

On a landscape ecology of a harlequin environment: the marine landscape

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The marine ‘landscape’, like its terrestrial counterpart, is characterized by a mosaic of resource and environmental patches, that is, a “harlequin environment” (sensu Horn and MacArthur 1972), created by, and embedded in, a matrix of otherwise relatively homogeneous conditions (Levin and Whitfield 1994). The notion of patchiness and heterogeneity in marine landscapes is well known at a range of spatial–temporal scales (Stommel 1963; Longhurst 2006). This notwithstanding, just how the multi-dimensional spatial structure of physical and biological forcing agents in marine environments (e.g., fronts, currents, eddies, prey patches) affect biota and influence key ecological processes lags behind that known for terrestrial environments. The general aim of this paper makes a case for more widespread application of the principles and concepts of landscape ecology to ecological studies of coastal, benthic and, pelagic systems, the latter of which has been especially slow or reluctant to consider the paradigm of landscape ecology. Landscape ecology is fundamentally an interdisciplinary science of heterogeneity (Wu and Hobbs 2002; Wu 2006). Issues of scale, heterogeneity,

patchiness and connectivity are widespread in these systems thus making a landscape ecology perspective germane to their study and management. I also argue that we need to overcome more general impediments between marine and terrestrial ecology insofar as sharing of empirical information, methodologies and theory if landscape ecology is to make greater inroads into the marine realm.

Patchiness and structure in the marine landscape

A range of biological, bathymetric, and hydrographic processes acting singly and in concert over time and space create marine patchiness. Abiotic features include, but are not limited to, salinity (Longhurst 2006), sea temperatures (Rayner et al. 2003), thermal refugia (Rose and Leggett 1990), upwelling of nutrients (Martin et al. 2002), and formation of hydrographic fronts (Longhurst 2006). Biotic influences extend from patchy predator–prey interactions such as cod (*Gadus morhua*) and capelin (*Mallotus villosus*) (Ciannelli and Bailey 2005) to patchiness in a range of marine organisms such as plankton (Steele 1989), sea grasses (Bell et al. 2008), kelp (Dayton et al. 1999), corals (Rowan et al. 1997), foraging behaviour in petrels and albatrosses (Pinaud and Weimerskirch 2007), squid (Weimerskirch et al. 2005), pelagic herring (Maravelias et al. 2000), larval fish (Frank et al. 1993), spawning distribution of walleye pollock

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(*Theragra chalcogramma*) (Bacheler et al. 2009), and intertidal algae (Underwood 1998). Largely missing, however, from many such studies is that patches are typically nested within larger-scale patches, forming nested patch hierarchies (Wu and Loucks 1995).

A fundamental aspect of life in this hierarchical patchwork of fluid media is that a great many marine organisms move along a hydraulic network (Pringle et al. 2009). Other organisms, such as highly migratory fish species (e.g., tuna) and marine mammals, may move counter to such flows, yet are directly or indirectly affected by varying connectedness in flow patterns. This fluid medium and its physical properties (e.g., temperature, current velocity, and salinity) govern primary productivity and the amount of energy available to higher trophic levels. In consequence, the transport of heat, mass, and momentum has tremendous significance for patch structure and the spatial characteristics of these patches in a larger ocean context. Stommel (1963), in his seminal work on scale in oceans, stressed the need for the ocean to be investigated geographically and hydrodynamically, noting that, by virtue of its vastness, there are critical discontinuities in space.

The paradigm of landscape ecology in a marine context

The paradigm of landscape ecology has made some inroads into the study of coastal systems (Bell et al. 2008; Hinchey et al. 2008; Pittman et al. 2011), but is poorly known for marine organisms and processes in pelagic systems (Moore et al. 2010). This is true despite that spatial and temporal discontinuities in energy and matter, which are characteristic of this fluid medium, are major drivers of biotic patterning (Legendre and Demers 1984). That is, they are only different in kind from those found in terrestrial landscapes. Hence, there is no compelling reason to suppose that the notion of “landscape” is confined to terrestrial landscapes. Several studies of intertidal and subtidal environments have explicitly adopted the central tenets of landscape ecology (e.g., Vidondo et al. 1997; Orr et al. 2005; Zajac 2008). For example, Orr et al. (2005) documented the complexities of input and accumulation of algal wrack, as spatial subsidies, on beaches as a function of factors such nearshore hydrodynamics and beach structure.

Arguably, sharing of the constructs between these researchers and terrestrial landscape ecologists occurs because these marine habitats have structural characteristics similar to terrestrial landscapes. For example, patches of organisms or habitat (e.g., mussel beds, meadows, coral reefs) in marine benthic landscapes are relatively easy to distinguish and often fixed in space (Paine and Levin 1981; Vidondo et al. 1997; Teixidó et al. 2002). Further, like terrestrial patches, marine patches that are seemingly fixed are subject to change over time owing to a variety of biological and physical forcings (e.g., fragmentation).

Beyond these coastal zone examples, a relatively small handful of studies have shown how landscape ecology extends beyond the benthos and into the water column. For example, Moore et al. (2010) found that depth and six landscape metrics helped predict demersal fish assemblage structure and spatial distribution. Ciannelli and Bailey (2005) used a landscape ecology approach to understand the link between landscape dynamics, climate forcing, and ecological interactions between cod and capelin in the Bering Sea. Mitchell et al. (2008) described complex spatial arrangements of phytoplankton using a landscape ecology approach. Pittman et al. (2004) used a landscape ecology perspective linking fish and prawns to their environment. Fauchald (2009) invoked the pattern-process dynamic in suggesting seabird-prey interactions should be viewed as a reciprocal spatial game where seabirds track prey density while prey evade predation by moving away from areas of high risk. Schick and Urban (2000) noted that, despite a terrestrial bias, the techniques of landscape ecology are germane to marine applications, and demonstrated this in an analysis of the spatial components of bowhead whale (*Balaena mysticetus*) distributions. Berger and Jelinski (2008) examined spatial patterns in maternal investment in red sea urchins (*Strongylocentrotus franciscanus*) along a near-shore marine terrestrial gradient. Stable isotope data show a winter shift in increasing amounts of refractory terrestrial detritus to mysid (order Mysida) diets in coastal British Columbia, Canada (Mulkins et al. 2002). Lastly, Treml et al. (2008) used a landscape ecology perspective for exploring connectivity of coral larvae and juveniles between distant patches via the use of a Eulerian advection–diffusion approach.

From an applied conservation perspective, Botsford et al. (2003) argued that models for marine protected

areas (MPAs) should adopt the principles of landscape ecology. Lipcius et al. (2005) made a case for incorporating landscape-driven metapopulation structures in marine protected area design and management. Similarly, Ciannelli et al. (2008) maintained that the identification of high quality habitat and the establishment of MPAs is significantly dependent on an understanding of fisheries spatial ecology. Gröber-Dunsmore et al. (2009) argued that landscape ecology provides a well-developed conceptual and operational framework for addressing issues of connecting among MPAs in terms of behaviour, growth, survival, and the spatial distribution of constituent species. The fundamental argument is that connectivity is a function of habitat area, quality and spatial arrangement, and the dispersal capabilities of individual species, which is central to terrestrial landscapes (Forman 1995).

Landscapes and seascapes: So where's the problem?

Notwithstanding the above examples where landscape ecology has permeated marine research, there is general absence of a landscape ecology perspective, especially in the pelagic realm. To some degree this is somewhat perplexing, as freshwater ecologists have been significantly influenced by Wiens (2002) and Poole (2002) insofar as viewing riverine landscapes from a landscape ecology viewpoint. Why might this be? First, the term “landscape” may insert a mental block because we tend to think of “landscape” as a terrestrial unit. Troll (1939) first coined the scientific term landscape ecology (landschaftsökologie) as “the study of the main complex of causal relationships between the life communities and their environment” that “are expressed regionally in a definite distribution pattern.” In other words, his focus was on “the land.” However, in a modern-day landscape ecology view, a landscape is often defined simply as an area that is spatially heterogeneous in at least one factor of interest, scaled relative to the organism (including its perception of the landscape, or its *umvelt*) or landscape process of interest (Forman 1995). Thus, a marine landscape may range in size from a few square metres, say that of a mature seastar, to hundreds of square kilometres for wide-ranging seabirds, dolphins, or tuna. Similarly, from a process view, Langmuir cells may be as fine-scaled as 4–6 m in depth and spaced

10–50 metres apart, whereas larger scale Ekman spirals are characterized by net water movement through a depth of 100–150 m (McWilliams et al. 1997). At even coarser scales, meso-scale fronts, for example, are typically between 10 and 100 kms long (Longhurst 2006). Correspondingly, many organisms, such as schooling fish and foraging seabirds, can be viewed as having a hierarchical patch structure (sensu Wu and Loucks 1995) in which high-density, small-scale patches are nested within low-density, large-scale patches (Fauchald 2009). Fauchald and Tveraa (2006) found that foraging patterns in Antarctic petrels (*Thalassoica antarctica*) was based on a spatially nested search strategy to locate coarse-scale patchiness in prey and then concentrate their search at finer spatial scales. Ciannelli et al. (2010) analyzed the vertical and horizontal distribution of Atlantic cod (*Gadus morhua*) eggs in relation to small-scale circulation and water column hydrography in a Norwegian fjord. They discovered that cod eggs were found in greater abundance (1) in shallow water layers and (2) in the inner portion of the fjord. In this spatial structure, eggs were found to be neutrally buoyant at shallow depths.

This brings me to the point that similarities between marine and terrestrial landscapes are particularly pronounced where properties of pelagic systems often derive from features that are geographically fixed or predictable. This includes physical features such as seamounts and certain bathymetric features, as well as geographically fixed biological units such as mangroves or salt marshes, or relatively sedentary species such as orange roughy (*Hoplostethus atlanticus*), flounder (*Platichthys flesus* L.), and coral reef fishes (Ciannelli and Bailey 2005). Technological advances in remote sensing and GPS are aiding in quantifying seascape structure (Moore et al. 2010).

However, as already noted, marine landscapes also have labile components (e.g., hydrography), and here terrestrial and marine landscapes *seemingly* diverge in major ways. For example, distributions of pelagic species are largely dictated by the intricacies of water flow, and by the coupling of physical and biological processes that promote the growth of planktonic populations (Steele 1991). Accordingly, the dynamic nature of pelagic systems and the prevalence of variability over large scales blurs the linkages between physical and biological processes, and spreads biotic interactions over spatial scales that greatly exceed those common to terrestrial systems (Steele 1989;

Block et al. 2011). Nevertheless, this is a scale issue, and it is the assertion in this paper that the same principles should hold true in terms of spatial patterns having manifold effects on ecological processes, irrespective of marine versus terrestrial system.

Another possible reason for the lack of penetration of landscape ecology into marine systems may result from those who consider the open ocean as a relatively homogenous and structurally simple environment relative to terrestrial systems (Brown 1980). This view holds that, while oceanographic fronts create discrete and fine-scale patches of temperature, salinity and biomass often change over the scale of hundreds to thousands of kilometres (Bost et al. 2009). Related is the perceptual constraint that much of the ocean dynamic is hidden from our view (Carlton 1998). Thus, there may be a tendency to assess marine-related phenomena in the context of human-scale perceptions, such that investigators tend to smooth over small-scale variation and pay little attention to short-term dynamics in their search to find constancy beyond the perceptual scale of a single human investigator. In essence, while human-scaled studies may reveal emergent properties and general patterns, these properties and patterns happen to manifest themselves at a scale coincident with the human scale. Further, Moore et al. (2010), among others, pointed out our perception of ocean is constrained by our ability to measure it, which is much different from terrestrial systems that we can visually see and, therefore, have an intuitive sense of the accuracy of our measurements. Stenseth et al. (2005) commented on differences between marine and terrestrial ecology and the role of perception thusly: “The world is also perceived differently from a ship struggling through the white waves of the Northern Atlantic than from under a spruce tree in the deep forest.” Similarly, Underwood (301:2005) remarked that terrestrial ecologists “... can actually see (or hear) [their study organisms] in nature, in groups, in real time or space. That is rarely true for ecologists studying fish or marine benthic invertebrates because of the opacity of the medium. Even when they can be seen it is for very short periods over very small time scales.”

Other impediments

There may be other, larger issues in biology that constrain application of landscape ecology thinking to

oceanography. First, whereas the study of variation is at the core of biology, typological thinking has long dominated much of biology (Mayr 1988), and hence Roitberg and Mangel (1997) argued that, mistakenly, we often perceive organismal responses to the environment as being fixed and stereotypical. This approach supports the optimization paradigm in ecology (Cody 1974; Gould and Lewontin 1979). Furthermore, moving beyond species, the ecosystem concept itself, while dating back some 80 years as a highly useful construct in terrestrial ecology, has not been as widely accepted in oceanographic systems given the openness of many marine ecosystem boundaries (Ciannelli et al. 2004). However, as articulated by O’Neill (2001), the concept of relative boundedness of ecosystems is simply a way to understand the controls on the dynamics of ecosystems. Furthermore, Cole (2005) noted that the problem of ecosystem definition for the open ocean is not necessarily as intractable as it may seem, using, for instance, geochemical mass balances as a way of understanding processes in marine ecosystems. In a similar approach, Ciannelli et al. (2004) applied ecosystem energetics and foraging theory to characterize the spatial extent of the Pribilof Archipelago ecosystem.

Conclusion

Steele (1989) was among the first to think about the “ocean landscape” from a landscape ecology perspective. Two years later, Steele (1991) argued for integration of marine and terrestrial theory and practice noting that, heretofore, they operated quite separately in that it was held “there was little relation between the studies in these two subdisciplines.” Cole (2005) built on this notion stating “... there are gaps between terrestrial, marine and freshwater ecology” for which “the bridges are fettered with obstacles.” He further commented that the “communication has not always been harmonious or even polite....” Almost 25 years post-Steele’s pleas, Webb (2012) similarly argued that “. . . marine and terrestrial ecology have developed largely as separate intellectual endeavours . . .” and “. . . the binary ‘marine-terrestrial’ misses many opportunities....” Rotjan and Idjadi (2013) made the case that while cross-systems ecology is lauded, it is seldom implemented. The need for cross-fertilization in terms of more and better exchange of empirical

findings and theory between terrestrial and marine ecologists seems largely unheeded. This paper adds to the halcyon call for greater integration, and that the paradigm of landscape ecology has a deserved place in the study and management of a broad range of marine landscapes.

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