ICES Journal of
Marine Science

ICES Journal of Marine Science (2017), 74(8), 2276–2279. doi:10.1093/icesjms/fsx070

Comment

Seascapes are landscapes after all; Comment on Manderson (2016): Seascapes are not landscapes: an analysis performed using Bernhard Riemann's rules. ICES Journal of Marine Science, 73:1831–1838

Susan S. Bell[1,*] and Bradley T. Furman[2]

[1]*Department of Integrative Biology, University of South Florida, 4202 E. Fowler Ave., Tampa, FL 33620, USA*
[2]*Department of Environmental Sciences, University of Virginia, 291 McCormick Rd., Charlottesville, VA 22904, USA*

**Corresponding author: tel: +1 813 9742542; fax: +1 813 9743263; e-mail: sbell@usf.edu*

Bell, S. S., and Furman, B. T. 2017. Seascapes are landscapes after all; Comment on Manderson (2016): Seascapes are not landscapes: an analysis performed using Bernhard Riemann's rules. ICES Journal of Marine Science, 73:1831–1838. – ICES Journal of Marine Science, 74: 2276–2279.

Received 27 March 2017; revised 27 March 2017; accepted 3 April 2017; advance access publication 20 June 2017.

Recently, Manderson (2016, Seascapes are not landscapes: an analysis performed using Bernhard Riemann's rules: ICES Journal of Marine Science, 73: 1831-1838) argued that landscape ecology approaches developed in terrestrial habitats have little practical application for the study of marine "seascapes". Here, we offer a contrasting perspective to this over-generalization. We first focus on historical uses of the term "seascape" to delineate the wide range of habitats that have been designated as such. After providing a brief overview of the study of seascape ecology, we argue that concepts and methodology originating from terrestrial disciplines have, in fact, provided an important cornerstone for investigating the dynamics of nearshore marine ecosystems. We present examples of coastal seascape research that have successfully applied terrestrial landscape theory and revisit points raised by Manderson regarding the application of landscape approaches to the marine environment. Overall, we contend that Manderson's thesis may apply to some, but not most, use of landscape constructs for investigating aquatic environments. Moreover, we suggest that the study of coastal landscapes will continue to yield valuable insight into the spatiotemporal workings of aquatic ecosystems, and that this particular avenue of ecological investigation will only increase in its relevance as human impacts intensify.

Keywords: benthic, biogenic, coastal, landscape, patch, pelagic, seascape, spatial scale, terrestrial.

Manderson (2016) (henceforth JM) considers seascapes to be identified mainly by chemical and physical characteristics of water masses. According to JM, strong contrasts between the spatial structure and temporal dynamics of water column constituents and terrestrial landscapes preclude a common approach to understanding marine and terrestrial realms. Adopting the analytic approach formalized by Riemann (Ritchey 1991), he reviews distinctive features of organisms that live on land and those that inhabit marine waters, and compares the physical conditions within which each group physiologically and behaviorally operates. JM lists other differences between terrestrial and marine settings that impede idea sharing such as: terrestrial landscapes are largely characterized by long-lived photosynthetic plants and soils of varying geological composition while seascapes are fueled by small planktonic organisms with hydrodynamics playing an integral role in the pelagic system or; pelagic seascape structure can change on the order of seconds while terrestrial landscapes generally change much more slowly.

Based upon these sets of attributes, JM wonders how concepts of landscape ecology could be of heuristic or practical value for studying seascapes. Further, he raises concern that our knowledge of marine system components is insufficient to build a working synthesis of seascape function, necessitating weak analogies with terrestrial systems to fill in conceptual blanks. JM surmises that seascape ecology "should not rest on the paradigms of terrestrial landscape ecology"; rather the guiding principles should be "... consistent with the importance of the properties and dynamics of the ocean fluid".

We, however, contend that JM's rejection of commonality in the study of landscapes and seascapes is too broad a declaration as it focuses too much on pelagic systems and fails to consider the many benthic habitats that have been foci of ecological study for decades. We argue that existing marine ecological work clearly mitigates the need for the analogies that so vexed JM, and that sufficient information on "patches" within most patch-mosaic models exists to build a viable conceptual synthesis of coastal seascapes. Below, we develop the suitability of landscape concepts for seascape ecology and revisit points raised by JM regarding the application of landscape approaches to the marine environment.

Most seascape studies tend to involve the formation (including self-organization; Rietkerk and van de Koppel, 2008; van der Heide *et al.*, 2012) or spatial arrangement of long-lived, biogenic structures that produce highly visible "patches" embedded within sand or rock matrices (Dunning *et al.*, 1992). Examples of research examining the structure and dynamics of habitat patch mosaics in intertidal and subtidal systems can be found for salt marshes, mangroves, seagrasses, oyster, mussel and/or coral reefs (see Boström *et al.*, 2011 for a review of the literature), and, more recently, kelps (Parnell, 2015). Importantly, landscape theory has been uniquely instrumental in promoting key conceptual and methodological shifts for (1) describing and sampling seascapes across multiple spatial scales (Levin, 1992; Pittman *et al.*, 2004; Furman *et al.*, 2015), (2) evaluating relationships between habitat configuration/connectivity and regional productivity, energy and flows, spatial subsidies, and invasive species introductions (Valentine *et al.*, 2007; Heck *et al.*, 2008; Meynecke *et al.*, 2008), and (3) incorporating concepts of spatial management into marine reserves (Carr *et al.*, 2003; Leslie, 2005; Gaines *et al.*, 2010; Huntington *et al.*, 2010).

If application of landscape principles to the marine environment was plagued with difficulties then it seems likely that research efforts on this topic would have declined over time. However, the term "seascape" has gained popularity among investigators since 2000 (Figure 1). To date, seascape-related work has looked at ecosystems characterized by marine angiosperms, macroalgae or biogenic reefs across a wide geography [e.g. Northern Europe (Bekkby *et al.*, 2008), Australia (Pittman *et al.*, 2004; Davis *et al.*, 2014), USA (Bell *et al.*,1999; Valentine *et al.*, 2007; Carroll *et al.*, 2012), Mediterranean region (Pagès *et al.*, 2014), Caribbean region (Pittman *et al.*, 2007a, b), Africa (Berkström *et al.*, 2013), and China (Han *et al.*, 2007)]. In one of the earliest studies, Ogden *et al.* (1994) proposed a spatial perspective of biotic interactions on coral reefs within a larger seascape. Concurrently, the term "marine landscape" was used when spatial structure was a central theme of investigation in the rocky intertidal (Paine and Levin, 1981), the open ocean (Steele, 1989), as well as seagrass beds (Robbins and Bell, 1994; Fonseca *et al.*, 2002).

As landscape approaches gained traction in marine ecology the term "seascape" became essentially interchangeable with "landscape" (Hinchey *et al.*, 2008; Boström *et al.*, 2011; Pittman *et al.*, 2011). For example, Abadie *et al.* (2015) used both "landscape" and "seascape" as terms in their study utilizing landscape metrics to compare dynamics of human- vs. naturally generated seagrass patches. Yet, acknowledging the strong overlap of coastal seascape

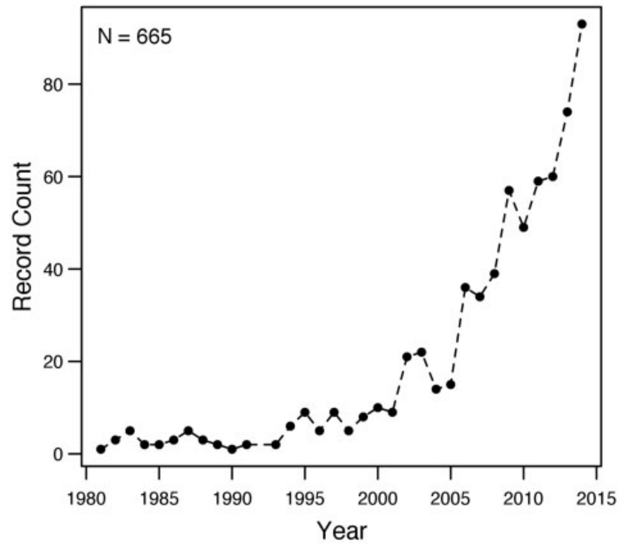

Figure 1. A full time-series of the number of studies containing the key word: "seascape" in either the topic or title fields of ISI Web of Knowledge records (apps.webofknowledge.com; accessed 29 December 2016).

ecology with concepts developed in terrestrial biomes is noticeably missed in JM's essay. Interestingly, in an extremely relevant discussion of marine–terrestrial contrasts, Dawson and Hamner (2008) outlined how "patch formation" in landscapes conceptually differed between pelagic and terrestrial settings; however, benthic marine and terrestrial systems adopt a very similar view of patch dynamics. These authors point out that comparison of marine vs. terrestrial settings has been too often conflated with marine pelagic vs. marine benthic contrasts, thereby impeding development of unifying frameworks. Accordingly, we support the need to distinguish the pelagic from the nearshore environment when gauging the usefulness of landscape ecological theory.

The improvement of tools to obtain spatial signatures of biogenic structures in intertidal and subtidal seascapes, as well as more precise and available characterizations of ocean surface features (i.e. chlorophyll, salinity, temperature) has already helped to advance the field of marine landscape ecology over the last two decades (Kavanaugh *et al.*, 2014; Barrell and Grant, 2015). JM contends that while terrestrial landscapes can be viewed easily, "seascapes are among the most remote and opaque ecosystems on earth". Methodological limitations exist for describing or quantifying seascape structure in some settings but such a characterization clearly does not apply to habitat types found in optically shallow waters or the intertidal zone, or when considering large-scale patterns in pelagic productivity (Manderson *et al.*, 2011). Of course, challenges to data collection in vast and remote (i.e. deep) underwater ecosystems remain, and remote sensing networks such as the IOOS (Manderson *et al.*, 2011), as well as the increasing affordability and functionality of technically advanced aerial and submarine drones, advance the capacity for data-driven observation of marine landscapes (Oliver *et al.*, 2013). Kavanaugh *et al.* (2016) aptly argued that enhanced data capacity may allow for improved translation of terrestrial concepts into the pelagic realm, particularly with regard to patch characterization techniques for the spatio-temporally dynamic pelagic setting. However, acknowledging the utility of, and need for, better data does not imply that current or historical approaches to understanding coastal seascapes are fundamentally flawed.

As tools for collecting and analyzing landscape-level information improve, we expect that the study of coastal seascapes, which provide highly-valued ecosystem services (Costanza *et al.*, 1997), will concurrently increase due to timely and practical concerns (e.g. threats from urbanization, climate change). For example, trophic transfer within and among habitat types, a service highly valued by human populations, is controlled by mechanisms produced and modulated by seascape components. Also, features such as faunal movement between habitat patches and faunal relationships to patch size only become apparent when viewed through the lens of landscape ecology (e.g. spatial subsidies of material and energy flows, habitat and population connectivity, habitat configuration). Although seascape support of higher trophic levels was addressed by JM, he failed to acknowledge that energy flow and connectivity are not products that can be gleaned from ocean observing systems unless they are properly compartmentalized and interpreted within a seascape framework. In fact, much of JM's thesis appears to condense seascape ecology to the development of habitat models for individual species, an approach highly supported by his own research (Palamara *et al.*, 2012; Manderson 2016). Unfortunately, though, this circumscribed sub-discipline does not fairly characterize the full scope of seascape ecology. IOOS and related technologies may allow detection of rapid changes in pelagic seascapes, however they do not yet replace the time-integrated approach used to delineate regions of seasonal productivity nor do they necessarily provide the framework for understanding seascapes at coarser spatial or longer temporal scales. The value of high-resolution data comes as no surprise to long-time practitioners of seascape ecology, but, in our view, access to more data (or lack thereof) does not warrant an overhaul of the theoretical underpinnings of research conducted on coastal landscapes.

Interest in seascape ecology has expanded as ecosystem services have come to the forefront of ecological investigation. Seascapes in coastal zones provide many valuable ecosystem functions and services, such as primary and secondary productivity, carbon sequestration, and nutrient cycling. Yet coastal seascapes are also areas highly modified via human activities such as dredging, watershed and land-use changes, coastal eutrophication, and the harvesting of marine species, thereby generating growing concern among coastal managers about the resilience of coastal settings at the spatial scale of seascapes. Moreover, work to date indicates that the temporal domain of seascape change may be much shorter (months to years) (McGlathery *et al.*, 2012) than the decades to centuries required to document terrestrial landscape dynamics (Turner *et al.*, 2001). Therefore, identifying and tracking seascape change has become increasingly tractable. Accordingly, a principle focus on investigating seascape structure and understanding seascape dynamics at the ecosystem level has emerged as a principal component of coastal management (Carr *et al.*, 2003; Browman and Stergiou, 2004).

Conclusion

In our view, JM's rejection of a landscape approach for understanding seascapes ignores the breadth of published literature, compresses the discipline to single-species applications, and places undue emphasis on difficulties faced by investigations in pelagic settings as indicative of problems plaguing seascape work as a whole. The argument that traditional landscape investigations are paradigmatically flawed, and exposed to error by way of analogy, seems unsupported because the habitat types comprising many coastal seascapes, the nutrient and energy fluxes connecting them, and their associated communities have been well-studied and therefore serve as useful components of seascape ecology. Although JM has identified the promise of IOOS-based modeling for coastal fisheries and its future applicability in selected topics of seascape ecology, IOOS and comparable systems merely provide a means to expand and sharpen our view of the seascape, opening new avenues of research at spatio-temporal scales finer than previously possible. We contend that expanding seascape work into the pelagic realm need neither lead to the upending of its foundations nor the supplanting of key concepts driving progress elsewhere in the marine realm.

Acknowledgements

We thank Mark Fonseca, Amber Stubler, and John Carroll for helpful comments on the manuscript.

References

Abadie, A., Gobert, S., Bonacorsi, M., Lejeune, P., Pergent, G., and Pergent-Martini, C. 2015. Marine space ecology and seagrasses. Does patch type matter in *Posidonia oceanica* seascapes? Ecological Indicators, 57: 435–446.

Barrell, J., and Grant, J. 2015. High-resolution, low-altitude aerial photography in physical geography. Progress in Physical Geography, 39: 440–459.

Bekkby, T., Rinde, E., Erikstad, L., Bakkestuen, V., Longva, O., Christensen, O., Isaeus, M., and Isachsen, P. E. 2008. Spatial probability modelling of eelgrass (*Zostera marina*) distribution on the west coast of Norway. ICES Journal of Marine Science, 65: 1093–1101.

Bell, S. S., Robbins, B. D., and Jensen, S. L. 1999. Gap dynamics in a seagrass landscape. Ecosystems, 2: 493–504.

Berkström, C., Lindborg, R., Thyresson, M., and Gullström, M. 2013. Assessing connectivity in a tropical embayment: fish migrations and seascape ecology. Biological Conservation, 166: 43–53.

Boström, C., Pittman, S. J., Simenstad, C., and Kneib, R. T. 2011. Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. Marine Ecology Progress Series, 427: 191–217.

Browman, H. I., and Stergiou, K. I. 2004. Perspectives on ecosystem-based approaches to the management of marine resources. Marine Ecology Progress Series, 274: 269–270.

Carr, M. H., Neigel, J. E., Estes, J. A., Andelman, S., Warner, R. R., and Largier, J. L. 2003. Comparing marine and terrestrial ecosystems: implications for the design of coastal Marine Reserves. Ecological Applications, 13: S90–S107.

Carroll, J. M., Furman, B. T., Tettelbach, S. T., and Peterson, B. J. 2012. Balancing the edge effects budget: bay scallop settlement and loss along a seagrass edge. Ecology, 93: 1637–1647.

Costanza, R., dArge, R., deGroot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., ONeill, R. V., Paruelo, J., *et al.* 1997. The value of the world's ecosystem services and natural capital. Nature, 387: 253–260.

Davis, B., Baker, R., and Sheaves, M. 2014. Seascape and metacommunity processes regulate fish assemblage structure in coastal wetlands. Marine Ecology Progress Series, 500: 187–202.

Dawson, M. N., and Hamner, W. M. 2008. A biophysical perspective on dispersal and the geography of evolution in marine and terrestrial systems. Journal of the Royal Society Interface, 5: 135–150.

Dunning, J. B., Danielson, B. J., and Pulliam, H. R. 1992. Ecological processes that affect populations in complex landscapes. Oikos, 65: 169–175.

Fonseca, M. S., Whitfield, P. E., Kelly, N. M., and Bell, S. S. 2002. Modeling seagrass landscape pattern and associated ecological attributes. Ecological Applications, 12: 218–230.

Furman, B. T., Jackson, L. J., Bricker, E., and Peterson, B. J. 2015. Sexual recruitment in *Zostera marina*: a patch to landscape-scale investigation. Limnology and Oceanography, 60: 584–599.

Gaines, S. D., White, C., Carr, M. H., and Palumbi, S. R. 2010. Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences of the United States of America, 107: 18286–18293.

Han, M., Sun, Y., and Xu, S. 2007. Characteristics and driving factors of marsh changes in Zhalong wetland of China. Environmental Monitoring and Assessment, 127: 363–381.

Heck, K. L., Carruthers, T. J. B., Duarte, C. M., Hughes, A. R., Kendrick, G., Orth, R. J., and Williams, S. W. 2008. Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. Ecosystems, 11: 1198–1210.

Hinchey, E. K., Nicholson, M. C., Zajac, R. N., and Irlandi, E. A. 2008. Preface: Marine and coastal applications in landscape ecology. Landscape Ecology, 23: 1–5.

van der Heide, T., Eklof, J. S., van Nes, E. H., van der Zee, E. M., Donadi, S., Weerman, E. J., Olff, H., and Eriksson, B. K. 2012. Ecosystem engineering by seagrasses interacts with grazing to shape an intertidal landscape. PLoS One, 7: e42060.

Huntington, B. E., Karnauskas, M., Babcock, E. A., and Lirman, D. 2010. Untangling natural seascape variation from marine reserve effects using a landscape approach. PLoS One, 5: e12327.

Kavanaugh, M. T., Emerson, S. R., Hales, B., Lockwood, D. M., Quay, P. D., and Letelier, R. M. 2014. Physicochemical and biological controls on primary and net community production across northeast Pacific seascapes. Limnology and Oceanography, 59: 2013–2027.

Kavanaugh, M. T., Oliver, M. J., Chavez, F. P., Letelier, R. M., Muller-Karger, F. E., and Doney, S. C. 2016. Seascapes as a new vernacular for pelagic ocean monitoring, management and conservation. ICES Journal of Marine Science, 73: 1839–1850.

Leslie, H. M. 2005. A synthesis of marine conservation planning approaches. Conservation Biology, 19: 1701–1713.

Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award lecture. Ecology, 73: 1943–1967.

Manderson, J. P., Palamara, L., Kohut, J., and Oliver, M. J. 2011. Ocean observatory data are useful for regional habitat modeling of species with different vertical habitat preferences. Marine Ecology Progress Series, 438: 1–17.

Manderson, J. P. 2016. Seascapes are not landscapes: an analysis performed using Bernhard Riemann's rules. ICES Journal of Marine Science, 73: 1831–1838.

McGlathery, K. J., Reynolds, L. K., Cole, L. W., Orth, R. J., Marion, S. R., and Schwarzschild, A. 2012. Recovery trajectories during state change from bare sediment to eelgrass dominance. Marine Ecology Progress Series, 448: 209–221.

Meynecke, J.-O., Lee, S. Y., and Duke, N. C. 2008. Linking spatial metrics and fish catch reveals the importance of coastal wetland connectivity to inshore fisheries in Queensland, Australia. Biological Conservation, 141: 981–996.

Ogden, J. C., Porter, J. W., Smith, N. P., Szmant, A. M., Jaap, W. C., and Forcucci, D. 1994. A long-term interdisciplinary study of the Florida Keys seascape. Bulletin of Marine Science, 54: 1059–1071.

Oliver, M. J., Breece, M. W., Fox, D. A., Haulsee, D. E., Kohut, J. T., Manderson, J. P., and Savoy, T. 2013. Shrinking the haystack: using an AUV in an integrated ocean observatory to map Atlantic Sturgeon in the coastal ocean. Fisheries, 38: 210–216.

Pagès, J. F., Gera, A., Romero, A., and Alcoverro, T. 2014. Matrix composition and patch edges influence plant–herbivore interactions in marine landscapes. Functional Ecology, 28: 1440–1448.

Paine, R. T., and Levin, S. A. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs, 51: 145–178.

Palamara, L., Manderson, J., Kohut, J., Oliver, M. J., Gray, S., and Goff, J. 2012. Improving habitat models by incorporating pelagic measurements from coastal ocean observatories. Marine Ecology Progress Series, 447: 15–30.

Parnell, P. E. 2015. The effects of seascape pattern on algal patch structure, sea urchin barrens, and ecological processes. Journal of Experimental Marine Biology and Ecology, 465: 64–76.

Pittman, S. J., Caldow, C., Hile, S. D., and Monaco, M. E. 2007a. Using seascape types to explain the spatial patterns of fish in the mangroves of SW Puerto Rico. Marine Ecology Progress Series, 348: 273–284.

Pittman, S. J., Christensen, J. D., Caldow, C., Menza, C., and Monaco, M. E. 2007b. Predictive mapping of fish species richness across shallow-water seascapes in the Caribbean. Ecological Modelling, 204: 9–21.

Pittman, S. J., McAlpine, C. A., and Pittman, K. M. 2004. Linking fish and prawns to their environment: a hierarchical landscape approach. Marine Ecology Progress Series, 283: 233–254.

Pittman, S. J., Kneib, R. T., and Simenstad, C. A. 2011. Practicing coastal seascape ecology. Marine Ecology Progress Series, 427: 187–190.

Robbins, B. D., and Bell, S. S. 1994. Seagrass landscapes: a terrestrial approach to the marine subtidal environment. Trends in Ecology and Evolution, 9: 301–304.

Rietkerk, M., and van de Koppel, J. 2008. Regular pattern formation in real ecosystems. Trends in Ecology and Evolution, 23: 169–175.

Ritchey, T. 1991. Analysis and synthesis: on scientific method—based on a study by Bernhard Riemann. Systems Research, 8: 21–41.

Steele, J. H. 1989. The ocean 'landscape'. Landscape Ecology, 3: 185–192.

Turner, M. G., Gardner, R. H., and O'Neill, R. V. 2001. Landscape Ecology in Theory and Practice: Pattern and Process. Springer, New York.

Valentine, J. F., Heck, K. L., Blackmon, D., Goecker, M. E., Christian, J., Kroutil, R. M., Kirsch, K. D., Peterson, B. J., Beck, M., and Vanderklift, M. A. 2007. Food web interactions along seagrass-coral reef boundaries: effects of piscivore reductions on cross-habitat energy exchange. Marine Ecology Progress Series, 333: 37–50.

Handling editor: David Secor