Managing Marine Ecosystems as Complex Adaptive Systems: Emergent Patterns, Critical Transitions, and Public Goods

George I. Hagstrom*and Simon A. Levin†

Department of Ecology and Evolutionary Biology, Princeton University

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Abstract

Complex adaptive system provides a unified framework for explaining ecosystem phenomena. Three ubiquitous features of ecosystems that arise from this framework are emergent patterns, critical transitions, and cooperative behavior. Focusing on marine ecosystems, we present numerous examples of each phenomenon, using the theory of complex adaptive systems to explain the universal features and common mechanisms shared by disparate ecosystems, as well as the important differences. Marine ecosystems provide important ecosystem services, and we analyze how complex management issues can be solved in the face of anthropogenic ecosystem and environmental pressures.

1 Introduction

Twenty years ago, as Ecosystems was setting out on its path to become one of the leading-edge outlets for progress in ecosystems research, it featured a special issue on viewing ecosystems as complex adaptive systems (Hartvigsen et al., 1998, Levin, 1998). Since that time, this perspective has seen impressive development, from both theoretical and applied perspectives (Filotas et al., 2014, Messier et al., 2015, Scheffer et al., 2012).

*georgehagstrom@gmail.com

†slevin@princeton.edu

GIH and SAL designed the study, carried out the research, and wrote the manuscript

In this paper, we will focus on three features of complex adaptive systems, through the lens of marine ecosystems. Complex adaptive systems are characterized first of all by emergent features, like food-web structure and nutrient cycling, that characterize community and ecosystem patterns at the macroscopic levels, but that have not been the major targets of evolution at the organismic level. Alternative stable outcomes are hence possible (Carpenter et al., 2001, Jacob, 1977, Staver et al., 2011a,b), as is the possibility for system flips from one basin of attraction to another (Carpenter et al., 1999, Scheffer, 2009, Steele, 1998). Two fundamental and interrelated challenges are therefore to understand the relationships among phenomena at diverse scales of time, space and organizational complexity, developing scaling laws and moment-closure techniques; and to resolve the public-goods and common-pool-resource conflicts that are unavoidable. These challenges arise in the description and management of any complex-adaptive ecosystem, but for definiteness we explore them in more detail for marine ecosystems.

2 Emergent Patterns in Ocean Ecosystems

The physicist Philip Anderson wrote that "more is different" (Anderson, 1972), highlighting the essential importance of emergent paterns for complex adaptive systems. Emergent patterns are large-scale structures or regularities that arise due to interactions that take place on small scales (Levin, 1998), and feed back to influence those small-scale interactions. In systems that contain living things, emergent patterns involve the coupling and coevolution of organisms and their environment: large-scale patterns of ecological properties such as trophic structure and nutrient usage are generated by small-scale interactions, but also influence the further development of those small-scale interactions and over long time scales may lead to changes in the physical and chemical environment. These processes have shaped the biosphere of the Earth, oxygenating the atmosphere and oceans, altering the temperature and climate, and creating new niches for life to occupy (Falkowski et al., 2008).

The ocean ecosystem exhibits numerous emergent patterns (Cullen et al., 2007), showing remarkable regularities in size spectra, correlations between the physical environment and morphology, and elemental stoichiometry. The Sheldon Spectrum (Andersen and Beyer, 2006, Sheldon et al., 1972, Stock et al., 2008) is the universally constant scaling law that there are equal amounts of biomass in each logarithimically spaced size class, and it emerges from the biophysical size scalings of different interacting processes in the ocean: metabolism, swimming speed, and trophic efficiency. An equally remarkable pattern is the so-called Margalef's Mandala (Kiørboe, 1993, Margalef et al., 1979), which accurately predicts the cell-size and motility

of phytoplankton as a function of the level of nutrients and turbulence in their environment.

The pattern of elemental stoichiometry in the ocean, which is sometimes called the Redfield ratio (Redfield, 1958), is both biogeochemically important and unresolved in its details. The Redfield ratio was discovered when Arthur Redfield noticed the striking similarity between the mean nitrogen-to-phosphorus ratio in organic matter, (N:P_{org}), and the ratio of inorganic fixed nitrogen to inorganic phosphorus in the deep ocean, (N:P_{deep}), the former of which is approximately 16:1 and the latter of which is approximately 14.7:1. Redfield hypothesized that this near equality was not due to either chance or phytoplankton adaptation, and was instead the result of phytoplankton altering the amount of available fixed nitrogen in the environment so that (N:P_{deep}) $\sim$ (N:P_{org}). Redfield proposed that diazotrophic phytoplankton, which can fix nitrogen from readily available dinitrogen gas in the ocean, tie the inorganic fixed nitrogen inventory to the inorganic phosphorus inventory in "Redfield" proportions. This idea was made mathematically explicit by Tyrrell and others (Lenton and Watson, 2000, Tyrrell, 1999), who showed that the supply of phosphorus to the ocean determines both the amount of fixed nitrogen in the ocean and the total primary producitivity of phytoplankton. This remarkable result suggested that, despite the fact that nitrogen directly limits the growth of phytoplankton in the majority of the surface of Earth's oceans, the total amount of exogenous nitrogen flux to the ocean is of no consequence to either nutrient limitation patterns or primary productivity. The concepts that (N:P_{deep}) $\sim$ (N:P_{org}) because of homeostasis mediated by diazotrophs and that phosphorus is the *ultimate limiting nutrient* are collectively known as the Redfield paradigm.

The Redfield paradigm illustrates the importance of nutrient usage patterns for the complex adaptive system that is the ocean: elemental stoichiometry is the ecological property through which phytoplankton interact with biogeochemical cycles, enabling them to coevolve with their environment. There have been two significant discoveries that cast doubt on the Redfield paradigm: the discovery of systematic deviations of phytoplankton populations from the Redfield ratio (Martiny et al., 2013, Teng et al., 2014), and the discovery that iron limitation is widespread in the ocean (Falkowski, 1997, Martin and Fitzwater, 1988, Mills et al., 2004). These discoveries threaten to upend the basis of the Redfield paradigm by suggesting that there is nothing special about the 16:1 ratio and by usurping the role of phosphorus as the nutrient regulating diazotrophy. Recent research has led to the elucidation of many aspects of the stoichiometric pattern, from the drivers of phytoplankton stoichiometry (Galbraith and Martiny, 2015, Klausmeier et al., 2004a, 2008, 2004b, Toseland et al., 2013) to its latitudinal variation (Martiny et al., 2013, Teng et al., 2014) to the implications for the coupled nitrogen, phosphorus, and iron cycles and biogeochemistry (Hagstrom et al., 2016, Weber and Deutsch, 2012, 2014).

2.1 Environmental Controls on Phytoplankton Stoichiometry

Although the Redfield ratio has been adopted as an intrinsic property of phytoplankton, Redfield was well aware of the fact that field populations of phytoplankton typically showed large deviations from this mean ratio. Numerous mechanisms have been proposed to explain the wide ranging observations of phytoplankton (N:P_{org}), the two most important of which are the *growth-rate hypothesis* (Klausmeier et al., 2004a) and the *frugality hypothesis* (Galbraith and Martiny, 2015, Klausmeier et al., 2004b). The growth-rate hypothesis is based on the constant stoichiometric composition of organelles and biological macromolecules such as ribosomes and proteins. Using simple physiological principles, it is possible to model the growth rate of a phytoplankton cell having a given allocation of biomass to each type of macromolecule (Shuter, 1979). Combined with the knowledge of the stoichiometry of each type of macromolecule, this provides a means of linking ecological fitness to stoichiometry. This approach was used by Klausmeier et. al. (Klausmeier et al., 2004a) to determine the stoichiometry of optimal phytoplankton strategies in different types of environments. They found that the optimal stoichiometry was never equal to the Redfield ratio, with optimal (N:P_{org}) ~ 40 in environments with limiting resources and (N:P_{org}) ~ 8 in environments with replete nutrients. This dynamic suggests that the Redfield ratio emerges from a locally heterogeneous mixture of resource limited patches at high (N:P_{org}) and resource replete patches at low (N:P_{org}), produced by random disturbances and upwelling events. This point of view was extended by Toseland et. al. (Toseland et al., 2013), who considered the differential impact of temperature on metabolic processes within cells and also considered the effect of varying cell size. Together these studies give mechanistic demonstrations of why oligotrophy is accompanied by high (N:P_{org}) and eutrophy is accompanied by low (N:P_{deep}).

Studies of element partitioning in cells show that regulation of ribosomes is not enough to explain the variations in (N:P_{org}) observed in natural phytoplankton populations. The cellular phosphorus pool is only partially accounted for by ribosomes, and in many cases less than one-third of the cellular phosphorus quota is in ribosomal RNA. The frugality hypothesis relies primarily on fluctuations in this non-ribosomal RNA pool in order to explain variations in (N:P_{org}). The basis of the frugality hypothesis is that phytoplankton take advantage of resources that are easy to acquire, and are frugal with their allocation of scarce resources. Thus when a resource is available, the intercellular quota increases, and when it is scarce the quota decreases. This basic mechanism is influenced by an inherent plasticity in the cellular quota of each element within a given cell. Cells have little capacity to change their carbon or nitrogen quotas, as these two elements are in common in every single biological molecule. Less-common elements like iron and phosphorus have highly plastic cellular quotas, and phytoplankton frugality means that the environment can dramatically influence

ratios of carbon or nitrogen to phosphorus and iron. When phosphorus levels are low, cells reduce phosphorus usage by limiting storage reserves and substituting SQDG (Sulfoquinovosyl diacylglycerol) for phospholipids (Mouginot et al., 2015, Van Mooy et al., 2006). When phosphorus is available, the opposite dynamic occurs and cells accumulate luxury phosphorus, driving up (N:P_{org}). Iron is even more plastic than phosphorus, and cellular quotas of iron can range over almost two orders of magnitude in response to changes in availability. The frugality hypothesis has been explored mathematically by Klausmeier et. al. (Klausmeier et al., 2004b), who developed a multi-nutrient cell quota model, and by Galbraith and Martiny (Galbraith and Martiny, 2015), who modeled phytoplankton (P:C_{org}) as a linear function of ambient phosphorus concentrations. Both hypotheses may play a role in explaining laboratory and field observations of (N:P_{org}).

2.2 Challenges to the Redfield Paradigm

The theory that phosphorus is the ultimate limiting nutrient (Karl, 2000, Tyrrell, 1999) and that the nitrogen cycle is controlled directly by the phosphorus cycle has been challenged by the discovery of latitudinal variations in stoichiometry and of iron limitation. A synthesis of field measurements of stoichiometric ratios in organic matter (Martiny et al., 2013) and inverse modelling studies of the carbon to phosphorus export ratio of organic matter (DeVries and Deutsch, 2014, Teng et al., 2014) showed that (C:P_{org} and (N:P_{org}) are significantly above the Redfield ratio in oligotrophic gyres, and significantly below it in high-latitude subpolar gyres and equatorial upwelling regions. Diazotrophs are predominantly found in oligotrophic regions depleted of nitrate and ammonium, implying that they occur only in ecosystems with (N:P_{org}) substantially greater than Redfield. This discovery violates one of the most important assumptions of Tyrrell's model, that diazotrophs compete with phytoplankton at the Redfield ratio. This resource competition establishes the setpoint of the deep ocean nitrogen inventory in Tyrrell's model. Iron limitation violates the Redfield paradigm in two ways: by limiting diazotroph populations, thus preventing any interaction between the nitrogen and phosphorus cycles, and by limiting the bulk plankton population, preventing nitrogen from being a limiting nutrient in certain regions and thus leading to an equal role for iron as the *ultimate limiting nutrient*.

Hagstrom et. al. (Hagstrom et al., 2016) developed a simple box model with three nutrients, three phytoplankton types, and regional differences in phytoplankton biogeography and N:P:Fe. The model predicted that the ocean can exist in six different states, each represented by the pair of nutrients limiting large phytoplankton and diazotrophs. The realized pattern of nutrient limitation was determined by resource-ratio-theory (Ward et al., 2013): the nutrients with the lowest supply ratio relative to demand were limiting

to phytoplankton. Primary productivity was controlled by all three of the nutrients limiting phytoplankton populations, implying that contrary to previous theories, nitrogen could be an ultimate limiting nutrient. Variations in the supply of iron to the low-and high-latitude boxes was sufficient to cycle the model through all of its states. When iron deposition levels were low, iron was an ultimate limiting nutrient in the low-latitude regions and either iron or nitrogen was an ultimate limiting nutrient in the high-latitude regions. As iron levels to each box increased, the ultimate limiting nutrients changed from iron to phosphorus in the low-latitude box, and iron to nitrogen to phosphorus in the high-latitude box. Nitrogen could be an ultimate limiting nutrient due to geographic restrictions on diazotrophy and due to differences in stoichiometry between diazotrophs and small phytoplankton, which allow nitrogen to stimulate primary productivity when diazotrophs are iron limited. Hagstrom et. al. also showed that the deep ocean nitrogen inventory is much more flexible than predicted by the Redfield paradigm, and is regulated by the stoichiometry of low-latitude phytoplankton, the supply rate of the ultimate limiting nutrient to the low-latitude regions, and the ratio of high-latitude to low-latitude upwelling. Our results suggested that $(N{:}P_{deep}) > (N{:}P_{org})$ in a phosphorus limited ocean, due to the high nitrogen to phosphorus ratio of organic matter in oligotrophic gyres.

Variable stoichiometry and iron limitation of diazotrophs are together a plausible mechanism for trigerring the fluctuations in the carbon cycle observed over geological time. Geoscientists have theorized that atmospheric CO_2 during glacial periods were caused by the increased aeolian flux in the dry glacial climate (Sarmiento, 2013). Increases in the strength of the carbon pump without corresponding increases in upwelling are impossible under the Redfield paradigm, which predicts that the surface ocean phosphorus would become depleted after only modest productivity increases. Hagstrom et. al. (Hagstrom et al., 2016) and Galbraith and Martiny (Galbraith and Martiny, 2015) showed that productivity can increase without increases in upwelling if the phytoplankton community shifts to higher $(N{:}P_{deep})$, which would be expected if surface ocean phosphorus declined or if nitrogen fixation increased.

Changes in the carbon pump may occur on much shorter time scales due to anthropogenic nutrient inputs. The flux of anthropogenic nitrate and potentially iron has increased dramatically since industrialization (Duce et al., 2008). There is evidence from longitudinal studies of ocean ecosystems, particularly the North Pacific Subtropical Gyre (Karl, 1999), showing a rapid change in numerous ecological properties, including declining cell size, increasing $(N{:}P_{org})$, declining phosphorus levels, and increased nitrogen fixation. Could these changes be part of a shift from an iron-limited system to a phosphorus limited one, driven by deposition of industrially produced iron or nitrate from Asia? The potential for ocean ecosystems to undergo rapid change in response to human activity has been well established by coral bleaching and fishery collapse, but

it remains to be seen how quickly stoichiometric ratios can shift. Shifts in nutrient-use efficiency may also dampen declines in the carbon pump due to increased stratification, as both inverse model studies (Teng et al., 2014) and theoretical models (Galbraith and Martiny, 2015) suggest that latitudinal gradients in carbon export are weak. This confirms work based on oxygen production in the euphotic zone of the oceans (Emerson, 2014) and challenges the idea that most export comes from region with phytoplankton blooms and strong upwelling.

Resource ratios set the interaction between ecosystem and environment and drive the emergence of ecological patterns. Although commonly treated as fixed constants, resource ratios can be changed by individual plasticity and natural selection. Mathematical models of biogeochemical cycles seldom allow for ecological or evolutionary plasticity in these ratios, even though the basic principles that regulate these ratios have been described. Incorporating the ecological constraints on elemental stoichiometry is an essential step in the development of comprehensive theories of the coevolution of phytoplankton and their environment. Evolutionary models of phyoplankton competing for multiple nutrients tend to evolve towards colimitation (Klausmeier et al., 2004b), and frugal phytoplankton, increase in fitness by making greater use of abundant resources and more frugal use of scarce resources, should be no exception to this rule. Combining flexible phytoplankton, biogeochemistry, and evolution into a single model is the next step in this fruitful line of research. The feedbacks between biological response to nutrients and the nutrient inputs themselves may be the ultimate regulator of ocean biogeochemistry.

3 Critical Transitions

The dynamics of the biosphere are punctuated by abrupt changes in response to gradual perturbations by either natural or anthropogenic forces (Scheffer, 2009). These abrupt changes are significant events both from ecological and economic points of view, and they are often irreversible: when the perturbations are reversed the altered state may persist (Carpenter et al., 2001). Examples of these critical transitions have become increasingly numerous as the anthropocene has advanced, threatening or destroying important ecosystem services thoughout the world. In the marine environment, marginal seas and other coastal ecosystems have borne the brunt of critical transitions, which include the collapse of coral reef ecosystems (Bellwood et al., 2004, Knowlton, 1992) and important fisheries (Berkes et al., 2006, Halpern et al., 2008) due to overfishing as well as the spread of anoxia and dead zones (Diaz and Rosenberg, 2008) near areas with large industrial output. Critical transitions are bifurcations: a small change in the system parameters leads to a drastic

change in system behavior(Scheffer, 2009). These discontinuous changes are often described by saddle-node bifurcations, which lead to the disappearance of a stable branch of equilibria and force the system to jump to a distant state. The presence of a critical transition is often accompanied by the existence of alternative stable states (Collie et al., 2004, Steele, 1998) and hysteresis, and the reversal of the perturbation that trigerred the critical transition may be unlikely to reverse the transition itself. As a result, a predictive capacity for critical transitions is urgently needed in the face of increasing anthropogenic perturbations to the biosphere.

The most important universal phenomenon accompanying a critical transition is the loss of stability of the equilibrium state, inspiring the development of a variety of techniques for predicting a critical transition or estimating the robustness of a given system state (Boettiger and Hastings, 2012a, Carpenter and Brock, 2006, Guttal and Jayaprakash, 2008, Held and Kleinen, 2004, Holling, 1973). Methods for detecting critical transitions fall into two classes, depending on the level of stochasticity of the underlying dynamics (Scheffer et al., 2012). When the dynamics are mostly deterministic, stochastic fluctations are confined to a small neighborhood of the equilibrium solution, which can be seen by considering the Ornstein-Uhlenbeck process:

$$dx = -r(x - \theta)dt + \sigma dW, \tag{1}$$

where W is the Wiener process. The variance of this process $\mathrm{var}(x(t)) = \frac{\sigma^2}{2r}$, and the autocorrelation $\mathrm{cov(x(s), x(t))} = \frac{\sigma^2}{r}\sinh(r(t-s))$, for $s < t$. During a critical transition, the dynamics along the least stable direction will have large amplitude and be well approximated by equation 1. Methods for detecting critical transitions take advantage of the fact that moments of the time-series blow up near the critical transition. The two classes of methods are based on summary statistics, such as variance (Carpenter and Brock, 2006) or autocorrelation (Held and Kleinen, 2004), or probabilistic estimation of the time at which $r = 0$ in equation 1 (Boettiger and Hastings, 2012a,b). These later methods have been developed recently and have been shown to be more robust than those based on summary statistics. Heavily stochastic systems will have fluctuations that can shift the system between alternative stable states (Scheffer et al., 2012), and thus require different early warning systems. A histogram of the time-series can be used to be estimate the size and shape of the basin of attraction of each equilibrium. Critical transitions can arise in more complex ways, and more theoretical work is required to understand which bifurcations arise in complex adaptive systems.

Spatial heterogeneity can change smooth critical transitions by allowing for the preservation of domains of each equilibrium state (Martín et al., 2015, van Nes and Scheffer, 2005). This smoothing depends on the diffusivity, and it can be explicitly shown that small diffusivity preserves patches of each state, changing

discontinuous first order transitions in continuous second order ones. Heterogeneity provides a novel mechanism for managing systems subject to critical transitions, as patches of the ecosystem can be designated as preserves in order to maintain both states. When the system is reversed, there will no longer be hysteresis as the preserves will act as nucleation centers for the original state.

In the following sections we present several examples of critical transitions in marine ecology and ocean science, discussing the mechanisms that generate alternative stable states, the implication of critical transitions for ecosystem health and the environment, and the development of early warning indicators and management techniques.

3.1 Overfishing: Collapse of Corals and Fisheries

Overfishing has driven critical transitions in many types of marine ecosystems, including coral reefs and fisheries. High rates of fishing selectively perturb parts of the marine food web, leading to complex nonlinear responses of both biota and environment. Ecologists have characterized numerous mechanisms that can give rise to alternative stable states in these systems, and we follow Knowlton (Knowlton, 1992) and others (Collie et al., 2004, Steele, 1998) in defining three broad classes of mechanisms: those based on single species interactions/Allee effects, those based on competitive interactions, and those based on predator prey interactions. The Allee effect (Allee, 1931) is the proportionality of specific growth rate to population density at low population levels, which typically leads to a population model with both stable high and low abundance equilibria. Allee effects are usually produced by intraspecies cooperation or a density dependent rate of finding mates, impyling the rare animals have difficulty surviving or reproducing. Two stable equilibria can also be generated by the competition of two similar species: if each species reduces the growth rate of the other when at high population levels, there will two stable equilibria, each with one dominant animal and one rare animal, which might be maintained by immigration from nearby regions. Predator prey interactions are typified by the functional response of the predator to the prey, and numerous types of functional response can produce alternative stable states (Collie et al., 2004). For instance, if per-capita predation is negatively dependent on prey abundance, alternative stable states can be expected (Knowlton, 1992). Overfishing can destabilize equilibria and lead to either a reorganization of the entire food web or the replacement of some of the species that are present.

Coral reefs are highly productive shallow water ecosystems organized around the symbiosis between calcifying corals and their microalgal endosymbionts and the presence of a traditional marine food web. The dominance of corals is maintained by top-down control of macroalgal populations by small reef fish. Coral

reef ecosystems have experienced unprecedented global collapse in the past 30 years, driven by bleaching, the disruption of the traditional food web, and extensive macroalgal growth (Bellwood et al., 2004, Knowlton, 1992, Mumby et al., 2007). Carribean reefs experienced a large-scale collapse in the 1980s, catalyzed by the replacement of small reef fish by the sea urchin *Diadema antillarum*, and the subsequent collapse of the latter due to viral outbreak (Knowlton, 1992). The release of grazer control lead to the replacement of corals by dense patches of macroalgae. Numerous mechanisms contributed to this ecological catastrophe, including the Allee effect, which prevented the recovery of the sea urchin population, unfavorable predator-prey interactions that suppressed grazing of macro-algae at high densities, and pathogenicity produced by overgrowth of the microbial loop (Kline et al., 2006). Field manipulations of reefs have been unsuccessful in restoring corals once they have collapsed, and strong hysteresis appears to be at work in the system.

Coral conservation efforts that rely on the spatial network of reefs have met with modest success. Coral reefs usually exist in large groups which are connected via ocean currents. The connectivity between reefs likely enhances the robustness of coral ecosystems, sparing reef fish, sea urchins, and corals from regional extinction after coral collapse (Mumby and Hastings, 2008, Nyström and Folke, 2001). Because of the role of overfishing in driving critical transitions on reefs, governments have designated no-take marine preserves in order to maintain a larger reservoir of healthy corals (Botsford et al., 2009). This program has been successful in slowing the death of coral reefs in some areas, but it is still an open problem to determine the optimal choice of marine preserves to maximize the robustness of the entire system. The solution of this problem will require a synthesis of techniques from dynamical systems, fluid mechanics, and ecology, and is an important problem for future research.

Overfishing has also led to the collapse of many of the most productive fisheries worldwide (Berkes et al., 2006, Halpern et al., 2008). Collapsed fisheries have been unable to recover due to the presence of alternative stable states (Choi et al., 2004). Various mechanisms have been discovered that could explain alternative stable states in these models, including mortality rates inversely proportional to school size, and the formation of schools of containing a small minority of the ecologically threatened fish (Collie et al., 2004). The collapse of the stock of demersal fish, including cod and haddock, in the northwestern Atlantic Ocean is a canonical example of the critical transitions that have plagued fisheries in the past century (Choi et al., 2004). The coastal shelf of the northwestern Atlantic ocean is a highly productive ecosystem, and high export of carbon supported a high biomass benthic community, providing energy for bottom feeders such as Cod and Haddock. The rate of exploitation of this fishery accelerated in the latter half of the 20th century, and total rates of removal of fish represented reached the same order of magnitude as the energy flow from

lower trophic levels. Stocks of small pelagic fish increased, but the supply of energy to the benthos declined, as did the populations of groundfish. By 1993, the size of the fish catch had declined to a few percent of its historical maximum, and a moratorium was placed on fishing. In the years since, groundfish have not recovered, and the benthic community is instead dominated by crustaceons, suggesting that the system is in an alternative stable state.

There is substantial economic and ecological interest in avoiding fishery collapse and in replenishing collapsed fisheries. Many entities are stakeholders in fisheries, including the fishermen, local communities, corporations, and the general public. As a result, efforts to manage fisheries must interface with the varied incentives of the different stakeholders, which has been a challenging problem. Behavioral economics and ecology have been used in concert to develop policies for successfully managing fish stocks, with mixed results. Even prior to widespread fishery collapse, fisheries were managed by targeting fish catches to an estimated maximum sustainable yield (Smith and Punt, 2001). This policy was unsuccessful, as poor modelling (especially of interactions), inaccurate stock assessment, and a lack of proper incentivization or enforcement methods lead to overexploitation of fish stocks. New policies have been developed since, with greater success. In particular, fisheries managed using individual catch shares and transferable quotas, which provide each fisher with an exchangeable right to a specific amount of fish per year, have shown greater robustness than those without (Costello et al., 2008). An even more intriguing idea is to abandone the species concept and to regulate fishing by size class only, which would much better preserve the ecosystem structure, preventing imbalances between predators and prey across trophic levels (Andersen et al., 2015). More work is needed to understand whether stable equilibria provide a good model for fisheries, and to find ecologically reasonable strategies that align naturally with management incentives.

3.2 Eutrophication: Interactions Between the Nutrient Cycles and the Food Web

Eutrophication is one of the most important causes of critical transitions in both coastal and lacustrine ecosystems (Doney, 2010, Scheffer and van Nes, 2004). Coastal ecosystems are highly productive ecosystems, contain large eukaryotic phytoplankton and a long food chain, consisting of macrozooplankton, copepods, and large fish biomass. Eutrophication usually occurs through the delivery of industrial fertilizers, high in fixed nitrogen and phosphorus, to coastal zones (Gray et al., 2002). The delivery of additional nutrients enhances primary productivity and the export of organic matter. Organic matter recycling consumes oxygen below the euphotic zone and in the benthos, and if productivity is sufficiently high, oxygen can be depleted

from either of these regions. Hypoxia and anoxia have a significant effect on metazoans, most of which cannot survive below some oxygen threshold. Oxygen depletion leads to the local extinction of large parts of the food web, beginning with benthic dwellers and demersal fish. Hypoxia in the bottom waters changes the biogeochemical cycling of phosphorus, causing phosphate to be released from iron phosphorus compounds as well as releasing sulfer compounds that buffer the system against reoxidation (Van Cappellen and Ingall, 1994). The sediments usually contain significant quantities of phosphorus, so the reversal of phosphorus burial is a significant feedback, leading to further eutrophication. Eventually, hypoxic conditions restructure the food web, leading to a switch from a traditional food web to one dominated by cyanobacteria, mixotrophs, the microbial loop, and filter feeders such as jellyfish (Oguz and Velikova, 2010, Uye, 2011). Even if external fluxes of nutrients are decreased, recovery of the original ecosystem structure may not happen.

This full process has played out in the Black Sea (Oguz and Velikova, 2010). Eutrophication due to agricultural activity in the Soviet Union and Eastern Europe led to severe hypoxia over the shallow western shelf. The traditional food web was replaced with one based on dinoflagellates and jellies, leading to collapse of Baltic Sea fiseries. After the dissolution of the Soviet Union, a recession in Eastern Europe led to a massive decline in agricultural output, but not to recovery of the Black Sea. Persistent anoxia continues to supply high levels of phosphorus, and fish species remain absent. The Black Sea scenario is becoming more prevalent throughout the world, especially in heavily industrialized areas. Coastal dead zones are becoming common and jellyfish are increasing in abundance throughout the oceans (Mills, 2001, Purcell et al., 2007). Eutrophication is one of the most significant threats to ocean ecosystems, as it can be nearly impossible to recover lost biodiversity after an anoxic event. Models for jellyfish-dominated food webs are in their infancy(Uye, 2011), and much work remains to be done before we understand how to properly remediate hypoxic or anoxic coastal waters.

This bifurcation is particularly interesting because it can operate on numerous different space and time scales, a feature which may give potential hints on how to both anticipate and mediate eutrophication driven oxygen depletion. Eutrophication of lacustrine ecosystems is common, and clearly leads to two alternative stable states: turbid, hypoxic, cyanobacteria-dominated lakes and clear, oxic, algae-dominated lakes (Carpenter et al., 1999). In this cases, remediation efforts based on the cessation of nutrient inputs and the introduction of small grazers has led to eventual reversal of the turbud state, though it seems impossible to apply such a manipulation on the scale of coastal systems (Scheffer and van Nes, 2004). It is apparent from the geologic record that the entire ocean has become anoxic for significant periods of time. These marine anoxic events (or MAEs) are examples of critical transitions on the global scale (Sarmiento et al.,

1988). Although the cause of MAEs is hotly debated, they are in many ways analogous to the smaller scale transitions that occur in coastal waters and lakes. MAEs are associated with mass extinctions of ocean life, with a switch from eukaryotic to cyanobacterial dominance amongst phytoplankton, and of a shift to extremely high C:P values in sediments (Butterfield, 2009). That the same series of mechanisms could be responsible for critical transitions on such differing space and time scales is an extraordinary feature of coupled biogeochemical cycles and a fascinating topic for future research.

3.3 Early Warning Systems for the Ocean Circulation and Climate

The theory of critical transitions has been extensively developed for climate and ocean phenomenon (Lenton, 2011, Lenton et al., 2009). The coupled-ocean atmosphere system is highly nonlinear, and the ocean circulation acts as an amplifier of climate fluctuations. Paleo-proxies indicate that the climate is highly dynamic, transitioning between cold glacial and warm inter-glacial periods on a time-scale driven by subtle Milankovich forcing (Rahmstorf, 2002). Positive feedbacks include the ice-albedo effect, greenhouse effects potentially driven by alterations in the soft-tissue pump, and inter-hemispheric temperature see-saws caused by the strengthening or weakening of the thermohaline circulation. Changes in the thermohaline circulation are important on shorter time-scales, and are capable of causing dramatic warming or cooling events such as the Damsgaard-Oeschger and Heinrich events. The thermohaline circulation is influenced by the strength of deep-water formation in the North Atlantic, which involves the sinking of cold, relatively fresh water in the subpolar North Atlantic. Decreases in salinity due the influx of meltwater (as in Heinrich events) led to a reduction in deep water formation rates, and this reduction is amplified due to high levels of precipitation over deep water formation regions. The thermohaline circulation can be described using bifurcation theory and alternative stable states, driven by changes in freshwater forcing.

Critical transitions of the climate system are high-impact events (Lenton, 2011, Rahmstorf, 2002), and many early warning indicators were developed originally with atmosphere-climate dynamics in mind (Held and Kleinen, 2004, Scheffer et al., 2009, 2012). The availability of both high-resolution time series data describing the state of the atmosphere and oceans and the availability of large-scale numerical models have aided the development and testing of early warning signals. Detailed study of paleo-data as well as simulations of climate under different scenarios of anthropogenic forcing have led to the identification of a list of potentially serious climate bifurcations, including alterations of patterns of monsoon rains, shutdown of the thermohaline circulation, melting of both arctic and antarctic ice sheets, and strengthening of ENSO events. Simulations of these phenomena simulataneously provide a test of early warning indicators, which

have proved promising but not definitive with model based (Boettiger and Hastings, 2012a,b). The combined use of early warning signals with measures of potential event impact is now accepted as key tool for management and government planning (Lenton, 2011, Lenton et al., 2009). Work remains to develop a better understanding of the inconsistency of early warning indicators for some critical transitions, and also to extend these indicators to ecological systems.

4 Public Goods: Extracellular Macromolecules in the Ocean

Public goods are ubiquitous features of social and ecological systems (Levin, 2014). In the marine environment, extracellular macromolecules such as iron-binding ligands (Boyd and Ellwood, 2010, Johnson et al., 1997), polysaccharides (Hassler et al., 2011, Passow et al., 1994), enzymes (Duhamel et al., 2010) and fixed nitrogen (Karl et al., 1997) act as public goods and sustain essential ecological and biogeochemical processes. Public goods production is only sustainable when it is favoured by natural selection, and numerous such selective mechanisms have been identified, for instance kin selection (Hamilton, 1964) and multi-level selection (Traulsen and Nowak, 2006, Wilson, 1975). These mechanisms, which are facilitated by spatial assortment (Damore and Gore, 2012), are effective in explaining the evolution of microbial cooperation in biofilms (Nadell et al., 2008a,b), but seem more difficult in the unstructured marine environment (Hutchins, 1995, Traving et al., 2015, Völker and Wolf-Gladrow, 1999). Marine microbes have developed clever adaptations that allow for public goods production even in highly turbulent conditions, including the modification of the phycosphere with extracellular polymers (Amin et al., 2012), the exploitation of microscale nutrient patches, organic gels (Verdugo et al., 2004), and sinking particles (Cordero et al., 2012), and the evolution of metabolic dependencies through adaptive gene loss (Morris et al., 2012). The theory behind these mechanisms sheds light on the types of public goods dynamics that may arise in the ocean, and helps identify the organisms expected to produce key public goods. Public goods couple dynamics that occur below the millimeter scale to those of entire ecosystems and biogeochemical cycles, and new modelling techniques must be developed to understand the global implications of these microscale processes.

4.1 Evolution of Cooperation in the Ocean

We define a public good as a chemical, behavior, or process that increases the fitness of organisms other than one that generated it. Because scroungers, which do not produce the public good, benefit from public goods production, they can also be able to invade populations of producers. Public goods games illustrate

the dynamics of these invastions (Wakano et al., 2009). In these games there are two types of organisms, a producer and a scrounger. The producer pays a cost c to generate the public good, which enhances the fitness of both other producers and scroungers, and the scroungers do not pay the cost. If there is no spatial structure, and the benefit is available to the entire population, the scroungers will dominate the producers and drive them to extinction, lowering the fitness of the entire community and leading to the 'tragedy of the commons'. In order for public goods production to be sustainable, structure is required to allow producers to benefit more from production than scroungers. Most such mechanisms rely on the spatial assortment of similar individuals (Damore and Gore, 2012). In structured environments such as a bacterial biofilm (Nadell et al., 2008b), producers of the public good will be clustered near their kin and near other producers, favoring continued public goods production. The criteria for the sustainability of public goods production is a variant of Hamilton's rule (Damore and Gore, 2012, Hamilton, 1964), which is most commonly given as:

$$rb - c > 0$$

where r is a measure of spatial assortment, b is the fitness benefit of the public good, and c is the cost of production. When assortment is included, there are numerous possible evolutionary outcomes depending on the specific details of the competition between producers and cheaters, including dominance of each type, equilibrium coexistence, or bistability. Characterizing the benefits of the public good realized by producers and scroungers is the key to understanding the evolution and stability of public goods.

The presence of public goods in the marine environment is theoretically challenging because of the relative lack of structure in the marine evironment, implying that the assortment factor r is close to 0. This can be seen through consideration of the fluid dynamics of the micro-environment experienced by phytoplankton and heterotrophic bacteria in the ocean. The smallest eddies in a turbulent flow have length scale equal to the Kolmogorov length $\eta = \left(\frac{\nu}{\epsilon}\right)^{1/4}$, ν is the kinematic viscosity of seawater and ϵ is the rate of turbulent energy dissipation (Frisch, 1995). Consider the relative motion of nearest-neighbor organisms separated by a distance λ, which is likely to be less than η even in oligotrophic ecosystems (Siegel, 1998). For $\lambda < \eta$, neighborhing organisms are embedded in a smooth (though temporally variable) shear flow with shear scale $\left(\frac{\epsilon}{\nu}\right)^{1/2}$. The nearest neighbor separation is governed by the largest Lyapunov exponent of the flow, implying a separation time scale $t_0 = \left(\frac{\nu}{\epsilon}\right)^{1/2}$. For the range of ϵ likely to be found in the euphotic zone t_0 is between 1 and 10 seconds. Thus microscale shears will rapidly separate neighborhing phytoplankton, preventing free floating organisms from having any relatedness to their neighbors. This simple analysis suggests that free

floating organisms experience a weakly structured microenvironment. For public goods production to be feasible in the ocean, producers must either extract benefits from their public goods before they become available to others, or they must use alternative mechanisms for generating ecosystem structure.

Despite the effects of turbulent mixing, there are numerous methods for generating ecosystem structure in the marine environment. The ocean is highly heterogeneous, filled with sinking organic matter particles, colloids, and gels (Azam, 1998). Many heterotrophic bacteria are motile and are able to colonize micropatches of organic matter, in the process generating persistent gradients in their population distribution and creating conditions favorable to public goods production. Various types of phytoplankton are able to alter their environment by producing extracellular polysaccharadies, which create structures in the ocean analogous to biofilms, fostering to interactions between bacteria and phytoplankton on ecologically relevant time scales (Amin et al., 2012). These associations are even stronger in colonial algae such as *Trichodesmium*, which generates a multitude of public goods. Ecosystem structure will not be required for public goods production if the public goods are 'leaky', but primarily benefit the producer. Leaky public goods are common in the ocean due to physiological constraints, and a theory known as the Black Queen Hypothesis (Morris et al., 2012) has been developed to explain how leaky public goods lead to the evolution of metabolic dependencies in the ocean.

4.2 Copiotrophs and Siderophore Production

The discovery that iron availability can limit the growth of phytoplankton and heterotrophic bacteria (Martin and Fitzwater, 1988) fundamentally changed our understanding of marine ecosystems and biogeochemical cycles. Iron is relatively insoluble in the ocean: high levels of dissolved oxygen in seawater causes rapid oxidation of Fe from its ferrous (Fe^{2+}) to its ferric (Fe^{3+}) form, which forms oxide compounds that rapidly precipitate out of solution and sink (Boyd and Ellwood, 2010). The residence time of iron in the ocean is less than 200 years, and the supply of iron is dominated by the flux of aeolian dust from terrestrial sources. More than 99% of the dissolved iron in the ocean is complexed with organic ligands and siderophores, without which scavenging losses would dramatically restrict phytoplankton growth in the majority of the ocean. Organic ligands and siderophores are archetypal public goods, and understanding the factors that control their levels is key to determining the availability of iron to phytoplankton and heterotrophic bacteria in the ocean.

Production of extracellular organic ligands is prohibitively costly for free living microbes (Hutchins, 1995, Völker and Wolf-Gladrow, 1999). High rates of loss of organic ligands due to diffusion would imply that

a solitary organism spends a significant fraction of its energy and nutrients on siderophore production. In a stable environment, these losses would be mitigated by gains from the public goods produced by nearby related organisms, but the ocean environment is too fluid for such a trait to be favorable by selection. This intuition has been supported by the near lack of siderophore production by marine phytoplankton (production is limited to a coastal strain of *Synechococcus* (Cordero et al., 2012), whereas every type of phytoplankton has genes for uptake of ligands and siderophores (Hopkinson and Morel, 2009)). Instead, the producers of siderophores in the ocean are heterotrophic bacteria (Cordero et al., 2012), which are roughly divided into two types: oligotrophs and copiotrophs (Koch, 2001). These two types of bacteria occupy different ecological niches in the ocean, and the differences between them are comparable to the differencs between K-strategists and r-strategists (Southwood et al., 1974). Oligotrophs are free floating bacteria that have simple metabolism, and which are able to thrive under low availability of carbon and nutrients. Their distribution in the ocean is similar to that of phytoplankton, and is roughly set by the action of turbulent mixing and bacterial growth. For the same reasons as phytoplankton, oligotrophs seldom contain the genes for siderophore production and are reliant on exogenous ligands for iron acquisition. Copiotrophs, on the other hand, rely on patches of nutrients, attaching themselves to organic particles, living phytoplankton, or gels and colloids. They are capable of rapid growth, and can become highly abundant in blooms (Gilbert et al., 2012). Distributions of copiotrophs are patchy, and they typically live in microenvironments with high concentrations of other bacteria. Copiotrophic bacteria seem to be the exclusive producers of siderophores in the ocean (Cordero et al., 2012).

Dense aggregations of copiotrophic bacteria resemble terrestrial biofilms, and the distinct environment surrounding the adhered particles is likely what allows them to be producers of siderophores. The high concentrations of producers and the sticky microenvironment surrounding organic particles minimize the loss of siderophores, and the adhesion of bacteria to particles guarantees that neighboring organisms remain neighbors for ecologically relevant timescales. Exploitation of patchy resources favors r-strategists that maximize their growth rate, leveraging intense public goods production to dominate uncolonized resource patches. Indeed, the dramatic increase in organic ligand concentrations observed in the days following iron fertilized phytoplankton blooms may be due to associated blooms of copiotrophic bacteria (Boyd et al., 2000). It has been shown that there is a connection between patch size and the ratio of producers to scroungers, with scroungers only reaching significant numbers on the largest of patches (Cordero et al., 2012). The factors that make copiotrophs natural producers of siderophores extend naturally to suggest that these bacteria produce other types of extracellular macromolecules and public goods. Incorporating the microscale dynamics of the

microbial loop into ecological models, resolving the drivers of recycling rates in the ocean, and determining the emergent patterns of nutrient recycling in the ocean are key goals for future reserach into biogeochemical cycles and marine ecosystems.

4.3 Leaky Public Goods and the Black Queen Hypothesis

An alternative set of public goods are provided by 'leaky' metabolic functions. Cellular processes such as nitrogen fixation, nitrate assimilation, and $HOOH$ detoxification produce strong benefits for the organisms that perform them, but also generate byproducts that can be used by other organisms. For instance, nitrogen fixing bacteria exude a significant fraction of the nitrogen that they fix (Garcia et al., 2013), nitrate that is assimilated by phytoplankton is remineralized to ammonium, and hydrogen peroxide detoxification reduces both its extracellular and intracellular concentration. The Black Queen Hypothesis (BQH) (Morris et al., 2012) states that these 'leaky' metabolic functions drive the evolution of metabolic dependencies in the ocean through adaptive gene loss. Many numerically prevalent marine microbes lack seemingly essential metabolic functions, and are dependent on populations of producers to maintain a survivable environment.

The BQH operates by a fundamentally different mechanism than the spatially assortative mechanisms discussed so far, though K-strategists like *Prochlorococcus* and oligotrophic bacteria are still the most common scrounger species. Leaky functions provide a much greater fitness benefit to the producer organism than to the scrounger, as the public good is mostly used in the original cell before it is lost to the extracellular environment. When producers are dominant, extracellular levels of the public good are high, and mutants that lose the ability to produce may have a fitness advantage. The presence of both producers and scroungers introduces a density dependent interaction, which is crucial for maintaining the production of the public good. As the level of producers decreases, so does the level of the public good, lowering the fitness of the scroungers but leaving the producers unaffected (or even increasing their fitness by increasing the availability of other resources). Eventually an equilibrium is reached where the scroungers are limited by the public good, and a small population of producers is maintained.

This mechanism can be seen operating at a global scale when fixed nitrogen is the public good (Hagstrom et al., 2016, Tyrrell, 1999). Fixed nitrogen is the proximate limiting nutrient for primary producers in over 60% of the global ocean, but diazotrophic organisms are able to generate fixed nitrogen from dissolved dinitrogen gas at a significant cost (Karl et al., 1997). Globally, diazotrophs constitute less than 1% of phytoplankton biomass, and their production of fixed nitrogen is just enough so that diazotrophs and non-diazotrophs have similar fitness. Furthermore, phylogenetic evidence indicates that diazotrophy was once

the dominant nitrogen acquisition strategy in marine phytoplankton, and that modern non-diazotrophic strains diverged from diazotrophs through adaptive gene loss. A similar process also explains the lack of *HOOH* detoxification genes in the marine cyanobacterium *Prochlorococcus* and the heterotrophic bacterium *Candidatus Pelagibacter*, both of which are K-strategists. These species are thus dependent on more complex organisms like *Synechococcus* to remove hydrogen peroxide, which is generated through the degradation of dissolved organic matter by light in the surface ocean, from the marine environment.

The ubiquity of adaptive gene loss and BQH dynamics has important implications for the structure of marine microbial ecosystems. Many metabolic processes are inherently leaky, and gene loss is common and often fitness enhancing. As a result, seemingly distinct marine organisms are ecologically linked through metabolic dependencies. Multiple loss of genes is likely to be adaptively favorable in K-strategists but not in producers (Morris et al., 2012), suggesting that evolution will favor the development of numerically common organisms supported by numerically rare 'Keystone' species, which exert an outsized influence of the ecosystem they inhabit. The implied importance of rare species suggests marine ecosystems are more complex than previously believed, and is likely an important insight into other types of microbial ecosystems where the BQH may apply, such as the human microbiome. The BQH may also explain other difficult problems in marine ecosystems, such as the high diversity of primary producers (the Paradox of the Plankton) (Hutchinson, 1961), by providing a new means for the evolution of coexistence.

4.4 Structuring the Marine Environment: Production of Extracellular Compounds and Signalling Molecules by Photosynthetic Phytoplankton

Phytoplankton produce extracellular compounds for a variety of different purposes. Diatoms, which are photosynthetic r-strategists capable of growing rapidly and to high concentrations, produce both extracellular polymers (Amin et al., 2012, Passow and Alldredge, 1995, Passow et al., 1994) and infochemicals (Brownlee, 2008, Vardi et al., 2006). These public goods have been hypothesized to play a variety of different roles: such as triggering aggregations, stimulating bacterial growth, signalling nutrient stress, or even triggering cell death in competitors. Similar activities have been observed in *Trichodesmium* colonies, which produce signalling molecules that influence both members of the colony and co-occurring heterotrophic bacteria as well as extracellular enzymes that increase the availability of inorganic nutrients bound in organic matter. These phytoplankton-regulated public goods processes play important roles in key biogeochemical processes such as the successional dynamics of blooms, the export of carbon from the euphotic zone, and the coupled dynamics of nitrogen, phosphorus and iron in the ocean.

Diatoms are siliceous marine algae responsible for roughly 50% of primary production in the sea, and are the dominant organisms in regions of strong upwelling. Mirroring the parrallels between copiotrophic and oligotrophic bacteria, Diatoms produce many different types of public goods. The phycosphere of a diatom (Bell and Mitchell, 1972) contains typically contains large amounts of photosynthate in the form of extracellular polysaccharides. These polysacharrides play many different roles. The production of polysaccharides (and other extracellular products) triggers the colonization of the diatom phycosphere and cell surface by heterotrophic bacteria, which rely on phtosynthetic exudates to fuel their growth. Though many types of ecological interactions are possible, diatoms are likely able to make use of inorganic nutrients and siderophores released by heterotrophic bacteria to help fuel their continued growth. These extracellular products change the phycosphere, making it stickier and enhancing the stability of diatom-bacterial associations and enhancing the probability that selection favors cooperation. This stickiness increases as diatoms become more nutrient stressed, leading to the formation of aggregations of diatoms that eventually sink out of the euphotic zone (Passow and Alldredge, 1995, Passow et al., 1994). These aggregation dynamics are reminiscent of bacterial biofilms, which are subject to competition between producers and scroungers of the extracellular polysacharides.

Infochemicals are public goods that primarily serve as signalling molecules, spreading information rather than energy or nutrients. The most famous example of infochemicals are Acyl Homoserine Lactones (AHLs), which are involved in bacterial quorum sensing (Nadell et al., 2008a), and diatoms produce a large number of such compounds including aldehydes (Vardi et al., 2006) and nitric oxide (NO). Diatoms produce aldehydes in response different types of stress, including predation or nutrient scarcity (Vardi et al., 2008). These compounds can trigger a variety of responses in other phytoplankton types, including programmed cell death, and thus represent a mechanism for diatoms to regulate the levels of their competitors and their own population. Much is unknown about the ecological role and implications of both signalling and aggregation in diatom populations, and further work is required to place these hypotheses on a firmer footing.

Trichodesmium, a colonial diazotroph that inhabits subtropical gyres, is also capable of public goods production. Though usually present at very low concentrations, *Trichodesmium* colonies can undergo bloom formation and reach high concentrations in optimal conditions. Due to the large size of colonies, *Trichodesmium* is a poor competitor for inorganic nutrients such as phosphate, which are often found at nanomolar concentrations in subtropical gyres. To acquire essential nutrients like iron and phosphorus, *trichodesmium* relies on public goods produced within its colonies and by associated heterotrophic bacteria.

One important extracellular product of *trichodesmium* is alkaline phosphatase (Dyhrman et al., 2007),

which cleaves phosphorus from dissolved organic molecules. It contributes to the rapid recycling of phosphorus in oligotrophic regions like the Sargasso Sea. Recycling is one of the most important processes undertaken by heterotrophic bacteria, as it enhances the availability of nutrients to phytoplankton. It has been observed that different elements are recycled at different rates (Monteiro and Follows, 2012). The C:N:P of sinking particulate organic matter consistently increases with depth, indicating that heterotrophic bacteria are preferentially recycling inorganic nutrients (Schneider et al., 2003). This bias in recycling processes enhances the efficiency of carbon export, leading to a greater transport of carbon per unit nitrogen and phosphorus delivered to the surface ocean. Theoretical (Hagstrom et al., 2016, Monteiro and Follows, 2012) and empirical studies show the potential importance of remineralization rates and establish the fact that rates vary by element and by region. Understanding the factors driving remineralization rates is as important as determining the physiological and ecological drivers of elemental stoichiometry, as both sets of nutrient ratios interact with nutrient delivery ratios to determine important ecosystem properties.

The production of alkaline phosphatase by *trichodesmium* is regulated by the external phosphorus concentrations (Ståhl-Delbanco and Hansson, 2002) and by the activity of epibiotic bacteria inhabiting the colonies (Van Mooy et al., 2012). These epibionts produce AHLs and other infochemicals, which seem to trigger alkaline phosphatase activity within colonies. In addition to quorum sensing triggered alkaline phosphatase production, *trichodesmium* undergoes other complex interactions with its epibionts. Colonies can undergo programmed cell death (Berman-Frank et al., 2004), leading to the sinking of both carbon and fixed nitrogen from the euphotic zone. Mass, autocatalyzed apoptosis seems to be an ubiquitous feature of marine phytoplankton (Bidle and Falkowski, 2004), but the ecological purpose is still unknown (Franklin et al., 2006) *Trichodesmium* may be a keystone species in subtropical gyres due to its production of fixed nitrogen, and a better understanding of the public goods processes that regulate its population and activity are necessary to accurately model subtropical gyre ecosystems and global scale biogeochemical processes.

4.5 Public Goods and Broad Scale Patterns in Ocean Ecosystems

Public goods are a mechanism that couple the microscale dynamics of marine organisms to macroscale ecological and biogeochemical processes. Dense aggregations, microscale patches, and leaky public goods enable producers to find niche space in the ocean. Despite the fact that many examples of public goods have been observed in the ocean, most of the important details about the role and dynamics of these goods remain elusive. The phycosphere has been relatively inaccessible to observational and experimental investigations, owing to the difficulties of making small scale measurements and the instability of the ocean environment.

New efforts are beginning to change this picture, leading to the generation of a wealth of information about the microscale dynamics of phytoplankton and the microbial food web (Stocker, 2012). The remaining challenges are formidable, but an improved understanding of public goods games in the ocean is a key ingredient in modelling macroscale processes in ocean ecosystems and biogeochemical cycles.

5 Future Challenges and Opportunities

The view of ecosystems as complex adaptive systems is powerful and has led to numerous insights, including those described here. Despite this success, the most interesting and challenging questions remain ahead. Ocean ecosystems are complex, spanning time scales from seconds to millenia and length scales from nanometers to ocean basins. The ocean environment is physically and chemically diverse, and the vast majority of marine organisms are uncharacterized. Futher complicating the situation is the interaction with human social dynamics, which have foiled attempts at managing and regulating the usage of the public goods in the ocean. Although complex adaptive systems provide a unifying framework for explaining many properties of ecosystems, these ideas have not been fully embraced by oceanographers, climate scientists, or marine biologists. This reticence has been partially due to practicality and the fact that the most important techniques were not widely known, having been developed in disparate fields. The past two decades have provided ecologists with easier access to high-performance computing, revolutionary new methods from molecular biology, systems biology, and network science, high-resolution data sets, and greater communication with researchers in other fields. These developments have removed the obstacles blocking a fuller embrace of complex adaptive systems. We propose three classes of methods and research directions that will be important in the coming decades: to incorporate diversity into marine ecosystems, to learn from new physical and biological data, and to account for the human element.

There is a conceptual gulf between modern ocean models and our understanding of marine ecosystems. The majority of ecosystem models represent the dynamics of a handful of different species or functional groups, making no attempt to resolve or reproduce the biodiversity (Franks, 2009). As an example, microbial organisms are typically modelled using fewer than three species or groups, but a drop of seawater typically contains thousands of distinct microbial ecotypes (Venter et al., 2004). Evidence has accumulated suggesting qualitative differences between the low and high diversity models: when diversity is high the ecosystem is more flexible and the community rapidly adapts to conditions, leading to a fundamentally different type of functional response than in the low-diversity case(Norberg, 2004, Norberg et al., 2001). Diverse ecosystems

seem to have a linear response to resource availability, whereas low-diversity models have a hyperbolic response, leading to decreased resource utilization rates. High diversity models better explain observed predation rates by zooplankton (Gentleman et al., 2003) and nutrient uptake rates by phytoplankton (Lomas et al., 2014) and are also able to reproduce emergent patterns without the fine parameter tuning required by low-diversity models (Follows et al., 2007). Trait-based models (Litchman and Klausmeier, 2008), which replace a discrete set of species by a continuous distribution over multidimensional trait space, are key to modelling diveristy, and they have been been used to understand the mechanisms controlling ecosystem properties and global emergent patterns (Fuchs and Franks, 2010). Work remains to make trait-based models suitable for broader use. Trait-based models are generally infinite-dimensional, so techniques based on moment-closures (Flierl et al., 1999, Merico et al., 2009) or perhaps equation-free-methods (Cisternas et al., 2004) are necessary if large-scale simulations are planned. Fortunately, even the simplest closures based on optimality principles have shown enormous promise (Smith et al., 2011), and we believe that the community should further develop these methods so that they can be used in the large-scale models upon which management and conservation decisions are based. For these efforts to succeed, there needs to be a greater emphasis on physiological measurments in laboratory and field settings, as well as a close collaboration with theorists. The potential gains are great, as it may be possible to derive simple, practical models that accurately incorporate biodiversity.

In the past 20 years there has been an explosion of new data on all aspects of marine ecosystems. Autonomous gliders and floats constantly collect data throughout the ocean, satellites monitor both physical and biological features of the marine environment in real time, and techniques from molecular and systems biology make it possible to infer the function and interaction of innumerable microbial organisms throughout the sea. This data represents a treasure trove that will shed a new light emergent patterns, critical transitions, and cooperation. The use of inverse modeling techniques, which combine physical and biological data to infer properties of marine ecosystems (DeVries and Primeau, 2011), has already overturned multiple closely held theories in biological oceanography, including the Redfield paradigm and the biogeography of export (Teng et al., 2014). These methods will become much more powerful in the near future, as higher resolution data sets enable us to reduce the uncertainty surrounding both physical and biological processes. Inverse models may be used to infer the ecosystem properties that are nearly impossible to measure, such as the relative rates of recycling in the ocean. Methods based on *-omics* have changed our understanding of the function and contituents of ocean ecosystems (Johnson et al., 2006, Venter et al., 2004, Viant, 2007). *-Omics* is the only tool available for studying most complex microbial interactions, but very few methods exist to extract

anything more than qualitative knowledge from these predictions. Techniques from systems biology make it possible to estimate metabolic function from metagenomic and metabolomic data (Turnbaugh and Gordon, 2008), and these tools have been combined with network-based methods to infer the ecological role and interactions of rare members of the each ecosystem (Kurtz et al., 2015, Levy and Borenstein, 2012). Most of these methods are in their infancy, and work needs to be done to understand how to reconcile the picture derived from systems biology with those from trait-based models and culture studies (see (Bruggeman, 2011) for an successful combination of these approaches). Higher data resolution time-series data should also improve our understanding of ecosystem dynamics. The nature of marine dynamics is unclear, and methods based on attractor reconstruction or the S-map have shown great promise for predicting food web dynamics in comparison to purely stochastic or equilibrium models (DeAngelis and Yurek, 2015, Ye et al., 2015). The collection of higher dimensional data sets containing more species has spurred the increased usage of these techniques, but it remains to reconcile the nonlinear dynamics that they predict with the equilibrium assumption at the heart of models of critical transitions. It may be that an equilibrium is recovered when the right moments of the species distribution are averaged, such as is observed when size classes are modeled instead of individual species. The model based framework for critical transitions is a promising start, and further work in this area is likely to yield new insights.

Perhaps the most important challenge facing ecosystems science is understanding how to manage the interactions of humans with their environment (Dietz et al., 2003). Nearly every ecosystem feels the effect of anthropogenic forcings, and ecosystem services are vanishing or under threat. Marine ecosystems have not been spared (Halpern et al., 2008), being faced with the potentially irreversible disappearance of both fish and mammal species, the bleaching of corals, acidification, global warming, the decimation of food webs and the spread of hypoxia. Ecology has revealed the mechanisms by which anthropogenic perturbations have altered the environment, and the primary obstacle to conservation has been the lack of human cooperation. To account for this, human behavior must become a factor that is explicitly modeled (Levin, 2006). The study of coupled human-natural systems has bloomed in recent years, and research has been performed to understand how to engineer cooperation in marine ecosystems (Levin and Lubchenco, 2008). Early work is promising, as insights from social sciences like economics and anthropology (Berkes et al., 2000) have been applied to fisheries management and other problems involving resource exploitation. As the Earth becomes more crowded and ecosystems become more stressed, the fate of future generations will rely on how well we manage and secure the public goods and common pool resources contained in our ecosystems.

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