



Contribution to the Themed Section: 'Seascape Ecology'

Quo Vadimus

Seascapes as a new vernacular for pelagic ocean monitoring, management and conservation

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For terrestrial and marine benthic ecologists, landscape ecology provides a framework to address issues of complexity, patchiness, and scale—providing theory and context for ecosystem based management in a changing climate. Marine pelagic ecosystems are likewise changing in response to warming, changing chemistry, and resource exploitation. However, unlike spatial landscapes that migrate slowly with time, pelagic seascapes are embedded in a turbulent, advective ocean. Adaptations from landscape ecology to marine pelagic ecosystem management must consider the nature and scale of biophysical interactions associated with organisms ranging from microbes to whales, a hierarchical organization shaped by physical processes, and our limited capacity to observe and monitor these phenomena across global oceans. High frequency, multiscale, and synoptic characterization of the 4-D variability of seascapes are now available through improved classification methods, a maturing array of satellite remote sensing products, advances in autonomous sampling of multiple levels of biological complexity, and emergence of observational networks. Merging of oceanographic and ecological paradigms will be necessary to observe, manage, and conserve species embedded in a dynamic seascape mosaic, where the boundaries, extent, and location of features change with time.

Keywords: biodiversity, conservation, landscape, ocean observations, pelagic, phytoplankton, seascape.

Beyond the yellow pine woods there lies a world of rocks of wildest architecture . . . towers and spires, pinnacles and slender domed columns, are crowded together, and feathered with sharp-pointed Engelmann spruces, making curiously mixed forests,—half trees, half rocks. Level gardens . . . in the midst . . . offer charming surprises, and so do the many small lakes with lilies on their meadowy borders . . . together forming landscapes delightfully novel, and made still wilder by many

interesting animals,—elk, deer, beavers, wolves squirrels, and birds. — John Muir, Our National Parks

Introduction

John Muir was one of the most persuasive naturalists and conservationists of the 19th and 20th centuries. Muir's capacity to weave

his observations into the language of grand emergent landscapes led to a transformation in the consciousness about conservation in United States. The idea of conserving whole landscapes, pieces of land on length scales of 10s to 1000s of kilometres, continues to be a driving force for environmental legislation (Mace, 2014). On terra firma, the landscape concept and development of landscape ecology science have informed our understanding of the controls on biodiversity, system responses to climate change or land-use strategies, and the application of ecosystem management practices (Turner *et al.*, 2003; Turner, 2005). Likewise, understanding and planning for marine pelagic ecosystem change will require a comprehensive and multi-scale seascape framework (Game *et al.*, 2009; Lewison *et al.*, 2015) that draws upon the domains of landscape ecology and oceanography.

Marine ecosystems face multiple stressors associated with global change, including warming, reduced oxygen, reduced pH, and reduced productivity (Gruber, 2011; Doney *et al.*, 2012). Projecting future change is problematic because individual pressures may have different and or overlapping spatial footprints (Bopp *et al.*, 2013; Boyd *et al.*, 2015) or affect ecosystems differently at local and global scales. Climate-related drivers can also interact with over- or selective harvesting, eutrophication, and land-use change (Perry *et al.*, 2010; Hidalgo *et al.*, 2012; Saunders *et al.*, 2015) leading to context dependency. Furthermore, geographic shifts are evident in species ranges (Pereira *et al.*, 2010; Sorte *et al.*, 2010), extents of whole ecosystems (Polovina *et al.*, 2008; Irwin and Oliver, 2009), and boundaries or dispersal corridors via shifting current regimes (Treml *et al.*, 2008; Ling *et al.*, 2009). Thus scale, context-dependency, and shifting geographies make it difficult for managers and policy makers to adapt to, plan for, or mitigate the multiple stressors on pelagic ecosystems (Crowder *et al.*, 2006; Muller-Karger *et al.*, 2014).

Since Muir's time, problems of environmental complexity, patchiness, and scale have become areas of intensive research for terrestrial and marine ecologists (Paine and Levin, 1981; Steele, 1991; Levin, 1992; Schneider, 2001). Terrestrial and marine benthic ecology draw from landscape ecology theory to address these issues, which also include spatial context sampling bias, and edge effects (Turner, 2005). Landscapes are conceptual models of systems shaped by the local geomorphology, environmental conditions, and biological processes (Wiens, 1976; Turner *et al.*, 2001; Turner, 2005). Landscapes are typically analysed as mosaics of habitats or patches in a region (Forman, 1995; Turner *et al.*, 2001). Landscape models describe the varying composition and shapes of different adjacent habitats (Forman and Godron, 1981), as well as the composite dynamics of individual patches and their interactions at adjacent hierarchical levels (Wu and Loucks, 1995; Moorcroft *et al.*, 2001).

The marine environment can also be viewed as a mosaic of distinct seascapes, with unique combinations of biological, chemical, geological, and physical processes that define habitats which change over time (Steele, 1991; Karl and Letelier, 2009; Kavanaugh *et al.*, 2014a). Intertidal zones, coral reefs, seamounts, and seagrass beds can be treated as flooded, marine versions of landscapes that structure mobile populations (Paine and Levin, 1981; Wedding *et al.*, 2011). Traditional definitions of seascape ecology have focused on the study of how relatively static habitat structure influences the ecological processes and the spatial patterns of marine species (Pittman *et al.*, 2011). However, pelagic seascapes are fuelled by planktonic processes, where the size and behaviour of organisms contribute to patch scales that are

coherent with dynamic physical oceanographic structures. Pelagic seascapes are shaped by hydrology and turbulence that varies in space, time, and depth. Thus to adapt tenets of landscape ecology to the pelagic realm, we must create a framework that allows for dynamic geographic shifts in planktonic habitat that influence the spatiotemporal patterns of ecological interactions and species distributions. In the next sections, we review the key differences between landscapes and seascapes and historical understanding of seascape structure in the pelagic realm. We then discuss the transfer of the landscape paradigm to modern oceanography through the maturation of synoptic time series from satellites and models, robust methods for classifying seascape patches in space and time, and emergence of autonomous observing systems and networks. Finally, we provide recommendations that facilitate the application of dynamic seascape ecology to marine resource management.

Pelagic seascapes are fuelled by microbes

Mostly invisible to the naked eye, photosynthetic phytoplankton are responsible for approximately half of the global primary production (Field *et al.*, 1998; Behrenfeld *et al.*, 2001), and form the biogeochemical and ecological foundation of pelagic ecosystems. Phytoplankton, bacterioplankton, and many zooplankton have rapid response times to physical perturbation or blooms, often with generation times-scales as short as a day. Observations of lower trophic level dynamics, the primary biophysical interactions of the seascape, require technologies that can measure quick changes in small life forms that are spread out over large areas, in often harsh and remote environments.

The cumulative distribution of variability, from subseasonal to interannual, and across different landscapes and seascapes, is in part, a function of the interaction between physical perturbations and of the life history of primary producers that supply and structure the rest of the ecosystem. This partitioning of variability, and thus the potential upon which natural selection to act, is much different from land to sea (Steele, 1985; Caswell and Cohen, 1995). For example, there are areas of the ocean and on continental masses where annual primary production levels are similar (Figure 1a), but the response time of marine primary producers is much more rapid than dominant terrestrial primary producers (Figure 1b) shifting the distribution of variance to higher frequencies. These are the time scales at which secondary consumers must respond, and the scales at which observers of these phenomena must sample to characterize, and predict these processes. Ultimately, these are also scales over which human activities should be managed in order to affect an outcome on a changing ecosystem services.

Seascapes in motion: advection vs. behaviour

Dispersal and diffusion create and maintain physical and ecological patchiness in terrestrial and aquatic systems (Okubo and Levin, 2001; Turner *et al.*, 2001). However, pelagic organisms inhabit a turbulent, moving fluid where advection interacts with organism size, swimming speed (Beamish, 1978; Blackburn and Fenchel, 1999; Hansen *et al.*, 1997) and behaviour (Keister *et al.*, 2011; Kiørboe and Jiang, 2013) to affect dispersal and migration scales and strategies. Particularly, at intermediate sizes and trophic levels, vertical migration, predator avoidance, and foraging or reproductive behaviour can affect aggregation (Folt and Burns, 1999), and our capacity to predict distributions from more easily observed or modelled physical phenomena.

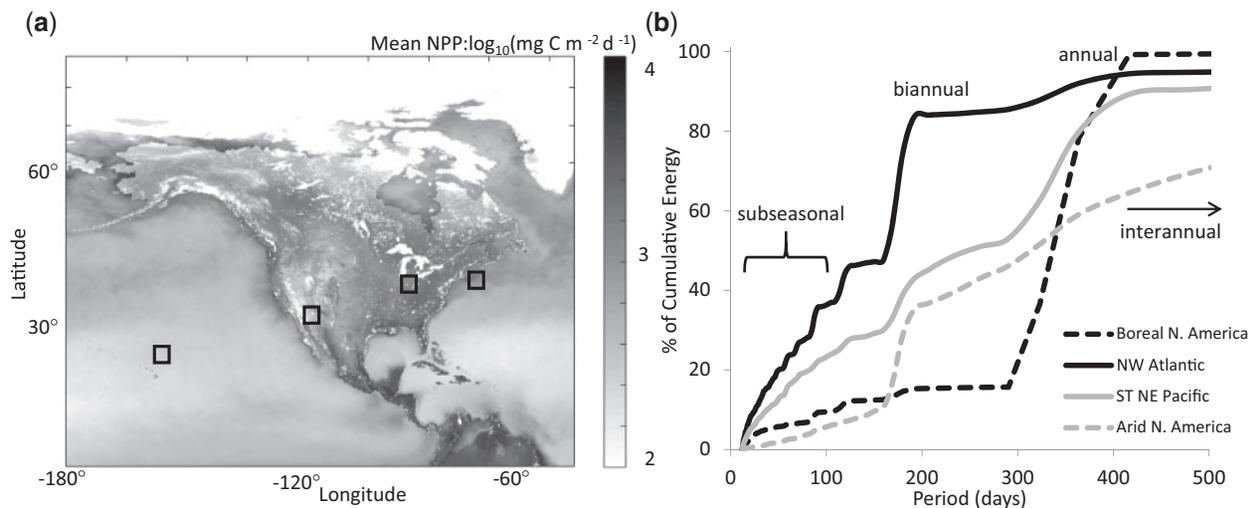


Figure 1. Temporal variability of comparable landscapes and seascapes. (a) Mean Net Primary Production on land and sea derived from Zhao *et al.* (2005), and Behrenfeld and Falkowski (1997). (b) Cumulative variability of primary producer standing stock derived from spectral analysis of time series within landscapes and seascapes (black boxes). Time series were spatially binned 8-d averages of Leaf Area Index in landscapes and Chl *a* in seascapes from the Terra and Aqua MODIS sensors.

The Reynolds number (Re) is a dimensionless number that relates the density (ρ), viscosity (μ) and velocity (U) of a body relative to the fluid to the length scale (L) of an object:

$$Re = \frac{\rho UL}{\mu}$$

where $\rho = \text{kg m}^{-3}$, $\mu = \text{kg m}^{-1} \text{s}^{-1}$, $U = \text{m s}^{-1}$, $L = \text{m}$.

The length scales of organisms moving through the marine environment span over seven orders of magnitude (Figure 2). At $Re < \sim 100$, an organism's movement through the fluid is limited by the viscosity of the fluid. The dispersal of neutrally buoyant, microscopic phytoplankton, therefore, is driven by advection, although some phytoplankton can escape physicochemical regimes by swimming vertically or adjusting buoyancy (Villareal *et al.*, 1999; Mitchell *et al.*, 2008).

Zooplankton and krill occupy an intermediate range of Re ; variation in ocean currents, life history stage, and behaviour determine the relative importance of advection compared to movement, growth, and death to the patch scale. Copepods and small euphausiids on average have swimming speeds that are slow relative to horizontal velocities, but fast relative to vertical velocities allowing them to utilize the depth gradients to their advantage (Keister *et al.*, 2011; Lindsey and Batchelder, 2011), but also smearing the apparent patch scale. Copepods swim slowly while foraging, but burst to a speed equivalent to 500 body-lengths per second to avoid being eaten (Kjørboe and Jiang, 2013). Larger zooplankton and fish aggregate in swarms or schools to avoid predation by their larger and faster predators (Parrish and Edelstein-Keshet, 1999). Within swarm heterogeneity is affected by foraging and reproductive behaviours (Folt and Burns, 1999), but also may be a response to smaller predators (Kaltenberg and Benoit-Bird, 2013). Thus, this intermediate control can influence trophic interactions, population connectivity, and very local to mesoscale patchiness of the system.

Large organisms can overcome physical water movement, through complex body structures, physiological adaptations, and behaviour (Nathan *et al.*, 2008). However, the location of large

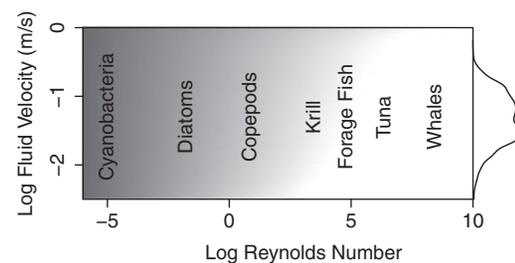


Figure 2. Reynolds number of potential seascape constituents and their environmental fluid velocities. Both axes are \log_{10} transformed. Reynolds number for marine organisms is shown only for adults and is primarily determined by size. Shading indicates the relative importance of advection relative to organism migration patterns, with darker grey showing greater importance. The normalized distribution of upper ocean (100 m) horizontal current speeds across the global ocean is shown in the right margin from the NOAA OSCAR product.

organisms is also related to advective and physicochemical components of seascapes, because of life history, physiological, or food web linkages. For example, the Re for an adult tuna is $\sim 10^6$, whereas juvenile tuna are planktonic with $Re < 100$, creating advective control of early life history patch scales that are similar to lower trophic levels. Large-scale seasonal migrations are often strongly related to temperature and productivity, both of which also have strong seasonal signals. Larger predators often aggregate at ocean frontal boundaries, where physical processes such as upwelling enhance local planktonic productivity and biomass (Polovina *et al.*, 2001; Woodson and Litvin, 2015). Indeed, spatial heterogeneity of the prey field may structure predators even with vastly different foraging strategies (Santora *et al.*, 2012; Benoit-Bird *et al.*, 2013). Thus, despite differences across size classes, trophic status, and behavioural complexity, there are coherent scales of "apparent" diffusivity (Okubo and Levin, 2001), where biological organization may align with physical organization, but due to multiple mechanistic processes.

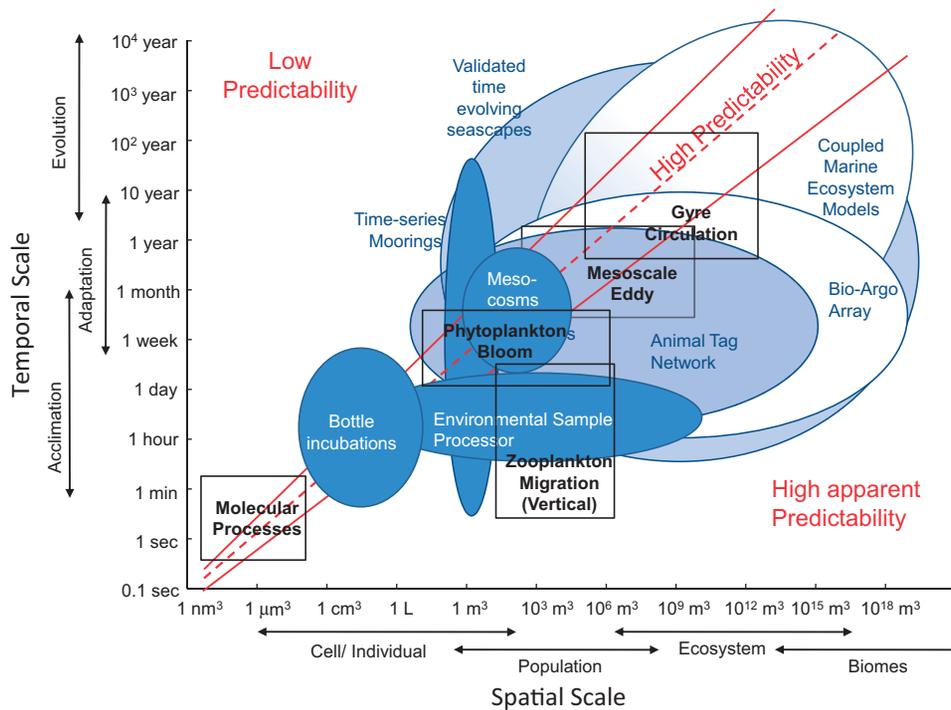


Figure 3. Stommel diagram showing time and space scales for typical biophysical phenomenon (squares) and our current observational capacity (ovals) (after Marquet *et al.*, 1993; Dickey, 2003). Shading denotes level of ecological complexity that the measurements provide with explicit community structure provided by the darkest shading. See text for further detail.

Seascapes organization and dynamic bio-physical hierarchies

Hierarchy theory has provided a means to scale between local mechanistic observations and regional and global models (Wu and Loucks, 1995; Wu, 1999). One focus of hierarchies within landscape ecology has been on spatial scales (Kotler and Wiens, 1990; Wu and Hobbs, 2002; but see Gillson, 2009); e.g. episodic erosion by rivers and streams results in hierarchical or fractal scaling of a tributary system (Burrough, 1981). Other hierarchies are defined in terms of food chain dynamics and directions of cascades; the role of evolution in population dynamics, of populations in communities, and communities in ecosystems; and the role of “functional” diversity in organizing an otherwise chaotic biosphere (Levins, 1969; O’Neill *et al.*, 1986, 1992; Lidecker, 2008; Devictor *et al.*, 2010).

Physical hierarchies, driven by atmospheric ocean interactions and ocean circulation features, have led historical studies of seascapes. Stommel (1963) recognized that physical ocean structures followed a power law cascade as energy dissipated from gyre circulation to small-scale turbulence (Kolmogorov, 1941; Okubo, 1971). Biological oceanographers and fisheries ecologists modified Stommel’s space–time diagram to depict dominant patch scales observed for phytoplankton, zooplankton, and fish (Haury *et al.*, 1978; Steele, 1978). Concurrently, oceanographers and limnologists recognized that the fractal nature of the physical phenomenon could be used to predict biological scales (Denman *et al.*, 1977; Fasham, 1978; Gower *et al.*, 1980). Experimental and modelling evidence have also demonstrated that phytoplankton aggregate at centimetre to metre scales (Mitchell *et al.*, 2008). Thus the biophysical structure of seascapes span the scales of intermittent turbulent eddies to

fronts or boundaries associated with vertical mixing, mesoscale circulation, and gyres.

The complex interdependency between energy dissipation, other physical processes, and biology is evident within the Stommel diagram (Figure 3). Many phenomena align along an axis in time–space dimensions with what would be predicted with either energy dissipation or apparent scale-dependent eddy diffusivity (Okubo, 1971). For example, the horizontal spatial scale of mesoscale eddies is set by the Rossby radius of deformation, where planetary rotational effects on ocean flow become important, with characteristic times-scales. Mesoscale (~10–100 km; days to weeks) and submesoscale (~1–10 km; hours to days) physical dynamics act to influence biological growth/loss and stir large-scale bio-geophysical property gradients, down to smaller scales (Mackas *et al.*, 1985).

The space–time hierarchy determines the capacity of different methods of observations to observe phenomena of interest (Figure 3). How observations translate to predictive ability is also a matter of continuity and persistence. For example, sampling at fine spatial scales gives little predictive capacity for large scale and long-term processes unless such fine-scale sampling is conducted over long periods. Conversely, sampling shorter term processes infrequently or over larger scales misses key features and characteristics of the processes being observed. This results in poor predictive skill and masks underlying mechanisms (from Wiens, 1989). However, a hierarchical seascape framework presents an effective means to translate local measurements to broader spatio-temporal scales, scales relevant for modelling the effects of global change and enabling whole-ecosystem management in the dynamic ocean (Kavanaugh *et al.*, 2014a).

While larger scale circulation patterns can drive linear covariation in biophysical properties (Figure 4a), physiological or

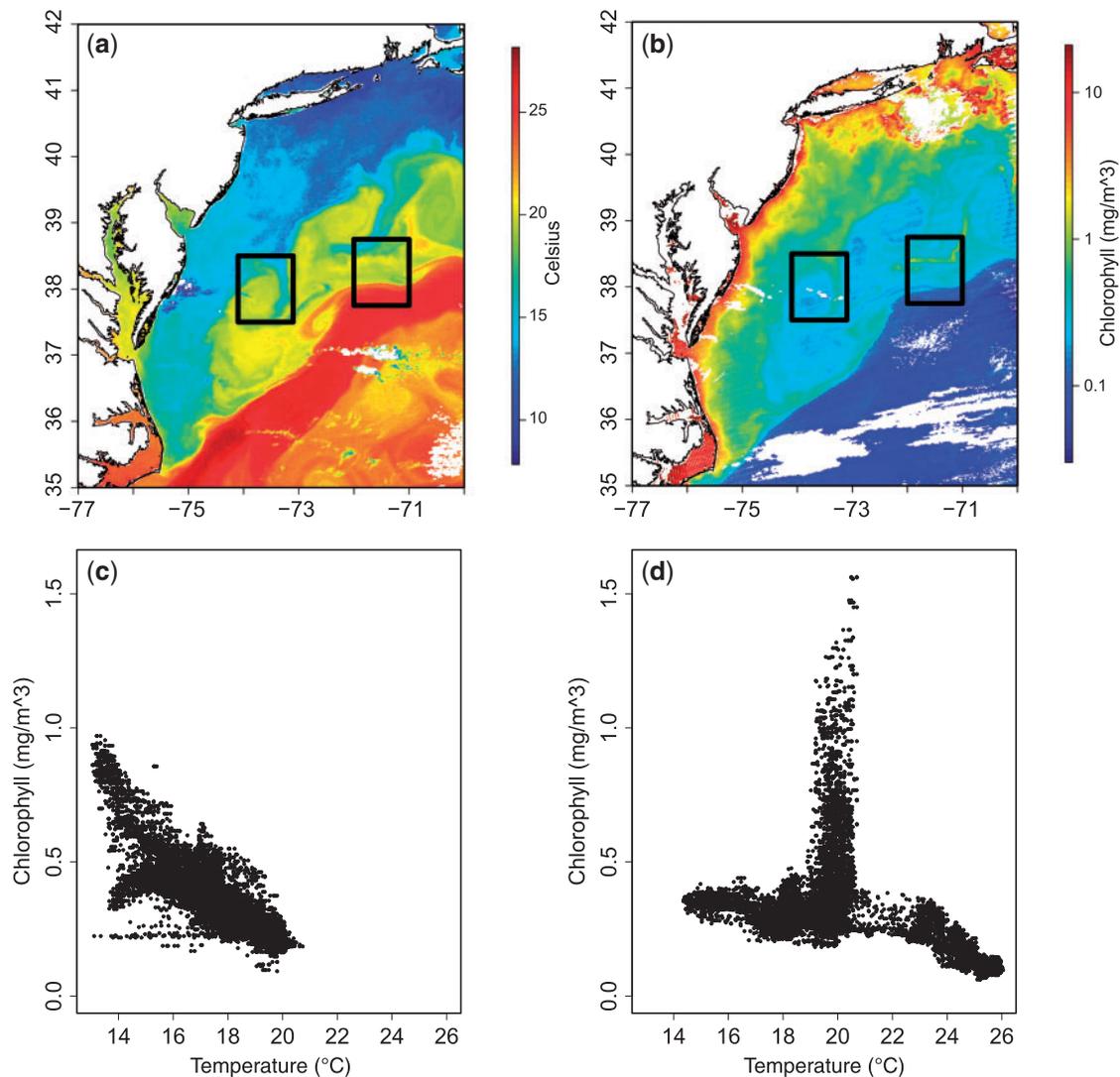


Figure 4. The 23 May 2015 sea surface temperature (a), chlorophyll (b), and the relationship between these two scape predictors in the western box (c) and the eastern box (d). In the western box, temperature and Chl *a* covary, suggesting that biological patterns are driven by regional physics with mixing occurring across a gradient from biomass-rich, cold coastal waters to biomass-poor open ocean conditions. A linear interaction would sufficiently characterize the seascape. In the eastern box, Chl *a* responds in a non-linear fashion to ocean physics with a local peak in Chl *a* values and Chl *a* variance occurring near 19–20 °C associated with the surface expression of the Gulf Stream front. A time-dependent reaction term, e.g. phytoplankton growth or buoyancy response, is necessary to characterize the seascape.

trophic processes may decouple biological and physical scales (Abbott and Letelier, 1998; Lovejoy *et al.*, 2001), particularly at scales < 1 km. Thus, locally, the relationship between physical forcing and biological response may be non-linear (Figure 4b). Indeed, non-linearities are common in biogeochemical (Gruber, 2011; Hales *et al.*, 2012), biophysical (Hsieh *et al.*, 2005), physiological (Jassby and Platt, 1976) and trophic (Litzow and Ciannelli, 2007; Brander, 2010) interactions. Therefore, the heuristic for seascape classification needs to consider a dynamic, hierarchical, and potentially non-linear multivariate topology.

Seascape classification

A major challenge in seascape ecology is the appropriate delineation of hierarchical categories, particularly, in regions where boundaries are diffuse and gradients are shallow (Hinchey *et al.*,

2008). While some argue that the patch mosaic paradigm may obscure underlying pattern–process relationship (Cushman *et al.*, 2010), we assert that the objective partitioning into emergent categories may actually illuminate mechanistic relationships, by disentangling driver responses of different, but adjacent systems (Hales *et al.*, 2012; Kavanaugh *et al.*, 2014b). Furthermore, with maturation of classification methods, synoptic time series, and *in situ* observing systems, oceanography can now employ a piecewise continuous approach (Platt and Sathyendranath, 1999, 2008), where both the mosaic (discrete patches) and continuous nature of the fluid environment within patches are recognized.

Pelagic classification approaches have different names, e.g. biomes, biophysical provinces, seascapes; all represent the practice of identifying water masses with particular biogeochemical features organized in a spatially coherent mosaic. Classification schemes became spatially explicit with the extensive data

provided by satellite-derived measurements (Platt and Sathyendranth, 1999; Longhurst *et al.*, 1995; Longhurst, 1998; Hooker *et al.*, 2000) and biogeochemical models (Sarmiento *et al.*, 2004; Dutkiewicz *et al.*, 2012). These divisions were based primarily on the spatial covariation of annual or multi-year climatological means.

However, climatologies do not adequately characterize dynamic ocean ecosystems (Hardman-Mountford *et al.*, 2008), thus there have been efforts to classify seascape on seasonal, interannual, and multiple spatial scales. Seasonal dynamics for coastal regions have been inferred with dynamic but discontinuous boundaries (Saraceno *et al.*, 2006; Devred *et al.*, 2007) or by explicitly including seasonal and spatial forcing in their assessments (Hales *et al.*, 2012). Others have applied *post hoc* classifications based on distributions of variables within subjective Longhurst province boundaries on seasonal and annual scales (Fay and McKinley, 2013; Reygondeau *et al.*, 2013). Objective and dynamic seascapes have been classified using satellite remote sensing data on basin (Kavanaugh *et al.*, 2014a) and global (Oliver and Irwin, 2008; Irwin and Oliver, 2009) scales by simultaneously clustering pixels in space and time. Each of these methods assumes that seascapes have unique multivariate distributions, that there are natural discontinuities or gradients that delimit seascapes, and that the boundaries change with time. Thus, modern seascape classification merges lower trophic level ecology, geography, and ocean dynamics using observations that are updated regularly and that provide a historical context for reference against which to measure change.

Classification efforts involve a multivariate covariance analysis and will benefit by the use of flexible parametric and non-parametric approaches that explicitly recognize that many processes and interactions in the ocean are non-linear. For example, fuzzy sets and copula (Fauvel *et al.*, 2006; Voisin *et al.*, 2014) have been used to approximate the underlying spatial structure of synthetic aperture radar (SAR) data. Neural networks or self-organizing maps (SOM; Kohonen, 2001) have been used in oceanography to classify coastal biophysical regions (Richardson *et al.*, 2003; Saraceno *et al.*, 2006), to define regions of mechanistic coherence in predictive models (Hales *et al.*, 2012), and to find drivers of net primary productivity (Lachkar and Gruber, 2012). In an extension of the hierarchical patch mosaic paradigm (Wu and Loucks, 1995), Kavanaugh *et al.* (2014a) combined a probabilistic SOM with a hierarchical agglomerative clustering algorithm to allow for non-linear interactions and hierarchical organization of seascapes.

Steps toward a seascape framework for conservation or management

The effects of global change and declining ecosystem health are evident in many regional marine systems (Halpern *et al.*, 2014). Seascape ecology can guide conservation, policy, and management strategies. Where and when possible, existing tools and paradigms can be modified to expedite this process and facilitate a cautious, yet deliberate transfer of ecological concepts from landscape ecology to the pelagic realm. Seascape ecology now has the tools to both characterize the spatial heterogeneity in a dynamic fluid environment, while there is also better technology to sample the rich diversity of life within seascapes. Below, we list five specific considerations to focus seascape ecology research in the near-term future.

Develop and test ecological theories

The main principles of landscape ecology (Risser, 1987; Forman, 1995), can be adapted to the sea (Steele, 1989, 1991). These include concepts about the development and dynamics of spatial heterogeneity, interactions and exchanges across heterogeneous landscapes (e.g. how disturbance or invasion is communicated between adjacent patches), influences of spatial heterogeneity on biotic and abiotic processes, and the management of spatial heterogeneity (e.g. forest cuts). Given the influence of advection on both patch-scale and organization, however, the heterogeneity of focus should not be just spatial, but spatiotemporal.

We have focused primarily on challenges associated with adapting the patch mosaic paradigm. Incorporating complementary paradigms, e.g. the gradient paradigm (Cushman *et al.*, 2010) will strengthen our understanding of the drivers of spatiotemporal patterns. This process needs to include a comparison of the efficiency of classification methods, evaluating the assumptions of underlying structure (e.g. hierarchical or diffuse systems), and validating seascape metrics at higher trophic levels (Oliver *et al.*, 2013; Breece *et al.*, 2016). Classification approaches also be complemented by edge or frontal detection techniques (Belkin *et al.*, 2009), and subsequent analysis of the interaction between persistence of features and community structure (Hidalgo *et al.*, 2015). If the underlying topology is maintained, patch boundaries should be demarcated by the discontinuities that result from strong gradients. Multi-scale gradient analysis (Alvarez-Berastegui *et al.*, 2014) can be compared to occupancy metrics within seascape categories (Breece *et al.*, 2016) to determine if habitat preferences can be predicted from the mean seascape state or gradual or abrupt gradients in the underlying hydrographical variables.

Studies should also assess the connectivity between seascape patches and the interactions between adjacent patches across multiple trophic levels and size classes (e.g. between open-ocean and coastal seascapes, or communication between gyres, transition zones). Convergent zones or open ocean fronts delimiting seascapes are ecotones (Ribalet *et al.*, 2010; Woodson and Litvin, 2015), and oceanographers can borrow from landscape theory on boundaries (Cadenasso *et al.*, 2003) to predict or generalize patterns of endemism, exchange, production, and connectivity. Network analysis and graph theoretic approaches may facilitate a lingua franca for conservation ecologists across marine and terrestrial realms (Saunders *et al.*, 2015).

Increase spatial, temporal, and spectral scales

The growing body of satellite based observations can provide multivariate and synoptic characterization of seascape structure. The polar-orbiting SeaWiFS, MODIS-Aqua, and VIIRS ocean colour sensors, have provided an extended time series of global, near daily, ocean colour observations since 1997, providing synoptic information to quantify lower trophic level dynamics at scales from 1 km to global. LIDAR (Young *et al.*, 2013) and polarimetry (Tonizzo *et al.*, 2011) may assist with quantifying ocean particle composition, in addition to facilitating atmospheric correction for ocean colour. Incorporating geostationary and hyperspectral ocean colour data into seascape classification or validation will increase temporal resolution and improve characterization of habitats and assemblages that are affected by tidal scale mixing, diurnal migration, and benthic vegetation (Davis *et al.*, 2007). For example, the multi-spectral radiometers on the

European Sentinel satellites can provide observations of a range of ocean and coastal parameters, at scales ranging from 10 m resolution data on a 5-d repeat cycle to 1 km resolution every few days. NASA's Pre-Aerosol, Clouds, ocean Ecosystems mission will provide high resolution ocean colour data, possibly with polarimetry to help understand ocean ecosystem and cloud dynamics. Observations from these satellites will be beneficial for mapping benthic and pelagic habitat quality, improve the capacity to detect phytoplankton community structure, and food quality for higher trophic levels. Integrating long wavelength sensors (e.g. radar and microwave) will allow for assessment of spatiotemporal habitat shifts associated with variation in winds (Rykaczewski and Checkley, 2008; Asch, 2015), sea surface topology (including currents and eddies: Cotté *et al.*, 2007; Gaube *et al.*, 2013), temperature, and sea ice (Kavanaugh *et al.*, 2015).

Merge observations with regional and global marine ecosystem models

Coupled regional and global models are tools that help integrate observations to advance understanding of the causes for a particular state of ocean ecosystems (Denman *et al.*, 2010). Model results can fill the gaps, particularly, in the vertical, to understand 3-D patterns of seascapes variables, nutrient dynamics, salinity and mixed layer depth. Once spatial patterns are validated, models can also be used to provide predictions of habitat shifts (Cheung *et al.*, 2010; Hazen *et al.*, 2013).

Integrate organismal level observations

Ship-based and autonomous platforms continue to advance our understanding of the distributions and interactions of pelagic organisms across many trophic and organizational levels. At higher trophic levels, ship-mounted sensors using active acoustic now enable 3-D acoustic imaging of aggregations of fish and large zooplankton (Korneliusson *et al.*, 2009), providing insight into pelagic ecosystem structure (Benoit-Bird and McManus, 2012) and multi-scale patchiness (Kaltenberg and Benoit-Bird, 2013). Several optical imaging sensors, with computer-based image analysis, exist and continue to be developed (Sieracki *et al.*, 2010). Animals are increasingly used as platforms for sensors by use of tags (archival and pop-up satellite), biologging (e.g. instruments attached temporarily to marine mammals) (Boehme *et al.*, 2010; Block *et al.*, 2011), and acoustic listening networks, in which animals with implanted sensors are detected at listening nodes (O'Dor *et al.*, 2009). The ability of autonomous underwater vehicles (AUVs) to track and detect telemetered animals is also becoming a significant tool for understanding seascapes (Grothues *et al.*, 2008; Clark *et al.*, 2013). AUVs provide greater environmental coverage than node-based detection, extend the depth capacity and spatial resolution of acoustic identification (Moline *et al.*, 2016), and facilitate evaluation of dynamic habitat preference of foraging pelagic species (Oliver *et al.*, 2013; Haulsee *et al.*, 2015; Breece *et al.*, 2016).

At lower trophic levels, pigments and microscopy remain critical to distinguishing different components of the phytoplankton and microbial assemblage. Multi- and hyperspectral optics can extend measurements of absorption and scattering spatially, and link in-water qualities to that measured by satellites. Imaging flow cytometry (Sosik and Olson, 2007; Sosik *et al.*, 2014) automates cell counts and discriminates among different types of individual phytoplankton and microzooplankton cells. Using a suite

of probes and chemical sensing arrays, the Environmental Sample Processor can detect specific microorganisms and proteins (Scholin *et al.*, 2009) and can archive of samples for microscopy and more detailed molecular analysis (Preston *et al.*, 2009). These are but a few of the technologies being developed that can provide organismal level information to identify and validate dynamic seascapes.

Complement existing management tools and embed seascape ecology and classifications into existing networks

Open-ocean environmental policies are beginning to embrace the concept of dynamic boundaries and subsequent management strategies (Game *et al.*, 2009), although coastal ocean policies are embedded in primarily static, place-based or population-based frameworks. Adaptive management is needed (Agardy *et al.*, 2011), because a static framework simplifies or ignores the dynamic nature of the boundaries of the systems it is trying to manage. From a conservation policy perspective, understanding the spatio-temporal dynamics of seascapes can help local and regional governments plan for, respond and adapt to these changes as well as build partnerships to mitigate jurisdiction mismatches (Crowder *et al.*, 2006). While dynamic seascape ecology serves to characterize basic spatiotemporal patterns of pelagic community structure and function, it can also inform biogeographic assessments for spatially explicit (Caldow *et al.*, 2015) or dynamic ocean management (Lewison *et al.*, 2015; Maxwell *et al.*, 2015). For example, Breece *et al.* (2016) determined that satellite-derived dynamic seascapes were highly predictive of the Endangered Species Act (ESA) listed Atlantic sturgeon (*Acipenser oxyrinchus*), during their spring migration. This study merged of AUV and satellite observations, metrics of occupancy by sturgeon and indices of seascape persistence. Because the ESA listing of Atlantic sturgeon potentially impacts major sink-gillnet fisheries, alternative energy development, and shipping practices in the Mid-Atlantic, these dynamic seascapes are likely to be used to help manage the human impact on this species.

How pelagic seascape ecology is incorporated into observational or management operational strategies may depend on specific conservation goals (Figure 5). Once the periodicity and extent of the processes of interest are defined, relevant technologies can be used to extend the observational capacity to higher frequencies, and horizontal and vertical resolution. For example, satellite-derived dynamic seascape classifications are an integral part of the Marine Biodiversity Observing Network (MBON; Duffy *et al.*, 2013; Muller-Karger *et al.*, 2014). A goal of the MBON is to better understand the effects of climate and coastal ocean dynamics on spatiotemporal dynamics of marine species distributions in order to inform state and federal management. In concert with ship, buoy, and AUV measurements, seascapes categories are being used as an objective extent to plan sampling, conduct rarefaction studies, inter-compare spatial and temporal patterns across trophic levels, test hypotheses of fisheries habitat affinities (Santora *et al.*, 2012), quantify seascape habitat diversity (Whitaker, 1977; Turner, 2005), and examine temporal shifts in habitat quality and availability within existing jurisdictional units.

A seascape observational/analysis framework needs to integrate with national and international observing networks (Figure 5). These include but are not limited to the Global Ocean Observing

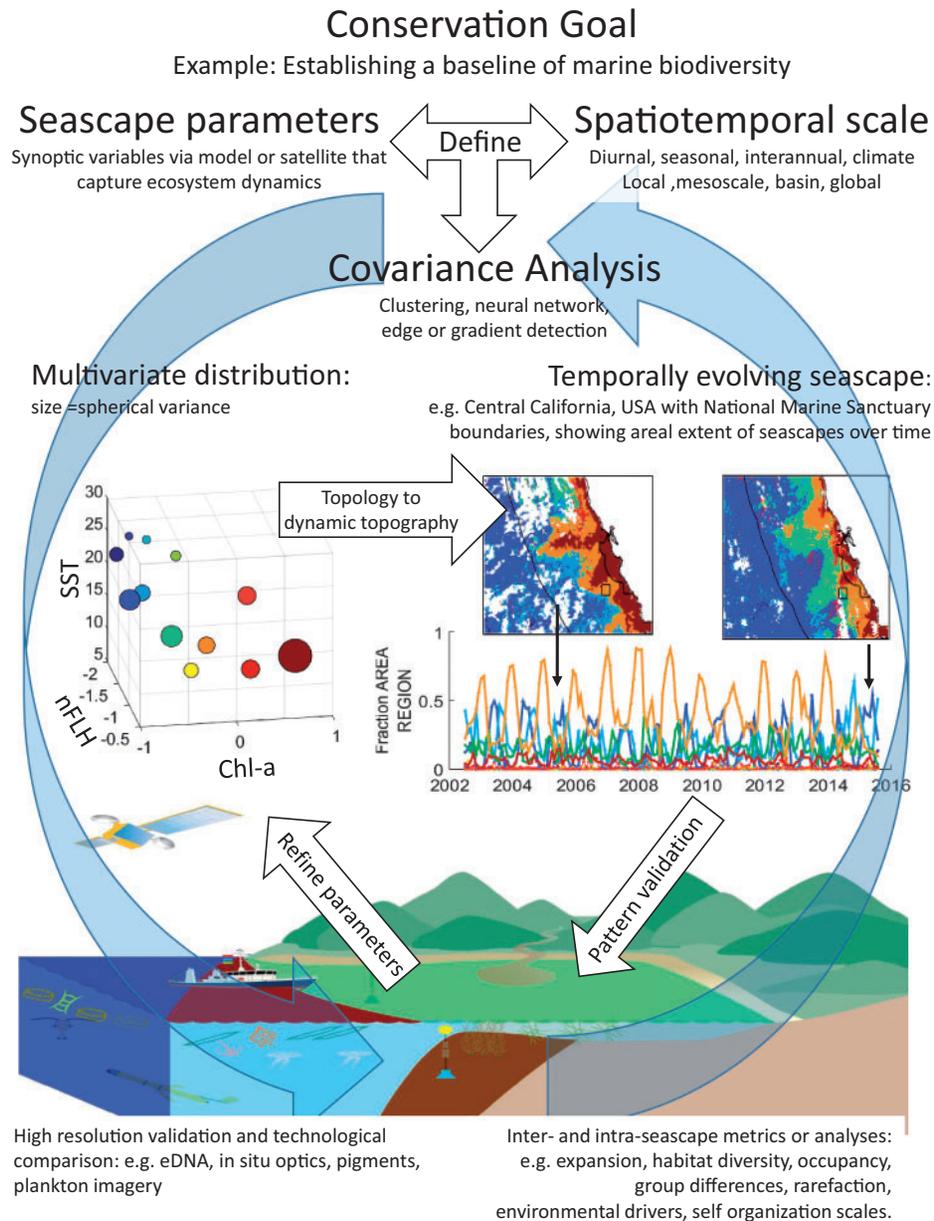


Figure 5. Seascapes as an observational and management tool. Blue arrows denote the interplay between mechanistic hypotheses testing and analyses of emergent patterns. The conservation goal, spatiotemporal scale, and parameters of interest may determine whether synoptic time series of satellite remote sensing (2-D), assimilated marine ecosystem models (3-D) or both are used to define seascapes. Higher resolution *in situ* data can provide vertical data, but also higher resolution organismal information than that provided by remote sensing reflectances or model functional types. Finally, in addition to informing conservation (e.g. rarefaction, patch and boundary analyses), management (trends and oscillations of major habitats) inter- and intra-seascape analyses can inform basic scientific inquiry such as dominant environmental drivers, and scales of biological self-organization (e.g. through partial-mantel tests).

System, the Animal Telemetry Network, Ocean Tracking Network, Ocean Observatories Initiative, Long-Term Ecological Research, ocean time series programs, in addition to the recent MBON. These observatories will provide the organismal data and environmental context necessary for a whole ecosystem understanding of coastal and oceanic systems (Oliver *et al.*, 2013). Conversely, the dynamic and hierarchical seascape framework will provide the biogeographic context to intercompare ecosystems (Murawski *et al.*, 2010) and scale observations to global phenomena.

Conclusion

Ocean ecologists have sought to characterize the hierarchical patch structure of the marine seascapes for over four decades. Adapting landscape ecology concepts to the dynamic open ocean had been hampered by lack of observational capacity and theoretical framework that can address a system fuelled by planktonic processes, moving and expanding patches, and multiple, yet interrelated scales of biophysical interactions. We now have the observational suite necessary and the opportunity to build operational seascape observing systems that integrate multiple

platforms, consider multiple levels of ecological complexity, and accounts for geophysical dynamics of pelagic ecosystems. By combining satellite remote sensing, marine ecosystem models, ship-based measurement and advanced autonomous measurements, we now can evaluate distributions, processes and spatio-temporal patterns of organisms and populations that reflect large variations from plankton to megafauna in mobility, life span, range, and behaviour. A hierarchical seascape observational framework will facilitate transfer and modification of landscape theory to the dynamic and advective marine realm, allow for scaling of mechanistic experiments and observations to patterns of global change, and contribute to real time monitoring and adaptive management of marine ecosystems.

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