceeding through a hierarchical filter to match the traits of class, genus, and species against habitat conditions, it is still not possible to predict at a low level (even if all traits were completely known) because selection is ultimately stochastic.

The concept of plankton functional types is similar to plant functional types, but oceanographic application emphasizes common effects on ecosystem functioning over common responses to environment. A prospectus for assessing the biogeochemical impact of plankton activities recognizes 10 provisional types: picoheterotrophs, picoautotrophs,

phytoplankton nitrogen-fixers, phytoplankton calcifiers, phytoplankton dimethylsulfide producers, phytoplankton silicifiers, mixed phytoplankton, protozooplankton, mesozooplankton, and macrozooplankton (Le Quéré *et al.*, 2005). This is clearly a mixed classification with some elements closely similar to trophic and size classes. Nevertheless, the idea of functional diversity is well accepted. Plankton functional types, appropriately clustered or ordinated, occupy an ecological trait space where the functional distance between types may be quite different from traditional measures of species differences (Weithoff, 2003).

Biogeochemical modeling of plankton functional types at the global scale requires sufficiently well-understood autecologies, a realistic type classification, and robust parameterizations: these are requirements perhaps not well met at present (Anderson, 2005). Nevertheless, it is understood that macroscopic patterns of functional types are a powerful way to study community structure. As an example, phytoplankton silicifiers, which are largely diatoms (but may also include silicoflagellates), can be indicated by their pigment composition or their spectral absorption characteristics. Inferences made from the broad distributions of fucoxanthin (measured by chromatography) and a water-leaving reflectance indicator (derived from satellite data) are consistent with known features of diatom distributions (Platt *et al.*, 2005). Although neither analytical chemistry nor spectral radiometry is incisive enough to provide an irrefutable diagnostic of diatoms, spatial mapping of proxy indicators allows the study of some plankton functional types at the large scale. Other plankton functional types have also been detected by satellites. These include calcifiers that detach high-reflectance coccoliths (Brown and Yoder, 1994), nitrogen-fixing *Trichodesmium* cyanobacteria that have a relatively unique spectral signature of high backscatter from gas vesicles, combined with the absorption and fluorescence of phycoerythrin (Subramaniam *et al.*, 2002), and bioluminescent bacteria which continuously emit light when concentrations of autoinducer are locally high (Miller *et al.*, 2005).

Phylogenetic Classification

It is in the sense of phylogeny that biological diversity is most widely understood. The arrangement of organisms according to their evolutionary relatedness in a nested hierarchy of taxonomic ranks is the basis on which marine autecology, conservation, and resource management is generally conducted. Many general ecological theories are strongly grounded in evolutionary relationships between species; therefore, it seems expedient to explore macroscopic patterns of plankton in that framework. However, to a considerable extent, those theories rely on human perception of morphology and lifestyle as a guide to differentiating between organisms. This guide fails us at the small scales of microbial plankton because organisms with a high ratio of surface area to volume appear to converge on relatively uniform morphological shapes such as spheres and rods. When organisms are very small, adaptive adjustments largely appear within the living volume rather than at the surface. Whereas macrobes tend to be diverse in shape and surface embellishments, microbes tend to be

diverse in metabolism and intracellular functionality. The nanoplankton are poised between the femtoplankton and picoplankton where the concept of morphospecies is conceded to be virtually untenable, and the microplankton, mesoplankton, and macroplankton where the concept is at least of arguable validity.

In microplankton and larger plankton, there is sufficient apparent confidence in taxon recognition of particular forms of diatoms, dinoflagellates, copepods, foraminiferans, and euphausiids that global distributions of these and others can be mapped for biogeographical study. Large-scale distributions of calanoid copepods are particularly well documented. Although taxonomic richness, evenness, and distinctness all decline from the tropics to the poles, they do so in different manners that are best explained by patterns of primary and secondary production consistent with Longhurst ecological geography (Woodd-Walker *et al.*, 2002). From the Continuous Plankton Recorder database, the information on greater than 100 taxa of calanoid copepods is sufficiently extensive in space and intensive in time that diversity can be examined in large contiguous ocean regions at diel, seasonal, and annual scales (Beaugrand and Ibañez, 2002). These multiscale considerations lead to a view that calanoid diversity is mainly regulated by temperature, hydrodynamics, stratification, and seasonal variability of the environment. But even so, a taxon as familiar as *Calanus* still cannot be regarded as taxonomically well described (Longhurst, 1998). In phytoplankton, when the richness of recognized species is examined in relationship to the surface area of the ecosystem, the familiar species–area power law is found, with an invariant exponent that spans many orders of magnitude in spatial extent (Smith *et al.*, 2005). Observations, or experiments, at one scale can therefore be used to inform at other scales. However, as with zooplankton, the taxonomy of even familiar species such as the diatom *Skeletonema costatum* may need revision (Sarno *et al.*, 2005).

In picoplankton (bacteria, archaea, and picoeukaryotes), the concept of species is vague but biological diversity can be inferred from nucleic acid sequences. “The individual is where the gene meets the environment” (Levin *et al.*, 2001); so if gene phylogeny equates to organism phylogeny, then genetically defined organismal units can also be expected to have a macroecology. Plankton phylogenetic trees are most commonly constructed from the small subunit ribosomal RNA gene. The structure and topology of the trees indicate a high degree of novelty and diversity in marine microbes. Were phylogenies better visualized as webs rather than trees, for example, because of prevalent lateral gene transfer, it would not change present consensus that the smallest organisms are also the most diverse.

In fact, the extent of diversity is even greater than that indicated by the dissimilarity of single genes. There is microdiversity. A group of coastal bacterioplankton showing nearly identical ribotype identity to *Vibrio splendidus* was estimated to consist of at least a thousand distinct genotypes (Thompson *et al.*, 2005). Similarly, oceanic bacterioplankton off California revealed greater than a thousand lineages from three clusters alone (Brown and Fuhrman, 2005). Some of this extensive diversity may be neutral with no selective advantage in the ecological context. Microdiverse clusters are thought to arise from periodic selection, but intracluster competition is not

strong enough to sweep (purge) members from the group. Yet, in at least one group of marine bacterioplankton, phylogenetically discrete clusters denoted by highly similar gene sequences are represented by ecologically differentiated units. These so-called ecotypes display different cellular characteristics, allowing them to partition environmental gradients in the ocean. In the photoautotrophic cyanobacterium *Prochlorococcus*, ecotypes are distributed in the ocean with respect to temperature, light, and nutrients in accord with functional capabilities conferred by their respective genomes (Johnson *et al.*, 2006). The global basin-scale distribution of *Prochlorococcus* ecotypes at the sea surface is consistent with prevailing environmental conditions resulting from physical oceanographic structuring of the water column (Bouman *et al.*, 2006).

The level of taxonomic resolution at which biogeographic and macroscopic patterns become evident is important in understanding evolutionary and community assembly processes. Genetic and genomic characterization of plankton suggest that some of the most finely resolved taxonomic units may not be distributed in random fashion. It follows that large-scale patterns should be discernible at higher taxonomic levels. At the genus level, the two marine cyanobacteria *Prochlorococcus* and *Synechococcus* have been mapped extensively in the ocean on the operational basis of cytometric characteristics. In the three Southern Subtropical Gyres (Bouman *et al.*, 2006), the surface distributions of the two genera are antiparallel (Pacific and Atlantic Oceans) or parallel (Indian Ocean) to each other (Figure 4(a)). In a bivariate plot of cell abundances, the data pairs seem to lie within a triangular polygon (Figure 4(b)). The orientation of the polygon indicates a large range of possible densities for *Prochlorococcus* at high densities of *Synechococcus*, but only a restricted high range for *Prochlorococcus* at low densities of *Synechococcus*. At the within-gyre scale, different processes evidently regulate the interaction between the two genera. At the larger between-gyre scale, there is a simple negative correlation between basin-averaged abundances of *Prochlorococcus* and *Synechococcus* in the order of Indian Ocean to Atlantic Ocean to Pacific Ocean (Figure 4(b)). This niche complementarity, earlier noted by Chisholm (1992) at a different spatiotemporal scale, is evident at a level of the taxonomic hierarchy higher than that of the interacting units, which are presumably the ecotypes or lower-level genomic variants. A decrease in the numerical abundance of *Prochlorococcus* is not fully offset by an increase in *Synechococcus*, but cells of the former are somewhat smaller on average than those of the latter, so there is a degree of ecological homeostasis in the combined cyanobacterial biomass.

It seems that different taxa can coexist by being sufficiently different or by being sufficiently similar. Taxa repulsion occurs when competition excludes others of moderate similarity. On the other hand, taxa attraction occurs when others are similar enough to avoid competition and results in self-organized clustered niches, a so-called paradox of the clumps (Nee and Colegrave, 2006). As evidence, the frequency distribution of phytoplankton species in Dutch lakes appears to be clustered along a niche axis defined by cell volume (Scheffer and van Nes, 2006). *Prochlorococcus* and *Synechococcus* share similar positions in the food web, physical cell size, dominant metabolic capabilities, and cellular biochemistry. For these

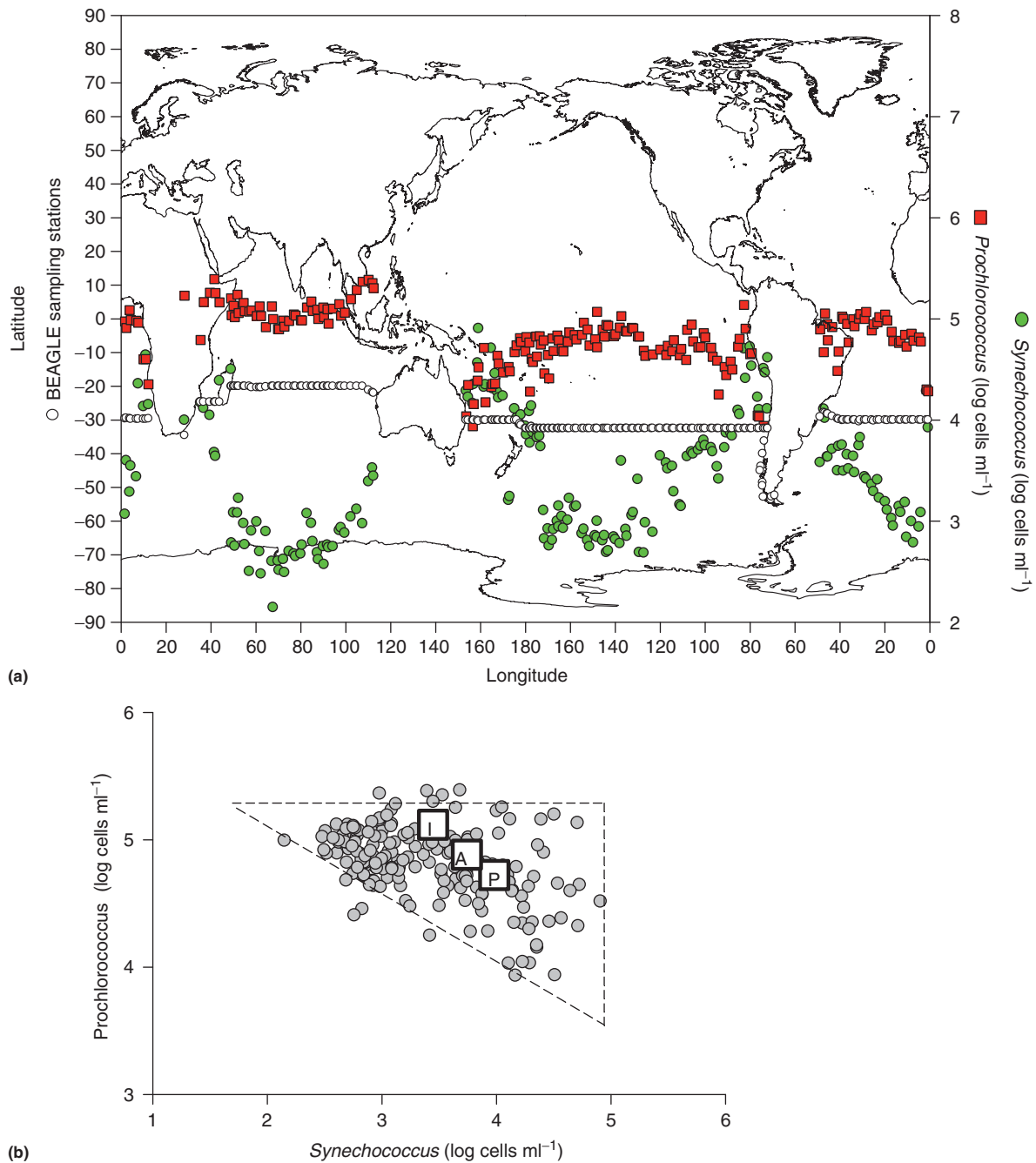


Figure 4 Abundance of *Prochlorococcus* and *Synechococcus* in the Southern Subtropical Gyres. (a) Map shows sampling stations in horizontal transects along 20° and 30° S, and U-shaped (upright or inverted) cell distributions in each ocean basin. (b) bivariate plot of cell abundance for individual stations, and ocean average values: I = Indian Ocean, A = Atlantic Ocean, P = Pacific Ocean. Triangular polygon is drawn by eye to envelop the data cluster.

picoplankton, the phylogenetic perspective becomes intimately enmeshed with those based on trophic linkages, size allotment, functional performances, and indeed also with biotic elemental composition.

Stoichiometric Emergence

All living beings are made of the same few classes of biomolecules (e.g., proteins, carbohydrates, lipids, nucleic acids,

nucleotides, and pigments), which are constituted from the same few elements, of which the three major ones are carbon (C), nitrogen (N), and phosphorus (P). A consideration of the C:N:P stoichiometry of plankton is in effect a multiscale analysis from elements and molecules up through the biological hierarchy to populations, communities, ecosystems, and even ultimately to the biogeosphere (Sterner and Elser, 2002). In this sense, ecological stoichiometry is the quintessence of macroscopic emergence from microscopic organisms. Despite perceived

biodiversity and biocomplexity in plankton systems, there is apparent biosimplicity in the stoichiometric equivalence of oceanic plankton biomass and deep dissolved inorganic nutrients in the atomic ratio of 106:16:1, well known as the Redfield ratio. The concept of an elemental composition common to the living and nonliving parts of the Earth is alluring because it lends easily to a teleological metaphor of the biosphere as a super-organism on which selection acts. However, as it is most widely understood, selection acts at a much lower level. It is the genomic instructions within individual organisms that provide controlling directions. Accordingly, the observed stoichiometry of marine seston is a high-level pattern resulting from nested processes leading from fast molecular biology to slow biogeochemistry; it is not a Gaian homeostasis (Levin, 2005).

The concept of a common elemental composition in plankton is useful for biogeochemistry because the laws of matter conservation and stoichiometric proportions allow nutrient inventory to be balanced amongst the major elements and also between the biota and the water. However, because the Redfield ratio is a macroscopic pattern, it may not necessarily be robust at local scales, for example, when used to calculate a nonsteady-state drawdown of dissolved nutrients from observed local biomass accumulation in multiphyletic plankton assemblages (Figure 5). The Redfield ratio is an empirical statistical average (Figure 5(a)) and not a

fundamental biochemical constraint. Stoichiometric plasticity is possible in photolithoautotrophs because the elements are obtained from disparate soluble inorganic forms (e.g., bicarbonate, nitrate, and phosphate) whose supplies are not necessarily coupled. Indeed, phytoplankton has a considerable capacity for intracellular storage of excess nutrients. By contrast, heterotrophs obtain their elements together in pre-formed food items. If there is stoichiometric similarity between an organism and its resources, then there is some degree of homeostasis (Sterner and Elser, 2002). In this respect, there is a distinction between autotrophs and heterotrophs: Homeostasis is less evident in phytoplankton than in chemooorganotrophic bacterioplankton and zooplankton.

Organisms, especially autotrophs, vary considerably in elemental composition. Systematic phylogenetic differences in C:N:P exist between major superfamilies of phytoplankton, indicative of ancestral phenotypes (Quigg *et al.*, 2003). Furthermore, microalgae exhibit considerable physiological plasticity of C:N:P in response to nutrient and light conditions (Geider and La Roche, 2002). The smallest cyanobacteria (*Prochlorococcus* and *Synechococcus*) are characterized by very high C:P ratios due to low cellular P (Bertilsson *et al.*, 2003). Under P-limitation, most of this element in the cyanobacteria is found in DNA, a nonscalable cell component that constrains both minimum cell size and elemental stoichiometry

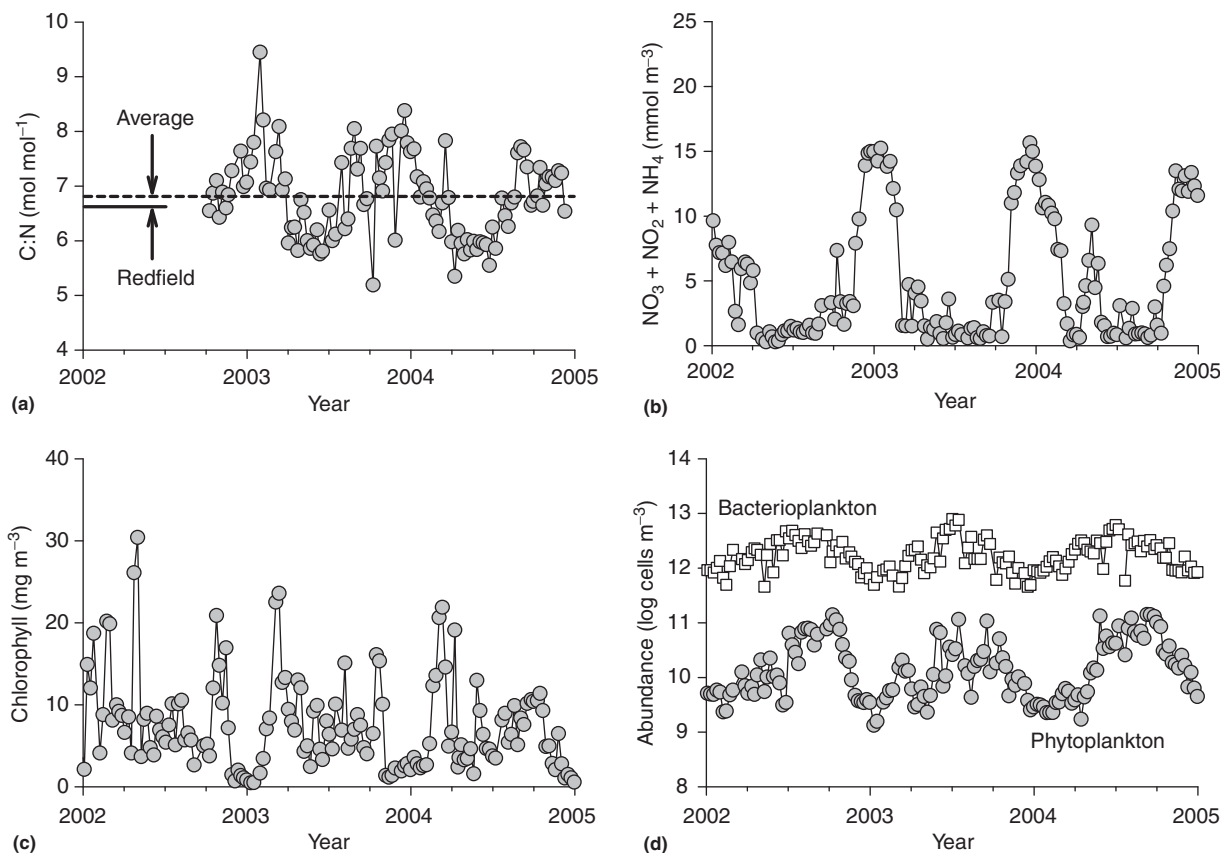


Figure 5 Time series of plankton and nutrients in Bedford Basin. (a) Particulate C:N atomic ratio showing the similarity of the average value to the Redfield ratio, (b) inorganic nitrogenous nutrients, (c) chlorophyll *a* concentration, and (d) numerical abundance of phytoplankton and heterotrophic bacterioplankton.

(Raven, 1994). Exponentially growing phytoplankton depend on intracellular growth machinery such as ribosomes which have a low N:P ratio; conversely, near-equilibrium slow-growth phytoplankton depend on resource-acquisition machinery such as nutrient-uptake proteins and chloroplasts which have a high N:P ratio. The appropriate mix of all these stoichiometric types results in the Redfield ratio (Klausmeier *et al.*, 2004). Oceanographic and atmospheric regimes that shift the relative availability of nutrients to phytoplankton may alter stoichiometric steady states, which might be discernible at regional and global scales.

Temperature Dependence

From Single Molecules to Biochemical Kinetics

Temperature affects the velocity of biochemical reactions which drive organism metabolism. Statistical thermodynamics is in essence a macroscopic rule used to predict the effects of temperature on chemical reactions. In an ideal gas at thermal equilibrium, it is impossible to describe the kinetic energy associated with each individual molecule, but Maxwell-Boltzmann distribution law shows that the probability of a molecule occupying a kinetic energy E is proportional to $e^{-E/kT}$ where k is Boltzmann constant (8.62×10^{-5} eV K⁻¹) and T the system's absolute temperature (K). There is an interesting resemblance between what this law represented (a bridge between microscopic physicists interested in single molecule dynamics and macroscopic physicists interested in whole systems dynamics) and the aim of macroecology as a discipline linking ecophysiology and community ecology.

Implicit in Maxwell-Boltzmann equation is the fact that as temperature increases the proportion of molecules with sufficient kinetic energy to react increases. This ultimately led Svante Arrhenius to formulate that the temperature dependence of reaction kinetics should scale as $e^{-E_a/RT}$ where R is the gas constant (8.31 J mol⁻¹ K⁻¹) and E_a is the activation energy of that particular reaction; reactions with higher E_a show stronger temperature dependence. The difference between Boltzmann's factor and Van't Hoff-Arrhenius equation is just that the former uses particle units (E in eV and k in eV K⁻¹) while the latter uses the molar scale (E_a in J mol⁻¹ and R in J mol⁻¹ K⁻¹). Because k and R are related by $k = R/(N_A \times j)$, where N_A is Avogadro constant ($N_A = 6.022 \times 10^{23}$) and a j conversion factor from electronvolts to Joules ($j = 1.602 \times 10^{-19}$ J eV⁻¹), both expressions have the same value. The more intuitive Q_{10} constant results from simplification of Van't Hoff-Arrhenius equation (Gillooly *et al.*, 2002).

From Biochemical Kinetics to Whole Organism Physiology

A second scaling step is needed to apply Boltzmann's-Arrhenius equation to the response of whole organism physiological rates to temperature. Although Boltzmann's-Arrhenius equation has been widely applied to biological systems, just recently the activation energy measured for whole-organism rates has been related to the activation energy of the main biochemical reactions that drive organism physiology (Gillooly *et al.*, 2001). Metabolic scaling theory proposes that because organism metabolism is mainly driven by mitochondrial respiration, the temperature dependence of

adenosine triphosphate (ATP) synthesis should determine the temperature dependence of whole-organism metabolic rate with an average activation energy for both processes close to 0.65 eV (or 62.7 kJ mol⁻¹) (Gillooly *et al.*, 2001). Although whole-organisms greatly depart from the ideal gas conditions for which Boltzmann's-Arrhenius equation was formulated and more complex explanations have emerged, the similar activation energy at both levels of organization is quite remarkable. For planktonic heterotrophs, whose metabolism is mainly driven by the synthesis of ATP, the activation energy for both respiratory (Lopez-Urrutia *et al.*, 2006) and growth rates (Rose and Caron, 2007) is close to the predicted value of 0.65 eV. But the temperature dependence of the metabolic rates of photosynthetic plankton has long been recognized to be lower than that of heterotrophs (Eppley, 1972) with values ranging from 0.29 to 0.39 eV (Lopez-Urrutia *et al.*, 2006; Rose and Caron, 2008). Allen *et al.* (2005) argued that the lower temperature dependence of land-plant photosynthetic rates (0.32 eV) is due to the kinetics of rubisco carboxylation and photorespiration. As temperature increases photorespiration increases relative to carboxylation thus reducing net carbon gain. The applicability of Allen *et al.* (2005) explanation to marine plankton depends on the assumption that CO₂ supply to Rubisco in marine plants, which have different diffusive characteristics and carbon concentration mechanism (Yvon-Durocher *et al.*, 2010), does not modify this theoretical explanation.

From Organisms to Communities, Biogeochemical Cycles, and Biodiversity

Regardless of the theoretical basis for the differential temperature dependence of the metabolic and growth rates of autotrophs and heterotrophs, the implication for to marine plankton community dynamics and biogeochemical cycles are far reaching. Huntley and Boyd (1984) showed that the zooplankton to phytoplankton production ratio would increase as temperature increases. Rose and Caron (2007) argued that phytoplankton blooms might occur more frequently in cold waters because the growth of grazers will be much lower than the growth of phytoplankton as temperature decreases. Laws *et al.* (2000) showed that the proportion of primary production exported to the deep increases with decreasing temperature because, at cold temperatures, the growth rates of heterotrophic decomposers are much lower so most organic matter is exported before it can be decomposed. Lopez-Urrutia *et al.* (2006) scaled the differential temperature dependence of planktonic respiration and photosynthesis to the metabolic balance of whole plankton communities and showed that as temperature increases the ratio of community production to respiration decreases.

Through its effects on organism metabolic rates, temperature also affects community structure. Higher cell division rates with increasing temperature might be responsible for the stronger DNA evolution and speciation rates observed in planktonic foraminifera toward the tropics (Allen and Gillooly, 2006). This kinetic energy hypothesis plays a fundamental role on the observed temperature dependent global patterns of marine biodiversity both in planktonic and other marine communities (Tittensor *et al.*, 2010).

Regional and Global Change

In addressing societal concerns for which plankton ecology is relevant, the dominant patterns are arguably to be sought at the macroscopic level. At this level, we will not always have both pattern and process firmly in place before responding to calls for prediction. Climate change, ecological regime shift, fisheries reallocation, and biodiversity loss occur across multiple scales, but impacts are most consequential at decadal and longer timescales, at large regional and global spatial scales. Modern management of marine resources based on ecosystem considerations requires us to look for evidence and impact of plankton change at the whole system level. Plankton, at least the small ones, live for only days or weeks. Thus, there is a need to link local interactions with regional–global patterns.

Such a linkage can be made when a testable theory is supported by sufficient data. The apparent universal scaling of biological attributes with body size is an important macroscopic pattern. Another is the dependence of metabolic rates on temperature and light (for phototrophs). Together, they underlie a general metabolic theory (Brown *et al.*, 2004), which scales individual rates of photosynthesis and respiration of constituent plankton organisms to ecosystem carbon flux rates of primary production and community respiration (López-Urrutia *et al.*, 2006). Photosynthesis is less dependent on temperature than respiration, and this leads to a prediction that the balance of biogenic carbon flux could be altered by climate change: Less CO₂ would be captured in the surface ocean as temperature increases.

Rules of community assembly prescribe the successional development of populations over a year. In the sea, unlike on land, the scales of variability are such that changing community patterns fit well in the physical context of hydrodynamics (Steele, 1998). Temperature, being an important determinant of both cell metabolism and water column stability, as well as an indicator of seasonal progression and climate change, is an ecosystem driver acting across many scales. Thus, it is perhaps not astounding, but remarkable nevertheless, that over a large region of the temperate and subarctic northwest Atlantic Ocean, there is a coherence in the wax and wane of phytoplankton cells over the annual cycle that is aligned by temperature (Li *et al.*, 2006a). By this rule, phytoplankton are not assembled according to taxonomy, size, or functional attribute, but only by virtue of being individual particulate autotrophic entities. In other words, it might be construed that the molecular basis for trophic mode is ascendant over any particular organismal form under these conditions.

Seasonal cycles recur annually, but the question is whether phase and amplitude remain the same from year to year. There is some evidence that such phenological change is occurring in plankton groups of the North Sea (Edwards and Richardson, 2004), with the implication that a temporal mismatch across trophic levels signals a decoupling of ecosystem components. On the Nova Scotian Shelf and Labrador Sea, there is other evidence that the seasonal means of phytoplankton biomass have been increasing in some areas, but decreasing in others. Indeed, it seems that these multiyear trends have propagated to the heterotrophic bacterioplankton because they also exhibit these trends: a case of coherent sign switching in the direction of long-term change (Li *et al.*, 2006b). Generation times of

phytoplankton and bacterioplankton are not greatly dissimilar, but become increasingly disparate from those of primary, secondary, and tertiary consumers at higher trophic levels. Do signals propagate through many levels with fidelity? A continental shelf ecosystem monitored for 40 years appears to show trophic cascades across four levels: large-bodied predators (benthic fish and seals), forage species (pelagic fish and macroinvertebrates), herbivorous zooplankton (calanoid copepods), and phytoplankton (green seston) (Frank *et al.*, 2005). This marine ecosystem is highly complex, and thus the signature of top-down control in the form of simple trophic cascade can be viewed as a macroscopic pattern. The actual details of grazing, forage, and predation are not important in a multidecade trend.

The enterprise of science, like nature, is hierarchical. International consortia work toward a capacity for global ecology; national networks are placed to embrace regional interests; and local alliances exist to address immediate concerns. However, a space–time hierarchy of institutional management of marine resources will not necessarily ensure appropriate normative behavior because human and ecological dynamics are mismatched in scale (Rice, 2001; Ehrlich and Levin, 2005). Moreover, multiscale considerations will inevitably be confronted by ecological fungibility (Steele, 1998), which is the substitutability of one entity by another of equal value or utility. Thus, at some level, the differences in biological patterns caused by historical contingencies and contemporary environmental factors become moot. If fungibility can be expressed in terms of energy flux, allometric linkage, adaptive attributes, functional performance, diversity indices, elemental balance, or other such concepts, then we may be able to see evidence of laws in ecology (Lawton, 1999). Part of the macroecological agenda is to delineate the range of natural variability in given ecosystems so that outliers may be identified, even if the process constraints on natural limits are not yet fully understood. From a management perspective, these limits may suggest points of natural thresholds that trigger precaution toward undesired system states. To describe how a large continental shelf ecosystem has devolved from one regime to another using indicators of ocean climate, plankton, invertebrates, fish, and human influence, and then to predict a potential fishery collapse in an adjacent ecosystem within a decade (Choi *et al.*, 2005) is a bold and consequential test of the empirical approach.

Concluding Remarks

Biological diversity is conceptualized by assigning living entities to different categories. Our perception of meaningful categories is based on what we observe. By and large, we observe whole organisms, namely the units that house the genes. However, it is possible to consider, and in fact construct by technology, an entire plankton community as the sum of all constituent genomes, a metagenome. Sequencing of the community genome yields information on ecological structure, function, and diversity that crosses multiple levels of the conventional biological hierarchy. Although such ecogenomic studies are nascent, comparative ecosystem analyses of metagenomes will undoubtedly yield patterns of macroscopic organization. Macroecology, by its holistic nature, is sometimes seen as an approach to rise above the repeating cycle of

data-intensive reductionism. A multiscale approach enables emergent patterns to consolidate myriad historical contingent events. Seemingly inexhaustible biodiversity can be telescoped to elegant biosimplicity.

See also: Marine Ecosystems. Microorganisms (Microbes), Role of. Ocean Ecosystems. Pelagic Ecosystems. Plankton, Status and Role of. Restoration of Animal, Plant, and Microbial Diversity. Scale, Concept and Effects of. Trophic Levels

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