

The emergence of regularity and variability in marine ecosystems: the combined role of physics, chemistry and biology

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SUMMARY: Marine ecosystems play an integral role in the functioning of life on earth. To predict how they will respond to global changes, and to effectively manage and maintain services upon which humans rely, we must understand how biological processes at the cellular level generate macroscopic patterns in the oceans. Here, we discuss how physics and biogeochemistry influence and constrain marine ecosystem structure and function, and outline key regularities and patterns of variability that models should aim to reproduce. We identify unanswered questions regarding how size-dependent physiological and ecological processes are linked to turbulent mixing, dealing specifically with how size structure is related to mixing over a range of spatial scales and how it is linked to the fate of primary production in the sea.

Keywords: variability, turbulence, scaling, abundance, trophic interactions, modelling.

RESUMEN: LA APARICIÓN DE REGULARIDADES Y VARIABILIDAD EN ECOSISTEMAS MARINOS: EL PAPEL COMBINADO DE LA FÍSICA, LA QUÍMICA Y LA BIOLOGÍA. – Los ecosistemas marinos juegan un papel integral en el funcionamiento de la vida sobre la Tierra. Para predecir cómo van a responder a cambios globales y para mantener los servicios de los cuales los humanos dependemos, tenemos que comprender cómo los procesos biológicos a nivel celular generan patrones macroscópicos en el océano. Examinamos cómo la física y la biogeoquímica afectan y limitan la estructura y función de los ecosistemas marinos, y exponemos importantes regularidades y patrones de variabilidad que los modelos deberían reproducir. Identificamos aspectos sin resolver sobre la relación entre procesos fisiológicos y ecológicos y la mezcla turbulenta. En concreto, cómo la estructura de tamaños está relacionada con la mezcla en un rango de escalas espaciales y cómo está conectada con el destino de la producción primaria en el mar.

Palabras clave: variabilidad, turbulencia, escalado, abundancia, interacciones tróficas, modelización.

INTRODUCTION

Perhaps the greatest mandate facing global society today is the achievement of a sustainable future. As we degrade our environments, we lose the services that ecosystems provide. Clearly, as a first step we must catalogue what those benefits are, that is, the things we take directly from systems, like food, fibre and fuels, the indirect benefits from climate mediation and carbon sequestration, and the most difficult to quantify:

the aesthetic and ethical. Such a cataloguing, however, is just a beginning, raising scientific challenges that cross disciplines from the molecular to the socio-political level, and that cross scales of space, time and complexity (Levin, 2010). What are the dimensions of biological diversity and ecosystem organization that underlie those services, and what mechanisms sustain their robustness and resilience (Levin and Lubchenco, 2008)? These challenges are particularly urgent for marine ecosystems, which are already providing evi-

dence of regional and basin scale decadal shifts (Kerr 2010; Hoegh-Guldberg and Bruno 2010; Schofield *et al.*, 2010).

Ecosystems and the biosphere are complex adaptive systems, deriving their features from evolutionary forces and ecological mechanisms operating far below the level of the whole system (Levin, 1998; 1999). As a consequence, the macroscopic patterns that characterize marine ecosystems are sustained by a combination of microscopic and macroscopic forces (Margalef, 1978). This means that we must develop approaches that allow us to scale from cells and individuals to ecosystems and the biosphere, deriving a statistical mechanics of ecosystem function (Levin, 1992). Scaling up cellular process to the biosphere requires not only the ability to predict overall biomass, but also an understanding of overall community diversity. Promising steps have been taken in this direction recently; for example Follows *et al.* (2007) explain aspects of the global distribution of specific classes of phytoplankton. There are, however, a variety of other regularities characteristic of marine ecosystems, and knowing these and how robust they are can provide us with not only a hierarchy of indicators of system decline, but also a set of targets for evaluating the success of modelling efforts.

Global net primary production and biogeochemistry are greatly influenced by the dynamics of marine ecosystems because biological processes catalyze and drive the flow of nutrients and energy in the oceans (Redfield, 1958; Margalef *et al.*, 1979; Raven and Falkowski, 1999). As a result, seemingly small changes in marine ecosystem processes (e.g. shifts in temperature and stratification) can have significant consequences for global biogeochemistry and the global carbon budget because the oceans harbour the largest carbon pool associated with the global carbon cycle. It is therefore essential to improve our relatively poor understanding of how marine ecosystems will respond to continued disturbance (Pomeroy, 1974; Azam *et al.*, 1983). Because metabolism and higher-order ecological interactions (competition, predation, etc.) are constrained by the chemical and physical environment, in order to predict how the oceans will respond to perturbations, it is critical to understand the links between the chemical environment, the physical mixing of water, and biological processes. For example, the increasing water column stratification has been hypothesized to underline the basin scale declines in phytoplankton productivity in the South Pacific (Behrenfeld *et al.*, 2006). This mirrors the purported centennial declines in global ocean productivity (Hoegh-Guldberg and Bruno, 2010) and the projected changes associated with altered ocean circulation (Schmittner *et al.*, 2005) can feed back to accelerate climate change (Cox *et al.*, 2000). Detecting these changes is difficult because long-term changes are superimposed upon natural climate cycles and high frequency fluctuations, and our quantitative understanding of the physical forcing of

ocean productivity remains a central challenge for biological oceanography.

The physical mixing of water, driven by the earth's rotation, local wind patterns and density gradients, creates spatial and temporal heterogeneity in ocean properties and provides the context for biological processes (Stommel, 1963). For example, chlorophyll *a* concentrations exhibit patterns of variability across a range of spatio-temporal scales (Fig. 1). Organisms experience significant variability in environmental conditions on time scales ranging from seconds to decades and from microns to thousands of kilometres (Haury *et al.*, 1978). Although the influence of physical variability on biological processes in the oceans has been appreciated for over half a century, the link between heterogeneity generated by physical processes and variability in ecosystem properties continues to be a focus of theoretical and empirical research in oceanography, in part because we still do not fully understand the links and feedback mechanisms (Bracco *et al.*, 2009). An appreciation for the influential role that biological processes play in determining carbon flow and biogeochemical cycling in the oceans (Sarmiento and Toggweiler, 1984; Fasham, 2003) has prompted modellers to incorporate detailed descriptions of the links between nutrient dynamics, primary production and trophic dynamics into purely physical models. The advent of increasingly detailed descriptions of biologically driven nutrient cycling in large-scale ocean models (Leonard *et al.*, 1999; Moore *et al.*, 2002; Lima and Doney, 2004; Litchman *et al.*, 2006; Follows *et al.*, 2007) warrants a review of the links between chemical, physical and biological processes operating over a range of scales and their combined impact on ecosystem structure and function. Our goals in this paper are to help synthesize our current understanding of the links between physics, biogeochemistry and variability in ecosystem properties and to identify key questions that need to be addressed to advance our understanding of the determinants of marine ecosystem structure. First, we briefly review how mixing generates variability and discuss links between physical variability and variability associated with biological processes. Next we highlight 3 regular features in marine ecosystems: community diversity, size structure and trophic structure, and pose questions about how each is related to physical variability. Finally, we discuss the biogeochemical consequences of biological feedbacks and some implications for modelling marine ecosystems.

THE PHYSICAL GENERATION OF VARIABILITY

The physically driven mixing that occurs in the oceans depends upon complicated flow patterns and transfer of energy and momentum over a range of spatio-temporal scales. Because spatio-temporal heterogeneity in the oceans is driven in large part by physics, fluid dynamics provides a null prediction for the

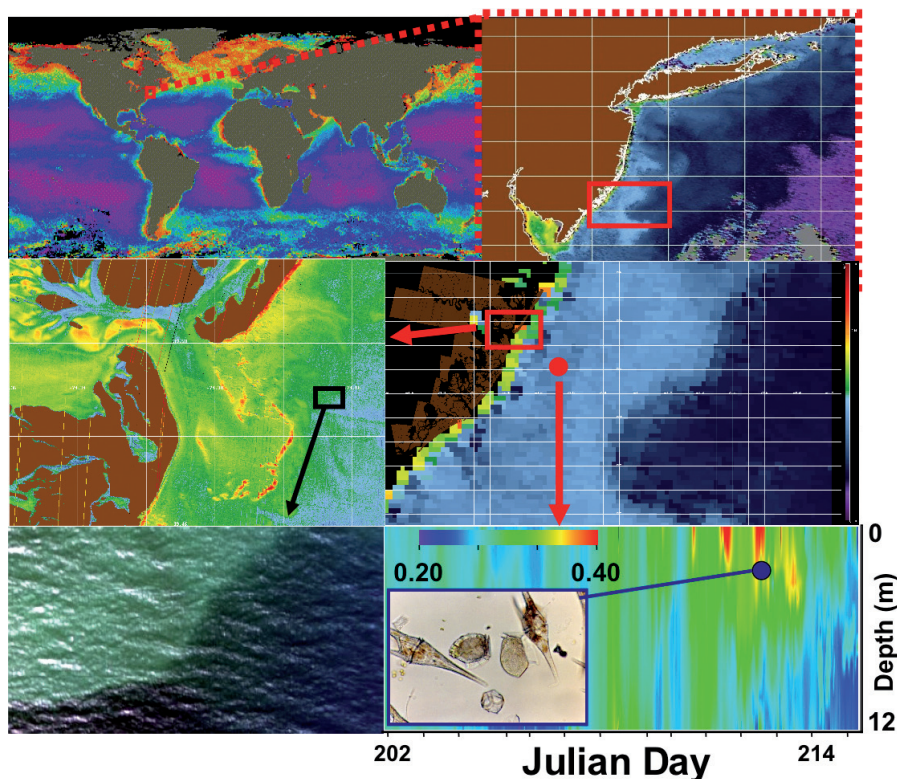


FIG. 1. – Variability in chlorophyll *a* over a range of scales.

relationship between spatial and temporal variability in ecosystem properties (Tennekes and Lumley, 1972; Margalef *et al.*, 1979; Levin, 1992; Falkowski and Oliver, 2007). Mixing begins at large spatial scales, where momentum is transferred as shear stress from the earth's rotation and wind to the oceans' waters, inducing flow. In the interior of the oceans at appropriate latitudes, flows can be characterized by simplified equations of motion with Coriolis terms dominating (Pond and Pickard, 1983). However, in other regions, the Gulf Stream for example, non-linear terms must be retained in equations of motion and the ratio of non-linear to frictional effects (the Reynolds number) is high, leading to the irregular mixing known as turbulence. Over a range of scales known as the inertial subrange, energy introduced by momentum is transferred with little dissipation, but is ultimately lost due to viscosity or molecular friction at scales smaller than the smallest eddies generated by turbulent mixing. The inertial subrange is delineated by Ozmidov lengths at the upper end and the Kolmogorov or inner length scale at the lower one. Kolmogorov's universal equilibrium theory posits that inner scales or microscales of length, time and velocity, all associated with the smallest eddies, are well approximated by simple functions of the kinematic viscosity of water ν ($10^{-6} \text{ m}^2 \text{ s}^{-1}$) and the energy dissipation rate per unit mass ϵ , which is assumed to equal energy input from larger scale eddies in the turbulent flow. The inner length, time and velocity scales are $(\nu^3/\epsilon)^{1/4}$, $(\nu/\epsilon)^{1/2}$, and $(\nu\epsilon)^{1/4}$ respectively and are much smaller than the largest eddies in turbulent flow,

rendering the small-scale structure in turbulent flow statistically independent of larger scale eddies when Reynolds numbers are large (Tennekes and Lumley, 1972). Ozmidov length scales tend to be of the order of metres and inner length scales tend to be of the order of centimetres. Kolmogorov's microscales and the associated frequency spectrum provide robust predictions for how three-dimensional turbulent mixing generates variability independent of biological processes in the inertial subrange.

Although the $k^{-5/3}$ energy spectrum, which predicts how variability scales with frequency (Kolmogorov, 1941a;b), has proven to be robust even when its basic underlying assumptions are not met (Phillips, 1991), relating observed biological variability to turbulent mixing is a challenge. First, the limitations of current instrumentation make resolving variability over the inertial subrange difficult. And second, deviations from the Kolmogorov prediction can be generated via multiple processes (Franks, 2005). For example, when plankton interactions (Powell and Okubo, 1994) and size structure (Poulin and Franks, 2010) are incorporated into models, spectral slopes can vary greatly. However, observed spatio-temporal variability that deviates from null expectation of the $k^{-5/3}$ energy spectrum suggests that additional processes or constraints are exerting influence over a range of scales. Deviations in variables associated with biological activity may indicate that biological processes are expending energy to dissipate energy inputs from physical processes, thereby maintaining spatial heterogeneity, or

disperse, effectively smoothing physically driven variability. Understanding the scales at which these deviations occur and what drives them is key because this is where predictions based only on physics break down. It is critical to identify these scales if we hope to understand and predict how marine ecosystems are likely to respond to perturbations amidst all the physically driven background variability.

The complete context for biology in marine ecosystems is provided by physical mixing, the light environment and redox conditions, largely determined by oxygen concentrations. Increased energy input from wind increases the degree of mixing in the surface ocean and serves to lower the pycnocline, increase nutrient inputs to the euphotic zone and maintain high oxygen concentrations, all of which have important consequences for biological processes. Over half a decade ago, Sverdrup (1953) pointed out how mixing could influence ecosystem processes. Using a simple model, he showed that it is necessary for the nutricline, whose depth is intimately tied to the depth of the pycnocline and energy input, to be shallower than critical light depth in order for significant primary production (e.g. phytoplankton blooms) to occur. This is perhaps the first example of how physical mixing and the chemical environment were integrated to make a general prediction about ecosystem response to a variable environment. Although Sverdrup's reasoning is logically sound, the interpretation of critical depth is inherently scale- and taxon-dependent (Smetacek and Passow, 1990), making its general application difficult. Nevertheless, phytoplankton growth results in severe drawdown of concentrations of limiting resources, namely nitrogen and phosphorus, but also creates anoxia and hypoxia from increased rates of decomposition in slightly deeper water, significantly altering redox state. As a consequence, variability in the chemical and physical environment in the oceans can be more predictable with depth than across space. For example, the abundance of different species can vary predictably with depth (Belyayeva, 1970; Letelier *et al.*, 1993; Bidigare and Ondrusek, 1996; Johnson *et al.*, 2006; DeLong *et al.*, 2006) as well as latitude (Davis and McGillicuddy, 2005) and longitude (Cavender-Bares *et al.*, 2001). In all cases, abundance of particular taxonomic groups is closely tied to the chemical and physical environment.

Mixing can influence phytoplankton community composition by changing the chemical environment and shifting life-history trade-offs, many of which are dictated by body size (Margalef *et al.*, 1979). Differential ability to acquire nutrients confers differential competitive ability in different environments, which means that distinct phytoplankton communities occur in disparate mixing regimes (Litchman *et al.*, 2006; Falkowski and Oliver, 2007). However, physically generated variability can also promote coexistence among species (Scheffer *et al.*, 2003). Mixing can reduce the disadvantage larger cells face from sinking faster than smaller cells (Smayda, 1970; Rodríguez *et al.*, 2001; Huisman *et al.*, 2002;

Irwin *et al.*, 2006) and from reduced surface to volume ratios, critically important in determining rates of nutrient uptake (Chisholm, 1992; Irwin *et al.*, 2006; Strom, 2008; Yoshiyama and Klausmeier, 2008). For example, cyclonic eddies have been shown to increase inorganic N concentrations and to increase the abundance of large species (Vaillancourt *et al.*, 2003). In stable environments, smaller body sizes characteristic of picoplankton are predicted to be optimal, but predation by zooplankton and increased nutrient supply increase optimal body sizes for phytoplankton (Jiang *et al.*, 2005; Irwin *et al.*, 2006). Increased mixing, turbulence in particular, also increases the susceptibility to predation by decreasing sensitivity to hydrodynamic signals (Hwang *et al.*, 1994; Gilbert and Busky, 2005) as well as modifying behaviour (Moison *et al.*, 2009) and cell morphology (Thomas and Gibson, 1990). Although much work has focused on nutrient acquisition and competition among phytoplankton taxa (Falkowski and Oliver, 2007; Yoshiyama and Klausmeier, 2008) as key determinants of community structure, the importance of higher trophic interactions has recently been stressed (Jiang *et al.*, 2005; Strom, 2008). Though we do not fully understand the advantages and disadvantages associated with changes in body size across different mixing regimes and chemical environments, the complex network of feedbacks between the chemical environment, biological nutrient transformations and heterogeneity are surely linked to organism body size.

IDENTIFYING SCALES ASSOCIATED WITH BIOLOGICAL REGULARITIES

Physically driven mixing is primarily responsible for generating variability at larger scales, which is subsequently transferred in a regular fashion over a range of intermediate scales and ultimately lost at the smallest scales (Kolmogorov, 1941a,b). Energy, which drives mixing, and chemical inputs are realized over large spatio-temporal scales (basin to mesoscale phenomena), but the majority of biological processing (e.g. metabolism, grazing and decomposition) is performed by microorganisms at cellular scales (micrometres to centimetres). This separation of scales can decouple biology from physics and makes identifying the scales at which decoupling occurs critical for predicting how ecosystems will respond to changes in circulation patterns and geochemical inputs. Over intermediate scales, of the order of 5–20 kilometres, variability in aggregated measures of biological activity, e.g. total biomass or primary production, is driven predominantly by physical mixing (Lekan and Wilson, 1978; Weber *et al.*, 1986; Yoder *et al.*, 1987), and phytoplankton have been shown to act as tracers over 10- to 100-km scales (Denman and Abbot, 1994). At smaller scales, community interactions (competition, predation, parasitism, etc.) are likely to be more instrumental in determining ecosystem properties. Similar scale dependence exists in the temporal realm. At frequencies of less than 24 h,

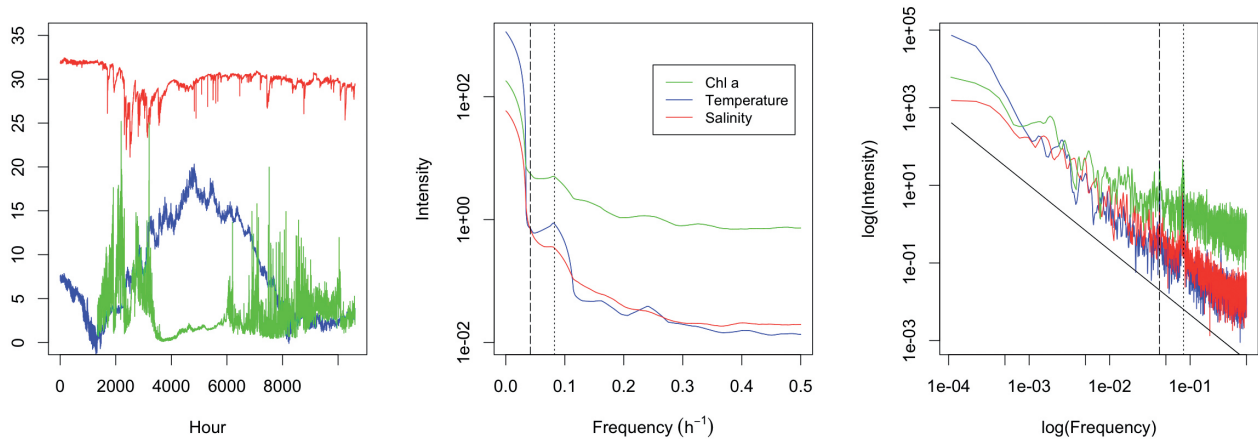


FIG. 2. – Variability in chlorophyll *a*, temperature, and salinity over a range of time scales. Left panel are the raw time series from Gulf of Maine Ocean Observing System (GOMOOS) buoy DO1, in Lower Harpswell Sound, from December 12, 2006 through March 31, 2008. Centre panel shows smoothed periodograms for the time series. Dashed line is 24 hour frequency and the dotted line is 12-hour frequency. Right panel shows log transformed variance spectra for the time series. Solid line is the $-5/3$ Kolmogorov prediction (see text) and the dashed and dotted lines are the same as in the centre panel.

variance spectra for chlorophyll *a* deviate from spectra for temperature and salinity, both of which appear to conform to the Kolmogorov prediction (Fig. 2). It is interesting to note the apparent concordance with the $k^{-5/3}$ energy cascade because the observed frequency range is presumably outside of or only partially overlaps the inertial subrange. Regardless of what is conspiring to generate variance spectra consistent with the Kolmogorov prediction over this frequency range, it is apparent that biological processes dictate patterns of variability in chlorophyll *a* at shorter time scales. In particular, a greater proportion of total variability in chlorophyll *a* concentration is generated at high frequencies, which could be the result of large individual plankton cells or aggregates (Levin *et al.*, 1989; Grünbaum and Okubo, 1994; Grünbaum 1994; Flierl *et al.*, 1999; Franks, 2005). Thus, it becomes important to understand how ecosystem processes respond to, and potentially feed back on, abiotically generated variability across scale in the marine environment. Determining the relative influence of abiotic and biological processes occurring across scales on observed ecosystem properties remains a challenge (Martin, 2003; Bracco *et al.*, 2009), and one that must necessarily be overcome to predict the response of ecosystem processes to continued perturbation.

The generality of spatial and temporal variability in aggregated measures of biological activity (biomass, chlorophyll *a*, etc.) has been the subject of intense study for decades. A close correspondence between variance spectra of physical variables, such as temperature and salinity, and measures of biological activity have been thought to implicate turbulent mixing as a key factor in generating spatio-temporal variability in ecosystem structure. However, Franks (2005) clearly articulates that variance spectra alone are not enough to unambiguously determine underlying causes of variability. Patterns of variability are more informative if put in the context of a model with dynamics at the appropriate

temporal and spatial scales. The end result of the interplay between physical mixing and ecological processes is often a heterogeneous or patchy distribution of biomass at the surface of the ocean (Abraham, 1998). For example, the interaction between mixing and rate of reproduction determines the degree of “patchiness” of phytoplankton (Denman *et al.*, 1977). The patches are more prevalent at intermediate spatial scales (5–20 km). If predators and prey within these patches disperse at roughly the same rates, which would occur if they are similar in size, mixing can increase their encounter rates, but a discrepancy in dispersal rates (predators and their prey can have Reynolds numbers differing by over 3 orders of magnitude) will reduce the potential for trophic interactions (Granata and Dickey, 1991). For larger plankton with longer generation times, smaller-scale spatial variability (≤ 1 km) can be generated by individuals that initially experienced variability associated with the largest turbulent features in the oceans, occurring over hundreds of kilometres (Abraham, 1998). The key determining factor is the relationship between the Kolmogorov length (approximately 1–10 mm) and velocity (approximately 0.1–1 mm s⁻¹) scales, and organism size (Granata and Dickey, 1991). If patches persist, they can stimulate further aggregation by other organisms and be exploited by predators at multiple higher trophic levels in a matter of minutes, potentially accelerating carbon flow through the microbial loop (Seymour *et al.*, 2009). Using dimensional arguments, Grünbaum (2002) derived a criterion for determining whether resource patches of particular size and longevity are available to foragers with particular foraging time scales. Increased variability or patchiness creates the potential for increases in biogeochemical rates. Aggregates increase spatial variability, and if a non-linear relationship exists between patch size or duration and rates of biogeochemical or ecological processes, gross fluxes could be altered. Patchiness in the distribution of phytoplankton can occur with depth

as well. Hydrodynamic torque can disrupt the ability of phytoplankton to orient with respect to gravitational torque, spinning phytoplankton and causing them to aggregate into thin dense layers in the euphotic zone (Durham *et al.*, 2009). Continued upward swimming of deeper phytoplankton further aggregates phytoplankton into patches that can persist for several minutes (see below for more discussion of thin layers).

Ultimately, the intrinsic time scale associated with a particular variable of interest will determine the extent to which turbulent mixing influences variability. Over long time scales and for variables with slow relaxation times, such as salinity and temperature, turbulent diffusion is the dominant process generating observed variability, but variability in small-scale phenomena, such as phytoplankton variance spectra, must be determined by short-time-scale processes, not turbulent mixing (Bracco *et al.*, 2009). As can be seen in Figure 2, variability in chlorophyll *a* concentration appears to be tightly linked to physically generated variability over intermediate time scales, but deviates from variability produced by physical mixing at short and long time scales. The departure of the chlorophyll *a* spectrum from salinity and temperature spectra at the shortest time scales suggests that biological processes are responsible for generating observed high frequency variability. In marine communities, patchiness is observed at almost every scale of observation—in the zooplankton and those that feed on them, in the phytoplankton, and in the underlying physical properties of the environment. Patterns of variability across trophic levels and departures from the spectra associated with abiotic features suggest that physical features may account for the patchiness on the largest scales, but that biological features—such as swimming behaviour of zooplankton—must be invoked to explain smaller-scale patchiness (Levin *et al.*, 1989; Levin, 1992; Bearon *et al.*, 2004). As a consequence, we should not be surprised that purely physical models often perform poorly when making predictions for dynamics that occur over the course of hours in marine ecosystems. We need to understand ecological and biogeochemical interactions at short time scales before we can accurately predict dynamics across all scales. Despite decades of intense study, a coherent statement linking turbulent mixing and variability is missing (Martin, 2003; Bracco *et al.*, 2009), in part because the influence of swimming on patterns of variability has yet to be fully explored (Granata and Dickey, 1991; Kamykowski *et al.*, 1992; 1998; Bracco *et al.*, 2009). It is clear that we still have much to learn about the causes of variability in biological processes at the finest scales, but that variability across intermediate scales can be well predicted from physical mixing alone. However, if we wish to scale up ecosystem dynamics from the scales at which they occur to scales meaningful to humans, it is critical to understand why biologically-driven variability deviates from physically driven variability at the smallest scales. One consolation is that the scales

at which statistical predictions from fluid dynamics fail are the scales at which experimentation is possible (Guadayol *et al.*, 2009).

REGULARITIES IN MARINE ECOSYSTEMS

Community structure and diversity

Although the highly variable marine environment creates the potential for myriad micro-environments and ecological interactions, marine ecosystems often exhibit striking regularities. As in terrestrial ecosystems, predictable gradients in species richness and community similarity, as well as oscillations in community structure, are found in the oceans. Using the intergenic spacer region between 16S and 23S rRNA to describe marine bacterial genotype diversity, Fuhrman *et al.* (2008) demonstrate a latitudinal diversity gradient for bacterial plankton with the highest sequence diversity found at the equator. This gradient in the richness of sequence diversity appears to be tightly linked to temperature. Additionally, the idea of β diversity, or the turnover of species across space, can be easily applied to marine plankton communities. Phytoplankton community dissimilarity, the result of β diversity, tends to asymptote at approximately 20 km both along and across the continental shelf in British Columbia (Mackas, 1984), whereas zooplankton community dissimilarity asymptotes at approximately 35 km across and at approximately 100 km along the shelf. These results suggest important characteristic horizontal scales for vertically integrated community structure that differ between trophic groups. Plankton community structure also varies predictably over time. Bacterial plankton exhibit regular annual fluctuations in community structure that are driven by both abiotic and biotic processes (Fuhrman *et al.*, 2006). Zooplankton community structure has also been linked to flow patterns in the oceans (Mackas *et al.*, 2001). Such predictable variability highlights the inherent scale dependence of observations (Levin, 1992). In general, estimates of variance increase with window or grain size and will attenuate in finite systems. The point at which variance saturates suggests a natural scale associated with the extent of underlying causal processes, which for the study of Mackas (1984) are approximately 20 km for phytoplankton, and either 35 or 100 km for zooplankton, depending on direction (along or off shore). Therefore, multi-species plankton models, set in the context of physical oceanography models, should exhibit patterns of β diversity and characteristic scales on the order of kilometres to tens of kilometres, consistent with empirical patterns (Starr and Mullin, 1981; Mackas, 1984). Additionally, there is increasing evidence that biological behaviour combined with turbulent shear can lead to the formation of small-scale features of a metre or less in both phytoplankton and zooplankton communities (McManus *et al.*, 2008; Cheriton *et al.*, 2009; Moline *et al.*, 2009), but these so-called “thin

layers” can also be produced by shear alone (Franks, 1995; Birch *et al.*, 2008). The biomass associated with these layers can represent the major feature present in the water column (Sullivan *et al.*, 2009). While presence of these thin layers has only been documented in the last decade, current and future efforts are focused on mapping their quantitative significance in the ocean. These small scale features will represent new challenges for ocean models, because they need to describe processes operating over non-hydrostatic scales.

Abundance-size scaling of plankton

The scaling of abundance with organism size also exhibits some uniformity across disparate habitats and environmental conditions, despite the fact that life-history trade-offs and ecological interactions vary with body size. One of the most striking regularities in marine ecosystems involves the biomass spectrum, which of course is intimately connected with the flow of energy across scales. Sheldon *et al.* (1972) observed that aquatic ecosystems exhibit a power law decrease in abundance as body size increases across a broad range of size scales from the smallest particles to the largest consumers. This has inspired a wealth of theoretical efforts to explain these patterns, largely couched in consideration of the trophic web (Kerr, 1974; Platt and Denman, 1977; Silvert and Platt, 1978; Stock *et al.*, 2008). There has since been considerable discussion about the exact value of the scaling exponent and the spatio-temporal scales over which we would expect uniform scaling to apply (empirically calculated exponents range from $-5/3$ to $-2/3$ (Finkel, 2007). Rodríguez (1994) argues that this “primary” scaling results from common constraints that all organisms face when acquiring resources, distributing them and metabolizing them. However, such robust size-abundance scaling breaks down when a narrower range of body sizes is considered or when local environmental conditions are driven primarily by physical processes. This argument leads to a fundamental question yet to be answered: how is robust size-scaling of plankton tied to physical mixing over a range of spatial scales and the intrinsic constraints placed on single-celled organisms in the marine environment? Data compiled by Chisholm (1992) show that picoplankton comprise virtually all plankton biomass in N-poor waters but comprise a small fraction of the total plankton biomass at higher nutrient concentrations, supporting the optimal body size relationships derived by Jiang *et al.* (2005) and reinforcing the notion that size-abundance scaling may be scale-dependent. Interestingly, picoplankton density is relatively uniform throughout the world’s oceans, which suggests that size structure of larger size classes may be “superimposed” on relatively constant picoplankton biomass.

Increased mixing, often driven by upwelling, increases local nutrient concentrations and diatom abundance, 2 to 3 orders of magnitude larger than cyanobacteria, which dominate the ensuing plankton biomass

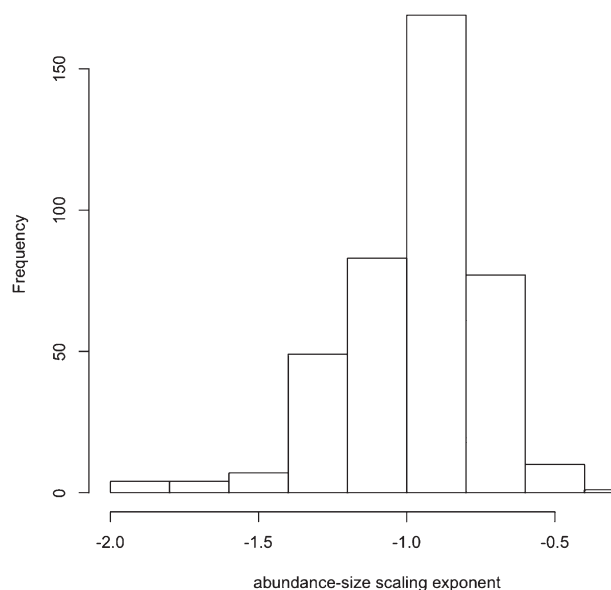


FIG. 3. – Abundance-body size scaling exponents for AMT cruises 12, 13 and 14. Body size is computed as length³.

(Rodríguez *et al.*, 2001) and change the slope of the size spectrum. Intermediate upward mixing velocities, of the order of 5 m d^{-1} , increase total carbon in the euphotic zone by buoying these larger species. The fact that the community size spectrum is well characterized by a power law implies that the same size scaling will hold for individual species that exhibit some degree of size polymorphism (Rinaldo *et al.*, 2002). Bacteria, despite varying forms and functional types, appear to conform to this prediction. Universal size scaling in marine ecosystems, which indicates the absence of a “preferred” body size, is certainly surprising given the variability in the chemical and physical environment of the oceans (Rinaldo *et al.*, 2002). Another way to phrase the above fundamental question is: what variance signature is required to reconcile the enormous shift in community composition observed by Chisholm (1992) with constant size scaling observed by many others? A single cause for the shape of the size spectrum is unlikely (Steele and Frost, 1977), but the self-organization occurring over ecological and evolutionary time scales implied by such consistent size scaling begs for an explanation (Rinaldo *et al.*, 2002). Poulin and Franks (2010) recently demonstrated how simultaneous top-down and bottom-up control can influence size structure, but such ecological dynamics have yet to be fully placed in the context of mixing across a range of spatio-temporal scales.

More recent analyses of abundance–body size scaling shed additional light on how body size is tied to organization in marine ecosystems. Data presented by Li (2002) and Cermeño *et al.* (2006) exhibit $-3/4$ power scaling of abundance with cellular C content and volume respectively. A histogram of size-abundance scaling exponents for different locations and depths for the Atlantic Meridional Transect (AMT) cruises 12, 13 and 14 is plotted in Figure 3. The modal value is

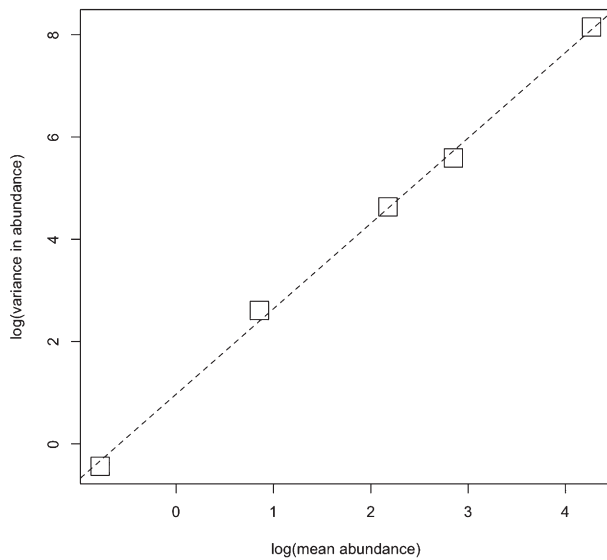


FIG. 4. – Taylor's power law for AMT phytoplankton size class data. Data transformed using natural logarithms. The slope of the log-log regression is 5/3 with $R^2=0.9975$

consistent with values in Li (2002) and Cermeño *et al.* (2006), but we see significant variability, presumably driven by heterogeneity among individual sites and depths. Surprisingly, no relationship exists between scaling exponent and latitude or depth (unpublished results). However, spatial variance exhibits robust scaling with mean abundance, which is obviously tied to body size. Taylor's power law (Taylor, 1961), in which the logarithm of variance in abundance is plotted as a function of the logarithm of mean abundance, for AMT phytoplankton size class data is shown in Figure 4. Because the scaling exponent is 5/3, the coefficient of variation for phytoplankton abundance decreases with mean abundance (Ballantyne, 2005), meaning that larger, less numerous phytoplankters exhibit more relative variation in abundance across space than do their smaller counterparts. It is not immediately obvious what is responsible for generating the exponent of 5/3, but such a consistent mean-variance scaling relationship is worthy of further study.

Trophic structure

The fact that the dominant groups of primary producers in the ocean are all single-celled organisms both reflects the importance of physical processes in structuring marine ecosystems and has important consequences for trophic dynamics and marine food webs. The physical stress associated with living near the surface of the open ocean, low nutrient availability and severe grazing pressure has exerted strong selection against larger body sizes. Building and maintaining large multi-cellular bodies requires too much energy and time to be a viable strategy. Because nutrient acquisition occurs across cell surfaces and occurs predominantly by diffusion, larger cells are at a distinct

disadvantage. Additionally, larger cells are often the primary targets of grazers because they take significantly longer to grow and divide, which exposes each individual cell to greater predation pressure. The major consequence of strong size selection is that the biomass of the primary producer pool in the ocean turns over on a time scale of days. All this primary production has to go somewhere and there are only 3 places for it to go: up the food web, into the microbial loop (Azam *et al.*, 1983) or out of the euphotic zone. The latter accounts for a minimal fraction of total production, 15% on average (Falkowski *et al.*, 1998), leaving the microbial loop and grazing food webs responsible for funnelling off the rest. Although the microbial loop can metabolize a significant fraction of primary production, the remaining primary production, not lost to respiration, is grazed and transferred up through the marine food web. However, changes in trophic structure can significantly alter the flow of C and other nutrients through food webs, affecting gross rates of respiration and C flux through the euphotic zone (Walsh, 1981). The transformation of primary production along these multiple pathways leads to another fundamental question: how is the proportion of primary production consumed by the microbial loop related to highly constrained size structure, and what is the relevant scale for addressing this question? The role of viruses and higher-order interactions on the flow of carbon and nutrients in marine ecosystems is surely linked to the size spectrum of the primary producers. Viruses may help retain nutrients in the euphotic zone but may also increase bacterial respiration by one third (Fuhrman, 1999). The importance of predation in dictating size spectra has long been known (Steele and Frost, 1977), but in order for us to be able to predict the effects of climate change on ecosystem processes, food web interactions must be put in the context of physical mixing (Fuhrman, 1999).

The efficient transfer of primary production up oceanic food webs, due in large part to the similarity in predator and prey sizes, has important implications for ecosystem structure. Higher trophic levels contain significant biomass relative to lower trophic levels, and changes in primary production are tightly linked to the production of fish biomass. In contrast to terrestrial ecosystems, inverted biomass pyramids can occur in marine ecosystems in the absence of significant fishing pressure because rates of production and turnover are so high in the oceans (Demartini *et al.*, 2008). As nutrient availability usually limits primary production and mixing influences nutrient availability (Oschlies, 2002; Vaillancourt *et al.*, 2003), changes in mixing regimes can be linked to changes in primary production (Walsh, 1981). Over evolutionary time, changes in primary production have influenced diversification and trophic complexity in marine ecosystems (Bambach, 1993). Across space, heterogeneity in primary production is intimately tied to mixing, especially in upwelling regions (Walsh, 1981), but local conditions can also influence patterns of pri-

mary production. For example, if wind speed exceeds 5 m s^{-1} , the energy input is great enough to smooth production to biomass ratios (Therriault *et al.*, 1978). The range of time scales associated with zooplankton grazing of primary production and subsequent consumption of zooplankton by fish larvae is consistent with the time scales of dominant variability in ocean currents (Denman *et al.*, 1989). However, higher-level trophic interactions can feed back to influence variability initially generated by physical mixing. Critical phytoplankton patch size increases in the presence of herbivory (Wroblewski *et al.*, 1975), and variability in phytoplankton biomass is influenced by krill predation as well as mixing (Weber *et al.*, 1986). However, variability in krill abundance is relatively constant over the range of scales associated with phytoplankton variance scaling, indicating that krill are less influenced by physical processes than are the primary producers. As a rule of thumb, more mixing means greater nutrient availability, which results in greater primary production and larger plankton (Irwin *et al.*, 2006; Falkowski and Oliver, 2007). Despite the importance of fine-scale variability, for some questions, averaging the effects of mixing across scales throughout the euphotic zone is still informative (Franks, 2002).

Regularities in size structure (for example the so-called Sheldon spectrum discussed above) and universal constraints on metabolism have enabled researchers to link biomass and energy fluxes at the level of unicellular organisms to far-ranging top predators. For example, the efficient transfer of primary production up through food webs has made it possible to estimate total potential catch throughout the world's oceans (Ryther, 1969; Walsh, 1981). Such efficient transfers through consumption enable relationships between biomass and size class, time scales associated with transfers between trophic levels and ecosystem respiration to be predicted from allometric dependence of growth and metabolism on body size (Platt and Denman, 1977; Denman *et al.*, 1989). Furthermore, the shape of the fish size spectrum has been used to infer the degree to which humans have exploited marine ecosystems (Jennings and Mackinson, 2003). Shifts in the size spectrum indicate that different components of marine ecosystems may exhibit differential responses to environmental heterogeneity generated by physical mixing, largely determined by body size. Models with additional trophic detail and explicit size structure suggest that transfers of biomass from smaller to larger size classes need to be more fully integrated in order to reproduce smoother empirically observed size spectra (Silvert and Platt, 1978). Stock *et al.* (2008) show that the observed power law distribution for abundance in size classes emerges from such a trophic model that balances ingestion by one size class with production by the level below, and that the slope of the log-log relationship is determined by the fraction of ingested prey converted to new biomass.

BIOLOGICALLY DRIVEN FEEDBACKS

Ecosystem processes can also exert feedbacks on the physical-chemical environment in the oceans. For a long time, questions about the generation of ecosystem structure have focused on determining whether physics drives biology or biology drives physics (Margalef, 1978; Bracco *et al.*, 2009). Depending on the property in question, the relative importance of physical versus biological processes can vary substantially. As described above, mixing strongly influences phytoplankton patchiness over tens of kilometres, but light absorption by phytoplankton can create a pressure gradient from a temperature gradient and induce a flow velocity (Edwards *et al.*, 2001), albeit small. However, biological feedbacks are more influential in determining the chemical environment in the oceans because biological processes are responsible for the majority of the chemical transformations in the sea. Chemical transformations occur orders of magnitude more rapidly because of biology, which is why biological processes dictate the biogeochemistry of the oceans. In nutrient poor regions of the oceans, competition for nutrients among phytoplankton is strong and results in significant drawdown of inorganic nitrogen (N) and phosphorus (P) concentrations, to almost un-detectable levels. But because N fixation is a biologically-driven process, N:P stoichiometry in the oceans is largely a product of ecosystem processes. It is perhaps the best example of an emergent property in ecosystem science.

The N:P stoichiometry of the euphotic zone has been the basis for much inference about ecosystem processes in the oceans, yet we do not fully understand how metabolism and nutrient requirements ultimately determine observed N:P (Klausmeier *et al.*, 2004). Departures of inorganic N:P stoichiometry from Redfield values typical of phytoplankton (C:N:P of 106:16:1) are widely used to infer nutrient limitation of phytoplankton and the magnitude of N fixation (Gruber and Sarmiento, 1997; Karl *et al.*, 2001; Cavender-Bares *et al.*, 2001; Deutsch *et al.*, 2007). For example, inorganic N:P in the North Atlantic during the summer and in the Pacific throughout the year is less than 16:1, potentially indicating strong selection for N fixation (Karl *et al.*, 2001; Cavender-Bares *et al.*, 2001). However, during the winter in the North Atlantic, large inputs of nitrate, resulting from wind-driven mixing, increase inorganic N:P to significantly greater than 16:1, suggesting greater relative P limitation. Such inference is predicated on the assumption that phytoplankton N:P does not vary from the Redfield value of approximately 16:1, and that phytoplankton draw the most limiting nutrient down to the lowest concentration. However, phytoplankton N:P varies with nutrient status/limitation (Geider and LaRoche, 2002; Bertilsson *et al.*, 2003) and as a function of inputs (Karl *et al.*, 2001), potentially confounding such inference through poorly understood feedbacks. Furthermore, models of coupled phytoplankton-nutrient dynamics require refinement to

eliminate a significant discrepancy between predictions for the relationship between phytoplankton N:P and inorganic N:P and empirically observed values (Ballantyne *et al.*, 2010). Despite intuition for what may govern the likely extremes of phytoplankton N:P (Klausmeier *et al.*, 2004), how the joint influence of phytoplankton nutrient uptake and nutrient recycling conspire to generate the Redfield value of 16:1 for deep water inorganic N:P, which integrates euphotic zone metabolism, is still a mystery. And because mixing has such a significant influence on nutrient concentrations and can mediate the effects of turbulence (Iverson *et al.*, 2010), nutrient dynamics associated with phytoplankton need to be more explicitly linked to physical mixing and the variability it produces.

IMPLICATIONS FOR MODELING MARINE ECOSYSTEMS

Modelling and predicting the global climate system, of which the oceans play an integral part, is one of the remaining grand challenges in science. The inherent difficulty stems from the fact that physics, chemistry and biology all interact to generate ocean dynamics, but not necessarily over the same spatio-temporal scales. Ocean circulation models are more advanced than their biological counterparts, because of historical considerations, but also because universal physical constraints have been accepted for over a century. We have learned much about the constraints on biological processes, but what we know has yet to be fully incorporated into physical models. We have also made many observations that can guide us in the processes of integrating physics, chemistry and biology into synthetic ocean ecosystem models, the type that will allow us to predict how the oceans will respond to continued and future perturbations. The following lays out suggestions for what needs to be incorporated into future models, and lists the biological properties that such synthetic models need to reproduce in order to be considered predictive.

First, models must be grounded in thermodynamics. Energetic considerations from equilibrium thermodynamics provide a basis for determining the possible metabolic pathways in a particular environment, and predicting the sequence in which redox reactions will occur in nature. Microbes that are able to generate energy at the highest rates seem to be better at competing for electron donors and acceptors, meaning that the most energetically favourable reaction will dominate over other less favourable reactions in a particular environment. As a consequence, microbial communities will exploit the most energetically favourable metabolic pathway (Morel, 1983), which has consequences for biogeochemical fluxes, community composition and evolution (Quigg *et al.*, 2003). In a homogeneous environment we should, in theory, be able to predict equilibrium concentrations of redox species as a function of *pe* and pH. Such predictions

should reproduce observed nutrient concentrations and should be tied to C flux between the oceans and the atmosphere. However, the environment for phytoplankton in the oceans is far from equilibrium, and thus, the interplay between equilibrium thermodynamics and variability needs to be addressed more directly in future modelling efforts.

Recent advances in DNA and RNA collection and sequencing techniques have the potential to provide insight into how microbial metabolism feeds back into physically generated heterogeneity and ultimately generates observed variability in ecosystem features. However, interpreting such data in the context of ecosystem functioning remains a significant challenge because mixing creates a dynamic environment (Falkowski and de Vargas, 2004). Additionally, the gap between raw DNA sequences collected in the oceans and gene expression and ecosystem function is far from being bridged, although recently *in situ* gene expression has been characterized for well studied taxa (Frias-Lopez *et al.*, 2008). The extent to which relatively easily collectible *in situ* genomic and transcriptomic data can inform future models needs to be determined. In particular, it would be very useful to compare patterns of spatial variability in gene presence and expression to empirical patterns of β -diversity for plankton described by Mackas (1984) and Starr and Mullin (1981). Such a comparison would identify meaningful scales for averaging over meta-genomes and transcriptomes for bacteria, which would complement our knowledge for phytoplankton and zooplankton.

Perhaps the greatest challenge lies in integrating size-dependent life-history trade-offs and ecological interactions with physically generated variability at similar scales. Litchman *et al.* (2006) and Follows *et al.* (2007) have made significant strides toward such integration, but at significantly coarser scales than those at which life-history trade-offs, predation and competition occur. Optimal phytoplankton size is tightly linked to nutrient availability (Falkowski and Oliver, 2007; Yoshiyama and Klausmeier, 2008) and buoyancy (Smayda, 1970; Rodríguez *et al.*, 2001), but placing trade-offs directly into the context of the Kolmogorov energy cascade is necessary to link microscopic interactions to ecosystem-level patterns. Size-structured trophic interactions, which are responsible for generating patterns of abundance across trophic levels (Stock *et al.*, 2008), must also be placed directly in the context of the energy cascade, because mixing influences encounter rates between prey and predators (Weber *et al.*, 1986).

Finally, there are key features that models need to reproduce. First, variability in biological variables needs to scale with a smaller exponent than predicted by the Kolmogorov spectrum at the finest scales. Second, biological variability must match predictions from physics over intermediate scales. Third, body size-abundance relationships should exhibit some variability, but on average should be characterized by an

exponent of close to -1 . And last, variability in the concentrations of inorganic N and P, as well as particulate N:P, should be bounded by long-term data sets.

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