



Contribution to the Themed Section: 'Seascape Ecology' Food for Thought

Seascapes are not landscapes: an analysis performed using Bernhard Riemann's rules

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

Received 15 July 2015; revised 18 March 2016; accepted 3 April 2016.

Applied seascape ecology rests on paradigms of terrestrial landscape ecology. Patches defined by persistent seabed features are the basic units of analysis. Persistent oceanographic features provide context while dynamic features are usually ignored. Should seascape ecology rest on terrestrial paradigms? I use Reimann's rules of analysis to identify differences between seascapes and landscapes. Reimann's method uses hypotheses about system function to guide the development of models of system components based upon fundamental "laws". The method forced me to avoid using terrestrial analogies in understanding of organism-habitat relationships. The fundamental laws applying to all organisms were the conservative metabolic requirements underlying individual performance and population growth. Physical properties of the environment; specifically those dictating strategies available to organisms meeting metabolic requirements, were the "laws" applying to the external environment. Organisms living in the ocean's liquid meet most metabolic requirements using strong habitat selection for properties of the liquid that are controlled by "fast", often episodic, atmospheric and tidal forces. Seascapes are therefor primarily driven by dynamic hydrography including mixing processes. In contrast, most terrestrial organisms are decoupled by gravity and physiological regulation from an atmospheric fluid that is metabolically more challenging. They show strong habitat selection for many essential metabolic materials concentrated on the land surface where slower biogeochemical processes including soil development drive ecological dynamics. Living in a liquid is different from living in a gas and resource use management in the oceans needs to be tuned to seascapes dynamics that is driven primarily by hydrodynamics and secondarily by seabed processes. Advances in ocean observing and data assimilative circulation models now permit the rapid development of applied seascape ecology. This development is essential now that changes in global climate are being rapidly translated into changes in the dynamics of the ocean hydrosphere that structures and controls ecological dynamics within seascapes.

Keywords: seascape ecology, landscape ecology, marine habitat ecology, analysis and synthesis, thought experiment.

Introduction

The management of natural resource use needs to be accurately tuned to the dynamics of ecosystems producing the resources. Spatial planning is currently considered to be the tool most useful for tactical management of resource use in marine ecosystems (Crowder *et al.*, 2006; Douvere, 2010; Norse, 2010). The approach apportions "common property" marine resources to conservation, fisheries, energy production, and other uses to balance tradeoffs among ecological, social, and economic objectives. Since it emphasizes apportionment in space, spatial planning relies on habitat classification that divides up seascapes based on locations of relatively

stationary and steep resource gradients. Usually topographic, geological, and biogenic features associated with the seabed define the primary gradients. Most classification frameworks get seascapes wet by placing seabed patch mosaics within broader scale oceanographic contexts defined by relatively stationary, persistent gradients in water column properties such as temperature, salinity, oxygen, and wave motions. Ocean currents controlling the transport of particles, including pelagic larvae, are sometimes considered (Mumby *et al.*, 2011). However, persistent, relatively stationary features associated with the seabed are usually the furniture on the oceanographic stage and the basic units of analysis and spatial

management. Dynamic water column properties and processes are often viewed as a nuisance and sometimes ignored. The paradigms of terrestrial landscape ecology including the patch-mosaic paradigm currently lie at the foundation of marine habitat classification and applied seascape ecology. Should applied seascape ecology rest on the foundation of terrestrial paradigms? The question is of great practical importance because marine ecosystems are changing rapidly in space and time as a result of global climate change while human demand for marine resources is also increasing. In this essay, I attempt to answer this question by performing a formal analysis of the basic ecological differences between seascapes and landscapes.

Method

Seascape ecology can be defined as a discipline describing the effects of interactions between heterogeneity in ocean properties and processes and individual organisms, their populations and ecosystems including human socio-ecological and economic activities. As whole systems emerging from interactions between organisms and the environment, seascapes invite the application of synthesis as the primary method for developing a coherent, “bottom up” understanding of whole system processes arising from causes at the level of system components. Analysis which applies a “top down” approach, using hypotheses about whole system function to guide the development of conceptual models about the ways interacting components could give rise to system function based upon fundamental “laws”, usually plays a supportive role. If we replace the phrase “heterogeneity in ocean properties and processes” with “heterogeneity in terrestrial properties and processes” in the definition of seascape ecology above, the objectives of seascape and landscape ecology are exactly the same. Furthermore, both disciplines rely on synthesis as the primary method of scientific inquiry.

The 19th century German mathematician Bernhard Riemann discussed the foundations and requirements of analysis and synthesis as scientific procedures in his investigation of “The mechanism of the ear” (reviewed by [Ritchey, 1991](#)). Analysis and synthesis are complementary and require different degrees of certainty in our knowledge of the whole system and its component parts. Analysis begins with a sufficient hypothesis about what the whole system “does”. This function then guides the development of conceptual models about the ways components may allow the system to accomplish its function. Analysis does not require components and their interactions to be understood with certainty; only that our conceptual models of them are consistent with fundamental laws. Analysis is best applied in early investigations of opaque systems whose functions are relatively clear but accomplished through interactions of components we don’t know with certainty. Synthesis, on the other hand, uses knowledge of components and their interactions to infer whole system function. As a result, synthesis requires relatively certain knowledge of system components and is a good starting point for the investigation of transparent systems. Performing synthesis on opaque systems can be tricky. When uncertain about the nature of components we often resort to analogy to explain how they may work and interact. Important discoveries have been made by likening components and their interactions to more familiar phenomena. For example, Nicolas [Carnot \(1824\)](#) developed a mechanistic theory of the heat engine by analogy to the flow of water over a waterfall (reviewed in [Gentner and Jeziorski, 1993](#)). However, analogies can also fail spectacularly when we force our understanding of a system to match expectations that are inconsistent with the true properties and processes underlying the system.

We are warm blooded, air-breathing creatures living along the interface between land and a transparent atmosphere abundant with gases essential to life. Our ecological intuitions are shaped by experience on terrestrial landscapes and with landscape components we easily observe. Applying synthesis as the primary method for understanding the ecology of terrestrial landscapes makes perfect sense. Landscapes are transparent to us and our terrestrial intuitions usually serve us well when we are forced to rely on analogy to describe interactions of components we do not fully understand. Seascapes, on the other hand, are among the most remote and opaque ecosystems on the earth to us. Our knowledge of marine organisms and their interactions with the environment is highly uncertain. Living in a liquid is different from living in a gas and our terrestrial intuitions can fail us as we draw analogies to describe the ways marine organisms interact with the liquid surrounding them. It is therefore risky to rely on synthesis as the primary method of investigation in the early development of seascape ecology. To avoid traps set by terrestrial intuition and analogies, I apply Riemann’s rules of analysis to explore the basic ecological differences between seascapes and landscapes.

An analysis of seascapes and landscapes using Bernhard Riemann’s rules

Every analysis begins with a hypothesis describing the function of the whole system. We must therefore decide what seascapes actually do. All ecologists can probably agree that the task of any functioning seascape is to provide resources sufficient to maintain important life history processes of individuals belonging to one or more species. Seascapes and the habitats composing them function only if they support living organisms over some time horizon. We can make our hypothesis about the function of seascapes relevant to the species populations by grounding it in classical ideas about the species niche. Niches are defined by external physical and biological variables and resources, including species interactions producing population growth rates greater or equal to zero ([Grinnell, 1917](#); [Elton, 1927](#); [Hutchinson, 1957](#); [Chase and Leibold, 2003](#); [Holt, 2009](#)). Niches are abstract “spaces”, defined by abiotic and biotic environmental variables that have no spatial or temporal dimensions. This follows Hutchinson’s concept of the basic niche as an abstract “hypervolume” defined by N environmental dimensions ([Hutchinson, 1957](#); [Hutchinson, 1978](#)). Habitats, on the other hand, are projections of species niches on the spatial and temporal heterogeneity of the external environment. Habitats are niches manifested in space and time (see also [Colwell and Rangel, 2009](#)).

We can use the niche-habitat concept to refine our hypothesis about what seascapes do. Seascapes supply the spatial and temporal diversity of resources required for one or more species to achieve population growth rates greater than or equal to zero. Using the duality of the niche-habitat concept to define the function of ecological systems forces us to identify important external environmental properties and processes structuring and controlling the dynamics of seascapes, landscapes, and their habitats purely based on their effects on organism performance rates underlying population growth. Every functioning landscape also supplies the diversity of specific resources required for one or more terrestrial species to achieve population growth rates greater than or equal to zero. The ecological function of seascapes and landscapes is exactly the same.

The next step in the analysis is to use the system function to guide the development of conceptual models of interacting components

based on fundamental “laws”. The components of seascapes are living organisms and the specific external environmental characteristics and resources that regulate, control, and limit performance rates underlying population growth. The fundamental “law” that applies to all living organisms is that cellular metabolism fuels individual performance and population productivity (Fry, 1947; Neill *et al.*, 1994; Brown, 2004; Sousa *et al.*, 2008; Sibly *et al.*, 2012). The core metabolic machinery and processes through which energy is acquired, transformed, and allocated to do biological work are conservative (Hochachka and Somero, 2002). For metabolism to occur: proteins, enzymes, nucleic acids, lipids and lipoprotein cell walls, and the structured water supporting them must be both stable and flexible. The dynamic stability of metabolic machinery and its sustained operation are extremely sensitive to specific conditions in the extracellular environment that are universally required. These specific extracellular conditions are defined by the availability of water, the nature and concentrations of solutes, the availability of molecular oxygen, and for plants, carbon dioxide. Pressure affects the availability of gases essential to specific metabolic pathways and enzyme structure. Temperature also affects the structural integrity of enzymes and regulates metabolic reaction rates. Finally raw materials serving as building blocks for metabolic machinery and as “fuel” for respiration, photosynthesis, and chemosynthesis are required. These materials include light, inorganic nutrients required by photosynthetic plants, chemical compounds for chemosynthesizers, as well as organic “food” for respiration. Our models of living organisms: the way they are structurally, physiologically and behaviorally designed; must be consistent with the law that organisms must meet these specific, universal and conservative requirements of metabolism. Organisms living in the sea and on land must meet exactly the same core metabolic requirements using structural adaptation, physiological regulation and behavioural habitat selection.

The fundamental “law” pertaining to the external environment must be its physical properties. Here, the sea and land are very different, particularly with respect to external environmental properties affecting the intracellular environment and metabolism (Table 1). We can use the specific metabolic requirements to organize a discussion of the physical properties of the environment and the degree to which organisms meet a requirement by habitat selection and, or mechanisms of internal regulation that allow for physiological decoupling from the external environment. Since seascape and landscape systems emerge from interactions between organisms and the environment, the approach should allow us to identify basic differences in the properties and processes structuring and regulating seascape and landscape systems.

The challenge of maintaining water-solute balance in tissues required for cellular metabolism is determined by the strengths of concentration gradients of water and solutes crossing from tissues to the external environment (Denny, 1993; Hochachka and Somero, 2002; Costa *et al.*, 2013; Larsen *et al.*, 2014). Organisms in seawater are exposed to much weaker concentration gradients for both water and osmotically active solutes than are terrestrial organisms surrounded by the atmosphere (Table 1). In the oceans, liquid water is certainly not a limited habitat resource. Furthermore, when compared with the atmosphere, osmotically active elements and compounds are abundant in seawater at concentrations relatively near those required by metabolically active tissues. Concentrations of hydrogen ions in seawater are also relatively close to concentrations necessary for the normal functioning of mitochondria and blood. Since water, salt, and pH content of the

external environment is relatively similar to concentrations required within metabolically active tissues, organism in the sea conform to, or rely on relatively weak physiological regulation and habitat selection for volumes of ocean liquid with required properties. In contrast, the atmosphere surrounding terrestrial organisms is largely devoid of biologically accessible water and solutes including hydrogen ions. To maintain concentrations of water, salts, and ions required by metabolically active tissues against strong concentration gradients, terrestrial organisms use strong physiological regulation of tissue water-ion balance to partially decouple internal from external environments. They combine internal regulation with strong habitat selection for patches of water and food containing essential ions concentrated by gravity along the interface between land and the atmosphere.

On the other hand, gases essential to respiration and photosynthesis are much scarcer in the sea than on land. Oxygen dissolved in seawater is about 2.5% of the concentration of the gas in the atmosphere (Denny, 1993; Table 1). Oxygen diffuses $\sim 10\,000$ times more slowly in seawater than air. In the ocean, most organisms inspire seawater to extract oxygen from solution using specialized structures like gills. Oxygen is an important limiting habitat resource in the sea and most marine organisms seek out volumes of ocean liquid with the oxygen concentrations necessary for specific levels of metabolic performance (Prince *et al.*, 2010; Trueblood and Seibel, 2012; Brady and Targett, 2013). Carbon dioxide concentrations are not low in the ocean, but diffusion of the gas is just as slow in seawater as it is for oxygen (Table 1). Carbohydrate synthesis would be limited by the slow diffusion of carbon dioxide for many photosynthetic marine plants if it were not for their small body sizes, high surface area to volume ratios and the ability to use bicarbonate as an alternative carbon source (Denny, 1993). The solubility and exchange of gases between tissues and the external environment are also affected by pressure. At sea level pressure is about 1.013 bar and increases 1.013 bar with each 10 m increase in water depth in the ocean. Decreases in pressure with each 10 m increase in altitude in the atmosphere occur nearly 1000 times more slowly ($0.0012\text{ bar } 10\text{ M}^{-1}$). In the atmosphere, concentrations of oxygen and carbon dioxide and their diffusivities and partial pressures are usually high enough that essential gases are not limited habitat resources except in subterranean and high altitude landscapes (Denny, 1993; Hochachka and Somero, 2002). Oxygen is, in fact, superabundant in most of the atmosphere and many terrestrial organisms have evolved metabolic pathways to cope with the oxygen toxicity (Hochachka and Somero, 2002).

Temperature sets the pace of metabolism and the thermal properties of seawater in the ocean and air in the atmosphere are also profoundly different (Denny, 1993; Kingsolver, 2009; Table 1). The heat capacity of the ocean is four times higher than the atmosphere while the rate of heat transfer by conduction is 23 times faster in seawater than air. The exchange of heat between objects with temperatures different from the surrounding fluid by free convection and forced convection occurs ~ 100 times, and 200 times faster in the sea than on land. High heat capacity and transfer rates combined with the huge volume of seawater in the ocean limits ranges and rates of change of temperature in the marine environment (Steele, 1991; Mamayev, 1996). Most organisms living in the ocean do not need strong internal mechanisms of thermoregulation to maintain body temperatures in the range required by metabolism. This is fortuitous because rates of convective heat transfer are so high in the sea that physiological thermoregulation is too costly for most water “breathing” organisms (Pauly, 2010). With oxygen in such short

Table 1. Physical properties of seawater surrounding organisms in seascapes and air surrounding organisms on landscapes, their ratios and effects on metabolic requirements and energetics.

Physical property (units)	Seawater (@20 °C and 3.5‰)	Air (@20 °C)	Ratio seawater:air	Effect on metabolism and energetics	Additional comments
Density (kg m ⁻³)	1024.76	1.205	850.4232	Relative effects of drag and gravity on particle transport, movement, and buoyancy	Tissue densities: fat = 930, muscle = 1065, bone = 2500, shell = 2700
Dynamic viscosity (N s ⁻¹ m ⁻²)	1.09 × 10 ⁻³	1.82 × 10 ⁻⁵	59.9560	Relative effects of drag and gravity on particle transport, movement, and buoyancy	
Pressure (bar)	11.0651	1.00125	11.0513	Gas partial pressures. Availability of O ₂ for respiration and CO ₂ for photosynthesis	Values are for 100 m below and 100 m above sea level
Water content (% by weight)	~100	2	50	Osmotic balance. Scaffold for metabolic machinery	Tissues: 65–90%
Concentration of solutes (% by weight)	3.5	1 × 10 ⁻⁴	3.5 × 10 ⁴	Osmotic balance	Tissues: 2.8–3.2%
Hydrogen ions in solution (−log[mol H ⁺ l ⁻¹])	7.8–8.4	0		Proper functioning of mitochondria and blood	Mitochondria: 7.5 Blood: 7.34–7.45 Dry air has no PH
Oxygen concentration (mol m ⁻³)	0.231	8.714	0.0265	Terminal acceptor in electron transport chain in aerobic respiration	
Oxygen diffusion coefficient (m ⁻² s ⁻¹)	2.1 × 10 ⁻⁹	2.03 × 10 ⁻⁵	1.03 × 10 ⁻⁴	Terminal acceptor in electron transport chain in aerobic respiration	
Carbon dioxide concentration (mol m ⁻³)	9.7 × 10 ⁻³	1.38 × 10 ⁻²	0.7055	Inorganic carbon source for sugar synthesis by plants	
Carbon dioxide diffusion coefficient (m ⁻² s ⁻¹)	1.77 × 10 ⁻⁹	1.60 × 10 ⁻⁵	1.11 × 10 ⁻⁴	Inorganic carbon source for sugar synthesis by plants	Many marine plants can use bicarbonate
Temperature range (°C)	−2 – 32	−88 – 58		Enzyme structure. Biochemical reaction rates	
Specific heat capacity (J kg ⁻¹ K ⁻¹)	4.18 × 10 ⁹	1.01 × 10 ³	4.157	Enzyme structure. Biochemical reaction rates	
Thermal diffusivity (m ⁻² s ⁻¹)	1.43 × 10 ⁷	2.15 × 10 ⁵	6.65 × 10 ⁻³	Enzyme structure. Biochemical reaction rates	
Thermal expansivity (K ⁻¹)	2.20 × 10 ⁴	2.15 × 10 ⁵	6.65 × 10 ⁻³	Enzyme structure. Biochemical reaction rates	
Thermal conductivity (W m ⁻¹ K ⁻¹)	0.6011	0.0261	23.0307	Enzyme structure. Biochemical reaction rates	
Free convection of heat			~100	Enzyme structure. Biochemical reaction rates	
Forced convection of heat			~200	Enzyme structure. Biochemical reaction rates	At equal Reynolds numbers
Light attenuation coefficient (m ⁻¹ for wavelength (λ) = 700 nm)	3	3.00 × 10 ⁻⁵	1.00 × 10 ⁵	Physical energy transformed into biochemical energy by plants. Sensory: Prey detection and predator avoidance	
Speed of sound (m s ⁻¹)	1521.5	343.4	4.4307	Sensory: Prey detection and predator avoidance	
Acoustic resistance (kg m ⁻² s ⁻¹)	1.56 × 10 ⁶	4.14 × 10 ⁻²	3767	Sensory: Prey detection and predator avoidance	
Acoustic attenuation (dB km ⁻¹ [1000 Hz])	0.01	1	0.01	Sensory: Prey detection and predator avoidance	
Electrical resistivity (Ω m ⁻¹)	2.00 × 10 ³	4.00 × 10 ¹³	5.00 × 10 ¹¹	Sensory: Prey detection and predator avoidance	

Compiled from Denny (1993), Vogel (1996), and Hochachka and Somero (2002).

supply, generating necessary internal heat in the sea requires complex structural and physiological adaptations that are metabolically expensive. The cost of maintaining body temperature a degree warmer than the surrounding environment by respiration is ~3400

times higher for an organism living in the ocean than for an organism living on land surrounded by the atmosphere (Denny, 1993). Temperature is tyrannical to organisms in the sea and most are “cold blooded” ectotherms whose metabolic rates are strongly

regulated by the temperature of the liquid surrounding them. Mobile marine organisms govern metabolic rates by selecting volumes of liquid at preferred temperatures that are often unique for specific life history stages and events (Magnuson *et al.*, 1979; Magnuson and Destasio, 1997).

In contrast, the heat capacity and heat transfer rates in the atmosphere are low. Temperature ranges and rates of change on land can therefore be extreme and exceed values required for normal, active metabolism on a seasonal or even an hourly basis (Denny, 1993; Hochachka and Somero, 2002). Many terrestrial organisms have combined strong physiological and behavioural regulation to manufacture biochemicals protecting metabolic machinery when conditions become damaging and to regulate internal body temperatures independently of atmospheric temperatures. Even “cold blooded” terrestrial organisms guard against the damaging effects of high and low temperatures and control whole body temperatures by synthesizing macromolecules, generating metabolic heat, by wetting and evaporative cooling, or basking in the sun light or shade available near the land’s surface (Angilletta, 2009). Temperature is an important habitat resource for terrestrial organisms too. However, thermal properties of the atmosphere demand a much greater degree of physiological and behavioural decoupling of body temperatures from ambient environmental temperatures. Slow heat transfer rates and the abundance of oxygen in the atmosphere make physiological decoupling from environmental temperatures energetically “cheap” for terrestrial organisms. Species geographic ranges appear shifting in response to rapid changes in environmental temperatures with climate change an order of magnitude more slowly on land than in the sea (Chuang *et al.*, 2009; Sorte *et al.*, 2010). Differences in species range shift speeds in terrestrial and marine ecosystems that are related to environmental temperature should reflect differences in constraints and opportunities for thermoregulation available to organisms immersed in the atmosphere’s gases or the liquid of the ocean.

The density and viscosity of water in the ocean and air in the atmosphere ultimately control the availability of the building blocks of metabolism, the generation of metabolic fuel, and the strategies organisms must use to search for and acquire them. The ocean liquid is ~850 times more dense than the gases in the atmosphere and much closer to densities of most living tissues (Table 1; Denny, 1993; Vogel, 1996). The dynamic viscosity of seawater; its resistance to stretching and shearing, is also ~60 times greater than the viscosity of air. The dominant forces controlling movements of particles, including living organisms, and dynamics of foodwebs are different in seascapes and on landscapes because of the differences in densities and viscosities of seawater and air.

In the sea, drag is the primary force controlling movements of materials and organisms because seawater densities and viscosities are so high. Gravity exerts secondary control over movement. A particle the size and density of a phytoplankton sinks 1020 times more slowly in seawater (@20°C and 3.5% salt concentration) than a pollen grain, the same size and density, does in air (@ 20°C; Vogel, 1996). Drag thins the oceans “soup”, dispersing slowly sinking materials required for metabolism that are easily carried downstream. Because most living tissues have densities close to densities of seawater, marine organisms without shells or tests are nearly neutrally buoyant. Most of the three-dimensional structure of the ocean hydrosphere is therefore accessible at little cost to organisms that can adjust buoyancy by changing the specific

gravity of their tissues slightly. These organisms then combine morphology and behaviour to manage and sometimes exploit the forces of drag in the moving ocean liquid. Even sessile organisms strongly associated with the seabed have body forms structured to efficiently manage and sometimes exploit the forces of drag with, for example, appendages that sift particles from turbulent flows of the ocean’s viscous “soup” (Vogel, 1996; Fish and Lauder, 2006).

Sunlight required for photosynthesis enters the sea surface but is attenuated ~100 000 times faster in seawater than in the nearly transparent atmosphere (Table 1). Organic particles are remineralized back into inorganic nutrients by bacteria as they sink slowly away from well-lit surface waters where mostly mobile, tiny, and short-lived marine plants can use them to synthesize carbohydrates. Vertical mixing and horizontal current flows caused by wind, differences in the salinity and temperature and thus density of the liquid, or tides are required to resupply nutrients to sunlit waters where plants can use them for photosynthesis. Nutrients and other organic compounds essential to metabolism are brought to the surface by divergent upwelling flows or from terrestrial sources upstream. They are carried downstream and concentrated along horizontal or vertical fronts where currents converge to “thicken” the soup (Bakun, 1996). Under these circumstances, ocean habitats are not “places”, but diffuse networks of horizontal and vertical flows that converge on nodes concentrating resources derived from sometimes remote upstream sources (Tew Kai *et al.*, 2009; Prants *et al.*, 2014; Prants, 2015). Foodwebs assemble along downstream transport pathways as the building blocks move toward convergent nodes. They assemble over time scales determined by the duration of the forces of wind, density and tide creating networked divergent, transport and convergent flows combined with the generation times and search capabilities of the organisms occupying different trophic levels (Olson, 2002). These diffuse networks are ephemeral oases built upon heterogeneities in the mixing of the ocean liquid because drag is the primary force controlling movement in the sea and episodic atmospheric and planetary tidal forcing control mixing. These are not just open and coastal ocean phenomena associated with large eddies, shelf break canyons, offshore banks, and coastlines (e.g. McGillicuddy *et al.*, 1999; Glenn *et al.*, 2004; Hu *et al.*, 2008; Allen and Hickey 2010). They also occur as structures like turbidity maxima that are essential engines of ecosystem productivity in coastal estuaries (Martino and Houde, 2010).

On terrestrial landscapes processes regulating the generation and availability of the materials and fuels for metabolism are very different because the density and viscosity of air are low enough that gravity is the primary force controlling movements. Terrestrial ecosystems are fuelled by relatively large, long-lived, stationary photosynthetic plants living along the interface between land and the transparent atmosphere where sunlight is abundant. Bacteria remineralize sources of nutrients deposited by gravity along with water in soils in proximity to the roots of plants and available light. The building blocks of terrestrial foodwebs are transported over short distances and brief periods of time except when ground-water flows intervene. On land, most crucial habitat resources are localized and diffuse slowly along the interface between land and the atmosphere. Slow geophysical and biogeochemical processes associated with soil development set the pace of terrestrial foodwebs that have slower, more persistent spatial dynamics than foodwebs in the sea that are regulated by much faster, often episodic hydrodynamic processes (Steele, 1985, 1989).

Summary and implications

Based on analysis performed using Bernhard Riemann's rules, seascapes are fundamentally different from landscapes because organisms living in the ocean's liquid and surrounded by the atmosphere's gases must meet the same core requirements of metabolism using very different mechanisms of internal regulation and habitat selection for external environmental properties. Seascapes and landscapes both provide resources supporting the viability of at least one population of organisms. **This ecological function, grounded in the duality of niche and habitat, requires that we identify environmental properties and processes structuring seascapes and landscapes purely based on effects on organism vital rates underlying population growth and inextricably linked to metabolism. In the analysis, the system function guided the development of models of the components of seascapes and landscapes, organisms and the external environment, in a manner consistent with fundamental laws. The universal requirements of metabolism were the laws that applied to organisms. The "laws" applying to the environment were its physical properties that are very different for seascapes and landscapes. Organisms living in the ocean's liquid face a shortage of oxygen required for respiration, energetic constraints on thermoregulation, but relatively weak demand for internal regulation of body temperatures and tissue ion-water balance. Most marine organisms combine strong habitat selection for volumes of ocean liquid with preferred oxygen partial pressures, temperatures, and salt concentrations. Furthermore, since seawater is dense and viscous and drag is the dominant force controlling movements, many marine organisms have access to the three spatial dimensions of the ocean hydrosphere in which the availability of essential metabolic building blocks and fuels are controlled by hydrodynamics. Seascapes are therefore primarily structured by hydrographic properties and hydrodynamics that control their ecological dynamics. The seabed and associated structures provide organisms with important refuges from predation, refuges from or access to high velocity current flows, as well as particle trapping surfaces that are relatively impermeable compared with discontinuities in density and current flow in the water column. Nevertheless, seascapes and the habitats composing them are primarily structured and regulated by properties and processes of the ocean liquid.**

In contrast, geography and biogeochemical processes associated with soil development along the interface between land and the atmosphere lie at the foundation of landscape ecology (Troll, 1950). Most terrestrial organisms are partially decoupled by gravity and strong physiological regulation from the dynamics of a thermally variable atmosphere largely devoid of water and salts but abundant with essential gases. Since gravity is the dominant force controlling movement, the atmosphere is inaccessible to most terrestrial organisms that show strong habitat selection for water, food, and other materials concentrated along the land surface. Biogeophysical properties and processes occurring along the interface between land and the atmosphere are the primary features structuring landscapes and driving ecological dynamics. Interactions between organisms with the external environment are different enough in the sea and on land that seascape ecology should not rest on the paradigms of terrestrial landscape ecology. Seascape ecology needs to rest on paradigms consistent with the importance of properties and dynamics of the ocean fluid in driving dynamics if it is to be effectively applied for resource use management in the sea.

Usually, new paradigms emerge from observations made with new tools, not vice versa. New tools are allowing us, right now, to

move beyond terrestrial paradigms and to integrate hydrography and hydrodynamics along with functionally important seabed features into a seascape ecology useful for adaptive management in the sea (Allen *et al.*, 2015). These tools are the data and models integrated into the regional Ocean Observing Systems currently being established around the world (Liu *et al.*, 2015). Ocean Observing Systems integrate measurements of ocean properties made by satellites in space, radar on the earth's surface, and robots underwater. The observations are assimilated into numerical ocean models that describe with greater accuracy, precision and transparency, the hydrography and hydrodynamics driving seascape dynamics at scales relevant to the population ecology and marine resource management (Carr *et al.*, 2010; Manderson *et al.*, 2011; Breece *et al.*, 2016). Regional data and models describing the dynamics of the ocean liquid can be integrated with descriptions of ecologically important seabed features into hydrodynamic information systems (HIS) used in applied seascape ecology in the same manner geographic information systems (GIS) are used in applied landscape ecology. HIS are already being used in innovative approaches that could be applied to tune adaptive management strategies to the dynamics of seascapes producing marine resources (Game *et al.*, 2009; Hobday and Hartog, 2014; Hobday and Pecl, 2014; Breece *et al.* 2016; Dunn *et al.* 2016).

Acknowledgements

I thank John Quinlan, Chris Roebuck, Jeff Pessutti, and Josh Kohut whose deep curiosity and intelligent insights into the ocean and the ways organism might live it have been inspiring and have shaped ideas I explored in this essay. I thank David Secor, a coeditor of this issue, for encouraging me to write the essay and pushing it into better shape. Finally, I thank John Lee and my wife Joyce Ferris for helping to make the essay more clear and intelligible.

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Handling editor: David Secor