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Introduction

Observing and managing seascapes: linking synoptic oceanography, ecological processes, and geospatial modelling

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The capacity to observe, retrieve, and model the physiographical and hydrographical features of the sea (i.e. seascapes) has surpassed our ability to integrate this information into the assessment and stewardship of marine ecosystems. However, current marine policy that mandates integrated ecosystem assessments demands temporally intensive and spatially extensive predictions of key populations and ecosystem processes and services, particularly those related to habitat use and distribution. In this sense, seascape ecology represents an operational linkage between basic oceanography and applied ecology and management that embraces spatially explicit models of the dynamic distributions of populations, communities and foodwebs through a joint consideration of observational data and ecological processes. For these reasons, the *ICES Journal of Marine Science* solicited contributions to the article theme set, "*Frontiers in seascape ecology*". In this introduction, we present current concepts and developments in seascape ecology, briefly summarize the 10 articles that appear herein, and discuss the most relevant challenges to this nascent discipline. The contributions included in this theme set illustrate the growing relevance of seascape ecology in the multidisciplinary management of marine ecosystems.

Keywords: ecosystem based management, ecosystems oceanography, fisheries oceanography, geospatial modeling, habitat ecology, integrated ecosystem assessments, ocean landscapes, ocean observing systems, operational ocean data products, seascape ecology.

Background and motivation for this article theme set

In the digital era, the capacity to observe, store, retrieve, and synoptically model environmental information has greatly surpassed our ability to integrate these data into the assessment and stewardship of our marine ecosystems. Nowhere is this better demonstrated than in seascapes (i.e. physiographical and hydrographical features of the sea) which, by their nature, are dynamic, diffuse, transient, and without obvious physical boundaries. New technologies allow us to observe key oceanographic variables at multiple scales across ocean basins, or more intensively in coastal and reef habitats. "Operationalizing" these variables through global availability and rapid delivery (telecommunications) permits translation of data into synoptic oceanography—classification and data visualization of water masses structured by constituent physics or energy flow (Kavanaugh *et al.*, 2016). Current marine policy that mandates integrated ecosystem assessments demands temporally intensive and spatially extensive predictions of key populations, and ecosystem processes and services. The nascent field of "seascape ecology" tries to reproduce dynamic oceanography and expand it to include a limited number of controlling ecological processes to make predictions about the complex nature of marine populations and their ecosystems. This discipline moves us away from traditional approaches to define spatial management domains either through stipulation (e.g. unit stock boundary, Secor, 2013) or through spatially implicit modelling (e.g. the Basin Model, MacCall, 1990). In a broad sense, seascape ecology embraces spatially explicit models of dynamic distributions of populations, communities, and foodwebs,
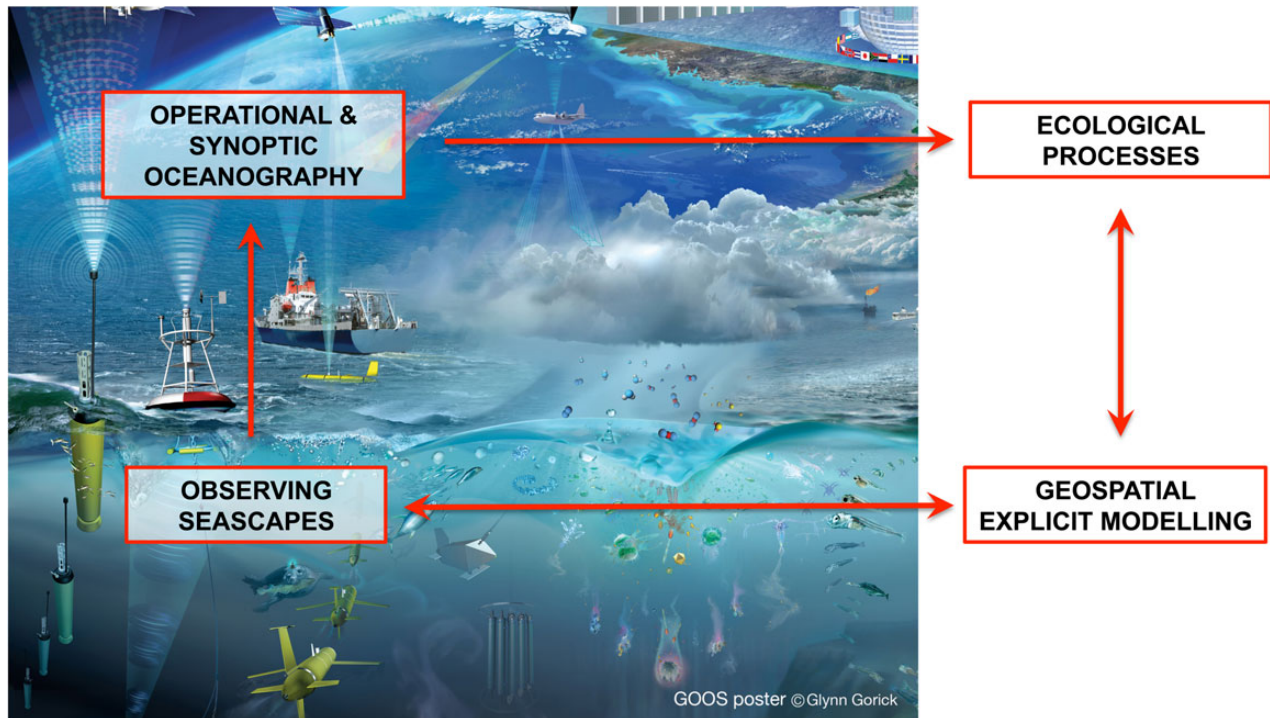
Figure 1. Seascape ecology entails a recursive approach, where observed oceanographic variables are made operational (accessible) and synoptic through wide bandwidth telecommunication. Knowledge of ecological and oceanographic processes is incorporated into spatially explicit models that permit predictions of the dynamic distributions of marine populations and related ecosystem properties (image adapted with the permission of the artist, Glynn Gorick; see also http://unesdoc.unesco.org/images/0018/001878/187825e.pdf).

doing so through joint consideration of observing data and ecological processes (Figure 1). Here, we adopt Manderson's definition: "seascape ecology is a science measuring the effects of the heterogeneity in the properties and processes of the ocean on the interactions of individual organisms, their populations and ecosystems including human socio-economic components" (Manderson, 2016).

Seascape ecology finds its roots in the concepts and analytical methods developed in landscape ecology for terrestrial ecosystems (Wedding *et al.*, 2011). Such a framework readily applies to coastal benthic environments, studies of which have long focused on habitat heterogeneity, patchiness, edge effects, and corridors. From this perspective, seascapes are merely "flooded landscapes" (e.g. seagrass beds, intertidal zones, reefs) with stationary and fixed patch structure and topographies (Pittman *et al.*, 2011). However, pelagic seascapes are fluid in nature; they are nonstationary with high diffusivity, advection, and turbulence (Manderson, 2016). Further, most benthic marine ecosystems may also reflect transience in their physical states that does not allow explicit characterization of spatial features that structure marine populations and communities. Physical variables within seascapes also show a broader range of scale-dependence in their actions than do terrestrial landscapes, requiring data to be collected and integrated across multiple scales (Kavanaugh *et al.*, 2016; Manderson, 2016; Scales *et al.*, 2016a). Therefore, techniques and metrics needed to characterize the pelagic seascape are far more challenging owing to the high frequency and spatial extent over which they must be observed (e.g. Bertrand *et al.*, 2014; Alvarez-Berastegui *et al.*, 2014; Scales *et al.*, 2016a). One of the main applications of seascape ecology, particularly from a dynamic perspective, is the understanding of habitat use and migrations over relevant time-scales—for instance, from hours to days in larvae, or from years to decades in populations. The increasing availability of data from ocean observing systems has the potential to provide near real-time benthic and pelagic habitat modelling of species of importance in a conservation and management context.

A principal goal of seascape ecology is to make efficient use of oceanographic data and ecological process models to predict the distributions and migrations of marine organisms. Such an integrative approach is highly relevant to efforts to assess and manage ecosystems that support major commercial fisheries as they are altered by climate change and other stressors (Link and Browman, 2014). In this sense, seascape ecology can provide a dynamic and adaptive framework over which important oceanographic properties and drivers of change occur. The tools of seascape ecology bear on all ecosystem attributes including habitats, foodwebs, ocean connectivity, species demography and spatial structure, anthropogenic impacts, and ecosystems services. For these reasons, and given the broad spectrum of implications and applications of seascape ecology, the *ICES Journal of Marine Science* solicited contributions to the article them set, "Frontiers in seascape ecology: new approaches to investigate dynamic benthic and pelagic habitats".

We sought contributions that would bring into sharper focus advances in seascape ecology that underlie more dynamic and real-time depictions and understanding of seascapes as drivers of ecosystems attributes, particularly on fish habitat use and migration. This included the dynamic influence of seascapes over relevant time-scales; near real-time habitat modelling; improvements in the parameterization of ecological and behavioural processes shaping benthic and pelagic habitat use and migration; and

temporal changes of scale-dependent processes influencing marine habitats. The contributions to this article theme set are strong evidence that seascape ecology is a growing and increasingly relevant discipline, marrying basic oceanography with applied ecology and management.

About the articles in this theme set: aligning observations with ecology

Seascape ecology has relied on developments in "operational oceanography", and on an improved understanding of mechanisms of the interaction between aquatic organisms and their physical environment. Kavanaugh *et al.* (2016) emphasize the basic influence of physical and energetic properties of the ocean, and how multi-scale synoptic measurements permit observation of ocean processes relevant from the microbe to the whale. Physical hierarchies emerge from processes that are structured by turbulence and advection, but also by high rates of energy dissipation and turnover. They illustrate how complex interdependence between energy dissipation, biology, and other physical processes triggers cross-scale interactions that require large amounts of data to reproduce context-dependent ecological outcomes (e.g. species distributions). Manderson (2016) examines basic physical differences between terrestrial and marine realms but concludes that the foundation of seascape ecology lies in the physiological and behavioural adaptations to life in water. This involves weak physiological regulation and strong habitat selection for ocean properties, structures, and dynamics. Although the perspectives of these two essays differ, Kavanaugh *et al.* (2016) and Manderson (2016) both emphasize how underlying component parts, for instance, the influence of a parcel of water on hourly or daily habitat selection, give rise to aggregate processes such as the dynamic distribution of fish populations. However, in practice, seascape ecology often entails an epiphenomenal approach involving statistical analyses of distributional data together with relevant operational oceanographic information and expected ecological responses.

From an applied point of view, Kavanaugh *et al.* (2016) presents a dynamic and hierarchical seascape framework to address the issue of integrating information across multiple spatial scales and international observing networks. This framework attempts to provide both a broad environmental context to model organismal data and a biogeographic perspective to compare ecosystems and to scale observations to global phenomena. At a mesoscale level, Alvarez-Berastegui *et al.* (2016) illustrate how the dynamic spawning habitat of a top predator with a high commercial value, bluefin tuna *Thunnus thynnus*, can be predicted using operational satellite data. This study, which employs sophisticated numerical modelling, opens new opportunities to implement dynamic spatial management of this species and to adjust larval indices to improve estimates of the spawning-stock biomass. Similarly, Alabia *et al.* (2016) develop an ensemble modelling approach that efficiently utilizes three-dimensional oceanographic information to investigate the habitat associations of Neon flying squid (*Ommastrephes bartramii*) in the North Pacific Ocean.

Seascape ecology also attempts to reveal underlying "ecological processes" that are often obscured when the driving mechanisms are dynamic or otherwise not well captured by asynoptic oceanographic information. For instance, ontogenetic, seasonal, and climate-driven changes in distributions are poorly resolved from distribution data alone. Petrik *et al.* (2016) effectively integrate interannual variability of ocean currents at different spawning locations to understand walleye Pollock (*Gadus chalcogrammus*) nursery habitat on the Bering Sea shelf, and how it affects juvenile survival in contrasting cold and warm years. This highlights the importance of combining information on the spatio-temporal distribution of spawners (when, where, and how many) with ocean currents to properly understand the influence of ocean connectivity on observed distribution patterns at nursery areas (e.g. Hidalgo *et al.*, 2012). Spawning areas are highly context-dependent and, in cold systems such as the Bering Sea, are generally well defined by species-specific ranges of temperature. Vestfals *et al.* (2016) demonstrate the contrasting responses to changes in temperature in the habitat use of two flatfish (Greenland halibut, *Reinhardtius hippoglossoides*, and Pacific halibut, *Hippoglossus stenolepis*) at opposite extremes of their distributional ranges in the eastern Bering Sea. Alvarez-Berastegui *et al.* (2016) illustrate methodologically how to combine mean values and gradients (i.e. rate of spatial variation) of hydrographic variables that capture the heterogeneity in seascape properties and processes at short spatial scales (i.e. fronts and mesoscale structures) that strongly influence the spawning habitat of bluefin tuna.

Spatio-temporal overlap in species distributions is often assessed to infer potential competition and depends on forage resources, oceanographic variables, and habitat physiography. The effect of these drivers is spatially variable, altering the strength of species overlap, and this aspect can be relevant to management. Puerta *et al.* (2016) explore patterns of spatial overlap between the octopus (*Eledone cirrhosa*) and the catshark (*Scyliorhinus canicula*), including shared diets and distributional preferences. The study combines seascape characteristics from surface waters (productivity and temperature) and community characteristics at the bottom (prey abundance, total density, and diversity) to differentiate areas of coexistence and those of competitive exclusion. Turner *et al.* (2016) investigate incidental catches of two riverine herring species (*Alosa pseudoharengus* and *Alosa aestivalis*) in the American Atlantic Herring (*Clupea harengus*) and Atlantic Mackerel (*Scomber scombrus*) fisheries, by characterizing bottom seascapes that influence their distributions and overlap with the targeted species.

Seascape genetics refers to how oceanographic variables and ecological processes structure population genotypes. Silva and Gardner (2016) show that environmental variation in the pelagic habitat can be a barrier to gene flow in New Zealand scallop (*Pecten novaezelandiae*) due to ecophysiological constraints associated with the low tolerance of scallops to high concentrations of either freshwater input or suspended sediment. Padrón and Guizien (2016) show, in contrast, the importance of disentangling the relative contribution of local demography (e.g. recruitment failure) and environmental connectivity in shaping seascape genetics of complex benthic metapopulations.

Improvements in "geospatial modelling" have allowed for a closer alignment between seascape observations and ecological processes. This implies a more conscientious consideration of the spatially explicit nature of ecological interactions. The studies included in this article theme set illustrate that one of the main analytical tools to model species distribution, in terms of habitat and seascape characteristics, are non-linear regression techniques (e.g. general additive modelling). These techniques have proven useful to differentiate local from regional effects of seascape characteristics and to incorporate them into a spatially explicit modelling framework (Bartolino *et al.*, 2012; Ciannelli *et al.*, 2012; Alabia *et al.*, 2016; Alvarez-Berastegui *et al.*, 2016; Puerta *et al.*, 2016; Turner

et al., 2016; Vestfals *et al.*, 2016). This statistical approach allows environmental drivers to be captured at spatial scales relevant to the ecological process of interest. This characteristic is of relevance because species distribution models are widely used nowadays to project potential species expansion or contraction under different climate change scenarios (e.g. Pinsky *et al.*, 2013). However, these models do not capture seascape information at the medium and short scales required for more fully dynamic modelling of spatial distributions, e.g. those occurring over weeks or months. An emerging and flexible geospatial technique that accommodates this limitation is ensemble niche modelling (Alabia *et al.*, 2016; Scales *et al.*, 2016b), which can capture the influence of oceanographic processes on species distributions at different spatial scales.

Seascape ecology represents an operational linkage between ocean science and "applied marine conservation and management". This can lead to improvement in the spatial planning of the use of coastal and reef areas (Silva and Gardner, 2016; Padrón and Guizien, 2016), or setting the methodological framework for near real-time prediction of favourable habitat for pelagic species of commercial importance (Alabia *et al.*, 2016; Alvarez-Berastegui *et al.*, 2016; Turner *et al.*, 2016). This may increase the resolution and effectiveness of management measures by including ecological processes in assessment models.

Conclusions and challenges

The refinement of information obtained from ocean processes, combined with an improvement in the accessibility of oceanographic variables, will play an important role in developing dynamic ocean management (Tintoré *et al.*, 2013; Hobday and Hartog, 2014). The studies included in this article theme set demonstrate that data, tools, and analytical frameworks are already at hand to develop near real-time forecasting of key ecological processes, particularly those related to the sustainability of marine ecosystems and economic activities such as fisheries. The field of "fisheries oceanography" has evolved considerably since the pioneering work of Hjort (1914) and his contemporaries. Nowadays, the increasing availability of operational information from ocean observing systems has prompted scientific and management agendas to make best use of such information, including temporally intensive and spatially extensive predictions that are driving a new era of research towards "operational fisheries oceanography" (e.g. Svendsen *et al.*, 2007; Manderson *et al.*, 2011; Alvarez-Berastegui *et al.*, 2016). Still, many challenges remain to effectively assimilate and integrate data and analyses across multiple scales to produce outcomes that provide robust ecological predictions. There is no single natural scale at which ecological phenomena can be studied because organisms and communities respond on a range of spatial, temporal, and hierarchical scales (Levin, 1992). For instance, distribution of demersal finfish, particularly those displaying vertical migrations such as gadoids, can be shaped by a combination of benthic static features and dynamic characteristics of the pelagic realm. In addition, the relative contribution of benthic and pelagic seascapes drivers can also change with ontogeny (e.g. from nursery to spawning areas).

The perspectives on seascape ecology contributed by Kavanaugh *et al.* (2016) and Manderson (2016) align well with the Movement Ecology Paradigm (Nathan, 2008), under which dispersal and movement of individuals can be predicted from first principles; hydrodynamics, energy transfer, and physiology. Although seemingly abstract, the marriage of these subdisciplines can produce effective management outcomes. As a recent example, operational

oceanographic variables in the California Current are collected, transmitted, and assimilated, and then filtered through a state-space habitat model for blue whales; the result is "Whale Watch" real-time alerts to mariners on regions prone to ship strikes (Irvine *et al.*, 2014, http://www.umces.edu/cbl/whalewatch). On the other hand, a challenge for both movement and seascape ecology is to better incorporate collective behaviours (e.g. Couzin *et al.*, 2005), which are fundamental to how individuals interact with their environment and can produce strong departures from predicted spatial dynamics (Bakun, 2010; Secor, 2015).

A nascent literature is demonstrating the capacity of seascape ecology to predict the dynamic spatial distributions of higher trophic level organisms (Manderson *et al.*, 2011; Alabia *et al.*, 2016; Alvarez-Berastegui *et al.*, 2016; Breece *et al.*, 2016; Queiroz *et al.*, 2016), although this has not as yet been incorporated into formal stock assessments. Simulation modelling, such as management strategy evaluation, can be conducted in parallel with conventional assessment models to improve the conversation between stock assessment scientists and seascape ecologists (Kerr and Goethel, 2013). However, the real challenge is to implement a transdisciplinary integration in which indicators of the spatio-temporal distribution of a species are explicitly included in analytical assessment schemes (e.g. Cadrin and Secor, 2009; Cooke *et al.*, 2016). This integration into applied research will require the development of novel parameterizations of key ecological and behavioural processes incorporating operational seascape information.

A growing body of research is directed towards long-term forecasting of species and ecosystem responses to climate change (i.e. to 2100, IPCC, 2014; e.g. Cheung *et al.*, 2015; Payne *et al.*, 2016, and references therein). However, it is our responsibility to balance our efforts on these long-term scenarios with accurate shorter term predictions, directly applicable to management aims, which are increasingly feasible through effective integration of operational environmental information (Godø *et al.*, 2014). Research on seascape ecology will continue to evolve towards meeting such needs.

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