Seascape ecology:

A new science for the spatial information age

s society undergoes a spatial data revolution fuelled by the rapid development of online maps, satellite navigation systems and geo-portals, a transformative shift is also underway in marine ecology. A new breed of marine ecologist, known as seascape ecologists, are bringing enhanced spatial awareness to ecological thinking, together with the tools to work with 'big data' and a desire to ask new types of applied research questions.

The latest generation of remote sensing data from water, air- and space-based platforms reveal unimaginable and intriguing structural complexity in our oceans. Yet, despite our best efforts to acquire and make accessible vast datasets that capture in detail the multidimensional patterning of the oceans, we still know surprisingly little about the ecological consequences of spatial patterning.

What is seascape ecology?

Seascape ecology deals with the causes and ecological consequences of spatial pattern in the marine environment, drawing heavily on conceptual and analytical frameworks developed in terrestrial landscape ecology. Seascape ecologists are interested in the spatially explicit geometry of patterns and the relationships between pattern, ecological processes and environmental change. A central tenet in landscape ecology is that patch context matters, where local conditions are influenced by attributes of the surroundings. instance, the physical arrangement of objects in space, and Visually captivating seascape patterns from the coastal zone to the open ocean are now being revealed in ever more detail by the latest generation of remote sensing devices. Simon Pittman, a marine spatial ecologist, explains the application of landscape ecology concepts and tools to marine and coastal data, which is providing vital information for marine management.

their location relative to other things, influences how they function. A landscape ecologist will ask different questions focused at different scales than other scientists, such as: What are the ecological consequences of different shaped patches, patch size, quality, edge geometry, spapatches across the landscape? At what scale(s) is structure most influential? How do landscape patterns influence the way that animals find food, evade predators and interact with competi-

tors? How does human activity alter the structure and function of landscapes?

Several guiding principles that exist at the core of landscape ecology have made major contributions to terrestrial landscape planning and conservation, but in marine systems our understanding is still in its infancy. For example: (1) environmental heterogeneity exists at multiple spatial scales to which organisms respond differently and at different scales; (2) connectivity is an important ecological pattern and process; (3) patch boundaries/edges influence ecological processes.

Seascape patterns

Just like life on land, the sea exhibits complex spatial patterning that can be mapped and quantified, such as gradients in plant communities across tidal saltmarshes or the intricate mosaics of patches typical of coral reefs. In the open ocean too, dynamic spatial structure in the form of water currents, eddies, temperature fronts and plankton patches can be measured readily. Physical processes

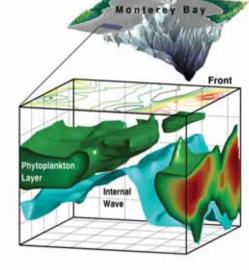


the environment and human activity can also directly create patch structure, modify mosaic composition and even completely remove elements of the seascape. Furthermore, climatechange induced shifts in species related to water temperature change and sea level rise are driving a gradual reconfiguration of the geography of species and habitats.

The patterns revealed by remote sensing devices are most often mapped and represented using two types of model: (1) collections of discrete patches forming mosaics e.g. as represented in two-dimensional benthic habitat map, or (2) continuously varying gradients in three-dimensional terrain models, e.g. in remotely sensed bathymetric data. In landscape ecology, patches can be classified into a binary patch-matrix model based on island biogeography theory where a focal habitat patch type (e.g. seagrasses) is surrounded by an inhospitable matrix (e.g. sand), or a patchmosaic of interconnected patches, where the interactions of the parts influence the ecological function of the whole mosaic. Both patch and gradient models have provided important insights into the spatial ecology of marine species and biodiversity.

Scale matters

Seascape ecologists recognise that one organism's habitat patch is to another a mosaic of patches. For example, the way



that an amphipod perceives, experiences and responds to the surrounding seascape will be different than a shark. Furthermore, this organism-seascape will relationship change throughout an organism's life, with juveniles responding differently than adults. Individuals, species and communities will respond to seascape patterning across a hierarchy of spatial scales.

So how do we select spatial scales for field investigations? Movement behaviour is one approach. In the Caribbean, we used acoustic telemetry to define day and night activity spaces for coral reef associated fish and then mapped that habitat at high resolution to examine the influence of seascape patterning on the movement process, thereby linking seascape ecology and behavioural ecology. The organism's activity space helps us to

anchor the scale selection to a known and functionally meaningful spatiotemporal scale that can then form the focal scale in a hierarchical approach.

The size of a seascape will thus be dependent on the research questions and the ecology of the organism or process of interest. In landscape ecology, this approach to scaling is called the 'organism-based perspective'. For many marine species, we do not have sufficient knowledge of movement patterns to select a meaningful focal scale and therefore an exploratory multi-scale approach to measurement of environmental patterning and analysis of organism-seascape relationships is appropriate.

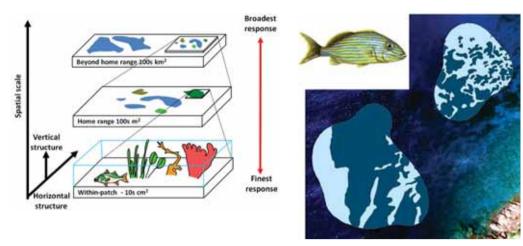
Nevertheless, whether the seascape is a 1m² patch of seagrass or a 10km radius area encompassing seagrass beds, adjacent coral reefs and mangroves, the analytical techniques and concepts applied can be the same. The problem of scale is not a new one for ecologists, but the challenge of ecologically meaningful scale selection is ever present.

Tools of the trade

Typically, seascape ecologists apply a suite of spatial pattern metrics, or spatial statistics, to quantify the geometry of patterning in the environment. Two families of metrics exist: (1) landscape metrics or indices that are applied to two-dimensional patch-matrix and patch-mosaic models of the environment (i.e. benthic habitat maps); and (2) terrain morphometrics that are applied to characterise the structure of three-dimensional digital terrain models (i.e. bathymetry).

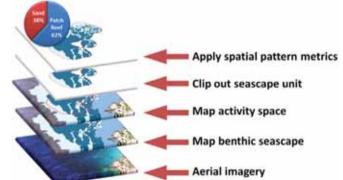
Landscape metrics are available in free online software such as FRAGSTATS or Patch Analyst, that quantify a wide range of structural attributes of composition (amount and variety of patch types) and configuration (spatial arrangement of patches). For example, area (e.g. area of patch type); edge (e.g. edge density); shape (e.g. fractal dimension); isolation/proximity (e.g. mean proximity index); diversity richness); (e.g. patch contagion/interspersion (e.g. clumpiness index) and connectivity indices. In contrast, terrain morphometrics more familiar to industrial metrologists and geomorphologists measure variables such as topographic complexity, curvature and slope from digital elevation models. Some metrics have well-documented ecological effects and others are less well known, or have yet to be evaluated, forming a major research focus.

Geographical Information Systems (GIS) enable seascape ecologists to work with and quantify geometry in maps. Multi-scale analysis is easily processed in a GIS using a moving-window analysis or by clipping out seascape units of varying sizes surrounding a biological survey location and applying pattern metrics. In this way, we treat the seascape unit much as we would a quadrat used to sample the abundance of benthic communities, albeit a larger unit area in most seascape applications. Furthermore, GIS combined with statistical modelling provides accurate, quantitative and cost-effective tools to model the geography of organismseascape relationships extending to spatial predictive mapping of species distributions.



Key findings

Since the early 1990s, landscape ecology approaches have been applied in several marine shallow subtidal and intertidal ecosystems, such as in seagrass ecosystems and salt marshes in the United States and Australia. These have primarily focused on the faunal response to structural attributes of individual patches (e.g. size, edge, shape, isolation). The influence of patch level structural attributes has been highly variable with no decisive generalities identified. Several studies, however, in subtropical Australia and the Caribbean found that the structural attributes of the surrounding seascape contributed significantly to explanations of the spatial variability in faunal diversity and abundance. For example, the juxtaposition of adjacent seagrass beds and coral reefs or mangroves results in a synergistic boost in the local diversity of fish and the biological productivity for some species. This is known as 'seascape complementation or supplementation'. In the Caribbean, a multi-scale seascape ecology approach demonstrated how benthic habitat maps can be used to identify optimal seascape types for fish species and fish assemblage diversity. A similar approach, but using terrain models instead of habitat maps, have shown topographic complexity to be an excellent predictor of habitat suitability for fish and coral species abundance and diversity. Reports of structural collapse of



coral reefs, however, are becoming widespread in the Indo-Pacific oceans and the Caribbean Sea. It is likely that a better understanding of the importance of three-dimensional physical structure on species distributions and diversity will allow us to more reliably forecast the ecological consequences of structural change including predicting species loss and range changes from reef collapse. In the open ocean, quantification of oceanic fronts and plankton patches has enabled ecologists to identify hotspots of productivity and diversity to inform the site selection process in placement of marine protected areas (MPAs) and network design.

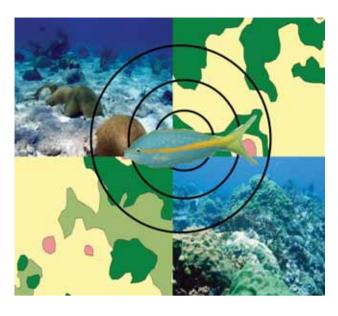
Bridging the gap

Marine managers receive ecological data from ecologists that is interesting and pertinent with high resolution detail, but with limited spatial distribution. A key utility of the seascape approach to ecology is the potential to provide ecologically meaningful information at spatial scales that are opera-

tionally relevant for decision making in marine management. Knowledge of the ecological consequences of seascape configuration can be used to help determine the best placement and design of MPAs to optimise restoration strategies, to understand the influence of structural and functional connectivity on biodiversity patterns and to better predict the effects of environmental change. Marine spatial planning efforts increasingly require spatial information on essential fish habitat, diversity hotspots and 'blue corridors' to incorporate ecological connectivity into the planning process. Seascape ecology techniques can be used to predict these priority locations cost-effectively. The multi-scale approach has now been effectively implemented in several locations worldwide to predict fish distributions, deep water corals, seabirds and cetaceans in support of marine spatial planning and MPA network design.

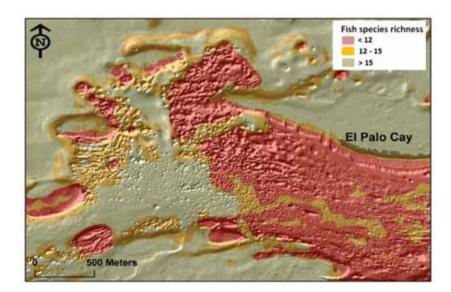
Future directions

Although much is made of the differences between marine and terrestrial environments. many commonalities exist in the way that organisms respond to structure in their environment. whether they are a bird or a fish on land or sea. The new generation of ecologists embracing big data and the spatial revolution is fast becoming equipped with the



tools to conduct sophisticated spatial analyses, although progress in marine applications is uncommon. The recent global surge in interest in marine spatial planning should fuel the evolution of conceptual and operational approaches seascape ecology.

The immediate focus of seascape ecology research should be to determine which theoretical constructs, analytical techniques and structural patterns or features from landscape ecology are relevant to marine organisms and their habitats. Gaining a better understanding of faunal-seascape relationships, including the identifications of threshold effects, is a major research priority. We now also need to build the evidence for causal linkages between patterns



and ecological processes, including the impact of changing patterns on predator-prey dynamics, animal movement pathways, foraging behaviour and individual growth rates. This can be examined through manipulative experiments, some of which will need to be opportunistic, given that the scale of interest may be too broad for conventional manipulations. In terrestrial systems, microlandscapes have been constructed in the laboratoto examine individual responses such as movement and habitat selection to differing patch structures. Computer simulation models also can be used to examine the effect of pattern on process.

Adoption of a multi-scale and multi-habitat landscape ecology perspective may move us closer to fulfilling the original vision for Ökologie (ecology), first defined by Ernst Haeckel in 1866 as "the science of the relationship of organisms to their surroundings". Landscape ecology helps define the relevance of the surroundings. Without such an approach, important pieces of the ecological puzzle will be missing. In a world where spatial data is a core component of decision-making throughout society, seascape ecologists have an academically rewarding challenge ahead and great potential to change the way we perceive and manage the marine environment. One has only to look at the rise of terrestrial landscape ecology in the past 30 years to obtain

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