



## Reply

### Response to Bell and Furman (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

Manderson, J. P. Response to Bell and Furman (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: 2280–2282; advance access publication 20 June 2017.

“... comparison of marine and terrestrial dynamics has more than theoretical interest. As we utilize marine and terrestrial environments, the consequences, deliberate or accidental, depend on the responses to physical and chemical change. The imposition of terrestrial standards for marine problems may produce too strict or too lax criteria—or most likely quite inappropriate ones”

*John H. Steele (1991) Can ecological theory cross the land-sea boundary?*

Bell and Furman (2017) contend that concepts and methods developed in terrestrial landscape ecology including the patch-corridor-matrix and patch-mosaic models originally developed by Forman (1995) and operationalized by McGarigal and Marks (1995) and others have been important cornerstones for the investigation of marine systems. In their comment, they emphasize heterogeneity in solid biotic and abiotic structures associated with the seabed in intertidal and shallow subtidal areas, and seem to suggest that patches defined by steep gradients in seabed structures should be treated as the fundamental units of analysis in “most” marine systems. They argue that the emphasis I placed in my *Food for Thought* essay (Manderson, 2016) on the importance of the ocean liquid in defining the habitats in the sea and in determining the pace of marine populations and ecosystems “may apply to some but not most marine aquatic systems”.

I agree with Bell and Furman that important advances have been made in marine ecology by applying the heuristic devices of terrestrial landscape ecology including the patch-mosaic model to research questions. The reverse is also true. Studies in intertidal

and shallow water ecology have improved our understanding of important ecological processes like disturbance dynamics that have informed terrestrial landscape ecology (e.g. Sousa, 1979; Turner *et al.*, 2001). However, to state that the ocean liquid defines habitat and the pacing of ecosystem processes in “some but not most marine aquatic systems” ignores the fact that all marine organisms live in seawater and that meeting life's fundamental requirements in a salty liquid is very different from meeting them in a gas. My objective in the essay was to use Riemann's analytical method as a tool to think about whether the fundamental principles of biology and physics might cause landscape paradigms, including the patch-mosaic heuristic, to “break” in the sea. I wanted to know whether further advances in seascape ecology and its effective application to the practical problem of managing human resource use in the sea might require a shift in emphasis from sharp gradients in solid structures associated with the seabed to the liquid; its properties and its fluxes.

Bell and Furman don't seem to contest the central argument I tried to develop using Riemann's rules of analysis. The argument rested upon the following “laws”. (i) All living organisms must meet the specific, conservative requirements of cellular metabolism including its energy requirements. Thus, all processes, at all levels of ecological organization from cells to whole ecosystems rest on the foundation of cellular metabolism. (ii) The physical properties and dynamics of the media in which an organism and its metabolism is embedded determine the specific strategies of behavioural habitat selection and internal physiological regulation required and available for meeting metabolic requirements. Ecosystems are textured by external environmental heterogeneity

in specific variables and processes that the organisms must respond to in order to meet metabolic requirements and close their life cycles. (iii) Organisms in the oceans and on land are embedded in media in different physical states with very different physical properties including those affecting metabolism and the behavioral and physiological strategies available to them for meeting metabolic requirements. From the perspective of the organism, different properties and processes texture seascapes and landscapes. Based on these “laws” I concluded that seascapes are primarily textured by heterogeneities in specific properties of the ocean liquid including its flows. Bell and Furman imply that I adopted a narrow “single species” perspective in my essay. I did adopt an “organism centered perspective” because ecologically relevant environmental heterogeneity in any ecosystem is defined by the responses of organisms. The eminent landscape ecologist John Wiens advocated for just this perspective when defining relevant environmental heterogeneity and its scales of variability for organisms living on terrestrial landscapes (Wiens, 1976; Wiens and Milne, 1989; Kotlair and Wiens, 1990; Wiens *et al.*, 1995).

In their comment Bell and Furman emphasize intertidal and shallow sub-tidal marine systems and particularly patches defined by sharp gradients in the types of solid structures associated with the seabed that are obvious to us as human observers. They contend that coastal and nearshore biomes that easily lend themselves to the patch-mosaic heuristic represent “most” marine systems. However, the biotopes Bell and Furman highlight only exist along the narrow boundary between land and sea where life’s media changes from a gas to a liquid. They discuss rocky intertidal areas and mangroves forests hosting organisms that must possess sophisticated structural and physiological adaptations to protect and maintain the integrity of their metabolisms in the face of extreme environmental conditions associated with living in *both* air and seawater. They discuss biotopes defined and supported by seagrass, kelp and hermatypic coral photosynthesizers that occur in water shallow enough that sunlight descends onto the seabed; seabeds that therefor limit the loss of nutrients from the photic zone. These benthic photosynthesizers are exempt from many of the nutrient limitations faced by photosynthesizers in *most* marine ecosystems in which mixing of the liquid is required to inject and concentrate nutrients in the photic zone. Bell and Furman also mention subtidal biomes including shellfish beds which are defined by sessile suspension feeders fully dependent on hydrodynamic processes to deliver the organic matter they require as fuel for metabolism. Like all the other biotopes Bell and Furman mention these exist in the coastal zone where the surface area to volume ratio of water is highest. Along this narrow fringe of water at the land-sea boundary the high-frequency environmental variability of the atmosphere which is predominately “white” or “blue” is damped and lengthened into lower frequency “red” and “brown” environmental variability characteristic of the ocean (Steele, 1985; Vasseur and Yodzis, 2004; Ruokolainen *et al.*, 2015). The amplitudes and frequencies of external environmental variability are reflected in the dynamics of populations and the ecosystems they compose (Turchin, 2003). Populations and ecosystems along the land sea-boundary are regulated by environmental forcings that fall midway along the spectrum between the “white” and “blue” environmental “noise” of terrestrial landscapes and the “red” and “brown” environmental “noise” characteristic of seascapes. Are Bell and Furman emphasizing biotopes representative of the *most* marine systems, or are they just

discussing the familiar ones that exist along the land-sea boundary, share some characteristics with terrestrial landscapes, and are accessible to landscape bound observers like ourselves?

The coastal biotopes Bell and Furman emphasize are shaped by some processes which are similar to those shaping terrestrial landscapes. Nevertheless, shallow water organisms live in a liquid instead of a gas and a shift in focus from solid seabed structures we easily recognize toward the hydrodynamic processes we find more difficult to observe has allowed us to better understand the structure and dynamics of coastal seascapes. One only needs to consider the ways coastal estuarine ecosystems are fundamentally organized by dynamic heterogeneities in the liquid including its flows that are created by tidal and wind driven mixing of tidal inflows of seawater and freshwater inflows derived from the atmosphere. We know estuarine ecosystems are built on the foundations of these heterogeneities in the liquid that include the spatially complex and dynamic circulation patterns that control trophic and life cycle coupling as well as the formation of vertical and horizontal fronts. Even in these shallow coastal systems gradients in the properties and processes of the liquid are the template upon which sessile and mobile plants and animals sort and assemble into communities, often on a seasonal basis, according to strategies of behavioral habitat selection and physiological regulation available to them for meeting the requirements of metabolism and life cycle closure (Attrill and Rundle, 2002; Whitfield *et al.*, 2012; Cloern *et al.*, 2017; and others).

I agree with Bell and Furman that landscape ecology and some of its heuristics have been useful for the study of seascapes. However, seascapes are ecosystems embedded in a salty liquid not a gas, and seascape ecology needs rest on foundations of physical and biological oceanography, including fisheries oceanography which are quite obviously pertinent and also have long and rich traditions (Hjort, 1914; Stommell, 1963; Steele, 1978; Sinclair, 1988; Schneider, 1994; Bakun, 1996; Mann and Lazier, 2006; and many others). Marine seascape ecology is becoming operationalized for the tactical management of human resource use in the sea. Operational products can only be effective if they explicitly incorporate the liquid and its essential role in structuring seascapes and controlling their dynamics. Integrating the liquid requires us to look upstream for causes and downstream for consequences over much larger spatial scales and shorter time scales than is the case on terrestrial landscapes. This is the lesson of the 2010 Deep Water Horizon Oil Spill whose impacts spread so rapidly over such large spatial extents because drag rather than gravity is the dominant force controlling movement in the sea. Integrating the liquid also forces us to accept that many patterns and processes in marine ecosystems may not recur in specific geographic locations for very long because the properties of the liquid, that have such strong effects on marine organisms and their abilities to meet the demands of metabolism and life history closure, are spatially dynamic. We are learning that lesson in the rapid shifts in distribution and productivity of marine populations and ecosystems occurring in response to anthropogenic climate change. Our failure to fully integrate the liquid and its dynamics into operational seascape ecology is creating crises of human governance that are particularly acute in temperate marine systems that are changing most rapidly in response to global climate change (Pinsky and Fogarty, 2012; Jensen *et al.*, 2015). The recognition that unforeseen problems can arise when terrestrial heuristics are applied to marine systems is not new. John

Steele recognized it over 25 years ago when he addressed the question “Can ecological theory cross the land-sea boundary” (Steele, 1991).

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## References

- Attrill, M. J., and Rundle, S. D. 2002. Ecotone or Ecocline: Ecological Boundaries in Estuaries. *Estuarine, Coastal and Shelf Science*, 55: 929–936.
- Bakun, A. 1996. *Patterns in the Ocean: Ocean Processes and Marine Population Dynamics*. University of California Sea Grant, San Diego, California, USA.
- Bell, S., and Furman, B. 2017. Seascapes are landscapes after all; Comment on Manderson (2106): Seascapes are not landscapes: an analysis performed using Bernhard Riemann’s rules: *ICES Journal of Marine Science*, 73: 1831–1838.
- Cloern, J. E., Jassby A. D., Schraga, T., Kress, E. S., and Martin, C. A., 2017. Ecosystem Variability Along the Estuarine Salinity Gradient: Examples from Long-Term Study of San Francisco Bay. *Limnology and Oceanography*, doi:10.1002/lno.10537.
- Forman, R. T. T. 1995. Some general principles of landscape and regional ecology. *Landscape Ecology*, 10: 133–142.
- Hjort, J. 1914. *Fluctuations in the Great Fisheries of Northern Europe Viewed in the Light of Biological Research*. Conseil Permanent International Pour l’Exploration de la Mer: Rapports et Procès-Verbaux des Réunions, vol. 20, 228 pp.
- Jensen, F., Frost, H., Thøgersen, T., Andersen, P., and Andersen, J. L. 2015. Game theory and fish wars: the case of the Northeast Atlantic mackerel fishery. *Fisheries Research*, 172: 7–16.
- Kotlair, N. B., and Wiens, J. A. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, 59: 253–260.
- Manderson, J. P. 2016. Seascapes are not landscapes: An analysis performed using Bernhard Riemann’s rules. *ICES Journal of Marine Science*, 73: 1831–1838.
- Mann, K. H., and Lazier, J. R. N., 2006. *Dynamics of Marine Systems*. 3rd edn. Blackwell, Malden, Mass.
- McGarigal, K., and Marks, B. J., 1995. Fragstats: spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW: 351, U.S. Forestry Service, Portland, Oregon.
- Pinsky, M. L., and Fogarty, M. 2012. Lagged social-ecological responses to climate and range shifts in fisheries. *Climatic Change*, 115: 883–891.
- Ruokolainen, L., Lindén, A., Kaitala, V., and Fowler, M. S. 2015. Ecological and evolutionary dynamics under coloured environmental variation. *Trends in Ecology and Evolution*, 24: 555–563.
- Schneider, D. C. 1994. *Quantitative Ecology: Spatial and Temporal Scaling*. Academic Press, San Diego.
- Sinclair, M. 1988. *Marine Populations: An Essay on Population Regulation and Speciation*. University of Washington Press, Seattle.
- Sousa, W. P. E. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, 65: 1918–1935.
- Steele, J. H. 1978 *Spatial Pattern in Plankton Communities*. Plenum Press, New York, London.
- Steele, J. H. 1985. A comparison of terrestrial and marine ecological systems. *Nature*, 313: 355–358.
- Steele, J. H. 1991. Can ecological theory cross the land-sea boundary?. *Journal of Theoretical Biology*, 153: 425–436.
- Stommell, H. 1963. Varieties of oceanic experience. *Science* 139: 572–576.
- Turchin, P. 2003. *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton.
- Turner, M. G., Gardner, R. H., and O’Neill R. V., 2001. *Landscape Ecology in Theory and Practice: Pattern and Process*. Springer-Verlag, New York.
- Vasseur, D. A., and Yodzis, P. 2004. The color of environmental noise. *Ecology*, 85: 1146–1152.
- Whitfield, A. K., Elliott, M., Basset, A., Blaber, S. J. M., and West, R. J. 2012. Paradigms in estuarine ecology – a review of the Remane diagram with a suggested revised model for estuaries. *Estuarine, Coastal and Shelf Science*, 97: 78–90.
- Wiens, J. A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics*, 7: 81–120.
- Wiens, J. A., Crist, T. O., With, K. A., and Milne, B. T. 1995. Fractal patterns of insect movement in microlandscape mosaics. *Ecology*, 76: 663–666.
- Wiens, J. A., and Milne, B. T. 1989. Scaling of ‘landscapes’ in landscape ecology, or, landscape ecology from a beetle’s perspective. *Landscape Ecology*, 3: 87–96.

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