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REVIEW

A biophysical perspective on dispersal and the geography of evolution in marine and terrestrial systems

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The fluid mechanics of marine and terrestrial systems are surprisingly similar at many spatial and temporal scales. Not surprisingly, the dispersal of organisms that float, swim or fly is influenced by the fluid environments of air and seawater. Nonetheless, it has been argued repeatedly that the geography of evolution differs *fundamentally* between marine and terrestrial taxa. Might this view emanate from qualitative contrasts between the pelagic ocean and terrestrial land conflated by anthropocentric perception of within- and between-realm variation? We draw on recent advances in biogeography to identify two pairs of biophysically similar marine and terrestrial settings—(i) aerial and marine microplankton and (ii) true islands and brackish seawater lakes—which have similar geographies of evolution. Commonalities at these scales, the largest and smallest biogeographic scales, delimit the geographical extents that can possibly characterize evolution in the remaining majority of species. The geographies of evolution therefore differ *statistically*, not fundamentally, between marine and terrestrial systems. Comparing the geography of evolution in diverse non-microplanktonic and non-island species from a biophysical perspective is an essential next step for quantifying precisely how marine and terrestrial systems differ and is an important yet under-explored avenue of macroecology.

Keywords: bacteria; biogeography; dispersal; island; nekton; plankton

1. PREAMBLE

Seminal works by physiologists and physicists (e.g. Aleyev 1977; Steele 1985; Okubo 1987; Vogel 1988, 1994; Denny 1993) have employed quantitative comparative methods to clarify how fluids affect form and function of living things in diverse freshwater, marine and terrestrial habitats. All organisms are challenged physically when moving through, moving with or staying stationary in fluids with suites of different properties. There has also been interest by ecologists and evolutionists in how rates and scales of dispersal, population structure and evolution differ between marine and terrestrial taxa (e.g. Mayr 1954; Schoener 1974*a*,*b*; Paulay & Meyer 2002; Carr *et al.* 2003; Kinlan & Gaines 2003). However, these two independently well-developed areas of research have not been integrated. Here, we review and explore a quantitative fluid dynamic framework to encourage comparisons in dynamically similar settings, settings where fluid dynamic differences are explicitly addressed, to clarify differences and similarities in dispersal and the geography of evolution in marine and terrestrial (and freshwater) environments.

2. INTRODUCTION

The complex processes influencing modern patterns of evolution, biogeography and biodiversity in marine taxa have been debated recently (Colin 2003; Taylor & Hellberg 2003; Warner & Palumbi 2003). Consensus remains elusive due to disparate or inadequate evidence (Warner & Palumbi 2003) and the lack of a formal framework for integration that explicitly addresses underlying assumptions thus hindering broader comparisons. For example, it has been argued repeatedly that the geography of evolution is fundamentally different in marine versus terrestrial and freshwater taxa, but there is no theory that suggests this should (or should not) be the case and thus no objective criteria for evaluating apparently dissonant evidence.

Mayr (1954), in his classic paper on the geography of marine speciation, examined the hypothesis that '[s]ince the ecology of marine organisms is fundamentally

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different from that of such typical land animals as mammals, birds, land snails, and butterflies, one might expect modes of speciation in the oceans that differ completely from the typical geographic speciation of land animals'. He concluded that this expectation was wrong. Despite Mayr's (1954) conclusion, a focus on supposed 'fundamental differences' between marine and terrestrial systems has remained a motif for over 50 years (e.g. Mayr 1954; Steele 1985; Smetacek & Pollehne 1986; Hamner 1988; CGER 1995; Thomson & Gilligan 2002; Secord 2003; Lourie & Vincent 2004). For example, Carr *et al.* (2003) concluded that 'the general pattern of high levels of intraspecific genetic diversity without pronounced spatial or geographic structure is well documented [in marine taxa and] reflects fundamental differences between marine and terrestrial animal species in the spatial scales of population and evolutionary processes'. Profound biological differences are presumed the logical evolutionary result of underlying and fundamental physical differences between these realms (Halley 2005).

The idea of an elementary distinction between marine and terrestrial systems has been so pervasive that it has delimited some areas of study. Marine biogeography, for example, is today considered to be a separate subdiscipline of biogeography (Lomolino & Heaney 2004), undertaken by different people using almost entirely different scientific infrastructure (Steele 1995; Sarkar 2005; see also Stergiou & Browman 2005). In the context of the geography of evolution, the dichotomy is perhaps most evident in studies of islands, which have played central roles in terrestrial biology (e.g. Darwin 1859; Wallace 1880; MacArthur & Wilson 1967; Grant 1998; Hubbell 2001) but have not been endorsed by marine biologists (Schoener 1974*a*; Knowlton & Jackson 1994; Thomson & Gilligan 2002). An assumption underlying some of these discussions is that there are no closed marine ecosystems (Hatcher 1997), certainly not on the scales seen in terrestrial environments. Paulay & Meyer (2002), when comparing patterns of connectivity in marine and terrestrial systems noted that, in contrast to terrestrial systems, there were neither known intra-island nor intra-archipelagic endemic marine species.

For over a century, the ocean has been viewed predominantly as a vast homogeneous habitat (Smetacek & Pollehne 1986) and marine species viewed as having great dispersal abilities and therefore large geographical ranges, large population sizes, high gene flow and slow rates of evolution (Day 1963; May 1994; Palumbi 1994; Carr *et al.* 2003; Jablonski & Roy 2003). Indeed, this is evidently the case for many marine species (e.g. Ely *et al.* 2005; Goetze 2005 and 15 references therein) and this aspect of ocean evolution thus represents a 'serious challenge' to the idea of allopatric speciation (Palumbi 1994; see also Goetze 2005), which is often considered the predominant mode of speciation in terrestrial organisms (Mayr 1954, 1963; Winston 1999, p. 48; see Schilthuizen 2001, p. 186). However, advances in our understanding of oceanography and marine molecular ecology are increasingly revealing that the ocean is more physically heterogeneous than we thought, with shorter dispersal, smaller geographical ranges, smaller population sizes and lower gene flow (Rosenblatt 1963; Field *et al.* 1997; Longhurst 1998; Jones *et al.* 1999; Darling *et al.* 2000; Carr *et al.* 2003; Selje *et al.* 2004; Goetze 2005). It is now clear that geographical speciation—including allopatric, parapatric and/or peripatric speciation—is common also in marine taxa (e.g. Mayr 1954; Palumbi 1994; Williams & Reid 2004; Dawson & Hamner 2005; Meyer *et al.* 2005).

It is conceivable that the starkness of the contrast between marine and terrestrial systems has remained a persistent motif in part 'by virtue of our being terrestrial organisms' which renders '[marine] pelagic systems … inherently inaccessible to us' (Smetacek & Pollehne 1986), then there may be 'a fundamental difference between … the ways we, as scientists, perceive[d] … events' (Hamner 1988; see also Steele & Henderson 1994; Halley 2005; Raffaelli *et al.* 2005), rather than between the events themselves. Here, we explore this proposition and, in doing so, outline an approach that applies the tools of fluid mechanics to increase our objectivity in comparing dispersal and the geography of evolution in marine and terrestrial (and freshwater) realms.

2.1. What is a fundamental difference?

We begin by considering what constitutes a 'fundamental difference', the term so frequently used in contrasts of marine and terrestrial realms. By definition (The Oxford English Dictionary), it is a distinction of the most basic kind from which many other dissimilarities derive that, in practice, are sufficient in magnitude to effectively preclude comparison. A commonly noted dichotomy (e.g. May 1994; Carr *et al.* 2003; Paine 2005) that supposedly indicates fundamental differences is the restriction to the ocean of entire phyla (e.g. jellyfish, ctenophores and other gelatinous zooplankton). Certainly, hundreds of thousands of marine species have no terrestrial conphyletic counterparts. Similarly, hundreds of thousands of terrestrial insect pollinators have no marine counterpart (Kearns *et al.* 1998; Raffaelli *et al.* 2005). Nonetheless, these faunistic differences are the consequences of relatively few independent evolutionary events (11 sea-to-land transitions (May 1994) and one coevolutionary radiation of plants-plus-insects) on which the million-or-more species-level differences are contingent. Inferring that land and sea are 'fundamentally different' owing to differences in phyletic diversity or fertilization (pollination) is not tenable. Inferring that land and sea are fundamentally different is also questionable because it conjoins marine benthic with marine pelagic environments (versus terrestrial systems) although the benthic and pelagic environments are distinguished by a comparable number of phyla (10 phyla, endemic to the benthos; see May (1994)). Moreover, lineages in 10 phyla did transition from a marine to terrestrial existence (May 1994) and subsequently there have been multiple re-invasions of marine habitats by terrestrial taxa (e.g. angiosperms, birds, mammals) some of which contribute to the many independent clades with species living at the interface of, or in, both realms (e.g. seabirds, semiaquatic mammals).

We conclude from the above (and other examples that follow) that supposedly fundamental differences are overly simplistic binary representations of more complex, potentially theoretically rich, suites of comparisons. Supposed fundamental differences say nothing quantitative about the actual number or the true magnitude of differences between marine and terrestrial systems. Finally, invocation of fundamental differences often involves arbitrary *a priori* criteria or subjective *a posteriori* conditions. Thus, there have been significant problems of formal logic with the frame of reference chosen for contrasting marine and terrestrial systems.

3. THE NEED FOR A COMPARATIVE FRAMEWORK

A more rigorous framework for comparing marine and terrestrial systems is clearly required, including quantitative and statistical analyses and clear formal logic. The methods used routinely in studies within marine and terrestrial environments may differ, but many yield data (e.g. measures of species diversity and distribution, movement, gene flow) that are suitable for comparison between those environments (Stenseth *et al.* 2005; e.g. Kinlan & Gaines 2003; Hillebrand 2004). Quantitative data alone, however, are insufficient. Measurements must be given context and meaning by their theoretical setting, so that hypotheses are supported or refuted theories can be modified (Rudwick 1985; Smetacek & Pollehne 1986; Hamner 1988; Thomson & Gilligan 2002; Raskoff *et al.* 2003). Unfortunately, there is a communication barrier between marine and terrestrial scientists (Stergiou & Browman 2005) and the quantitative and theoretical milieu for integrative marine and terrestrial studies is impoverished (see also Paine 2005).

The semantics of language used by terrestrial and marine scientists to describe the non-random and uneven grouping of organisms or resources, i.e. ‘patchiness’, provides an example of realm-specific terminology that has confounded integration. Historically, ‘patches’ in pelagic systems studied by oceanographers were aggregations of organisms against a background of lower density, whereas the ‘patches’ in terrestrial substrate-oriented systems studied by ecologists were places where localized disturbances had eliminated organisms within a background of higher density (Hamner 1988). While these different usages did reflect the predominant structures of the respective systems, they did not reflect a marine–terrestrial difference *per se*. The structural differences also distinguish a wide variety of other pelagic (marine, limnetic or aerial) from substrate-oriented (land, intertidal or benthic) systems (Hamner 1988). Marine and ecology texts have since converged on an oceanographic definition of patches (e.g. Nybakken 1997, p. 455; Ricklefs & Miller 1999, p. 272; Castro & Huber 2003, p. 452; figure 1) consistent with its usage in realm-neutral disciplines such as metapopulation dynamics (Levins 1969, 1970, cited in Hanski (1989, 1999), thus focusing our attention on the systems rather than on the lexicon. Accordingly, it has become apparent that a ‘focus on near shore (coastal) marine systems … suggests [marine and terrestrial] differences may not be so pronounced (Dayton & Tegner 1984)’ (Carr *et al.* 2003; see also Drakare *et al.* 2006; Gray *et al.* 2006).

This indicates that efforts to reconcile marine and terrestrial conceptual frameworks may often have failed to be convincing (Hamner 1988) because many compared marine pelagic with terrestrial surface-oriented habitats (e.g. Smetacek & Pollehne 1986; Steele 1995). Yet marine plankton communities ‘differ markedly from most other biological communities on earth’ including other marine situations such as surface-oriented benthic communities (Dayton 1984). Consequently, marine–terrestrial contrasts have been conflated with marine–marine contrasts, and a strong conceptual framework for comparing life in the marine realm with life on land has not been developed.

3.1. The fluid environment

Aleyev (1977, p. 1) detailed the need for a ‘biohydrodynamic conception of life’ in pelagic systems, and many others have described the consequences of life in moving fluids, whether the fluid is air or water (e.g. Vogel 1988, 1994; Denny 1993; Denny & Wethey 2001; Mann & Lazier 2006). We believe a perspective that explicitly considers the fluid environment is also necessary for understanding the geography of evolution and scales of evolution in marine and terrestrial (and freshwater) realms.

Comparisons of marine and terrestrial systems have focused on the marine pelagic and they mostly have ignored the air, the other major potentially uninterrupted fluid environment on Earth. This is noteworthy because, even when comparing surface-oriented habitats (e.g. land to marine benthic), the overlying fluid is important in the dispersal of propagules (e.g. anemochorous grass seeds, planktonic macroalgal spores, insects). Yet fluid environments are relatively easily compared and differences are quantifiable (e.g. Denny (1993); see also Nybakken 1997; Pelletier 2002) even though precise values vary with measurement conditions. For example, surface seawater is approximately 96.5% water and 0.5% oxygen; in contrast, air is utmost 1.5% water (1 atm, 20°C, 100% specific humidity) and approximately 20% oxygen. The specific heat capacity of seawater (approx. $3850\ \mathrm{J\ kg^{-1}\ K}$) is approximately four times that of air (approx. $1030\ \mathrm{J\ kg^{-1}\ K}$). Sound travels faster (approx. 4.39 times, at 20°C), electrical resistivity is greater (approx. 10^{16} times) and oxygen replenished slower (approx. 10^{-4} times) in seawater than in air. Two of the most apparent and commonly noted differences are that seawater is more dense and viscous (at 20°C, 34.84‰, 1 atm: density $\rho = 1024\ \mathrm{kg\ m^{-3}}$ and dynamic viscosity $\mu = 1.072 \times 10^{-3}\ \mathrm{kg\ m^{-1}\ s^{-1}}$) than air (at 20°C, 1 atm: $\rho = 1.205\ \mathrm{kg\ m^{-3}}$ and $\mu = 18.08 \times 10^{-6}\ \mathrm{kg\ m^{-1}\ s^{-1}}$; Vogel 1981). Measurements over appropriate spatial and temporal scales can therefore characterize pertinent aspects of the fluid environments of the organisms being compared, quantify the differences and be used to posit realistic hypotheses of marine–terrestrial differences that consider how the fluid environments are experienced by the organisms being compared.

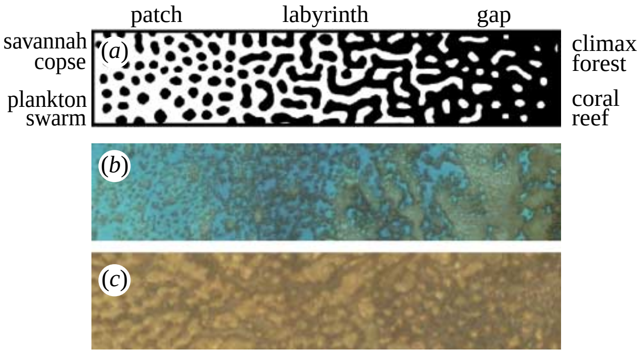

Figure 1. Patterns of environmental heterogeneity which have been used to illustrate basic differences in process in marine (plankton swarm) versus terrestrial (climax forest) systems are actually two ends of a continuum, each with analogues in the other realm. (*a*) Simulations using cellular automata produce different distributions of groups of organisms (black)—in patches, labyrinths or interspersed with gaps—on a background of bare habitat (white; redrawn from Rietkerk *et al.* (2004)). The distribution of organisms depends on interactions between biotic fine-scale positive feedback (increasing in strength from left to right) and a background of coarse-scale negative feedback (constant grain and strength, therefore relatively stronger towards the left). Decreasing or increasing the grain of interactions results in smaller or larger features, respectively. Interactions between biotic (e.g. compensatory biological mechanisms, functional interactions among species), plus abiotic (e.g. disturbance, physical heterogeneity), factors are the major influences on patchiness (Krohne 2001, p. 289) and, therefore, with the scale of dispersal and gene flow, determine the shapes of geographical mosaics (*sensu* Thompson 2005). (*b*) A 1.0 km long swath from barrier reef, on the right, to patch reefs, on the left, forming a mosaic with the lighter sandy sediment bottom (17° 00′19.38″ S, 146° 16′24.16″ E); image captured from the Google Earth mapping service, copyright 2007 DigitalGlobe. (*c*) A 0.4 km long swath of vernal pool grassland, Merced, California (37° 23′24.02″ N, 120° 16′26.67″ W), in which the landscape changes from predominantly grassland on the left to predominantly vernal pool on the right; image captured from the Google Earth™ mapping service, © 2007 Europa Technologies.

3.2. From the perspective of the organism

From a human perspective and from the perspective of any other species that does not successfully exploit both environments, marine and terrestrial realms differ physically in ways that are often biologically insurmountable. Marine–terrestrial comparisons of dispersal and the geography of evolution, however, are not made in the context of single species; they must compare pairs of marine and terrestrial taxa in their native environments (e.g. Kinlan & Gaines 2003). Consequently, comparisons should account for differences between realms in terms of the biologically relevant ways in which the hydrologic and aerial environments differ with respect to their incumbent organisms.

Fluid mechanics provides one suite of tools for comparing the hydrologic and atmospheric environments of organisms. One example is the Reynolds number ($Re=\rho \times l \times U \times 1/\mu$), which summarizes how fluid density (ρ) and dynamic viscosity (μ) interact with an organism's morphology (size and shape, but particularly length in the direction of flow, l) and speed (U) to influence the flow environment it experiences. Equality of Re for two flow regimes guarantees that the physical character of the flows will be the same irrespective of the fluid (Vogel 1981). Thus, different organisms living in different fluids can, in theory and practice (figure 2), experience very similar flow environments; flow is laminar in air or water if $Re<{\sim}2000$ and turbulent if $Re>{\sim}2000$; the fluid's inertia dominates the organism's motion in air or water if $Re\ll 1$ but the organism's momentum dominates if $Re\gg 1$. As a general guide, the order of magnitude of Re is the best indicator of an organism's flow environment (Vogel 1981), in part because an organism will experience a range of flow environments during its daily activities. Thus, Re is a useful scaling parameter for comparing (or contrasting) the lives of different organisms in different fluids.

Another approach for comparing biologically relevant physical differences in marine and terrestrial systems was introduced by Steele (1985). He recognized that the differing densities and viscosities of water and air would affect the temporal and spatial extents of variation, i.e. 'weather', including circulation, fronts and waves (Steele 1985, 1995; Steele & Henderson 1994). Although similar structures such as convergence zones and internal waves form in both fluids (e.g. Drake & Farrow 1988, 1989; Garrison 2002), such features are typically shorter lived in atmospheric than pelagic systems. The less dense, less viscous air can move and change more swiftly leading to less autocorrelation among measurements made on similar time scales (Steele 1995). As a result, on short (ecological) time scales, physical differences in the fluids are expected to lead to predominantly random environmental variation (termed white noise; variance $[v] \propto$ frequency $[f]$) in terrestrial environments but variability is positively autocorrelated over time (red noise; $\sim v \propto f^{-2}$) in marine environments (Steele 1985; figure 3).

These differences in environmental fluctuations or 'density independent' processes (Lawton 1988) are expected to have biological consequences (Steele & Henderson 1994). For example, an organism with a given lifespan will generally experience a greater range of conditions, as well as greater rate of change, in an environment characterized by white noise rather than by reddened noise (assuming the same long-term mean and variance). Thus, white-noise environments might select for organisms with greater tolerance of change and extremes. On the other hand, the redder the environmental variation, the more probable is a longer run of bad (or good) conditions, which increases the expectation of a population crash (or boom; Lawton 1988; Cuddington & Yodzis 1999) and might select for characteristics that favour persistence (e.g. resilient resting stages).

In fact, different colours of environmental variation do not segregate among realms (figure 3). For example, although short-term (i.e. high frequency) variation in precipitation takes the form of white noise, flow in rivers on the same temporal scale is considerably reddened (figure 3*c*), the thermal inertia of the sea reddens temperature variation of adjacent 'maritime'

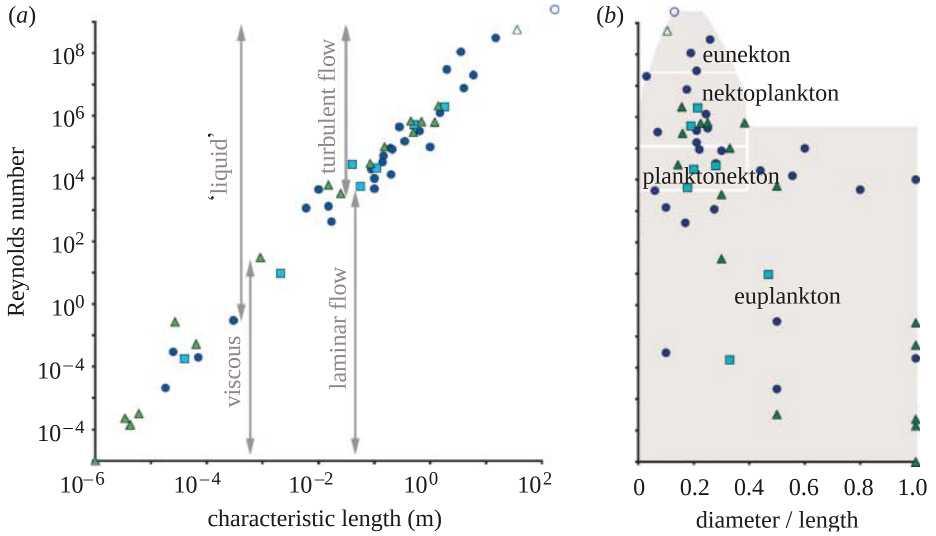

Figure 2. Comparisons of seawater, freshwater and air as experienced by some marine (dark blue circles), aquatic (light blue squares) and terrestrial organisms (filled green triangles). (*a*) Variation of fluid environment, described by Reynolds number Re, with the characteristic length l and typical speeds of movement of organisms (adapted from www.natureinterface.com/e/ni05/P048/; see also Okubo 1987; Mann & Lazier 2006). Regressions of Re on l for aquatic ($Re=1.79l+6.13$; $n=7$, $r=0.99$, $p<0.001$), marine ($Re=1.78l+6.11$; $n=26$, $r=0.98$, $p<0.001$) and terrestrial ($Re=1.79l+6.30$; $n=16$, $r=0.98$, $p<0.001$) taxa were not statistically different in slope ($F_{2,43}=0.009$, $p=0.99$) nor intercept ($F_{2,45}=0.500$, $p=0.61$). (*b*) Four classes of movement are used by diverse marine, aquatic and terrestrial organisms due to common constraints of fluid dynamics (adapted from fig. 1 in Aleyev (1977)). A Boeing 737 (open green triangle) is included in the analyses to illustrate that movement through the air at this extreme does not deviate from the relationship in (*a*) or classification in (*b*), although attaining such values is energetically unfeasible for terrestrial organisms. The fluid environment of Typhoon class submarines is indicated by an open blue circle. The characteristic length of organisms such as jellyfish that deform their whole body to swim may vary several fold (as will any ratio thereof) depending on the stage of the swimming stroke.

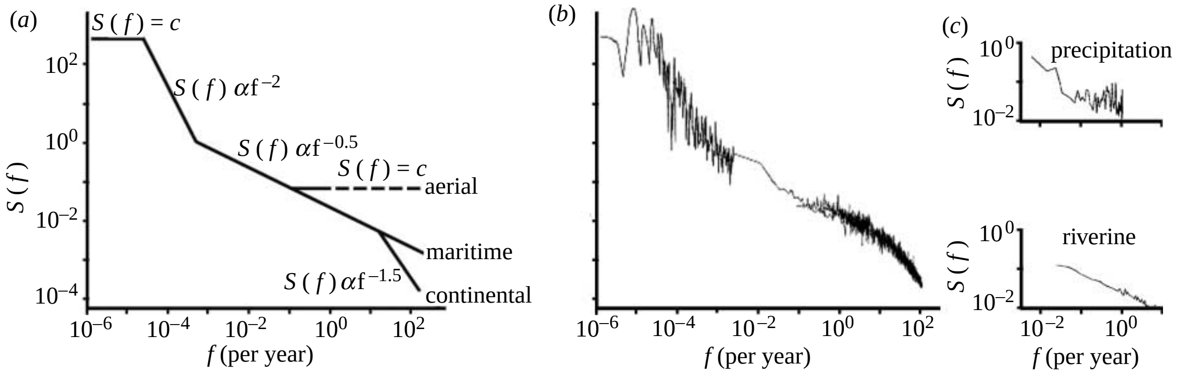

Figure 3. Noise (random variation) in environmental variables is generally well described by an inverse power law, $1/f^{\beta}$ (where f is the frequency of variation and superscript β, a constant), the form of which varies with temporal scale and environment. (*a*) Schematic of predominant patterns in environmental noise predicted on the basis of empirical observations and modelling of temperature variation (redrawn from Steele (1985) and Pelletier (1997)); c, a constant. (*b*) Example power-spectral density of local atmospheric temperature using combined low-frequency data inferred from the Vostok ice core and high frequency data from continental instrumental records (redrawn from Pelletier (2002)). (*c*) White noise in precipitation may be 'reddened' by processes that modify water movement into and through river beds.

coastland (figure 3*a*,*b*; Marshall *et al.* 2001; Halley 2005), and continental temperature records are also reddened presumably in part by the thermal inertia of land or vegetative cover (figure 3*a*,*b*). On longer time scales (approx. decadal and longer), the interaction between the atmosphere and ocean becomes greater and marine and terrestrial systems show similar patterns of variation (figure 3*a*). This is perhaps most evident in coupling on multi-year scales giving rise to phenomena such as El Niño Southern Oscillation and the Pacific Decadal Oscillation with important consequences in both environments. At century to millennial and longer scales, the ocean and atmosphere 'probably respond … as a single system' (Steele 1995) with a reddened spectrum (Steele & Henderson 1994). Such long-term, large-scale environmental changes have influenced the distribution of near shore marine benthic, planktonic and terrestrial land biotas (Addicott 1966; Hughen *et al.* 2004; Williams *et al.* 2004) although response times may vary between realms (Hughen *et al.* 2004) due, in part, to ecological thresholds (Maslin 2004).

These examples indicate two comparative approaches that should improve on the existing tendency to

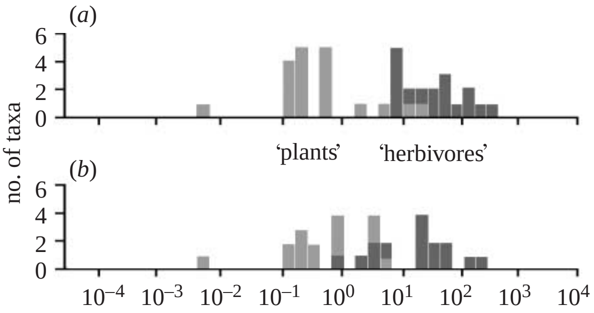

Figure 4. Evolutionarily averaged dispersal distances can be similar in ecologically comparable (*a*) terrestrial and (*b*) marine organisms. Dispersal scales of benthic marine primary producers (macroalgae and angiosperms; lower, light grey) and marine herbivores (invertebrates and fishes; lower, dark grey) with their terrestrial counterparts, land plants (upper, light grey) and herbivorous insects (upper, dark grey) estimated from genetic data ($n=16$ to 19). Redrawn from Kinlan & Gaines (2003).

qualitatively contrast organisms in dissimilar physical contexts in order to intuit the importance of biological differences. One is to quantify and explore differences between the physical environments as one component of quantitative comparisons of biology. The other is to compare marine and terrestrial organisms in physically similar settings; we discuss these in the next two sections.

3.3. Comparing physically dissimilar settings to understand biological differences

The strength of this approach is that there is no limit to the comparisons that can be made. The most disparate or very similar situations can be compared; each realm might even be represented by organisms drawn from multiple biophysical settings. Moreover, it transposes the existing framework of qualitative marine–terrestrial contrasts into a more quantitative and statistical comparative framework. Precedent for this approach is established, for example, in terms of the influence of fluid dynamics on individual morphologies (e.g. Vogel 1994), ecologies (Aleyev 1977) and population dynamics (e.g. Cuddington & Yodzis 1999) although it remains to be formalized as an evolutionary research strategy. Possibly, the greatest advances will be made by adopting the philosophy and methods of macroecology (Brown 1995; or macroevolution) to discover general relationships between metrics of the biophysical environment, such as *Re* and *Cd* (coefficient of drag), and a wide range of biological attributes, for example, size, shape, metabolic rate, dispersal distance, gene flow, range size and rates of speciation. If there are biophysical generalities of consequence across marine and terrestrial realms, correlations should be visualized as significant relationships with shapes and boundaries of statistical distributions that reflect shared constraints on variation, as has been found for metabolic rate and development time (Gillooly *et al.* 2001, 2002).

One of the difficulties, however, is identifying specific causes of macroecological patterns because variation may occur in many intrinsic and extrinsic factors or their interactions over ecological and evolutionary time scales. For example, dispersal ability (e.g. planktonic larval duration) should have a large influence on dispersal distance, yet dispersal of benthic and land animals and plants varies greatly in sometimes unpredictable ways (Knowlton & Keller 1986; Noonan 1990; Kinlan & Gaines 2003) possibly due to environmental heterogeneity, individual variation, selection, life history, behaviour and historical events. Thus, evolutionarily averaged dispersal distances of land and marine 'plants', for example, show considerable overlap and are more similar (angiosperms, median$=$0.29 km; macroalgae, seagrasses and mangroves, median$=$0.86 km; Kinlan & Gaines 2003) than one might expect from simple predictions based on dispersal distance as a function of sinking rates of dispersive propagules, which should be about 60-fold greater in the aerial setting according to predictions by the Stokes equation ($Re<1$, 1 atm, 20°C; note that the distances through which the propagules of terrestrial plants and marine macrophytes can sink and still encounter viable habitat are of similar magnitude). Marine species do, in general, tend to have 'fatter-tailed dispersal kernels' (Kinlan & Gaines 2003) and a higher frequency of larger ranges (i.e. 'cosmopolitanism … is greater' in the terms of Rapoport (1994)), as expected, but the quantitative differences remain to be fully explained by physical and biological differences. The approach of comparing physically dissimilar settings to understand biological differences, therefore, will benefit from being coupled with more 'controlled' comparisons to test specific hypotheses identified by the broad-brush of macroecology and macroevolution.

3.4. Comparing marine and terrestrial organisms in physically similar settings

The strength of this approach is that it minimizes the difference between physical settings and focuses on specific subsets of organisms, making it simpler to assess the causes of any observed differences. This strategy has also been espoused for investigating similarities between animals and plants and for comparing population dynamics (Bradshaw 1972, p. 25; Lawton 1988). As deduced above, studies comparing marine and terrestrial organisms in similar physical situations most reasonably should compare organisms in pelagic and aerial habitats, or should compare organisms that comprise marine benthos with those constrained to the land. For consistency, such comparisons would benefit from considering organisms that experience similar flow environments and similar colours of environmental variation. Comparisons meeting these criteria include those pairing pelagic and aerial nekton, pelagic and aerial plankton or benthic and land organisms over multi-decadal and greater, i.e. micro- to macroevolutionary, time scales.

The unexpectedly similar evolutionarily averaged dispersal distances of land and marine 'plants' (figure 4) strongly suggests that this approach has merit. This suggestion is supported by the similar evolutionarily averaged dispersal distances of land and marine 'herbivores' (phytophagous insects, median$\approx$40–60 km; benthic invertebrates, median$\approx$21 km;

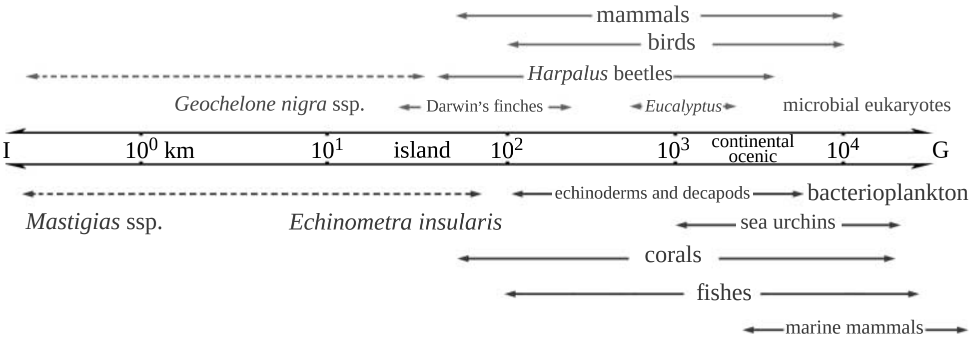

Figure 5. Insular to global species ranges in terrestrial and marine taxa. Simplified schematic showing considerable overlap in the geographical ranges, from insular (I) to global (G; approximate maximum linear extent) of some terrestrial (upper, light grey) and marine (lower, dark grey) taxa, including examples of some of the most narrowly and widely distributed taxa. *Harpalus* (Noonan 1990), *Eucalyptus* (Edwards & Westoby 1996), mammals and birds (Brown *et al.* 1996; von Hippel 2001), *Geochelone nigra* ssp. (Galapagos tortoise; see http://library.sandiegozoo.org/FactSheets/tortoise_galapagos/tortoise_map.htm), echinoderms and decapods (O'Hara & Poore 2000), sea urchins (Emlet 1995), corals (Veron 2000), some whales (e.g. blue, humpback; see: http://www.jncc.gov.uk/Publications/cetaceanatlas/) and fishes (e.g. from 1°-endemic species to albacore, bigeye and yellowfin tunas; see: http://kosfic.yosu.ac.kr/kos_home/ocean_gis/FAO/mapbrief.html). Dashed lines represent, by inference, population ranges, although some populations will have larger distributions. Island, continental and oceanic scales are indicated approximately. The figure is intended to be demonstrative rather than comprehensive.

Kinlan & Gaines 2003; figure 4) and by similar geographical ranges of marine (benthic and pelagic) and terrestrial (land and aerial) taxa, which range from extremely narrowly distributed insular biotas to globally distributed species irrespective of realm (figure 5). Even at this level, however, the diversity of organisms and situations is large and the factors contributing to variance potentially are numerous and difficult to parse. More clear examples are required. The best examples may come from the two biogeographic extremes that have only become available for comparison in the last few years. The first concerns the genetic structure of aerial and marine micro-organisms (i.e. organisms with mass less than 10^{-5} g and length less than 500 μm; Martiny *et al.* 2006) on global scales; the second concerns evolution in terrestrial and marine islands. We discuss these in the next two subsections.

3.4.1. The biogeography of micro-organisms. Traditionally, the marine plankton has been considered to have no terrestrial analogue. Without question, marine plankton are far more numerous, often much larger and phyletically more diverse than plankton in other fluids. However, there is also abundant cellular material in the atmosphere, including pollen, spores, bacteria, algae (including marine plankton), fungi and viruses ranging in size from tens of nanometres to millimetres (Jaenicke 2005; see also Wilkinson 2001). The microbial portion of this aerial plankton experiences a fluid environment very similar to the fluid environment of marine microbes. For example, an aerial microeukaryote of diameter 6 μm (Finlay 2002) has $Re=3.2\times10^{-4}$ and $U=1.3\times10^{-4}$; a marine heterotrophic flagellate nanoplankter of diameter 18 μm (Lenz 2000) has $Re=2.1\times\ 10^{-3}$ and $U=1.8\times\ 10^{-4}$ (at 20°C, 1 atm, assuming density of microbes is 1030 kg m^{-3} (giving a 12 μm organism the 1 ng mass typical of microeukaryotes; Finlay 2002), U is calculated using Stokes equation). Thus, in terms of fluid dynamics, aerial microbiota may be a close analogue of the marine microbial plankton. Hypothetically, given a suite of simplifying assumptions (such as physically similar large-scale environmental variation on relevant time scales; see figure 3), a variety of aerial and marine microbes should have similar dispersal abilities, realized dispersal distances and gene flow and geographical ranges (figures 5 and 6).

Evidence on dispersal and biogeographic patterns in aerial and marine microbes is somewhat sparse, due in part to limited geographical sampling of typically widely distributed taxa and the varied import given to DNA analyses versus phenotypes in inferences of species entities (Dolan 2005; Fenchel 2005; Mitchell & Meisterfeld 2005; Esteban *et al.* 2007). The initial picture is that marine bacterioplankton are very widely dispersed but not ubiquitous. Ribotypes often have global distributions that segregate along broad climatic bands (Baldwin *et al.* 2005; Pommier *et al.* 2005; Follows *et al.* 2007) or ecologically relevant depth strata (DeLong *et al.* 2006). Cosmopolitanism appears as an occasional trait (Pommier *et al.* 2005), presumably in species with very wide ecological tolerances. Terrestrial bacteria dispersed aerially show analogous patterns of distant but not ubiquitous dispersal (e.g. Isard *et al.* 2005; Prospero *et al.* 2005; Kellog & Griffin 2006) and compositionally similar soil bacterial communities clustered in similar soils regardless of geographical distance (e.g. arid or semi-arid ecosystems versus temperate–tropical forests; Fierer & Jackson 2006) such that 'distance–decay' patterns indicate non-cosmopolitan distributions due predominantly to environmental heterogeneity (Green & Bohannan 2006). Molecular data indicate that marine and terrestrial bacteriophages also show frequent continental scale migration (Breitbart *et al.* 2004; Silander *et al.* 2005) and while some genotypes or taxa may occur in multiple environments (Breitbart *et al.* 2004), the occurrence of at least some others appears to be determined by selection (Silander *et al.* 2005; see also Teira *et al.* 2006*a*,*b*). Generally, these results are

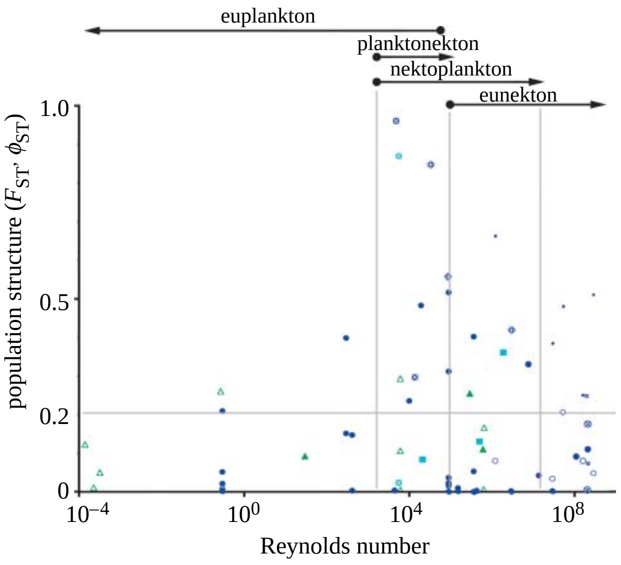

Figure 6. Relationship between Reynolds number (*Re*) and population subdivision (F_{ST} or ϕ_{ST}) for some marine (dark blue circles), freshwater (light blue squares) and terrestrial (green triangles) organisms. Organisms with very small *Re*, such as marine and aerial microplankton, are unable to influence fluid dispersal and are expected to have high gene flow (low F_{ST} and ϕ_{ST}) and very large geographical ranges. Organisms with very large *Re*, such as marine mammals and large birds, have locomotory abilities that far exceed the influence of fluid dispersal and are also expected to have high gene flow and very large geographical ranges. These taxa with potentially high dispersal typically have F_{ST} or ϕ_{ST} less than 0.2 (see light grey horizontal line), indicating at least one successful migrant per generation, i.e. sufficient in theory to prevent geographical differentiation. Organisms with intermediate *Re*, such as large insects, small birds and many reef fishes, are often able to avoid passive fluid dispersal but unable to move very large distances due to biomechanical or energetic restrictions; they are expected to have various degrees of connectivity and range-sizes, including many instances of low gene flow (high F_{ST} and ϕ_{ST}). The light grey vertical lines delimit the different classes of motility identified by Aleyev (1977). Differences in population subdivision between organisms with similar *Re* may indicate the influences of behaviour, life history, physical discontinuities (environmental filters), chance and other events on gene flow. Solid symbols, mitochondrial DNA; open symbols, nuclear DNA. Note that estimates of gene flow in marine mammals based on analyses of mitochondrial DNA (small solid circles) are inflated relative to those based on nuclear DNA due to female social structure (e.g. Bérubé *et al.* 1998; Burg *et al.* 1999; Durand *et al.* 2005). Pairs of crossed squares and circles with the same or similar *Re* highlight examples in which physical isolation or environmental filters contribute to high population subdivision (Bérubé *et al.* 1998; Dawson *et al.* 2002; Dawson & Hamner 2005). Crossed diamonds show examples in which life histories, in these cases vivipary or brooding or adult migration, contribute to high population subdivision (Bernardi 2000; Planes *et al.* 2001; Bowen *et al.* 2005).

consistent with the adage, for both marine and terrestrial microbes, that potentially ‘everything is everywhere …’ so particular distribution patterns occur because ‘… the environment selects’ what species are found where (Baas Becking 1934, cited in Fenchel (2005); Lowe *et al.* (2005) and Finlay (2002)), but so little is known about bacterial distributions that consistency with one hypothesis is far from support for that hypothesized mechanism to the exclusion of all others (Green & Bohannan 2006; Sogin *et al.* 2006; Telford *et al.* 2006, 2007; Pither 2007).

Large-scale dispersal and small-scale heterogeneity, rather than regional or global trends, may dominate the geographical occurrence of microbes, but a wide variety of dispersal scenarios and geographies are expected owing to differences in the sizes of microeukaryotes, the vagaries of dispersal mechanisms and distribution of habitats (Wilkinson 2001; Šlapeta *et al.* 2006). Thus, molecular analyses of marine foraminifera evince not only regional affinities consistent with physical or ecological limits to gene flow (Darling *et al.* 2007) but also long-distance dispersal (e.g. Darling *et al.* 2000; Esteban *et al.* 2007; see also Brown & Hovmøller 2002). Most studies to date suggest that neither marine nor soil bacteria show the latitudinal diversity gradient (Baldwin *et al.* 2005; Fierer & Jackson 2006), but there are recent exceptions (Pommier *et al.* 2007) which may be common among larger microbes (e.g. tintinnids; Dolan *et al.* 2006; see Finlay 2002); indeed, organisms with large, but subhemispheric, ranges are expected to show strong broad peaks in latitudinal diversity under the mid-domain model, with patterns of local species richness being modified by small-scale environmental heterogeneity (Colwell *et al.* 2004, 2005). Both aquatic and soil bacteria apparently deviate from island biogeographic theory (*sensu* MacArthur & Wilson 1967) because diversity patterns are inconsistent with distance–colonization predictions (e.g. Fierer & Jackson 2006; see discussion in Green & Bohannan 2006). Typically, small *z*-values (0.03–0.16; Reche *et al.* 2005; Fierer & Jackson 2006) for species–area curves suggest molecular studies of microbes, surveying patterns over large geographical scales generated on multi-generational time scales, have sampled ‘fragments’ within contiguous habitat in a single, or few, very large ‘mainlands’ (Fenchel & Finlay 2005). However, exceptions exist on surprisingly small spatial scales in aquatic (less than 180 l) and terrestrial (less than 100 m^2) ‘islands’ that are in very close proximity (centimetres to tens of metres) to each other ($0.25 \leq z \leq 0.47$; Bell *et al.* 2005; Noguez *et al.* 2005; van der Gast *et al.* 2005).

3.4.2. Islands.

The dichotomy between studies of the geography of evolution in terrestrial and marine systems is epitomized by the contrasting roles of islands. For over 150 years, islands have been central to evolutionary biology, ecology and conservation in diverse terrestrial and freshwater ecosystems from mountain tops to ancient lakes (e.g. Darwin 1859; Lack 1947; MacArthur & Wilson 1967; Grant 1998), but comparable studies of insular marine systems are relatively rare (see Whittaker 2006).

The relative dearth of island studies in the marine environment is a consequence of the historical characterization of ocean environments and their resident populations as few, large and homogenous, which is inconsistent with an island perspective. Also, early investigations of species diversity on a variety of marine islands (e.g. Schoener 1974*a*, *b*, 1978; Connell 1978; Smith 1979; Bohnsack & Talbot 1980; Thomson & Gilligan 1983; Anderson 1998) were inconclusive about (e.g. Schoener 1974*a*,*b*; Smith 1979), or contrary to (e.g. Connell 1978; Schoener *et al.* 1978), island biogeography theory. Commensurately, oceanic islands which so clearly differed in terrestrial biota were found to have comparatively much more similar marine biotas. For example, endemism in freshwater/terrestrial taxa in Hawaii averages 48% and in some groups can be as high as approximately 95%, but in marine taxa averages only 10.6% and is only 23% in reef and shore fishes (Sterrer 1998; Randall 1998; see also Wagner & Funk 1995; Paulay & Meyer 2002; Drew & Roderick 2005). Thus, although some studies found some evidence consistent with some predictions of island biogeographic theory (e.g. Schoener 1974*a*,*b*; Dauer & Simon 1976; Molles 1978), the concept of ecological and evolutionary islands appeared to be of little consequence to marine biologists (Knowlton & Jackson 1994; see absence of discussion from Nybakken (1997) and Castro & Huber (2003); cf. treatment in Ricklefs & Miller (1999), Krebs (2001), and Krohne (2001)). However, few of the early studies actually supported this viewpoint because they often deviated from the assumptions of island biogeography (e.g. Schoener 1974*a*,*b*; Smith & Rule 2002) or made comparisons across inappropriate scales (e.g. Thomson & Gilligan 2002) and were therefore not relevant tests of the theory.

The growth of molecular biology, satellite oceanography and chemical tagging methods (among other technologies) since the early 1990s has provided alternative perspectives. Studies applying these techniques have often emphasized abundant cryptic taxa (Knowlton 1993, 2000; Goetze 2003; Dawson 2004; Fukami *et al.* 2004), considerable oceanographic structure with ecological and evolutionary consequences (Longhurst 1998; Sotka *et al.* 2004; Hare *et al.* 2005), interacting biological and physical restrictions on dispersal (Dawson *et al.* 2005; Cowen *et al.* 2006), a high percentage of self-recruitment (Swearer *et al.* 1999; Cowen *et al.* 2000; Jones *et al.* 2005) and strong phylogeographic structure on scales of tens of meters to tens of kilometres (Taylor & Hellberg 2003; Dawson & Hamner 2005). Re-evaluating all available data leads to the conclusion that a variety of processes, acting at various spatial and temporal scales, influence modern patterns of marine biogeography (see also Rosenblatt 1963).

Several studies now have described marine patterns broadly consistent with island biogeography and island evolution (e.g. species–area and diversity–distance relationships (Bellwood & Hughes 2001), founder events (Paulay & Meyer 2002; Meyer *et al.* 2005), and disproportionately many average-sized species (Robertson 2001; see also Rosenblatt 1963; cf. Foster 1964) on Pacific islands). However, these often have limited implications for the existence of marine islands because, like their predecessors, few have explicitly tested the assumptions and predictions of relevant island theory and many acknowledge limitations on available data for adequate tests (e.g. Hubbell 1997; Bellwood & Hughes 2001). A good opportunity for comparing and contrasting island biogeography in familiar marine settings with terrestrial settings is provided by the islands of Oceania because the geographical matrix for terrestrial and shallow-water benthic marine organisms are the same (Paulay & Meyer 2002) but, as for other comparisons, it is essential that islands be defined in terms of the organisms being considered. Available data indicate that land masses surrounded by seawater within archipelagos are often islands from the perspective of terrestrial organisms but not from the perspective of marine organisms (Paulay & Meyer 2002).

To date, the most clear examples of island ecology and evolution in marine systems come from marine lakes: bodies of seawater entirely surrounded by land. These systems clearly are marine habitat islands and meet the assumptions of island biogeographic theory (Dawson & Hamner 2005). Patterns of molecular diversity in *Mastigias* jellyfish populations isolated in these marine lakes (Dawson & Hamner 2005) are consistent with the predicted genetic consequences of island biogeography (Johnson *et al.* 2000). Preliminary surveys of macroinvertebrates reveal the predicted (MacArthur & Wilson 1967) positive correlation of species diversity with area and negative correlation of species diversity with colonization distance (M. N Dawson, L. E. Martin & L. J. Bell 2003–2006, unpublished data). Moreover, *Mastigias* populations in five different lakes each represent different subspecies due to divergent morphologic evolution within 5000–15 000 years from a common ancestor in the surrounding lagoon (i.e. mainland) that has retained essentially the same morphology for several millions of years (M. N Dawson & N. Hanzawa 2006, unpublished data) consistent with the pattern of punctuated equilibrium proposed to typify evolution in peripheral environments (Mayr 1963; Gould & Eldredge 1974). Marine lakes also are meritorious because they capture mixed marine and atmospheric signatures (Martin *et al.* 2005) providing a link between oceans, semi-enclosed lagoons and coastal terrestrial systems that typically are expected to show different amplitudes and colours of physical and biological variation.

Importantly, marine lakes, which have a small subset of the regional marine biota (e.g. Hamner & Hamner 1998; M. N Dawson, L. E. Martin & L. J. Bell, unpublished data) plus endemics (e.g. Fautin & Fitt 1991; Dawson 2005*a*), are geographically widespread and occur in clusters analogous to terrestrial archipelagos. Marine lakes are, like oceanic islands, ‘simpler microcosm[s] of the seemingly infinite complexity of continental and oceanic biogeography … [which] provide the necessary replications in natural ‘experiments’ by which evolutionary hypotheses can be tested’ (MacArthur & Wilson 1967; see also Hamner 1982).

3.5. Marine macroplankton

By identifying situations that are comparable, we sidestepped the issue of the ‘[macrop]elagic species … with high rates of adult migration’ (Kinlan & Gaines 2003) such as gelatinous zooplankton. If we now consider these, do they cause a problem for the biophysical framework? No. Scyphozoa are included in figures 2 and 6 (Aleyev 1977; Dawson & Hamner 2003, 2005). Mayr’s (1954) analyses, recent genetic results (e.g. Dawson 2005*b*,*c*), and ocean modelling (Dawson *et al.* 2005) indicate considerable geographical isolation and cryptic speciation in these organisms. Moreover, of the few gelatinous zooplankton compared to date, holoplankton, which should have higher dispersal than meroplankton, does tend to have less phylogeographic structure than meroplankton (Dawson 2004).

Yet, it has been suggested that even some holoplankton experience habitat islands in the form of ocean gyres (Goetze 2005). However, high dispersal over long distances within gyres (200–9100 km), large effective population sizes (10^8–10^9) and ecological separation of these species of copepods (Goetze 2005) indicates that such gyre-wide populations are better interpreted as mainland, rather than island, populations (see also Rosenzweig 1995, pp. 211–212). This alternative interpretation could be tested; diversity–area relationships in fragments of mainlands differ in z-value from those of islands (Rosenzweig 1995, p. 8) providing a method for objectively identifying and defining islands from the biophysical perspective.

4. DISCUSSION

Marine and terrestrial systems have historically been considered fundamentally different. However, this conclusion is poorly substantiated due to methodological and conceptual inadequacies underlying many contrasts. The historical dichotomy between marine and terrestrial systems has been strongly influenced by our perceptions of the systems, perceptions that were reinforced by qualitative investigations which ignored or conflated potentially important considerations, such as sources of within- versus between-realm variation. The dearth of quantitative comparisons and theory is a long-standing deficiency recognized by Steele (1995, pp. 15 and 16), who wondered if there would be ‘methods and theories that can apply to [different realms]’ and ‘a set of case studies from marine, freshwater, and terrestrial environments that provide the basis for comparisons’.

4.1. Methods and questions that apply to both realms

Despite long histories of collecting different data in marine and terrestrial systems (Stenseth *et al.* 2005), many methods can now be applied, or have parallel approaches, in both realms. For example, aggregation and migration of aerial ‘meroplankton’ (e.g. insects) and ‘nekton’ (e.g. birds) are studied using radar (Drake & Farrow 1989; Westbrook & Isard 1999), while studies of their marine analogues now use acoustics (e.g. Bertrand *et al.* 2003; Holliday *et al.* 2003; Brierley *et al.* 2005). Similar approaches for tracking individual movements and environmental conditions are applied in both realms (e.g. isotope analyses (Bearhop *et al.* 2005; Jones *et al.* 2005); telemetry (Stenseth *et al.* 2005); satellite imagery (Longhurst 1998; Gage *et al.* 1999)) and a panoply of molecular methods yield exactly the same types of data that are easily compared across realms (e.g. Kinlan & Gaines 2003). Analytical approaches in, for example, biogeography are equally applicable to data from marine and terrestrial systems (e.g. Marshall & Liebherr 2000; Santini & Winterbottom 2002; Wojcicki & Brooks 2005; but see Siddall 2005), and the coupled biophysical models increasingly employed to study dispersal of marine larvae (e.g. Cowen *et al.* 2000, 2006; Dawson *et al.* 2005; Galindo *et al.* 2006) can be expected to promote similar approaches to studying aerial dispersal (e.g. Gage *et al.* 1999). Here, we have demonstrated that fluid mechanics is a fruitful approach for studying dispersal and the geography of evolution in both marine and terrestrial realms.

Similarly, although historically a broad array of questions has been asked independently of both marine and terrestrial systems (Stergiou & Browman 2005), the long-standing enigma of the geographical mode and tempo of evolution touched on in this paper can now be addressed in both realms within a single framework. This beginning synthesis emphasizes that differences between marine and terrestrial systems in terms of dispersal distances, species’ ranges and modes and rates of evolution and speciation (figures 4 and 5) are differences in degree or frequency as opposed to categorical differences between realms.

As evidence accrues that evolution can happen on much smaller scales in marine systems than commonly thought (e.g. Taylor & Hellberg 2003; Dawson & Hamner 2005) due to environmental heterogeneity (Gilg & Hilbish 2003; Sotka *et al.* 2004; Hare *et al.* 2005) a synthesis for marine and terrestrial systems seems increasingly tangible. Such a synthesis will necessarily consider a wide diversity of species and situations (e.g. Palumbi 1992; Bernasconi *et al.* 2004) and will benefit from an explicitly formulated initiative in macroecology (*sensu* Brown 1995), an approach that has been underused in marine systems and marine–terrestrial comparisons (Rafaelli *et al.* 2005). In the meantime, well-chosen case studies including the extremes will indicate the realm of possible outcomes for the remaining majority of species on the planet.

We have identified two case studies—global microplankton and island species—that provide bases for direct comparisons of marine, freshwater and terrestrial taxa. Of these, the study of island species is likely to be most profitable in the near-term because studies of small ecosystems with well-delineated boundaries and fluxes are logistically more simple than global studies of marine and aerial plankton. There is already a wealth of data and theory describing diversity and evolution on terrestrial islands, the outstanding requirement is only for collection of more data describing evolution in unambiguous marine islands, such as brackish marine lakes (Dawson & Hamner 2003, 2005; Dawson 2006) and probably the most remote oceanic islands (e.g. Robertson 2001).

4.2. Unified solutions?

Establishing a quantitative and theoretical comparative framework for dispersal and the geography of evolution in marine and terrestrial systems has important practical applications. Historically, owing to perceived fundamental differences between the realms, applying terrestrial conservation approaches to marine systems has been considered problematic (Angel 1993; Steele 1995; Secord 2003). Identifying shared patterns and processes will therefore underwrite the modern practice of considering marine protected areas (MPAs) and MPA networks as analogues of terrestrial parks and corridors (e.g. Carr *et al.* 2003) and will benefit integrated conservation strategies (Stoms *et al.* 2005). Better understanding of factors that influence connectivity in aerial and marine plankton may lead to shared approaches (e.g. Carter & Prince 1981; Harvell *et al.* 2004; McCallum *et al.* 2004) that inform efforts to curb taxa that spread disease and blight crops on land (e.g. Drake & Farrow 1988; Brown & Hovmøller 2002) as well as efforts to maintain the larval dispersal that replenishes stocks of food organisms and essential biological components of ecosystems in the seas (e.g. Steneck 2006). Ultimately, the value of better integrating marine and terrestrial studies, either generally or in a specific instance, will be demonstrated or refuted by whether integration provides useful new perspectives and resolves old controversies and whether there is a broad or narrow adoption of the approach.

5. CLOSING REMARKS

We have described a biophysical framework for comparing dispersal and the geography of evolution in marine and terrestrial systems. Our goal has been to illustrate the merits of quantitative and theoretically justified comparisons, a point that can be illustrated by considering a cliché: one supposedly should not compare ‘apples and oranges’, yet when considered as two examples of fruits of flowering plants, they clearly share many attributes whose states merely differ. We have provided examples that demonstrate similarities between some marine and terrestrial systems. We believe other similarities will be discovered using this approach. Importantly, the approach also provides a conceptual framework for objectively investigating differences between marine and terrestrial (and freshwater) taxa, as well as among marine taxa and among terrestrial taxa.

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