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A one ocean model of biodiversity

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ABSTRACT

The history of life is written in the ocean, and the history of the ocean is written in DNA. Geologists have shown us that hundreds of millions of years of ocean history can be revealed from records of a single phylum in cores of mud from abyssal plains. We are now accumulating genetic tools to unravel the relationships of hundreds of phyla to track this history back billions of years. The technologies demonstrated by the Census of Marine Life (CoML) mean that the ocean is no longer opaque or unknowable. The secrets of the largest component of the biosphere are knowable. The cost of understanding the history of ocean life is not cheap, but it is also not prohibitive. A transparent, open ocean is available for us to use to understand ourselves. This article develops a model of biodiversity equilibration in a single, physically static ocean as a step towards biodiversity in physically complex real oceans. It attempts to be quantitative and to simultaneously account for biodiversity patterns from bacteria to whales focusing on emergent properties rather than details.

Biodiversity reflects long-term survival of DNA sequences, stabilizing “ecosystem services” despite environmental change. In the ocean, mechanisms for ensuring survival range from prokaryotes maintaining low concentrations of replicable DNA throughout the ocean volume, anticipating local change, to animals whose mobility increases with mass to avoid local change through movement. Whales can reach any point in the ocean in weeks, but prokaryotes can only diffuse. The high metabolic costs of mobility are offset by the dramatically lower number of DNA replicates required to ensure survival. Reproduction rates probably scale more or less inversely with body mass. Bacteria respond in a week, plankton in a year, whales in a century.

We generally lack coherent theories to explain the origins of animals (metazoans) and the contributions of biodiversity to ecosystems. The One Ocean Model suggests that mobile metazoans paved the way for their own energetic life styles by decreasing the amount of primary production sinking to feed the benthic anaerobic prokaryotes. Increasing metazoan mobility and diversity ensured that less and less production sank and accelerated development of the aerobic oceans they require. High biodiversity among middle-sized organisms stabilizes the system, but rapid environmental changes can decrease diversity in a positive feedback loop ending in mass extinction events and the return of the anaerobes. The oceans have gone through this cycle several times. Global warming may be a mild flu compared to “the revenge of the microbes”.

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1. Introduction

The Census of Marine Life (CoML) arose from a 1995 US National Research Council volume *Marine Biodiversity* co-authored by Fred Grassle (NRC, 1995). Fred approached the Alfred P. Sloan Foundation to help resolve the issue that no country in the world, including the US, could meet the condition for cataloging marine biodiversity set forth in the UN Convention on Biological Diversity. After exploring the problem the Sloan Foundation sponsored the first meeting of the CoML Scientific Steering Committee, with Fred

as its Chair, under the aegis of the Intergovernmental Oceanographic Commission in Paris in 2000. Under this SSC the concept and organization grew into “a decade long program to assess and explain marine life’s diversity, distribution and abundance—past, present and future”. The scope of the known, unknown and unknowable in six Ocean Realms was outlined in *The Baseline Report* (O’Dor, 2003) and plans for global Realm Projects were outlined in a launch at the Smithsonian Museum of Natural History.

The Census has done a remarkable job of assessing and made good progress explaining geographic patterns, but there is still a lot more to talk about in its Synthesis phase between now and 2010. This article expands the second goal of explaining the observed diversity and distribution and will be developed further

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Table 1
Approximate size and time dimensions of marine life.

	Blue-green bacteria (<i>Synechococcus</i>)	Krill (<i>Euphausia superba</i>)	Whales (<i>Balaenoptera musculus</i>)
Length (m)	1×10^{-6}	5×10^{-2}	25
Weight (kg)	5×10^{-16}	1×10^{-3}	1×10^5
Speed (km h ⁻¹)	0.0001	1–4	20–50
Life cycle	<1 day	>1 year	>10 years
Global biomass (MT C)	43 million	20 million	3 million
Years on planet	2 billion	100 million	10 million

The range of size in a single food chain illustrates the diversity of marine life (adjusted from Fig. 5, O'Dor, 2003).

during Synthesis. Life originated and has been evolving for some four billion years in the ocean, so it is likely the only place we can hope to unravel the big picture of diversity and its maintenance. One problem is that on the time scale of evolution the ocean is constantly changing as plate tectonics alter shapes and currents, so physical changes can mask biological ones. By looking at the inherent properties of life across the size range of organisms, the One Ocean Model described below explores emergent properties of life in a single ocean construct that may help explain how ocean life responds to external forcing.

The 2003 *Baseline Report* briefly explored the scale of the challenge of understanding ocean biodiversity with the multi-dimensional single food chain shown in Table 1—from microbes to whales, from size to speed to biomass to life cycle to age. Although we are primarily aware of the things we see in or eat from the ocean, they are a minute fraction of the total life in the ocean. A vast body of research over the last few decades has shown us how complex the ocean ecosystem is across this size spectrum and how unpredictable the consequences of changing these relationships can be. Can we model the full spectrum of ocean biodiversity to better design the kinds of oceans we can live with sustainably, or must we stand back, marvel at the complexity and leave them alone? This is a first tentative step in that direction and a Synthesis contribution to the New Estimates of Biomass project.

CoML has come to be viewed as an authoritative source of information on marine biodiversity and is asked many questions by the media and the public. Among the more common ones are:

1. How much biodiversity is there?
2. Why is there so much?
3. How did it get there?
4. How much biodiversity is enough?

The last one is the most dangerous, often asked by managers and policy makers, it translates to, “What is the downside of allowing reduced biodiversity?” (Palumbi et al., 2009). This article moves towards answering that question by considering the full range of diversity over size scales and time. Considering how biodiversity might arise and decline in one simple, static, stable ocean roughly equivalent in dimensions to today's oceans consolidated reveals some surprisingly complex interactions.

2. Methods

Define a simple, baseline model ocean focused on metazoan ocean biodiversity. Make it 10,000 km in radius, 4 km deep, approximately equivalent to all present oceans combined (Fig. 1), with diffusion but no currents and no ballast water. Assumptions are listed below, some based on discoveries made by CoML projects and others from other disciplines:

1. The various types of prokaryotes spread from a central source to equilibrate ocean diversity by diffusion at least a billion

years ago. The revelation of 100 times previously predicted microbial diversity in the “rare biosphere” using 454 DNA sequencing (Sogin et al., 2006), supports the concept that, arguably, “everything is everywhere” in the Microbial Ocean Realm (Whitfield, 2005), which has always been about mixing, not isolation (DeLong et al., 2006). The global details of how it works are not clear, but the assumption that each liter of seawater from top to bottom contains every prokaryotic gene is not too far off and is supported by researchers outlined below. Prokaryotes essentially invented ALL of the enzyme systems used in metazoan metabolism and many that are not.

2. Metazoans distribute themselves based on size and mobility. They invented ways of coordinating activities on a large scale and of moving around. Nerves and muscle are perhaps the best examples, but mesoglea, shells, cartilage and bone are others. “The emergence of metazoans remains the salient mystery in the history of life” (Lipps and Signor, 1992). Pelagic organisms disperse in a generation. Benthic organisms take longer or are dependent on currents to distribute their larvae.
3. Sustainable oxygenated, oceans of the sort we are used to and can live with depend on a balance between the prokaryotes and eukaryotes. Widely distributed prokaryotes provide what are called “ecosystem services” throughout the ocean by breaking complex chemical substrates into simple ones that can be recycled using chemical or photosynthetic energy. In fact, they do not do this as a service but as a source of energy to increase their own numbers to take advantage of changing conditions in the local liter of seawater they inhabit. Diverse forms of mobile metazoans move local production around to maintain a balance that appears essential to stabilizing “our kind” of ocean.
4. Plate tectonics create “new” oceans over time, and, perhaps, biodiversity equilibration in these oceans can be examined to test this model.

3. Results

3.1. One Ocean space–time continuum

For cyanobacteria, krill and blue whales we have reasonable estimates of maximum speeds (Ehlers et al., 1996; Kils, 1982; Kermack, 1948), but we do not know how long they can sustain them. We have compared maximum swimming speeds to the ‘rule of thumb’ estimate for rates of cruising of 1 body length s⁻¹ and the differences are not dramatic. The result is that even at their remarkable maximum velocity these bacteria cannot outrun the Brownian motion of molecules, so it would take them at least 10,000 years to disperse 10,000 km in One Ocean. The directed currents in real oceans do not ensure uniform dispersion, but even the very slow thermohaline conveyor belt would be faster (0.004 km h⁻¹). Krill could do it in a generation and whales in a few weeks as shown in Fig. 2. The maxima would require that the organisms know where they are going and navigate directly there.

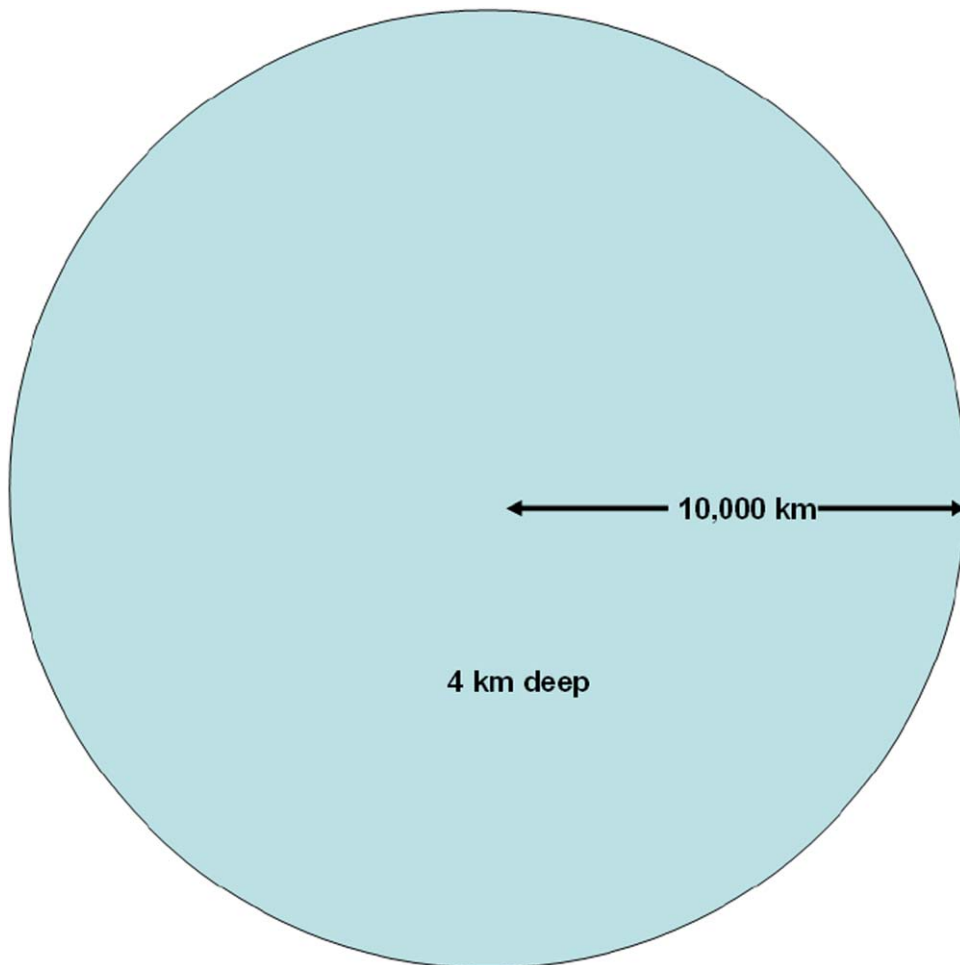


Fig. 1. The One Ocean Model representing the present global oceans consolidated in a single circular ocean of their average depth.

This is certainly possible for whales and probably krill, once they know they have been someplace and want to return, but it seems rather improbable for the first trip to a new place they have never been. We can assume that neither communicates with GPS satellites, but there is evidence that they may use lunar navigation (Manuel and O'Dor, 1997; Manuel et al., 1997) as well as a suite of other kinds of information.

Fig. 2 also includes a random walk model that assumes random changes in direction at the same speeds (Wilensky, 1997) to provide more realistic estimates. Whales live long lives, all at large size and still manage less than a generation, but krill are pushed out to 100 generations. Brownian motion still dominates prokaryotes. We looked at giant squid as another example, but their details were hard to model as they grow from tens of microgram to hundreds of kilograms in a few years at most. With directed motion giant squid dispersion might be possible in a generation, but multiple generations would be required for a random walk.

Many organisms remain associated with the bottom throughout their lives, and we have added a gastropod snail with a published track record (Taylor, 2001) to represent them. This snail needs somewhere between 20 and 10,000 generations to disperse. Bouchet et al. (2002) carved out multiple cubic meters of coral reefs along a 300 km line in New Caledonia and sampled them comprehensively for biodiversity. Coral reefs are prime examples, and are known as the rain forests of the ocean. Looking at gastropod molluscs, which were typical, Bouchet found that most are rare with 15–20% of species occurring at only one site in this small, seemingly homogeneous area! Perhaps long equilibration

times relative to the species' reproductive cycle are a major factor. In the real ocean many similar species appear to act as "stand-ins" to stabilize ecosystems and take advantage of "loopholes", each being optimally adapted to a slightly different set of conditions (Bakun and Broad, 2003).

3.2. Optimal size and metazoan diversity

Fig. 3 assembles maximum adult size data for the groups that contribute the most to biodiversity in the pelagic environment (Clarke, 1966; FishBase; SeaLifeBase). Over 80% of bony fish and squid are less than a half meter long, which puts them clearly in the multi-generation category in even the most optimistic model. On the other hand, many sharks and mammals (not shown), which are live bearers, start larger, grow faster and can potentially disperse in a generation like the blue whale.

What are the advantages of achieving large size? Prokaryotes seem to get bigger linearly increasing surface area to volume ratio and chemical exchange (Gallardo and Espinoza, 2007). Metazoans appear to have evolved from unicells by ingesting each other to reorganize as organelles (Margulis, 1993). In a cell-eat-cell world the bigger cell has a clear advantage. If the metabolic rate per unit mass also declines, for whatever reason, it cannot be a bad thing. There has been a debate for decades over why this decline has a slope of -0.25 (Hemmingsen, 1960; Hochachka et al., 2003), which we are not going to enter except to say that it is not 0 (constant) and it is not -0.33 (surface area to volume ratio). Fig. 4

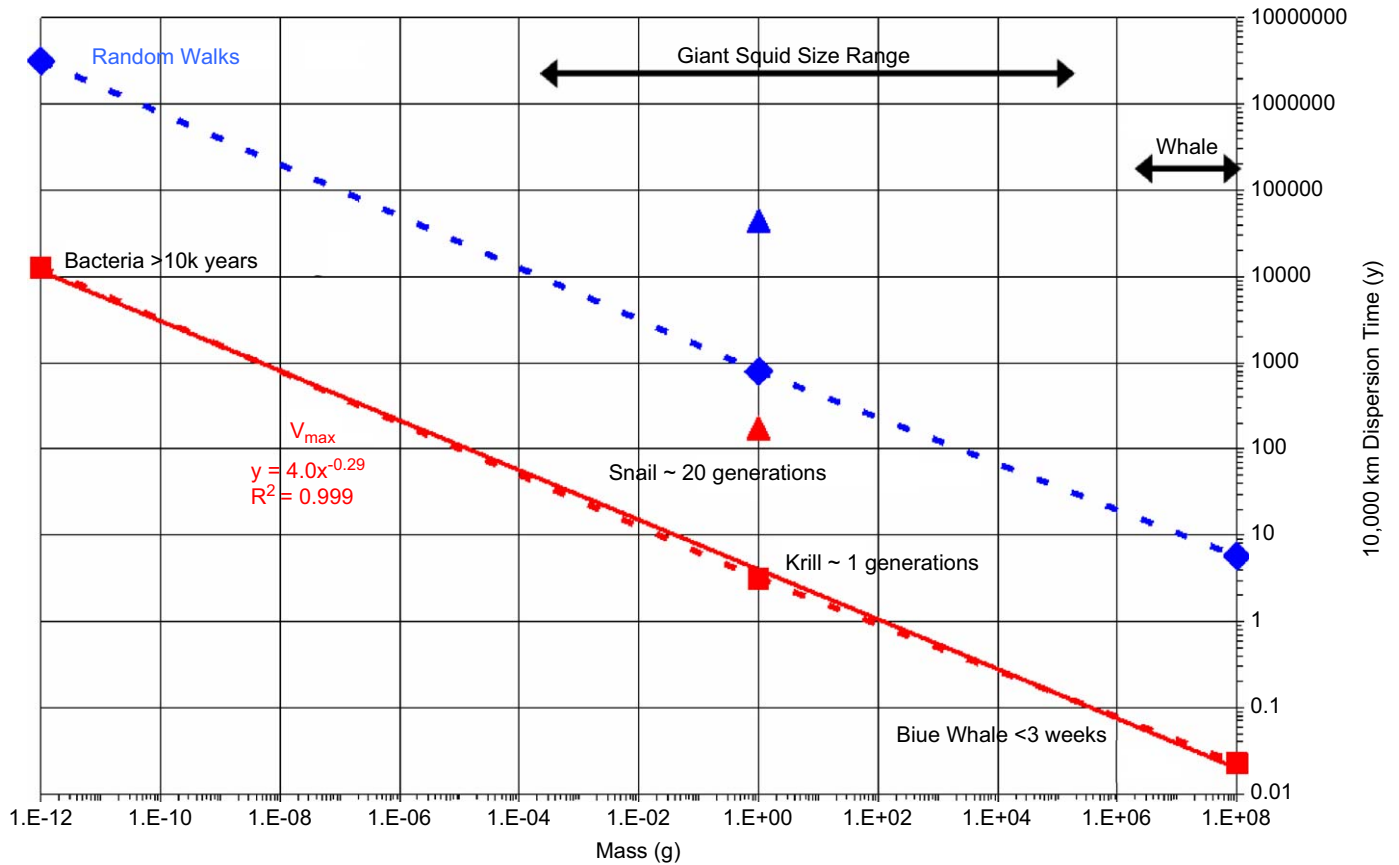


Fig. 2. This one ocean space–time continuum provides a range of dispersion times for water column species from maximum measured maximum velocities (squares) to random walks (diamonds) relative to organism sizes, with a benthic snail (triangle) for comparison.

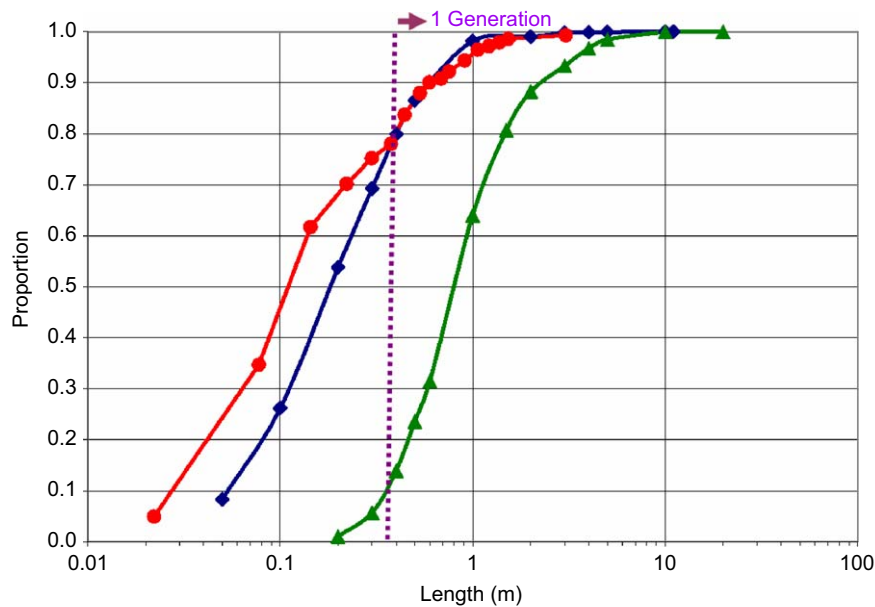


Fig. 3. Cumulative spectra of maximum size for pelagic groups: approximately 1000 shark species (triangles), bony fish (13,000, diamonds) and squid (300, circles) from the Ocean Biogeographic Information System, FishBase, SeaLifeBase and Clarke (1966). 80% of fish and squid fall in the multi-generational dispersion size range.

illustrates the tradeoffs between being big and getting big. Big animals not only save on the cost of their basal metabolism, they also have lower costs of transport (e.g. fish swimming, Beamish, 1978). However, even a fast growing tropical squid that matures in 150 days has to catch and remove from the ecosystem 6 times as

much biomass as it creates (19% gross conversion efficiency). Growth in most species costs a lot more. The standard efficiency between trophic levels in ecological models is 10% (Pauly et al., 2000), so it is not easy or cheap to get big. But, when you get bigger, both the cost of “being there” (basal metabolism) and of

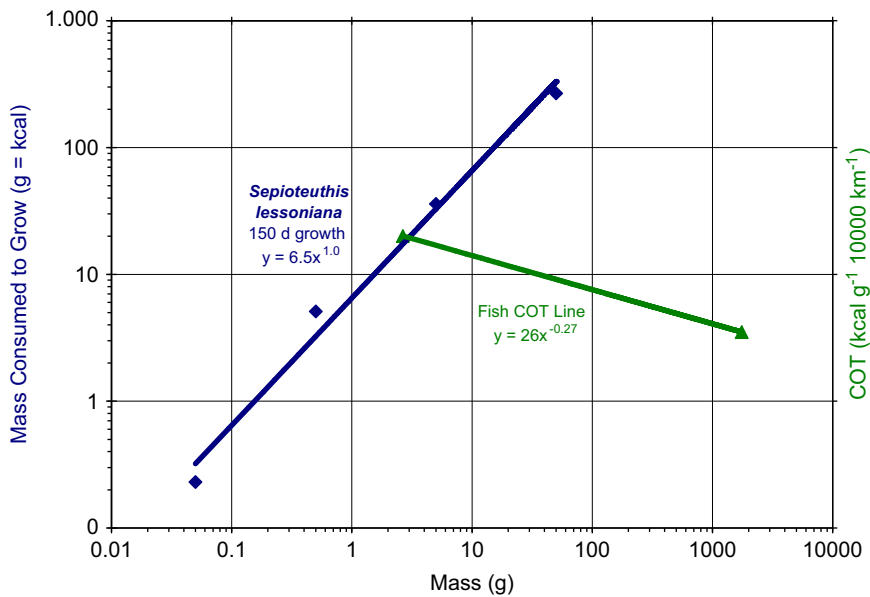


Fig. 4. Optimizing cost of growth versus cost of transport. Getting big costs energy even for the most efficient metazoans (squid, 19% conversion efficiency to 50 g weight using the approximation that 1 g equals one kilocalorie, diamonds; Segawa, 1987). Being big saves energy in terms of both resting metabolism and cost of transportation (Fish, triangles, COT; Beamish, 1978).

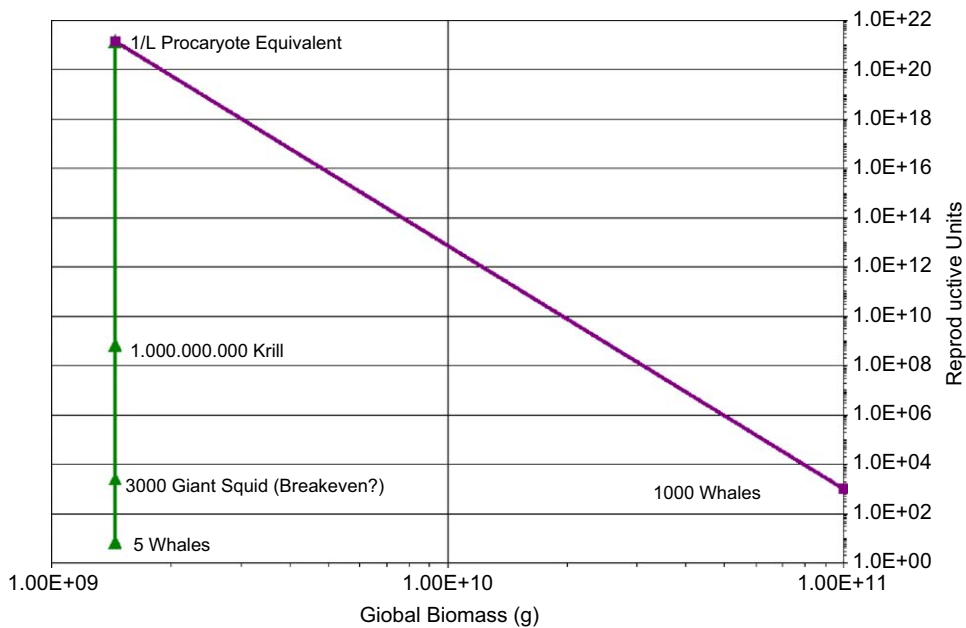


Fig. 5. Optimizing biomass versus survival. The biomass required to put one bacterium of a single species in every liter of seawater in One Ocean compared to the number of reproductive pairs of some representative marine metazoans. The strategy of being big ties up orders of magnitude more biomass than being small and dispersed.

“getting there” (cost of transport) decrease relative to individual animal mass. Thus, evolving larger metazoans has some advantages for individuals, but may not be the cheapest way to stabilize an ecosystem.

A competing optimization is the amount of biomass required for a species to survive. Sogin et al. (2006) showed that most prokaryotic “operational taxonomic units” occur as singularities once per liter. Fig. 5 shows the calculated total biomass required for a single prokaryote cell to be present in every liter of seawater in One Ocean. It is about 2 billion grams. If these prokaryotes had to support a basal metabolism their impact would be high, but many exist in resting stages, so their “being there” strategy puts lower energy demands on the ecosystem. Just considering

biomass without accounting for the cost of creating it, this equates to hundreds of millions of pairs krill, which is certainly enough to maintain a stable global population. But, it equates to only 5 pairs of blue whales, which is certainly not. Giant squid come out in the thousands of pairs which might be enough, but is probably on the edge. A thousand pairs of blue whales weigh in at over 50 times the biomass required to put one bacterium of a species in every liter of sea water. The cost of creating this biomass puts an even greater burden on the ecosystem. This suggests that you have to be very good at what you do to get that big, and you had better hope that what you eat is a stable part of the ecosystem. So, it looks like “being there” is probably a safer strategy than “getting there”, even if you are at the top of the

“getting there” pyramid, which may explain why the microbes keep wiping us out.

3.3. Diversity and stability

Berner et al. (2007) and Ward (2008) argue that while the most recent geological mass extinction can be clearly tied to a meteor impact, numerous previous extinction events, which came close to forcing metazoans to more or less start over from scratch, appear simply to result from some minor mistakes by us “getting there” types, that allowed the “being there” types to regain control of the ocean. The biomarker compounds around the other events suggest that they occurred over much longer periods and likely involved anaerobic bacteria taking over major parts of the ocean and pumping hydrogen sulfide into the atmosphere that even pushed the extinctions on to land. Ward (2008) warns, “At the end of the Permian the microbes nearly prevailed. Their day will come again.” Did Andy Warhol (1968) say that bacteria get 15 millennia of fame?

4. Discussion

4.1. Origins of diversity

For the purposes of this volume at least, we will accept that life on Earth originated at a deep sea vent (Baross and Hoffman, 1985; Pace, 1991; Shock, 1992) and will refer to the “mother of life” vent as the Grassle Knoll, for reasons that should be obvious in the context of honoring the first biologist to visit one. The tree of life for the first 3 billion years has proven to be quite complicated involving horizontal gene transfer as well as the usual vertical, reproductive kind (Doolittle, 1997), but the view that everything prokaryotic is everywhere at some low level of concentration, perhaps as functional genes, if not as whole genomes seems plausible, if not proven.

On the grand scale biodiversity is not about how much, it is about how long. Dawkins (1976) points out, “Darwin’s ‘survival of the fittest’ is really a special case of a more general law of *survival of the stable*.” Evolution allows biodiversity to accumulate over time as long as catastrophe is avoided, although there is evidence of differential extinction rates between groups and of equilibration (Sepkoski, 1998). Locally at least, rare is common (Bouchet, 2006) and “stand-ins” stabilize ecosystems (Bakun and Broad, 2003). Fitness lets species dominate an ecosystem by bulking up their biomass and offspring, but this may not be the only strategy for long-term survival, particularly if the system changes or single species dominance changes the system.

4.2. Failures of diversity

A good, if daunting, example of destabilization emerged recently off the coast of Namibia. Bakun and Weeks (2004, 2006), Weeks et al. (2004) report on a gas release “dead-zone” (Rabalais et al., 2007), where so much hydrogen sulfide rose in the water column that elemental sulfur plumes more than 300 km long were visible from satellites as the reducing gas consumed all of the oxygen and left tons of dead fish in its wake. Removing organic fuel from highly productive upwelling zones before it sinks to the bottom to feed anaerobic bacteria is not the kind of ecosystem service we normally think about, but it turns out to be a crucial one—a new role for the middle-sized. The authors suggest that a lasting collapse of a 10 million-ton sardine population from massive overfishing over decades may have replaced an occasional problem of small stocks into a chronic one.

They argue that when abundant these fish capture a large fraction of the phytoplankton production before it sinks to the anaerobic sediments. In their continued absence the anaerobes accomplish a return to the Proterozoic (Fennel et al., 2005)!

This supports a model where metazoans helped end the Proterozoic by dispersion. If diverse forms of mobile metazoans remove and move primary production before it reaches the abyss, this stabilizes our kind of ocean. High diversity removes more production in more ways at different scales and different depths. The optimizations in Figs. 4 and 5 suggest that we can expect stable ecosystems to contain high diversity among middle-sized metazoans with many alternate food chains emerging as local conditions vary. A few very large, mobile species can survive with the alternate strategy of avoiding local change. Decreasing metazoan diversity can produce a positive feedback loop, further reducing diversity as a result of toxic anaerobic products such as hydrogen sulfide as seen in past extinction events (Ward, 2008; Berner et al., 2007).

The conclusion seems to be that metazoans function as mobile vacuum cleaners that capture energy and disperse it, inadvertently keeping the anaerobes under control. This is consistent with Ward’s 2008 view that interruptions of metazoan ecosystems lead to destabilization and prokaryote domination with a temporary return to low oxygen conditions and mass extinctions among metazoans. How many sardines does it take to prevent an extinction event? An excellent question, and one that we ought to answer before managers let fishers experiment to find out “How much biodiversity is enough?” If we do not manage the ocean to maintain biodiversity, will this be the consequence? We do not really have answers to these questions yet, and it remains unclear if we have smarter strategies than the microbes in the long term. It is worth noting that the organisms that benefit most from high atmospheric oxygen are we mammals. We get big without being small, but require high oxygen tensions to keep fetuses alive (Falkowski et al., 2005).

4.3. Can we test the one ocean model?

Suppose one asked how long it takes an ocean of a certain size with so much diversity over such a large range of scales to reach equilibrium? Evidence would suggest that the equilibrium is never the same (Sepkoski, 1998), but there is probably some sort of equilibrium. We might hypothesize that biodiversity reflects long-term survival of DNA sequences, stabilizing ecosystem services despite environmental change. In the ocean, mechanisms for ensuring survival cover the spectrum from prokaryotes maintaining low concentrations of replicable DNA throughout the ocean volume, able to take advantage of local change, to animal mobility allowing movement to avoid local change. The high metabolic costs of mobility are offset by the dramatically lower number of DNA replicates required to ensure survival.

A small ocean likely equilibrates faster than a large one. We actually have examples and can age them paleontologically (Fig. 6) as a test of this hypothesis (Valentine and Moores, 1974). The real ocean has not been as simple as One Ocean for hundreds of millions of years. Real oceans have complex physical features, are far from uniform and move in complex ways due to density variations, etc. Is it possible to relate real diversity to an oversimplified model? CoML has demonstrated a remarkable suite of tools to record diversity from the smallest to the largest and from top to bottom. As oceans are created by geology and expand they record their rates and the diversity of many microscopic species with shells, like foraminifera (Rutherford et al., 1999). Perhaps it is possible to meld the understanding from geology, oceanography and biology in these many “test oceans” to complete the picture

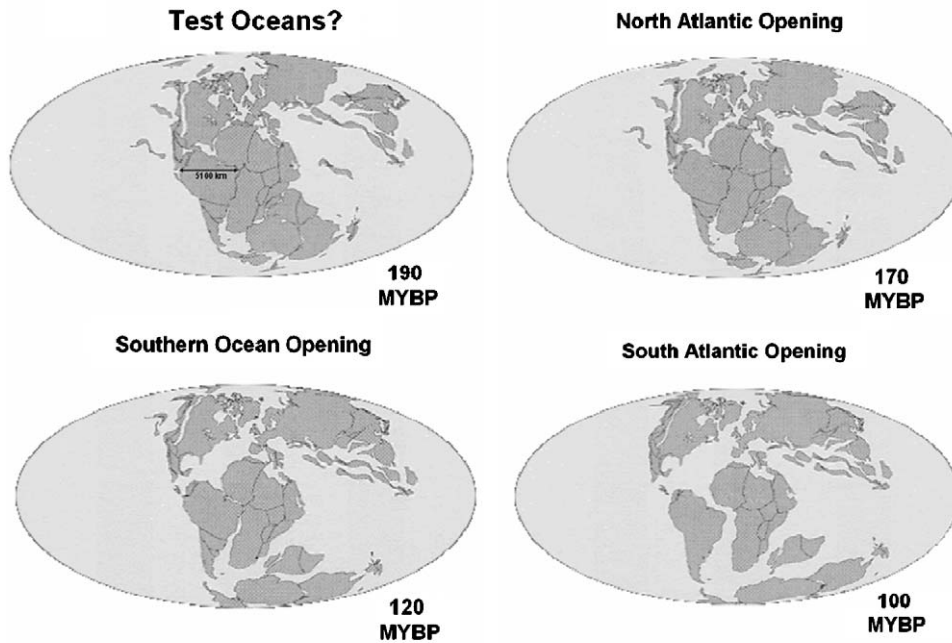


Fig. 6. Plate tectonics creates new oceans that must increase their biodiversity over time. Can we reconstruct biodiversity equilibration rates in these test oceans? Images from University of California Museum of Paleontology (<http://www.ucmp.berkeley.edu/geology/anim1.html>).

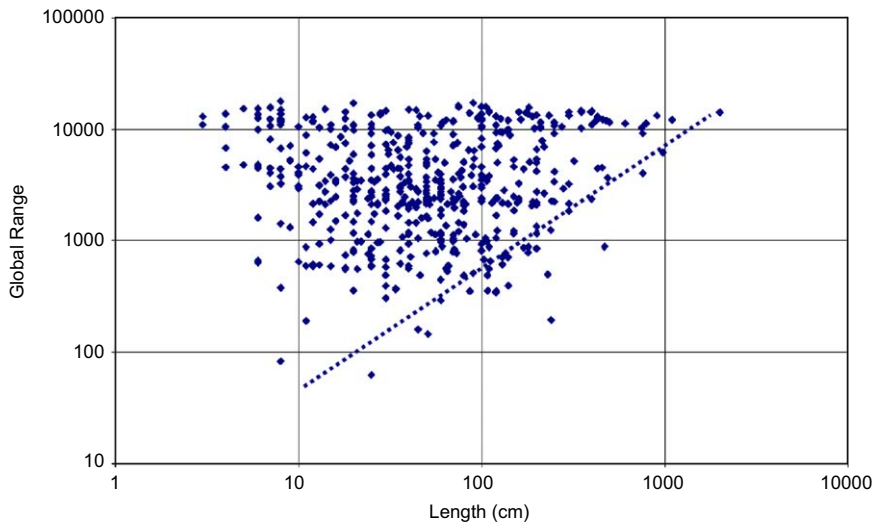


Fig. 7. A comparison of the maximum length of 1000 fish species with over 100 records in OBIS to the range of their distribution. The range size of a species is estimated as the median of all possible distances between pairs of observations of that species. Some fish produce planktonic larvae that are distributed by currents so that their range is independent of size. The lower limit of this distribution shows a relation of length and range for those species that distribute themselves based on their own swimming speed. Adult fish size from SeaLifeBase, courtesy Nicolas Bailly.

and reconstruct the origins of biodiversity by comparing the processes in the many to the model in the One. The details of these processes are beyond the scope of this article, but could be a future expansion of the concept.

As an example, Fig. 7 compares the maximum length of 1000 fish species with over 100 records in OBIS to the range of their distribution. The lower limit of this distribution shows a relation of length and range. These are likely species that distribute themselves based on their own swimming speed. The scatter in the graph likely relates to species that produce planktonic larvae that are distributed by currents, so that their range is independent of size. Sorting this out for species in a test ocean with known currents would be a logical next step.

5. Conclusions

Lovelock's latest book (2006) argues that the reduction in planetary biodiversity is testing Gaia's capacity to compensate for the addition of greenhouse gases to the atmosphere. The idea that the Earth is a giant homeostatic mechanism still makes some scientists nervous, but from horizontal gene transfer among prokaryotes to mobile metazoans stabilizing ecosystems by moving to the places where there is the most for them to eat, there do seem to be many opportunities for One Ocean to be self-regulatory. Geology shows us that from time to time the system has gone into wild oscillations in oxygen concentration and species richness (Berner et al., 2007), but it seems capable of

returning to a stable state as diversity accumulates. The current stable state is arguably a balance between the big and the small, which it is not about winning, but about breaking even.

This conversation with RKO's 92-year-old mother may be a good summary of the importance of marine biodiversity (Mathes, 2007).

“What good does the ocean do me here in Kansas City?”

“It provides half the oxygen you breathe: would you like to breathe twice as often?”

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