Food for Thought

Comparison of marine and terrestrial ecosystems: suggestions of an evolutionary perspective influenced by environmental variation

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†Deceased. This article arose from a work in progress with the co-authors when Prof John Steele passed away. It was produced from material in early drafts, copious notes from meetings and discussions such that this work was re-constructed using mostly John’s original voice on an issue that he very much wanted people to contemplate and deliberate.


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The transition of plants and animals from sea to land required adaptation to a very different physical and chemical environment. In this paper, we focus on the consequences of the differences between the magnitude of the variability of ocean and atmospheric dynamics, with the ocean environment (in particular temperature and currents) being two to three orders of magnitude less variable than that on land. We suggest that greater insights on possible responses of marine vs. terrestrial systems to rapid climate change can be gained by considering that terrestrial vertebrates, invertebrates and plants have evolved from marine organisms that, pre-Cambrian, had early life history developmental stages as planktonic larvae. Marine larvae were/are adapted to the predictable and minimal range of temperature changes and regularities in ocean currents, as most organisms utilize the energy in these currents as an “auxiliary” source for predictable gamete and larvae dispersal. Post-Cambrian, on land, no such simple strategy was available; instead, most terrestrial organisms have evolved reproductive strategies and behaviours to eliminate, or at least minimize, the consequences of much larger atmospheric variability. Adapting our future use of these systems sensibly will require greater understanding of how the two regimes respond to rapid climate change.

Keywords: climatic change, marine–terrestrial comparisons, physical–biological coupling.

Introduction

About 500 million years ago, give or take a few million years, the oceans were teeming with life and the land was a desert. We assume the invasion of the land began when simple plants—green slime—spread inland from coastal ponds, enhancing the oxygen in the air for animals to follow (Lenton and Watson, 2011); first the invertebrates, crustaceans having common ancestors that evolved into insects; then the more complex transformations from fish to quadrupeds. Within 100 million years there were fully developed terrestrial ecosystems that provided the basic material from which we and all contemporary life on land are derived. Some of the organisms within these ecosystems developed the capability to alter their environment (in particular us humans with our use of land for farming) in ways that marine organisms never achieved. How did terrestrial life—the Johnny-come-lately in the ecosystem game—develop the capabilities to manage or mismanage the world? Why had the earlier frontrunners in the sea not gotten there first? And, what are the drivers that have led to the present-day differences? Apparently it was too difficult to start from scratch on land (Lenton and Watson, 2011), so the tedious and complicated process we call evolution, with all its constraints, was required to transform the marine ecosystem, into a terrestrial one. This

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adaptation required the transformation of elegant sequences in the sea, where plants, herbivores and carnivores increase in an orderly fashion in body size, life span and ambit, to a messy, non-systematic grouping on land with short and long-lived plants, large warm-blooded herbivores, and social insects with lifespans not related to temporal and spatial scales (Figure 1).

Popular writing (Gordon and Olson, 1995; Fortey, 1999) covers the adaptations to the “statics” of the terrestrial environment (Denny, 1990), such as the effects of gravity on plant structures, the problems of desiccation, the elimination of waste products, and other physiological processes that are the subject of paleontology. The tendency is to give primacy to the terrestrial perspective, with titles such as “Concepts of Adaptation in Aquatic Animals: Deviations from the Terrestrial Paradigm” (McFall-Ngai and Manahan, 1990), or “Why life histories evolve differently in the sea” (Strathmann, 1990). This tendency is understandable, but we believe that an appreciation of the intricacies involved in deriving terrestrial solutions from marine origins is critical to an understanding of the evolution of terrestrial species as well as relationships between species at the ecosystem level in both regimes.

The main thesis in this paper is that, behind the need to adapt to the very different opportunities presented by the terrestrial environment, one of the main drivers was the adaptation to the much more variable atmospheric component of the terrestrial environment. We suggest that between evolutionary constraints and the need to deal with much higher variability in the environment, that terrestrial organisms evolved life-history traits, especially developmental life-history traits (egg and juvenile), and behaviours that were needed to dampen and eliminate the effects of much higher environmental variability. The basic premise that underlies

![Figure 1](https://academic.oup.com/icesjms/article/76/1/50/5161207)
our desire to ask readers to re-look at the comparisons between present-day terrestrial and marine ecosystems is to provide readers with the information about the contrasts in environmental variability between the regimes and to better appreciate the particular forms and processes we find on land and how they may be affected by rapid climate change, by understanding how these may have evolved from life in the sea. This paper will focus on the consequences of the very different space and time scales of the physical dynamics in the two regimes, while recognizing the constraints imposed by the very different static properties of the two systems.

We propose to focus on three principal solutions (illustrated in Figure 2) to the environmental challenges raised by the transition to the use of the land. The point is to view these transitions in the light that they are bounded by evolutionary constraints, especially within developmental life-history traits that require a very predictable stable environment: The three solutions are: (i) that some terrestrial plants evolved very much longer lifespans to smooth out the short-term but large-amplitude environmental perturbations; (ii) many invertebrates and vertebrates built nests to provide an environment that moderated or removed them and especially their eggs from this variability; and (iii) some vertebrates also created their own regular internal environment by becoming warm-blooded and viviparous. We contrast the possible response for adaptation to open-sea predictably low environmental variability with the possible reasons related to high environmental variability and demonstrate these three possible solutions by contrasting differences in evolutionary adaptation by superficially similar marine and terrestrial species. We suggest that it is important to consider the possible environmental variability drivers behind early life history traits by demonstrating the divergent consequences of the evolution of those traits in the two regimes and that looking at the differences between modern marine and terrestrial species in this light will allow more accurate predictions of what will be the consequences of rapid climate change in the contrasting regimes.

Our motivation is concern about how we think about affective adaptation to future rapid climate change, especially as the human achievement of combining two of the original strategies for adaptation to a terrestrial environment: “invertebrate” nest making on the largest scale, with efficient viviparous reproduction.

This has required major disruption of the first adaptation—long-term ecological stability built upon long-lived perennial plant communities—to achieve high production of selected annual species. Not only has this affected biodiversity; possibly more significant, dependence on annual plants removes the natural ability to dampen out climatic fluctuations at the decadal to century scales, and requires large-scale human intervention. Thus, the original challenge in the transition to land—independence from the effects of environmental variability—has become the ultimate adaptation we still need to make in understanding how to best manage our land and seas under rapid climate change. Future climate looks set to be far more variable than we humans have experienced in the last 10,000 years since our species started to become dependent on annual plant production (Pearce, 2007).

The major sections of this paper set out below are firstly “The transition to the land” which describes the range of transitions to the land across plants, invertebrates, and vertebrates via the relevant physical processes in the oceans and atmosphere, with examples of ecological adaptations at the species level. The second major section of this paper is “Comparative study: rapid climatic change” which considers the consequences for rapid climatic change of the different adaptations. The arguments in this review about relationships between physical and biological processes and marine and terrestrial communities, and the generalizations about broad groups such as “plants” or “invertebrates”, do not have the authority of physical laws. Rather, they invoke consensus of opinion or preponderance of evidence. We do not try to describe the detailed processes determining the evolution of traits and the estimation of evolutionary trade-offs (Stearns, 1992). Thus, the “conclusions” try to discern patterns that may illuminate certain ecological processes and evolutionary sequences, and in doing so provide insight into particular important sectors of our environment that the world has come to rely on in many contrasting parts of our world.

**The transition to the land**

**Importance of low environmental variability during early (developmental) life-histories**

Evolution is a long-term process of adaptation to the environment. The challenges for organisms invading the land were, initially, posed by the utterly different physical conditions between the two regimes. We think of the adaptation of individual species to “static” properties, such as the structural problems posed by gravity and oxygen supply, or of physiological processes required for temperature control and to prevent desiccation. But there were also problems raised by the difference between the levels of predictable variability and rates of change in the different environments. We are aware of the millenial-scale glaciations driven by the Malenkovich Cycles (Kerr, 1987), or, at the other extreme, of the global extinctions caused by meteorites or volcanoes. Both of these have tested the ability of life on land and in the sea to resurrect their ecosystem patterns with new components. But between the millenial-scale trends and the occasional global catastrophes, there is the need to adapt to the daily, monthly, or yearly variations in the environment. And, especially, to evolve modes of reproduction and rearing of young that maximize survival over generations. The early stages in the life cycle have the greatest exposure to the environment and display great diversity in the processes that have been developed by terrestrial plants and animals. It is in this phase that we find the very different solutions...
evolved in the sea and on the land in relation to the very different characteristics of the two regimes.

For most of us land-based inhabitants, the weather is a habitual topic of conversation. Its unpredictability beyond a few weeks is now established scientifically. Even the seasonal cycles can be quite variable. The predictability of weather a year ahead is about the same as for three weeks from now. Uncertainties about the temperature, the humidity, the wind strength and direction can affect our plans for outdoor activities. We find that most terrestrial animals devote a great deal of their acquired energy to mitigating the consequences of this unpredictability; especially for the reproduction and nurture of their young.

In the sea, most animals release large numbers of eggs or larvae to the water to be carried along by currents with broadly predictable trajectories and speeds to their next habitat that will provide food. This “auxiliary” source of energy (Mann and Lazier, 1991) is widely used by marine animals for transport of their young and does not have anywhere near the comparable level of predictability in the atmosphere. On land, many animals provide shelter for their offspring within their bodies or in specially constructed nests, and provide parental care by actively foraging for food for their young. Why have these very different strategies for parental care evolved in the two regimes? It is not that the alternatives are infeasible. *Nephrops norvegicus* ("scampi") creates extensive burrows, comparable to those of rabbits, in the muddy sea bed and carries its eggs until they are ready to hatch but then releases them to the currents with no more parental care. Within clams, branch fish, skates are oviparous as they lay pouches containing a few large eggs, known as “maidens’ purses”, and most sharks are viviparous but all parental care ends once young are released (Wourms and Lombardi, 1992). But within the superclass viviparous but all parental care ends once young are released. Carries its eggs until they are ready to hatch but then releases them to the currents with no more parental care. Why have these very different strategies for parental care evolved in the two regimes? It is not that the alternatives are infeasible. *Nephrops norvegicus* ("scampi") creates extensive burrows, comparable to those of rabbits, in the muddy sea bed and carries its eggs until they are ready to hatch but then releases them to the currents with no more parental care.

**Physical differences between regimes**

**Levels of variability**

The answer to the differences between the marine and terrestrial regimes must, in part, be attributed to the contrasting physical differences between them. Plankton and most fish are close to being neutrally buoyant and, unlike the birds and the bees, do not expend significant energy in staying suspended. The sea, unlike the air, contains the nutrients necessary for plant growth so that a complete food web can exist without a solid base. Thus most marine life depends on the microscopic plants in the water column for the energy and nutrients to support their food webs. But this does not account for the lack of parental care in the life cycles of the great majority of marine animals. For an explanation of the predominance of strategies based on the release of eggs or larvae to the “care” of the physical environment, we need to consider the differences between the marine and terrestrial habitats in terms of their oceanic and atmospheric environments and look more closely at the dynamics as well as the statics.

The ocean and the atmosphere are both subject to the same laws of fluid dynamics, but it is because of their very different physical properties (e.g. density, thermal expansion coefficient, and viscosity), that the time scales in the ocean are much longer and the spatial scales for comparable features are much shorter (Figure 1). This is especially true for eddies in the open ocean or cyclonic systems in the atmosphere, where most of the kinetic energy is found and which are generated by essentially random processes. The atmospheric eddy scales are much shorter in time (days vs. weeks) and larger in space (10^4 vs. 10^2 km) than ocean eddies (Gill, 1982; Clark, 1985). It is these features that introduce the variability in air currents, temperature, and rainfall that will affect the plants and animals. Over the continental shelf, where direct atmospheric forcing of the ocean is particularly important, oceanic time (but not so much space) scales are influenced by atmospheric processes. It is only on short time scales (10 s of minutes or less) that the differing molecular properties of air and water constrain heat transport between an organism and the environment. From Figure 3, it is clear that the transition to land involved the challenge of variability at quite different scales and would have required adaptation to much more rapid and much larger-scale variance.

In a classic paper, Hasselmann (1976) developed stochastic climate models to show how the nonlinearities in the combined ocean-atmosphere system converted short-term “weather” forcing into long-term ocean responses with red spectra, where variance decreases with increasing frequency. To get data on spectra for time scales from days to millennia, one has to patch together instrumental and geophysical records (Figure 3). The reconstructed long time series (Figure 3a–c), using temperature, sea level, and geophysical data and eliminating regular solar or lunar cycles, confirm Hasselman’s insights and show the terrestrial environment with a near “white” power spectrum on scales from days to centuries, whereas the ocean is “red” (Figure 3). “White” spectra have relatively equal energy at all frequencies, whereas for “red” spectra, the energy increases with decreasing frequency. An analysis (Figure 3d) by Vasseur and Yodzis (2004) of surface air temperatures over sea, inland, and at the coast at ecological time scales confirms this general pattern in the slope (-β) of the power spectra and shows that intermediate coastal regions have more variable responses that span the land-ocean range. Specifically, the spectra from over the ocean have the steepest slopes, hence longest time scales, and records from over land have the flattest spectra, hence the shortest time scales. The large range of intermediate values in coastal regions is caused in part by the fact that, in water of less than about 200 m depth, the open ocean definition of space-time scales (Figure 1) and of power spectra (Figure 3b) have to be modified. Generally, these data compilations confirm Hasselmann’s (1976) intuition about the role of ocean-atmosphere interactions in transforming the variability in the atmospheric drivers to an ocean-based system with very great millennial variance and, relatively, minimal variability at yearly to decadal scales. It is this transformation in scales that is central to our argument about the ecological and evolutionary consequences.

According to Pelletier (1998), at time scales longer than about 1 000 years, the atmosphere and the oceans are in thermal equilibrium, so that these two sectors will have the same variance.
Therefore, at millennial scales, the land and sea form a single system. A schematic presentation of the combined spectra and their relation to ecological time scales (Figure 4) summarizes the effects of the transition to land. What are the implications of these differences in the magnitude and time scales of variability for ecological processes?

The critical early life stages of nearly all marine species and of most terrestrial animals have time scales from days to a year. Based on the differences in the oceanic and atmospheric temperature spectra, at these time scales, the variability of the ocean environment can be two to three orders of magnitude less than that on land. At these same scales, the spectral slope of the ocean environment is much steeper than that on land. This spectral slope means that day-to-day variability is more dominant (compared to lower-frequency changes) over land than in the ocean, where the longer time scales dominate. Different variables, such as winds/currents, may have different spectral properties than temperature, but we anticipate that generally the oceanic spectrum will remain “redder”. Given the differences in variability and its time scales, then, it is not surprising that the trade-offs in how animals and plants have evolved to ensure the survival of their offspring in relation to terrestrial and marine environmental variability can be so different.

Predictably of currents in oceans vs. atmospheres

As well as the differences in temporal variance, in the ocean there are solid boundaries to constrain the currents. In consequence, instead of the atmospheric fronts and high or low pressure systems sweeping erratically across the continents, in the ocean we see predictable current systems at a wide range of scales, from the oceanic gyres (Talley et al., 2001) of the Gulf Stream in the North Atlantic and the Kuroshio in the North Pacific, to the anti-clockwise circulation in the North Sea driven by the Baltic outflow (Hill, 1998); and, at smaller scales, the tidal motions that can generate clockwise flow around fishing grounds such as Georges Bank off New England (Simpson, 1998). None of these current systems is “as regular as clockwork”, but it is not merely we
Red to pink noise: oceans compared to coastal/fresh water

But ecology seldom or never has all-or-nothing solutions to environmental challenges. This concern is expressed in the concept of trade-offs between different traits (Stearns, 1992). Evolution can be seen as a search for loopholes (Bakun and Broad, 2003) in any trade-offs between different traits (Stearns, 1992). Evolution can respond to begin life as fish on the seabed of the Bank (Smith and Morse, 1985). It is important to recognize that the physical processes are quite different in these three examples. The common factor is the passive but directed transport of larvae as part of the three life cycles. These examples illustrate the general dependence on physical current systems for "similar" marine and freshwater aquatic animals to partially resolve this issue. Furthermore, many if not most of the transitions to land occurred from brackish or freshwater organisms (Gordon and Olson, 1995; Petit and Hampe, 2006).

Oceans

At one extreme are cod, which release millions of tiny eggs providing very little stored food in each egg and relying on numbers to propagate the species. At the other extreme are the cartilaginous fish (sharks), which are oviparous or viviparous, producing 2–100 offspring in each reproductive cycle. Then, in between, are viviparous redfish (Sebastes spp.), which release a few tens of thousands of fully formed young. However, the predominant response of marine fish families has been to adopt a "hands-off" approach, with 85% being broadcast spawners (Winemiller and Rose, 1992). In comparison, families in freshwater display a much greater diversity of reproductive strategies, showing that the overriding factor is transition from the regularities of ocean systems, rather than just the adaptation to air. The distinction is most evident in the life cycles of catadromous and anadromous fish. The former, such as eels, feature a pelagic larval stage, whereas salmonids, such as salmon (Salmo salar), lay very large eggs in nests on the upper reaches of rivers.

There are similar descriptions for invertebrates (Thorson, 1950; Marshall et al., 2012). The free-swimming crustaceans that dominate the plankton obviously have eggs and nauplii that are at the mercy of the currents, but the offspring of bottom-living crustaceans such as lobsters (e.g. Homarus americanus), which carry their eggs for months, have also a later pelagic phase where the young molt and grow before settling back on the seabed.

Again, there are exceptions. Thorson (1950) proposed that high-latitude benthos had fewer planktonic larvae, but later work by Marshall et al. (2012) showed that this applied in the Antarctic but not the Arctic. Marshall and Thorson look for explanations in terms of productivity and temperature. Could the difference be explained in terms of the current patterns? Circumpolar currents in the Antarctic have no return path at the regional scale and so are comparable to atmospheric systems.

Coastal

Estuaries provide a great diversity of physical environments and current systems, forming interfaces between freshwater and marine environments. Highly fecund oysters and other estuarine shellfish use a strategy of multiple spawns of millions of eggs, which is believed to be a way to play the environmental lottery (North et al., 2008). But the main feature is larval vertical migration over a few tens of meters, to use vertical gradients in currents to counteract the kilometers of net seaward transport and ensure long-term residence (Carriker, 1951; North et al., 2008). This widespread dependence by broadcast eggs and larvae on estuarine currents to retain larvae where there is good habitat forms a
further illustration of the use of “auxiliary” energy sources for marine reproductive strategies.

**Freshwater**

Mussels provide an interesting contrast between marine and freshwater life cycles. The widespread blue mussel (*Mytilus edulis*) lives on rocky marine shorelines and is a broadcast spawner. Pearly mussels (*Unionacea*), which live in rivers and lakes, have what could be considered a bizarre life cycle. They have a specialized larva, the glochidium, which is a parasite of the gills of fish where they can derive some nutrients (Strayer *et al.*, 2004). We suggest that what looks bizarre once considered in the context of this essay is merely an adaption to stop larvae from being flushed out of the one-way river system and an evolved behaviour to serve the role of retention of larvae in good habitat (as described in the “Predictably of currents in oceans vs. atmospheres” section).

**Evolutionary constraints within “white noise” terrestrial environments**

**Vertebrates**

There is a predominant pattern for the early life phases of marine organisms that couples ecological behaviour to physical regularities in the chosen environment; patterns that are absent in closely related freshwater species. We must presume that the rewards (larvae survival) outweigh the risks that arise from the variability associated with these physical systems. When we turn to the land, the trend has been in the other direction; a decoupling from the use of the physical environment. As they passed from a relatively slowly changing temperature regime to one that could change rapidly and unpredictably, some vertebrate groups evolved from cold- to warm-blooded, accepting the greater energy costs. But the greatest developments were in the reproductive cycles, with the more recently evolved vertebrate class (mammals) becoming predominantly viviparous. Many invertebrates still produce very large numbers of eggs, but the general trend has been towards smaller numbers of offspring that are given increasing care, feeding, and protection in nests, culminating in vertebrate egg-laying as a strategy to decrease environmental exposure (Royle *et al.*, 2012).

**Invertebrates**

Whatever the details of the strategy for any particular terrestrial species, the common factors involve the expenditure of significant energy and resources on the separation of the offspring from the large and unpredictable fluctuations in their environment. In contrast to viviparous reproduction for warm-blooded vertebrates, many of the invertebrate strategies involve the use of "nests". Furthermore, these structures often require cooperative efforts by a few to hundreds or thousands of other members of the species. Wilson (2012), in "The Social Conquest of the Earth", has described the wonderful variety of communal structure and behaviour of the ants he has studied and has concluded that nest building is the defining feature of the social ant communities that achieved a level of organization comparable to humans, and some millions of years earlier. In the sea, the crustaceans are a dominant component of the food web. Copepods are a critical link between phytoplankton and fish. Furthermore, they evolved to living on and in the seabed in a way that seems pre-adapted to life on land. But there is no evidence of complex communities, or of communal nests. Nearly all the marine arthropods use a planktonic phase as an essential part of their life cycle, whereas, according to Wilson, on land the evolution of social systems and protected reproductive cycles went hand-in-hand. It is this combination that produced what Wilson calls "eusociality", where groups contain multiple generations and are prone to performing altruistic acts as part of their division of labour.

According to Wilson (2012), “all animal species that have attained eusociality, without exception, at first built nests that they defended against enemies”. We would suggest that these nests were first built as defense against the very variable and unpredictable environment. The more complex structures achieved greater isolation from the external conditions but required more division of labour and more social interaction. Contrast that with the yearly spawning aggregations of cod or haddock. There is quite a lot of "behaviour" in the male-female interactions and inherited "knowledge" of the spawning sites, but no real social patterns and certainly no parental assistance. Between that and the social insects, there is a range of intermediate solutions described by Wilson (2012), from a snapping shrimp species, which has a queen and workers inhabiting sponges, to birds and crocodilians, where the young leave the nest when they mature and disperse to breed and build nests on their own. Wilson (2012) regards dispersal as a barrier to eusociality. However, if, in the sea, egg or larval dispersal provides a more successful life cycle (i.e. higher survival of both larvae and adults—possibly from use of less energy in parenting) for a predominant number of species, then this difference in survival in the “redder” vs. “whiter” environments, is the critical division for responses to the environments on land and in the sea. This difference in fitness is the trade-off between the advantages of pelagic egg and larval transport and of complex parental involvement in long-term evolution.

**Plants**

Another challenge concerned the response of plants to the large-scale variability in the terrestrial atmosphere compared to the sea. We still do not appear to know as much as we would like about the early adaptations to air and the acquisition of nutrients (Gensel, 2008). But the later developments indicate two strategies. The first expansion came with the evolution of seed-bearing trees and perennial grasses. One solution to the problems posed by the vagaries of weather was to produce large numbers of wind-borne seeds over an extended life time on a very much longer, almost climatic (>100 s of years), time scale. There is an obvious comparison to the early life stages of fish, particularly gadioids. Both trees and fish have very high mortality of the early stages, followed by a long maturity with low death rates (Figure 5). Thus, some features of the predominant marine adaptation can be transferred to land by greatly increasing the lifespan and so averaging out the annual to decadal weather variability (Petit and Hampe, 2006). But the greatest development occurred just over 100 million years ago. The evolution of flowering plants transferred the problem of dispersal of pollen from the wind to insects as an energetically acceptable solution encouraging great diversity in both components. But the time scales have now become a problem. At climatic scales of centuries, the dispersion rates for deciduous trees of less than a kilometer per year (Davis and Shaw, 2001) could cope with post-glacial poleward spread but
would be inadequate to meet the predicted rates of rapid climate change resulting from present human activities. The importance of why we need to appreciate the differences in evolutionary adaption between the regimes in terms of environmental variability and rapid climate changes is taken up in the “Comparative study: rapid climatic change” section.

**Comparative study: rapid climatic change**

As we move into an unprecedented period of rapid climate change (Pearce, 2007) it is important to more fully understand how the marine and terrestrial regimes, their ecosystems and species, have evolved differently via the expected environmental variability. There is at least modelling evidence that those regimes with environmental variability in the “red” noise spectrum may face increasing extinction risk with rapid climate change (Mustin et al., 2013). The more accurately we can predict how species and ecosystems will react to climate change, the better we can use our ability to adapt management practices for our land and sea resources. This section provides a few examples of what the temporal and spatial differences may be in terrestrial vs. marine systems.

**Forests (land/white noise)**

The most recent and therefore most accessible large shift in climate was the recession from the last ice age that had its maximum about 18 000 years ago. The changes in forests in northeastern North America have been well documented by Margaret Davis and others (Davis, 1981; Davis and Shaw, 2001). The gradual northward move in the ice edge is followed fairly closely by the expansion of the hardwoods. For the future the question is how these forests (or their remnants) would respond to further climatic change induced by human activities. Davis and Zabinski (1994) simulated this by using a climate model projection as the basis for a distribution of one common evergreen, hemlock (*Conifera maculatum*). In more recent studies, Davis and Shaw (2001) have emphasized the differences between the predictions of northward movement of temperature contours and estimates of spreading rate for tree communities. They conclude that current climate projections for the 21st century necessitate range shifts of 300 to 500 km per century, in contrast to commonly observed migration rates in the past of 20 to 40 km per century. Even the exceptional examples from the fossil record, of 100 to 150 km per century, are far below the rates required to track climate changes in the future. Therefore, the evolution of forest systems towards the use of long time scales to integrate higher environmental variability may not be able to respond to rapid climate change as it happens.

**Pelagic fish (oceans/red noise)**

These rates of change and their corresponding distributions can be compared to the temporal/spatial patterns observed for dominant pelagic fish, such as anchovy (e.g., *Engraulis encrasicolus*) and sardine (e.g., *Sardina pilchardus*). The populations of these species have roughly cyclical changes in abundance with a period of 40–50 years, and correspondingly large amplitude changes in distribution with increases of 20–40 degrees latitude and longitude (2 000–3 000 km), (Chavez et al., 2003). The 30-year expansion in range of the California sardine (*Sardinops sagax caerulea*) is therefore comparable to the 10 000-year change in hardwoods. Managed fishing effort, such as targeted fishing of top predators can also lead to major increases in prey species abundance that can result in large extensions in their distribution. The very marked increase in abundance of sand lance (*Ammodites americanus*) in the northwest Atlantic is an example of a fishery-induced change (Sherman et al., 1981; Steele, 2012). But, as with the sardine and anchovy examples, the change in abundance corresponded to a considerable spatial expansion in distribution close to the latitudinal scale of the millennial change in forests, but occurring in just a few years. Therefore, marine systems seem capable of more rapid, but also more dramatic whole regime shift responses (Steele, 1998).

**Reef systems (coastal/pink noise)**

However, it is not a complete land-sea dichotomy as there are the coral reef ecosystems, with the symbiosis between very long-lived animal systems and microscopic plants imposing almost “terrestrial” time scales for coral grazers. Reefs have several terrestrial features: fine-structured solid substrate, long-lived basic food supply to fish, coastal rather than purely marine physical air-sea environment. Coastal environments have spectral exponents intermediate to slopes to ocean vs. land (Figure 3D, Vasseur and Yodzis, 2004). Nevertheless, almost all coral reef fish have a pelagic larval phase and formed the basis for the lottery hypothesis (Sale, 1978). Almany et al. (2007) indicates that dispersion from and return to the reef is more limited than previously supposed, but overall the trade-offs in favour of using “auxiliary energy” appear to hold generally for coral reefs. These constraints may be the basis for reefs’ being diversity “hot spots” comparable to tropical forest systems, and potentially subject to the same concerns about the negative consequences of rapid climatic change (Burrows et al., 2011).

**Coda**

We hope we have shown how life cycles on land and sea are related not only to the divergent static properties of the two regimes but depend on the quite distinctive general responses to environmental variability. The very long time and short spatial scales of landscape provide a trade-off against the relatively short time...
and long space scales encountered on emerging from the sea. These “solid” scales on land provide opportunities for long life spans for many plants, and so determine the terrestrial insulation from shorter-term environmental fluctuation. Together, these scales promote functional diversity (Petchey and Gaston, 2002) on land as the basis for sustainability. In contrast, the relatively short time scales of marine responses allow for regime shifts (Scheffer, 2009) in the sea and encourage adaptability (Steele, 1998). Sustainability and adaptability are the ecological processes at very different time scales imposed in each regime in response to their combination of contrasts in environmental variability and static properties (Levin and Lubchenco, 2008).

The story in this essay has followed the divergent development of marine ecosystems that used the auxiliary energy in ocean currents as a critical component of their early life cycle, and the regularities in the physical systems to determine their spatial patterns, as compared to terrestrial systems that followed the alternative path of developing life cycles that minimized the irregularities in their environment by length of life, internal temperature control, or external housing. The persistence of both systems over millions of years is an indication of their relative stability under their very different constraints. The recent utilization of fossil fuels by humans has allowed terrestrial systems to break the rules inherent in our evolutionary past and exceed the limitations that these imposed. It is ironic that the solution to our present “climate change” problems is to develop terrestrial ecosystems that rely on energy derived from unpredictable (wind) and relatively rapid, temperature changing sources (solar) and also from the most regular potential sources of energy (tides and ocean currents), thereby finally combining the options that all of our evolutionary ancestors, marine and terrestrial, have used. Let’s hope it works.

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