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THEME SECTION

# Seascape ecology: application of landscape ecology to the marine environment

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CONTENTS





# Practicing coastal seascape ecology

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ABSTRACT: Landscape ecology concepts developed from terrestrial systems have recently emerged as theoretical and analytical frameworks that are equally useful for evaluating the ecological consequences of spatial patterns and structural changes in the submerged landscapes of coastal ecosystems. The benefits of applying a spatially-explicit perspective to resource management and restoration planning in the coastal zone are rapidly becoming apparent. This Theme Section on the application of landscape ecology to the estuarine and coastal environment emerged from a special symposium at the Coastal and Estuarine Research Federation (CERF) 20th Biennial Conference (Estuaries and Coasts in a Changing World) held in Portland, Oregon, USA, in November 2009. The 7 contributions in this Theme Section collectively provide substantial insights into the current status and application of the landscape approach in shallow marine environments, and identify significant knowledge gaps, as well as potential directions for the future advancement of 'seascape ecology'.

KEY WORDS: Landscape ecology · Seascapes · Spatial pattern · Spatial planning

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### Emergence of seascape ecology

Measurement of spatial patterns plays a central role in monitoring environmental change and for studying the multi-scale processes that drive organism distributions and biodiversity. A conceptual and analytical framework for studying seascapes (i.e. wholly or partially submerged marine landscapes) currently does not exist, but landscape ecology appears to offer a suitable approach for studying the spatial ecology of marine species and communities (Fig. 1). Landscape ecology, developed over a half century ago primarily for managing terrestrial environments, focuses on the causes, changes and ecological functions associated with spatial patterns. The discipline of landscape ecology has developed a unique set of concepts and analytical tools, which combined with a holistic and interdisciplinary perspective has made valuable contributions to the understanding and management of terrestrial environments (Turner et al. 2001, Gergel & Turner 2002). Our lack of knowledge on seascape patterns and their ecological consequences represents both a major void in our understanding of marine and coastal ecology and an exciting new frontier for research (Fig. 1). Although seascape ecology is on the verge of entering mainstream marine ecology, the level of familiarity is still comparable to that reported by terrestrial landscape ecologists in the 1980s, whereby 'ideas were new and were received with a mixture of skepticism and excitement' (Turner 2005). In part, this is due to the persistent limited exchange of perspectives and concepts between terrestrial ecologists and the coastal science community (Kneib 1994, Stergiou & Browman 2005) and the dominance of a relatively fine scale and single scale approach in estuarine and marine ecology (Pittman & McAlpine 2003). Furthermore, the interdisciplinary approach, spatial data types, tools and techniques used in landscape ecology are more typical of geographical sciences than those traditionally applied in coastal ecology, although quantitative spatial techniques are now being taught to the new generation of coastal ecologists (Wright et al. 2007).

### Resolution of seascape patterns

Coastal environments exhibit physical patterns that are shaped by many interacting processes, including human activity, at a range of scales in time and space (Fig. 1). Widely recognized spatial patterns include the dendritic networks of tidal channels in coastal wetlands, the spatial zonation of biotic communities across tidal salt marshes and rocky shores, and the intricate mosaics of patches that characterize seagrass beds, coral reefs, mangrove forests and tidal marshes (Boström et al. 2011, this Theme Section). Such broad scale and structurally complex spatial patterns are now being revealed in increasing detail by the latest generation of remote sensing devices mounted on underwater vehicles, floating platforms, survey ships and air- and spacecraft. Although patterns detected by remote sensing imagery are often visually captivating, it is

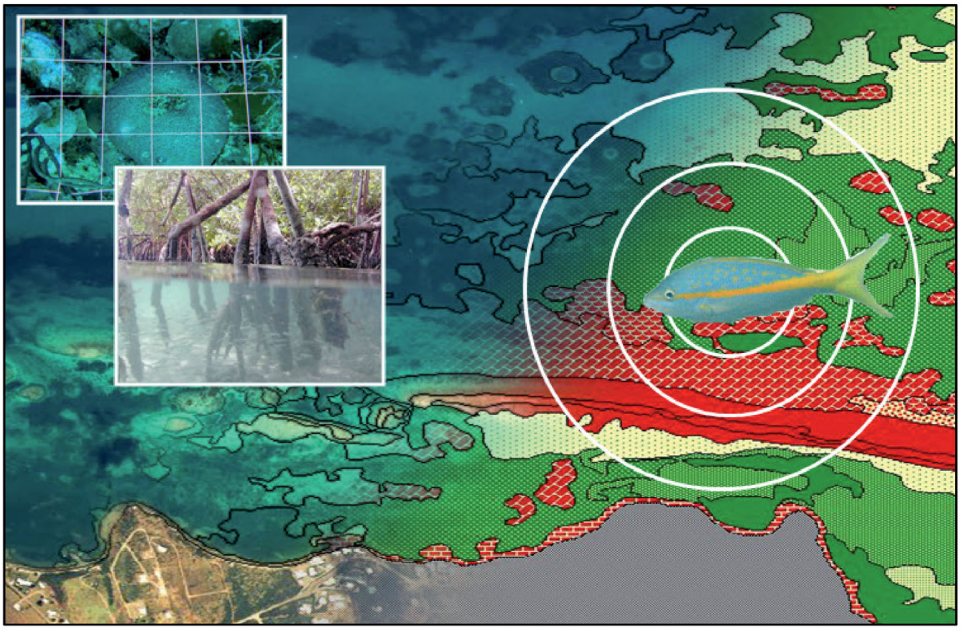

Fig. 1. Landscape ecology analyzes the effects of spatial patterns such as patch structure (e.g. coral cover, seagrass height, mangrove root density) and geometric properties (e.g. patch size, connectivity) on organisms and communities at various temporal and spatial scales

their ecological implications that are scientifically intriguing and most relevant to society. Understanding the relationship of observed patterns, such as those depicted in benthic habitat maps, to the provision of ecosystem goods and services is increasingly important in the face of rapid human-induced changes to the coastal zone. While seascape patterns may be most obvious in the coastal zone, they are not confined to nearshore ecosystems; in the open ocean, dynamic multi-dimensional spatial structure in the form of water currents, eddies, temperature fronts, plankton and seabird patches can be mapped and measured with modern spatial technologies. The application of landscape ecology to the pelagic realm is exceedingly rare. Innovative concepts and analytical techniques are required to interpret these spatially-explicit data and to make these findings applicable to marine management, if coastal and marine spatial planning (CMSP) is to be effective in the sustainable management of global marine resources.

## Thematic highlights

This Theme Section emerged from a special full-day conference symposium at the Coastal and Estuarine Research Federation (CERF) 20th Biennial Conference (Estuaries and Coasts in a Changing World) held in Portland, Oregon, USA, in November 2009. A total of 20 speakers from around the world made oral presentations on a wide range of topics addressed through a landscape ecology perspective. We present a collection of 7 papers based on that symposium that include 2 reviews (Boström et al. 2011, Wedding et al. 2011, this Theme Section) and a range of applications of landscape ecology concepts and tools applied to coastal seascapes. Since the early 1990s, the landscape ecology approach has been applied primarily to shallow-water subtidal and intertidal ecosystems (Robbins & Bell 1994), with the majority of studies carried out in seagrass beds (49%) and tidal marshes (32%), with fewer studies in coral reefs (11%) and mangroves (6%) (Boström et al. 2011). Few seascape studies have considered the consequences of spatial patterns on ecological processes; instead, they have focused on statistical associations between species distributions and seascape geometrics (Boström et al. 2011, Wedding et al. 2011). Notable exceptions include research in the 1990s conducted with a strong focus on predator–prey interactions and movements of nekton in seagrass and salt marsh landscapes on the east coast of the United States (Irlandi et al. 1995, Irlandi & Crawford 1997, Kneib 1997, Micheli & Peterson 1999, Hovel & Lipcius 2001). However, few have developed uniquely marine concepts or metrics. Wedding et al. (2011) reviewed the application of spatial pattern metrics to marine environments and found only one truly unique marine metric, while all others were derived from terrestrial landscape ecology.

Historically, the number of papers applying landscape ecology concepts to coastal environments has remained relatively low, with an average of 5 papers published per year between 1978 and 2010 (Boström et al. 2011). The 7 papers in this Theme Section make a comparatively major contribution to the emerging body of knowledge. As coastal scientists and managers begin to embrace landscape ecology, it is apparent that many of the concepts and analytical techniques are equally applicable to coastal environments, and that much can be gained from the insights and lessons learned from terrestrial applications in order to hone the emerging sub-discipline of seascape ecology. The urgency in understanding the impacts of changing spatial patterns on land and sea is heightened by the rapid global loss and degradation of coastal habitats such as coral reefs, seagrasses, mangroves and salt marshes. The trans-boundary and multidisciplinary nature of landscape ecology provides a suitable approach to address land–sea connectivity. Santos et al. (2011, this Theme Section) and Oliver et al. (2011, this Theme Section) consider the effects of inputs from coastal upland watersheds on the condition and spatial arrangement of marine biotic assemblages that form important shallow water seascapes.

Benthic habitat maps are the marine equivalent of terrestrial vegetation maps and land use or land cover maps and facilitate the application of landscape ecology to quantify the surface structure of the seafloor. Using benthic habitat maps that differ in spatial and thematic (i.e. number of map classes) resolution, Kendall et al. (2011, this Theme Section) explored the effects of seascape patterns on fish assemblages. Kendall et al. (2011) and Santos et al. (2011) conducted an exploratory multi-scale analysis using Geographical Information System (GIS) tools to quantify 2-dimensional seascape geometry. With a strong focus on movement ecology, Hitt et al. (2011, this Theme Section) coupled acoustic tracking technology with benthic habitat maps to explore a new frontier in behavioral landscape ecology, by characterizing individual diel movements of fishes within a coral reef seascape. A stochastic stage-based modeling approach was taken by Mizerek et al. (2011, this Theme Section) to evaluate the potential effects of varying fishing pressure and stocking enhancement in seascapes that included submerged aquatic vegetation (SAV) at different levels of fragmentation. All of the contributions to the Theme Section demonstrate the importance of studying spatial patterns through the application of landscape ecology concepts and tools and the implications for the management of coastal and marine resources.

### Future foci in seascape ecolgy

We envisage that the focus on CMSP and spatial prioritization for biodiversity conservation will dramatically increase spatial data acquisition and availability (e.g. habitat maps and remote sensing images of coastal areas). Making sense of these patterns will require a landscape ecology approach for developing and testing novel ecological hypotheses, with substantial potential for providing ecological information at spatial scales that are operationally relevant to management. Perhaps the greatest challenge and defining objective of landscape ecology in both terrestrial and aquatic realms, is to determine the mechanisms by which spatial patterns influence key ecological processes. Some progress has been made in the past 30 yr but much greater effort will be required to reach the same level of practical benefits to coastal management that has already been reached in terrestrial conservation. There are many new and exciting challenges for seascape ecology research; only a few have been addressed to date. Key topic areas include (1) a better understanding of the influence of upland landscape patterns and processes on adjacent seascapes; (2) determining the relevance of seascape structure for key ecological processes such as organism growth, survival (including predator–prey dynamics) and movement; (3) identifying and mapping optimally connected seascapes and movement corridors; (4) determining which of the structural attributes of seascapes drive biotic assemblages and the distribution of biodiversity; (5) quantifying and understanding the impacts of global climate change on seascape patterns, including spatial shifts in seascape structure, fragmentation and loss of seascape elements; and (6) the identification of threshold effects or tipping points in seascape structure resulting in abrupt changes in ecological functions and processes. A glimpse into the wealth of new ecological knowledge that has emerged from terrestrial landscape ecology over the past 3 decades indicates the enormity of the task ahead for marine and coastal ecologists. The inevitable emergence of seascape ecology fits into a broader paradigm shift toward greater spatial awareness in academic studies, the public sector, industry and across human society in general (Goodchild 2010).

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*Contribution to the Theme Section 'Seascape ecology'*

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# Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges

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ABSTRACT: We review the progress made in the emerging field of coastal seascape ecology, i.e. the application of landscape ecology concepts and techniques to the coastal marine environment. Since the early 1990s, the landscape ecology approach has been applied in several coastal subtidal and intertidal biogenic habitats across a range of spatial scales. Emerging evidence indicates that animals in these seascapes respond to the structure of patches and patch mosaics in different ways and at different spatial scales, yet we still know very little about the ecological significance of these relationships and the consequences of change in seascape patterning for ecosystem functioning and overall biodiversity. Ecological interactions that occur within patches and among different types of patches (or seascapes) are likely to be critically important in maintaining primary and secondary production, trophic transfer, biodiversity, coastal protection, and supporting a wealth of ecosystem goods and services. We review faunal responses to patch and seascape structure, including effects of fragmentation on 5 focal habitats: seagrass meadows, salt marshes, coral reefs, mangrove forests, and oyster reefs. Extrapolating and generalizing spatial relationships between ecological patterns and processes across scales remains a significant challenge, and we show that there are major gaps in our understanding of these relationships. Filling these gaps will be crucial for managing and responding to an inevitably changing coastal environment. We show that critical ecological thresholds exist in the structural patterning of biogenic ecosystems that, when exceeded, cause abrupt shifts in the distribution and abundance of organisms. A better understanding of faunal–seascape relationships, including the identifications of threshold effects, is urgently needed to support the development of more effective and holistic management actions in restoration, site prioritization, and forecasting the impacts of environmental change.

KEY WORDS: Landscape ecology · Seascape · Fragmentation · Scale · Edge effects · Patch size · Thresholds · Connectivity



## INTRODUCTION

Landscape ecology is a multidisciplinary field that combines the spatial approach of geography with functional ecology. For terrestrial ecosystems, landscape ecology has provided an important conceptual and analytical framework to understand ecology through a focus on understanding the causes and ecological consequences of spatial patterns in the environment (Wiens 1995b, Turner 2005). The unique spatially-explicit and multi-scale framework of landscape ecology has influenced our perception of species–envi-

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ronment relationships and has led to significant advancements in the design of terrestrial conservation strategies worldwide (Wiens 1999, Liu & Taylor 2002). More recently, landscape ecology has been explicitly incorporated into coastal conservation strategies such as marine protected area (MPA) network design (Leslie 2005, Leathwick et al. 2008).

There are many ways to define a landscape, but from an ecological perspective a landscape is an area of land containing a mosaic of habitat patches, often within which a particular 'focal' or 'target' habitat patch is embedded (Dunning et al. 1992). More broadly, we define a seascape as a spatially heterogeneous area of coastal environment (i.e. intertidal, brackish) that can be perceived as a mosaic of patches, a spatial gradient, or some other geometric patterning quantified from either benthic or pelagic environments. Seascape structure is commonly represented as a patch matrix, with focal patches (e.g. vegetation) viewed as 'islands' embedded in a matrix (e.g. sediment) that affects animal movements and survival depending on relative isolation. This model, derived from the theory of island biogeography (MacArthur & Wilson 1967), has proven useful in studies of seagrass meadows depicted as simplified binary seascapes, whereby seagrasses are focal patches and the surrounding unvegetated sand is the matrix (McNeill & Fairweather 1993, Robbins & Bell 1994). In particular, the patch matrix model has been applied to study the spatial processes and ecological consequences of fragmentation in seagrass meadows measured by changes in seagrass patch size, the number of patches, and their relative isolation (Bell et al. 2001, Hovel & Regan 2008). In contrast, the patch mosaic model is a competing construct that represents structural heterogeneity as a collection of different patch types, where the interactions of the parts influence the ecological function of the whole mosaic (Wiens et al. 1993, Wiens 1995a). In the patch mosaic model, a homogeneous matrix does not exist and instead the composition (abundance and variety of patch types) and spatial configuration (geometric structure) of mosaics is of central importance. In addition, an important third model has recently emerged that represents structural heterogeneity as a continuous gradient without discrete patch boundaries, such as with a digital terrain model of bathymetry or sea surface temperature (McGarigal & Cushman 2002, Pittman et al. 2009).

Despite the demonstrated applicability of landscape ecology concepts and techniques to coastal environments, particularly in shallow-water benthic ecosystems, seascape ecology has only slowly emerged during the past 2 decades, with relatively few practitioners and limited impact on mainstream marine ecology (Johnson & Gage 1997, Wiens 2002, Turner 2005). From the historical perspective of terrestrial landscapes, aquatic ecosystems were simply elements in the broader landscape, resulting in a lag in the application of landscape concepts to submerged ecosystems (Kneib 1994). Increasingly, however, coastal ecologists and managers are asking complex multi-scale questions that can best be addressed with a landscape ecology approach. Thus, we suggest that many of the central concepts and analytical approaches developed for terrestrial applications are equally applicable to the study of aquatic benthic environments, including both semi-terrestrial environments of the shoreline (salt marshes) and subtidal and intertidal seascapes composed of e.g. coral reefs and molluskan reefs. Many coastal organisms are closely associated with benthic structure, which is analogous to a land surface. Although submersion in water rather than air likely has a different effect on mobility, dispersal, and rates of ecological processes, variation in seascape structure (e.g. patch dynamics, edges, and proximity of one patch type to another) is intuitively and empirically known to influence coastal fauna. As the body of knowledge in seascape ecology expands, syntheses and meta-analyses are important in identifying generalities emerging from faunal responses to spatial patterning, and for comparing spatially-explicit responses in coastal environments.

Coastal environments are of major importance for secondary production, trophic transfer, and coastal biodiversity (Hughes et al. 2009). They may also provide the highest economic value of all natural ecosystems (Costanza et al. 1997, McArthur & Boland 2006, Duarte 2009) (Table 1). Intertidal marshes and mangrove forests represent critical transition zones linking terrestrial and coastal environments and often control the fluxes of materials and energy across land–seascapes (Valiela et al. 2000, Ewel et al. 2001, Levin et al. 2001). Furthermore, many important coastal biogenic habitats (e.g. tidal marshes, seagrass meadows, and coral reefs) occur in close proximity to densely populated coastal regions and as such are now among the most heavily used and impacted environments on earth (Weslawski et al. 2004, Lotze et al. 2006). Annual loss rates of the 5 most important biogenic habitats range between 1 and 9% (Duarte et al. 2008). Total global loss estimates of seagrasses, salt marshes, coral reefs, and mangroves average 30% (Nicholls et al. 1999, Valiela et al. 2001, Wilkinson 2008, Waycott et al. 2009), and losses of oyster reefs may exceed 85% (Beck et al. 2009) (Table 1). Loss drivers often involve multiple interacting stressors (Table 2), including localized impacts such as mariculture, dredging, pollution, and species invasions, as well as broader-scale impacts such as over-harvesting, watershed development, and global climate change (Snelgrove et al. 2004). Several

negative feedback links between ecosystem goods and services and loss drivers exist. For example, as many biogenic habitats support food resources critical for humanity, impacts such as mangrove mariculture further accelerate habitat loss, which, in turn, impairs other ecosystem goods and services. The negative impacts operate across a range of scales in time and space, and affect the integrity of coastal ecosystems in ways that are not yet fully understood.

While the consequences of total habitat loss for associated communities are becoming well documented (Airoldi & Beck 2007), there is little understanding of how coastal organisms respond to fragmentation and other changes in the spatial configuration of ecosystems, or whether responses are similar across ecosystems and taxa. In addition, the fact that spatial patterning of biogenic habitats can be perceived and quantified at a range of scales across a spatial hier-

Table 1. Summary of total global loss, annual loss rates, global diversity, loss drivers, and examples of ecosystems goods and services provided by the coastal biogenic ecosystems included in this review. Loss drivers and ecosystem services are not ranked in order of importance, as the relative role of each factor in each ecosystem might vary greatly between regions. Data sources: [a]Waycott et al. (2009); [b]Nicholls et al. (1999); Solomon et al. (2007); [c]Wilkinson (2008). [d]Oyster diversity refers to a minimum number of native, wild reef-forming oyster species in a global risk assessment (Beck et al. 2009), not the total global oyster species diversity; [e]Valiela et al. (2001); [f]Waycott et al. (2009); [g]Duarte et al. (2008); [h]Duarte et al. (2008); [i]Valiela et al. (2009); [j]Dennison (2009); [k]Kunza & (2008); [l]Polidoro et al. (2008); [m]Tomlinson (1986). nd: no data

| | Seagrass meadows | Salt marshes | Coral reefs | Oyster reefs | Mangrove forests |
|---|---|---|---|---|---|
| Global loss (%) | 29[a] | 13–30[b] | 34[c] | 85[d] | 35[e] |
| Annual loss rate (%) | 7[f] | 1–2[g] | 4–9[h] | nd | 2.1–3.6[i] |
| Diversity | 60[j] | 43[k] | 845[l] | ~40[d] | 75[m] |
| Loss drivers | Eutrophication | Construction | Acidification | Overfishing | Mariculture |
| | Dredging | Sea level rise | Eutrophication | Disease | Construction |
| | Mooring | Die-back | Climate change | Sedimentation | Forestry |
| | Overfishing | Invasive species | Overfishing | Eutrophication | Sea level rise |
| Ecosystem goods and services | Biodiversity | Biodiversity | Biodiversity | Food | Food |
| | Food | Food | Food/Fisheries | Biodiversity | Timber |
| | Export of materials | Export of materials | Ecotourism | Stabilization | Biodiversity |
| | Ecotourism | Ecotourism | Stabilization | Filtering | Ecotourism |
| | Stabilization | Stabilization | Carbon sequestration | Carbon and nutrient sequestration | Stabilization |
| | Carbon and nutrient sequestration | Contaminant and nutrient interception | | | Carbon and nutrient sequestration |

Table 2. Summary of mechanisms causing habitat fragmentation in coastal biogenic habitats. Sum scores from 1 to 5 indicate low to high generality of specific fragmentation mechanisms across systems. Note that habitat fragmentation also involves positive effects in terms of population growth by spatial spread through seedlings, colony fragments, and recruiting individuals

| Disturbance type | Fragmentation mechanism | Seagrass meadow | Salt marsh | Coral reef | Mangrove forest | Oyster reef | Sum |
|---|---|---|---|---|---|---|---|
| Physical | Storm events/sand scour | + | + | + | + | + | 5 |
| | Tsunami | + | + | + | + | + | 5 |
| | Construction | + | + | + | + | + | 5 |
| | Dredging | + | + | | | + | 3 |
| | Hydrologic alterations | | + | | + | + | 3 |
| | Siltation/sedimentation | + | | + | | + | 3 |
| | Propeller scarring | + | | | | + | 2 |
| | Anchoring | + | | | | | 1 |
| | Loss of adjacent habitat | | | | | + | 1 |
| Biological | Natural spreading | + | + | + | + | + | 5 |
| | Invasive species | + | | | | + | 2 |
| | Grazing/bioerosion | + | | + | | | 2 |
| | Diseases and parasites | + | | | | + | 2 |
| | Overfishing | + | | + | | | 2 |
| | Competition | + | | + | | | 2 |
| | Bioturbation | + | | | | | 1 |
| | Bleaching | | | + | | | 1 |
| Chemical | Eutrophication | + | | + | | | 2 |
| | Toxic compounds | + | + | + | + | + | 5 |

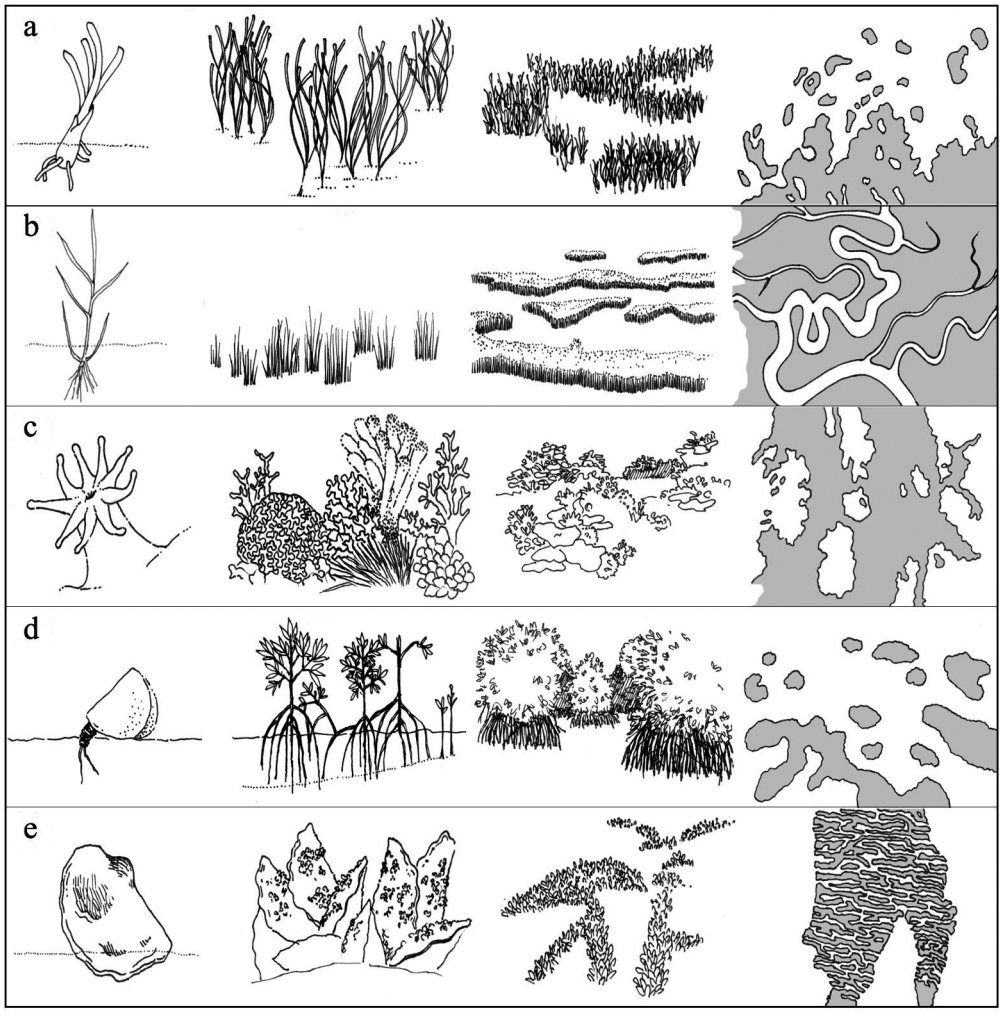


Fig. 1. What is a patch? Artistic representation of the hierarchical structure of the 5 coastal biogenic habitats studied: (a) seagrass, (b) salt marsh, (c) coral reef, (d) mangrove, and (e) oyster reef. For comparative purposes, figures are not drawn to scale. The dimension of the study area (extent) increase from left to right (1–10 cm, 10 cm–10 m, 10–100s m, 100s m–10s km) while resolution (grain) increases from right to left. The vertical dimensions of habitats range from a few centimeters (seedlings and oyster shells) to several meters (mangroves and coral reefs)

archy (Fig. 1) adds ambiguity to the use of terms such as 'patch' and 'fragmentation,' further complicating interpretation of responses across habitats. We adopt the definition of habitat fragmentation as being a complex process (not a state) seldom resulting in the mere splitting of habitat, but involving multiple changes such as habitat loss, increased isolation, and changes in patch quality (Fahrig 2003).

Most coastal biogenic habitats exist as components of functionally connected coastal mosaics, so loss or degradation of a particular habitat is likely to impair the integrity of neighboring patches and disrupt links in the ecosystem as a whole. For example, seagrass meadows and salt marshes play a significant role by subsidizing energy to adjacent and even distant ecosystems (Kneib 2000, Guest & Connolly 2006, Heck et al. 2008, Meynecke et al. 2008). For seagrass-associated species, the spatial arrangement of patches (interpatch distances, contiguity, juxtaposition) can influence important processes such as predator–prey relationships by affecting refuge availability for prey and feeding efficiency for predators, and rate of movement between their habitats (Irlandi & Crawford 1997, Micheli & Peterson 1999, Grober-Dunsmore et al. 2007). Also, a seascape that is functionally connected for one organism may be disconnected for another because of individual or species-specific differences in physiological, anatomical, behavioral, life-history, and other ecological characteristics; thus, landscape corridors can be viewed as barriers to or paths of movement, depending on the fauna or process of interest. Direct quantitative estimates of actual ecosystem connectivity are still rare (Gillanders et al. 2003, Grober-Dunsmore et al. 2009), but are needed for the ecologically meaningful design and management of coastal reserves (Crowder & Norse 2008, Palumbi et al. 2009). Thus, it is important to synthesize the wide range of individualistic responses by fauna to seascape structure in order to determine whether generalities exist and why similar responses may occur across taxa and functional groups. Landscape ecology holds great promise to increase our understanding of pattern–pattern and pattern–process

relationships in ecology, as it provides an appropriate conceptual and analytical framework to quantify, analyze, and interpret spatial information on seascape structure, function, and change across multiple spatial scales.

The purpose of this paper is to review landscape ecology applications in coastal ecosystems. As seascape ecology encompasses many different research approaches and ecosystems (Hinchey et al. 2008 and this Theme Section), we focus here mainly on a subset that encompasses some of the most frequently studied structural attributes of patches and seascapes, including fragmentation, patch size, patch shape, and patch edge effects on faunal communities, in 5 key habitats: seagrass meadows, salt marshes, coral reefs, mangrove forests, and oyster reefs. In order to evaluate the generality in organism–seascape relationships across species, habitats, and ecoregions, we address the following 5 questions: (1) How has landscape ecology been applied to study relationships between individual organisms or ecosystem processes and seascapes? (2) Which attributes of seascape structure and response variables have been studied? (3) Are faunal response patterns and biological processes in changing seascapes linear, or do nonlinearities and critical thresholds exist? (4) What are the advantages of a seascape ecology approach, and what are the implications for coastal management including restoration efforts, MPA management, and spatial planning? (5) What are the key future research priorities for seascape ecology in coastal ecosystems?

## MATERIALS AND METHODS

We used personal libraries and citations in literature reviews (Boström et al. 2006a, Connolly & Hindell 2006, Grober-Dunsmore et al. 2009) to identify peer-reviewed articles on landscape ecology applications to the study of coastal biogenic habitats. In most cases, we focused on the effect of spatial patterning for individual focal habitats, rather than the influence of the surrounding seascape context, primarily because the majority of studies had taken a single focal patch approach. However, we recognize that there are several notable exceptions (e.g. studies in which a multiscale, patch mosaic approach was applied). Our main inclusion criterion was that the study must contain a quantitative measure of one or several patch/landscape metrics (e.g. patch area, edge length, patch richness, nearest neighbor distance) that was then linked to a faunal response (e.g. variation in density, diversity, secondary production). Faunal groups included benthic invertebrates, fishes, and birds. Floral responses and abiotic patterns and processes (e.g. sediment dynamics, hydrodynamics) that interact with seascapes were outside the scope of this review. Mapping and modeling surveys using aerial photographs and geographic information systems to analyze patterns and dynamics in coastal ecosystems were not included unless patterns were quantitatively linked to a faunal response variable. Experiments in mesocosms were also excluded, but *in situ* manipulations of spatial structure using artificial seagrass units or artificial reefs were included. The connectivity literature relevant to coral reef ecosystems reviewed by Grober-Dunsmore et al. (2009) was also excluded. Complementary database searches using ISI Web of Knowledge (http://apps.isiknowledge.com) were conducted for the time period 1978 (earliest relevant study found) to June 2010 by entering partial words using wildcards (e.g. mangrove*, coral*) combined with the following key words; landscape ecology, seascape, fragmentation, patch, and edge. The search included title, abstract, and key word within a record. To avoid redundancy with previous reviews, particularly with the seagrass literature, which was thoroughly reviewed through 2004 (Boström et al. 2006a, Connolly & Hindell 2006), we searched primarily for seagrass seascape publications for the period 2004 to 2010. The total seagrass seascape literature (59 publications) allowed for a more detailed analysis of the generality of organism responses to patch size and edge effects than any other ecosystem. Both, seagrass and artificial seagrass studies were included. Following Connolly & Hindell (2006), we classified individual faunal responses (usually differences in density or richness) as a significant positive effect, significant negative effect, or no effect. For example, a positive effect was recorded for species/taxa exhibiting a statistically significant increase in abundance with increasing patch size, or significantly higher abundance at the edge than in the interior of seagrass patches. Individual species scores and results for the same species/taxa at different sampling periods within a single study were treated separately.

## RESULTS

### Application of landscape ecology in studies of organism–seascape relationships

We included a total of 118 papers spanning the time period 1978 to 2010 and covering 17 countries (Appendix 1). The literature survey indicates a cumulative increase, but very little growth in the rate of applying landscape ecology to coastal environments (Fig. 2). Over that time span, there has been a steady average output of ~5 papers $yr^{-1}$, often emerging from thesis research. Few research institutions include seascape

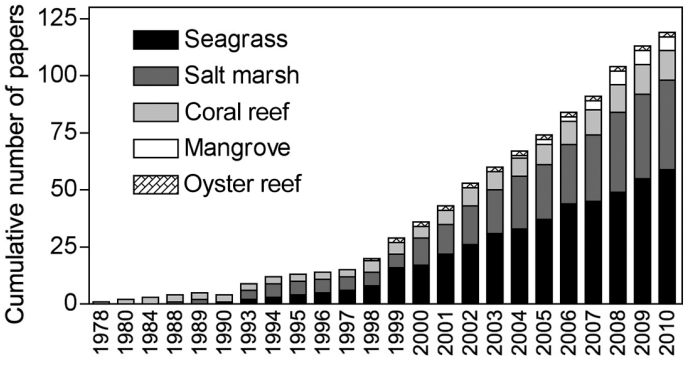


Fig. 2. Cumulative number of studies in coastal biogenic ecosystems applying landscape ecological principles to explain faunal responses

ecology as a primary focal area. Our understanding of seascape ecology is largely based on studies carried out in seagrasses (49% of total number of studies) and salt marshes (32%), while far fewer studies have been conducted in coral reefs (11%), mangroves (6%), and oyster reefs (2%). There is also a considerable geographic bias in the studies, with most carried out in the USA and Australia (Fig. 3a). This is particularly evident in the seagrass and salt marsh literature. Seagrass ecosystems from regions such as the Caribbean, Indonesia, Africa, and Europe were under-represented in our survey, which limited our ability to generalize results across species and ecoregions.

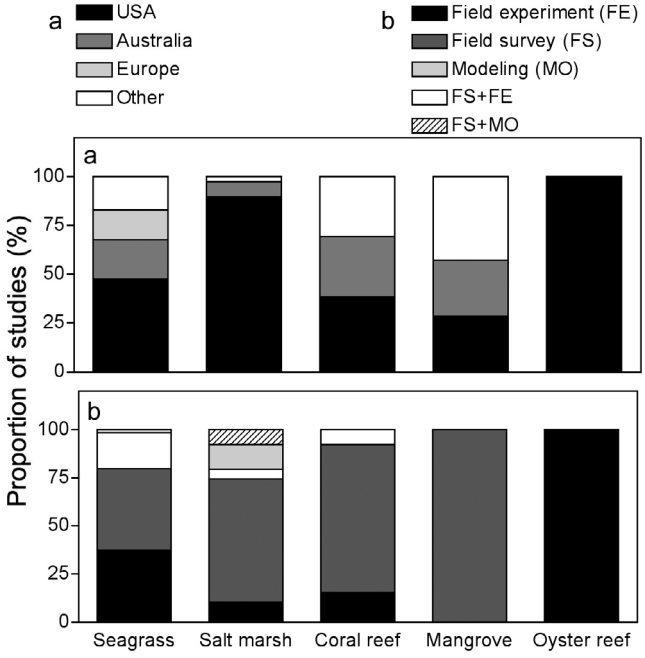


Fig. 3. (a) Geographical regions and (b) methodological approaches covered in the seascape literature (1978–2010, Appendix 1) linking seascape metrics to faunal response variables

The majority (60 to 90%) of the studies within each biogenic system took a binary patch matrix approach (focal versus non-focal habitat) and focused on the faunal response to individual patch attributes (e.g. edge, size, perimeter:area ratio), while fewer (7 to 40%) studied organism responses from a patch-mosaic perspective. In terms of methods, the seagrass publications indicate about equal contribution of descriptive and experimental approaches (often using artificial seagrass units; Appendix 1), and to some extent (18%) a combination of both approaches, while manipulative field studies in marsh, mangrove, and coral reef habitats are still scarce (Fig. 3b). Very few oyster reef studies applied landscape concepts (Eggleston et al. 1998, 1999), even though landscape ecology was suggested to provide a useful conceptual framework to understand oyster reef ecology and restoration (Eggleston 1999). Several studies have quantified mosaics of multiple patch types across a range of spatial scales, although in most cases the seascapes were linked to faunal communities sampled in a single focal patch type (coral reefs, mangroves). Exceptions include a study that developed predictive maps of fish species richness across the seascape by integrating fish survey data collected in multiple patch types with benthic maps (patch mosaics) and surface complexity from bathymetry (continuous gradients) (Pittman et al. 2007). Very few studies have directly quantified seascape connectivity, although it is increasingly acknowledged as an important process in coastal ecology and for the design of effective management strategies (Gillanders et al. 2003, Mumby et al. 2004, Ray 2005, Weinstein et al. 2005, Meynecke et al. 2008, Grober-Dunsmore et al. 2009).

## Spatial and temporal scaling in seascape studies

### Spatial scales

The perception of seascapes varies greatly depending on site, organism characteristics (e.g. size, life stage, mobility), or the process of interest; therefore, no single spatial (grain and extent) or temporal (duration, temporal replication) scale for seascape studies can be defined (Wiens & Milne 1989, Doak et al. 1992). Typically, scale selection is based on arbitrary choices, convention, or the type of question being addressed. The ecological rationale for scale selection is usually underdeveloped and unreported (Meentemeyer 1989, Pittman & McAlpine 2003). In the studies reviewed, the spatial extent ranged from 100 $m^2$ to 2000 $km^2$, with seagrass, marshes, and coral seascapes representing the systems that were studied on multiple spatial scales. Direct comparisons of the spatial extent of sur-

veys are problematic because the term 'site' may range from 1 to 400 $km^2$, and refer to sampling locations within seascapes or to geographically (latitudinally) separated locations 100 to 1000s of km apart. Rarely are spatial scales aligned with specific ecological processes, such as a species home range area (but see Hitt et al. 2011, this Theme Section).

Unsubstantiated relative terminology such as 'small' and 'large' can also be misleading. For instance, in geography, a large-scale map is one of higher spatial resolution than a small-scale map. To avoid confusion, we advocate the use of 'fine-scale' and 'broad-scale' as relative terms, instead of 'large' and 'small' to be consistent with convention in landscape ecology. Quantitative estimates of actual spatial scales will avoid ambiguity. Not surprisingly, our review found that the definition of small (S), medium (M), and large (L) patches in seascapes ranged markedly across habitats, studies, and target species. For example, the following patch sizes were noted in seagrass studies of infauna: S = 17–37, M = 41–72, L = 82–147 cm in diameter (Hirst & Attrill 2008), epifauna: S = 0.6–6, M = 6–30, L = 33–87 $m^2$ (Tanner 2006), fish: S = 980–2300, M = 3375–4090, L = 5335–6630 $m^2$ (Jelbart et al. 2007). Likewise, the terms 'seascape scale' and 'seascape level' are uninformative and ambiguous and should not be used (Allen 1998, King 2005). In salt marshes, Kneib (1994) generally defined questions addressing fish feeding ecology at S = 0.1–1, M = 10–100, and L > 1000 m scales. Relative patch sizes for other marsh fish and benthic invertebrate studies have varied considerably: S < 3000, L = 4000–80 000 $m^2$ (Guest & Connolly 2006), S = 70–240, L = 822–4347 $m^2$ (Long & Burke 2007), and S = < 1250, M = 49 000–96 100, L > 441 500 $m^2$ (Rozas & Minello 2010). In contrast, investigations of fish in patch reefs report remarkably similar patch size ranges: 2.5–60 $m^2$ (Molles 1978), 0.3–60 $m^2$ (Ault & Johnson 1998a,b), and 0.6–64 $m^2$ (Chittaro 2002). Maximum spatial scales of coral reefs typically span 700 to 2300 $m^2$ (Acosta & Robertson 2002) or may exceed 15 ha (Grober-Dunsmore et al. 2008). The spatial scale of experimental oyster reef work typically has been restricted to 0.25 to 5 $m^2$ patches (Eggleston et al. 1998, 1999).

### Temporal scales

Biogenic habitats are temporally dynamic, often characterized by rapidly changing patch composition and spatial configuration due to disturbance events such as storms and freshwater flows (Santos et al. 2011, this Theme Section), high interannual fluctuations in recruitment, and seasonal changes in species abundance (Bologna & Heck 2000, Shervette & Gelwick 2008). Temporal variability has often been addressed by repeated sampling events ranging from hours (Darcy & Eggleston 2005, Jackson et al. 2006b), months (Acosta & Robertson 2002, Smith et al. 2010), to several years (Webb & Kneib 2002, Gorman et al. 2009). When time has explicitly been incorporated as an explanatory variable, usually strong interactions have been found between spatial pattern metrics and time (Hovel & Lipcius 2001, Johnson & Heck 2006). For instance, edge effects in seagrasses may show inconsistent patterns among months (Fonseca et al. 1990, Horinouchi 2009), and strong diurnal variation of fish abundance may break down associations between fish and seagrass seascape configuration (Jackson et al. 2006a). In addition, inconsistent effects of seascape configuration demonstrated by interactions between time and patch size appear to be common across species (fish and decapods) and habitats (seagrass meadows, oyster reefs, and coral reefs) (Molles 1978, Eggleston et al. 1998, Jelbart et al. 2006, Johnson & Heck 2006).

## Spatial pattern metrics and faunal response variables

### Summary of trends across ecosystems

The most commonly used spatial pattern metrics and target taxa in the 5 habitats examined are summarized in Fig. 4. The 5 most frequently applied landscape attributes and spatial phenomena in seagrass and salt marsh studies are spatial configuration (e.g. number of patches, total edge, mean fractal dimension), patch size, patch shape, edge effects, and percentage cover. Key target faunal groups studied in seagrass meadows and salt marshes included fishes, decapods, and motile epifauna. Twelve distinct faunal response variables were identified, but there appeared to be no trend in regard to which variables were used to measure responses across the 5 ecosystems (Fig. 5). The majority of response variables were measured with short duration 'snap shot' faunal surveys, often with no spatial or temporal replication and sometimes limited to a single season. The most common faunal community variables studied in seagrasses were the number of individuals and number of species, while salt marsh studies have emphasized production-related variables such as biomass, body size, and growth. Few studies have directly linked salt marsh spatial configuration to nekton diversity or infaunal species diversity (Kneib 1997). The emphasis in coral reef studies has been on determining the influence of patch size, habitat configuration, and more recently surrounding seascape composition on fish density and species richness (Fig. 4c,h), while the potential influence of coral reef configuration on invertebrates has rarely been addressed. Increasing aware-

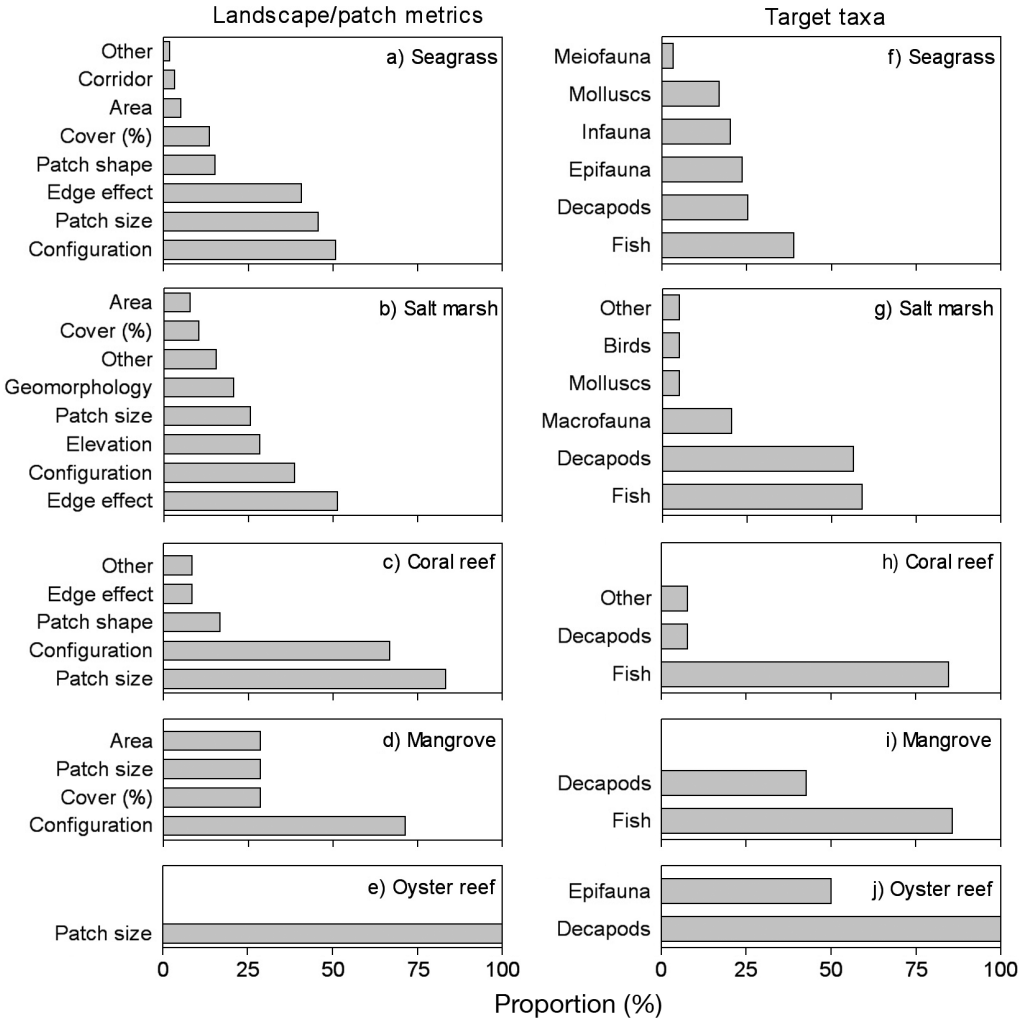


Fig. 4. Summary of (a–e) spatial pattern metrics applied to explain (f–j) target faunal groups in the 5 biogenic ecosystems studied. Patch size includes studies reporting habitat area measurements. Configuration refers to various landscape indices used to quantify the component habitat, e.g. number of patches, total edge, mean fractal dimension, total core area, contagion. Detailed descriptions of these metrics provided by McGarigal & Marks (1994). For salt marshes (b), geomorphology refers to channel network complexity (width, length, order, slope), and elevation to e.g. inundation regime, water depth, and edge elevation. Decapods refer almost exclusively to shrimps/prawns and crabs, while epifauna, macrofauna, and infauna refer to sampling of whole invertebrate assemblages

ness of the multi-habitat movements of many common fish in coral reefs has resulted in a shift toward patch-mosaic studies that quantify seascape composition and, in fewer cases, the geometric properties of seascape configuration (Kendall et al. 2011, this Theme Section). Our understanding of the causes and ecological consequences of structural patterns in oyster reefs and influence on associated fauna is restricted mainly to studies of patch size effects on macrofauna and decapods (Fig. 4d,i) and requires more focus. Despite the importance of mangroves for coastal and offshore fisheries (Faunce & Serafy 2006) and the loss of mangroves globally, effects of mangrove seascape configuration and mangrove patch size have only been addressed in a handful of studies, with the majority focusing on fish (Fig. 4e,j).

## Patch size effects

*Seagrass meadows.* Fish and invertebrate responses to differences in seagrass patch size were very consistent in the seagrass literature. About 70% of invertebrate and 75% of fish responses to patch size were not statistically significant (Fig. 6a,b). This suggests that fish and invertebrates are insensitive to changes in patch size at the spatial scales represented in the published literature. A major caveat here is that these results are probably de-

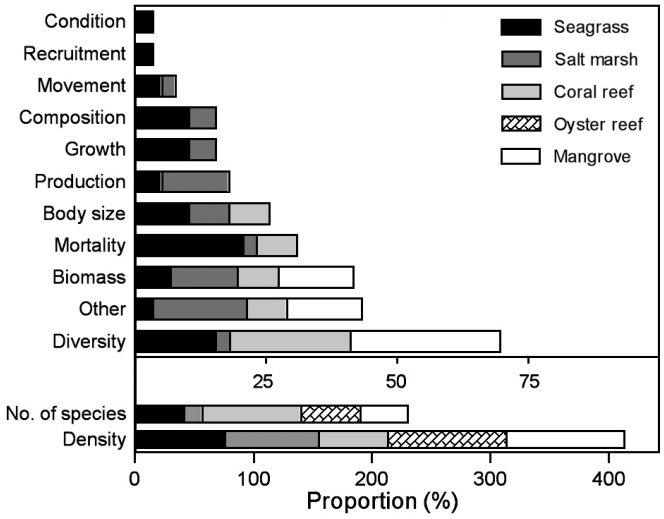


Fig. 5. Faunal response variables measured to investigate the influence of landscape or patch features on the 5 biogenic ecosystems. Density: number of individuals or abundance. No. of species: number of taxa or species recorded. Diversity: calculated diversity indices for faunal assemblages, e.g. Shannon-Wiener H′, Simpson Index (Jackson et al. 2006b, Reed & Hovel 2006). Production: animal secondary production, see e.g. Minello et al. (2008). Mortality incorporates studies reporting prey survival and predation pressure in relation to spatial pattern metrics. Biomass: a static measurement of the amount of animal biomass reported as dry or wet weight. Other: more rarely reported response variables such as number of functional groups, catch per unit effort, or cohort size. Movement: animal movement ranges measured *in situ* (Pittman et al. 2007) or estimated using simulation models (Haas et al. 2004). Composition: studies investigating influence of spatial configuration on the composition of infaunal or epifaunal assemblages using multivariate statistics (e.g. Frost et al. 1999, Tanner 2003, Mills & Berkenbusch 2009)

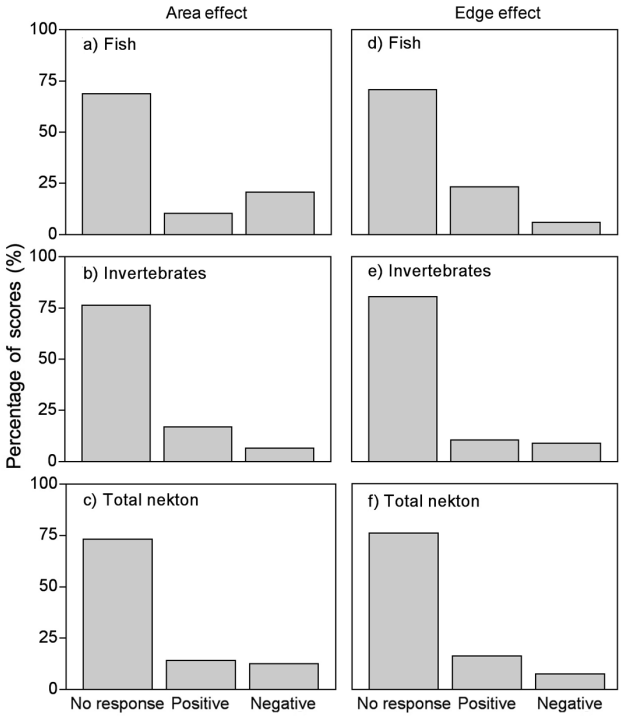


Fig. 6. Summary of (a,d) fish and (b,e) invertebrate as well as (c,f) total nekton responses to area (patch size) and edge effects (edge–interior comparisons) in seagrass seascapes. Only statistically significant responses in species density or richness are included. For details, see 'Materials and methods' and Connolly & Hindell (2006). Area effects are based on the following studies: Bell & Westoby (1986), McNeill & Fairweather (1993), Eggleston et al. (1998, 1999), Bell et al. (2001, 2002), Hovel & Lipcius (2001), Laurel et al. (2003), Tanner (2006), Jelbart et al. (2006, 2007), Johnson & Heck (2006), Hirst & Attrill (2008), and Mills & Berkenbusch (2009). Edge responses are based on results reported by Fonseca et al. (1990), Bologna & Heck (2002), Hovel & Lipcius (2002), Hovel et al. (2002), Sánchez-Jerez et al. (1999), Uhrin & Holmquist (2003), Tanner (2006), Jelbart et al. (2006), Smith et al. (2008), Horinouchi (2009), Macreadie et al. (2010), Smith et al. (2010), and Vonk et al. (2010)

pendent on arbitrarily defined differences between small versus large patches, rather than ecological processes (see 'Results — Spatial and temporal scaling in seascape studies'). The relative portions of significantly positive (increasing fish density or richness with increasing patch size) and negative (decreasing fish density with increasing patch size) responses were 10 and 20%, respectively. The partly dissimilar corresponding scores for invertebrate responses (17% positive and 7% negative) suggest that overall invertebrate density and richness are more likely to increase than decrease with increasing patch size. When scores were pooled for all fauna, the proportions for no response, positive response, and negative response were 76, 17, and 7%, respectively (Fig. 6c). Patch size effects on infauna are still understudied. Hirst & Attrill (2008) found no impact of the size range 17 to 147 cm in diameter on infaunal abundance and diversity, suggesting that even very small patches have high faunal diversity and abundance, and thus may have high conservation value. In another study from the UK, Bowden et al. (2001) sampled small (diameter <15 m) and large (diameter >30 m) *Zostera marina* patches and found a higher number of infaunal taxa, but not higher density and diversity ($H'$), in large patches compared to small.

*Salt marshes.* A few investigations of patterns in more mobile macroinvertebrates such as crabs have reported marsh patch size effects. In Chesapeake Bay (USA), Long & Burke (2007) found higher densities of fiddler crabs (*Uca* spp.) in a large (800–4300 $m^2$) marsh than in a small (60–240 $m^2$) marsh, but did not explicitly test patch size effects. As an indirect indication of patch effects on crabs, Guest & Connolly (2006) found that carbon flows supporting the red-handed shore crab *Parasesarma erythrodactyla* were higher in large (0.4–8.1 ha) than in smaller (<0.3 ha) mangrove/marsh (*Avicennia marina*, *Sporobolus virginica*) patches. Although there is considerable descriptive information

on nekton composition and abundance relative to total marsh area, few studies have related nekton density to individual patch size or density, and the documented relationships vary considerably by species. Meynecke et al. (2008) provided one of the few comparisons of fish biomass by patch size across a comprehensive seascape mosaic composed of seagrass, mangrove, marsh, other wetlands, mud, and sand patches (Queensland, Australia). In 1 of their 2 study regions, they found that fish catch was best explained by marsh and wetland patch density. Meyer & Posey (2009) described similar findings from North Carolina (USA) marshes, where the resident mummichog (killifish) *Fundulus heteroclitus* was found exclusively in the marsh and at greater densities in continuous marsh vegetation than in isolated patches, while the co-occurring transient pinfish *Lagodon rhomboides* was found in both the marsh plain and adjacent tidal flats. The abundance and productivity of avifauna has also been correlated to marsh size and patch density, but the relative importance varied with scale and surrounding land use. Landscape context was found to be particularly important for birds visiting New England marshes, where Shriver et al. (2004) found species richness to be 20% higher in larger marsh patches, but the effects of road density and marsh isolation varied according to the level of surrounding development. Spautz et al. (2006) found that each of 4 bird species in San Francisco Bay, California (USA), showed affinity for specific marsh plants and vegetative structure, but marsh size and adjacent development were also important predictors of abundance, while effects of finer-resolution spatial pattern metrics were insignificant for birds responding to the marsh and ecotone mosaic across 0.5 to 2 km.

*Coral reefs.* Sale & Douglas (1984) sampled fish communities on 20 coral patch reefs of varying surface area (2.71 to 28.35 $m^2$) on the Great Barrier Reef and found significant positive correlation ($r = 0.67$) with species richness. Similarly, in the US Virgin Islands, Grober-Dunsmore et al. (2007) found that coral reef patch size was significantly correlated with fish species richness ($r = 0.43$, $p < 0.001$), and Chittaro (2002) found a significant positive species–area relationship, where area explained 66 to 96% of the variation in species richness. This relationship appeared to be scale dependent, because at finer spatial scales (0.6 to 64 $m^2$), patch reefs contained 35% more species than contiguous coral reefs, while at broader spatial scales (100 to 200 $m^2$), the number of species on contiguous coral reefs was similar to that of patch reefs (Chittaro 2002). Overall, other habitat characteristics also played a role, and contiguous coral reefs with greater habitat richness contained more fish species per area than less habitat-rich patch reefs of equal size. To determine whether a single large patch supported more fish than several small patches (the so called 'single large or several small' [SLoSS] debate, see also McNeill & Fairweather 1993 for an analogous seagrass study), Acosta & Robertson (2002) surveyed fish on coral reefs in Belize and found greater abundance on relatively large (mean = 2300 $m^2$) coral reefs than on a cluster of 3 small (mean = 740 $m^2$) patch reefs. However, results for species richness from rarefaction analyses indicated that both species richness and species evenness were similar between a single large coral reef and 3 smaller reefs of equivalent total area.

*Mangroves.* In Australia, the proportion of mangroves in the seascape was only weakly positively correlated with the density of fish assemblages sampled in mangroves, but made a significant contribution to explaining fish species richness (Pittman et al. 2004). In Florida, mangrove area was a significant predictor in only 2 of 15 fish–seascape models, where it was negatively correlated with the density of juvenile barracuda *Sphyraena barracuda* and total fish density (Drew & Eggleston 2008). The perimeter:area ratio of mangrove islands, however, was a significant predictor of juvenile gray snapper *Lutjanus griseus* abundance. Halpern (2004) measured the amount of mangroves and their proximity to coral reefs in the Virgin Islands and found no relationship between the density of adult schoolmaster snapper *L. apodus* on coral reefs, but he found a significant relationship for the yellow-fin morjarra *Gerres cinereus* when data where pooled for entire islands. In the Philippines, a weak positive correlation was found between mangrove area and the catch of 4 families of commercial fish (Paw & Chua 1991).

*Oyster reefs.* In intertidal and subtidal areas, oyster reefs form landscape mosaics with patches ranging in size from single shells to kilometer-wide reefs (see Eggleston 1999 for a synthesis) (Fig. 1). Eggleston et al. (1998) revealed evidence of decreasing shrimp densities with increasing oyster patch size (0.25 to 4.0 $m^2$), while the first benthic stages of blue crabs showed opposite patterns. In addition, Eggleston et al. (1999) reported significantly fewer large macrofauna species in small (0.25 $m^2$) oyster shell patches compared to mixed patches (oyster shell and seagrass) and seagrass patches of the same size. In terms of small macrofauna, large (1 $m^2$) oyster shell patches supported more species than seagrass and mixed patches of the same area.

## Edge effects

*Seagrass meadows.* Although the seagrass–sand boundary represents a zone with abrupt transitions in many environmental and biological variables, most (75%) faunal taxa showed no significant edge responses (Fig. 6d–f). Fishes, however, showed proportionally more (25% of scores) positive edge effects (i.e.

higher abundance and/or richness) than invertebrates (10% of scores). Fewer data are available on infaunal responses to seagrass patch edges, but the density of polychaetes has been shown to peak at patch edges in different regions and seagrass landscapes (UK: Bowden et al. 2001; Australia: Tanner 2005; USA: Bologna & Heck 2002), although opposite patterns (i.e. interior aggregations) have also been observed (Bell et al. 2001).

*Salt marshes.* Almost half of the published marsh studies we reviewed reported faunal responses to patch and corridor edges. Descriptive studies have usually adopted 1 of 2 approaches: (1) sampling along gradients across edges, or (2) comparing different landscapes with varying amounts of edge $km^{-2}$ (edge density). Browder et al. (1989) modeled shrimp abundance in Louisiana (USA) and found a strong positive relationship between brown shrimp *Farfantepenaeus aztecus* catch and the total length of marsh edge, and a relationship between wetland loss (manifested as fragmentation) and the amount of marsh edge. Subsequent empirical and modeling studies of faunal density along vegetated marsh edges compared to interior marsh and mudflat (matrix) areas also demonstrated consistent evidence of greater fish and shrimp concentrations within 1.25 to 3 m of the marsh edge (Baltz et al. 1993, Minello et al. 1994, Peterson & Turner 1994, Cicchetti & Diaz 2000, West & Zedler 2000, Minello & Rozas 2002, Haas et al. 2004, Roth et al. 2008). However, most of these studies were conducted in the northern Gulf of Mexico. On the US Atlantic coast, Kneib (2003) demonstrated a positive relationship between nekton production and edge density within a 200 m radius of sampling locations on the interior intertidal marsh plain. Webb & Kneib (2002) also identified a relationship between the amount of intertidal marsh edge and the abundance of white shrimp *Litopenaeus setiferus* in adjacent subtidal channels of Georgia (USA) salt marshes. An investigation of the fine-scale distribution of benthic infauna relative to edge in a Gulf of Mexico marsh indicated that infauna were negatively related to the distance from the marsh edge, with the greatest densities occurring during winter and early spring when predator abundance was low (Whaley & Minello 2002). However, this pattern is not consistent across taxa or regions. For example, Kneib (1984) reported a variety of intertidal distribution patterns for different taxa of benthic invertebrates with distance from the marsh edge on Sapelo Island, Georgia (USA). On the US Atlantic coast, preferred epibenthic crustacean prey (e.g. tanaids and talitrid amphipods) of marsh nekton often tend to be more abundant at greater distances from the edge into the interior of the marsh plain (Kneib 1992, Covi & Kneib 1995). Lewis & Eby (2002) investigated the spatial patterns of gastropods (periwinkle snails) and blue crab, their predators, along the edge of a North Carolina (USA) *Spartina alterniflora* marsh and found that pursuant to the concept of increased inhibition of crab foraging with increasing distances into dense *S. alterniflora* marsh, snail densities increased positively with increased distance from the marsh edge. Although responses were found to be highly taxa specific, Fleeger et al. (2008) also found that marsh edge (as well as adjacent tidal channel wall) exhibited the strongest response by invertebrates to experimental predator removal and nutrient additions.

*Coral reefs.* Acosta & Robertson (2002) found 30% more edge-habitat fish species on small (700 $m^2$) reefs exhibiting a higher perimeter:area ratio than large (2300 $m^2$) reef patches, and fish species composition was markedly different when comparing the bottom edges of patch reefs with the reef top. Vanderklift et al. (2007) examined fish communities at varying distances (0 to 1100 m) from rocky reefs in Western Australia and observed an abrupt decline of small predatory fish within the first 30 m from the reef, indicative of a negative edge effect. Similarly, Dorenbosch et al. (2005) in the western Indian Ocean observed an edge effect for coral reef-associated species and generalist species, where fish densities and species richness decreased significantly within 30 m of the patch reef boundary.

## Fragmentation effects

*Seagrass meadows.* Because fragmentation is a dynamic process, not a state, there is a need to distinguish the static, postfragmented state or habitat patchiness from active habitat fragmentation. In the majority of studies examined here, fragmentation was approached by studying the static arrangement of different-sized natural and artificial patches, or by making comparisons between continuous and patchy configurations considered to represent different levels of fragmentation (e.g. Mizerek et al. 2011, this Theme Section). However, despite the prevalence of anthropogenic (propeller scarring, anchoring, dredging, trawling) and non-anthropogenic (storms) disturbances, there have been few attempts to conduct natural experiments or to experimentally fragment habitat and measure immediate responses (but see Reed & Hovel 2006, Macreadie et al. 2009). In a novel experimental design comparing patchiness with active fragmentation, Macreadie et al. (2009) found higher fish densities in actively fragmented treatments compared with non-fragmented controls, and more species in actively divided patches compared to a static arrangement of patches of the same total area. These results are among the first to indicate that fragmentation is not analogous to patchiness, and that fragmentation

effects might be compensated by edge effects and crowding, especially in fish assemblages dominated by habitat specialists (e.g. pipefish). When comparing continuous (>2 ha) and fragmented seagrass (patch size range: 6 to 9 $m^2$), Frost et al. (1999) found no effect of seascape configuration on infaunal density, diversity (19 taxa, $H'$ = 2.40 to 2.49), silt content and rhizome biomass, but configuration had a significant influence on the composition of the infaunal community. Similarly, in a comparison of fragmented (patch size range: 1 to 200 $m^2$) and continuous meadows (>1000 $m^2$) in 2 intertidal inlets in New Zealand, Mills & Berkenbusch (2009) found significant effects of seascape configuration on infaunal community composition. In the same study, density of individuals and the number of taxa (range 48 to 52) was significantly lower in fragmented landscapes at both study sites, while diversity ($H'$ = 1.8 to 2) showed inconsistent patterns in relation to configuration between sites. In the Gulf of Mexico (USA) Rakocinski et al. (2008) contrasted an exposed, fragmented (mean cover: 12%, mean patch size: 85 $m^2$) and a sheltered, less fragmented (mean cover: 45%, mean patch size: 645 $m^2$) seagrass meadow and recorded 4× higher total invertebrate abundance and 10× higher gastropod densities in the less fragmented meadow, but no effects on species richness (86 taxa) and diversity ($H'$ = 2.3 to 2.8). Interpretation of configuration effects is difficult due to confounding effects of wave exposure, and rarely have studies accounted for the interacting effects of hydrodynamics on faunal distributions (but see Turner et al. 1999).

*Salt marshes.* Few studies have tracked changes in ecological responses with the actual temporal fragmentation of marshes, while many have only assumed marsh structure indicative of slow disintegration (e.g. Minello & Rozas 2002). Fragmentation or increase of non-vegetated matrices appears to result in mostly positive faunal responses until thresholds are reached. Browder et al. (1989) predicted increases for brown shrimp production until salt marsh fragmentation reached a threshold (60% cover), after which shrimp production was expected to decline. Rozas et al. (2007) found that fish and decapod populations decreased by 34 to 95% over a 7 yr period during which 61% of a Texas (USA) marsh converted to open water. Much of this effect was likely manifested through a 71% decrease in marsh edge over that period.

*Coral reefs.* Few studies have addressed the influence of the spatial arrangement of coral reef patches across the seascape on faunal distributions, and therefore little is known about the potential impact of fragmentation. On the Great Barrier Reef, Australia, Ault & Johnson (1998a) recorded higher species richness on the larger patchy coral reefs than contiguous coral reefs. Patch reef assemblages, however, were more dynamic in time and space. On contiguous coral reefs, fish assemblage composition was more predictable and was best explained by within-patch structural attributes such as benthic composition, depth, and topographic complexity. To examine the influence of patch isolation on fish assemblages, Overholtzer-McLeod (2006) constructed arrays of artificial patch reefs with different inter-patch distances (5 to 50 m) in the Bahamas. The spatial configuration of patches influenced important predator–prey interactions affecting both the magnitude of total predation and the existence of density-dependent mortality for 2 common coral reef-associated species. Juvenile mortality rates for yellowhead wrasse *Halichoeres garnoti* and beaugregory damselfish *Stegastes leucostictus* were density dependent on reefs that were relatively isolated, but density independent on reefs that were more closely spaced. In the Pacific, Molles (1978) surveyed fish assemblages on rocky reefs of varying sizes (2.5 to 60 $m^2$) and found a significant negative correlation between reef isolation (6 to 60 m apart) and number of fish species, and a significant positive correlation with patch reef area.

*Mangroves.* We found only 1 study that explicitly quantified the spatial configuration of mangrove patches as a predictor of coastal faunal distributions. This study did not, however, track the process of fragmentation, but sampled mangroves varying in spatial configuration. For density of fish using mangroves at high tide, Pittman et al. (2004) found that mean nearest neighbor distance of mangroves was the most significant variable in explanatory models (path coefficient [pc] = 0.59, $t$ = 2.19, $p < 0.01$), although this appeared to influence species differently. Few species, however, preferred the more 'fragmented' patches, yet those that did were some of the most abundant schooling species in the samples and were well adapted to exist in open sandy areas.

## Effects of channel geomorphology and inundation regime in salt marsh seascapes

The distribution and abundance of marsh fauna can often be explained by the geomorphic structure of channels (e.g. complexity, density, depth) because these are the primary corridors for movements into and out of marshes and adjoining ecotones for most mobile coastal fauna (Figs. 7 & 4b). Furthermore, faunal responses to channel networks can be explained by both passive (tidal hydrology) and active (behavioral) selection processes. Desmond et al. (2000) found higher fish densities in 1st-order than in higher-order channels. Visintainer et al. (2006) also found that lower-order channels contained higher densities of small fish species, but species richness and densities of juveniles of

Fig. 7. Tidal marsh channel seascape in Cadiz Bay Natural Park, Spain. Photo: J. C. Muñoz

larger species were greater in higher-order (larger) channels. Tidal channel size rather than channel order may be a more important determinant of faunal assemblage structure; for instance, Rozas et al. (1988) found that the highest catch per unit effort (CPUE) of fishes accessing a Virginia (USA) marsh was found in the small 'rivulets' that dissected channel banks, where 41% of the fishes were captured even though the entrance to rivulets only accounted for 3% of the subtidal channel length. Similarly, Allen et al. (2007) suggested that although the highest nekton abundance and richness were found in shallow, broad tidal channels that filled/emptied slowly, differences in nekton abundance among channels ranged from 3× to 30× on the same day. There may actually be trade-offs between occupation of different tidal channel networks. Kneib (2009) found that mummichogs in Georgia (USA) *Spartina alterniflora* marshes were more dense in complex channel networks (headwaters) but that their field growth rates were greater in simple networks located closer to larger, open waters of the estuary. Similar responses might also be the case for subtidal populations of mysids (*Neomysis kadiakensis*), which Dean et al. (2005) found to incur significant adult mortality when imported into a San Francisco Bay, California (USA), marsh through a 4th-order tidal channel.

Tidal channel metrics have also been linked to trophic support of nekton in marsh-ecotone seascapes. Hood (2002a,b) illustrated how tidal channel allometry in Pacific Northwest tidal wetland complexes (emergent marsh, scrub-shrub, and forested wetland ecotone) related to the export probability of juvenile salmon prey (adult flies, aphids) as a function of channel size (perimeter, mouth area) and emergent marsh area. Larger and more complex channel networks that integrated emergent marsh with wetland ecotone had higher amounts of organic material in channel sediments and a greater abundance of benthic surface deposit feeders. At a finer scale, microtopographic patches and elevation zones in marsh plains can also provide sources and sinks of invertebrate fish prey as well as low-tide refugia for resident marsh nekton (Kneib 1994).

Hydroperiod is the ultimate control of access to the marsh and adjacent ecotones, and inundation frequency and duration may obscure effects of even large marsh edge or patch variability especially where meteorological effects drive microtidal regimes and marshes can experience extended periods of submergence (Rozas 1995, Kneib 1997). Many studies of nekton access to, and occupation of, marshes and ecotones relate nekton densities and production to inundation frequency and duration, arguing that nekton penetrating the marsh plain derive food and refuge from predation that is otherwise less available in lower tidal elevations (e.g. Rozas 1995). Rozas & Reed (1993) found higher densities of penaeid shrimp in low *Spartina alterniflora* marshes than in medium *Spartina* or high *Distichlis* marshes even when all 3 were submerged, seemingly driven by inundation time and depth irrespective of marsh edge. Kneib (2000) compared the density of white shrimp *Penaeus setiferus* and mummichogs on the marsh at high and low intertidal elevations under a range of tidal inundation durations; results showed that distance from the marsh edge (elevation) was less important than inundation duration, especially for white shrimp. In a study that actually related flooding frequency and duration to marsh edge, West & Zedler (2000) found that the southern California (USA) salt marsh edge, where they documented increased fish catches, was tidally inundated to a depth of at least 20 cm an average of 15.6 % of the time compared to only 9.3% of the time on the adjacent marsh plain.

## Importance of patch context and connectivity in coral and mangrove ecosystems

### Patch adjacency and proximity

Multi-scale analysis of fish–seascape relationships by Grober-Dunsmore et al. (2007) demonstrated that the amount of seagrass surrounding coral reefs was positively correlated with fish density and species rich-

ness. As much as 48 to 58% of the variation in fish assemblages on coral reefs was explained by the amount of seagrass in surrounding areas. In particular, the coral reefs with large amounts of seagrass in close proximity (<100 m) supported the highest abundance of grunts (Haemulidae) and snappers (Lutjanidae). The amount of seagrass within 100 m radius was the most significant spatial scale for explaining fish–seascape relationships in SW Puerto Rico (Pittman et al. 2007), Queensland, Australia (Pittman et al. 2004), and elsewhere (in the US Virgin Islands; Kendall et al. 2003). Further evidence for the importance of patch adjacencies comes from multi-habitat studies that have not taken a landscape ecology approach. In Belize, spiny lobsters, particularly juveniles, were significantly more abundant in mangroves and coral islands surrounded by seagrass (Acosta 1999), and the biomass of several fish species more than doubled where coral reefs existed in close proximity to extensive mangroves (i.e. 35% of coastline; Mumby et al. 2004).

### Structural and functional connectivity

Limited evidence suggests that connectivity is likely to be as vital a seascape attribute in coastal ecosystems as it is in terrestrial ecosystems. Seascape connectivity is rarely studied as a spatially-explicit process linking benthic patterns to animal movements. Information on broad-scale movements across mosaics of patch types, however, suggests that seascape patterns will be an important variable for many benthic and demersal species that undertake diel migrations, ontogenetic shifts, and seasonal and spawning migrations between adjacent patches and across continental shelves (Kneib 2000, Pittman & McAlpine 2003). In Queensland, Australia, Meynecke et al. (2008) found that structural connectivity of the seascape was the single most influential variable for fisheries. In particular, connectivity indices for mangroves, salt marsh and channels explained the largest proportion (30 to 70%) of variability in fisheries catch, indicating that connected tidal wetlands are important for fisheries. The CPUE of a key species, barramundi *Lates calcarifer*, was best explained by the number of wetland patches, mangrove connectivity and wetland connectivity ($r^2 = 0.38$, n = 28).

### Ecological thresholds in species–habitat relationships

We identified both, non-linear species responses and threshold levels in coverage in the seascape literature (Table 3). In general, fish and mobile epifauna appear to be robust to even extreme changes in seagrass cover (Pittman et al. 2004, Reed & Hovel 2006). Three studies demonstrated a positive parabolic relationship between seagrass patchiness and fish abundance, suggesting that continuous vegetation cover and/or large patches may be suboptimal for many fish species (Salita et al. 2003, Gorman et al. 2009, Thistle et al. 2010). Similarly, nekton populations in salt marshes may benefit from early stages of fragmentation and show positive curvilinear relationships to increasing fragmentation, but populations decline at ~60% (Browder et al. 1989) or <30% marsh cover (Minello & Rozas 2002, Haas et al. 2004). Species richness of coral reef fish may also show considerable declines when surrounding seagrass coverage drops below 30% (Grober-Dunsmore et al. 2009), but threshold responses related to focal (coral) habitat configuration have not been demonstrated; however, see Pittman et al. (2009) for complexity related thresholds in coral reef ecosystems.

## DISCUSSION

### Habitat fragmentation

Fragmentation of habitat is an important driver of species loss and degradation of ecosystem functions in many terrestrial ecosystems (Didham 1997, Hanski 2005). The term 'habitat fragmentation,' however, remains conceptually ambiguous because it involves both reduction in area and change in configuration. Furthermore, many habitat fragmentation studies have not examined the phenomenon as a dynamic process, but instead have sampled patchy habitats, sometimes along a gradient. The use and application of the term is further complicated by our poor ability to discriminate between natural and human-induced changes in natural environments, and because organisms perceive patchiness in different or contradictory ways (Haila 2002). Our review of the coastal fragmentation literature provided no exception for several reasons. Firstly, the mechanisms causing fragmentation are widely different in different regions (Table 2). Secondly, there is a wide range in the spatial and temporal scales at which habitat fragmentation has been studied. Thirdly, organisms seem to respond to the process of fragmentation in different ways, and little direct evidence is available to assess behavioral responses. All of these factors make the study of coastal fragmentation very challenging and inhibit our ability to directly compare studies, identify general patterns, or predict consequences across systems, and ultimately design coastal reserves based on relevant information.

Habitat fragmentation is a complex process (not a state) seldom resulting in the mere splitting of habitat (sensu Fahrig 2003). Rather, in coastal (and terrestrial) systems, fragmentation typically involves multiple

Table 3. Examples of studies identifying nonlinear faunal responses to changes in habitat configuration (fragmentation)

| Habitat and Component species | Response variable | Target taxon | Measure and estimate of configuration threshold | Source |
|---|---|---|---|---|
| **Seagrass** | | | | |
| *Zostera marina* + *Halodule wrightii* | Survival, siphon weight | Mollusks | 70% cover | Irlandi (1994)[a] |
| *Thalassia hempirichii* + *Cymodocea rotundata* | Catch (%) | Fish | 60% cover | Salita et al. (2003)[b] |
| *Zostera capricorni* | Abundance, species richness | Fish, decapods | 20% cover | Pittman et al. (2004) |
| *Zostera marina* | Abundance, species richness | Epifauna | 10% cover | Reed & Hovel (2006) |
| *Zostera marina* | Mortality | Fish | 25 $m^2$ patch area | Gorman et al. (2009)[c] |
| *Thalassia testudinum* | Species richness | Fish | 30% cover | Grober-Dunsmore et al. (2009) |
| *Zostera marina* | Density | Fish | $D_p$ = 1.4, $D_A$ = 0.85–0.92, $\beta_{P/A}$ = 0.4–0.6[d] | Thistle et al. (2010) |
| **Salt marsh** | | | | |
| *Spartina alterniflora* | Abundance | Decapods | 30% cover | Minello & Rozas (2002) |
| *Spartina alterniflora* | Production | Fish, decapods | 2000–3000 m edge within a 200 m radius | Kneib (2003)[e] |
| Simulated landscape | Survival, growth, density, mobility, time in vegetation | Decapods | 50% cover with high amount of edge | Haas et al. (2004)[f] |
| **Tidal creek** | | | | |
| Six land cover categories | Abundance, food web structure | Infauna | 20–30% impervious cover | Holland et al. (2004)[g] |

[a]Below-ground biomass and shoot density (but not aboveground biomass and shoot length) differed across configuration treatments

[b]A positive parabolic shape was recorded, with equally high fish catches at both extreme ends (16 and 94% cover, respectively) of the fragmentation gradient

[c]Percent predation on tethered age 0 cod measured in patches within the size range 1 to 80 $m^2$

[d]Scaling coefficient indicating $D_p$ = fractal dimension of perimeter, $D_A$ = fractal dimension of area, $\beta_{P/A}$ = scaling coefficient indicating convolution and landscape patchiness and how perimeter:area estimates change with scale of measurement; for details, see Thistle et al. (2010)

[e]Landscape complexity threshold was measured as the amount of intertidal creek edge within a 200 m radius of nekton collection sites (see 'Discussion — Non-linearities in animal–habitat configuration relationships' for details)

[f]Individual-based simulation modeling study testing the importance of percentage vegetation cover and edge cells in 4 marshscapes: little edge and high amount (50%) of vegetation with little and high amount of edge, and low amount (30%) of vegetation and little and high amount of edge

[g]When impervious cover (i.e. surfaces dominated by roads, parking lots, sidewalks, buildings) in tidal creek ecosystems exceeded 20 to 30% cover, reduced abundance of stress-sensitive macrobenthic taxa and shrimp as well as food web alterations were recorded

interlinked changes including increased isolation of patches, habitat loss, and changes in the number, shape, size, quality, and species composition of patches. While fragmentation can be reliably assumed to be a directional process in some ecosystems (e.g. wetland loss associated with subsidence of the northwestern Gulf of Mexico coastal marshes, Minello & Rozas 2002), and thus a 'fragmentation state,' other ecosystems may undergo variable natural processes of fragmentation and reconsolidation, wherein it is difficult to know the direction of change. Even in seagrass meadows, the best studied coastal seascape, any difference in a faunal response variable between a small and a large patch cannot usually be explained by a mere size effect, as differences in patch quality (e.g. changes in shoot density and thus water flow, amount of drift algae, number of opportunistic/competing species, and grain size), patch horizontal isolation (e.g. distance to the nearest patch of the same or contrasting habitat), patch vertical isolation, and patch shape (e.g. edge:area ratios) all influence the organisms inhabiting different patches. Furthermore, very few studies have separated the effects of fragment size, loss, and quality (Caley et al. 2001, Healey & Hovel 2004). In a small-scale field experiment separating the effects of coral reef fragmentation from degradation (bleaching), Caley et al. (2001) demonstrated that both total abundance and species richness showed weak responses to fragmentation, and both variables declined in response to degradation of coral colonies. This study further demonstrated species-specific responses to habitat fragmentation, with crabs and shrimps showing increasing and decreasing abundance patterns, respectively.

Response scales covered in experimental work (without confounding effects of factors such as habitat complexity and patch shape) have been short (hours to weeks), so patterns manifested over months and years might remain undetected. Conversely, while repeated

sampling of patchy natural systems address these issues and identify effects, emerging findings are usually confounded by habitat complexity combined with site and time-specific responses. Such methodological trade-offs suggest that complementary approaches using repeated, small-scale manipulations in combination with broad-scale interannual surveys would be more productive approaches to tackling complex animal–habitat relationships in seascapes.

### Edge effects

Edge effects were originally defined by Odum (1958) as the tendency for increased population density and species richness at the junction between 2 communities. The boundaries or transition zones between patch types often exhibit abrupt changes in physical structure, community biomass, assemblage composition, and sometimes provide navigable pathways for migrations and sites for spawning (Johannes 1978). This is likely to occur because mixing of species from 2 adjacent patch types and preferential use of edges offers greater access to resources in multiple patches. However, the majority of studies (70 to 75%) that have examined edge effects in coastal fishes and invertebrates have found no persistent response to edge (neutral edge response). Of the remainder, a positive response was found more often than a negative one, particularly for fish. In terrestrial avian literature, positive responses to edges are also more commonly found than negative edge responses (Sisk & Battin 2002). Avoidance of edges is more likely to be a response of a habitat specialist adapted to patch interior conditions than a generalist using resources in multiple patch types. Furthermore, edges within a patch type can differ due to both the internal heterogeneity of the patch and the patterning of the surrounding seascape. In our synthesis, the majority of studies examined edge responses for patches of seagrasses. A stronger edge effect was evident for coral reefs, marshes, and mangroves than for seagrass meadows, which likely corresponded to a more distinctive contrast in structural complexity that characterizes the edge where it adjoins lower-complexity soft sediments. In salt marshes, the prevalent paradigm is that access to marsh resources, such as prey on the marsh plain or exported prey, occurs along the marsh–channel interface such that a greater edge (or area:perimeter ratio) will have a higher attraction and function for mobile coastal fauna. Similarly, increased concentration of zooplankton and meiofauna along seagrass edges might be an explanatory mechanism for greater nekton abundance along seagrass edges (Macreadie et al. 2010). Most edge response studies are short-duration observations, conducted during daylight hours and carried out with no *a priori* predictions. This is likely to bias results, because many species make nocturnal forays across ecosystem boundaries to feed or use edges only when risk from predation is reduced.

### Infaunal responses to seagrass configuration

Infaunal responses to seagrass patch attributes and habitat configuration are still understudied compared to epifauna and fishes. This is unexpected, because such responses are likely important in explaining spatial distributions of higher trophic levels in patchy environments. Generally, studies have focused on 3 topics: (1) patch size effects (Bowden et al. 2001, Hirst & Attrill 2008); (2) patch edge effects (Bell et al. 2001, Bowden et al. 2001, Bologna & Heck 2002, Tanner 2005, Boström et al. 2006b); and (3) effects of broad-scale habitat configuration/fragmentation (Frost et al. 1999, Turner et al. 1999, Rakocinski et al. 2008, Mills & Berkenbusch 2009). Broad-scale (1 to 50 km) fragmentation studies on infauna are still few, and confounding effects of exposure, depth, habitat complexity, and time complicates direct comparisons of configuration effects (Rakocinski et al. 2008, Mills & Berkenbusch 2009), but see Turner et al. (1999) for separation of the influence of patch, landscape, and temporal variability on infauna. Unlike epifauna and fish, infauna appear to be less influenced by aboveground structure (except during the settling phase for some taxa), and the key mechanism maintaining high density and diversity is sediment stability provided by the belowground rhizome network.

While most infauna taxa appear to be more abundant in large patches or show similar densities in both small and large patch sizes, some taxa (e.g. oligochaetes, nematodes, and the polychaete *Capitella* sp.) seem to occur at higher densities in small patches. Such patterns may be explained by differences in infaunal life-history and functional traits. Reproductive type, feeding habits, and larval type have been identified as important factors influencing dispersal and community development and composition (Bremner et al. 2006). Other inconsistencies such as low versus high densities of Capitellidae along patch edges in Australia and the UK, respectively (Bowden et al. 2001, Tanner 2005), and between various polychaete families (Tanner 2005) also have been reported. Other taxa that seem to be edge specialists are tanaids and isopods (Bowden et al. 2001, Tanner 2005). The mechanisms causing such interior–edge differences are poorly understood, but species-specific susceptibility to predation, differing grain size, and organic content preferences or dissimilar feeding modes and reproductive strategies across infaunal taxa are all possible factors that warrant further study. How-

ever, prevalence for fragmented (edge) habitats might vary between taxon and site (Mills & Berkenbusch (2009). Thus, although tanaids (*Leptochelia savignyi*) and amphipods (Phoxocephalidae sp.) were found in higher numbers in continuous meadows at one site, they exhibited much higher abundances in fragmented seagrass at the other study site. Such results are likely influenced by the relative position of the patches in relation to site-specific environmental gradients (Mills & Berkenbusch 2009).

### Non-linearities in animal–habitat configuration relationships

As coastal biogenic habitats are fragmented or lost (Tables 1 & 2), a central question is whether animal population size or some other relevant ecological response variable will change linearly in relation to changes in habitat configuration, or whether faunal responses are characterized by non-linear relationships and sudden changes or so called 'critical thresholds' as reported for terrestrial landscapes (Swift & Hannon 2010). Non-linearities occur in both seagrass patch growth — and thus seascape formation (Sintes et al. 2005) — and in physical processes (wave attenuation) in coastal habitats (Koch et al. 2009), but similar responses by animals inhabiting these systems have not been synthesized.

One of the earliest examples of potential seascape configuration thresholds implied that transfer of secondary production increased abruptly when seagrass cover decreased from 99 to 70%, while no further increase in energy transfer was recorded in very patchy (23% cover) seagrass landscapes (Irlandi 1994). Fonseca & Bell (1998) proposed a critical coverage level of 50 to 59% in seagrass ecosystems, below which loss of integrity decreases with increasing habitat fragmentation. The seascape literature currently includes several other examples of potential thresholds and non-linear species–habitat relationships. Mobile fauna seem to tolerate significant changes in seagrass vegetation cover. For example, Pittman et al. (2004) identified a linear decrease in density and diversity of fishes and decapods as seagrass cover decreased along a gradient until ca. 20% seagrass cover, where an abrupt decline in fauna was recorded. Similarly, Reed & Hovel (2006) showed that removal of up to 50% of seagrass had minor impact on the number, richness, and composition of seagrass epifauna, while a shift in epifaunal species richness and density was only evident in plots with 90% habitat removal.

Strong positive parabolic relationships between seagrass cover and fish abundance have also been recorded, with highest fish abundances in both continuous (95% cover) and discontinuous (16% cover) seagrass landscapes. This result suggests that conditions are suboptimal for fish at 55 to 65% cover (Salita et al. 2003). Also in a temperate seagrass seascape consisting of patches between 1 and 80 $m^2$, predation risk of juvenile cod was best described with a parabolic function, where predation losses were highest at a threshold patch size of 25 $m^2$ (Gorman et al. 2009). Perhaps the most convincing evidence of strong parabolic relationships between fish and seagrass ecosystem configuration is from Newfoundland, Canada, where Thistle et al. (2010) found strong parabolic relationships between fish density and eelgrass patchiness across several fish species and spatial scales (Table 3). Furthermore, recent work on the multi-scale relationships between 3-dimensional topographic complexity and fish distributions has detected distinct threshold effects for some coral reef species that exhibit a sensitive dependence for architecturally complex reefs (Pittman et al. 2009). Explanations put forward to explain parabolic relationships between fish and habitat configuration include food availability, predation risk, or a combination of both. For instance, juvenile cod (*Gadus morhua*) forage for zooplankton and invertebrates over the unvegetated matrix, and reduce their own predation risk by using the structure provided by patchy vegetation (Laurel et al. 2003, Thistle et al. 2010). Also, pipefish respond to increased food availability (e.g. copepods) along seagrass patch edges (Smith et al. 2008, Warry et al. 2009). However, strong diurnal patterns may also influence spatial patterns of fish foraging in patchy seagrass seascapes (Jackson et al. 2006b). In seagrasses, predation risk is higher along edges (Irlandi 1994, Bologna & Heck 1999a, Peterson et al. 2001) as well as in larger patches and connected ecosystems due to higher predator densities (Hovel & Lipcius 2001, Laurel et al. 2003). Thus, predation may explain avoidance of very patchy as well as continuous vegetation, causing parabolic distributions (Salita et al. 2003).

Despite the association of salt marsh nekton with ecosystem edges (see 'Results — Spatial pattern metrics and faunal response variables — Edge effects — Salt marshes'), and parabolic models suggesting a maximum amount of edge in marsh seascapes with 60 to 70% cover (Browder et al. 1989, Minello & Rozas 2002), few quantitative values for critical thresholds unique to tidal marsh seascapes have been described to date. On the other hand, simulation models suggest that survival of brown shrimp peaks at intermediate levels of fragmentation patterns in marsh seascapes characterized by large amounts of edge habitat, while less and more severe disintegration results in lower shrimp survival and density estimates (Browder et al. 1989, Haas et al. 2004) (Table 3). There is a scarcity of examples that describe the shape of population response curves to marsh–water configurations. However, sigmoid relationships between nekton produc-

tion and salt marsh landscape pattern have been demonstrated. For example, Kneib (2003) described steep declines in both resident and migrant nekton production when the amount of marsh edge within a 200 m radius of a sampling point dropped below a 3000 m threshold. However, duration of tidal inundation, i.e. intertidal foraging time for nekton, was believed to influence any underlying relationship between marsh edge and nekton production derived from intertidal resources. In a broader watershed view, there appear to be thresholds in relationships between detectable environmental effects on physical, chemical, and biological components of tidal marsh creeks and the amount of impervious surface in adjacent upland areas (e.g. Lerberg et al. 2000, Holland et al. 2004) that are similar to those reported for freshwater riverine watersheds (Booth & Jackson 1997).

### Applications in coastal management and spatial planning

Although strong evidence of biotic response to some spatial patterns in coastal ecosystems would argue for incorporating the underlying concepts into coastal restoration and protection strategies and designs, the published literature has yet to provide much guidance or case studies. Despite numerous terrestrial studies that argue for restoration of fragmented landscapes to increase biodiversity and abundance of targeted at-risk taxa (Palmer 2009), this has generally not been substantiated for coastal restoration.

The application of a landscape ecology approach in the management of salt marshes has provided a broader view of the importance of maintaining spatial heterogeneity to accommodate not only the requirements of multiple species (Larkin et al. 2008), but also an explicit consideration of humans as integral components of coastal seascapes (Weinstein 2008). Some large-scale preservation and restoration efforts in marsh ecosystems in the USA have specifically relied on applying recognized relationships between the marsh seascape, tidal hydrodynamics, and the export of fish production to the open estuary (Weishar et al. 2005). Relationships between channel geomorphology, tidal activity, and use of marsh ecosystems by faunal components have been applied to evaluate restoration projects in California (Larkin et al. 2008) as well as manipulations of the marsh seascape for mosquito control in New Jersey (Lathrop et al. 2000). In addition, the regional focus on the importance of edge in the production of fisheries species also has driven a number of smaller-scale marsh restoration projects in the Gulf of Mexico (Rozas et al. 2005, 2007, Rozas & Minello 2007). Furthermore, modeling results suggest that salt marsh nekton population size may benefit from simulated addition of channel edge (Minello & Rozas 2002). Allometric form (outlet width and depth, channel length, perimeter, and surface area) of tidal channels may constitute valuable templates for tidal channel restoration. For example, Hood (2002a) argued that allometric relationships that can be related to ecological performance (e.g. anadromous fish use), benefit restoration design and assessment by (1) loosening size-related constraints on replication for landscape-scale studies; (2) maximizing physical and ecological predictability; (3) providing insight into undocumented human disturbances; and (4) suggesting allometry-based design goals and criteria for success.

For conservation efforts to be successful, the abundance, proximity, and composition of different habitat types within patch mosaics needs to be considered. Coral reefs and mangroves exhibit complex spatial patterning at a range of spatial scales (Fig. 1), yet relatively few studies have quantified the seascape composition and spatial configuration. The majority of work has focused instead on the juxtaposition of habitat types and their relative proximity or the absence/loss of key habitat types on faunal distributions. Many of these studies did not adopt a landscape ecology approach whereby spatial attributes of patch structure and patch context are quantified. The influence of patch types adjacent to coral reefs and mangroves has long been known as an important factor determining the structure and ecological function of these interconnected systems (Nagelkerken et al. 2001). Where patch mosaics have been analyzed, seascape composition and organization appears to elicit a stronger faunal response than spatial configuration. This has clear implications for both the way we approach the study of fish–habitat relationships and for conservation efforts. Research on juvenile fish species in mangrove seascapes indicates that higher survival is associated with certain seascape types. For example, certain fish species with life histories that require habitat-specific ontogenetic shifts may successfully transition through all life stages only when mangroves exist in close proximity to seagrasses and coral reefs to provide sufficient stage-specific food resources and predator refugia (Nagelkerken et al. 2001, Pittman & McAlpine 2003).

Identification of functionally integrated seascape types involves a perceptual shift away from a focus on single patch types to a consideration of interrelated functions provided by mosaics of habitat types (Pittman et al. 2007). This information can be used to help design restoration strategies or to ensure that a suite of resources is protected so that the seascape functions well for the support of species, assemblages, and communities of interest. This will guide investments that are targeted at achieving ecologically meaningful goals and objectives and increase the likelihood of success in con-

servation. Such information can also assist in identifying essential fish habitat, which would also be enhanced through consideration of seascape types versus the more conventional individual patch types, particularly for multi-habitat species. Although commonly implemented in terrestrial environments and known as 'conservation design,' few coastal examples exist where restoration actions are strategically chosen to enhance faunal populations through ecologically functional seascape configurations. One large-scale example from a salt marsh in Delaware Bay (USA) was described by Teal & Peterson (2005) and associated contributions. Landscape ecology concepts related to size and shape, connectivity and spacing, and diversity of target habitats have been incorporated into MPA design criteria (Roberts et al. 2003, McLeod et al. 2009). Fewer studies have incorporated seascape structure in comparative studies of MPA effectiveness. This is problematic because most MPAs are sighted around areas of local interest which may include the best examples of coastal ecosystems. Therefore, it is important to account for variability in the underlying seascape composition and configuration in explaining variability in performance and in untangling the relative influence of compliance or enforcement or other factors. Likewise, the seascape structure surrounding an MPA may influence the ecological functioning inside the MPA. Ultimately, the achievement of more sustainable and ecologically functional coastal seascapes will require more adherence to protecting and restoring the natural ecosystem processes that promote natural 'designs' rather than 'designing' restoration and preservation.

## Future research priorities for seascape ecology

### Habitat fragmentation

The results of our synopsis of the state of this science suggests that the next generation of fragmentation research should (1) more clearly address what type of seascape change (e.g. patch fragmentation) is measured, such as the effects of a static arrangement of patches illustrating the (long-term) end result of a naturally patchy system, or the (short-term) effects of active habitat fragmentation mimicking stochastic disturbance events; (2) consider the portion of sensitive (ecologically specialized) versus insensitive (habitat generalist) species in the system in order to evaluate acute versus chronic seascape scenarios; (3) identify risk regions, i.e. highly fragmented areas under risk of likely loss due to future anthropogenic pressures, or due to the negative cascading effects that loss of a habitat might have on adjacent elements in the seascape; and (4) design surveys and experiments to identify and assess the generality of possible nonlinear faunal responses and critical thresholds to changes in habitat configuration across species and systems.

### Edge effects

Ries & Sisk (2004) provided a predictive framework for faunal responses (changes in abundance) to edges based on an assumption that the relative availability of resources between patches is a key driver of responses. If access to prey assemblages drives nekton edge responses, future edge studies could focus more on explicit tests of that hypothesis in different seascapes, and routinely incorporate prey species sampling in descriptive and experimental edge studies (Smith et al. 2008, Warry et al. 2009). Studies are now needed in different biogenic ecosystems to examine species and even life history-stage specific sensitivities to edge that could also be influenced by behavioral and anatomical attributes such as mobility, access to mates, body size, schooling and other predator evasion tactics, and diet.

### Animal movements and connectivity

Relationships among seascape patterns, connectivity, and animal movements are among the most overlooked applications of landscape ecology to coastal environments and likely to be an area of intense activity as the data, tools, and technology needed to address this topic become more widely available. In particular, more studies are now required to gain a broader and deeper understanding of the link between patch connectivity and coastal organism distributions. This will allow us to identify optimal seascape types and determine whether thresholds or tipping points exist in structural connectivity that if exceeded could disrupt functional connectivity such as the transitioning between critical stages of the life cycle.

### Oyster reefs

The processes and faunal interactions in many coastal habitats have not been effectively examined in the seascape context e.g. macroalgae/kelp systems, but among those we examined, oyster reefs are clearly understudied from a landscape point of view. This is surprising given their high global loss rates (Beck et al. 2009), their importance for coastal ecosystem function (Peterson et al. 2003), and their critical role as links in coastal seascapes (Micheli & Peterson 1999, Shervette & Gelwick 2008). As oyster reefs form landscape mosaics with patches ranging in size from single shells

to kilometer-wide reefs (Fig. 1), future manipulative work should focus on the role of patch size, shape, elevation, and isolation to determine how these features affect ecosystem processes and associated faunal diversity. Such experiments may be particularly valuable for understanding optimal reef design in restoration programs (Grizzle et al. 2006).

Thus, while previous studies have provided a good basis for understanding coastal organism–seascape links and patterns, future research efforts should aim at linking spatial patterning of biogenic ecosystems and their component habitats to organism behavior and ecosystem functioning (Lima & Zollner 1996). This requires novel interdisciplinary approaches, better use of the latest technology and analytical methods (Treml et al. 2008), and perhaps most importantly, an in-depth understanding of the biology of marine organisms, including life cycle analysis, recruitment patterns and bottlenecks, movement behavior, and residence times.

## CONCLUDING REMARKS

Landscape ecology principles have not been applied extensively to coastal ecosystems, with most examples and arguably greatest advances gained from studies of vegetated soft sediment patch types such as seagrass meadows and salt marshes. In addition, studies using a seascape approach on other important ecosystems such as coral reefs and mangrove forests are emerging. Thresholds in animal–habitat associations in coastal biogenic ecosystems appear to be common but also species, habitat, and site specific. Conversely, studies of faunal interactions with variation in the broader seascape composition and organization are still poorly represented. Although dominant (and well documented) mobile species of fish and epifauna seem robust in the face of habitat loss at smaller scales, extrapolations across species and organism groups, habitats, and spatio-temporal scales should be avoided. Significant efforts are now needed to expand seascape ecology to seagrass and salt marsh systems outside the US and Australia, and thus provide critical comparative framework to assess the generality of results obtained during the first 30 yr of seascape ecology. From a theoretical perspective, seascape ecology has great potential to enhance our understanding and management of coastal environments. Substantial efforts are now required to apply and evaluate landscape ecology concepts and analytical techniques to coastal species and ecosystems, and thus further develop this exciting new frontier in coastal science. Technological advances in acoustic and optical remote sensing, geographical information systems, spatial analysis, and acoustic technologies can provide the data and tools to facilitate multi-scale analyses and track movements of individuals. Together with the realization that important changes are occurring to biogenic ecosystems at a range of scales, these technological catalysts are set to propel seascape ecology and the associated conceptual frameworks into mainstream coastal ecology.

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**Appendix 1.** Chronological summary of the 118 studies included in this review. FE: field experiment, FS: descriptive field survey, ASU: artificial seagrass unit. Time (d: days, wk: weeks, mo: months, yr/yrs = year/years) refers to the duration of the study; nd: no data

| Ecosystem | No. | Country | Region | Method | Time | Source |
|---|---|---|---|---|---|---|
| Seagrass | 1. | USA | North Carolina | FE | mo–yrs | Fonseca et al. (1990) |
| | 2. | Australia | New South Wales | FS, FE, ASU | mo | McNeill & Fairweather (1993) |
| | 3. | USA | North Carolina | FE | wk | Irlandi (1994) |
| | 4. | USA | North Carolina | FE | d–wk | Irlandi et al. (1995) |
| | 5. | USA | North Carolina | FE | mo | Irlandi (1996) |
| | 6. | USA | North Carolina | FS, FE, ASU | mo | Irlandi (1997) |
| | 7. | USA | North Carolina | FE, ASU | wk | Eggleston et al. (1998) |
| | 8. | Germany | Baltic Sea | FE | mo | Reusch (1998) |
| | 9. | USA | Florida | FE | d-wk | Bologna & Heck (1999a) |
| | 10. | USA | Florida | FE, ASU | wk | Bologna & Heck (1999b) |
| | 11. | USA | North Carolina | FE, ASU | wk | Eggleston et al. (1999) |
| | 12. | UK | Devon | FS | d | Frost et al. (1999) |
| | 13. | USA | North Carolina | FE, ASU | mo | Irlandi et al. (1999) |
| | 14. | USA | California | FE | wk–mo | Reusch & Williams (1999) |
| | 15. | Spain | Alicante | FS | mo | Sánchez-Jerez et al. (1999) |
| | 16. | New Zealand | North Island | FS | mo–yr | Turner et al. (1999) |
| | 17. | USA | Florida | FS, FE, ASU | mo–yr | Bologna & Heck (2000) |
| | 18. | USA | Florida | FS | mo–yr | Bell et al. (2001) |
| | 19. | UK | Isles of Scilly | FS | d | Bowden et al. (2001) |
| | 20. | USA | Florida | FE | d | Brooks & Bell (2001) |
| | 21. | USA | Virginia | FS, FE, ASU | d | Hovel & Lipcius (2001) |
| | 22. | USA | Maine, Florida | FE | h–wk | Peterson et al. (2001) |
| | 23. | Spain | Alicante | FS | mo–yr | Barberá-Cebrián et al. (2002) |
| | 24. | USA | Florida | FS, FE | mo | Bologna & Heck (2002) |
| | 25. | USA | Virginia | FS, FE | d–wk | Hovel & Lipcius (2002) |
| | 26. | USA | North Carolina | FS | yr | Hovel et al. (2002) |
| | 27. | USA | California, North Carolina | FS, FE | h–d | Hovel (2003) |
| | 28. | Canada | Newfoundland | FE, ASU | mo–yr | Laurel et al. (2003) |
| | 29. | The Philippines | Bolinao | FS | mo | Salita et al. (2003) |
| | 30. | Australia | South Australia | FE, ASU | wk–mo | Tanner (2003) |
| | 31. | Puerto Rico | La Parguera | FS | mo | Uhrin & Holmquist (2003) |
| | 32. | Australia | Queensland | FS | mo–yr | Pittman et al. (2004) |
| | 33. | USA | California | FE, ASU | mo | Healey & Hovel (2004) |
| | 34. | Australia | South Australia | FS | mo | Tanner (2005) |
| | 35. | Italia | Capo Feto | FS | d | Fernandez et al. (2005) |
| | 36. | USA | North Carolina | FE, ASU | d–mo | Darcy & Eggleston (2005) |
| | 37. | USA | North Carolina | FE, ASU | d–yrs | Hovel & Fonseca (2005) |
| | 38. | USA | Texas | FS | mo–yrs | Burfeind & Stunz (2006) |
| | 39. | USA | California | FE | mo | Reed & Hovel (2006) |
| | 40. | Australia | South Australia | FS, FE, ASU | wk–mo | Tanner (2006) |
| | 41. | UK | Jersey | FS | d–mo | Jackson et al. (2006a) |
| | 42. | UK | Jersey | FS | d–mo | Jackson et al. (2006b) |
| | 43. | Australia | New South Wales | FS, FE, ASU | mo | Jelbart et al. (2006) |
| | 44. | USA | Alabama, Florida | FS, FE, ASU | wk-mo | Johnson & Heck (2006) |
| | 45. | Australia | New South Wales | FS | mo–yr | Jelbart et al. (2007) |
| | 46. | USA | California | MO | nd | Hovel & Regan (2008) |
| | 47. | UK | Torbay | FS | d | Hirst & Attrill (2008) |
| | 48. | Australia | Victoria | FS | mo | Smith et al. (2008) |
| | 49. | USA | Mississippi | FS | mo | Rakocinski et al. (2008) |
| | 50. | Australia | Victoria | FE, ASU | d–yr | Warry et al. (2009) |
| | 51. | Australia | Victoria | FE, ASU | d–yr | Macreadie et al. (2009) |
| | 52. | New Zealand | South Island | FS | mo | Mills & Berkenbusch (2009) |

(continued on next page)

**Appendix 1** (continued)

| Ecosystem | No. | Country | Region | Method | Time | Source |
|---|---|---|---|---|---|---|
| | 53. | Canada | Newfoundland | FS, FE | mo–yr | Gorman et al. (2009) |
| | 54. | Japan | Moroiso Bay | FS | mo–yr | Horinouchi (2009) |
| | 55. | Thailand | Trang | FS | mo–yr | Horinouchi et al. (2009) |
| | 56. | Australia | Victoria | FE, ASU | d | Macreadie et al. (2010) |
| | 57. | Australia | Victoria | FS | mo | Smith et al. (2010) |
| | 58. | Canada | Newfoundland | FS | mo–yr | Thistle et al. (2010) |
| | 59. | Indonesia | South Sulawesi | FS | mo–yr | Vonk et al. (2010) |
| Salt marsh | 1. | USA | Virginia | FS | – | Rozas et al. (1988) |
| | 2. | USA | Louisiana | MO | mo–yr | Browder et al. (1989) |
| | 3. | USA | Louisiana | FS | yr | Baltz et al. (1993) |
| | 4. | USA | Georgia | FE, FS | d–yr | Kneib (1994) |
| | 5. | USA | Louisiana | FS | mo | Peterson & Turner (1994) |
| | 6. | USA | Texas | FE | yr | Minello et al. (1994) |
| | 7. | USA | Virginia | FS | mo | Cicchetti & Diaz (2000) |
| | 8. | USA | Texas | FS | mo–yr | Rozas & Zimmerman (2000) |
| | 9. | USA | South Carolina | FS | mo | Lerberg et al. (2000) |
| | 10. | USA | California | FS | mo | Desmond et al. (2000) |
| | 11. | USA | California | FS | mo–yr | West & Zedler (2000) |
| | 12. | USA | Georgia | MO | h–yr | Kneib (2000) |
| | 13. | Australia | Queensland | FS | mo | Thomas & Connolly (2001) |
| | 14. | USA | North Carolina | FS, FE | – | Lewis & Eby (2002) |
| | 15. | USA | Georgia | FS | yr | Webb & Kneib (2002) |
| | 16. | USA | Texas | FS | mo | Whaley & Minello (2002) |
| | 17. | USA | Texas | FS, MO | mo | Minello & Rozas (2002) |
| | 18. | USA | Georgia | FS | yr | Kneib (2003) |
| | 19. | USA | New Jersey | FS | mo | Able et al. (2003) |
| | 20. | USA | Massachusetts | FS | yrs | Palmer (2004) |
| | 21. | USA | South Carolina | FS, MO | yr | Holland et al. (2004) |
| | 22. | USA | New England (multiple states) | FS | yrs | Shriver et al. (2004) |
| | 23. | USA | Louisiana | MO | yr | Haas et al. (2004) |
| | 24. | USA | California | FS | yr | Dean et al. (2005) |
| | 25. | USA | California | FS | mo | Visintainer et al. (2006) |
| | 26. | Australia | Queensland | FS | mo | Guest & Connolly (2006) |
| | 27. | USA | Virginia | FE | yr | Long & Burke (2007) |
| | 28. | USA | South Carolina | FS | mo–yr | Allen et al. (2007) |
| | 29. | USA | Texas | FS, MO | yrs | Rozas et al. (2007) |
| | 30. | USA | Texas | MO | mo | Minello et al. (2008) |
| | 31. | USA | California | FS | yrs | Kelly et al. (2008) |
| | 32. | Australia | Queensland | FS | yrs | Meynecke et al. (2008) |
| | 33. | USA | Texas, Louisiana | MO | yr | Roth et al. (2008) |
| | 34. | USA | Massachusetts | FE | yr | Fleeger et al. (2008) |
| | 35. | USA | California | FE | yrs | Larkin et al. (2008) |
| | 36. | USA | Georgia | FS | mo-yrs | Kneib (2009) |
| | 37. | USA | North Carolina | FS | mo | Meyer & Posey (2009) |
| | 38. | USA | Louisiana | FS | mo | Rozas & Minello (2010) |
| | 39. | China | Shanghai | FS | mo | Jin et al. (2010) |
| Coral reef | 1. | USA | California | FE, FS | yr | Molles (1978) |
| | 2. | USA | Virgin & Marshall Islands | FS | d–wk | Gladfelter et al. (1980) |
| | 3. | Australia | Queensland | FS | mo–yr | Sale & Douglas (1984) |
| | 4. | Australia | Queensland | FS | yr | Ault & Johnson (1998a) |
| | 5. | Australia | Queensland | FS | yr | Ault & Johnson (1998b) |
| | 6. | Australia | Queensland | FE | d–mo | Caley et al. (2001) |
| | 7. | Belize | Glovers Reef | FS | mo | Acosta & Robertson (2002) |
| | 8. | USA & British | Virgin Islands | FS | mo–yr | Chittaro (2002) |
| | 9. | Africa | Zanzibar | FS | wk–mo | Dorenbosch et al. (2005) |
| | 10. | Bahamas | Lee Stocking Island | FE | h–mo | Overholtzer-McLeod (2006) |
| | 11. | USA & British | Virgin Islands | FS | mo | Grober-Dunsmore et al. (2007) |
| | 12. | Japan | Okinawa | FS | mo–yr | Hattori & Kobayashi (2007) |
| | 13. | USA & British | Virgin Islands | FS | mo–yr | Grober-Dunsmore et al. (2008) |
| Mangrove | 1. | USA & British | Virgin Islands | FS | wk | Halpern (2004) |
| | 2. | Australia | Queensland | FS | yr | Manson et al. (2005) |
| | 3. | Malaysia | Western peninsular Malaysia | FS | yr | Loneragan et al. (2005) |
| | 4. | Puerto Rico | La Paguera | FS | mo–yrs | Pittman et al. (2007) |
| | 5. | UK | Cayman Islands | FS | d | Marlow et al. (2007) |
| | 6. | USA | Florida | FS | mo–yrs | Drew & Eggleston (2008) |
| | 7. | Australia | Queensland | FS | yr | Meynecke et al. (2008) |
| Oyster reef | 1. | USA | North Carolina | FE | wk–mo | Eggleston et al. (1998) |
| | 2. | USA | North Carolina | FE | wk | Eggleston et al. (1999) |
| Total | 118 | | | | | |

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# Quantifying seascape structure: extending terrestrial spatial pattern metrics to the marine realm

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ABSTRACT: Spatial pattern metrics have routinely been applied to characterize and quantify structural features of terrestrial landscapes and have demonstrated great utility in landscape ecology and conservation planning. The important role of spatial structure in ecology and management is now commonly recognized, and recent advances in marine remote sensing technology have facilitated the application of spatial pattern metrics to the marine environment. However, it is not yet clear whether concepts, metrics, and statistical techniques developed for terrestrial ecosystems are relevant for marine species and seascapes. To address this gap in our knowledge, we reviewed, synthesized, and evaluated the utility and application of spatial pattern metrics in the marine science literature over the past 30 yr (1980 to 2010). In total, 23 studies characterized seascape structure, of which 17 quantified spatial patterns using a 2-dimensional patch-mosaic model and 5 used a continuously varying 3-dimensional surface model. Most seascape studies followed terrestrial-based studies in their search for ecological patterns and applied or modified existing metrics. Only 1 truly unique metric was found (hydrodynamic aperture applied to Pacific atolls). While there are still relatively few studies using spatial pattern metrics in the marine environment, they have suffered from similar misuse as reported for terrestrial studies, such as the lack of *a priori* considerations or the problem of collinearity between metrics. Spatial pattern metrics offer great potential for ecological research and environmental management in marine systems, and future studies should focus on (1) the dynamic boundary between the land and sea; (2) quantifying 3-dimensional spatial patterns; and (3) assessing and monitoring seascape change.

KEY WORDS: Seascape ecology · Landscape indices · Landscape metrics · Seascape structure · Spatial pattern metrics · Spatial scale



## INTRODUCTION

Landscape ecology has been widely applied in the terrestrial environment to understand the relationships between spatial patterns and ecological processes at a range of spatial and temporal scales (Forman & Godron 1986, Turner 1989, Wiens 2002). In landscape ecology, the scientific study of spatial patterning requires the quantification of the structural geometry of landscapes (Gustafson 1998). To address this task, landscape ecologists have developed spatial tools and spatial pattern statistics specifically to quantify the geometric properties in mapped surfaces. There now exists a wide range of metrics for the

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examination of relationships between spatial structure, ecological function, and landscape change (Gustafson 1998). Spatial pattern metrics have been classified broadly into 3 categories that quantify: (1) landscape composition, e.g. the abundance and variety of patch types, without reference to spatial attributes of the geometry; (2) configuration, e.g. the spatial arrangement of individual patches and mosaics of patches; and (3) fractal dimension, e.g. the shape complexity of a patch or landscape (Turner et al. 2001, Mandelbrot 1982) (Table 1). Spatial pattern metrics provide a consistent method with which to compare landscape structure and to monitor change at a range of spatial scales, thus providing ecologists and resource managers with a suite of tools that have contributed to effective management decisions in conservation and planning (Botequilha Leitão et al. 2006).

Computer software has been produced by landscape ecologists and statisticians to facilitate the application of metrics. The most widely used landscape metric applications are the software packages FRAGSTATS (www.umass.edu/landeco/research/fragstats/fragstats.html) and Patch Analyst (http://flash.lakeheadu.ca/~rrempel/ecology/). Spatial pattern metrics can be quantified for both vector-based and raster-based maps (Fig. 1).

Like landscape ecology, the marine counterpart, seascape ecology, focuses on the causes and consequence of spatial patterning (Hinchey et al. 2008, Li & Mander 2009), including implications of human activity (Costanza et al. 1990). Seascapes have been represented using several different conceptual models with varying cartographic properties (i.e. spatial and thematic resolution). The 'patch-matrix' model is a common representation of seascape structure based conceptually upon island biogeography theory, where the map classification is binary with focal 'high quality' patches embedded in a matrix of 'lower quality' habitat (Fig. 2A). The focus of this patch-matrix model has been on patch attributes such as area (i.e. species–area relationships), biotic response to patch edges, perimeter:area ratios, patch shape, and inter-patch distances or isolation (Fig. 2B). More recently, entire mosaics of patches have also been examined to assess the effect of the seascape surrounding a focal patch, thereby providing information on the patch context (Brennan et al. 2002).

Conclusions on the suitability of landscape ecology concepts and techniques to marine ecosystems vary among studies, with some evidence that patch and seascape structure such as edges, patch size, and the spatial configuration and composition of patch mosaics have a significant influence on marine organisms (Grober-Dunsmore et al. 2009, Boström et al. 2011, this Theme Section). In contrast, for seagrass ecosystems, where the majority of research has been conducted, results from patch level studies have been equivocal and highly variable among species and ecosystems (Boström et al. 2006).

In general, landscape ecology concepts developed and evaluated primarily for terrestrial environments have been used in marine studies on the assumption

Table 1. Summary of commonly used metrics for quantifying landscape pattern from 2D categorical maps arranged into 3 broad categories following Turner et al. (2001) and McGarigal et al. (2002). Algorithms and descriptions of mathematical formulas are provided in McGarigal et al. (2002)

| Metric | Level | Type | Description |
|---|---|---|---|
| **(1) Landscape composition (quantifies type of landscape cover type present and relative amount)** | | | |
| Proportion | Mosaic | Structural | Proportion of landscape occupied by cover type |
| Richness | Mosaic | Structural | Number of patch types composing the mosaic |
| Evenness | Mosaic | Structural | Relative abundance of different patch types |
| Diversity | Mosaic | Structural | Composite measure of richness and evenness |
| **(2) Spatial configuration (quantifies the spatial arrangement and orientation of patches/mosaic)** | | | |
| Contagion | Mosaic | Structural | Distinguishes between overall clumped or dissected mosaic patterns |
| Patch area | Patch-based | Structural | Total area of patch |
| Patch perimeter | Patch-based | Structural | Perimeter of a patch |
| Perimeter:area ratio | Patch-based | Structural | Index of patch shape complexity |
| Connectivity | Patch-based | Functional | Average distance between patches |
| Proximity index | Patch-based | Structural | Degree to which patches in landscape are isolated from other patches |
| Area-weighted average patch size | Patch-based | Structural | Frequency distribution of patch sizes |
| Core area | Patch-based | Structural | Area unaffected by the edge of the patch |
| **(3) Fractal dimension (quantifies the shape complexity of a patch or landscape)** | | | |
| Mean patch fractal dimension | Patch-based | Structural | Average patch shape complexity |

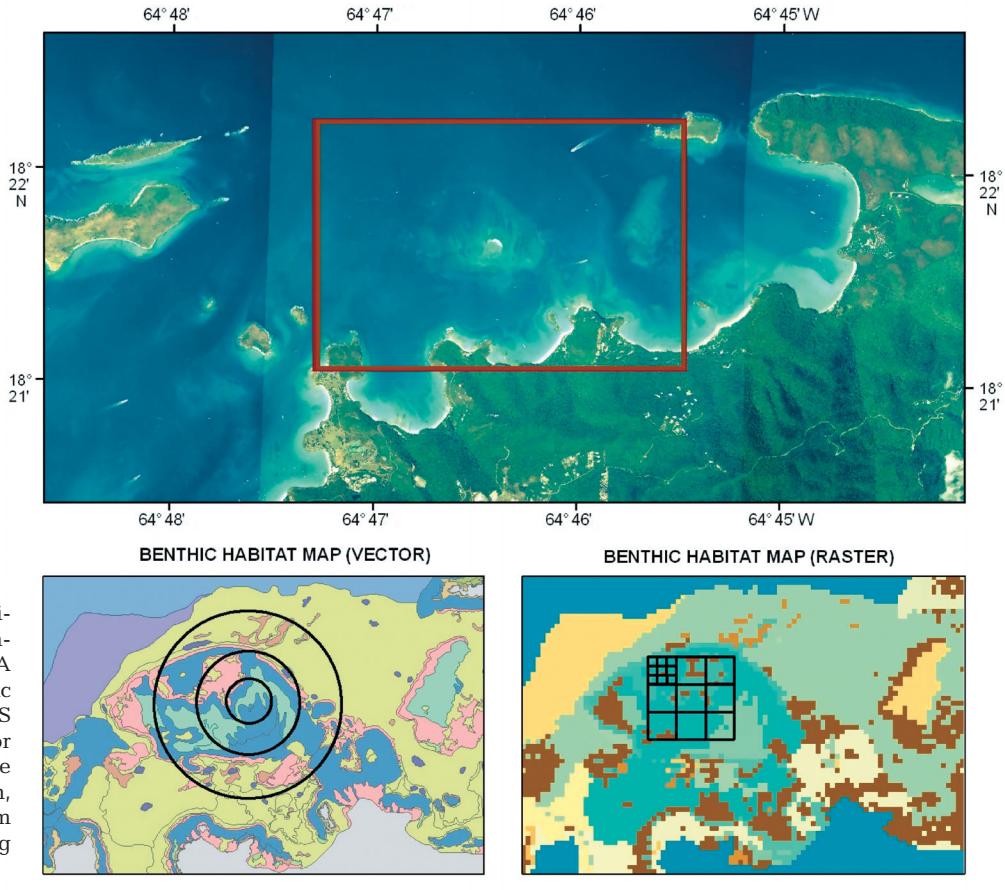


Fig. 1. Example of multi-scaled approach to derive seascape metrics using NOAA Biogeography Branch benthic habitat maps of St John, US Virgin Islands; from vector data (bottom left), using the increasing radius approach, and raster data (bottom right), using the moving window approach

that the approach is equally applicable to marine species and habitats. The rationale for this assumption is that some generalities will exist in the organism and community response to structural patterns whether they are in water or in air. However, it is not yet known whether some of the fundamental differences between terrestrial and marine systems may affect the transfer of techniques from land to sea. Further, in landscape ecology studies that have applied spatial pattern metrics, the approach is often exploratory and the selection of metric(s) and the spatial scale of analyses are typically unsupported by ecological rationale. The lack of guidelines on utilizing and implementing landscape metrics in the marine environment presents a notable knowledge gap that requires urgent attention to support future applications of metrics to seascapes.

Considering the issues surrounding landscape metrics and their relatively recent rise in marine ecology, our overarching goal was to assess the potential for the application of spatial pattern metrics to seascapes. In order to address this goal, we had 3 key objectives: (1) determine how many studies have applied spatial pattern metrics to quantify seascapes; (2) highlight uniquely marine spatial pattern metrics; and (3) discuss the importance of considering spatial, temporal, and thematic resolution.

## METHODS AND SCOPE OF REVIEW

**Definitions of seascape ecology and spatial pattern metrics.** Seascape ecology is the application of landscape ecology to the marine environment, and currently is almost entirely based on concepts and techniques developed for terrestrial species and habitats (Kneib 1994, Robbins & Bell 1994). Within the context of this review, spatial pattern metrics, sometimes referred to as landscape metrics or indices, are applied to characterize and quantify the spatial structure of seascapes. Spatial pattern metrics have evolved from the original need to quantify the complex spatial heterogeneity represented in remotely sensed images (both aerial photography and satellite imagery). There are 2 major types of metrics that are applied to specific data types (e.g. point data, 2-dimensional [2D] categorical maps, and continuously varying 3D surfaces; Burrough 1981, Legendre & Fortin 1989, Li & Reynolds 1995, McGarigal et al. 2009). In this paper, we focused primarily on the quantification of spatial pattern metrics that are applied to 2D maps of the seafloor, such as benthic habitat maps (e.g. maps with horizontal patterning, but no vertical dimension). Marine ecologists are now also applying spatial pattern metrics (terrain metrics) to continuously varying 3D surface models; thus some examples are included in this review.

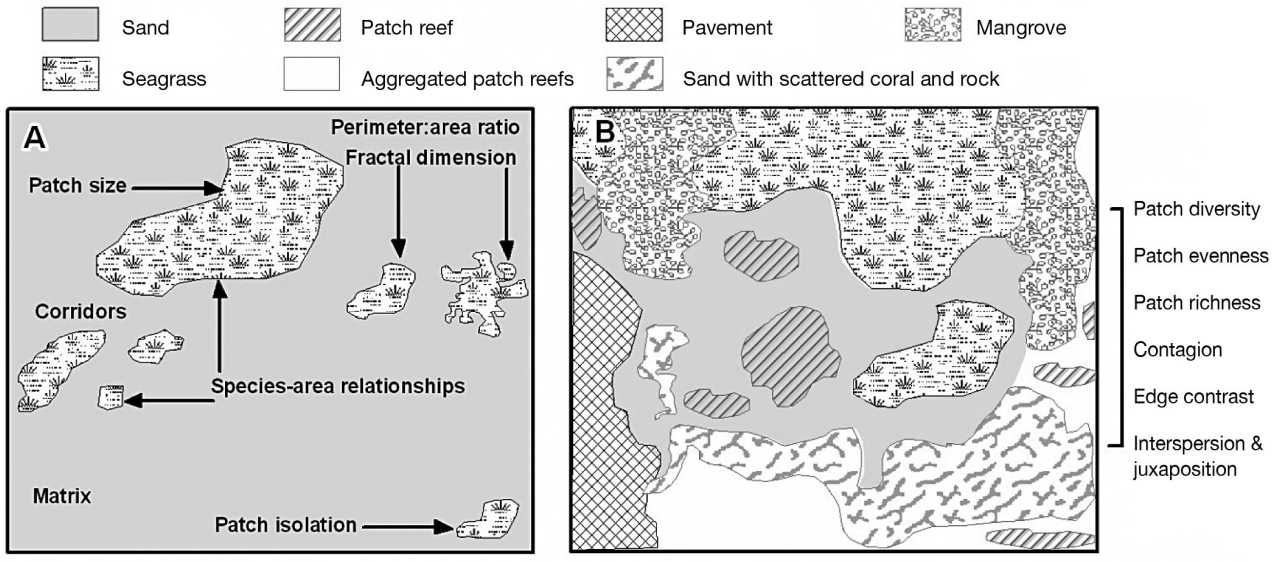


Fig. 2. Examples of 2 different seascape models. (A) Binary seascape with focal patches (seagrasses) that contrast sharply with the surrounding homogeneous and potentially 'hostile' matrix (bare sand). (B) Marine patch-mosaic model, where the seascape is spatially and compositionally complex, cannot be simply categorized into discrete binary elements

**Literature search and selection.** Marine applications of spatial pattern metrics were sourced primarily from the ISI Web of Knowledge's Web of Science (www.isiknowledge.com/) over a 30 yr period (1980 to 2010) using relevant key words and search strings (Table 2 and see Table S1 in the supplement at www.int-res.com/articles/suppl/m427p219_supp.pdf). The asterisk was used as a wildcard in ISI to allow for singular or plural words to be identified in the same search. In addition to these articles from the ISI search, several supplementary articles were included in the review from bibliographic lists cited in these ISI articles. Research articles were examined and only included in this marine spatial pattern metric review if they met the following criteria:

(1) The article was published in a peer-reviewed journal in the English language.

(2) Spatial pattern metric(s) were used to quantify seascape structure in the article and not just mentioned in the text.

(3) Spatial pattern metric(s) were applied to 2D categorical maps or continuously varying 3D surfaces.

The articles examined were based on a review of a strictly qualified subset of the literature, and as a result, the conclusions are relevant specifically to studies that have applied spatial pattern metrics to marine environments. The studies were reviewed and attributes were recorded in a database that included author, article title, publication year, journal, volume, issue, key word, landscape pattern metric, quantification, data representation, data type, minimum mapping unit (MMU), and extent (Table S2 in the supplement).

**Structure of the review and synthesis.** Relevant papers were reviewed to examine (1) the number of studies that applied spatial pattern metrics to quantify seascapes; (2) uniquely marine spatial pattern metrics; and (3) importance of considering spatial, temporal, and thematic resolution. The results of the literature search are synthesized and organized by the 2 major groupings of metrics we have identified (e.g. 2D categorical maps and continuously varying 3D surfaces). From the selected papers and the broader literature on multivariate ecological modeling, we discuss and highlight many of the analytical techniques that have been used effectively to identify the most influential metrics, and to link this spatial variability to the ecology of spe-

Table 2. Key words used in ISI literature review for marine applications of spatial pattern metrics. The asterisk is used in ISI as a wildcard in order for singular or plural words to be identified in the same search. Numbers in the left column denote the key words used to find studies and are also used in Table S1 in the supplement

| | |
|---|---|
| TERRESTRIAL | |
| 1. | 'landscape metric*' |
| 2. | 'landscape indice*' |
| MARINE | |
| 1. | 'seascape*' AND 'metric*' |
| 2. | 'marine' AND 'landscape*' AND 'metric*' |
| 3. | 'seascape*' AND 'indice*' |
| 4. | 'marine' AND 'landscape*' AND 'indice*' |
| 5. | 'marine landscape ecology' |
| 6. | 'seascape structure' |

Table 3. Overview of modeling techniques and relevant attributes in seascape ecology case studies. nMDS: non-metric multidimensional scaling

| Source | Focal patch type | Seascape model | Spatial pattern metrics | Measure of spatial autocorrelation | Variable reduction method | Ecological modeling |
|---|---|---|---|---|---|---|
| Pittman et al. (2004); Queensland, Australia | Seagrasses; mangroves | 2D patch mosaic with vertical attributes in patch classes | %cover; total edge; no. patches; patch size; contrast weighted edge density; core area; nearest neighbor; proximity; patch richness; evenness; contagion; interspersion/juxtaposition | Not measured | Cluster analysis; hybrid MDS; principal axes correlation | Structural equation modeling |
| Manson et al. (2005); Queensland, Australia | Mangroves; offshore fisheries | 2D patch mosaic | Area; perimeter; no. patches; mean patch area & perimeter of mangroves; length coastline; area of shallow water | Not measured | PCA | Regression trees & stepwise multiple regression |
| Grober-Dunsmore et al. (2007); US Virgin Islands | Coral reefs; seagrasses | 2D patch mosaic | Patch size; perimeter to area ratio; %cover | Not measured | None | Stepwise multiple regression & linear regression |
| Pittman et al. (2007a); Puerto Rico | Coral reefs; seagrasses; sand | 2D patch mosaic & gradient model | %cover; patch richness; SD of water depth | Moran's I | None | Regression trees |
| Pittman et al. (2007b); Puerto Rico | Mangroves; coral reef ecosystems | 2D patch mosaic | %cover; patch richness; distance to shore | Moran's I | nMDS & similiarity percentages (SIMPER) | ANOVA |
| Drew & Eggleston (2008) | Seagrass; mangroves | 2D patch mosaic | Habitat area; island perimeter to area ratio; no. mangrove patches; diversity, distance to nearest major channel, depth contour | Not measured | None | Multiple regression with backward elimination |
| Grober-Dunsmore et al. (2008); US Virgin Islands | Coral reefs; seagrasses | 2D patch mosaic | Patch size; perimeter to area ratio; %cover; diversity; patch richness | Not measured | PCA | Stepwise multiple regression using principle components |
| Meynecke et al. (2008); Queensland, Australia | Coastal wetlands; offshore fisheries | 2D patch mosaic | Area; no. patches; patch density; length coastline; river length; connectivity index | Not measured | PCA | Stepwise multiple regression using principle components |

cies. The final 2 sections highlight current knowledge gaps and research questions to help guide future applications of spatial pattern metrics to the marine environment.

## RESULTS

### Literature review

#### Marine applications of landscape metrics

The first published ecological studies using metrics to quantify spatial patterns emerged in the early 1980s for terrestrial systems (Romme 1982, Forman & Godron 1986, Krummel et al. 1987, O'Neill et al. 1988). In the marine environment, edge metrics such as the amount of land–water interface were recognized as important predictors of coastal species distributions in the late 1980s (Browder et al. 1989), although the structural attributes of individual patches had been considered from at least the 1970s (e.g. species–area relationships; Neigel 2003). However, it was not until more recently that pattern metrics were applied to quantify marine habitat mosaic composition and configuration (Garrabou et al. 1998, Andréfouët et al. 2001). Metrics have now been applied to Antarctic benthos (<10s of $m^2$), and at broader spatial scales (10s to 100s of $m^2$) to seagrass, saltmarsh, mangrove, and coral reef ecosystems (Table 3).

Over the past 30 yr, a total of 556 terrestrial research papers focused on the subject of landscape metrics (e.g. based on a 'landscape metric*' query in ISI) or indices (e.g. based on 'landscape indice*' query in ISI), compared to 40 marine papers that contained 1 or more of these search terms. Of the 40 marine studies, only 23 met our specific selection criteria that required the actual application of spatial pattern metrics to quantitatively measure seascape structure (Table S1 in the supplement). Consequently, this review focuses on these

23 studies, of which 18 quantified spatial patterns from 2D categorical data and 5 applied surface metrics or morphometrics to continuously varying 3D surfaces (e.g. seafloor bathymetry from multibeam or light detection and ranging [LiDAR] data).

## Application to 2D seascapes

The majority (78%) of seascape studies quantified metrics based on a patch-mosaic model representing 2D seascape structure. Of the 18 seascape metric studies based on 2D data, 7 were conducted in estuarine, mangrove, and seagrass communities (Turner et al. 1999, Manson et al. 2003, 2005, Pittman et al. 2004, Sleeman et al. 2005, Drew & Eggleston 2008, Meynecke et al. 2008), 6 studies were conducted in coral reef ecosystems (Andréfouët et al. 2001, Grober-Dunsmore et al. 2007, Pittman et al. 2007a,b, Grober-Dunsmore et al. 2008, Prada et al. 2008), 2 studies in Antarctic benthic communities (Teixido et al. 2002, 2007), and the remaining 2 in the subtidal zones of Mediterranean rocky shores (Garrabou et al. 1998, 2002).

Multiple spatial pattern metrics were applied to quantify landscape composition, and contagion spatial configuration (patch-based and mosaic), and patch complexity (patch-based) (Table 4; Table S2 in the supplement). Specifically, 10 of the studies applied metrics at the patch level (e.g. individual patch types) and 7 to entire seascape mosaics comprising multiple patch types. Nine metrics measuring landscape composition were applied, with patch area being the most prevalent metric (n = 5), followed by habitat diversity and richness (n = 3) and evenness (n = 2).

In total, 24 different spatial pattern metrics were applied to quantify the spatial arrangement, orientation, or shape of seascape patches. Most metrics were standard pattern metrics from terrestrial landscape

Table 4. Summary of 2D spatial pattern metrics applied in the reviewed literature. 'Contagion' quantifies the level of clumping or aggregation in landscape elements. *Spatial pattern metrics adapted or developed uniquely for seascape ecology studies

| Spatial pattern metric | No. of studies | Major habitat type in study |
|---|---|---|
| **Landscape composition — 9 metrics** | | **(of 7 studies using composition)** |
| Habitat area | 5 | Coral reef, Antarctic benthic, mangrove |
| Habitat diversity | 3 | Coral reef, Antarctic benthic, mangrove |
| Patch richness | 3 | Coral reef, Antarctic benthic |
| Habitat richness | 2 | Coral reef |
| Evenness | 2 | Coral reef, Antarctic benthic |
| Habitat perimeter | 2 | Mangrove |
| Patch diversity | 1 | Coral reef |
| Percent cover | 1 | Coral reef |
| Mean depth | 1 | Coral reef |
| **Spatial configuration (contagion) — 2 metrics** | | **(of 2 studies using contagion)** |
| Interspersion | 1 | Antarctic benthic |
| Contagion index | 1 | Intertidal |
| **Spatial configuration (patch-based) — 22 metrics** | | **(of 10 studies using configuration)** |
| Patch mean size | 4 | Intertidal, coral reef, mangrove |
| Number of patches | 4 | Mangrove, intertidal |
| Perimeter:area ratio | 3 | Coral reef, mangrove |
| Mean patch area | 2 | Mangrove, seagrass |
| Mean patch perimeter | 2 | Mangrove, seagrass |
| Mean shape index | 2 | Intertidal, mangrove |
| Area weighted mean shape index | 1 | Intertidal |
| Landscape shape index | 1 | Intertidal |
| Patch size standard deviation | 1 | Intertidal |
| Patch size coefficient of variation | 1 | Intertidal |
| Total edge | 1 | Intertidal |
| * Coral habitat intersecting boundary/ Coral habitat inside boundary | 1 | Coral reef |
| Patch size variability | 1 | Intertidal |
| Patch shape | 1 | Intertidal |
| * Distance to nearest feature (e.g. prop root) | 1 | Mangrove |
| Coefficient of variation | 1 | Mangrove |
| Mean proximity index | 1 | Mangrove |
| * Mangrove–water interface | 1 | Mangrove |
| * Length of coastline | 1 | Mangrove |
| Fractal dimension | 1 | Seagrass |
| Nearest neighbor | 1 | Seagrass |
| * Hydrodynamic aperture | 1 | Coral reef |

ecology (e.g. contagion, perimeter:area ratio, interspersion), with 5 being adapted specifically to the marine environment. The 1 truly unique marine metric we encountered was hydrodynamic aperture (total aperture and degree of aperture) developed to measure the morphological openings in the carbonate rims of Pacific atolls. Apertures are channels that allow water, nutrients, and biological exchanges between the ocean and the interior lagoon environments of atolls (Andréfouët et al. 2001, 2003). In addition, unique derivatives of commonly used terrestrial edge metrics have been developed for coastal wetlands, such as the linear extent of the mangrove–water interface (Manson et al. 2003), and the marsh–water interface used as a predictor of brown shrimp production in Louisiana saltmarshes (Browder et al. 1989). Bartholomew et al. (2008) developed an edge metric that quantified the ratio between marine reserve boundary that intersected coral reefs and the area of coral reefs within marine reserves. This metric provided a proxy for boundary permeability to examine the influence of reserve boundary placement on the retention potential of recovering exploited fish populations.

Mean patch size and number of patches (n = 4) were the most commonly applied metrics used to quantify seascapes, followed by perimeter to area ratio (n = 3), mean patch area, mean patch index, and mean patch perimeter (n = 2). Of the marine applications of pattern metrics, 67% involved an evaluation of the relationships between ecological patterns in the marine environment. Garrabou et al. (1998) characterized the spatial dynamics of mosaics of colonizing organisms on Mediterranean rocky shores using digital photographs and GIS to map benthic communities at relatively fine spatial scales (310 $cm^2$ plots). At a broader scale, Meynecke et al. (2008) characterized the coastal seascape in Queensland, Australia, and applied metrics to determine the links between seascape structure and offshore fisheries productivity. In coral reef ecosystems, studies focused primarily on the influence of seascape structure on coral reef fish assemblages, trophic guilds, and species of concern. Two studies in the Caribbean explored the linkages between mangroves (Pittman et al. 2007a) and seagrass habitat (Grober-Dunsmore et al. 2007) for fish species and assemblages.

Seventeen percent of the studies applied metrics to monitor spatial dynamics across a range of temporal scales. Garrabou et al. (2002) utilized pattern metrics to monitor change of benthic communities on rocky subtidal substratum over a 2 yr period. Manson et al. (2003) applied 7 spatial pattern metrics to document change in mangrove communities from vegetation maps over a 25 yr period. In Antarctic benthic communities, Teixido et al. (2007) applied 2 metrics (class area and number of patches) to measure benthic community change across a gradient of disturbance due to iceberg scouring. Unlike terrestrial studies where change over time is a prominent component of studies, seascape studies have not pursued this to any notable degree, and this is an area of research that has great potential to expand in the future.

### Application to 3D seascapes

Of the 5 seascape metric studies based on continuously varying 3D surfaces (e.g. LiDAR or multibeam derived bathymetry), 4 were conducted in coral reef ecosystems and the other study was carried out in shale beds off the coast of California (Table 5). The most commonly applied morphometric was rugosity (n = 3), followed by slope and mean depth (n = 2). Overall, 8 morphometrics were applied, of which 7 were used to quantify habitat complexity in the marine environment. For example, Wedding & Friedlander (2008) found that variance in depth (within a 75 m radius) explained most of the variation in numerical abundance and species richness compared to other spatial pattern metrics applied to continuously varying 3D surface data. Pittman et al. (2009) compared 8 morphometrics at multiple spatial scales to identify the best predictors of fish and coral species richness and abundance. Slope of the slope, a measure of the habitat complexity, emerged as the most influential spatial predictor for a wide range of coral reef associated faunal species (Pittman et al. 2009).

## Influence of spatial, thematic, and temporal resolution on pattern metrics

The 2 main components of scale, viz. grain (e.g. spatial resolution of the data) and extent (e.g. geographic area of the study site), have been well studied and are

Table 5. Summary of 3D spatial pattern metrics applied in the reviewed literature. Of 5 studies in total, the major habitat types to which the metrics were applied were coral reef, mangrove, and seagrass. See Pittman et al. (2009) for description of common 3D spatial pattern metrics

| Spatial pattern metric | No. of studies |
|---|---|
| **Landscape composition — 8 metrics** | |
| Rugosity | 3 |
| Slope | 2 |
| Mean depth | 2 |
| Variance in depth | 1 |
| Standard deviation of depth | 1 |
| Slope of slope | 1 |
| Plan curvature | 1 |
| Fractal dimension | 1 |

known to affect the behavior of individual spatial pattern metrics, and therefore, the understanding of ecological relationships (Urban et al. 1987, Wiens 1989). For instance, as grain is increased with an unchanging extent, the number of patches in the landscape decreases (Lepczyk et al. 2007). Another often neglected map characteristic that can influence the results from spatial pattern metrics is the thematic resolution, e.g. the amount of detail in a map represented by the number of classes (Kendall & Miller 2008, Castilla et al. 2009, Kendall et al. 2011, this Theme Section).

When thematic maps (e.g. benthic habitat maps) are used to represent structure in the marine environment, issues related to map accuracy, cartographic bias, error propagation, and uncertainty become increasingly important and must be assessed (Lunetta et al. 1991, Hess 1994, Shao & Wu 2008) (Figs. 3 & 4). Remotely sensed data are available in a broad range of spatial resolutions, and the resolution of the imagery used to derive spatial pattern metrics can affect the results of the subsequent analysis (Manson et al. 2003). Within the subset of seascape papers reviewed, the geographic extent ranged from a photo quadrat at 310 $cm^2$ (Garrabou et al. 1998) to an estuarine region that extended along the entire coast of Queensland, Australia (Meynecke et al. 2008). Spatial resolution of the data ranged from a vector data set with an MMU of 4 $mm^2$ (Garrabou et al. 2002) to a raster data set with a pixel size of 10 m (Meynecke et al. 2008). Prada et al. (2008) explored the effects of changing the grain size (e.g. 4 $m^2$ and 400 $m^2$ MMU) of habitat maps on 7 commonly used pattern metrics and found habitat richness to be the only metric that remained constant. Kendall & Miller (2008) found that changing the spatial resolution of benthic habitat maps (100 $m^2$ to 4048 $m^2$ MMU) resulted in disproportionate changes in the area, perimeter, and other values among feature types, but had little effect on the relationship between seascape structure and fish community composition (Kendall & Miller 2010). Subsequently, however, species level analyses by Kendall et al. (2011) found that different resolution maps changed the strength of correlations for several fish associated with coral reef edges and sandy areas, but results were consistent regardless of map resolution for comparisons involving area of seagrass and habitat diversity.

The Caribbean seascape ecology studies reviewed (Grober-Dunsmore et al. 2007, 2008, Pittman et al. 2007a,b) used existing maps with predetermined cartographic characteristics including spatial and thematic resolution. Thematic resolution, as well as the quality and resolution of the imagery from which the map was derived, can have important impacts on the quantification of patch or habitat diversity. This is particularly important in studies of biodiversity patterns. Habitat diversity in terrestrial systems has been found to be positively correlated with animal species diversity, which is consistent with the 'habitat heterogeneity hypothesis' (Tews et al. 2004). In contrast, habitat richness and diversity of seascapes have not emerged as important explanatory variables for faunal diversity at the spatial scales examined in seascape ecology studies. This important difference between marine and terrestrial studies has not yet been sufficiently addressed in ecology and requires more detailed comparative and multi-scale analyses. In addition, very few studies (marine or terrestrial) have used diversity metrics such as taxonomic diversity and distinctness (Clarke & Warwick 1999) to quantify seascape and landscape habitat diversity. Taxonomic indices account for diversity across hierarchical levels of classification that can be equally applicable to a benthic map classification as to a multi-species community. For instance, weightings can be assigned to different levels of a map classification, such that 4 classes from the same level in the hierarchy (e.g. sparse seagrass, dense seagrass, macroalgae, algal turf – all marine plants) would be less taxonomically diverse than 4 more structurally different classes (e.g. boulders, patch reef, seagrass, sand). Conventional diversity metrics such as patch richness and Shan-

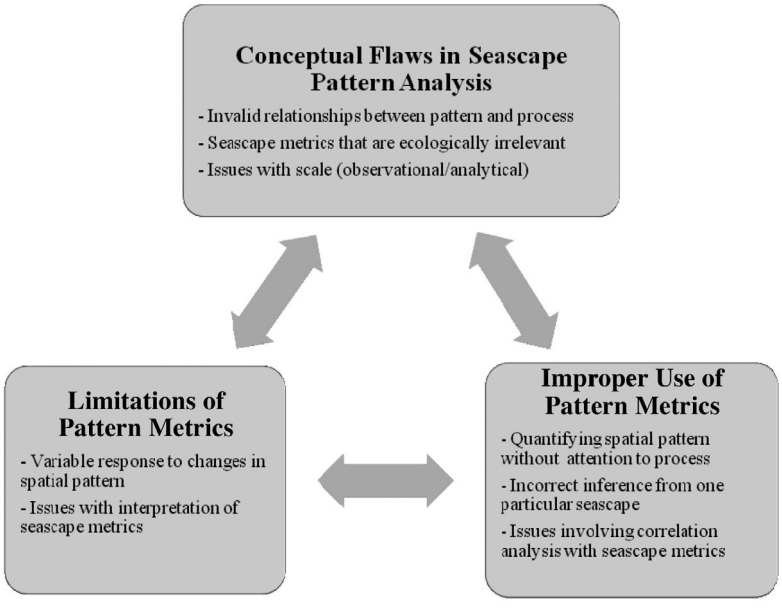


Fig. 3. Three types of problems in landscape analysis with pattern metrics: conceptual flaws, improper uses, and inherent limitations of landscape indices. Each type manifests in several forms that overlap with the other types. Modified from Li & Wu (2004)

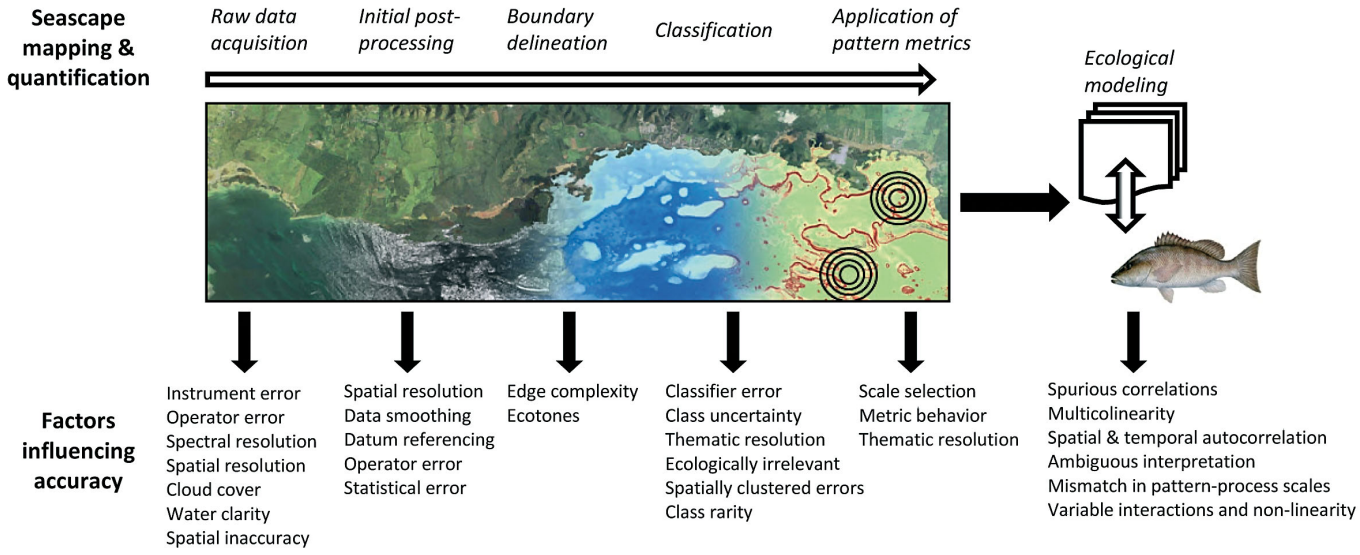


Fig. 4. Factors potentially influencing accuracy during the steps involved in seascape mapping, characterization, and quantification

non diversity would assign an equal score to these structurally and functionally different seascapes. Future studies in landscape ecology should examine a range of diversity metrics with consideration given to the functional relevance of the thematic resolution of any given habitat map.

### Data considerations and analytical techniques

Potential misuses of pattern metrics can easily arise for 2 main reasons: (1) quantifying patterns without considering ecological processes and causal relationships, and (2) failing to deal with caveats of correlation analysis (Li & Wu 2004). The first reason is self-explanatory and an important consideration for all areas of ecology. The second reason requires some explanation and discussion of analytical solutions. Data in landscape ecology, particularly spatial pattern metrics, are typically non-normally distributed, exhibit multicollinearity, spatial autocorrelation, and often include irrelevant variables. Multicollinearity has implications for certain statistical modeling techniques, such as multiple regression (Graham 2003). Multicollinearity occurs because many of the metrics share some component (often geometric) derived from a core suite of interrelated measures such as patch area, edge length, shape, and inter-patch distance to quantify different attributes of spatial pattern often resulting in strong collinearity (positive and negative) between metrics (Li & Reynolds 1993, Riitters et al. 1995). Nonetheless, similar metrics can still capture slightly different attributes of spatial structure, and a single metric may not capture sufficient structural variability (e.g. spatial arrangement and composition) to explain complex organism responses to spatial patterning (Cushman et al. 2008). Much effort has been directed toward finding parsimony amongst the wealth of spatial pattern metrics available (Riitters et al. 1995, Gustafson 1998, Cardille et al. 2005). Cushman et al. (2008) examined 49 class-level metrics and 54 landscape-level metrics applied to 3 geographically distinct regions and identified a reduced set of metrics that consistently described the major attributes of landscape configuration.

Exploratory analyses can be crucial to identifying a suite of potentially important patterns through correlative techniques as a precursor to refining the subsequent steps toward explicitly determining causality. Although the pattern-pattern approach is often criticized in science, it is clear that progress in ecology can be accelerated by first identifying and describing patterns (Underwood et al. 2000). We focus here on a brief review of multivariate statistical techniques that have been developed to increase interpretability of pattern-pattern relationships from analysis of complex multiscale ecological data sets (Table 3). We do not include linear regression, although we recognize its utility for modeling in landscape ecology, where it is sometimes used as a secondary step after orthogonal decomposition of multivariate data through ordination techniques. Our focus is not on the details of the algorithms themselves, but rather on highlighting the applications of the techniques in landscape ecology.

#### Ordination

Ordination is a family of techniques that reduces high dimensionality data into fewer variables, each of which represents a continuum or gradient in the data

that may be visualized in a 2D or 3D plot. The derivative variables are composites of environmental data and can be used as predictor variables in ecological modeling. Principle components analysis (PCA) has frequently been used to reduce the large number of sometimes collinear pattern metrics into a more parsimonious suite of variables (McGarigal & McComb 1995, Cushman et al. 2008). PCA has been used to reduce the dimensionality of the multivariate data and to describe seascape structure based on the size and significance of the component loadings. For example, Meynecke et al. (2008) regressed 3 principal components (PCs), representing independent gradients in coastline characteristics and seascape composition and connectivity, against reported catch of individual fish and crustacean species, to highlight the importance of wetland connectivity. However, Grober-Dunsmore et al. (2008) regressed PCs of seascape structure against reef fish variables and explained less variability than did individual pattern metrics. PCA is a useful tool, but is influenced by sample size and assumes that the suite of variables change linearly along underlying gradients (Gauch 1982). In addition, non-linearity and inclusion of many collinear variables can result in distorted ordinations using standard PCA (McGarigal & Cushman 2000).

Non-metric multidimensional scaling (nMDS) is an ordination technique that does not assume linearity and uses a similarity matrix rather than a correlation or covariance matrix and where samples are ranked according to their similarity. Pittman et al. (2007b) applied cluster analysis and nMDS using Plymouth Routines in Multivariate Ecological Research (PRIMER) to characterize seascape types from a small selection of pattern metrics that measured seascape composition (abundance of patch types and overall patch richness). Similarity percentages (SIMPER) were calculated to quantify the similarities and dissimilarities of the seascape structure within and between seascape types. Canonical correspondence analysis (CCA; Jongman et al. 1995), a hybrid of ordination and multiple regression, has been used effectively in explaining patterns of variation in organism distributions. CCA performs well with non-orthogonal and collinear gradients, making it suitable for complex landscape ecology analyses (Cushman & McGarigal 2002), and has been used as a secondary step in the variable selection process to calculate the statistical significance when a variable is added into a model (Cushman & McGarigal 2004).

### Structural equation modeling

Structural equation modeling (SEM) can provide accurate and meaningful models in the presence of multicollinearity by incorporating collinear variables and non-linear variables explicitly in the model, rather than excluding them, or combining them into orthogonal components (Graham 2003). In SEM, the overriding concept is that a correlation may not imply causation, but the existence of a causal relationship implies some correlation. The possibilities can be tested as competing hypotheses. Models can be built and visualized using path diagrams to represent the working hypothesis about the causal relationships among variables (Shipley 1999). The relative effect of 1 variable is communicated using a standardized path coefficient analogous to partial regression coefficients. Parameter estimation is done by measuring the goodness of fit between the actual data matrix (correlation or covariance) representing the relationships between variables and the estimated data matrix of the best fitting model. Pittman et al. (2004) used SEM and path models to explain spatial patterns in fish and prawn distributions and diversity as influenced by habitat structure at multiple spatial scales. SEM was used to decompose correlations into direct and indirect components and examine the relative importance of within-patch structure (leaf length, sediment grain size) versus seascape composition and configuration (represented by a set of spatial pattern metrics). Competing models were tested using a range of goodness of-fit statistics and a final model selected on the basis of overall performance of the measures of model fit.

### Machine-learning algorithms

Over the past decade, many advanced algorithms have been developed to efficiently explore and model complex patterns in complex data (Hastie et al. 2009). Some of the most successful examples are 'ensemble' techniques that use many models developed through iterative training and testing to learn and improve upon the errors of predecessors (Elith et al. 2006). Tree-based ensemble techniques, such as boosted regression trees and random forests have recently been used to model fish–seascape relationships at a range of spatial scales and to assess the relative importance of variables, to model interactions between variables, and to identify ecological thresholds (Leathwick et al. 2006, Pittman et al. 2009, Knudby et al. 2010). These machine-learning techniques are robust to collinearity and the presence of irrelevant predictors and therefore do not require prior variable selection or data reduction. Additional machine-learning techniques that offer great utility include multivariate adaptive regression splines and neural networks (Linderman et al. 2004).

## FUTURE MARINE APPLICATIONS OF SPATIAL PATTERN METRICS

### Landscape ecology at the boundary of land and sea

Landscape ecology approaches offer great promise for examining functionally important structural boundaries at the land–sea interface (Kneib 1994), and can extend the progress made with understanding and managing the land–water interface for terrestrial freshwater environments (Naiman & Decamps 1997). Tidal wetlands including some saltmarshes and mangroves, where the land–sea interface is dynamic over the tidal cycle, present a unique challenge for the application of spatial pattern metrics. Measuring such dynamic structure would require the application of metrics over a time series of imagery or quantification of features that provide a reliable proxy. Adequately quantifying dynamic patterns, however, may require new metrics. The easily mapped shallow-water and semi-terrestrial environments at the land–sea interface offer great opportunities to develop, apply, and test pattern metrics. Several commonly used metrics in hydrology, such as drainage density and measures of dendritic network complexity and channel morphology, as well as patch-based metrics such as marsh–water interface and edge:perimeter ratio have been applied successfully to examine the spatial ecology of saltmarshes (Kneib 1991, 1994, Feagin & Wu 2006). Future remote sensing techniques will increase the thematic resolution of seascape maps, and new variables that reveal more detailed spatial patterns in soil and water conditions across saltmarsh seascapes could be quantified using spatial pattern metrics. The adaptation of conventional landscape indices together with new metrics that can account for dynamic linear features, changing water volumes, wave action, and edaphic variables may increase the ability of statistical models to predict the distribution of species and assemblages. Understanding the consequences of changing spatial patterning will increase our ability to predict the impact of human modifications to coastal environments and guide effective restoration activities (Feagin & Wu 2006, Kelly et al. 2011).

### 3D seascape structure

Detailed seafloor terrain models are becoming increasingly accessible and reliable with technological advances and the proliferation of marine remote sensing. The 3D models that result from seafloor acoustic, laser, and optical mapping provide an opportunity to examine the relationship between benthic morphology, including topographic complexity and marine organisms and communities (Brock & Purkis 2009). Morphometrics commonly used in geomorphology and industrial engineering to quantify surface features and complexity have performed well as predictors of fish diversity and species distributions across coral reef seascapes (Wedding et al. 2008, Pittman et al. 2009). The current limitation with morphometrics, and similarly with many of the spatial pattern metrics, is the lack of information on the ecological mechanisms that drive the pattern–pattern relationships. Nevertheless, inclusion of morphometrics in the suite of metrics applied to seascapes will likely offer new insights in the study of the reciprocal link between pattern and process (McGarigal et al. 2009).

### Quantifying seascape change

Spatial pattern metrics combined with remote sensing data offer a cost-effective suite of spatial tools for surveillance and monitoring of seascape change. Remotely sensed imagery to document change in marine and coastal habitats over time is becoming increasingly important as anthropogenic stresses change coastal environments. Shallow water marine ecosystems such as seagrass, salt marsh, coral reef, and mangrove systems are globally threatened with an estimated loss of 30% in the past few decades (Valiela et al. 2009, Waycott et al. 2009). Detection of coastal habitat changes may be greatly enhanced by the application of spatial pattern metrics because they can provide important information beyond simple estimates of areal losses and gains. Habitat change can be a spatially complex process. Pattern metrics can quantify fragmentation rates and identify threshold effects or tipping points in ecosystem function (Grober-Dunsmore et al. 2009). For example, Manson et al. (2003) applied 7 spatial metrics to analyze mangrove change in Queensland, Australia, between 1973 and 1999 and found significantly altered spatial configuration, with implications for the movement and dispersal of marine fauna. With rapid loss and alteration of coastal ecosystem structure underway, it is now imperative to find cost-effective and reliable ways to quantitatively monitor changes and predict the ecological consequences.

## CONCLUSIONS

Comparative studies and careful evaluation are required to support the judicious application of landscape ecology principles, concepts, and analytical techniques in the marine environment. Seascape structure (e.g. the composition and spatial configuration) of the marine environment is perceived differently, through the

lens of landscape ecology, than conventional ecology. The development of spatial pattern metrics unique to the marine environment should be conducted with a strong ecological rationale in mind and with an aim to better understand the linkages between spatial patterns and ecological processes. Although we have focused entirely on shallow coastal applications, spatial pattern metrics could potentially offer new insights on pelagic ecosystems. Oceanic fronts, plankton patches, and spatial gradients in biophysical conditions across continental shelves are spatial patterns that have ecological consequences, yet are rarely quantified with pattern metrics. Seascape ecologists could benefit from lessons already learned in terrestrial landscape ecology. In particular, more effort should be focused on the *a priori* identification of ecologically relevant metrics to characterize spatial patterns. Research on the quantification of spatial patterns in the marine landscape should develop with an awareness of the evolution of terrestrial metrics, and with due attention to the limitations and pitfalls that arose as landscape pattern analysis became more widely applied and critically assessed. Future work on seascape metrics must achieve a balance between applying the fundamental metrics based on established terrestrial landscape ecology and expanding the theoretical basis of landscape ecology to address the unique set of challenges that must be confronted when working in the marine environment.

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# Quantifying freshwater-induced fragmentation of submerged aquatic vegetation communities using a multi-scale landscape ecology approach

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ABSTRACT: Species composition and abundance of nearshore submerged aquatic vegetation (SAV) of Biscayne Bay, Florida, USA, are influenced by pulsed delivery of fresh water from canals that drain the Everglades and adjacent urban and agricultural areas. In the present study, we evaluated whether freshwater inflows were correlated with the spatial structure (e.g. patchiness, fragmentation, spatial heterogeneity) of SAV. SAV patches were delineated using aerial photographs and object-based classification, and the SAV seascape structure was characterized at different spatial scales (200 m to 1 km from shore) using landscape metrics. The area closest to shore (200 m buffer) was identified as the area with the highest heterogeneity in SAV seascape structure; areas beyond this buffer did not differ significantly in landscape metrics. Within the 200 m buffer, SAV seascapes clustered into continuous SAV structures (CSS) and fragmented SAV structures (FSS). CSS had a higher proportion of the benthos covered by larger SAV patches with simpler boundaries. FSS had a higher density of smaller SAV patches with complex shapes and a lower proportion of the substrate covered by SAV patches. Neither structure type was distributed randomly along the shoreline. CSS were prevalent in areas with high and stable salinity. FSS were prevalent in areas influenced by freshwater discharges where salinity is low and variable, highlighting how the pulsed release of fresh water may adversely influence the structure of SAV seascapes, potentially resulting in fragmentation of the benthic community. Thus, this seascape approach provides a tool to assess the influences and effectiveness of the Everglades Restoration Project in Biscayne Bay.

KEY WORDS: Submerged aquatic vegetation · Seagrass · Landscape ecology · Seascape structure · Salinity patterns · Water-quality influences · Habitat fragmentation · Everglades restoration



## INTRODUCTION

Submerged aquatic vegetation (SAV) communities provide key ecological services such as organic carbon production and export, nutrient cycling, sediment stabilization, enhanced biodiversity, and trophic transfers to adjacent habitats in tropical and temperate regions (Orth et al. 2006). Significant patterns of decline and shifts in community structure have been documented for these communities worldwide (Duarte 2002, Waycott et al. 2009). Among the main causes of this decline are chemical pollution, eutrophication, physical impacts, and trophic-structure modifications (Duarte 2002, Orth et al. 2006). Associated with declines in SAV biomass are losses in the habitat value that these ecosystem engineers provide as essential refuges and as sources of nutrition to a large number of resident and transient macrofaunal organisms (Costanza et al. 1997, Orth et al. 2006).

Perturbations to SAV communities are most commonly quantified at fine spatial resolution by *in situ* observations and descriptions of SAV shoot/ramet den-

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sity or percent cover (Waycott et al. 2009). Comparatively, methodologies that consider processes occurring over larger spatial scales are rarely considered (Robbins & Bell 1994, Kendall 2005, Mellin et al. 2009). Nevertheless, large-scale spatial SAV habitat patterns (e.g. habitat size, fragmentation, arrangement) can influence ecological patterns and processes such as faunal recruitment, dispersal, survivorship, and connectivity (Pittman et al. 2004, 2007, Mellin et al. 2007, Hovel & Regan 2008), highlighting the need to evaluate the role of disturbances on the structuring of large-scale SAV spatial patterns. Concepts and analytical techniques developed in terrestrial landscape ecology provide a framework that can be readily adapted to assess large-scale SAV patterns and disturbance impacts. A landscape generally refers to a heterogeneous area composed of locally interacting ecosystems made up of homogenous units called habitat patches (Grober-Dunsmore et al. 2008). Adapting this term to marine systems, a SAV seascape can be considered as a heterogeneous mosaic of SAV patch habitats across a broad homogenous matrix (e.g. sand, mud, hard substrate). Thus, approaches developed in landscape ecology are ideal for quantifying spatial patterns of SAV patches because of the natural tendency of these communities to form variable-sized patches (Boström et al. 2006, Connolly & Hindell 2006). In the present study, we utilized landscape metrics (referred to as spatial pattern metrics hereafter) to quantify the composition (e.g. diversity and abundance of patches) and configuration (e.g. spatial arrangement, position, orientation, size-frequency) of SAV patches across the seascape within Biscayne Bay, Florida, USA, a shallow subtropical lagoon that is heavily influenced by human activities including water management (Lirman et al. 2008a,b).

Tropical and subtropical marine ecosystems such as coral reefs, mangroves, and SAV patches are ecologically interconnected through the movement of fish and invertebrate species as well as inorganic and organic nutrients (Parrish 1989, Beck et al. 2001, Beets et al. 2003, Nagelkerken & van der Velde 2004a,b, Orth et al. 2006, Davis et al. 2009). Habitat composition and configuration across the seascape are known to influence connectivity patterns among habitats (Pittman et al. 2007), and several studies have shown that species abundance and diversity are directly related to habitat heterogeneity (Nagelkerken et al. 2001, Jelbart et al. 2007). A heterogeneous seascape may support high species diversity by enhancing recruitment opportunities, providing a wide range of resource types (e.g. food items, space use for attachment or shelter), and influencing the outcome of biological interactions such as competition, predation, and foraging behavior (Parrish 1989, Irlandi & Crawford 1997). Thus, impacts of water quality on the structure of SAV communities within the seascape can have significant cascading effects on higher trophic levels.

Previous research in Biscayne Bay has shown that abundance and species composition of SAV are directly related to salinity patterns, with areas containing low and highly variable salinity (i.e. adjacent to canals that discharge fresh water into littoral areas) exhibiting lower SAV species abundance and high variability in percent cover within patches (Lirman et al. 2008a,b, Lirman & Serafy 2008). While response patterns to salinity have been documented at the within-patch scale, it is expected that spatial pattern metrics such as mean patch size, shape complexity, and patch density will also capture spatial heterogeneity of SAV, as species-specific responses may cascade to the seascape level and translate into differences in the composition (e.g. total area, percent cover by patch type) and configuration (e.g. size, patch density, patch shape, patch complexity) of the SAV seascape. In this study, we evaluated, for the first time, the potential influence of freshwater inflow on the structure of SAV communities in a coastal subtropical lagoon with a landscape approach commonly used to evaluate structural attributes of terrestrial landscapes. We hypothesized that (1) SAV seascape structure would be significantly different in areas with distinct salinity patterns; (2) higher SAV fragmentation would be observed in areas with extreme salinity values and high salinity variability; and (3) the influence of freshwater deliveries (and salinity) on SAV spatial pattern metrics would be concentrated on the habitats closest to shore where salinity patterns are more dynamic.

## MATERIALS AND METHODS

**Study area.** The study area for this project was located in western Biscayne Bay, Florida, USA (Fig. 1). Biscayne Bay is a shallow subtropical lagoon located adjacent to the city of Miami and downstream of the Florida Everglades system. The hydrology of the Everglades has been severely modified over the last 100 yr by the construction of a massive water management system that has altered the quantity, quality, and delivery of fresh water into the coastal bays (Davis & Ogden 1994, Browder & Ogden 1999). Historical hydrologic patterns that were dominated by sheetflow across the landscape have been replaced by canals as the main method of delivery of fresh water into the littoral habitats of Biscayne Bay. Areas where pulsed canal discharges take place experience drastic fluctuations in salinity over short periods, especially in the wet season (July to September) when water is released in pulses into coastal bays, mostly for flood management.

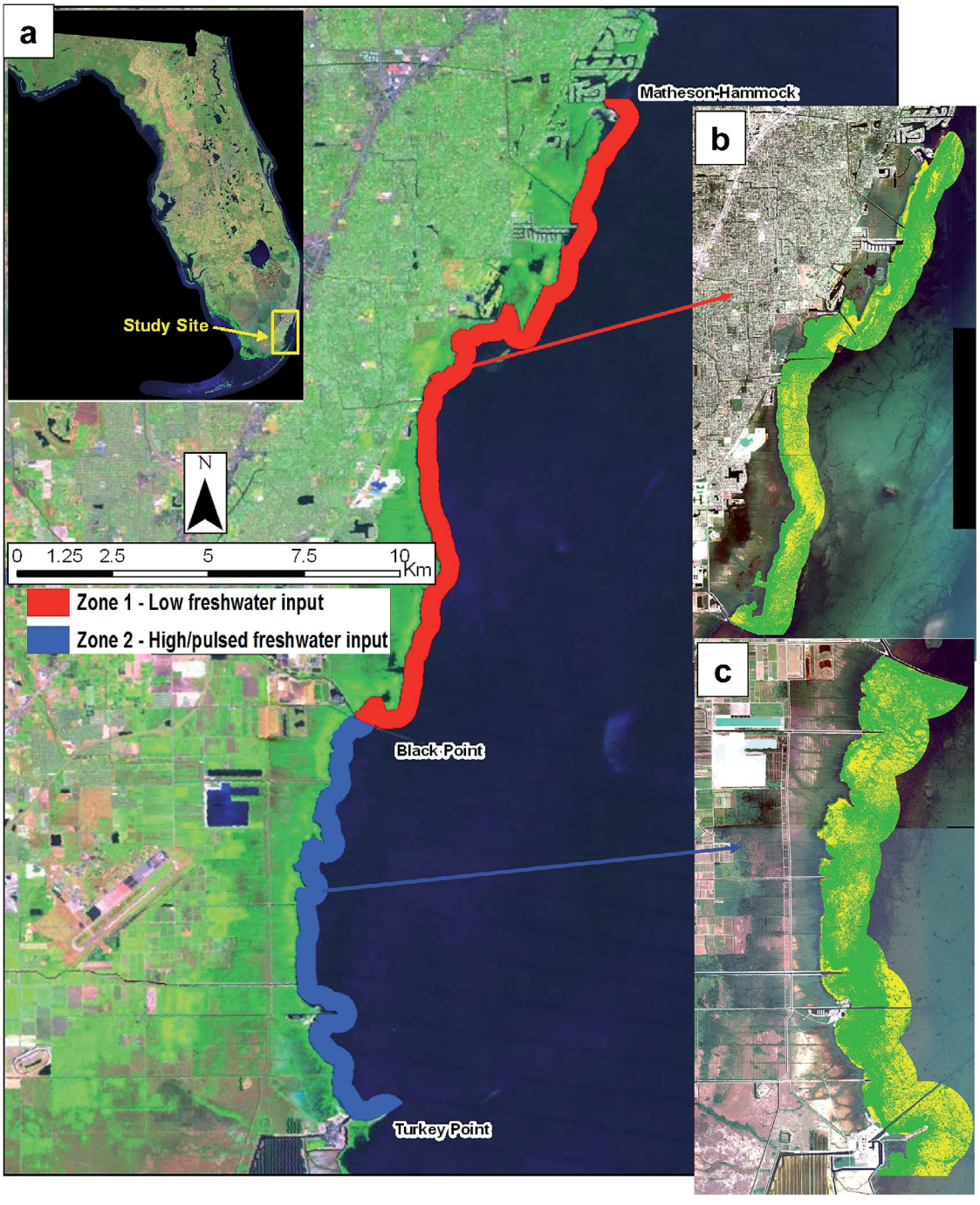


Fig. 1. (a) Study area in Florida, USA, with the delineation of the salinity zones, and the submerged aquatic vegetation (SAV) thematic map for (b) Zone 1 and (c) Zone 2. SAV dominant patches appear in green and SAV sparse patches in yellow. Thematic maps are drawn to different scales

Salinity patterns in Biscayne Bay are controlled by precipitation, freshwater runoff, canal flows, groundwater, and tidal oceanic influx that create distinct spatial and temporal patterns of salinity (Alleman 1995, Wang et al. 2003, Lirman et al. 2008a,b; South Florida Water Management District: www.sfwmd.gov/portal/page/portal/pg_grp_sfwmd_watershed/biscayne_bay_minimum375/tab744033?project=1303&ou=440). Habitats with low and variable salinity are found along the western margin due to the influence of canals as well as overland and groundwater sources (Caccia & Boyer 2005, Stalker et al. 2009). The present study concentrated on nearshore habitats (<1 km from shore) bordered by fringing mangrove habitats. The study region

was divided into 2 major zones that encompassed a total area of 38.9 $km^2$ (Fig. 1). Zone 1 (21.8 $km^2$) extended from Matheson Hammock to north of Black Point, and Zone 2 (17.1 $km^2$) extended from south of Black Point to Turkey Point (Fig. 1). These zones were delineated based on distinct salinity regimes as previously described by Caccia & Boyer (2005) and Lirman et al. (2008a,b). Zone 1, an area with limited input of fresh water from canal structures, is characterized by higher and more stable salinity patterns. In contrast, Zone 2 is significantly influenced by pulsed freshwater inflows from canals that create a nearshore environment with low and highly variable salinity.

Nearshore benthic habitats of Biscayne Bay are dominated by SAV communities composed of seagrasses and macroalgae (Zieman et al. 1989, Lirman et al. 2008a). These SAV communities, as well as the fringing mangrove shorelines, provide habitat for a large number of commercial and recreational fishery species such as pink shrimp (Diaz 2001), gray snapper, hogfish, and spotted seatrout (Serafy et al. 1997, 2003, Faunce et al. 2002).

**Delineation of SAV patches and construction of thematic habitat maps.** High-resolution (0.3 × 0.3 m pixel size) aerial photographs taken in May 2005 and provided by the Florida Fish and Wildlife Conservation Commission and Fish and Wildlife Research Institute were used to delineate different classes of SAV patches. The images were processed using ArcGIS v9.3 (ESRI) and ENVI v4.5 (ITT Visual Information Solutions) as follows: (1) the shoreline was delineated and digitized with a vector line, followed by the creation of a 1 km buffer, (2) the aerial photographs were re-sampled from 0.3 m resolution to 1 m resolution to provide more efficient processing and mapping results; and (3) the 1 km buffer and the re-sampled images were combined to delimit the desired area of study (i.e. nearshore SAV habitats).

An object-based supervised classification was performed with the ENVI v4.5 Feature Extraction module (ITT Visual Information Solutions: www.ittvis.com/ProductServices/ENVI/Tutorials.aspx) to delineate and classify SAV patches and to create a thematic SAV map. The object-based image classification used here optimized the delineation of exterior and internal (patch internal discontinuities) SAV patch boundaries and provided better discrimination between SAV classes under varying water depth and image quality than per-pixel based image classification methods. Since objects (i.e. image segments with distinct homogenous spatial, textural, and spectral characteristics) are used instead of individual pixels, results do not have 'salt and pepper' effects or erroneously classified pixels across the image (Kelly & Tuxen 2009). Also, the segmentation of the images into objects with distinct properties (e.g. tone, color contrast, texture, shape) helped distinguish the borders between different classes. The minimum patch size delineated by the Feature Extraction procedure was 100 $m^2$.

Due to the optical limitations of the aerial photographs used (e.g. high variance of sun glint and color contrast, limited spectral information), the object-based classification was limited to 2 SAV patch classes: (1) SAV dominant (patches with >30% SAV cover); and (2) SAV sparse (patches with ≤30% SAV cover). This classification scheme (i.e. SAV sparse and SAV dominant) was based on groupings of SAV samples that were identified by adapting the approach described by Mumby & Harbourne (1999). The benthic data used for this classification were obtained from field surveys conducted in March to May 2005 using the Shallow Water Positioning System (SWaPS), a boat-based platform that collects geo-tagged images of the bottom (Lirman et al. 2008a). The high-resolution (10 MP) images of the bottom collected by SWaPS were analyzed on the computer screen to determine the percent cover of each SAV taxon. The percent cover of the different taxa from each site surveyed (n = 153 sites) was examined in an agglomerative cluster analysis based on a resemblance matrix of Bray-Curtis similarities. Clusters with 50% similarity were identified, and used in a 'similarity percentages' (SIMPER) routine in PRIMER v6 (Clarke & Warwick 2001), which decomposes average Bray-Curtis dissimilarities between all pairs of clusters. The SIMPER analysis identified threshold cover values of 30% as the main feature responsible for splitting sites into 2 robust groups (SAV dominant and SAV sparse).

Although remote sensing by aerial photographs has proven to be efficient and accurate in this study, aerial photographs provide limited taxonomic resolution for benthic classification. Thus, in this study, patches composed of macroalgae were not distinguished from patches of similar cover, but dominated by seagrasses. The lack of taxonomic resolution restricts our results and conclusions to broad categories (SAV sparse and SAV dominant). The use of aerial images has also increased the potential for omission (e.g. classes not assigned in the thematic map, but identified in the reference data) and commission errors (e.g. class assigned in the thematic map, but not in the reference data) in our analyses. Overall, the SAV sparse class was subject to high values of omission errors possibly caused by the inability to distinguish spectrally barren areas with organic sediments and high detritus cover versus areas with sparse SAV. Therefore, some of the barren areas with organic sediments and high detritus cover were classified as SAV dominant. In addition, commission errors could be caused by the similarity of spectral features among barren areas, areas with sparse SAV, and areas with high cover of drift algae.

Drift algae tended to show optical characteristics similar to light-brown sediments and senescent SAV material. Future studies with multispectral imagery would be required for the documentation of taxa-specific patterns in structural metrics and to limit the occurrence of omission and commission errors.

**Groundtruthing methods.** A subset of the georeferenced benthic images obtained in 2005 was randomly selected (100 images per zone) as groundtruth points for the accuracy assessment of the classified thematic map. The value of SAV cover estimated for each image (values for macroalgae and seagrasses were added together to obtain a single aggregate SAV value) was compared to the value obtained for the same location extracted from the classified map. Accuracy was calculated as the proportion of images that matched the SAV class extracted from the thematic map. Using a confusion matrix, the SAV dominant class showed higher user accuracy (81% in Zone 1, 80% in Zone 2) than SAV sparse (47% in Zone 1, 55% in Zone 2). Since the user accuracy is a measure of the reliability of class in a thematic map, only the SAV dominant class was considered for further statistical analyses (e.g. spatial patterns of SAV seascape structures).

**Multi-scale SAV seascape characterization.** Following the mapping process, a group of circular extraction buffers was created around a set of 45 randomly selected points along the shoreline of Zones 1 and 2 (Fig. 2a). These points served as the centers of the extraction buffers used to clip and obtain the delineated SAV patches within areas at increasing distances (i.e. scale) from shore. The buffers delineated were analyzed to establish the spatial scale at which the SAV seascape structures (described below) showed the highest heterogeneity (i.e. differences in spatial pattern metrics) within nearshore habitats (Fig. 2b).

The process of extracting the spatial pattern metrics from each buffer was automated using ArcGIS ModelBuilder (www.esri.com). In total, 4 metrics were extracted to quantify the SAV seascape composition or configuration at the class level (SAV dominant and SAV sparse) based on metrics calculated with Patch Analyst v4 and FRAGSTAT (McGarigal et al. 2002, Rempel 2008). These spatial pattern metrics were percentage of the landscape occupied by a given class (ZLAND), fractal dimension of patches (DLFD), mean patch size (MPS), and patch density (PDENS; Table 1). Mean patch size, shape complexity, and patch density (number) have been used in landscape ecology studies to assess the fragmentation dynamics of terrestrial habitats (Trzcinski et al. 1999, Turner et al. 2001, Botequilha et al. 2006).

In a preliminary analysis, 100 m extraction buffers were used (100 m is the extension of the buffers used as strata in the benthic surveys conducted by Lirman et al. 2008b). The 2 buffers (100 and 200 m) closest to shore were identified using an analysis of similarities (ANOSIM) analysis as the buffers that differed significantly from all other buffers. However, a pairwise test indicated that the 100 and 200 m buffers did not differ

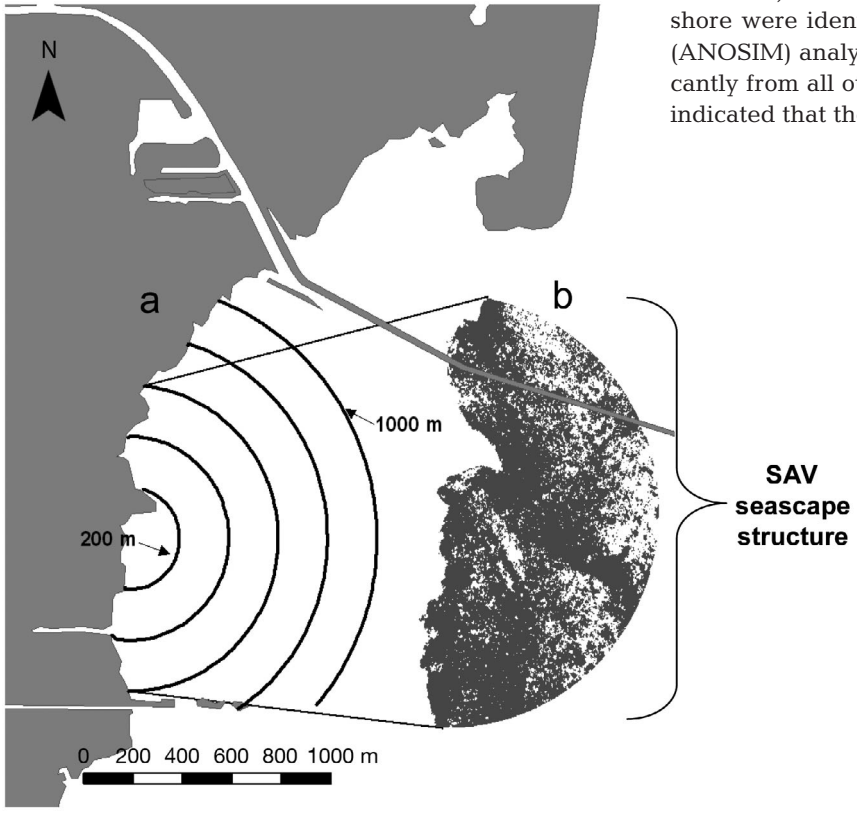


Fig. 2. Illustration of the multi-scale seascape approach. The multi-scale seascape approach was composed of (a) extraction buffers with radius from 200 m to 1 km from shore used to extract the submerged aquatic vegetation (SAV) seascape at different scales, and (b) the characterization and definition of SAV seascape structure within each extraction buffer (i.e. scale) based on spatial pattern metrics: proportion of the landscape (ZLAND), mean patch size (MPS), double log fractal dimension (DLFD; shape complexity), and patch density (PDENS)

Table 1. Spatial pattern metrics calculated based on McGarigal et al. (2002). There are 2 types of general categories: metrics that calculate composition and metrics that calculate configuration. Within these categories, the metrics are classified based on the aspect of the landscape pattern measured

| Metric | Code | Category | Aspect | Description |
|---|---|---|---|---|
| Percentage of landscape | ZLAND | Composition | Area/density | Percentage of the total landscape made up of the corresponding class |
| Double log fractal dimension | DLFD | Configuration | Shape | Measure of patch perimeter complexity<br>Values range from 1 (simple form) to 2 (more complex form) |
| Mean patch size | MPS | Configuration | Area/density | Average size of a particular class<br>Units: ha |
| Patch density | PDENS | Configuration | Area/density | Number of patches of a certain class divided by the total landscape area<br>Units: patches $ha^{-1}$ |

from each other. Based on this, a 200 m radial increment was chosen for all further analyses. Thus, the radius of the extracting buffers around each site increased from 200 m to 1 km at increments of 200 m. Therefore, each sampling site (n = 45 sites) had 5 buffers, yielding a total of 225 extraction buffers.

**Statistical analyses.** All descriptive statistics were generated with SPSS v17.0. The spatial pattern metrics were $\log_{10}(x + 1)$ transformed. Multivariate tests were run with PRIMER v6 (Clarke & Warwick 2001) to analyze for differences in the SAV seascape structures among buffers and zones. To test differences in SAV seascape structures between treatments (i.e. buffers, zones) a 1-way ANOSIM was performed on the Euclidean distance similarity matrix of the spatial pattern metrics (Clarke & Warwick 2001). The scale (i.e. buffer extension) with distinct SAV seascape structures was identified using the 1-way ANOSIM pairwise tests, and a combination of a simple agglomerative hierarchical clustering (CLUSTER, PRIMER) and non-metric multidimensional scaling (MDS) plots with buffer size as the main treatment (Clarke & Gorley 2006). These tests were used to identify the buffer extension in which spatial pattern metrics were significantly dissimilar from the rest of the buffer extensions considered. A subsequent cluster analysis of sites at the selected scale was performed to identify groups with distinct SAV seascape structures. A series of similarity profile permutation tests (SIMPROF, PRIMER) were incorporated into the CLUSTER routine to identify statistical differences among clusters (Clarke & Gorley 2006).

## RESULTS

### SAV spatial pattern metrics

In Zone 1, SAV dominant and SAV sparse classes covered 68.9% (15.0 $km^2$) and 30.7% (6.7 $km^2$) of the seascape, respectively (Fig. 1b). In Zone 2, the SAV dominant class covered 66.0% (11.3 $km^2$) and the SAV sparse class covered 33.8% (5.8 $km^2$) of the seascape (Fig. 1c). Based on the SAV dominant class, spatial pattern metrics showed significant differences between buffers, with some degree of overlap indicated by a small global R value (ANOSIM test, $R < 0.2$, $p < 0.001$). ANOSIM pairwise tests indicated that the 200 m buffer was the spatial extent where significant dissimilarities in spatial pattern metrics between buffers and zones were observed (illustrated by MDS, CLUSTER; Fig. 3). Differences among buffers (Fig. 3) and zones (Fig. 3a) disappeared when larger distances (and larger buffers) were evaluated. Based on these results, the 200 m buffer was selected for all subsequent analyses. The 45 sampling sites used to evaluate spatial pattern metrics at the 200 m buffer scale clustered into 7 groups (CLUSTER; Fig. 4). Groups B and C, and groups F and G were joined together based on their similarities (Fig. 4).

Based on the value distributions of the ZLAND, MPS, PDENS, and DLFD, the groups identified in the CLUSTER analysis were further classified into 2 distinct classes (Fig. 5). The groups of sites identified in Fig. 4 were classified as either fragmented SAV seascape (FSS) or continuous SAV seascape (CSS) structures. Groups A, D, and E were classified as CSS, and groups B and C, and F and G as FSS. The latter (B, C, F, and G) had, on average, the lowest proportion of the seascape dominated by SAV (low ZLAND values), and presented high densities of smaller SAV patches (higher PDENS) with complex shapes and boundaries (higher DLFD; Fig. 5). Sites with a CSS structure had a higher portion of the seascape occupied by SAV dominant patches (Fig. 5). The low patch density values and high mean patch size values indicate that these groups were characterized mainly by large, continuous SAV patches with simple boundaries (i.e. less convoluted boundaries). Differences in the spatial pattern metrics between CSS and FSS groups were statistically significant (1-way ANOVA, $p < 0.01$; Fig. 5).

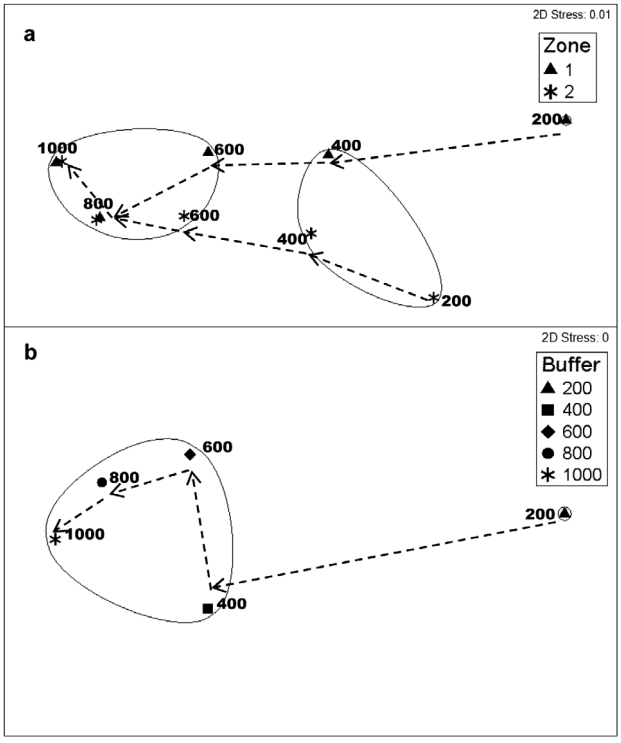


Fig. 3. Multi-dimensional scaling (MDS) plots of the mean spatial pattern metrics in (a) Zones 1 and 2 by distance-to-shore buffers, and (b) by buffers. The length of the dashed arrows is proportional to the level of dissimilarity. Contours represent the highest resemblance level (Euclidean distance) from a simple agglomerative hierarchical clustering. The highest submerged aquatic vegetation seascape metrics dissimilarity between buffers and zones occurred at the 200 m buffer. Stress values represent the measure goodness of fit of the MDS plot

### Seascape structure and salinity patterns

To evaluate the relationship between seascape structure and salinity patterns, we explored (1) the distance between the location of each site and the mouth of freshwater canals; and (2) the mean salinity and salinity variability (i.e. standard deviation) at each location obtained from the Biscayne Bay Hydrodynamic model (Wang et al. 2003) for the 2 yr prior (2004–2005) to the field surveys conducted for this study.

The sites identified as CSS and FSS were not distributed randomly along the shoreline (Fig. 6a). The groups classified as FSS (groups B, C, F, and G) were significantly closer (i.e. shorter mean distance) to the mouth of freshwater canals than the groups classified as CSS (groups A, D, E; 1-way ANOVA, $p < 0.05$; Fig. 6d). A higher proportion of the sites described as having FSS (19 of 28) were located in areas with a higher concentration of canals (6 canals discharge in Zone 2 compared to only 2 in Zone 1). In contrast, groups with CSS structures (11 of 17) were in areas with lower concentrations of canals (Fig. 6a,d). Moreover, the FSS groups within Zone 1 were only found adjacent to the 2 canals in this area.

Based on the output of the salinity model, the groups classified as CSS had statistically higher mean salinity and lower salinity variability compared to sites classified as FSS that had lower mean salinity and wider salinity fluctuations (1-way ANOVA, $p < 0.05$; Fig. 6e,f).

## DISCUSSION

Two classes of SAV patches, SAV dominant (>30% benthic cover) and SAV sparse (<30% cover), were delineated within the nearshore habitats of the study area using object-based classification of aerial photographs. Moreover, the multi-scale seascape approach used here identified the 200 m buffer extension as the scale at which SAV seascape characteristics differed among sites. The clustering of SAV seascape characteristics within this scale revealed 2 main SAV seascape structures: continuous SAV seascape (CSS) and fragmented SAV seascape (FSS). FSS, defined here as habitats with low SAV coverage, large numbers of small patches, and higher patch shape complexity, were prevalent in areas of Biscayne Bay where point sources of fresh water discharged from water management canals create environments with low and variable salinity. CSS were found mainly in areas of the bay removed from canal-based freshwater discharges. Thus, this study indicates that water management practices that regulate freshwater discharges into littoral areas of coastal lagoons may have structural impacts on the SAV seascape structures within the area of influence of freshwater pulses. This finding extends previous research that has shown that SAV species' distributions and abundances are highly influenced by their salinity tolerances (Montague & Ley 1993, Fourqurean et al. 2003, Lirman & Cropper 2003, Lirman et al. 2008a,b, Herbert & Fourqurean 2009). Moreover, these findings are consistent with those reported by Bell et al. (1999, 2007), who showed that losses in productivity and biomass are associated with the formation and persistence of fragmented areas and gaps within the SAV seascape.

Studies that have used remote sensing to assess SAV spatial dynamics have often only considered SAV coverage and change patterns over a single, broad scale (Ferguson & Korfmacher 1997, Cole et al. 2002, Hernandez-Cruz et al. 2006, Dekker et al. 2007, Moore et al. 2009), and have rarely applied landscape theory or metrics (Bell et al. 2007). In landscape ecology, there is a consensus that there is not a single, 'best scale' for research and that overemphasis on either very small or very large scales is not recommended (Kent 2005). Thus, to have a robust understanding of spatial pat-

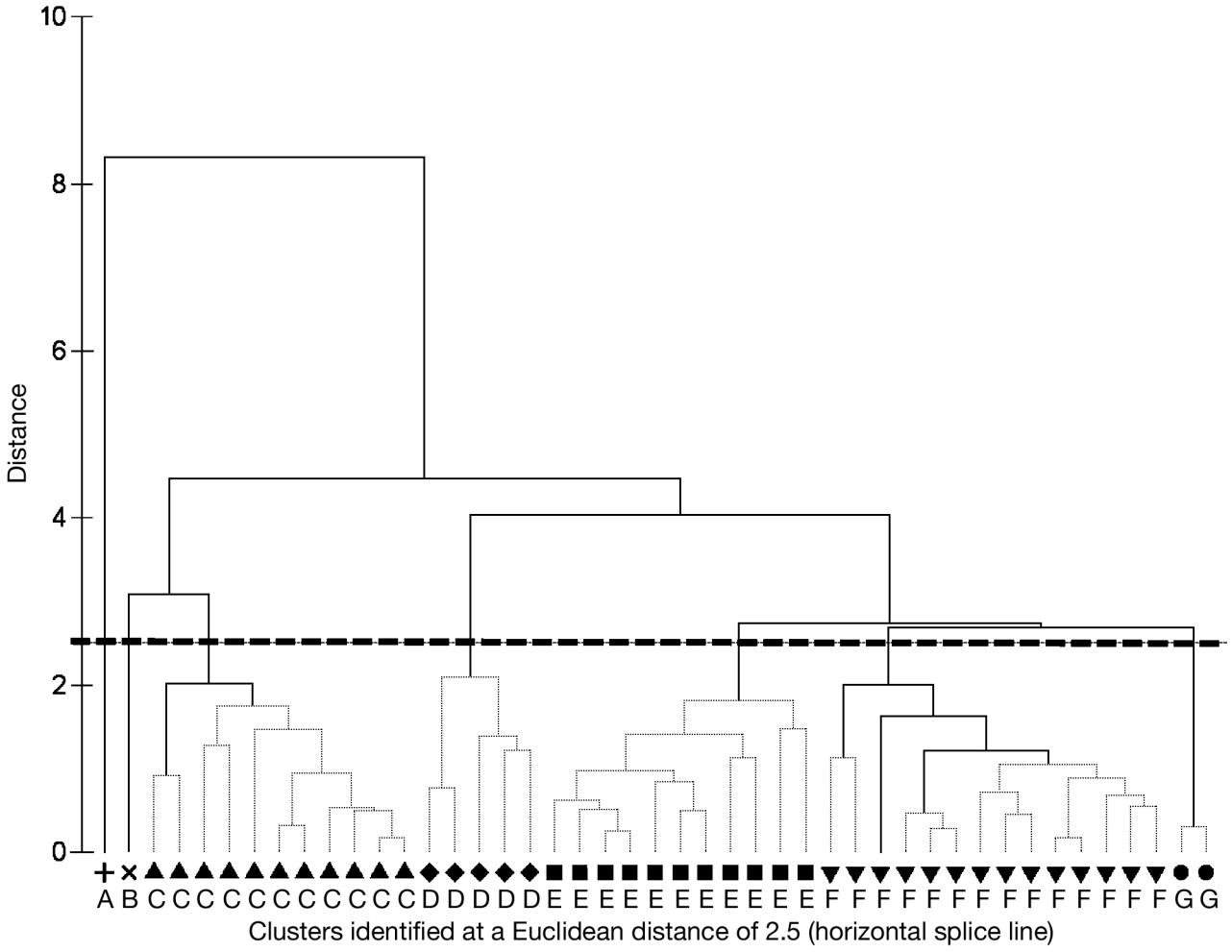


Fig. 4. Clustering of sites based on seascape characteristics measured within the 200 m buffer. Clustering labels defined at the Euclidean distance 2.5 (black horizontal dashed line). Dotted lines indicate where the SIMPROF test found no statistical evidence of sub-structure within these groups

terns within landscapes, it is important to quantify habitat spatial heterogeneity explicitly at multiple scales (Levin 1992, Wu et al. 2002, Shen et al. 2004, Kendrick et al. 2008). Factors and processes important at 1 scale are frequently not important or predictive at another scale, and information is often lost if spatial data are not considered at multiple scales (Turner et al. 1989). When only the total aerial coverage of SAV dominant patches was compared between the 2 zones surveyed in Biscayne Bay, no significant differences were detected. However, when a multi-scale approach was used and spatial pattern metrics were evaluated at increasing distances from shore and buffer sizes, the 200 m buffer was identified as the scale at which SAV seascape characteristics differed significantly among salinity zones. Thus, this study highlights the significance for the monitoring of SAV spatial distribution to incorporate multi-scale approaches to examine the underlying driving processes of SAV spatial patterns.

Spatial pattern metrics are known to be spatially correlated and scale-dependent (Wu 2004), and are also sensitive to changes of scale (Turner et al. 1989, 2001). Accordingly, comparisons of spatial pattern metrics quantified at different scales may reflect scale-related errors or effects rather than true differences in landscape patterns (Turner et al. 2001). The spatial pattern metrics selected in this study (i.e. percentage of landscape, fractal dimension, patch size, patch density) are known to be robust and stable across multiple scales (e.g. Saura & Martinez-Millan, 2001). Thus, the SAV seascape patterns described for Biscayne Bay can be considered a result of the distribution and spatial arrangement of driving factors and not an artifact of scaling effects.

Sublethal stressors known to influence the structure of SAV seascapes may alter vital processes such as photosynthesis, growth, and reproduction. The impacts of these factors (e.g. nutrients, depth, light, and

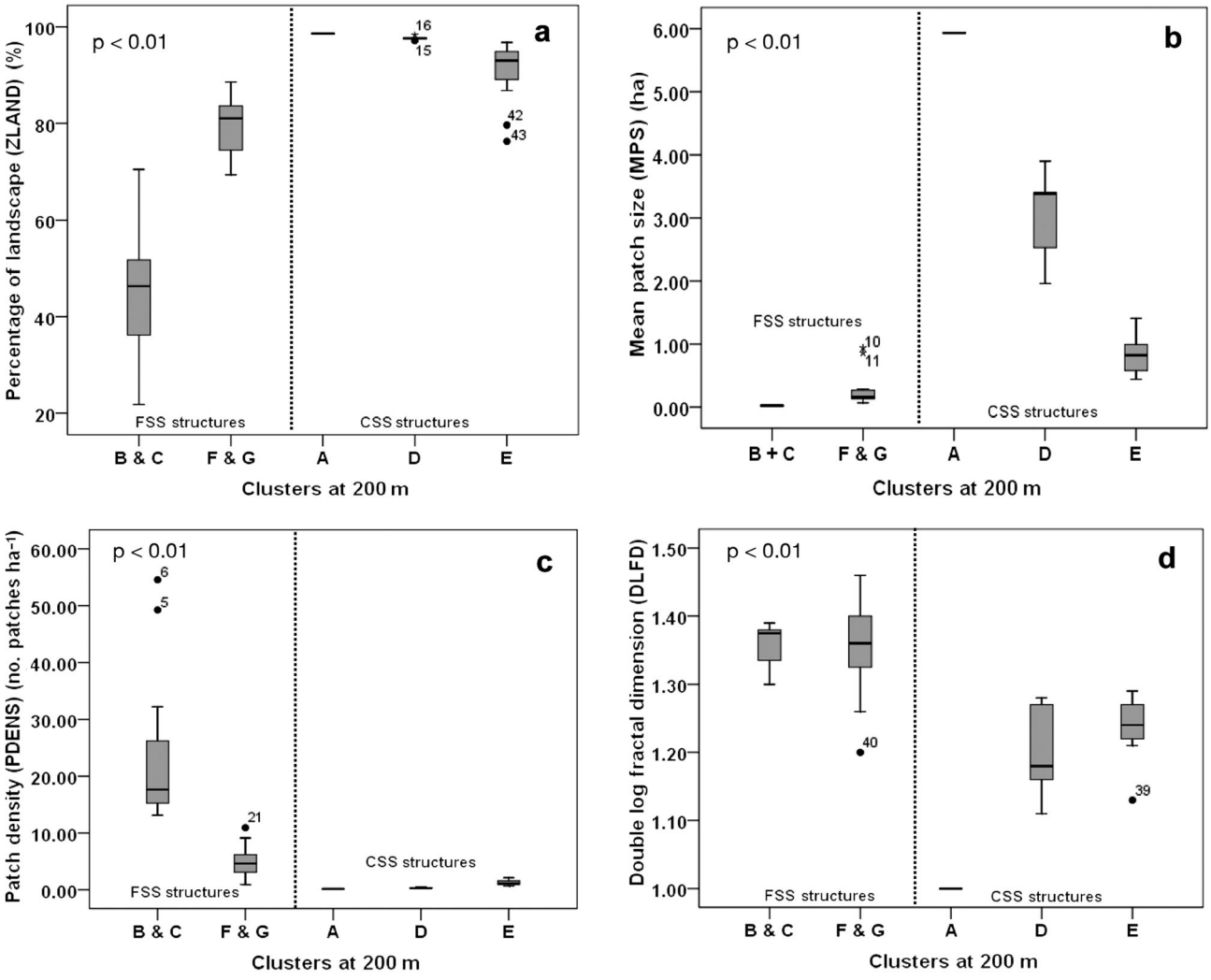


Fig. 5. Value distribution of (a) proportion of the landscape (ZLAND), (b) mean patch size (MPS), (c) patch density (PDENS), and (d) double log fractal dimension (DFLD) within the groups identified in the cluster analysis (Fig. 4). Based on these 4 spatial pattern metrics, these groups were classified as continuous submerged aquatic vegetation (SAV) seascape (CSS), and fragmented SAV seascape (FSS) structures. The dotted line in the box plots separates the groups classified as CSS and FSS. The differences between the spatial pattern metrics within CSS and FSS were statistically significant (1-way analysis of variance, $p < 0.01$). Horizontal lines: median; boxes: 25th–75th percentile; whiskers: data range; black dots and asterisks: outliers (with site number)

salinity zonation, space competition) are commonly species-specific and are based on the physiological tolerances or requirements of species and assemblages (Frederiksen et al. 2004, Boström et al. 2006, Bell et al. 2007). While SAV seascape characteristics and salinity patterns are clearly spatially correlated in western Biscayne Bay, the formation and persistence of gaps and the shrinkage or removal of SAV patches can be potentially associated with other driving variables such as temperature, dissolved oxygen (DO), currents, and nutrient availability. However, Lirman & Serafy (2008, 2009) showed that in the shallow environments of nearshore Biscayne Bay, no differences in depth, light penetration, temperature, and DO are found between the 2 areas compared in this study in the dry season, when the aerial imagery for this study was collected. A lack of spatial patterns in DO, temperature, and turbidity between the zones examined in this study was also reported by Caccia & Boyer (2005). Sediment depth, also known to influence the distribution and abundance of seagrasses (Zieman et al. 1989), exceeded 25 cm throughout the study area (Lirman et al. 2003), providing ranges suitable for seagrass meadow formation (Zieman 1972).

Nutrients in the water column were not measured here, but previous studies have shown correlations between freshwater and nutrient inputs into this P-limited lagoon (Fourqurean & Robblee 1999, Four-

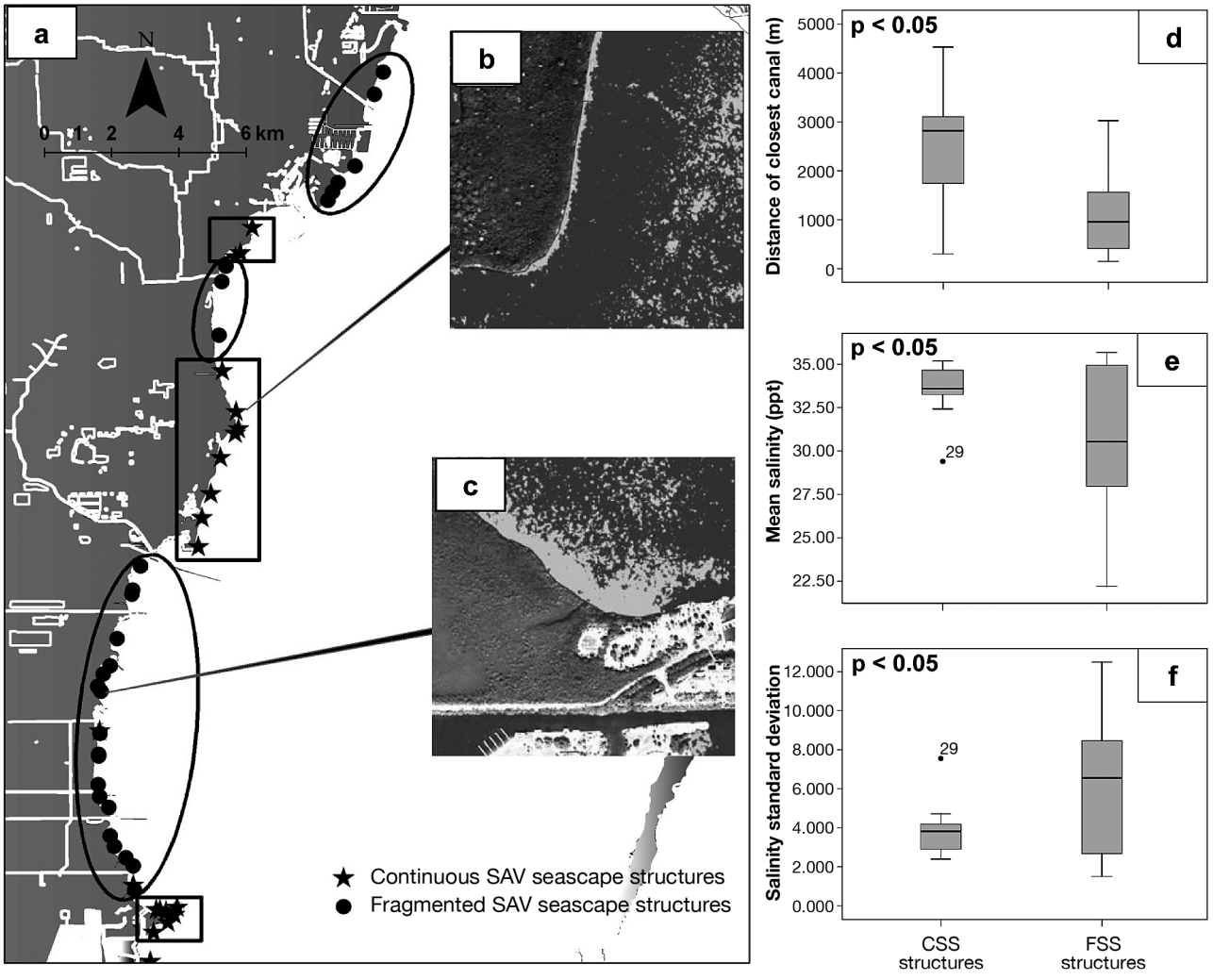


Fig. 6. (a) Spatial distribution of sites identified in the clustering analysis (Fig. 3) based on seascape characteristics measured within the 200 m buffer. Groups with continuous submerged aquatic vegetation (SAV) seascape (CSS) structures are represented by black stars, and groups with fragmented SAV seascape (FSS) structures are represented by black filled circles. Areas with higher proportions of groups with FSS structures are bordered with black ovals, and areas with higher proportions of groups with CSS structures are bordered with black rectangles. Canals and major streams are illustrated with white lines. Illustration of (b) CSS structure and (c) FSS structures. Boxplots (see Fig. 5 for boxplot limits) illustrate the values distribution of (d) distance of the closest canal, (e) mean salinity, and (f) salinity standard deviation within the clusters classified as FSS and CSS (1-way analysis of variance, $p < 0.05$)

qurean et al. 2003, Biber et al. 2004, Caccia & Boyer 2005, 2007). Thus, nutrient availability, together with freshwater pulses, may play a synergistic role in determining SAV patch structure in the study area. Nutrient loadings have been linked to direct and indirect negative effects on the productivity and spatial assemblages of SAV species (Orth et al. 2006, Waycott et al. 2009). For example, light availability can be reduced by phytoplankton blooms and suspended organic matter associated with high nutrient loads (Fourqurean & Robblee 1999, Duarte 2002, Fourqurean et al. 2003). In addition, increased nutrients have been linked to high epiphyte and drift algae biomass that can control seagrass biomass and distribution through light limitation and competition for nutrients (Holmquist 1997, Biber et al. 2004, van Tussenbroek et al. 2007). Until the separate (and potentially synergistic) impacts of salinity and nutrient availability on SAV seascape structure have been experimentally determined, observed patterns in Biscayne Bay cannot be causally linked to one or the other factor.

Hydrodynamic forces have been suggested as potentially more important structuring features in the SAV seascape than other driving variables that control the physiological responses of macrophytes (Bell et al. 1999). Factors such as tidal currents and wave expo-

sure have been shown to directly influence SAV patch size, shape, and distribution (Robbins & Bell 2000, Bell et al. 2007). For example, Fonseca & Bell (1998) reported that SAV seascape characteristics such as percent cover and seagrass bed perimeter-to-area ratio declined with increasing mechanical disturbance produced by waves and tidal currents. Frederiksen et al. (2004) found that *Zostera marina* formed continuous meadows only in sheltered areas. Acute disturbances such as storms have also been found to be dominant factors structuring and maintaining seascape heterogeneity, and transitions between vegetated and barren areas (Ramage & Schiel 1999, Robbins & Bell 2000). Hydrodynamic forcing is clearly a key structuring factor on SAV seascapes, but there is a low likelihood that mechanical disturbances are a major driver within our study area, especially at the 200 m scale (buffer with highest heterogeneity in SAV seascape structure). The zones surveyed here are of shallow and fairly uniform depth and are sheltered by a mangrove coastline. Finally, while storms and hurricanes have impacted the study area historically (Manzello et al. 2007), the short distance separating the 2 areas assessed is clearly smaller than the area of influence of any single storm.

Even if the role of mechanical factors as a structuring force at the scale of our study is likely minor, the characteristics of the SAV patches may indeed influence the susceptibility of the SAV seascape to future storm events. Previous studies have identified a critical patch size (<25 $m^2$ for patches of the temperate seagrasses *Zostera* spp.) beyond which the likelihood of patch mortality decreases significantly (Olesen & Sand-Jensen 1994, Ramage & Schiel 1999, Kendrick et al. 2005). Thus, continuous SAV seascapes may be more resistant and resilient to physical disturbances than fragmented SAV seascapes since the homogeneous root-rhizome matrix stabilizes the sediment and less patch edge is exposed to damage from waves or currents (Ramage & Schiel 1999, Frederiksen et al. 2004). Large patches have higher potential for resource accumulation to support patch growth (Kendrick et al. 2005), and the high mortality associated with small SAV patches could be linked to lack of mutual protection and firm anchorage leading to higher susceptibility to physical disturbances and nutrient stress (Duarte et al. 2007). Within this context, future changes in salinity patterns caused by restoration may have long-term negative impacts in terms of SAV patch persistence if further seascape fragmentation takes place.

While the focus of the present study was the spatial and structural characteristics of SAV seascapes and spatial correlations with salinity patterns, the potential for these impacts to propagate up the food chain and affect higher trophic levels deserves further consideration. The use of SAV habitat patches as transient and permanent habitat by fish and invertebrates highlights the need to better understand how the value of ecological services provided by SAV habitats may change with modification on the SAV seascape structure. Biscayne Bay has one of the longest and most detailed records of mangrove fish communities (Serafy et al. 2003, Faunce & Serafy 2006), providing a unique opportunity to assess how distinct SAV seascape patterns influence the abundance and diversity of fish communities, and the connectivity and synergistic functions of multiple critical habitats in heterogeneous seascape. In the near future, this spatially explicit fish dataset will be related to the SAV seascape patterns recorded in this study to ascertain the role of seascape structure on fish habitat utilization patterns.

In summary, using a multi-scale seascape approach adapted from landscape ecology, the seascape structure of SAV communities in Biscayne Bay (Florida, USA), was found to be spatially correlated with areas of pulsed freshwater releases into littoral areas. SAV communities in the area of influence of freshwater releases had structural characteristics consistent with fragmented habitats, including high density of small patches and a higher proportion of sparse SAV patches. While patch structure of SAV seascapes can be driven by a number of biological and physical factors, the spatial data collected in this study area indicated that salinity patterns (and correlated nutrient availability) are likely the main factor influencing the observed SAV spatial patterns. Results presented here show that previously reported impacts of salinity at the individual and species levels scale up to a landscape level within this shallow coastal system. Due to the implementation of a multi-scale approach, these spatial patterns were discerned and related to potential processes, which otherwise could be precluded and masked by broad and single scale quantification of aerial extent of SAV patches. Coastal and estuarine monitoring and management at the ecosystem level should apply multi-scale and multidisciplinary methodologies not only to understand spatial features of essential marine habitats, but also to understand the functional linkages between habitats in a heterogeneous seascape, and the abundance, movement, and growth of ecological and economically important marine species.

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# Seagrass habitat loss and fragmentation influence management strategies for a blue crab *Callinectes sapidus* fishery

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ABSTRACT: Marine biodiversity is increasingly threatened by multiple processes, and management strategies therefore must explicitly address the synergistic effects of multiple threats to marine species. The effects of harvesting and habitat degradation may be magnified for many coastal marine fishery species that rely on structurally complex nursery habitats to enhance survival and growth of postlarval and juvenile life history stages. Fishery management strategies that do not account for processes reducing juvenile survival and growth may overestimate the amount of biomass that can be taken; similarly, conservation and restoration strategies for nursery habitats that do not account for variable recruitment may fail. We used the blue crab *Callinectes sapidus* as a case study to investigate the population-level effects of harvest and seagrass habitat loss and fragmentation. We used available data to parameterize a stochastic stage-based model to test combinations of management strategies, namely reduced harvest rates and introductions of juvenile crabs to nursery habitat. Under a no-harvest scenario, large continuous areas of seagrass supported the largest blue crab populations. However, when harvest rates exceeded 20%, median population abundance was maximized in seascapes composed of smaller, fragmented seagrass patches. Populations in isolated patches of seagrass benefitted more from the introduction of crabs rather than harvest reduction, but the opposite was true for crab populations inhabiting highly connected seagrass seascapes. Management of species that use seagrass beds as nursery habitat must consider the spatial context of multiple threats and their potential synergies to maintain population persistence.

KEY WORDS: Habitat fragmentation · Fishing · Blue crab · *Callinectes sapidus* · Seagrass · Seascape · Reintroduction



## INTRODUCTION

Conservation and natural resource management practices typically address single threats to populations, communities, and ecosystems, but rarely consider synergistic interactions between threats (Myers et al. 1996, Calkins et al. 1998, Mellink et al. 2002). However, in order to effectively manage populations, it is essential to establish a better understanding of the synergies between threats, particularly in how they influence risks of decline or extinction (Marschall & Crowder 1996, Myers 1996, Davies et al. 2004, Ewers & Didham 2005). For many marine organisms, 2 major threats to population persistence are overharvesting and habitat degradation. These threats may be magnified for the large number of coastal marine fishery species that rely on structurally complex nursery habitats to enhance survival and growth of postlarval and juvenile life history stages. For these species and many others, habitats such as subtidal and intertidal seagrass beds, salt marshes, and oyster reefs provide refuge from predation and abundant foraging opportunities, but increasingly are degraded and fragmented (Beck et al. 2001), which threatens to disrupt linkages between early life history stages and recruitment to the fishery (e.g. Irlandi et al. 1995, Hovel & Lipcius 2002).

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Fishery management strategies that do not account for processes reducing juvenile survival and growth may overestimate the amount of biomass that can be taken; similarly, conservation and restoration strategies for nursery habitats that do not account for variable recruitment may fail.

In this study, we used the blue crab *Callinectes sapidus* in Chesapeake Bay, USA, as a case study to determine how loss and fragmentation of a key estuarine nursery habitat interacts with harvesting to dictate population persistence. Here, we define fragmentation as the breaking apart of habitat into spatially isolated patches, a process which often accompanies habitat loss (i.e. habitat fragmentation per se: Fahrig 2003). The blue crab forms one of the most valuable single-species fisheries along the east coast and gulf coasts of the USA; however, in estuaries such as Chesapeake Bay, blue crab populations are in decline (Fogarty & Lipcius 2007) at least in part due to excessive fishing pressure (BBCAC 2005). Moreover, eelgrass *Zostera marina*, the primary nursery habitat for blue crab in Chesapeake Bay (Moody 1994, Perkins-Visser et al. 1996), has declined by 80% from historical levels due to non-anthropogenic (e.g. storms, digging predators) and anthropogenic (e.g. nutrient loading, sedimentation, propeller scarring) causes (Orth & Moore 1983).

In Chesapeake Bay, harvest, habitat loss, and habitat fragmentation all may reduce blue crab population size (Hovel & Lipcius 2001, Sharov et al. 2003, Fogarty & Lipcius 2007), but studies evaluating these threats, and management options to overcome them, have not considered their potential interactions. Moreover, the effects of seagrass habitat fragmentation and loss on blue crabs may be complex. Whereas loss of seagrass reduces the availability of refuge and foraging habitat, and seagrass patchiness increases the risks associated with movement among patches (Micheli & Peterson 1999), relative survival of tethered juvenile blue crabs is higher in small isolated patches than in larger continuous patches. This likely is due to reduced predator abundance in sparse, highly fragmented seagrass seascapes (Hovel & Lipcius 2001). Additionally, the effects of seagrass loss and fragmentation on blue crab survival and abundance vary ontogenetically, seasonally, and with crab density (Hovel & Lipcius 2002).

Our goal in this study was to determine how the loss and fragmentation of seagrass habitat may influence the success of different blue crab management scenarios (reductions in harvest and stock enhancement; blue crabs are hatchery-reared and released into the bay as a stock enhancement strategy). To do this, we constructed simulated seascapes consisting of seagrass patches embedded within a matrix of unvegetated sediment and used a stage-based matrix model to subject crabs within seagrass habitat to a variety of harvest and stock enhancement scenarios. Although blue crabs settle and mature within a variety of habitat types (Fogarty & Lipcius 2007), we chose to use a patch-matrix seascape consisting only of seagrass (habitat) and unvegetated sediment (non-habitat) to explicitly model the effects of fragmentation and loss of the primary blue crab nursery habitat in Chesapeake Bay, for which information is available on survival and abundance. Our model addressed 2 primary questions: (1) What combination of seascape configuration and harvest rate results in the largest population of blue crabs over the long-term (50 yr)? (2) Under what combination of seascape configuration and harvest rate is seeding of juvenile blue crabs most effective as promoting persistence of blue crab populations?

## MATERIALS AND METHODS

**Population models.** We modified an existing deterministic stage-based model for blue crab populations in Chesapeake Bay (Miller 2001) to include spatial heterogeneity, stochasticity, density dependence, and habitat-dependent survival rates for juvenile stages (see Miller 2001 for full description of blue crab life history and justification for model structure). Environmental variability was represented as a probability distribution for each survival rate, transition rate (i.e. growth rate from smaller to larger stages), and fecundity in the matrix model. We constructed the stage-based stochastic models in the software platform RAMAS Metapop® (Akçakaya & Root 1998) to simulate the population dynamics under a range of harvest, seeding/stocking, and seagrass loss and fragmentation scenarios. This platform propagates variability across parameters via Monte Carlo simulations. We explain below how each model parameter was estimated, how environmental variability is represented for each parameter, the type of density dependence modeled, and how spatial heterogeneity and management scenarios were implemented in the models.

**Selection of seascape types.** We first identified 4 seascape types (henceforth simply 'seascapes') based on a series of aerial photographs taken of the lower York River in Chesapeake Bay, an area in which wave and current scouring, digging predators, and boating and fishing practices create a mosaic of seagrass seascapes that vary from undisturbed, continuous seagrass cover to small, isolated seagrass patches (Hovel & Lipcius 2001). Four seascapes were selected from the aerial photographs to represent the full range of average seagrass patch sizes and isolation between patches: continuous (connected) seagrass, large patches of seagrass isolated from one another, small patches close to one another, and very small isolated patches of seagrass

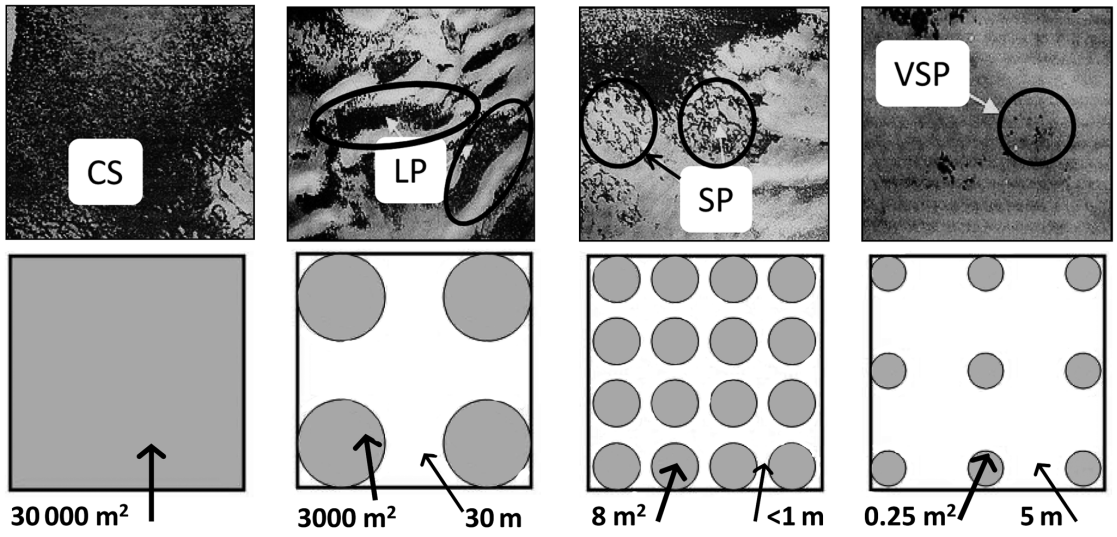


Fig. 1. *Zostera marina*. Aerial photographs of eelgrass beds (dark patches) in the lower York River, Chesapeake Bay (upper panels), and visual schematic of the layout of seagrass beds in each model representing different fragmentation types (lower panels). From left to right: continuous seagrass (CS), large isolated patches (LP), small close patches (SP), and very small isolated patches (VSP). The area of the box is held constant (30 000 $m^2$), and the amount of seagrass varies in each model based on patch size and isolation by unvegetated sediment. Size of seagrass beds not to scale. Color photographs and detailed habitat descriptions are provided in Hovel & Lipcius (2001)

(Fig. 1). These 4 seascapes provide the spatial underpinnings for 4 separate population models. The models differ in 2 key ways: (1) the number of large and adult blue crabs supported by the available seagrass habitat, and (2) the survival rates for small crabs, as indicated by field data (Hovel & Lipcius 2002). The link between the seascapes and the population model is provided by these 2 components (see below for more detail).

The average size of the patches, as well as the area of unvegetated sediment between patches, varied across the 4 seascapes (Fig. 1, Table 1; refer to Hovel & Lipcius 2001 for aerial maps). For consistency, each seascape was set within a 30 000 $m^2$ spatial context (i.e. for each scenario the average sized patch was repeated, with the average distance between patches, to fill a total area of 30 000 $m^2$; Fig. 1). This spatial scale was chosen (1) to isolate seascapes for exploration of spatial structure on population dynamics, and (2) to investigate management actions which occur on localized scales. Continuous patches average 3 ha in area, hence the other seascapes were scaled to match this within their respective spatial context (Fig. 1). These seascapes were used in separate models representing unique scenarios where the total amount and configuration of seagrass habitat differed in each.

**Stage-based matrix model.** The life history of this species is best described by 4 stages which are defined according to carapace width (CW): megalopae, small age 1 crabs, large age 1 crabs, and adults (see Miller 2001 for CW). In this model, individuals transition between stages across 2 seasons annually, summer and winter (Fig. 2), according to the equation:

$$\begin{bmatrix} N_1(t+1) \\ N_2(t+1) \\ N_3(t+1) \\ N_4(t+1) \end{bmatrix} = \mathbf{A}_{\text{summer}} \times \mathbf{A}_{\text{winter}} \times \begin{bmatrix} N_1(t) \\ N_2(t) \\ N_3(t) \\ N_4(t) \end{bmatrix} \quad (1)$$

where $N_i(t)$ for $i = 1, \ldots, 4$ is the number of megalopae, small age 1 crabs, large age 1 crabs, and adults, respectively, in year $t$. The annual time step begins with the winter season (December to May) and ends at the conclusion of the summer season (June to November). $\mathbf{A}_{\text{summer}}$ and $\mathbf{A}_{\text{winter}}$ are the transitions in the winter and summer, represented by the following matrices:

$$\mathbf{A}_{\text{winter}} = \begin{bmatrix} 0 & 0 & aw_{13} & aw_{14} \\ aw_{21} & 0 & 0 & 0 \\ aw_{31} & 0 & 0 & 0 \\ 0 & aw_{42} & aw_{43} & aw_{44} \end{bmatrix}$$

$$\mathbf{A}_{\text{summer}} = \begin{bmatrix} as_{11} & 0 & 0 & 0 \\ 0 & as_{22} & 0 & 0 \\ 0 & as_{32} & as_{33} & 0 \\ 0 & 0 & 0 & as_{44} \end{bmatrix} \quad (2)$$

where $aw_{ij}$, $as_{ij}$ are the winter and summer transition rates, respectively, from stage $j$ to stage $i$.

All parameters were either derived from functions of 2 fundamental parameters, number of female offspring ($B$) and natural mortality ($M$) (Miller 2001 and Table 1), or based on direct observational data (Hovel & Lipcius 2002; Table 1, Fig. 3). To estimate the annual number of female offspring ($B$), we assumed a 50:50 sex ratio and

Table 1. Definition and estimated value of blue crab model parameters (modified from Miller 2001). Estimated values are either based on Hovel & Lipcius (2002) or calculated as functions of the fundamental parameters $M$ and $B$ as indicated below. Values are means ± 1 SD (parentheses) or range (brackets). NA: not applicable

| Symbol | Parameter | Value |
|---|---|---|
| $M/2$ | Seasonal natural mortality | 0.274 (0.137) |
| $B$ | Maternity | $1.6 \times 10^6$ [$7.5 \times 10^5$, $8.0 \times 10^6$] |
| $as_{11}$ | Zoea/megalopae survival | $1.2 \times 10^{-5}$ ($6 \times 10^{-6}$) |
| $as_{22}$ [a] | Summer megalopae to overwintering juvenile transition rate | Dependent on habitat fragmentation (see Fig. 3) |
| $as_{32}$ [a] | Summer small age 1 to overwintering large age 1 transition rate | Dependent on habitat fragmentation type (see Fig. 3) |
| $as_{33}$ | $e^{-M/2}$ | 0.760 (0.094) |
| $as_{44}$ | $e^{-M/2}$ | 0.760 (0.094) |
| $aw_{13}$ | $0.66 \times Be^{-M/2}$ | 802909 (1000000) |
| $aw_{14}$ | $Be^{-M/2}$ | 1216528 (1414214) |
| $aw_{21}$ [a] | Overwintering juvenile to summer small age 1 transition rate | Dependent on habitat fragmentation (see Fig. 3) |
| $aw_{31}$ [a] | Overwintering juvenile to summer large age 1 transition rate | Dependent on habitat fragmentation (see Fig. 3) |
| $aw_{42}$ | $e^{-M/2}$ | 0.760 (0.094) |
| $aw_{43}$ | $e^{-M/2}$ | 0.760 (0.094) |
| $aw_{44}$ | $e^{-M/2}$ | 0.760 (0.094) |
| $K_{CS}$ [b] | Adult carrying capacity in continuous patch (across 30000 $m^2$) | 27530 |
| $K_{LP}$ | Adult carrying capacity in habitat with large isolated patches (across 30000 $m^2$) | 4730 |
| $K_{SP}$ | Adult carrying capacity, per patch, in small close patches (across 30000 $m^2$) | 19880 |
| $K_{VSP}$ | Adult carrying capacity, per patch, in very small isolated patches (across 30000 $m^2$) | 5100 |
| $S_{CS}$, $D_{CS}$ | Average size ($m^2$) of individual patches & average distance (m) between patches for continuous patch | 30000; NA |
| $S_{LP}$, $D_{LP}$ | Average size ($m^2$) of individual patches & average distance (m) between patches for large isolated patches | 3000; 30 |
| $S_{SP}$, $D_{SP}$ | Average size ($m^2$) of individual patches & average distance (m) between patches for small close patches | 8; <1 |
| $S_{VSP}$, $D_{VSP}$ | Average size ($m^2$) of individual patches & average distance (m) between patches for very small isolated patches | 0.25; 5 |

[a]A perturbation of 10% in $as_{21}$, $as_{31}$, $as_{22}$, and $as_{32}$ simultaneously resulted in a perturbation of 18% in median population threshold
[b]A perturbation of 10% in $K_{CS}$ alone resulted in a perturbation of 12% in median population threshold

halved the number of offspring for an average size adult female blue crab (3.2 million; Prager et al. 1990) to yield 1.6 million female offspring per average size female adult per year. Since estimates of the standard deviation were unavailable, the published range of values for number of offspring was used to establish standard deviations for parameters expressed as functions of $B$ (SERC 2006; Table 1). Since the annual census (in the model) is taken just before the birth pulse, it is necessary to include a mortality factor for offspring from birth to the census. We therefore multiplied the average value of $B$ by a mortality factor to convert maternity into fecundity (Table 1). Fecundity of large age 1 crabs is reported as ~66% of adult fecundity (Miller 2001). Due to the considerable uncertainty in the birth rate, we performed a sensitivity analysis on this parameter to determine the impact of changes in this parameter on model output (see 'Materials and methods — Sensitivity analysis' below).

Juvenile and adult survival rates are functions of annual natural mortality, which is based on maximum life expectancy of individuals. The Chesapeake Bay blue crab maximum age ($t_{max}$) is postulated to be 8 yr (Rugolo et al. 1998), and this was used to predict a natural mortality rate calculated as $\ln(M) = 1.44 - 0.982 \times \ln(t_{max})$ (Hewitt & Hoenig 2005) resulting in $M$ = 0.548. Natural mortality is represented in the seasonal submatrices; therefore, the estimated rate for a 6 mo period is 0.274 (= $M/2$). The uncertainty and variability is represented by a lognormal probability distribution for $M$ with a mean of 0.274 and a conservative 50% coefficient of variation.

Two population-level factors varied between each of the seascapes: seasonal survival rates of small age 1 crabs, and number of subadult and adult crabs for each seagrass habitat seascape. In the summer and winter seasons of 1998, Hovel & Lipcius (2002) used tethering experiments to assess relative differences in survival rates of small age 1 blue crabs across 4 seagrass fragmentation levels in Chesapeake Bay. These average survival rates of juveniles for each seascape (Fig. 3) were then increased by 10% to partially account for a relative effect of tethering (Pile et al. 1996). These were then partitioned into transition rates to summering small age 1 ($aw_{21}$) and summering large age 1 crabs ($aw_{31}$) for overwintering juveniles, and overwintering small age 1 ($aw_{22}$) and overwintering large age 1

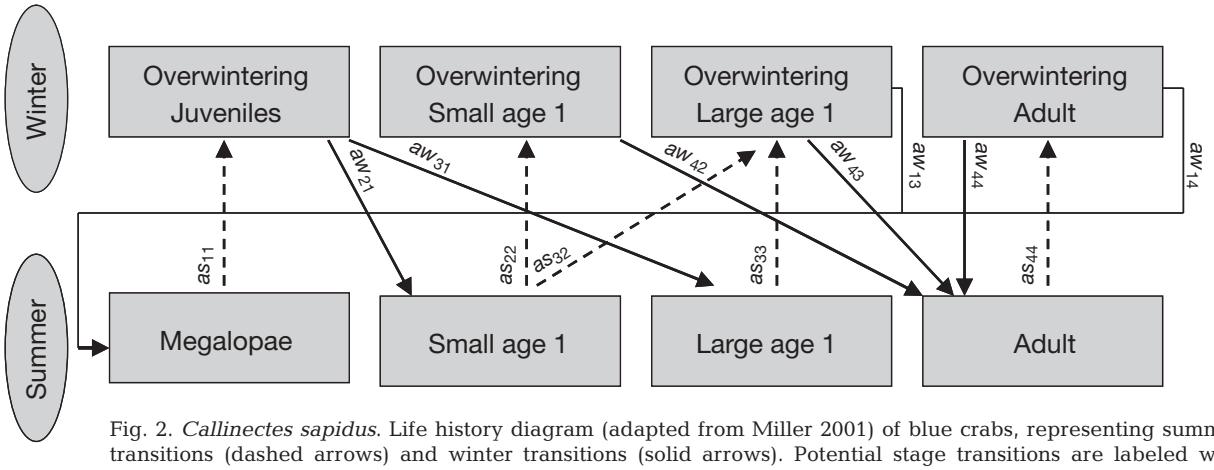


Fig. 2. *Callinectes sapidus*. Life history diagram (adapted from Miller 2001) of blue crabs, representing summer transitions (dashed arrows) and winter transitions (solid arrows). Potential stage transitions are labeled with transition probabilities (see Table 1 for definitions)

crabs ($aw_{32}$) for summering juveniles, at a ratio of 85:15 (based on Rothschild et al. 1988). Due to uncertainty and unknown temporal variability in these estimates, a lognormal distribution with a coefficient of variation of 50% was used for this transition probability. This level of variability was later perturbed in a sensitivity analysis to ascertain its importance in overall management rankings.

Of the total number of eggs produced and released by blue crabs, larval survival through the zoeal and megalopal stage is low, primarily because of predation and variable resource availability in the pelagic environment. The mean survival rate through this initial stage of the blue crab life cycle was assumed to be ($1.2 \times 10^{-5}$) to ensure a positive deterministic intrinsic growth rate for all seascapes. Again, a 50% coefficient of variation with a lognormal distribution was assumed because of the inherent variability and uncertainty. For parameters calculated as functions of the independent variables $M$ and $B$ in Table 1, means and standard deviations were estimated from the distributions resulting from stratified sampling, and subsequent convolution, of the respective functions of $M$ and $B$. Lognormal distributions were then assumed for these parameters with the estimated means and standard deviations.

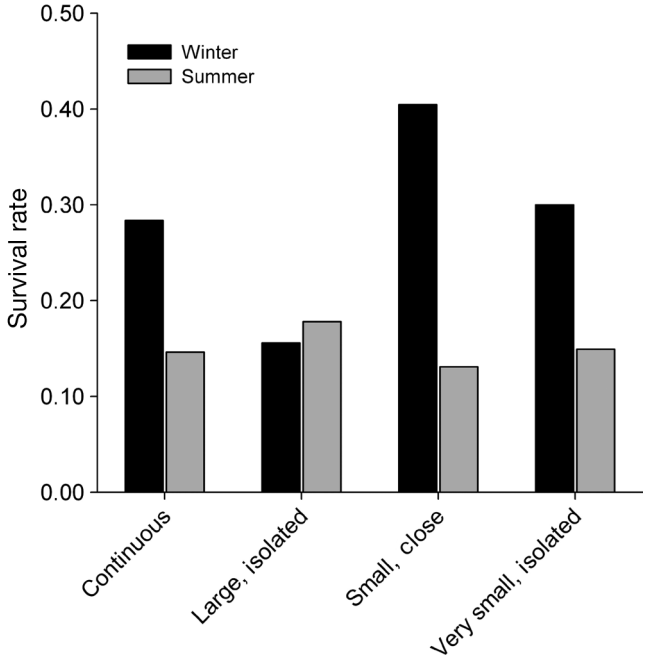


Fig. 3. *Callinectes sapidus*. Winter and summer small age 1 blue crab survival rates per habitat fragmentation type (Hovel & Lipcius 2002, K. A. Hovel unpubl. data)

**Density dependence.** Hovel & Lipcius (2001) observed that the number of blue crabs 50 mm CW or larger depended strongly on the seascape and amount of habitat present. We incorporated this into the model by assuming the Beverton-Holt function for blue crabs 50 mm CW or larger (i.e. crabs in the large age 1 and adult stages). The Beverton-Holt function models density dependence (i.e. a decline in population growth rate as population size increases) as a function of carrying capacity and was originally developed to include contest competition for fisheries models (Beverton & Holt 1957). In the absence of information about the smaller stages, carrying capacities were not applied to megalopae, juvenile, or small age 1 crabs. Carrying capacities for each seascape were set based on the average number of blue crabs of this size found during trawl surveys in each seascape (Hovel & Lipcius 2001) and by restricting crabs to seagrass habitat in the model. These were then scaled to correspond to the dimensions of the total simulated spatial area considered for each seascape (30 000 $m^2$ for each type; Table 1). The trawling surveys showed that as the size of seagrass patches increased so did the numbers of subadult and adult blue crabs present across patchy areas. While subadult and adult blue crabs are found in a much larger array of habitats, including unvege-

tated areas, the trawling data collected by Hovel & Lipcius (2001) indicate that some dependence of adult and subadult stages on the amount of nursery habitat is plausible. While the carrying capacities applied here underestimate the actual carrying capacity possible, they provide an empirically-based consistent lower bound that can be used across all scenarios for ranking and comparing outcomes of management and seascape. The seascape characteristics are defined by the carrying capacity of each seascape and the juvenile survival rates (Figs. 1 & 3, Table 1). In this model, individuals do not occupy coordinates in space; rather, the population is aggregated and its dynamics within a seascape are governed by the demographic and habitat parameters for that particular scenario. In order to restrict focus to population dynamics in the seascape without the potentially confounding effects of alternative spatial structures, each seascape is modeled separately and in isolation of the other seascapes.

**Management strategies.** To assess the impacts of harvesting in various habitats, we applied the same fishing pressure to populations in each of the seascapes. A constant adult harvest rate (i.e. a constant proportion of the adult stock), which is currently believed to be optimal for maximum sustainable yield, was applied to each model at the end of each time step. Current management of the Chesapeake Bay blue crab stock recommends a fishing mortality rate threshold of 0.7, which preserves a minimum of 20% of the spawning potential of an unfished stock (CBSAC 2005, Miller et al. 2005). This rate corresponds to ~50% annual removal. Adult harvest rates of 30, 20, and 10% were also tested to examine the effect of a range of reduced fishing mortality rates on population persistence. For all scenarios, harvest or seeding/stocking of juveniles started in Year 25 of the model simulations to allow populations to initialize and average population dynamics to stabilize before removal of individuals.

To determine how the interaction of introductions, harvesting, and habitat fragmentation impact blue crab population dynamics, we simulated annual introductions of 100, 200, 400, and 800 small age 1 blue crabs from Years 25 to 50 for each seascape in conjunction with constant harvest rates of 20, 30, and 50%.

**Sensitivity analysis.** We performed a sensitivity analysis on the population model in the absence of management actions. The analysis was performed only for the continuous seagrass seascape, but the results apply across all seascapes because only carrying capacities and small age 1 blue crab survival rates varied among seascapes. Each of the parameters in the model, including coefficients of variation, and the fundamental parameters $M$ and $B$, were perturbed by ±10% (see Table 1 for the full list of parameters, all of which were individually perturbed in separate sensitivity analyses). Sensitivity was defined as the relative difference in median population threshold before and after the perturbation. The model was deemed sensitive to a parameter if the sensitivity was greater than the initial extent of the perturbation (10%). The sensitivity of model results to the type of density dependence was tested by changing density dependence to a Ricker function (i.e. scramble competition) and exponential growth with a ceiling. Selected combinations of parameters were also perturbed simultaneously to measure the effect of compounding uncertainty in multiple parameters.

**Simulations.** The initial abundance for model simulations for each seascape was 35 000 total individuals across all stages. Our aim was to compare the effects of fragmentation and habitat loss on population dynamics without the confounding effects of differences in initial population size. We therefore assumed equal total initial population size across all seascapes. The total abundance was then distributed across stages according to the stable stage distribution for the relevant seascape. Stochasticity was incorporated through Monte Carlo simulations for 1000 replications over a 50 yr period to account for natural variation in both the environment and the demographics of the population.

The median of the final population sizes (i.e. population abundance in Year 50) across the 50 yr trajectories (n = 1000) was used to rank population persistence across each harvest, introduction, and seascape scenario tested (Burgman et al. 1993, Akçakaya et al. 1999). Hereafter this metric is referred to as the median population threshold; it is a measure of the central tendency of the population abundance after the model is run for 50 annual time steps.

## RESULTS

### Interactive effects of seascape and harvest rate on blue crab populations

In the absence of harvest, the largest median population threshold was supported in continuous seagrass (Fig. 4). Although a higher harvest rate reduced the median population threshold across all seascapes, the optimal seascape configuration for blue crabs shifted from continuous seagrass to patchy seagrass as a higher fraction of the population was harvested. Continuous seagrass still supported the largest median population threshold with harvest rates set at 10%, but under harvest rates of 20% and greater, there was a shift in optimal habitat from continuous seagrass to small close patches of seagrass. Population declines due to increasing harvest were steepest in continuous

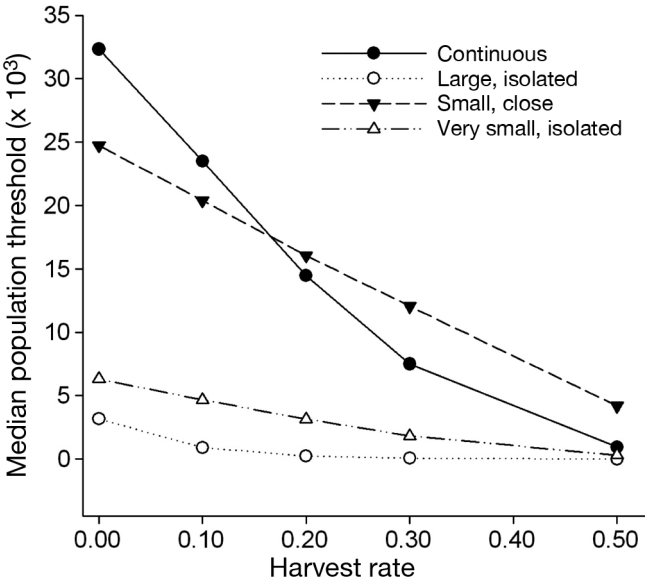


Fig. 4. *Callinectes sapidus.* Median population threshold at the end of 50 yr under a range of harvest rates across the 4 seagrass fragmentation types

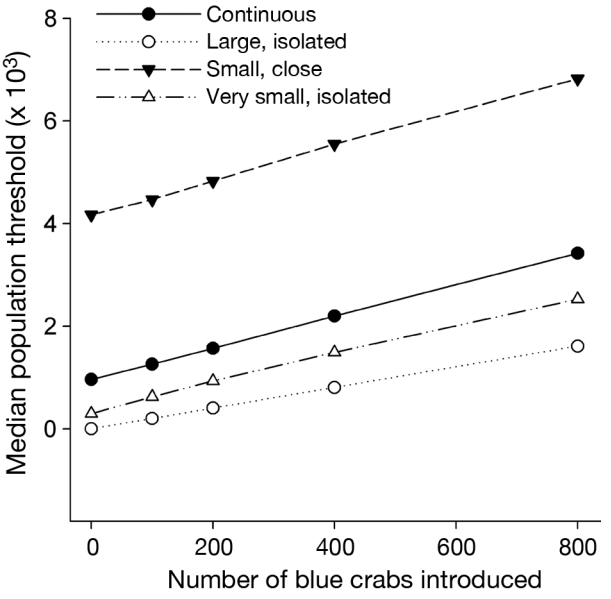


Fig. 5. *Callinectes sapidus.* Median population threshold for small age 1 blue crabs introduced annually within each of the seagrass fragmentation types under a 50% annual harvest rate

seagrass, followed by seascapes composed of small, close seagrass patches. While the population in large isolated patches had the least dramatic decline with increased harvest rates, it was nearly extirpated with a harvest rate of 50%.

### Effects of stock enhancement on blue crab populations

Under a 50% harvest rate, introductions caused the greatest absolute population increase in small close patches, whereas the greatest relative increase occurred in large isolated patches (Fig. 5). This trend reversed when the lowest absolute and relative increases were considered: large isolated patches displayed the lowest absolute population increase, whereas the lowest relative increase occurred in small close patches.

A general distinction emerged between the relative effects of harvest reduction versus introductions for large, isolated patches and continuous seagrass (Fig. 6). The smallest relative increase in median population threshold with introductions occurred in a seascape of continuous seagrass (a similar pattern emerged for the small close patches; results not shown). In this seascape, reductions in harvest rate from 50 to 30% and 20% had greater impacts on population persistence than blue crab introductions (Fig. 5). The maximum number of introductions tested here (i.e. 800 $yr^{-1}$) never increased the median population threshold more than when reducing the harvest rate alone. Furthermore, the similar slopes of the response graphs for each harvest level indicate that the effect of introductions on median population threshold is almost identical (Fig. 6).

In a seascape of large, isolated patches of seagrass, the relative effects of introductions and reduced harvest were reversed (a similar pattern emerged for the very small isolated patches; results not shown). The relative increase in median population threshold with introductions outweighed that of harvest reduction. Hence, the benefit of supplementing populations in a seascape of isolated seagrass patches was greater than the benefit of reducing the harvest rate alone. The median population threshold with 400 introductions under a 50% harvest rate in large, isolated patches of seagrass was greater than that with no introductions and a harvest rate reduced to 20% (Fig. 6).

### Sensitivity analysis

The greatest change in model output occurred with a simultaneous increase in the summer and winter survival rates of juvenile blue crabs (a relative change of 18% in model output with 10% changes in both parameters). This indicates that if these parameters are both in error then model results may change by a disproportionate amount to the extent of the error. It also suggests that if both seasonal survival rates of this blue crab stage were to increase, there may be a significant impact on the population growth. Adjustments to the carrying capacity and a change from contest density dependence to exponential growth with a ceiling resulted in relative changes in model output of up to

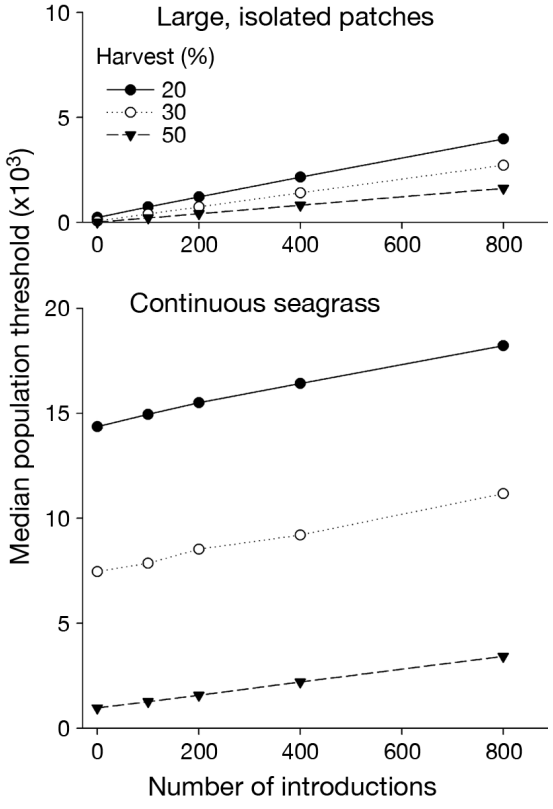


Fig. 6. *Callinectes sapidus.* Median population threshold under a range of harvest rates (20, 30, 50%) and number of small age 1 blue crabs introduced (0, 100, 200, 400, 800) within seascapes of connected seagrass (based on the continuous seagrass habitat) and a seascape of isolated patches of seagrass (based on large isolated patches)

12%. Perturbations of 10% to all other parameters, including coefficients of variation for all parameters, resulted in relative changes to model output of less than 10%, indicating that the model results are fairly insensitive to parameter errors of this magnitude.

## DISCUSSION

Many marine fishery species use shallow coastal habitats such as seagrasses, oyster reefs, and salt marshes as refuge and foraging areas, all of which commonly are degraded and fragmented. Habitat loss, habitat fragmentation, and overfishing therefore may synergistically threaten a variety of fishery species such as blue crabs that have high economic, ecological, and cultural significance (Paolisso 2002). Our model suggests that the influence of seagrass seascape structure on blue crab persistence varies with harvest rate. In the absence of harvest, continuous seagrass seascapes are optimal habitat for blue crab population persistence, because even though high predator abundance reduces juvenile blue crab survival, this habitat supports the largest number of crabs. Seascapes composed of small seagrass patches that are isolated by short distances also promoted population persistence in the absence of harvest. Adults may be less likely to congregate in these patches of seagrass due to fewer resources, or more visibility to predators, and young crabs can temporarily leave the safety of a patch to move the short distances across unvegetated sediment to nearby patches without a significant increase in mortality (Moksnes et al. 1997). Both of these habitat configurations accommodated higher abundances than the 2 isolated patch configurations.

When harvest rates greater than 10% were implemented, population persistence was maximized in seascapes composed of small close patches of seagrass rather than continuous seagrass. Even when 50% of the adult population is harvested annually, the population abundance increased more quickly in small close patches than in the other seascapes due to high survival rates for small age 1 crabs. Thus it is possible that this survival rate is sufficient to sustain the population under a 50% harvest rate.

These results have implications for the fishery. At the conclusion of the 50 yr time period, the total number of crabs harvested was greatest in small close patches of seagrass even though continuous seagrass can accommodate a larger number of adult crabs. The amount harvested decreased annually in the continuous habitat because the population could not recover sufficiently before the next harvest event. The larger average growth rate allows the population in small close patches to recover more quickly after a harvest. Therefore, under a 50% harvest rate, the amount harvested annually in a habitat of small close patches remains fairly constant.

There was a significant increase in the median population threshold when harvest rates were reduced for connected patches of seagrass. A reduction in the harvest rate in connected habitats resulted in a much higher number of adults than for isolated patches. Continuous seagrass promoted the highest abundance for a harvest rate of 10% because so few adults are removed that the population can quickly increase to pre-harvest numbers. However, it is unlikely that this low harvest limit would be implemented (Paolisso 2002, Rosenberg 2003). Reducing the harvest rate below 50% for populations in isolated patches does not result in a large increase in median population threshold simply because the population begins at a small size when harvesting begins. It is clear that successful management of the population by solely reducing the harvest rate depends on the habitat conditions and the number of adult crabs present. The interesting issue here is that the seascapes with the highest proportional

cover of seagrass (and therefore the highest carrying capacities) are not necessarily optimal for crab survival. Understanding the apparent trade-off between patchiness and juvenile survival rate appears crucial in managing this fishery across a heterogeneous seascape. Further research to determine the effectiveness of increasing small age 1 crab survival could also promote recovery after harvest.

The extent to which introductions improve population persistence also depends on seagrass configuration. Large isolated patches with 800 crabs introduced annually gave a median population threshold equal to that of 400 crabs introduced in very small isolated patches and 200 crabs introduced in continuous habitat. The relative change in populations due to crab introductions was greater in patch configurations with lower abundances. Under a 50% harvest rate in conjunction with introductions, small close patches remained the best habitat for population persistence because of the larger population abundances and the faster growth rate resulting in relatively quick recovery from harvest, irrespective of the number of crab introductions. The stock of individuals available for introductions is usually limited. Therefore, efficient management may require different levels of introductions for different seascapes. Populations in large isolated patches benefit the most from introductions because the relative increase in abundance is greatest in these patches. If absolute increase is of most interest, then populations in small close patches benefit the most from introductions. However, populations in small close patches start out relatively high in the absence of introductions, so maximizing relative increases may be more appropriate for management.

The way in which seascape structure and harvest interactively affect different life history stages is critical to consider for effective management of fishery species (Botsford et al. 1997, Huxel & Hastings 1999) and rather than relying on one management strategy to improve population persistence, a combination of approaches may be most effective. For example, in our model, the benefits of reducing fishing pressure outweigh population increases from crab introductions in seascapes with high connectivity (i.e. continuous and small close patches of seagrass). A reduction in harvest allows the population to increase to larger numbers than those in isolated patches. Conversely, introducing a large number of individuals to large or very small isolated patches without reducing harvesting pressure is usually more beneficial than reducing harvest alone. This is because populations in isolated fragments have slow population growth and hence introducing individuals results in faster (albeit artificial) population growth than relying on background population growth alone. In small isolated seagrass patches, introducing 800 individuals and harvesting 50% of the adult population results in the same median population threshold as for a 30% harvest rate and 200 crab introductions. The former alternative allows for an almost double harvest rate but it requires great effort to rear and introduce small age 1 crabs annually (Zmora et al. 2005).

Our model incorporates winter and summer survival rates of small age 1 crabs, which were experimentally estimated in different seascapes that existed within a single sub-estuary within Chesapeake Bay. The results of the model therefore address how harvest, habitat loss and fragmentation, and introductions affect population persistence at a local scale. At this scale, the combined effects of harvesting and habitat loss and fragmentation, in addition to the potential of introductions to promote persistence, can be evaluated in isolation of additional and potentially confounding factors that may be present elsewhere in the Bay. To describe the population dynamics of the entire population throughout the bay more accurately, comparable research should be extended to other regions. Additionally, environmental factors not included in our model, such as salinity, water temperature, and depth, may influence blue crab survival (Jensen et al. 2005) and could be incorporated into future models. Future models also may consider a patch-mosaic approach to simulating blue crab habitat, rather than the patch-matrix approach we used in our study. The patch-mosaic approach allows for more realism by incorporating a variety of habitat types into seascapes, but requires data on blue crab densities and density-dependent survival within multiple habitat types, as well as rates of movement among habitat types, much of which is not available at present.

One ecological component we did not incorporate into our model is dispersal of individuals across seascapes with combinations of different configurations of fragmentation and habitat loss. Furthermore, models for each seascape assumed that individuals move between seagrass patches without increased mortality, although patch isolation may reduce blue crab movement and survival (Micheli & Peterson 1999). Adults are known to travel large distances, particularly females that may travel the entire length of Chesapeake Bay to release eggs at the bay mouth (Turner et al. 2003), and may move between patches due to competition and/or lack of resources. Density-dependent dispersal has been documented in newly settled blue crabs (Reyns & Eggleston 2004), but studies quantifying average dispersal distances are lacking. Incorporating stage-dependent dispersal between habitat patches into a metapopulation model could help capture the dynamics over larger spatial scales and possibly identify source and sink populations.

Efforts to restore seagrass beds are essential for overall ecosystem health, but in order to promote persistence of populations that rely on seagrass as nursery habitat, additional factors, aside from an increase in total acreage, may be important. Habitat configuration is a key component to survival during various life history stages of many invertebrate species. Our model shows that a large area of continuous seagrass habitat is suboptimal for population persistence in the presence of harvest when juvenile survival rates are affected by habitat fragmentation and loss in nonlinear ways. An efficient seagrass restoration strategy should not only increase the amount of vegetation but should also incorporate favorable habitat configurations and structure (Beck et al. 2001). Planting seagrass to reduce the isolation of existing patches will likely promote the survival of younger or smaller life stages and could potentially increase the existing habitat for juveniles, both of which may help increase future population size. Restoration projects therefore should not just focus on the total amount of seagrass restored, but also consider the spatial layout of restoration, and harvest should be considered in the context of the spatial arrangement of seagrass beds.

Human population growth leads to increased environmental degradation due, in part, to an accelerated depletion of resources and unknown synergistic effects of multiple threats (Harte 1996). The harvest of economically valuable species is often targeted as the cause of decline. While this threat can be significant, harvesting can mask the consequences of additional factors because of potential synergies (Ewers & Didham 2005). The simultaneous evaluation of harvesting, habitat loss, and habitat fragmentation describes how population persistence can be dependent upon various combinations of threats and how management must recognize and address population level responses to these threats.

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# Patterns of scale-dependency and the influence of map resolution on the seascape ecology of reef fish

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ABSTRACT: Detection and perception of ecological relationships between biota and their surrounding habitats is sensitive to analysis scale and resolution of habitat data. We measured strength of univariate linear correlations between reef fish and seascape variables at multiple spatial scales (25 to 800 m). Correlation strength was used to identify the scale that best associates fish to their surrounding habitat. To evaluate the influence of map resolution, seascape variables were calculated based on 4 separate benthic maps produced using 2 levels of spatial and thematic resolution, respectively. Individual seascape variables explained only 25% of the variability in fish distributions. Length of reef edge was correlated with more aspects of the fish assemblage than other features. Area of seagrass and bare sand correlated with distribution of many fish, not just obligate users. No fish variables correlated with habitat diversity. Individual fish species achieved a wider range of correlations than mobility guilds or the entire fish assemblage. Scales of peak correlation were the same for juveniles and adults in a majority of comparisons. Highly mobile species exhibited broader scales of peak correlation than either resident or moderately mobile fish. Use of different input maps changed perception of the strength and even the scale of peak correlations for many comparisons involving hard bottom edge length and area of sand, whereas results were consistent regardless of map type for comparisons involving area of seagrass and habitat diversity.

KEY WORDS: Landscape ecology · Scale · Coral reef · Home range · Habitat



## INTRODUCTION

Recent studies have shown that the distribution and abundance of reef fish can be influenced by seascape factors such as the areas of adjacent seagrass, soft bottom, and hard bottom in the vicinity (Kendall et al. 2004a, Kendall 2005, Dorenbosch et al. 2006, Grober-Dunsmore et al. 2007, Pittman et al. 2007, Tuya et al. 2010). Many of these studies relied on particular benthic maps as a source of independent variables with which to establish relationships between fish and their surrounding habitat. Benthic maps are, however, abstract representations of actual seafloor features and have particular spatial and thematic characteristics that are profoundly affected by the processes and source data used to produce them (Turner et al. 1989, Benson & MacKenzie 1995, Saura 2002, Andréfouët et al. 2003, Kendall & Miller 2008, Prada et al. 2008). Spatial characteristics include the number of patches, their size, shape, and edge length. Thematic characteristics include the number and types of categories used to describe seafloor features. For coral reef ecosystems, Andréfouët et al. (2003) found that map-based measurements of coral atolls differed by as much as 28% depending on the spatial resolution of satellite data. Kendall & Miller (2008) found that increasing thematic resolution greatly increased the number, diversity, and total edge length of map polygons, whereas changing the spatial resolution resulted in disproportionate changes in the area, perimeter, and other values

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among feature types. Given the influence of spatial and thematic resolution on the quantification of seascapes, we hypothesized that map differences could influence the sensitivity of seascape ecological studies as well.

Map resolution may affect the detection and measurement of seascape influences on fish distribution in several ways. The amount of mapped habitat deemed essential to a particular species can be altered. Small or rare patches of habitat can be subsumed into larger features as map resolution is coarsened. Many species use edges or ecotones between habitat patches (Shulman 1985, Sweatman & Robertson 1994, Dorenbosch et al. 2005, Pittman et al. 2007, Valentine et al. 2007, Vanderklift et al. 2007), and such boundaries can be greatly simplified or even removed depending on map characteristics (Kendall & Miller 2008).

Seascape composition can affect fish ecology at several levels of biological organization. At the broadest level, species diversity, richness, and total abundance of fish have been partly explained by seascape variables (Kendall 2005, Grober-Dunsmore et al. 2007, Pittman et al. 2007). At lower levels of organization defined according to trophic roles or mobility and therefore with similar habitat or space requirements, fish guilds may have greater correlation with seascape elements when considered separately from the rest of the fish assemblage (Grober-Dunsmore et al. 2007). Individual species would be expected to have even higher correlation with seascape features without the added variability from multiple species of a guild that utilize slightly different niches or habitats. Highest fish–seascape correlations are expected for individual life stages of species considered separately. All such fish utilize the same discrete spatial scale and habitat types (Kendall et al. 2003, Grober-Dunsmore et al. 2007), and correlations would not be reduced by the added variability associated with the different scales of seascape utilization and habitat preferences among life stages.

The strength of fish–seascape correlations are likely scale-dependent and based on fish size, mobility, taxonomy, life stage, and habitat requirements (Kramer & Chapman 1999, Pittman et al. 2004, Kendall 2005, Grober-Dunsmore et al. 2007). Body size in some reef fish has been positively correlated to home range size (Kramer & Chapman 1999, Overholtzer & Motta 1999). Similarly, juveniles of a given species, by virtue of their relatively smaller size, are expected to interact with adjacent seascape features at shorter distances than adults (Kendall et al. 2003, Grober-Dunsmore et al. 2007). The abundance of those species that utilize a single rock, coral head, or burrow for most of their life history, termed resident species, would be expected to exhibit correlations only with habitat measures for their immediate vicinity. A good example are fish in the genus *Stegastes*, which defend territories of 1 to 5 $m^2$ for food and breeding purposes (Itzkowitz 1977, Luckhurst & Luckhurst 1978). Those species that range more widely across larger or multiple habitat patches, termed mobile species, would not be expected to be correlated with just the habitats in the immediate vicinity of a focal patch and instead would have correlations with seascape features at distances of 10s to 100s of meters away. Examples include haemulids (Tulevech & Recksiek 1994, Burke 1995), acanthurids (Morgan & Kramer 2004), and scarids (Chapman & Kramer 2000, Mumby & Wabnitz 2002). Finally, those species that range widely across the seascape, termed transient species, would likely have correlations with seascape features at even greater distances. Such species include many fish in the families Carangidae and Lutjanidae (Chapman & Kramer 2000).

The scale of fish–seascape interactions can be identified by evaluating a local fish assemblage in relation to the surrounding mosaic of habitat patches (Irlandi & Crawford 1997, Pittman et al. 2004, Kendall 2005, Grober-Dunsmore et al. 2007, Vanderklift et al. 2007). The spatial extent of elements to include in such analysis is critical, and analyses should seek to systematically vary the spatial scale and distances over which fish and seascape associations are measured (Addicott et al. 1987, Wiens 1989, Riitters et al. 1997, Sale 1998, Kendall 2005). If the spatial extent used is too small, only weak fish–seascape correlations will be found, because seascape elements used by the taxa considered are not included in the analysis. Conversely, if the analysis is conducted at a spatial extent that is too broad, weak correlations will again be found, but this time because too many seascape elements not used by the taxa under consideration are being included. Correlations will be maximal at an intermediate extent that matches the scale of habitat use. Once quantified across a range of scales, correlation strength can be examined to find the scale that best correlates fish with their surrounding habitat. Use of this 'best' scale approach to empirically define the ecological scale has recently emerged in a handful of terrestrial (Pearson 1993, Karl et al. 2000, Ricketts et al. 2001, Steffan-Dewenter 2003, Holland et al. 2004, 2005) and marine studies (Kendall 2005, Grober-Dunsmore et al. 2007).

Both the scale and strength of fish–seascape correlations can be influenced by map resolution. If only the perception of correlation strength is altered, it is not a serious problem if the objective is merely to identify the scale of peak correlation. However, it is of concern if accurate measurement of correlation intensity is the goal. Of greater concern is when map type alters both correlation scale and magnitude, resulting in a complete misperception of a fish–seascape association.

The real seascape that fish inhabit and are influenced by is depicted in greatest detail by maps with very high spatial and thematic resolution. Thus, high-resolution maps are expected to yield the highest fish–seascape correlations when an association exists and also the lowest correlations when no association is present. Highly detailed maps are, however, costly and time-consuming to produce. Maps generalized into coarser thematic and spatial properties are cheaper and faster to produce, but these changes often have unknown consequences on the perception of fish–seascape correlations.

In the present study we investigated several interrelated aspects of ecological scale by simultaneously varying (1) the size of habitat measurements used as independent variables, (2) both the spatial and thematic resolution of map data, and (3) the life stage, mobility guild, and fish assembly groups used as dependent variables. Our complementary hypotheses (1 to 5, below) seek to disentangle the effects of these issues in detecting and accurately perceiving fish–seascape relationships:

(1) Reef fish are significantly correlated with seascape variables (area of sand or seagrass, length of hard bottom or reef edge, and habitat diversity).

(2) Correlation strength will vary with the spatial scale of the analysis.

(3) Thematic and spatial resolution of maps will affect correlation strength and scale. Highest resolution maps will yield the highest correlations.

(4) Range in correlation strength will be highest for individual life stages of species followed by guilds, and lowest for whole community metrics.

(5) Resident fish species will have highest correlation with seascape variables at shorter distances than mobile, followed by transient species, and juveniles of a given species will have highest correlation with seascape variables at shorter distances than adults.

## MATERIALS AND METHODS

This study was based on the fish communities and seascape around Buck Island Reef National Monument (BIRNM), US Virgin Islands, which is comprised of seascape features typical of Caribbean coral reef ecosystems (Fig. 1). Dependent variables were based on fish surveys, and independent variables were based on 4 types of benthic maps.

**Fish survey data.** Underwater visual surveys were used to census fish on 588 sites on reefs and hard bottom within and around BIRNM between January 2002 and May 2006. Due to random placement, each site was surrounded by a unique combination of habitat elements. At each georeferenced site, a diver swam along a randomly selected compass heading for 15 min and recorded all fish within 5 cm size classes that were observed within a $25 \times 4$ m belt transect (100 $m^2$) to the lowest possible taxon.

A hierarchical approach was taken in selecting response variables to test hypotheses relating fish distribution at several organizational levels from whole community to particular life stages of individual species (Table 1, columns 1 & 2). Variables included total fish abundance and overall species richness; species richness and fish abundance within the mobility guilds of resident (R), mobile (M), and transient (T) (Grober-Dunsmore et al. 2007); and the abundance by life stage of 6 common reef fish species. The 6 species were chosen to include those with (1) representation from diverse family and trophic groups, (2) known life history and habitat preferences, and (3) relatively common occurrence in the study area across a range of seascape settings. Abundances of these species were also separated into juvenile and adult categories, respectively, for life stage-specific analysis.

**Mapping and quantifying seascape structure.** Four maps of the benthic habitat around BIRNM were produced using 2 levels of spatial and thematic resolution, respectively (Kendall & Miller 2008). Maps were created by visual interpretation of orthorectified aerial photographs (Kendall et al. 2001). A relatively large minimum mapping unit (MMU; size of the smallest feature to be mapped) of 4000 $m^2$ and a much smaller MMU of 100 $m^2$ were used. A hierarchical classification scheme was used to attribute maps at both spatial scales into 17 subcategories nested within 3 main categories in a scheme structurally similar to those used to produce reef ecosystem maps elsewhere (FMRI & NOAA 1998, Mumby & Harborne 1999, NOAA NCCOS 2004). Main categories were unconsolidated sediment, submerged vegetation, and hard bottom. Subcategories of unconsolidated sediment were sand and mud. Subcategories of submerged vegetation were seagrass and algae in varying degrees of patchiness. Subcategories of hard bottom were patch reefs, linear reefs, colonized pavement, bedrock, pavement with sand channels, spur and groove, and scattered coral/rock. Maps with 17 classes served as high thematic resolution maps. Subsequently, we dissolved the boundaries and aggregated the polygons of these high thematic resolution maps to the 3 thematic class level for use in the analyses as maps with low thematic resolution. This process resulted in 4 maps of BIRNM using the same approach but with different spatial and thematic characteristics (Fig. 2).

Four variables were selected to quantify seascape structure that were representative of broad classes of 'landscape pattern metrics' and suspected to play a role in reef fish community structure: (1) area of seagrass or

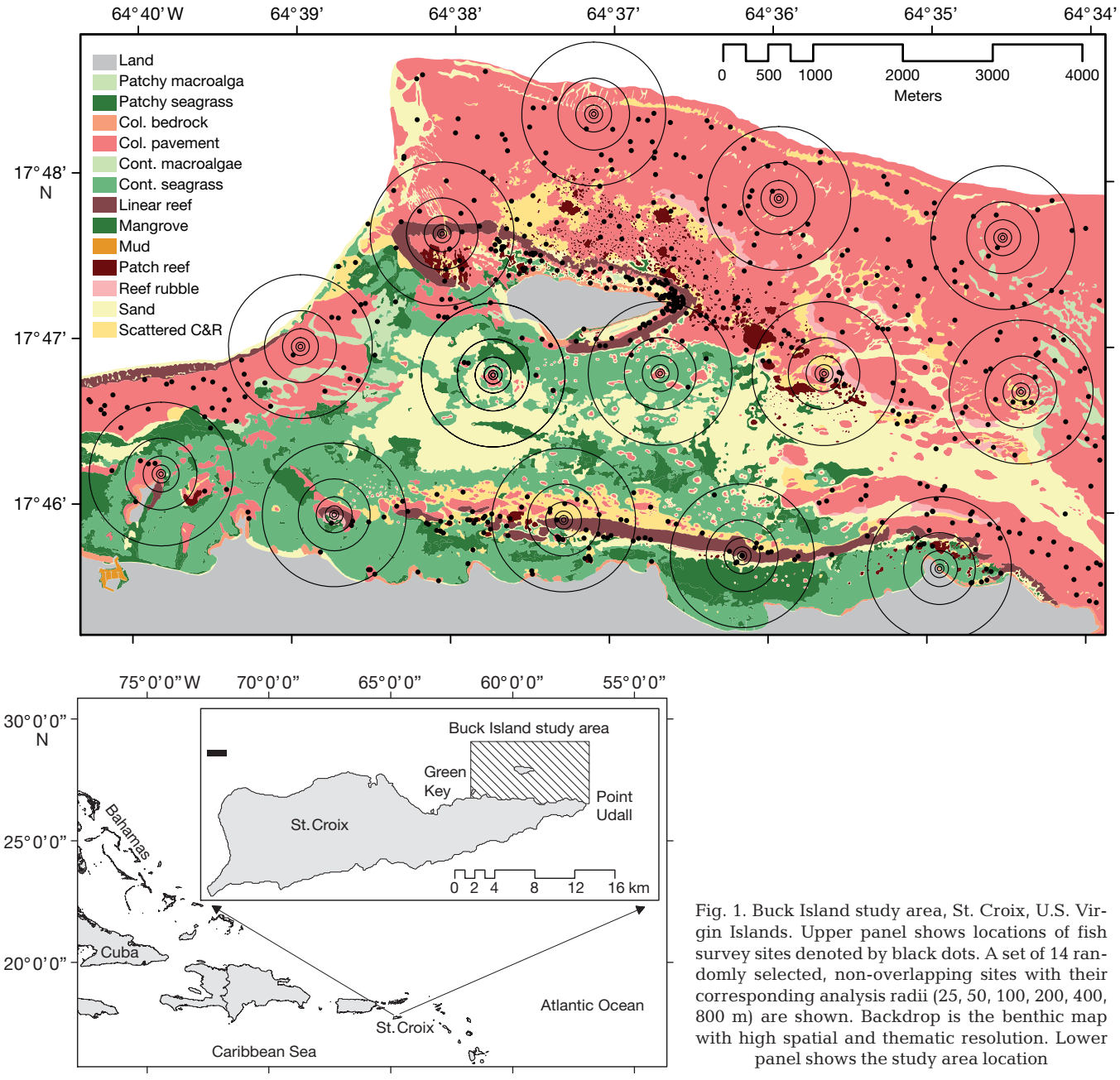


Fig. 1. Buck Island study area, St. Croix, U.S. Virgin Islands. Upper panel shows locations of fish survey sites denoted by black dots. A set of 14 randomly selected, non-overlapping sites with their corresponding analysis radii (25, 50, 100, 200, 400, 800 m) are shown. Backdrop is the benthic map with high spatial and thematic resolution. Lower panel shows the study area location

submerged aquatic vegetation (SAV), (2) length of hard bottom edge, (3) area of sand or unconsolidated sediment (map with high or low thematic resolution, respectively), and (4) habitat diversity (Shannon-Wiener Index). Area of seagrass around reefs is suspected to enhance abundance of lutjanids (snappers), haemulids (grunts), and other fish on reefs (Randall 1965, Ogden 1976, Kendall et al. 2003, Kendall 2005, Grober-Dunsmore et al. 2007). Reef edges have been implicated as a key ecotone shaping fish communities on reefs (Dorenbosch et al. 2005, Vanderklift et al. 2007), including piscivores (Shulman 1985, Sweatman & Robertson 1994, Valentine et al. 2007, Vanderklift et al. 2007), herbivores (Wernberg et al. 2006), and those species that use hard bottom as structural refuge but forage over soft bottom (Ogden 1976, Burke 1995). Sand and seagrass bottom provides settlement habitat for many reef fish species and may therefore eventually impact adult abundance on nearby reefs (Shulman & Ogden 1987, Shulman 1985, Parrish 1989). Diversity of habitat types may be positively correlated with the diversity of the fish community (Ward et al. 1999) and has been suggested as a surrogate for overall biodiversity in marine reserve selection (National Research Council 2001).

Table 1. Scale (m) of maximum fish–seascape correlation among all map types. SAV: submerged aquatic vegetation; (–) variable pairs with no correlations above |r| = 0.2 for any map type. Bottom rows summarize the changes in perception of fish–seascape correlation due to map type. [a] and [b] are defined in the bottom 2 rows and denote 2 types of altered perception. All 104 correlation plots are provided in the supplement at www.int-res.com/articles/suppl/m427p259_supp.pdf where numbers (Suppl. 1–Suppl. 4) and letters (Panels a–z) indicate seascape and fish variables, respectively (e.g. habitat diversity and fish abundance is Supplement 1, Panel a).

| Fish variables | Habitat diversity Suppl 1 | Seagrass/ SAV area Suppl 2 | Sand/sediment area Suppl 3 | Hard bottom edge length Suppl 4 | Panel |
|---|---|---|---|---|---|
| **Whole community** | | | | | |
| Fish abundance | – | – | – | – | a |
| Species richness | – | 800[a] | 800[bb] | 800[ab] | b |
| **Mobility guild** | | | | | |
| Resident fish abundance | – | – | 25[bb] | – | c |
| Resident species richness | – | 800[a] | – | 800 | d |
| Mobile fish abundance | – | – | – | – | e |
| Mobile species richness | – | – | – | 50[bbb] | f |
| Transient fish abundance | – | – | 800[bb] | – | g |
| Transient species richness | – | – | 800[bb] | – | h |
| **Species (abundance)** | | | | | |
| *Acanthurus coeruleus* | | | | | |
| Juvenile | – | – | – | 800[aaa] | i |
| Adult | – | – | – | 800[aab] | j |
| Total | – | – | – | 800[aaa] | k |
| *Cephalopholus fulvus* | | | | | |
| Juvenile | – | 800[a] | 25[bb] | 800[ab] | l |
| Adult | – | 800 | 100[bb] | 800[ab] | m |
| Total | – | 800 | 25[bb] | 800[ab] | n |
| *Haemulon flavolineatum* | | | | | |
| Juvenile | – | – | – | – | o |
| Adult | – | 800 | – | 50[abb] | p |
| Total | – | 800 | – | 50[abb] | q |
| *Ocyurus chrysurus* | | | | | |
| Juvenile | – | 800[bbb] | – | – | r |
| Adult | – | – | – | – | s |
| Total | – | 100[abb] | – | – | t |
| *Sparisoma viride* | | | | | |
| Juvenile | – | 800[a] | – | 800[aab] | u |
| Adult | – | 400[a] | – | 800[abb] | v |
| Total | – | – | – | 800[aa] | w |
| *Stegastes planifrons* | | | | | |
| Juvenile | – | 800[a] | – | 800[ab] | x |
| Adult | – | 800 | – | 800[a] | y |
| Total | – | 800[a] | – | 800[ab] | z |
| No. of comparisons with at least one map type with \|r\| > 0.2 | 0 | 14 | 7 | 17 | |
| No. of times one of the other 3 map types had a peak \|r\| at the same scale but a significantly lower value. [a]each occurrence | na | 8 | 0 | 22 | |
| No. of times one of the other 3 map types had a peak \|r\| at a different scale. [b]each occurrence | na | 5 | 14 | 17 | |

**Multiscale analysis.** The dominant scales at which components of the fish assemblage are correlated with their surrounding habitat mosaic were identified using a multi-scale approach. The seascape pattern metrics were calculated around each of the 588 fish survey sites within circular sample units for all 4 map types, respectively (Fig. 1). To determine which analysis scale 'best' related to a fish community variable, seascape metrics were calculated at a range of distances from very small, including only seascape elements directly at the fish census site, through broad scales that included the mosaic of habitat elements beyond the distance that fish were likely to be influenced. The smallest distance was 25 m to incorporate each 4 by 25 m fish survey. Habitat metrics were also calculated at increasing distances of 50, 100, 200, 400, and 800 m radii around each survey (Kendall 2005) (Fig. 1).

Univariate linear regression was used to determine the basic relationship between a given fish variable and the seascape variables at each analysis distance. The strength of the relationship as a function of spatial scale was evaluated using the Pearson correlation coefficient (r) that resulted from the regression. This was chosen over other regression-based statistics, such as $R^2$, to characterize relationships because it ranges from –1 to +1, and therefore both positive and negative relationships between variables can be perceived.

To maintain independence among samples, especially where larger analysis diameters (e.g. 800 m) would result in very similar seascape values around adjacent survey sites but maximize use of the data, a resampling approach was taken using the software Focus v2.1 (Holland et al. 2004). Based on distances between survey points, a non-overlapping subset of random survey sites was repeatedly drawn from the entire pool of 588 surveys (1 subset shown in Fig. 1). Preliminary analysis revealed that 1000 iterations of the resampling procedure and their corresponding correlation statistics produced a stable and unimodal set of r values with very low

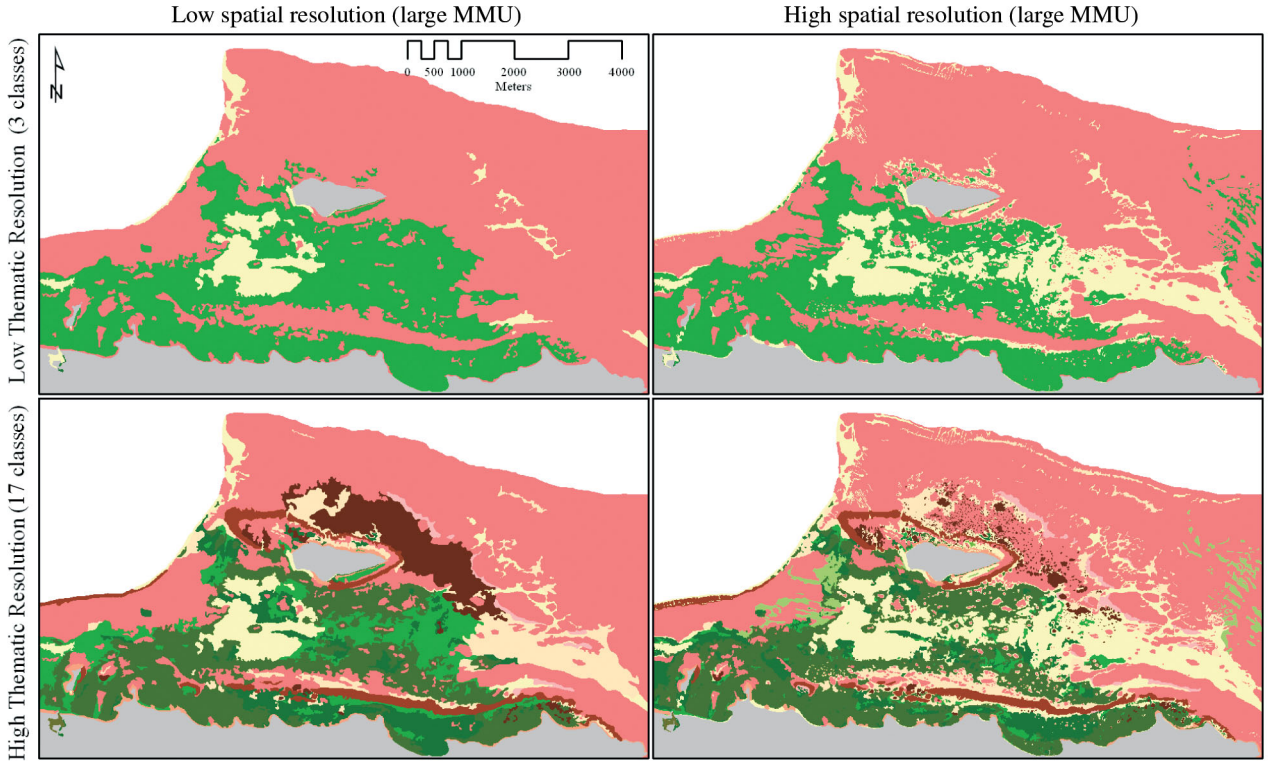


Fig. 2. Four map types of the study region. Counterclockwise from upper left is the map with low spatial and thematic resolution, low spatial but high thematic resolution, high spatial and thematic resolution, and high spatial but low thematic resolution. Grey denotes land. White denotes unmapped area beyond the shelf edge. Green tones denote seagrass/submerged aquatic vegetation categories. Tans denote sand/sediment categories. Reds denote coral reef/hard bottom categories. See Kendall & Miller (2008) for quantitative differences among maps

standard error for all variables and analysis scales. The sampling process was conducted at all 6 analysis scales for each combination of *x* and *y* variables, respectively. The mean and standard error of the correlation coefficients from each scale were plotted and the scale of greatest correlation (maximum |r|) was identified for each pair of fish and seascape variables. The resampling analysis was conducted for each of the 4 map types, and the results for each fish and seascape variable were plotted on the same chart to visualize the effect of map type on fish–seascape correlations.

**Hypothesis testing.** Four outcomes were possible for each fish–seascape combination in Table 1. The simplest case was when no correlation was found between a fish variable and seascape variable for any map type or analysis scale. Another possibility was that a significant correlation existed at one or more scales and all map types yielded similar results. It was also possible that one or more analysis scales yielded a significant correlation, but the results were different depending on the map type. In this case maximum |r| value among map types could occur at the same scale but achieve significantly different values, or maximum |r| values among map types could occur at entirely different scales. The results of each of the 104 fish and landscape comparisons were tallied into one of these 4 categories using the rules defined in the hypotheses below.

*Hypothesis 1. Reef fish are significantly correlated with seascape variables (area of sand or seagrass, length of hard bottom or reef edge, and habitat diversity):* With Bonferroni correction for testing 6 scales at once, nearly all mean r values were significantly nonzero due to the very narrow standard error of the mean (SEM) values. Even r values between +0.1 and −0.1, which would account for <1% of the variability in the fish–seascape relationship, were statistically significant. To infer ecological relevance, a much higher and more conservative |r| of 0.2 was therefore selected as a cutoff for identifying more important ecological relationships and to reduce the probability of Type I errors.

*Hypothesis 2. Correlation strength will vary with the spatial scale of the analysis:* A simple ANOVA evaluated whether all 6 analysis scales yielded a maximum r value ($|r| > 0.2$) at the same scale for each fish–seascape variable pair and map type. Where a significant ANOVA was found, a Tukey's-type multiple means comparison determined which scales differed. A more conservative $\alpha = 0.001$ was used to define significant differences due to the narrow SEM values that resulted from the resampling procedure.

*Hypothesis 3. Thematic and spatial resolution of maps will affect correlation strength and scale. Highest resolution maps will yield the highest correlations:* To evaluate the possibility that peak r values occurred at the same scale but had significantly different values among map types, the scale with the highest r value was identified and the mean r values among map types were tested for significant differences using a conservative Tukey's-type multiple means comparison procedure ($\alpha = 0.001$). To evaluate the possibility that peak r values occurred at different scales for different map types, peaks in |r| values by map type were identified visually. The relative frequencies of these possible outcomes were tabulated for each seascape variable at the bottom of Table 1.

To determine if there was a map type that consistently had the highest or lowest |r| values for each of the 4 seascape variables, comparisons with significant results were evaluated further. When a $|r| > 0.2$ was present, maps yielding significantly higher or lower |r| than the rest were tallied for each seascape variable.

*Hypothesis 4. Range in correlation strength will be highest for individual life stages of species followed by guilds and lowest for whole community metrics:* Maximum |r| values for each of the 104 variable combinations were grouped and plotted by those that tested: (1) abundance of individual life stages (juvenile or adult) of particular species, (2) total abundance of particular species, (3) abundance or species richness of the mobility guilds, and (4) the whole assemblage variables of overall abundance or species richness. Plotted |r| values were separated by map type and coded by seascape variables. The range and distribution of extreme values was compared among levels of organization of the fish variables for each map type.

*Hypothesis 5. Resident fish species will have highest correlation with seascape variables at finer scales than mobile, followed by transient species, and juveniles of a given species will have highest correlation with seascape variables at finer scales than adults:* The scale of peak correlation between juveniles and a given landscape variable was identified for each map type and simply compared to the scale of peak correlation for adults. The distance of peak correlation of juveniles relative to adults was described as one of the following: juvenile < adult, adult < juvenile, or when the scale of peak correlation was the same for both of these life stages, juvenile = adult. The hypothesis that resident fish have higher correlations with seascape variables at finer scales than mobile, followed by transient fish, was evaluated in similar fashion. Habitat diversity was not evaluated because r values were very low across all scales and no clear peaks in correlation were observed.

## RESULTS

### Hypothesis 1—Fish are correlated with seascape variables

Linear correlations between fish and individual seascape variables were low overall and explained a low percentage of the variability in fish distributions (see the supplement at www.int-res.com/articles/suppl/m427p259_supp.pdf). Of the 2496 mean r values calculated, only 220 (~11%) exceeded the selected significance level of $|r| = 0.2$. The strongest association was $|r| = 0.5$ between the abundance of *Cephalopholus fulvus*, a small grouper and the amount of hard bottom edge. Habitat diversity was not significantly correlated with any fish variable at any scale (Table 1) (e.g. Fig. 3).

Despite the lack of strong correlations between individual seascape variables and fish distributions, some relationships between fish and specific attributes of the seascape were found. Length of hard bottom edge was correlated with more of the fish variables (17) than any other seascape feature (Table 1). Species richness, resident species richness, mobile species richness, and abundance of all species except for *Ocyurus chrysurus* were related to length of hard bottom edge. Highest |r| values found with hard bottom edge length were for *Acanthurus coeruleus* adult and total abundance, *Cephalopholis fulvus* adult and total abundance (neg-

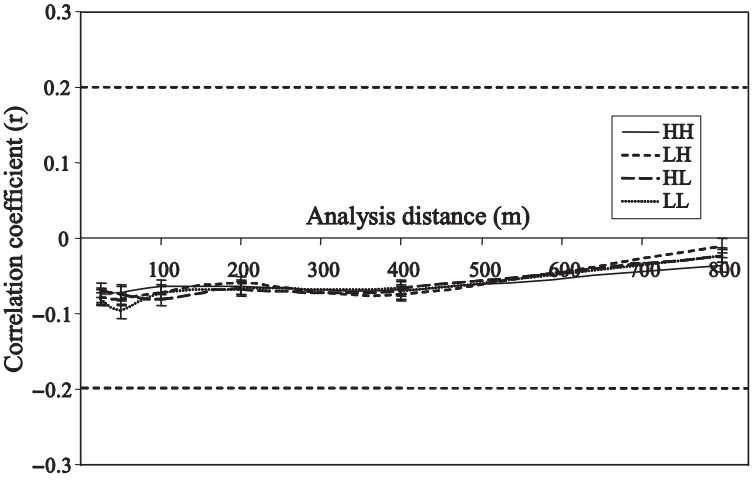


Fig. 3. Correlations of habitat diversity and fish species richness by analysis distance for all 4 map types. HH: map with high spatial and thematic resolution. LH: map with low spatial and high thematic resolution. HL: map with high spatial and low thematic resolution. LL: map type with low spatial and thematic resolution. Observations between the horizontal dashed lines ($|r| < 0.2$) denote non-significant results

ative correlations), and *Sparisoma viride* juvenile and total abundance. Area of seagrass/SAV was correlated with total species richness, species richness of resident fish, and abundance of at least one life stage of all species considered except for *A. coeruleus* (Table 1). The highest |r| values found with seagrass/SAV were for *Stegastes planifrons* juvenile and total abundance, and *C. fulvus* juvenile, adult, and total abundance (negative correlations). Species richness and abundance of transients, abundance of residents, and overall species richness all had positive correlations with area of sand/sediment (Table 1).

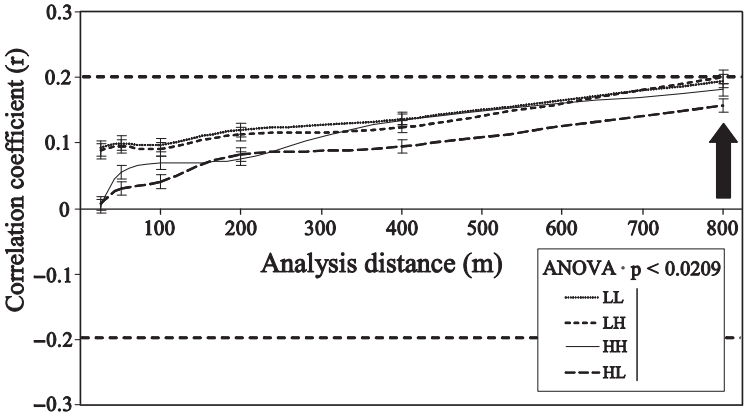


Fig. 4. Correlations of seagrass/submerged aquatic vegetation and *Haemulon flavolineatum* adult abundance by analysis distance for all 4 map types. Where a significant correlation was found (|r| > 0.2 as indicated by the horizontal dashed lines), the scale with the strongest relationship is noted with the black arrow. Vertical lines adjacent to the legend denote map types that have correlations that are not significantly different from each other at the scale with highest correlation. See Fig. 3 for abbreviations

### Hypothesis 2—Correlation strength varies with analysis radius

This hypothesis was accepted for all comparisons with significant r values, although the results differed by seascape variable (Table 1). Most peak correlations involving area of seagrass/SAV occurred at the broadest scale considered (800 m, e.g. Fig. 4). Transient richness and abundance had highest correlation at 800 m with sand/sediment area, whereas resident abundance had highest correlation at 25 m.

Patterns for correlations between individual species and seascape variables were less predictable (Table 1). The abundance of adult *Cephalopholis fulvus* had highest correlation with sand/sediment area at 100 m, whereas overall and juvenile abundance had highest correlation at 25 m. Most peak correlations with length of hard bottom edge occurred at the 800 m scale except for total and adult abundance of *Haemulon flavolineatum* and species richness of mobile species that occurred at 50 m. All peak |r| values showed positive relationships except for *C. fulvus*, which showed strong negative correlations.

### Hypothesis 3—Map resolution affects correlation strength and scale

Support for this hypothesis was equivocal among seascape variables, with spatial and thematic resolution influencing some results but not others. For fish–habitat diversity comparisons, all 4 map types yielded similar results, with |r| values rarely exceeding 0.1 across all scales (e.g. Fig. 3). For seagrass/SAV area, the scale of highest correlation was the same for all 4 map types in all but one of the 14 comparisons with significant results. In contrast, all sand/sediment area results were strongly influenced by map type. Maps of the same spatial resolution resulted in similar r values at all spatial scales, whereas maps with differing spatial resolution resulted in very different values across scales (e.g. Fig. 5). More specifically, the abundance of adult *Cephalopholis fulvus* had highest correlation with sand/sediment area at 100 m, whereas overall and juvenile abundance had highest correlation at 25 m. These were perceived as positive relationships only when maps with low thematic resolution were used. For length of hard bottom edge, map type significantly influenced the results for all but one of the 17 comparisons with at least one |r| > 0.2. Only species richness of residents was consistently correlated with hard bottom edge by all 4 map types (Fig. 6). For the 16 other comparisons, use of different map types resulted in either significantly lower r at the same scale or even a peak in r at an entirely different scale.

Changes in perception of fish–seascape correlation due to map type are summarized at the bottom of Table 1 (i.e. either peak in correlation at different scale or peak at the same scale but different strength). Map type had no effect on correlations involving habitat diversity with no significant correlations observed with any map. When map type had an effect on the sand/sediment results, maximum |r| value occurred at completely different scales (14 occurrences) rather than simply peaking at the same scale but at a significantly lower value (0 occurrences). In contrast, seagrass/SAV and hard bottom edge relationships showed some of each type of difference. Overall, the 2 types of differences occurred with approximately equal frequency.

The number of times that each map type had the highest or lowest |r| value when a |r| > 0.2 was present is tallied in Table 2. Only hard bottom edge comparisons yielded a consistent pattern. Maps with high spa-

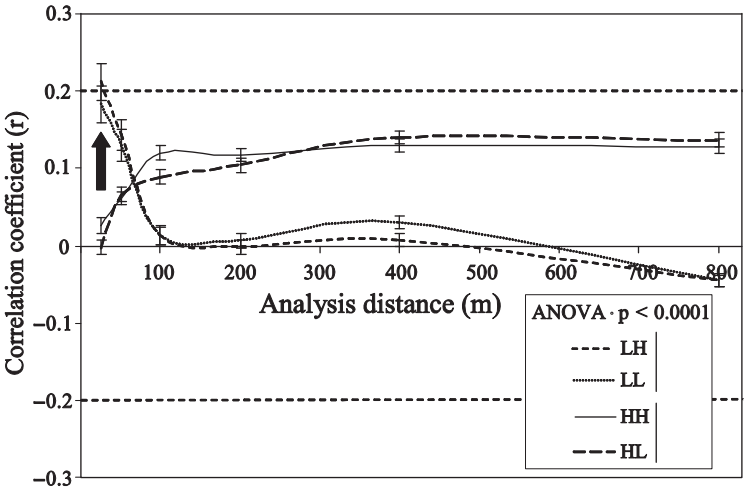


Fig. 5. Correlations of sand/sediment area and resident fish abundance by analysis distance for all four map types. See Figs. 3 & 4 for definitions and abbreviations

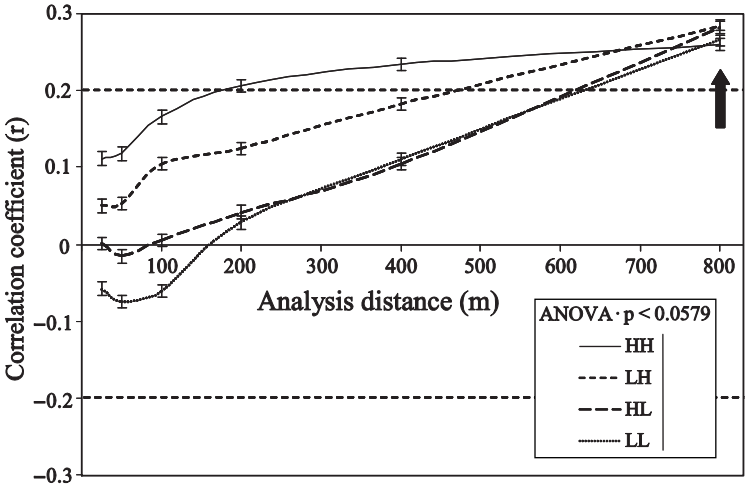


Fig. 6. Correlations of hard bottom edge and resident species richness by analysis distance. See Figs. 3 & 4 for definitions and abbreviations

tial and thematic resolution most often had |r| values significantly higher than other maps. Maps with low spatial and thematic resolution also had significantly lowest |r| values in the most comparisons. No single map type consistently differed from the others for the other 3 seascape variables.

### Hypothesis 4—Range in correlation strength varies by life stage, guild, and whole community variables

Maximum |r| values showed similar minima, maxima, and ranges among individual life stages of the 6 focal species and when all life stages were grouped together. Values for mobility guilds and whole fish community results were also similar to each other but quite different from those based on individual species (Fig. 7). Findings were therefore grouped into these 2 broader categories, respectively. Of the 104 fish–seascape combinations tested, at least 11 of the highest maximum |r| values were for species-level analyses. This was true for all map types except for high spatial and low thematic resolution, which had only 4 of the highest values (Fig. 7d). Species-level analyses also had a higher range of values (~0.4), much higher than the range for guild or community comparisons (~0.2) (Fig. 7a–c). The exception was again for analyses based on maps with high spatial and low thematic resolution, which differed from this pattern in that the range of values was lower (~0.3) (Fig. 7d). Also of note, nearly all of the highest |r| values were for comparisons involving hard bottom edge length and seagrass/SAV, whereas nearly all of the lowest values were for correlations between habitat diversity and individual fish species.

### Hypothesis 5—Mobility guilds and life stage will affect distance of peak correlation

Overall, 38% (9 of 24) of the comparisons had maximum correlations at the same scale for resident, mobile, and transient species (Table 3). The next most common result (30%, 7 of 24 of the comparisons), occurred when transient species had a larger scale of correlation than either resident or mobile species (which had a common scale of peak correlation). The expected result of r value trends: resident < mobile < transient, occurred in only one of the 24 comparisons evaluated. Also of note, no fish–seascape correlations based on mobility yielded the same results for all 4 map types, and differences were unpredictable and inconsistent.

Overall, 56% (40 of the 72) of the comparisons evaluated had maximum correlation at the same scale for both adults and juveniles of a given species (Table 4). Juveniles had a finer scale of peak correlation in only 15% (11 of 72) of the comparisons, whereas adults had finer scales of peak correlation in 30% (21 of 72) of the comparisons. Of note, when a difference was found in comparisons involving seagrass/SAV, it was always that adults had a finer scale of peak correlation than juveniles. All 4 map types generally resulted in the same patterns. Exceptions to this were for *Ocyurus chrysurus* and *Cephalopholis fulvus*. For *O. chrysurus*, use of maps with high spatial resolution resulted in

Table 2. Tally of the number of times each map type had the highest or lowest |r| value when a significant result was present. SAV: submerged aquatic vegetation

| Map resolution | Habitat diversity | Seagrass/ SAV | Sand/ sediment | Hard bottom edge length |
|---|---|---|---|---|
| **Significantly highest \|r\| value** | | | | |
| High spatial high thematic | 0 | 0 | 0 | 4 |
| High spatial low thematic | 0 | 0 | 0 | 0 |
| Low spatial high thematic | 0 | 0 | 0 | 1 |
| Low spatial low thematic | 0 | 1 | 0 | 0 |
| **Significantly lowest \|r\| value** | | | | |
| High spatial high thematic | 0 | 0 | 0 | 0 |
| High spatial low thematic | 0 | 0 | 0 | 3 |
| Low spatial high thematic | 0 | 0 | 0 | 0 |
| Low spatial low thematic | 0 | 0 | 0 | 4 |

juveniles having finer scales of peak correlation than adults. When low spatial resolution was used, the inverse pattern was perceived. For *C. fulvus*, use of maps with high spatial resolution resulted in adults having finer scales of peak correlation than juveniles. When low spatial resolution was used, the inverse pattern was perceived. It should be noted that inference regarding scales of peak correlation by life stage are limited to only the 6 focal species tested, whereas results for mobility guilds a more broadly robust and are based on all species observed.

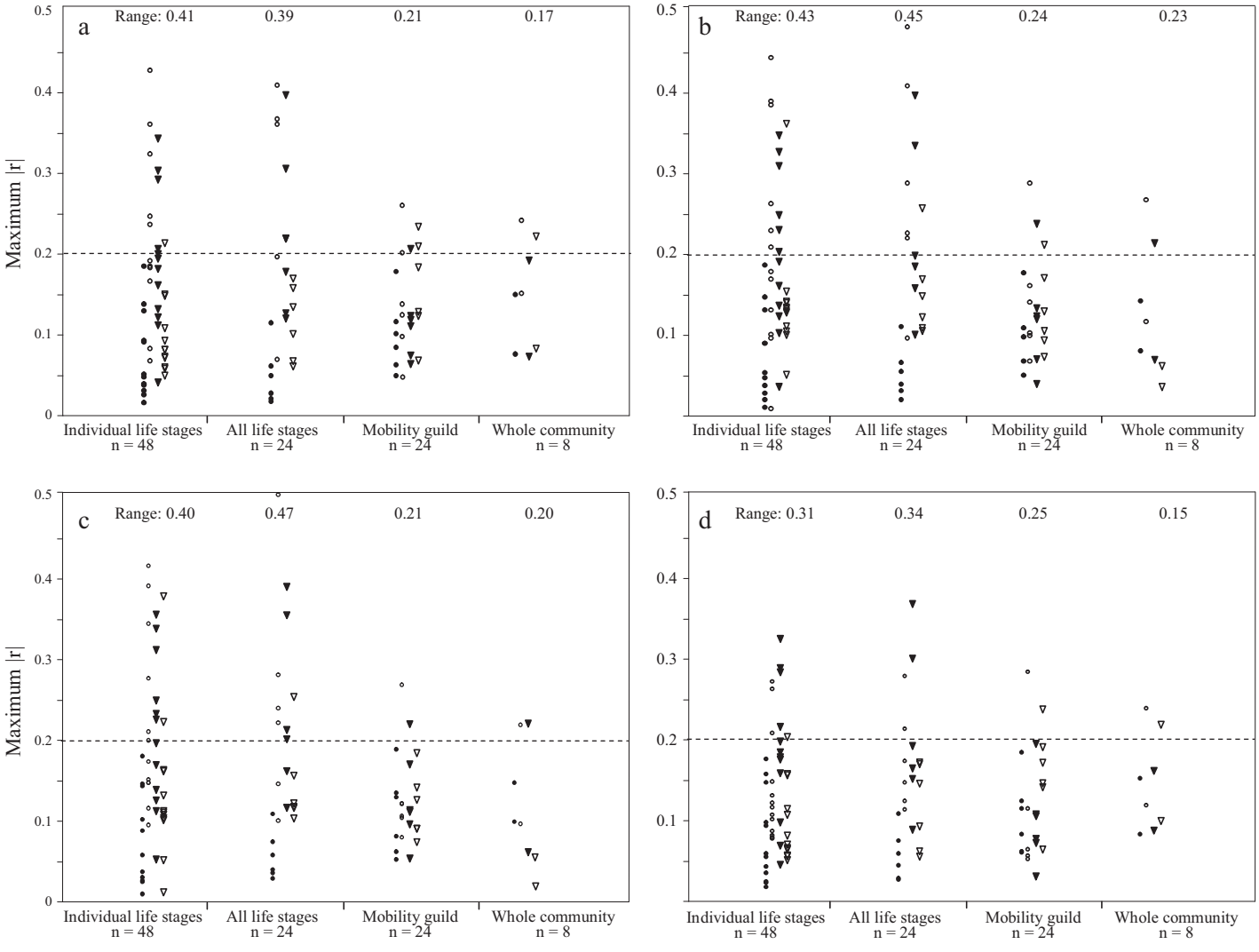


Fig. 7. Maximum |r| values for all 104 *x* and *y* variables investigated in the study using maps with (a) high spatial and thematic resolution, (b) low spatial and high thematic resolution, (c) low spatial and thematic resolution, and (d) high spatial and low thematic resolution. Results are grouped by level of organization of the fish variables. Symbols denote the landscape variables associated with each |r| value. •: habitat diversity; ○: hard bottom edge length; ▼: seagrass/SAV; ▽: sand/sediment

Table 3. Relative scale of maximum |r| values for resident (R), mobile (M), and transient (T) fish within the 4 map types. SAV: submerged aquatic vegetation

| | High spatial high thematic | High spatial low thematic | Low spatial high thematic | Low spatial low thematic |
|---|---|---|---|---|
| **Hard bottom edge length** | | | | |
| Fish abundance | R = M < T | M < R = T | R = M < T | R = M < T |
| Species richness | R = M = T | R = M = T | R = M < T | R = M = T |
| **Seagrass/SAV** | | | | |
| Fish abundance | R = M = T | R = M < T | M < R < T | R < M < T |
| Species richness | R = M = T | R = M < T | R < M = T | R < M = T |
| **Sand/sediment** | | | | |
| Fish abundance | R = M = T | T < R = M | R = M = T | R = M < T |
| Species richness | M < R = T | T < R = M | R = M = T | R = M = T |

Table 4. Relative scale of maximum |r| values for juveniles (J) versus adults (A) of each of the 6 focal species within the 4 map types. SAV: submerged aquatic vegetation

| | High spatial high thematic | High spatial low thematic | Low spatial high thematic | Low spatial low thematic |
|---|---|---|---|---|
| **Hard bottom edge length** | | | | |
| *Acanthurus coeruleus* | J = A | J = A | J = A | A < J |
| *Cephalopholis fulvus* | J = A | J = A | J = A | J = A |
| *Haemulon flavolineatum* | J = A | J = A | J = A | J = A |
| *Ocyurus chrysurus* | J < A | J < A | A < J | A < J |
| *Sparisoma viride* | J = A | A < J | J = A | A < J |
| *Stegastes planifrons* | J < A | J = A | J = A | J = A |
| **Seagrass/SAV** | | | | |
| *A. coeruleus* | A < J | A < J | A < J | A < J |
| *C. fulvus* | J = A | J = A | J = A | J = A |
| *H. flavolineatum* | J = A | J = A | J = A | J = A |
| *O. chrysurus* | A < J | A < J | A < J | A < J |
| *S. viride* | A < J | A < J | A < J | A < J |
| *S. planifrons* | J = A | J = A | J = A | J = A |
| **Sand/sediment** | | | | |
| *A. coeruleus* | A < J | A < J | J = A | J = A |
| *C. fulvus* | A < J | A < J | J < A | J < A |
| *H. flavolineatum* | J = A | J = A | J < A | J < A |
| *O. chrysurus* | J = A | J = A | J = A | J = A |
| *S. viride* | J = A | J = A | J = A | J = A |
| *S. planifrons* | J < A | J < A | J < A | J < A |

## DISCUSSION

A central question asked in the present study is 'How much of the pattern in fish distribution can be explained using landscape variables?' The seascape pattern metrics selected for study were considered to be among those with the greatest explanatory power over fish distributions based on prior research. Results suggest, however, that each of the seascape variables studied here explain only a relatively small proportion (~25%) of the variability in the distribution of fish in coral reef systems.

Similar studies in a variety of systems have generally yielded a similar range of correlation values to those found here. Landscape variables explained 2 to 64% of the variability in bird and insect communities (Ricketts et al. 2001, Pearman 2002, Steffan-Dewenter 2003, Holland et al. 2004), and although less-studied, findings from multiscale studies of reef fish are similarly wide ranging, with 11 to 94% of the variability explained between seascape and fish variables (Kendall 2005, Grober-Dunsmore et al. 2007). Linear correlation between fish species richness on sand sites with area of nearby hard bottom reached maximum values of r = 0.33 in a separate study at BIRNM (Kendall 2005). Grober-Dunsmore et al. (2007) reported linear correlations between reef fish community variables and area of seagrass as high as 0.97 and were often in the range of ~0.5 to 0.6 around the nearby island of St. John, U.S. Virgin Islands. These differences in results for ecologically similar coral reef ecosystems from the same geographical area are likely the result of differences in sampling design between the 2 studies. Studies by Kendall (2005) and the results here were based on a large number of spatially random survey sites, whereas findings of Grober-Dunsmore et al. (2007) were based on a subset of selected coral reef sites chosen specifically to quantify the effects of variation in the amount of nearby seagrass cover and to minimize confounding variables such as differences in coral cover, rugosity, depth, and distance from shore. In contrast, our study provides a more comprehensive, ecosystem-wide measure of the strength of the relationships across the complete range of coral reefs in the study area.

What seascape variables had the highest or most correlations with the fish variables? Habitat diversity has been considered as a proxy for fish diversity in the selection of marine reserves (National Research Council 2001). Terrestrial studies have shown a relationship between habitat diversity and biotic diversity for a range of taxa (Kohn & Walsh 1994, Kerr & Packer 1997, Ricklefs & Lovette 1999, Fox & Fox 2000). However, our results suggest that habitat diversity is a very poor predictor of fish species richness or indeed any compo-

nent of the fish community considered. A possible explanation is that benthic maps of the type used here may not capture the aspects of habitat diversity to which fish respond. It is also possible that, although we evaluated a wide range of variables representing the fish assemblage, the species and assemblages considered may be habitat generalists or have considerable plasticity in suitable habitats (Ricklefs & Lovette 1999). Our results bolster growing evidence against using habitat diversity at the seascape scale, as depicted in benthic maps, as a proxy for predicting overall fish and biotic diversity (Donaldson 2002, Pittman et al. 2007, Grober-Dunsmore et al. 2008).

Area of seagrass/SAV was correlated with several of the fish community variables, including at least one life stage of most species tested. This confirms prior studies on species suspected of association with seagrass/SAV and further quantifies those relationships (Dorenbosch et al. 2005, 2006, Kendall 2005, Grober-Dunsmore et al. 2007, Valentine et al. 2007). Correlations were also found for species not previously thought to be related to area of seagrass (e.g. *Cephalopholis fulvus*, *Sparisoma viride*, and *Stegastes planifrons*). This demonstrates the importance of seagrass/SAV as an influence on fish distribution on reefs generally, not just those considered obligate users. It also indicates that a variety of direct and indirect mechanisms can operate that influence abundance of particular species or guilds. Sand/sediment area predicted several of the fish variables, although not as many as expected given this bottom type's role in settlement and foraging of many species.

Length of hard bottom edge was correlated with more of the fish variables than any other landscape feature. This underscores its role as an important habitat margin to a diversity of reef fish (Dorenbosch et al. 2005, 2006, Valentine et al. 2007). Edges between reef types and soft bottom often have high rugosity that offers structural refuge supporting a diversity of reef species (Pittman et al. 2007).

Correlations were found between diverse elements of the fish community and seascape features at a wide range of distances. Systematically changing the size of the analysis window and comparing fit among the models allowed the neighborhood that explains the highest amount of variability (highest |r|) in the fish data to be identified. The distance or neighborhood with the strongest correlation has been interpreted as the most ecologically influential or relevant scale for each combination of biotic and seascape variable (Holland et al. 2004, Kendall 2005). For many comparisons no significant relationships were found for any fish variables at any scale. In these instances, a number of factors may be responsible. Fish variables may be more closely related to a seascape variable not tested in this study, or the relationship may be non-linear and insensitive to our linear-regression-based approach. It could also be that the seascape maps did not adequately capture the necessary detail of the seascape parameters that were tested. Fish may even be responding to seascape features beyond our maximum analysis distance.

Ecologically meaningful explanations are present for many of the observed patterns in neighborhood distance and associations with particular landscape variables. Species richness of fish was positively correlated with area of sand/sediment, area of seagrass/SAV, and length of hard bottom edge. Correlation with these variables increased with analysis distance such that maximum r values occurred at the 800 m scale, a broader scale of peak correlation than identified by prior research (400 m by Kendall 2005; 500 m by Grober-Dunsmore et al. 2007). It has long been thought that the area of surrounding seagrass increases the number of fish species on hard bottom sites by providing foraging areas for some species (Randall 1965, Ogden 1976, Nagelkerken et al. 2000), transfer of energy to reefs (Meyer et al. 1983, Meyer & Shultz 1985), nursery habitat (Dorenbosch et al. 2005, Adams et al. 2006, Dorenbosch et al. 2007, Verweij et al. 2008), and enhanced recruitment (Shulman & Ogden 1987, Cocheret de la Morinière et al. 2002). Similarly, area of surrounding sand bottom may result in enhanced recruitment to nearby hard bottom sites of the many species that initially settle in sand habitat to avoid reef and reef edge predators (Helfman et al. 1982, Shulman 1985, Shulman & Ogden 1987). Species richness may be enhanced by length of hard bottom edge through several mechanisms. Hard bottom edge must be transited for juvenile fish undergoing ontogenetic shifts following settlement in sand or seagrass (Shulman 1985, Shulman & Ogden 1987, Cocheret de la Morinière et al. 2002), it is a preferred hunting ground of some piscivores (Helfman et al. 1982, Quinn & Ogden 1984, Sweatman & Robertson 1994), and is the optimum location to seek structural refuge to minimize travel distance from reef to soft bottom for species that undergo such daily foraging migrations (Kendall et al. 2003, Tuya et al. 2010). Hard bottom edge represents a key ecotone habitat for many species (Wernberg et al. 2006, Valentine et al. 2007, Vanderklift et al. 2007), and also indicates the presence of bathymetric complexity between reef types or reef and soft bottom, which has been positively correlated with species richness of fish (Luckhurst & Luckhurst 1978, Gratwicke & Speight 2005a,b, Pittman et al. 2007).

Ecologically meaningful correlations were also found between individual species and seascape variables. Strong negative correlations were observed between *Cephalopholis fulvus* and length of hard bottom edge and area of seagrass/SAV. In both cases r values steadily decreased with analysis distance to a maxi-

mum at the 800 m scale. This species utilizes flat hard bottom often sparsely colonized by corals, sponges, and gorgonians (Pittman et al. 2008), a bottom type often described as pavement that typically covers broad areas (Kendall et al. 2004b). Hard bottom edges or a large area of seagrass nearby would mean that there is less of their preferred flat hard bottom habitat. Logical ecological correlations were also observed between seascape variables and *Haemulon flavolineatum* adult and overall abundance. This species feeds solitarily over seagrass and soft bottom at night but schools over reefs and hard bottom during the day (Randall 1965, Ogden 1976). Area of seagrass positively influenced abundance on reef sites by providing a large foraging area (Burke 1995, Nagelkerken et al. 2000, Kendall et al. 2003), especially at long analysis distances that may correspond to a broad foraging range. High correlation with hard bottom edge, especially at very short analysis distances, is logical, too, because optimality theory predicts that *H. flavolineatum* will utilize reef sites near reef edges (Kendall et al. 2003). Such proximity minimizes energy costs and daily travel time from resting sites on reefs to adjacent seagrass foraging areas. This relationship was apparent only when maps with high spatial and thematic resolution were used.

More difficult to explain were the strong correlations observed between other variables. For example, a positive correlation was observed between *Stegastes planifrons* and both area of seagrass/SAV and length of hard bottom edge. High correlations were measured at the 800 m analysis scale. This highly resident species settles directly onto reefs (Tolimieri 1995, Gutierrez 1998) and spends its benthic life associated with the same coral head or <~1 $m^2$ territory (Luckhurst & Luckhurst 1978, Robertson et al. 1981). That either of these landscape variables or this analysis distance have a direct influence on fish abundance is doubtful. These seascape variables may instead be correlated with some other environmental factor, some indirect effect may be responsible, and we are reminded that correlation need not be obviously linked to causation.

In many comparisons, use of different input maps resulted in a changed perception of either the strength of peak correlation at a given scale, or the scale at which peak correlations occurred. The latter case represents a more serious problem in that both the spatial dimensions as well as the intensity of the relationship are perceived differently. Such events call for the most careful consideration of the consequences of relying on a particular map type. These 2 types of misperception occurred with different frequency depending on the seascape feature tested. Studies relying on the amount of hard bottom edge length and area of sand need to be cautiously interpreted due to the large number of cases where map type changed the perception of the fish–seascape correlation. Spatial resolution of maps often completely changed the perceived relationships between fish and their area of surrounding sand/sediment. In all cases, use of high spatial resolution maps resulted in lower r values or even negative r values compared to low spatial resolution maps at the same analysis scale. Perception of correlation strength between fish and hard bottom edge also depended on the type of input maps used. While the general patterns of increasing correlation with scale were similar among all 4 map types, the values of the correlation were often significantly different. Maps of the study site exhibited a doubling of edge length for hard bottom features when high spatial resolution was used to create them (Kendall & Miller 2008). Many reef edges that fish interact with, such as small patch reefs in sand and sand channels in hard bottom, only appeared when high spatial resolution was used. In contrast, results were quite consistent for seagrass/SAV area regardless of map type. Continuous seagrass beds were characterized quite consistently at the 2 map scales used in the present study, but patchy beds showed large differences (Kendall & Miller 2008). For habitat diversity, all 4 map types performed similarly in that none had significant correlations with any fish variables.

Is there a particular map type that is best for seascape ecological studies of reef fish? Our results suggest that the answer depends on the seascape variables of interest. Maps with high spatial and thematic resolution had most of the significantly highest correlations for comparisons involving hard bottom edge, whereas maps with low spatial and thematic resolution were often lowest. This indicates that results of studies using hard bottom edge are likely inaccurate when using lower spatial or thematic resolution maps. In contrast, all 4 map types performed similarly for seagrass/SAV, indicating that even simple, inexpensive to produce maps do just as well as highly detailed, expensive, time-consuming maps in studies involving this variable. Also of relevance are the plots of maximum r values by level of organization of fish variables. All map types yielded a similar range of results except for maps with high spatial but low thematic resolution. This map type had lower sensitivity to detecting the highest and lowest peak correlations that were observed more consistently among the other map types. This indicates that mapping only a few bottom types with great spatial detail may be least effective in seascape ecological studies. Why such maps would perform more poorly than those with low thematic as well as low spatial resolution is unclear.

Maximum correlations between seascape variables and individual species achieved a wider range and more extreme values (highest and lowest) than comparisons involving either guilds or the entire fish

assemblage. Variables representing more than a single species had more moderate peak correlations. This is likely because the habitat preferences and scales of movement of the many species included in such variables get averaged together and limit extreme values. In contrast, individual species had both highest and lowest values since each species interacts with a more discrete set of habitats at similar scales. This pattern did not however, separate the results of individual life stages from all individuals of the focal species, as was expected, nor did it distinguish between mobility guilds and whole community metrics.

Scales of peak correlation were the same for juveniles and adults in over half of the comparisons. The expectation based on terrestrial literature (Holling 1992, Gehring & Swihart 2003, Holland et al. 2005), that juveniles would have a shorter distance of maximum correlation than adults, rarely occurred (but see Grober-Dunsmore et al. 2007). This suggests that seascape influences on the distribution of juvenile fish may operate at scales often as broad as those for their adult stages. Typical scales of seascape interaction for mobility guilds were somewhat more in line with expectations (Pearman 2002), in that transients had broader scales of peak correlation than either resident or mobile fish in a large number of comparisons. Still, however, scale of influence was the same for all 3 mobility guilds in many comparisons, again indicating that in many cases even resident fish are influenced by their surrounding seascape at distances as broad as those for transients. Despite peak correlation at similar scales, the mechanisms responsible are almost certainly indirect given present understanding of the very small home range of resident species and juveniles of the 6 focal species (Itzkowitz 1977, Luckhurst & Luckhurst 1978, Overholtzer & Motta 1999, Bell & Kramer 2000, Watson et al. 2002). Map type generally did not influence the results of peak scale for adult versus juvenile fish. In contrast, results of mobility guild analysis differed in unpredictable ways depending on map type, again indicating that caution be used when studying mobility guilds using a single map type.

Most prior seascape ecological studies base results on one type of map; whatever is available. Little consideration appears to have been given to the influence of map type on the conclusions reached. Terrestrial investigations have shown that the characteristics of input maps can influence results of landscape ecology studies (Stohlgren et al. 1997, Karl et al. 2000). Results here also suggest that use of a single map type in the marine environment can lead to an incomplete or even incorrect perception (i.e. undetected, weakly measured, inversely signed, thought to occur at the wrong scale) of habitat utilization and scale at which organisms interact with their seascape.

Based on the findings here, the following advice can be given to those interested in mapping coral reef ecosystems to study seascape ecology of reef fish, to model species distributions, or in making spatially explicit management decisions using benthic maps. Hard bottom should be mapped with high spatial resolution above all else since this most affects reef edge depictions. Time and money permitting, hard bottom should be mapped with high thematic resolution as well and separated into its various reef types. Many studies are presently concerned with hard bottom edge and proximity to hard bottom habitat (Sweatman & Robertson 1994, Dorenbosch et al. 2005, Wernberg et al. 2006, Valentine et al. 2007, Vanderklift et al. 2007, Tuya et al. 2010). Extrapolating their mostly *in situ* studies to seascape scales using benthic maps carries with it particular concerns. Sand should be mapped with high spatial resolution to pick up key features such as sand channels in hard bottom and halos separating hard bottom from seagrass (Kendall & Miller 2008). In contrast to these bottom types, seagrass mapped at coarse thematic and spatial resolution appear to effectively evaluate the seascape ecology of a variety of fish species and will result in similar values when more detailed maps are used. Given these findings, prior seagrass studies probably do not need to be concerned about their results changing if different map types were used (e.g. Pittman et al. 2004, Kendall 2005, Grober-Dunsmore et al. 2007). Results involving hard bottom or sand, however, could change measurably were different maps to be used as input. Habitat diversity, as measured by the type of benthic maps used here, is simply not representative of fish diversity or any other measure of the fish community at any scale and should not be considered as a surrogate or proxy variable for overall biodiversity. To keep these recommendations in perspective, however, seascape variables that were used here were for common bottom features. Habitat specialists that are obligate users of a particular reef type, for example, would need to be studied with a map of sufficient spatial and thematic complexity to capture such features.

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# Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem

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ABSTRACT: Many common fishes associated with Caribbean coral reef ecosystems use resources from more than 1 patch type during routine daily foraging activities. Few studies have provided direct evidence of connectivity across seascapes, and the importance of benthic seascape structure on movement behavior is poorly known. To address this knowledge gap, we coupled hydro-acoustic technology to track fish with seafloor mapping and pattern analysis techniques from landscape ecology to quantify seascape structure. Bluestriped grunts *Haemulon sciurus* and schoolmaster snapper *Lutjanus apodus* were tracked over 24 h periods using boat-based acoustic telemetry. Movement pathways, and day and night activity spaces were mapped using geographical information system (GIS) tools, and seafloor structure within activity spaces was mapped from high-resolution aerial photography and quantified using spatial pattern metrics. For both fish species, night activity spaces were significantly larger than day activity spaces. Fish exhibited a daytime preference for seascapes with aggregate coral reef and colonized bedrock, then shifted to night activity spaces with lower-complexity soft sediment including sand, seagrass, and scattered coral/rock. Movement path complexity was negatively correlated with seascape complexity. This demonstrates direct connectivity across multiple patch types and represents the first study to apply quantitative landscape ecology techniques to examine the movement ecology of marine fish. The spatially explicit approach facilitates understanding to the linkages between biological processes and the heterogeneity of the landscape. Such studies are essential for identifying ecologically relevant spatial scales, delineating essential fish habitat and designing marine protected areas.

KEY WORDS: Seascape ecology · Spatial pattern · Acoustic tracking · Home range · Fish movements



## INTRODUCTION

Coral reef ecosystems typically exist as mosaics of patch types (i.e. coral reefs, seagrasses, sand, mangroves) exhibiting complex spatial patterns in biophysical structure. Many common species of fish connect multiple patch types through routine daily foraging movements, ontogenetic shifts, and seasonal and spawning migrations (Parrish 1989, Chapman & Kramer 2000, Pittman & McAlpine 2003). Diel migration, a widespread phenomenon for fish such as grunts and snappers, links adjacent patch types that are used for different purposes (e.g. foraging and refuge; Ogden & Buckman 1973, Parrish 1989, Krumme 2009). Routine migratory movements are thought to optimize survival by maximizing growth rate and minimizing risk from predation by preferential utilization of areas that provide suitable food and refuge (Dahlgren & Eggleston 2000).

Our knowledge of fish movements across the seascape has come primarily from underwater visual observations (Friedlander & Parrish 1998, Nagelkerken et al. 2000, Mumby et al. 2004), from extractive net and trap sampling (e.g. Beets & Friedlander 1998, Halpin 2000, Hammerschlag & Serafy 2010), and chemical isotope signatures (Kieckbusch et al. 2004, Nagelkerken & van der Velde 2004). Such techniques,

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however, provide only low-resolution reconstructions of movement pathways (stable isotopes) or indirect evidence of connectivity inferred from spatial distribution patterns of different life stages or size classes (Gillanders et al. 2003). Furthermore, conventional fish distribution studies are usually restricted to daytime sampling, often conducted at arbitrary spatial scales, and are typically subject to a range of geographical and temporal biases in sampling design (Pittman & McAlpine 2003). Manual acoustic tracking of fish movements combined with high-resolution global positioning system (GPS) technology provides a direct measure of individual fish movement pathways and space-use patterns over time that is not restricted to daylight hours (Holland et al. 1996, Lowe et al. 2003, Topping et al. 2005).

An additional knowledge gap exists in the linking of fish movement behavior to the underlying benthic seascape structure. Landscape ecology, the study of the ecological consequences of spatial patterning, provides an appropriate conceptual and analytical framework for examining fish–seascape relationships for highly mobile species (Robbins & Bell 1994, Pittman et al. 2004). In terrestrial landscape ecology, movement behavior has long been recognized as an important link between process and pattern (Lima & Zollner 1996, McIntyre & Wiens 1999). It is now becoming apparent that the spatial patterning of the benthic seascape, such as the spatial arrangement of patches, the size and shape of patches, and edges influence the distribution of fish and ecological processes such as movement, growth, and predator–prey relationships (Irlandi & Crawford 1997, Pittman et al. 2004, Grober-Dunsmore et al. 2009, Boström et al. 2011, this issue, Kendall et al. 2011, this issue). Conventional ecological studies, however, rarely quantify benthic structure at spatial scales broad enough to encompass even the routine daily space use patterns of the organisms of interest (Pittman & McAlpine 2003).

Advances in geographical information system (GIS) tools have improved our ability to quantify space use patterns in marine animals and the structure of the seascape over which they traverse (Pittman & McAlpine 2003). Although great progress has been made in the field of movement ecology, marine studies have not considered the influence of the spatially explicit patterning of the benthic seascape on movement and habitat utilization patterns (Lima & Zollner 1996). We propose that by combining spatially explicit movement studies with quantitative landscape ecology, a more complete understanding of species–habitat relationships and seascape connectivity can be developed.

We applied a novel approach to movement ecology in the marine environment through the coupling of concepts and quantitative tools from landscape ecology, together with conventional hydro-acoustic tracking techniques and habitat mapping from remote sensing. We demonstrate how seascape structure can be quantified at functionally relevant spatial scales, as determined by the space use patterns of the organisms of interest. Multiple individuals of 2 ecologically important fish species with widespread occurrence across the Caribbean region, bluestriped grunt *Haemulon sciurus* and schoolmaster snapper *Lutjanus apodus*, were acoustically tracked throughout their diel cycle (24 h). These fish are important carnivores that rest in areas with sufficient structural complexity to provide daytime refuge (e.g. large branching corals, patch reefs, boulders) and then migrate to seagrass beds for nocturnal foraging on benthic invertebrates and small fishes (Ogden & Ehrlich 1977, Burke 1995, Cocheret de la Morinière et al. 2003a,b). Such movements are considered to be key vectors for the cross-boundary transfer of energy and nutrients (Clark et al. 2009) and facilitate coral and seagrass growth through nutrient flux (e.g. Meyer et al. 1983, Meyer & Schultz 1985, Layman et al. 2011). Despite their ecological importance, the detailed diel space use patterns and the scheduling of daily activities, such as diel migrations, remain poorly understood.

The primary hypotheses regarding the influence of seascape structure on diel movement patterns of *Haemulon sciurus* and *Lutjanus apodus* include: (1) If foraging takes place at night and resting during the day, then activity spaces will be larger and more complex in shape at night than during the day. (2) If seagrass patches are important as nocturnal foraging areas, then fish should spend a larger proportion of the night over seagrass when compared to other available patch types. (3) If day and night activity spaces are used for different functions, then we expect the composition and spatial configuration of the seascape including size and shape to differ in day versus night areas. (4) In more spatially heterogeneous seascapes, the movement path of individual fish is expected to be more convoluted or tortuous, reflecting more complex individual navigational decisions in response to spatially varying seafloor structure.

## MATERIALS AND METHODS

**Study sites.** Fish were acoustically tracked between July 2008 and March 2010 at 2 locations in the US Virgin Islands: Great Lameshur Bay, St. John, and Brewer's Bay, St. Thomas (Fig. 1). Great Lameshur Bay is located on the southeastern coast of St. John within the Virgin Islands National Park. The interior of Great Lameshur Bay (18° 18′ 54″ N, 64° 43′ 23″ W) is dominated by 2 seagrass species (*Syringodium filiforme* and

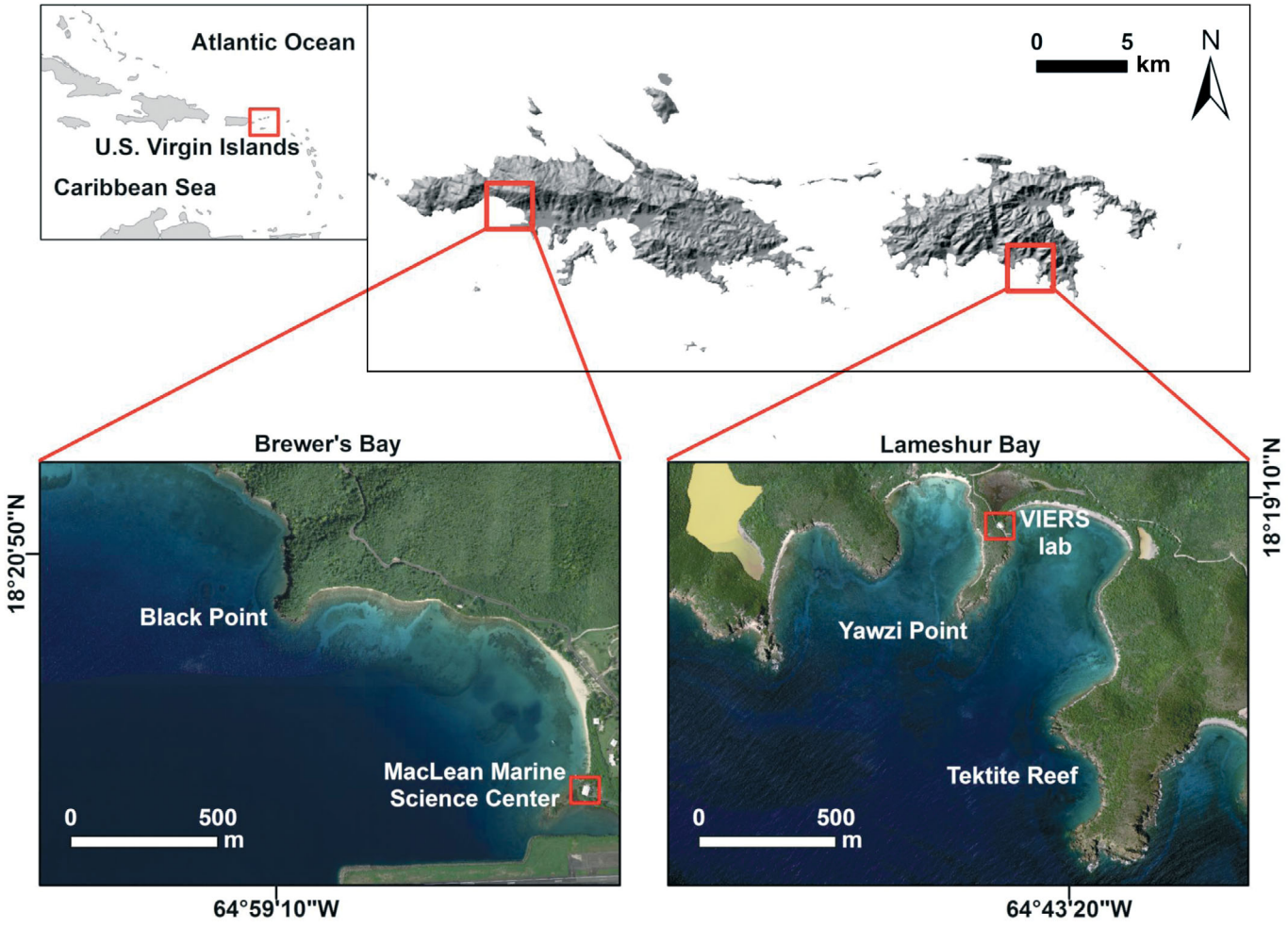


Fig. 1. Study locations for fish tracking within the US Virgin Islands; Brewer's Bay (left) and Lameshur Bay (right)

*Thalassia testudinum*) and is bordered along the northern and eastern shoreline by extensive fields of small (<4 $m^2$) boulders and cobblestones. Much larger (≥4 $m^2$) submerged and semi-submerged boulders can also be found around southwestern and southeastern promontories and are typically colonized by sponges, gorgonians (*Gorgonia ventalina*, *Pseudoplexaura* spp., *Plexaurella* spp.), hard corals (*Millepora alcicornis*, *Porites astreoides*, *Montastraea annularis*), and the endangered elkhorn coral *Acropora palmata*. Fringing coral reefs on the southeastern (Tektite Reef) and southwestern (Yawzi Point) coasts are dominated by *M. annularis* (Fig. 1). A nearly contiguous sand zone (3 to 10 m width) circles the bay and separates the seagrasses interior to the bay from adjacent patches of fringing reef. Brewer's Bay (18° 20′ 34″ N, 64° 58′ 51″ W) is located on the southwestern coast of St. Thomas. Brewer's Bay also has interior seagrass beds, small boulder and cobblestone fields, large boulders surrounding a promontory (Black Point), and *M. annularis*-dominated fringing coral reefs (Fig. 1).

**Tagging and tracking.** A total of 6 individuals of each target fish species, *Haemulon sciurus* and *Lutjanus apodus*, were obtained using baited fish traps set for 48 h on sandy patches adjacent (<5 m) to benthic structures near their daytime resting locations (i.e. patch reefs, boulders). Each specimen (>24 cm total length, TL) had a V9-2L continuously 'pinging' acoustic transmitter with 1 s ping rate (dimensions 9 × 29 mm, carrier frequencies 75 to 84 kHz; Vemco) surgically implanted into its abdominal cavity. Fish were kept in flow-through seawater holding tanks at either the MacLean Marine Science Center (St. Thomas) or the Virgin Islands Environmental Resource Station (VIERS) laboratory (St. John) until they exhibited normal behavior (i.e. freely swimming), which was typically within 2 h of surgery. Tagged fish were then transported in aerated containers to the site of capture and released by a snorkeler to ensure safe descent to the substratum.

Continuous tracking methodologies (e.g. Lowe et al. 2003, Topping et al. 2005, Papastamatiou et al. 2009) were used to quantify diel movement behavior and

habitat utilization patterns. Tracking began no earlier than 24 h post tag implantation to allow fish to re-acclimate to the habitat and to minimize the effects of surgery on movement behavior (Papastamatiou et al. 2009). All continuous tracking was conducted for an interval of 24 h from a 17 foot motorized catamaran equipped with a directional hydrophone (Vemco model VH110) and acoustic receiver (Vemco model VR100). Prior to the study, the range (~200 m) and accuracy (2 to 5 m) of the hydrophone were tested in each bay. A researcher manually operated the hydrophone, which allowed for 180° tilting and 360° rotation and hastened transmitter signal acquisition. GPS fixes were acquired at 15 min intervals using a hand-held GPS. Fixes were only taken when the transmitter signal strength was repeatedly greater than 85% while the hydrophone was pointed facing directly downward below the vessel (i.e. perpendicular to the substrate).

**Quantifying activity spaces and movement paths.** All activity space estimations were performed using the ABODE extension (Laver 2005) in ArcMap GIS v. 9.2 (ESRI). A 95% kernel utilization distribution (KUD) was calculated from GPS fixes acquired for each fish during diurnal and nocturnal periods that spanned 24 h. The KUD is a probability distribution that represents the area in which a fish can be found 95% of the time during the tracking event. Here the 95% KUD was only calculated for the diurnal and nocturnal time periods to make specific diel movement comparisons (e.g. Tolimieri et al. 2009). Diurnal and nocturnal periods were defined based on the United States Naval Observatory sunrise/sunset time charts (http://aa.usno.navy.mil/data/docs/RS_OneYear.php) for Charlotte Amalie (St. Thomas) and Coral Bay (St. John), whereby night began at sunset and day began at sunrise.

Measures of tortuosity were analyzed for diurnal and nocturnal movement pathways of each fish using estimates of the fractal dimension (*D*), as described by Nams (2005) and Papastamatiou et al. (2009). The fractal dimension of a movement path is a measure of the convolutedness of a movement pathway and typically varies between 1 (straight line) and 2 (patch completely covers a plane). Recent work has raised concerns about calculating overall *D* values for movement paths that are correlated random walks (i.e. when the overall movement path is random but successive points are correlated; Nams & Bourgeois 2004, Papastamatiou et al. 2009). Therefore, we used Fractal version 5.0 to compare the movement paths and their mean fractal *D* values across multiple spatial scales, and then calculated the fractal mean only for paths that deviated significantly from a correlated random walk (CRW) model. Fractal v. 5.0 detects deviations from a CRW model by calculating observed and expected (generated by CRW model) net distance traveled values for each movement path and then calculates the mean difference between them (see Nams & Bourgeois 2004).

**Mapping and quantifying seascape structure.** Benthic habitat maps with a minimum mapping unit of 4 $m^2$ were hand digitized from aerial photography (ground resolution 0.3 × 0.3 m) of St. Thomas and St. John using the Habitat Digitizer Extension in ArcGIS 9.3 (Kendall et al. 2001); 9 patch types—aggregate coral reef, colonized bedrock, colonized boulder, patch coral reef (individual), rocky reef, sand, sparse seagrass with 10–30% cover, dense seagrass with 30–90% cover, and scattered coral/rock in unconsolidated sediment (SCR)—were classified from the aerial photography. Colonized substrates were sparsely covered with a variety of scleractinian corals, gorgonians, and sponges. Since little is known about the appropriateness of a single thematic resolution when mapping seascapes for ecological studies, we used a hierarchical scheme to allow for selection of 2 levels of thematic resolution (i.e. a detailed and a coarse benthic habitat map) to quantify seascape structure (Pittman et al. 2004, Kendall & Miller 2008). The detailed thematic resolution benthic habitat map was created using all 9 patch types, and coarse map was created using only 3 patch types: (1) hardbottom (all types of reef, pavement, and boulder combined), (2) sand (including SCR), and (3) seagrasses.

**Benthic map accuracy.** To assess and validate the accuracy of the benthic habitat maps, reference points (n = 204) were randomly generated on each map according to an area-weighted, stratified random sampling protocol using the GIS-based NOAA Sampling Design Tool (Menza 2008). Reference points were located in the field with a handheld GPS receiver, the patch type was independently evaluated by a snorkeler, and underwater photographs were taken for additional verification. For final accuracy assessment, we compared the benthic habitat map reference point data to *in situ* data by constructing an error matrix for each map to show overall accuracy (the sum of correct classifications, divided by the total number of reference points), producer's accuracy (percentage of correct classifications per patch type), and user's accuracy (percentage of correctly classified points divided by the number of validation points per patch type). The Tau coefficient ($T_e$) was used to measure the improvement of classification accuracy compared to a random assignment of map units to map categories (Ma & Redmond 1995).

For the detailed benthic habitat map with 9 patch types, the overall accuracy of the Lameshur Bay and Brewer's Bay maps was 89.2 and 78.4%, respectively; however, the user's accuracy for sparse seagrasses (10–30% cover) was 50% for the Lameshur Bay map due to difficulty differentiating between sparse sea-

grass and sand. Map accuracies for the coarser benthic habitat maps with 3 patch types were 95.1% for Lameshur Bay and 91.2% for Brewer's Bay.

Because coarse versions of the maps with only 3 patch types (hard bottom, sand, and seagrass) improved overall map accuracies, all but 2 spatial pattern metrics were applied to the more accurate coarser-resolution map. The detailed map with all 9 patch types, however, was used to examine fish residency times within patch types and to calculate patch richness within activity spaces. Patch richness is the number of patch types within day and night activity spaces. Polygons representing day and night activity spaces were overlayed on the benthic habitat maps, and used to clip out the seascapes using a GIS tool. Spatial pattern metrics were applied to the seascapes using Patch Analyst 4 extension (Elkie et al. 1999) for ArcGIS 9.3 and FRAGSTATS (McGarigal et al. 2002). Metrics included the area of each patch type, the number of patch types (i.e. patch richness), the shape index, and edge metrics such as total edge and contrast-weighted edge density. Raster data were used to calculate the shape index, which equals the patch perimeter (number of raster cells) divided by the minimum perimeter (number of raster cells) possible for a maximally compact patch (square raster format) of the corresponding patch area (McGarigal et al. 2002). Contrast-weighted edge density is a measure of patch edge per unit area proportionate to the degree of contrast in the seascape (McGarigal et al. 2002).

**Statistical analysis.** Paired *t*-tests were used to examine the statistical difference between day and night movement path complexity, activity space size, activity space shape index, patch richness, and seascape. Data were $\log_{10}$ or fourth-root transformed to meet the parametric assumptions of normality; $D$ was $\log(D-1)$ transformed (sensu Nams 2005). To test whether movement path complexity was positively correlated with seascape complexity, we used linear regressions to compare the fractal $D$ values to total edge, contrast-weighted edge density, patch type area, and patch richness of the seascape. To measure similarities between the multivariate seascape structure of day and night activity spaces and to test for significant differences, non-parametric, multivariate analyses were conducted in PRIMER 6 (Clarke & Gorley 2006). Multivariate data were fourth-root transformed to allow intermediate and low values to make a contribution (Clarke & Green 1988) and were averaged across time period (i.e. day and night) and species. Ordination by non-metric multidimensional scaling (nMDS) was applied to matrices of Bray-Curtis pairwise similarities (Clarke et al. 2006) to examine between-sample patterns of seascape structure in a 2-dimensional plot. Analysis of similarity (ANOSIM; Clarke & Green 1988, Clarke 1993) was used to test for significant differences in multivariate seascape structure within and among *Haemulon sciurus* and *Lutjanus apodus* day and night activity spaces. We used similarity percentage analysis (SIMPER, Clarke 1993) to identify the seascape metrics contributing most to differences in the seascape structure.

## RESULTS

### Fish activity spaces

Adult *Haemulon sciurus* and *Lutjanus apodus* were tracked for 24 h between July 2008 and March 2010 (Table 1). All fish except H1 exhibited increased night movement activity that resulted in either an expansion

Table 1. *Haemulon sciurus* and *Lutjanus apodus*. Summary data of 6 *H. sciurus* (H1–H6) and 6 *L. apodus* (L1–L6) tracked in Great Lameshur and Brewer's Bays, US Virgin Islands, between July 2008 and March 2010. The ratio between night (N) and day (D) activity space areas calculates the magnitude of the difference between the 2 activity spaces. Activity space areas are calculated from rasterized polygons of 95% fixed kernel utilization distribution estimates. Distance between day and night activity spaces is calculated as the Euclidean distance between the centroid of each activity space. TL: total length; dates are given as m/d/y

| ID | TL (cm) | Tag frequency (kHz) | Tag date | Track date | Distance D to N (m) | Day area ($m^2$) | Night area ($m^2$) | Ratio (N/D) |
|---|---|---|---|---|---|---|---|---|
| H1 | 24.5 | 84 | 7/13/2008 | 7/14/2008 | 70.2 | 12487 | 8836 | 0.7 |
| H2 | 29.7 | 78 | 10/9/2008 | 10/23/20080 | 2.4 | 281 | 609 | 2.2 |
| H3 | 29.5 | 81 | 6/2/2009 | 6/4/2009 | 187.6 | 175 | 12621 | 72.1 |
| H4 | 30.6 | 75 | 8/1/2009 | 8/26/2009 | 332.7 | 283 | 15663 | 55.3 |
| H5 | 29.3 | 78 | 9/16/2009 | 9/30/2009 | 171.8 | 764 | 4861 | 6.4 |
| H6 | 29.0 | 78 | 3/25/2010 | 4/6/2010 | 329.6 | 2678 | 25267 | 9.4 |
| L1 | 38.3 | 78 | 1/8/2009 | 1/13/2009 | 9.5 | 332 | 2651 | 8.0 |
| L2 | 29.5 | 84 | 4/9/2009 | 4/22/2009 | 11.0 | 627 | 2859 | 4.6 |
| L3 | 30.1 | 78 | 6/2/2009 | 6/11/2009 | 485.7 | 1700 | 19459 | 11.4 |
| L4 | 33.1 | 84 | 8/1/2009 | 9/2/2009 | 360.2 | 4277 | 19187 | 4.5 |
| L5 | 25.1 | 63 | 12/9/2009 | 12/14/20090 | 277.9 | 163 | 9062 | 55.6 |
| L6 | 31.0 | 75 | 1/2/2010 | 1/9/2010 | 52.7 | 644 | 6482 | 10.1 |

of the day activity space or a re-location to a new night activity space via a nocturnal migration. As a result, the size and shape of day and night activity spaces varied widely among all individuals (Table 1, Figs. 2–4); 8 of the 12 diurnal activity space areas recorded for *H. sciurus* and *L. apodus* were smaller than 800 $m^2$ (mean ± SE: 2034 ± 1016 $m^2$), whereas all but 1 of the 12 nocturnal activity space areas was larger than 2600 $m^2$ (10 630 ± 2262 $m^2$; Table 1). For both *H. sciurus* and *L. apodus*, the mean area of night activity spaces was significantly greater than the mean area of day activity spaces (*H. sciurus*: $t = -2.90$, $p = 0.034$; *L. apodus*: $t = -6.12$, $p = 0.002$), thus hypothesis $H_1$ was accepted (Table 2). There was no significant difference between *H. sciurus* and *L. apodus* mean activity space area when day and night activity spaces were combined ($t = 0.0684$, $p = 0.946$). There also was no significant difference between the shape of day and night activity spaces for either species (*H. sciurus*: $t = 0.232$, $p = 0.826$; *L. apodus*: $t = -2.485$, $p = 0.056$), indicating that the shape complexity between day and night activity spaces did not change significantly. In addition to complexity, the shapes of activity spaces tended to be elongated and generally encompassed a distinctive high-contrast edge between patch types such as hardbottom and softbottom areas. Day and night spaces were geographically separated. The average distance between the centroids of day and night activity spaces was highly variable, ranging from 2.4 to 332 m (182.4 ± 54.6 m) for *H. sciurus* and 9.5 and 485.7 m (199.5 ± 83.1 m) for *L. apodus* (Table 1).

### *Haemulon sciurus* seascape use

For *H. sciurus*, the number of patch types (patch richness) within night activity spaces was not significantly different from day activity spaces ($t = -2.33$, $p = 0.067$). The area of dense seagrasses (30–90% cover), colonized bedrock, and sand was significantly greater in night than day activity spaces, and aggregate coral reef area was greater in day than night activity spaces (Fig. 5A,B). Day residence time for *H. sciurus* was highest in aggregate coral reef, followed by colonized bedrock, sand, and dense seagrasses (Fig. 5A). Despite having low areal cover in day and night activity spaces, colonized bedrock was the second-most used patch type during the day (Fig. 5A) and the most used at night (Fig. 5B). Furthermore, the second-highest residence time recorded for *H. sciurus* at night was in seagrass, which encompassed the largest proportion of most night activity spaces (Fig. 5B). Use of aggregate coral reefs decreased more than 55% at night, while use of colonized bedrock and dense seagrasses increased more than 10% at night (Fig. 6A).

### *Lutjanus apodus* seascape use

In contrast to *Haemulon sciurus*, patch richness was significantly higher in *L. apodus* night activity spaces than in day activity spaces ($t = -3.50$, $p = 0.017$). All 9 patch types had greater areas in the night activity spaces than in the day activity spaces (Fig. 5C,D). During the day, *L. apodus* demonstrated habitat utilization patterns that were similar to those of *H. sciurus*; their highest residence times were recorded in hardbottom patch types, such as colonized boulder, aggregate coral reef, and sand (Fig. 5C). At night, *L. apodus* residence times were highest in sand, aggregate coral reef, colonized boulder, and colonized bedrock patch types, respectively (Fig. 5D). From day to night, residence times decreased most in colonized boulder patch types and increased by more than 15% in sand (Fig. 6B). During the day, 3 patch types were used by both species (i.e. aggregate reef, colonized bedrock, and sand), although average aggregate coral reef and sand areas in *L. apodus* activity spaces were more than 50% less than those found in *H. sciurus* activity spaces (Fig. 5A,C). Average colonized bedrock area in *L. apodus* diurnal activity spaces was twice that of *H. sciurus* (Fig. 5A,C). Six patch types had greater areas within night activity spaces of *L. apodus* than in *H. sciurus* night activity spaces (Fig. 5B,D). Residence time in seagrasses was significantly higher at night, but only when combining the 2 species. Thus, $H_2$ was accepted only for both species combined and was rejected for individual species due to inter-species variability in habitat utilization patterns (Table 2).

### Similarity of day and night seascapes

For *Lutjanus apodus*, day and night seascapes were structurally similar (average similarity = 89%), with moderate separation between groups and no statistically significant difference detected (ANOSIM $R = 0.41$, $p > 0.05$). At the level of individual patch types the use of sand patches was greater in the night than within day seascapes, and notably, seagrasses were absent from day seascapes and present (albeit relatively small areas) in night seascapes. For *Haemulon sciurus*, day and night seascapes were structurally more dissimilar (average similarity = 65%) than for *L. apodus*, but high overlap between groups was measured, resulting in no significant difference ($R = 0.28$, $p > 0.05$). The greatest contribution to dissimilarity was the markedly higher average area of sand and seagrasses frequented by fish in night seascapes, accounting for 61% of the dissimilarity. Hardbottom area and total edge contributed 20.0 and 16.3%, respectively, and patch richness contributed least (<1.8%) to the group differences, with a similar number of patch types observed in day and night seascapes for both species.

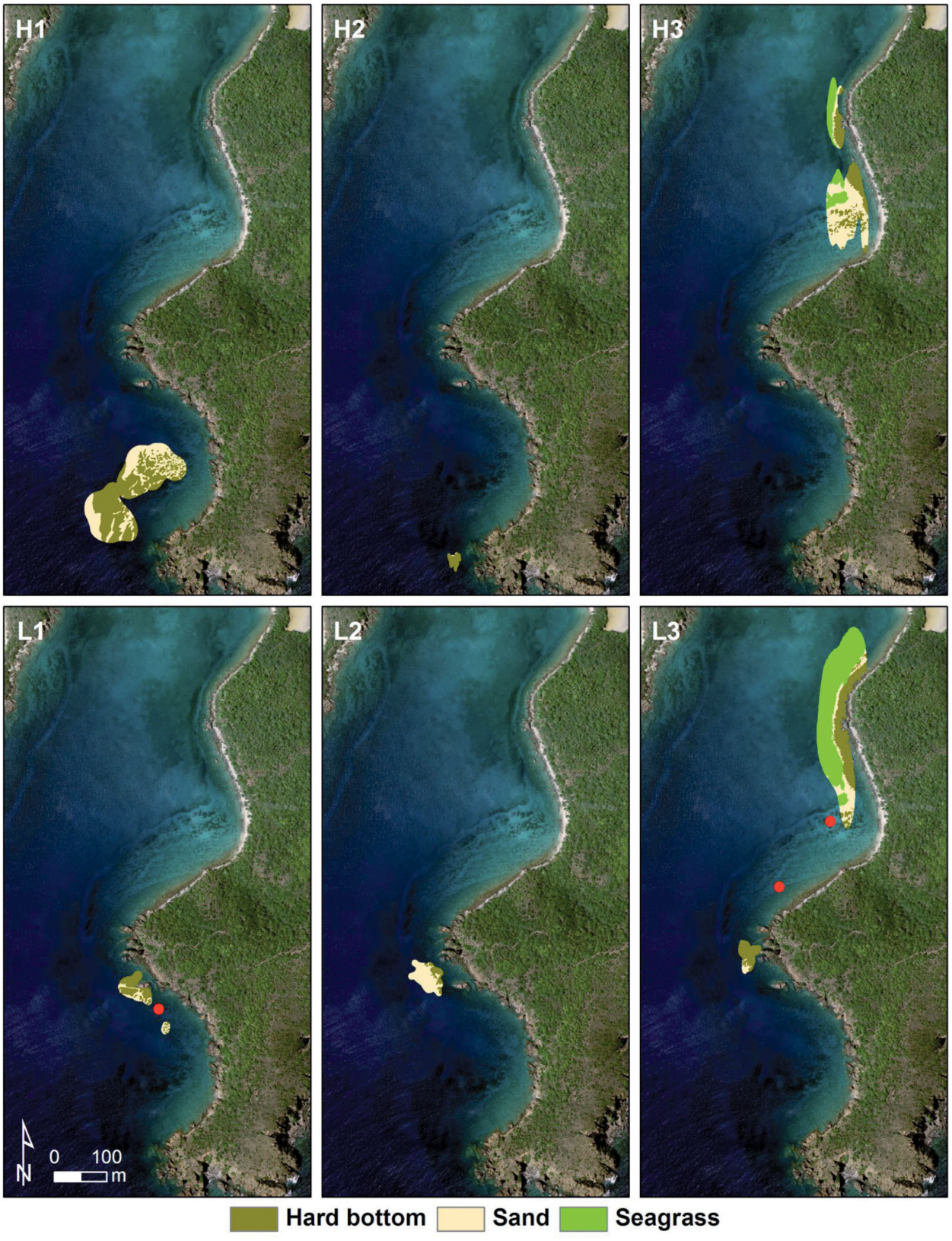


Fig. 2. *Haemulon sciurus* and *Lutjanus apodus*. 95 % kernel utilization distribution diurnal and nocturnal activity space estimates for *H. sciurus* (H1–H3) and *L. apodus* (L1–L3) tracked in Lameshur Bay, St. John. The red dots represent points acquired during the migration between day and night activity spaces

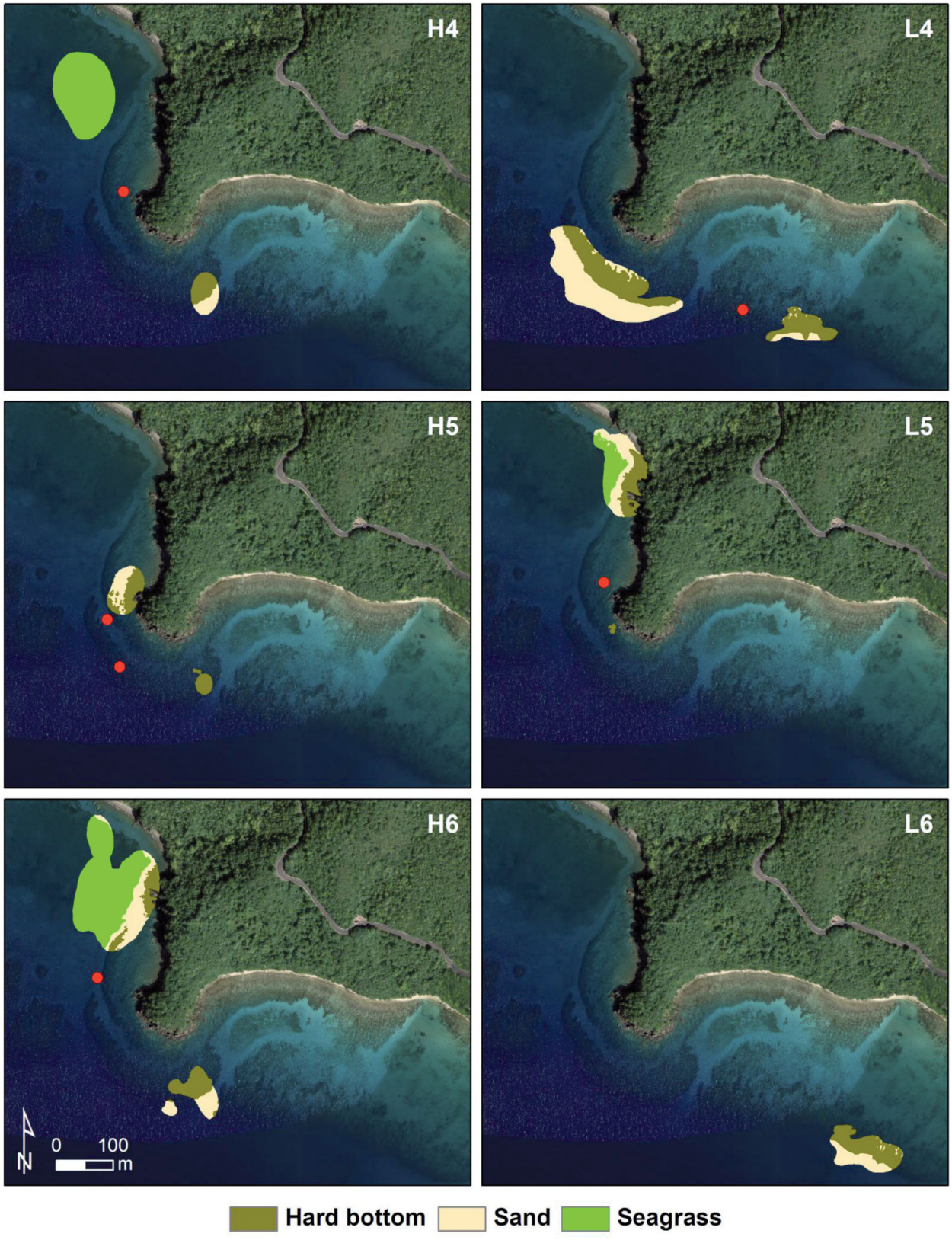


Fig. 3. *Haemulon sciurus* and *Lutjanus apodus*. 95% kernel utilization distribution diurnal and nocturnal activity space estimates for *H. sciurus* (H4–H6) and *L. apodus* (L4–L6) tracked in Brewer's Bay, St. Thomas. The red dots represent points acquired during the migration between day and night activity spaces

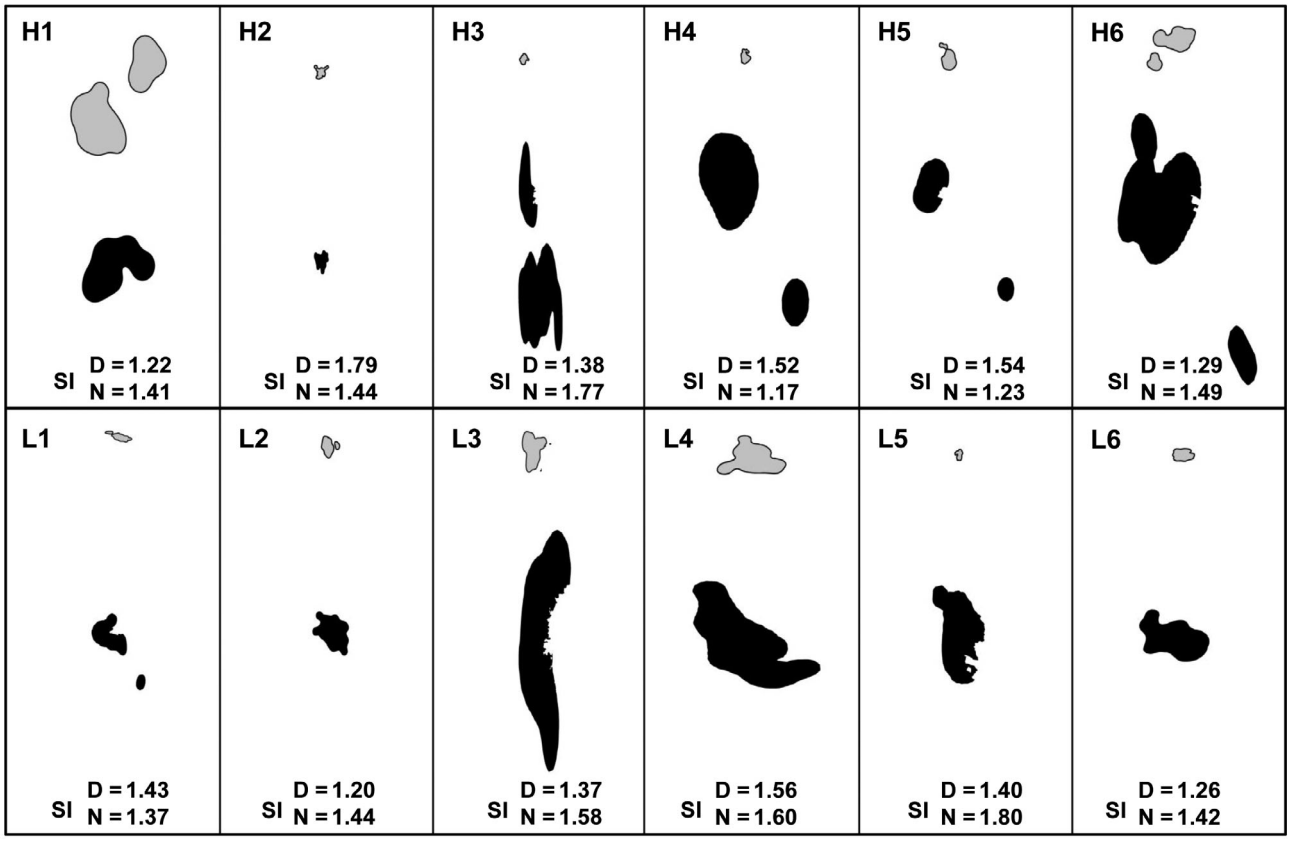


Fig. 4. *Haemulon sciurus* and *Lutjanus apodus*. Shape of day (gray) and night (black) activity spaces for *H. sciurus* (H1–H6) and *L. apodus* (L1–L6). SI: shape index values for day (D) and night (N). All activity spaces are projected at the same scale

Table 2. *Haemulon sciurus* and *Lutjanus apodus*. Interpretation of the results of hypothesis testing for relationships between day and night activity spaces, movement behavior and seascape characteristics. Alternative hypotheses were accepted or rejected based on statistical significance ($p < 0.05$)

| Hypothesis | Test result | Results statement |
|---|---|---|
| $H_1$: Night activity spaces are significantly larger than diurnal activity spaces | Accepted | Both *H. sciurus* and *L. apodus* night activity spaces were significantly larger than day activity spaces |
| $H_2$: Residence time in seagrasses is significantly higher at night than during the day | Only accepted when species were combined | Combined residence time of *H. sciurus* and *L. apodus* in seagrasses was significantly higher at night than during the day |
| $H_3$: Seascape structure is significantly different between day and night activity spaces | Rejected | Seascape structures of day and night activity spaces were not significantly different for *H. sciurus* and *L. apodus* |
| $H_4$: Complexity of the movement paths is positively correlated with seascape complexity (i.e. patch richness, total edge, and contrast-weighted edge density) | Rejected | Movement path complexity was negatively correlated with total edge and area of hardbottom and sand for *H. sciurus* and *L. apodus*. Movement path complexity was negatively correlated with patch richness for *H. sciurus* only |

### Structural differences between multivariate seascape types

Following hierarchical cluster analysis of seascape metrics, 3 groups (A, B, C) were clearly identified based on 75% dissimilarity in multivariate seascape structure. Two-dimensional nMDS ordination plots offered a very good representation of the similarity between seascapes with low stress values and were used to characterize seascape types with high within-group similarity (Fig. 7). Heterogeneity was lowest in Seascape A, highest in Seascape B, and somewhat variable in

Seascape C (Fig. 7). Seascape A was characterized by smaller activity spaces, lower patch richness, total edge, hard bottom, and sand area, and very little seagrass area. The low heterogeneity habitat of Seascape A was primarily day activity spaces (Fig. 7), with fish undergoing relatively tortuous movement pathways ($D \geq 1.53$); the 8 largest $D$ values recorded were in Seascape A. Highest heterogeneity Seascape B habitat exhibited the highest occurrence of seagrasses. Differences in activity space area, patch richness, total edge, and area of sand contributed to Seascape B's dissimilarity from A and C. Seascape B was comprised entirely of night activity spaces (Fig. 7). Seascape C represented an intermediate seascape type with moderate heterogeneity defined by intermediate sized day and night activity spaces. Fish used hardbottom habitat and patchy sand with no seagrasses present, but a high density of edges, particularly edges with high contrast between adjacent patch types (i.e. sand–reef interface).

### Path complexity–seascape relationships

Comparisons between mean fractal $D$ and seascape structure were restricted to 22 samples where movement paths deviated significantly from a CRW model.

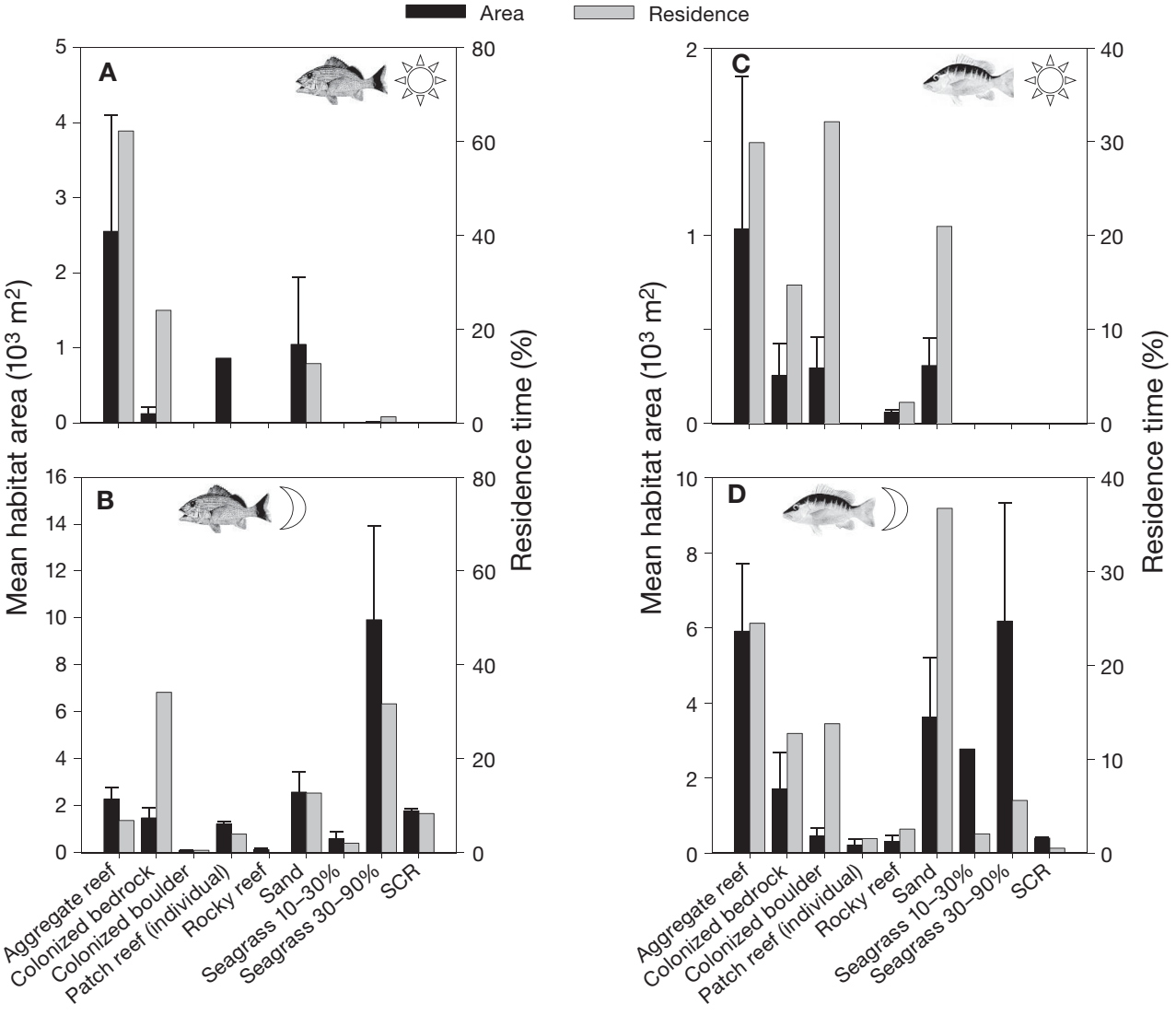


Fig. 5. *Haemulon sciurus* and *Lutjanus apodus*. Plot of residence time (%) and mean patch type area ($m^2$) of aggregate coral reef, colonized boulder, colonized bedrock, individual patch reef, rocky reef, sand, scattered coral/rocks in unconsolidated sediment (SCR), sparse seagrasses (10–30% cover), and dense seagrasses (30–90% cover) used by 6 *H. sciurus* (A, B) and 6 *L. apodus* (C, D) in their day and night activity spaces. Note: $y$-axis scales differ between day and night activity spaces. Error bars absent from area columns with single data points. Error bars: ± SEM

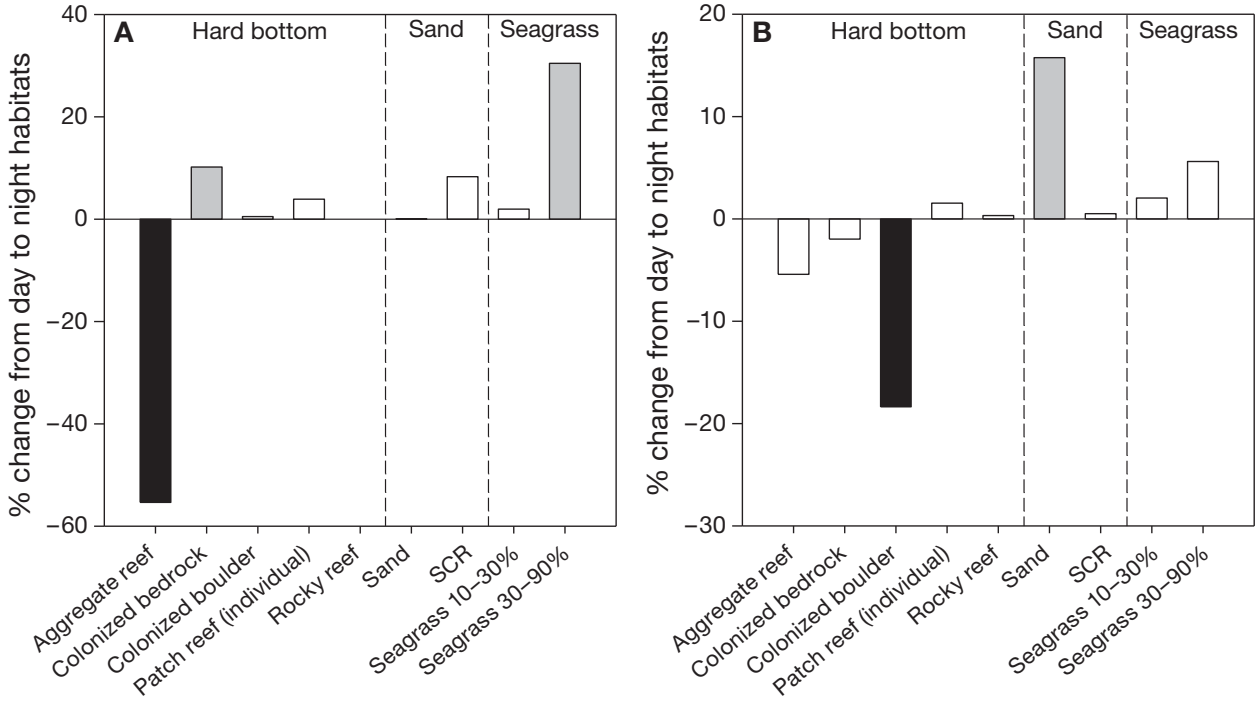


Fig. 6. *Haemulon sciurus* and *Lutjanus apodus*. Percent change of residence times for patch types within day and night activity spaces for: (A) *H. sciurus* and (B) *L. apodus*. Black bars indicate >10% decrease in residence time, gray bars indicate >10% increase in residence time, and white bars indicate <10% change in residence time. Patch types are grouped into 3 coarse categories (hardbottom, sand, seagrass) for comparison. SCR: scattered coral/rocks in unconsolidated sediment

For the entire diel cycle (day and night combined), there was no significant difference in path complexity ($t = -0.058$, $p = 0.95$) between *Haemulon sciurus* and *Lutjanus apodus.* Mean *D* was relatively high for both species (*H. sciurus*: 1.78 ± 0.18; *L. apodus*: 1.70 ± 0.11), indicating very convoluted or tortuous movement patterns. Day movement paths were significantly more tortuous than night movement paths for both species (*H. sciurus*: $t = -8.30$, $p = 0.0037$; *L. apodus*: $t = -3.37$, $p = 0.0199$). Of the 22 mean *D* values analyzed, the 8 most tortuous ($D \geq 1.84$, e.g. Fig. 8A) paths occurred during the day and the 7 least tortuous ($D \leq 1.36$, e.g. Fig. 8B) paths occurred at night.

Linear regressions between path complexity (*D*) and 5 individual pattern metrics revealed negative linear relationships for 27 of 30 bivariate regressions, of which 8 were strong (Table 3) and statistically significant negative relationships. Stronger relationships were detected across the entire diel activity space (day and night seascapes combined). Overall, relatively low heterogeneity seascapes, with greater area of hardbottom and sand patches, relatively low edge (i.e. large continuous patches), and low to medium patch richness, were navigated by more complex fish movement pathways. Hypothesis $H_4$, which predicted more complex pathways across more complex seascapes, was rejected at the spatial and thematic resolution of our study (Table 2). More specifically, the path complexity of *Haemulon sciurus* decreased as total edge, hardbottom area, sand area, and patch richness increased, with slightly stronger linear relationships modeled for night activity (Table 3). Similar relationships (although less strong) emerged for *Lutjanus apodus*, with the strongest negative linear relationships for path complexity and area of hardbottom benthic classes (Table 3). Area of seagrasses was excluded from the linear regression analysis due to a high proportion of 0 values in the data.

## DISCUSSION

In our diel movement study, we found that both grunts and snappers move across spatially heterogeneous patch mosaics through routine daily movements that encompass seascapes over 100's of $m^2$. These benthic seascapes represent an important component of the ecological neighborhood quantified at the level of the individual (sensu Addicott et al. 1989). We provide direct evidence of both inter-species and intra-species variability in space use patterns, including the size and shape of activity spaces. Species differences are likely to be determined by species specific life-history traits, predation pressure, competitors and dietary requirements. In addition, individualistic differences may reflect organism ex-

perience, condition, and behavior. Similarly, acoustic tracking of 2 snapper species in the Bahamas found substantial fine-scale intra-population variability in movement patterns (Hammerschlag-Peyer & Layman 2010). Although the movement patterns in our study varied among individuals, our results demonstrated that both fish species shared similar sun-synchronous scheduling of diel migrations and some similarities in generalized habitat utilization patterns. As in terrestrial fauna (Bolnick et al. 2003), we suggest that intra-population variation is not rare in marine fish and can have a significant effect on ecological processes and therefore caution is required before such complexities are simplified in favor of broad generalizations, which can lead to sub-optimal decisions and uncertain results in conservation planning and ecosystem-based fisheries management. Our study represents an important first step towards applying a landscape ecology approach to behavioral marine ecology that will increase our understanding of marine animal movements across heterogeneous seascapes. Based on our knowledge of the multi-habitat use patterns of coral reef associated fish and the spatial scales at which fish use their environment, we advocate a shift in perspective from the study of individual patch types (e.g. seagrass beds or coral reefs) to a focus on determining how fish use and respond to seascape mosaics.

### Diel behavior patterns and seascape use

The scheduling of migration behavior was closely tied to sunset and sunrise, a phenomenon also described for French grunts *Haemulon flavolineatum*, white grunts *H. plumierii*, and other species (McFarland et al. 1979, Dorenbosch et al. 2004, Krumme 2009). *H. sciurus* and *Lutjanus apodus* departed daytime resting areas at sunset and returned from nighttime feeding areas at sunrise. Although direct evidence of foraging activity during nighttime tracking periods was not obtained, other studies suggest that these 2 species feed primarily at night (Rooker & Dennis 1991, Clark et al. 2009, Hammerschlag et al. 2010). As hypothesized, night activity spaces of *H. sciurus* and *L. apodus* were significantly larger than day activity spaces. Maximum night activity spaces of 25 267 $m^2$ and 19 459 $m^2$ for *H. sciurus* and *L. apodus* were 70 and 11 times greater than their corresponding day activity spaces. Maximum distances between the centers of day and night activity spaces were 332 m for *H. sciurus* and 485 m for *L. apodus*. Other studies have reported similar scales of movement; for instance, Beets et al. (2003) and Verweij & Nagelkerken (2007) observed *H. sciurus* and *L. apodus* moving estimated distances of 230 to 767 m from day resting areas to nighttime foraging areas. Thus, day and night activity spaces and combined diel activity spaces provide an ecologically meaningful unit for scaling the environment in habitat-use studies (Pittman & McAlpine 2003).

*Haemulon sciurus* and *Lutjanus apodus* had broadly similar seascape utilization patterns, generally showing a shift from high relief hardbottom habitats (i.e. coral and rocky reef and boulders) in the day to low relief softbottom habitats (i.e. sand and seagrasses) at night. During night excursions, both species used many more habitats than during the day. Habitat utilization patterns for *H. sciurus* in Brewer's and Lameshur Bays corroborated generalities from previous studies which highlighted the importance of seagrasses for nocturnal foraging in grunts (Ogden & Ehrlich 1977, Burke 1995,

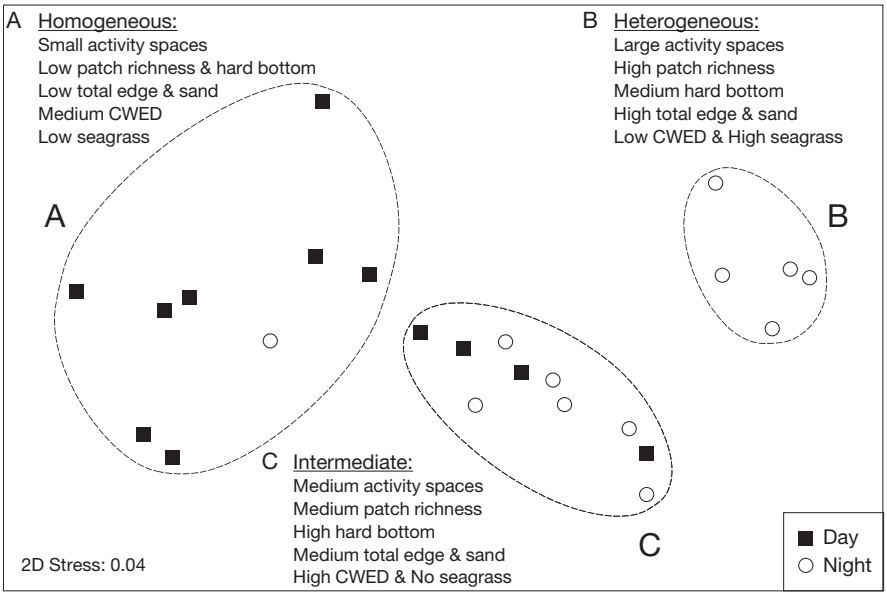


Fig. 7. Dissimilarity among diurnal and nocturnal activity spaces using non-metric multidimensional scaling plots (nMDS) showing relative dissimilarity in seascape composition (area of hardbottom, sand, and seagrass, patch richness) and configuration (total edge, contrast weighted edge density, CWED) for all samples. Hierarchical cluster analysis identified 3 cluster groups (i.e. seascape types A–C) based upon 75% dissimilarity

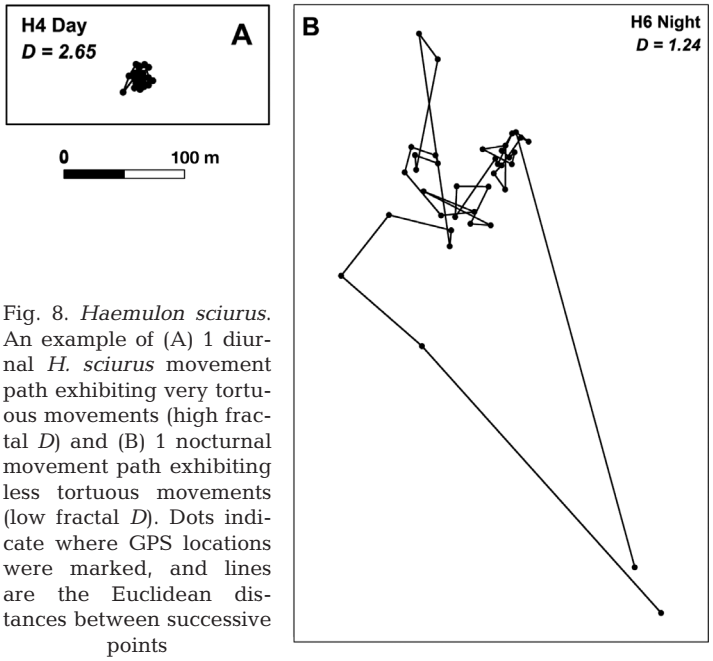


Fig. 8. *Haemulon sciurus*. An example of (A) 1 diurnal *H. sciurus* movement path exhibiting very tortuous movements (high fractal *D*) and (B) 1 nocturnal movement path exhibiting less tortuous movements (low fractal *D*). Dots indicate where GPS locations were marked, and lines are the Euclidean distances between successive points

Table 3. *Haemulon sciurus* and *Lutjanus apodus*. Linear regressions between diurnal and nocturnal seascape metrics (total edge, contrast weighted edge density [CWED], hard bottom area, sand area, and patch richness) and the response variable (mean fractal *D*) for *H. sciurus* and *L. apodus*. Significant ($p < 0.05$) values are highlighted in **bold**. + or – indicates directionality of the relationship

| Seascape variable | *H. sciurus* $R^2$ | p | Relationship | *L. apodus* $R^2$ | p | Relationship |
|---|---|---|---|---|---|---|
| **Total edge** | | | | | | |
| Day + Night | **0.79** | **0.0006** | – | **0.78** | **0.0002** | – |
| Day | 0.67 | 0.0916 | – | 0.62 | 0.0627 | – |
| Night | 0.76 | 0.0527 | – | 0.51 | 0.11 | – |
| **CWED** | | | | | | |
| Day + Night | 0.16 | 0.2488 | – | 0.03 | 0.5756 | – |
| Day | 0.03 | 0.7889 | + | 0.16 | 0.4288 | – |
| Night | 0.01 | 0.8912 | – | 0.36 | 0.2044 | + |
| **Hard bottom** | | | | | | |
| Day + Night | **0.81** | **0.0004** | – | **0.72** | **0.0005** | – |
| Day | 0.63 | 0.1111 | – | 0.63 | 0.0594 | – |
| Night | 0.69 | 0.0794 | – | 0.57 | 0.0843 | – |
| **Sand bottom** | | | | | | |
| Day + Night | **0.75** | **0.0012** | – | **0.60** | **0.0030** | – |
| Day | 0.30 | 0.3369 | – | 0.45 | 0.1466 | – |
| Night | **0.88** | **0.0184** | – | 0.20 | 0.3703 | – |
| **Patch richness** | | | | | | |
| Day + Night | **0.42** | **0.0426** | – | 0.31 | 0.0594 | – |
| Day | 0.24 | 0.3984 | + | 0.08 | 0.5946 | – |
| Night | 0.60 | 0.1264 | – | 0.32 | 0.2377 | – |

Cocheret de la Morinière et al. 2003a,b). Clearly the juxtaposition of hard- and softbottom patch types is important in defining suitable seascapes for *H. sciurus*. Our seascape ecology approach, however, also revealed that hardbottom areas such as colonized bedrock are important for *H. sciurus* at night. In contrast, *L. apodus* spent only a small proportion of its time over seagrasses compared to *H. sciurus* and instead demonstrated a clear preference for hardbottom and unvegetated sand during nocturnal periods. Further studies are required to determine whether this observed pattern reflects habitat requirements that are affected by the close proximity to higher relief areas that provide greater refuge from predators, or whether this is inter-species habitat partitioning due to competition or differences in diet (Gladfelter & Johnson 1983, Burke 1995).

Dietary analysis indicates that *Haemulon sciurus* feeds primarily on benthic crustaceans and mollusks including shrimps, small portunid and xanthid crabs, and bivalve mollusks abundant in seagrass beds (Randall 1967). Nagelkerken et al. (2000) found that densities of macro-invertebrate prey (i.e. Tanaidacea and Copepoda) most commonly consumed by *H. sciurus* were higher in seagrass and algal beds than in other biotopes, which may explain *H. sciurus* showing higher residence times in soft sediment habitats. Higher residence time over hardbottom and sand patches for large, reef-dwelling *Lutjanus apodus* may be directly attributable to their preference for small demersal fishes (Rooker 1995, Cocheret de la Morinière et al. 2003a,b), particularly juvenile scarids and acanthurids, which are known to heavily graze areas immediately adjacent to reefs (Randall 1965). Our findings revealed that diel space use patterns are more spatially complex and variable than was previously known, since some fish use a wide range of patch types during the day and night and do not always migrate directly between resting and foraging activity spaces at sunset and sunrise. Nocturnal foraging in seagrass beds, therefore, may be a facultative behavior for some individuals and species, particularly *L. apodus,* which may be more generalist than *H. sciurus* (Verweij et al. 2006). Nagelkerken et al. (2000) suggested that intraspecific competition and evasion of predators may lead to inclusion of some patch types that are sub-optimal foraging areas, but offer higher refuge function.

Our results are likely to be location specific, but the high variability between sites and within species highlights the need for further tracking studies that explore geographical variability, as well as inter-species variability in seascape utilization patterns. Acoustic tracking studies are capable of revealing the detailed spatial movements that when combined with benthic habitat maps will provide more complete information on habitat utilization patterns.

Very little is known about the development of specialized movement tactics when fish navigate across spatially heterogeneous seascapes; this presents a new frontier in behavioral landscape ecology.

### Path complexity and seascape structure

Daytime movement paths were significantly more tortuous than nocturnal paths for both species. The highly convoluted, back and forth movements, often resulting in relatively small activity spaces, are indicative of sheltering behavior (Turchin 1996, Nams & Bourgeois 2004). Unexpectedly, both species exhibited a less complex movement pathway over more spatially heterogeneous seascapes as evidenced by highly negative correlations between the fractal dimension of the pathway and seascape characteristics, such as total edge and patch richness. However, the strongest negative relationship was modeled for *Haemulon sciurus* nighttime path complexity and area of sand, which could be due to more directed linear movements over open sandy areas with low refuge function and low prey abundance. Further studies are required to examine foraging behavior and prey distribution throughout activity spaces. These findings provide insight into the complex movement ecology of these 2 species. Our counter-intuitive finding that movement paths were more complex in more homogeneous seascapes may be influenced by our focus on 2-dimensional structure. Future studies should also include structural characteristics of the 3-dimensional seafloor terrain that would quantify vertical relief, an important variable determining the refuge function of the seascape. Boat-based acoustic surveys or airborne hydrographic light detection and ranging (LiDAR) are capable of mapping detailed seafloor bathymetry within fish activity spaces to provide 3-dimensional terrain models of the seascape (Costa et al. 2009). Since the nocturnal activity spaces were more heterogeneous, adopting less tortuous (straighter) movements may increase the likelihood of fish encountering desired patches of food (Zollner & Lima 1999). In controlled experimental microlandscapes, McIntyre & Wiens (1999) manipulated the spatial arrangement of resource patches and observed low $D$ values for the movement paths of a terrestrial beetle, *Eleodes extricata*, when resource patches were randomly distributed. Experiments with controlled microseascapes, analogous to microlandscapes (Wiens et al. 1995), could be used to further examine the influence of seascape patterning on faunal behavioral decisions, understand navigational strategies across seascapes with different patterning, and identify structure–function threshold effects. *H. sciurus* and *Lutjanus apodus* were also observed making rapid, directed linear movements during twilight migrations, a strategy thought to reduce predation risk by minimizing the time spent in unfavorable patch types (Zollner & Lima 1999). During these movements, a few successive detections were recorded (difficult to obtain due to the speed of movement, Figs. 2 & 3) within sand corridors between habitat types or along the edges of reefs, indicating that the fish used edge features as easily navigable corridors between day and night activity spaces. Very little is known about the mechanisms associated with edge permeability and attraction of fish to edges, although edge effects have been reported for marine fish and invertebrates (Boström et al. 2006).

### Relevance of seascape types

High variability in seascape structure across day and night activity spaces resulted in relatively low dissimilarity between groups, particularly for *Lutjanus apodus*. The fact that *L. apodus* seascapes for day and night activity spaces were structurally more similar to each other than were day and night spaces for *Haemulon sciurus* suggests that the 2 species differ in the way that they differentiate when selecting habitat, but that the selection is unlikely to be a random one. Although both species are widespread and known to utilize a wide range of patch types, it appears that *L. apodus* may be more of a seascape generalist than *H. sciurus*, which showed a distinctive twilight migration to locate softbottom areas with seagrasses for nocturnal foraging. Statistical identification of seascape types as an approach for characterizing suitable habitat can be applied as a cost-effective tool to identify beneficial combinations or configurations of patch types. This technique is also useful for classifying the relative position of fish species along a gradient of seascape generalist to specialist. It is likely that the seascape type approach may prove more discriminatory when applied to seascape specialists.

Furthermore, the inshore–offshore ontogenetic habitat shifts from embayment nurseries to non-bay coral reefs reported for grunts and snappers elsewhere in the Caribbean (Verweij & Nagelkerken 2007, Grol et al. 2011) may not be typical. Instead, we propose that in some bays where coral reefs and seagrasses exist in close proximity, individuals that require both resources may simply expand their home range with maturity rather than shifting to deeper non-bay coral reefs.

### Management implications and further studies

This study demonstrates ecological connectivity between mosaics of different patch types and highlights

that multiple resources are important to fish at the scale of hundreds of meters. Although the level of dependence on each component patch types is unknown for many species, it is clear that to address habitat conservation for the species studied here, decision makers must consider the functional integrity of seascapes rather than focusing primarily on individual patch types. Although *Haemulon sciurus* and *Lutjanus apodus* are commonly referred to as coral reef fish, it is apparent that much of their time is spent in non-reef patch types, and the juxtaposition of both hard- and softbottom patch types combines to define suitable seascape types for the persistence of species. This information can be used to parameterize species distribution models to predict suitable areas and therefore to map essential fish habitat (EFH). This task is made more complicated by strong intra-population space use variability, but consideration of individualistic responses may be necessary to accurately map the potentially broad spectrum of patch types used by species, particularly those that appear to be seascape generalists. Consequently, our sample size of 6 individuals per species may have been insufficient to completely characterize what may be a very diverse set of routine movement patterns. We strongly advocate that more fish-habitat use studies be conducted over the daily home range extent and over multiple days for individual fish; this is particularly important when research is used to identify EFH.

For the short duration of our study, we found relatively high site fidelity within daily activity spaces that could be easily protected by fairly small marine protected areas, although protecting the life stages through ontogenetic shifts and migration to potential spawning aggregation sites for these species is likely to require larger protected areas. The movement data can be used to understand the spatial scales of nutrient and trophic fluxes occurring between day resting areas and night feeding areas. Further studies are required to determine the thresholds in seascape configuration that make some areas unsuitable or sub-optimal and others suitable. Some seascapes will enhance connectivity, growth, and survival, and the identification of these optimal seascapes is a valuable tool for marine management and particularly important for biodiversity conservation and for protection of endangered species. More detailed studies coupling high-resolution tracking with high-resolution seafloor mapping can be used to understand the behavioral response to structural features including the use of landmarks, provide insights on fish navigation, and to identify and predict migration pathways. Incorporating information on spatial patterns of food availability and foraging rates together with observations of predator and competitor interactions will link key ecological processes to seascape structure. More broadly, the spatially-explicit understanding of movement ecology is essential to guiding scale selection in ecological studies and for the development of a mechanistic foundation for seascape ecology analogous to key early development in terrestrial landscape ecology (Ims 1995, Wiens 1995, Lima & Zollner 1996).

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# Relating landscape development intensity to coral reef condition in the watersheds of St. Croix, US Virgin Islands

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ABSTRACT: Land-based sources of pollution are a major threat to the health of coral reefs. We report, for the first time, a study that relates coral reef condition to human modifications of the landscape. Stony coral community richness, cover, colony size, and density were assessed along with 3-dimensional coral cover in the near-shore waters of St. Croix, US Virgin Islands, in 2006 and 2007. Land use/land cover data (LULC, 2.4 m resolution) and a landscape development intensity (LDI) index, an indicator of human activity calculated from the LULC data, were used to explore relationships with coral indicators. The LDI index was more robust than other indicators of human activity, exhibiting negative correlations with stony coral colony density, taxa richness, colony size, and total coral cover. High variability observed in coral density and taxa richness was better explained when percent natural land and average coral station depth were considered along with the LDI index. Percent impervious surface in the watershed was negatively correlated with 1 coral condition indicator, total coral cover. The LDI index is an effective landscape indicator of human impact on St. Croix corals, highlighting the link between land-based human activity and marine ecosystems. Further development of this tool will aid in land use planning and prioritization of conservation efforts.

KEY WORDS: Coral reef condition · Coastal watersheds · Land-cover/land-use · Landscape development intensity (LDI) index



## INTRODUCTION

Coral reefs are productive and diverse ecosystems that provide valuable ecological services such as harvestable fish, a beautiful seascape that attracts tourists, and protection of vulnerable shorelines from storms and wave action (Moberg & Folke 1999). Protection and restoration of coral reef ecosystems are fundamental management goals for regions of the world where corals are found. However, sustainable coral reef management is hindered, at least in part, by uncertainty surrounding the impacts to coral reefs of the many and varied human-generated stressors (Richmond 1993, Hughes & Connell 1999, Downs et al. 2005). Coral reef ecosystems may be impacted by local pressures such as landscape development (Dubinsky & Stambler 1996, Burke & Maidens 2004, Fabricius 2005), by regional pressures such as over-harvesting of fishery stocks (Valentine & Heck 2005), and by global pressures such as rising sea surface temperatures and ocean acidification stemming from increased atmospheric $CO_2$ (Wilkinson 1996, Hoegh-Guldberg et al. 2007). The variability and interaction of these stressors can confound management strategies for conservation and restoration of coral reef ecosystems. Moreover, effects of local watershed stressors may be masked and difficult to document.

Increases in terrigenous pollutants entering the ocean result from land use changes in coastal and inland watershed landscapes. Clearing land, creating impervious surfaces, and applying fertilizers, herbicides, and pesticides can act in concert to accelerate terrestrial runoff of sediments and associated chemical contaminants known to cause decline in coral ecosystems (Wolanski et al. 2004, Warne et al. 2005, Richmond et al. 2007). Physical smothering and mortality of reef-building scleractinian (stony) corals occurs with prolonged exposure to high levels of sediment. Sediment trans-

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ported to reefs may inhibit stony coral photosynthesis directly by attenuating light (Rogers 1979), or indirectly when energy is diverted to mucus production to slough sediment off coral surfaces (Riegl & Branch 1995). Negative consequences for corals exposed to sediments include loss of cover (Cortés & Risk 1985), impaired fertilization (Gilmour 1999), decreased larval settlement and survivorship (Babcock & Smith 2000), reduced growth (Dodge et al. 1974, Miller & Cruise 1995), and altered community structure (Loya 1976, for review see Rogers 1990, Fabricius 2005). Despite recognition of these problems, protection of corals from watershed pollution has been limited (Richmond et al. 2007).

An obstacle to effective management at local scales is the lack of quantitative information that links coral condition to human activities on land. This requires both coral condition and human activity indicators. Stony coral indicators are highly valued for coral reef management because stony corals form the permanent infrastructure of a coral reef and provide habitat and nursery grounds for nearly all reef inhabitants (Dahl 1973, Fisher 2007). However, to be useful for relating reef condition to human activity, coral condition indicators must also be sensitive to anthropogenic disturbance over global and regional factors that affect coral condition. This requires testing candidate indicators at sites located across a human activity gradient (Fore et al. 2008). A recent study in St. Croix, US Virgin Islands, found that measurements of stony coral size, taxa richness, and colony density (among others) were sensitive to distance from an active industrial area (Fisher et al. 2008). Consequently, these measurements were candidates for investigating relationships between reef condition and human activities in the watershed.

Although development of indicators for human activity has been challenging (Mack 2006), a landscape development intensity (LDI) index, calculated from land-use/land-cover (LULC) data, has shown great promise for quantifying human disturbance (Brown & Vivas 2005). The LDI index has been successfully related to pollutant loads (Brown & Vivas 2005), to the ecological condition of wetlands in both the midwest (Mack 2006, 2007) and southeast USA (Brown & Vivas 2005, Reiss & Brown 2007), and has been adopted into condition assessment protocols for aquatic ecosystems by several US states. LDI represents the cumulative anthropogenic impact in terms of nonrenewable energy to a landscape unit; in this case, a watershed. The basis for the LDI lies in spatially explicit, high-resolution LULC data that offer valuable information for landscape ecology studies (Wu 2006).

Here, the LDI was applied in a novel context that explores potential extension of landscape ecology methods to the seascape. In this exploratory comparison, stony coral condition was related to watershed LULC and LDI values. We also compared the capacity of other potential human activity indicators to predict coral reef condition using multivariate analysis. If significant relationships between human activity and coral condition were found, the expectation was that watersheds with greater human impact would be associated with reduced coral reef condition. The methods and relationships discovered have potential use for the development of water quality standards based on coral condition (i.e. biological criteria, Fore et al. 2008, 2009) and for local land-use zoning, planning, and permitting as pertains to the conservation and restoration of sustainable coral reef ecosystems.

## MATERIALS AND METHODS

**Coral condition data.** Coral survey data were collected during 2 surveys in the coastal waters of St. Croix (US Virgin Islands) using the US Environmental Protection Agency's (USEPA) stony coral rapid bio-assessment protocol (Fisher 2007). Stations were selected for the 2006 survey in 4 coastal zones, viz. 3 zones near centers of human activity and 1 zone with minimal human activity, to test the responsiveness of coral indicators (Fig. 1, Fisher et al. 2008). Stations were selected for targeted sampling following snorkel reconnaissance for the best available habitat (i.e. highest coral cover) at approximately constant intervals from predetermined locations. In the second survey (2007), stations were selected randomly from 'coral and hardbottom' areas identified on benthic habitat maps (Rohmann et al. 2005, NOAA; http://ccma.nos.noaa.gov/ecosystems/coralreef/usvi_pr_mapping.html). Sites were selected using a probabilistic approach to avoid redundancy yet allow spatial extrapolation of results to the entire region (Hughes et al. 2000, USEPA 2008). Site selection was confined to coral and hardbottom areas within 1.5 km of shore and <12 m depth (Fig. 1).

One transect was surveyed at each station. Survey transects were established by placing a tripod on the substrate which held an upright pole in place, and a 2 m wide annulus (radial belt) was surveyed 3 to 5 m from the pole. Data were recorded from either a full annulus (360°; transect area = 50.2 $m^2$) or a half annulus (180°; transect area = 25.1 $m^2$) if colony density was very high. Data for full-annulus transects were collected in half-annulus segments and averaged to obtain a single station value. All stony corals (order Scleractinia) described by Humann & Deloach (2002) and 1 reef-building hydrocoral (*Millepora complanata*) were included in the survey. Because goals of the 2 surveys did not include coral recruitment, only colonies >10 cm in diameter were documented. Coral species, colony dimensions, and approximate % live tissue were

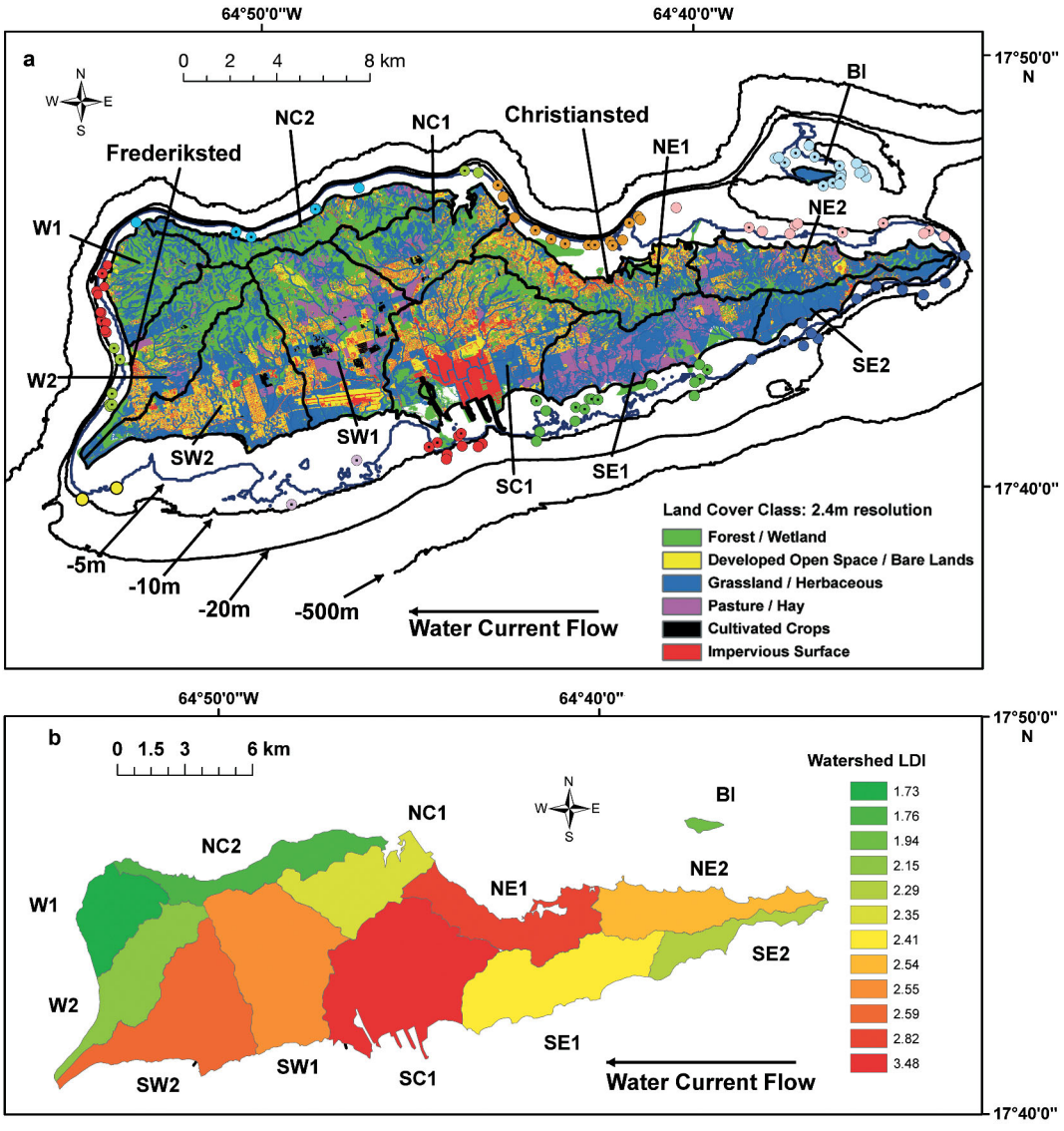


Fig. 1. (A) St. Croix watersheds and associated coral stations from 2006 (circles with dots) and 2007 (circles). Clusters of stations that share a common color (colors are not related to those used to indicate land use) were associated with the adjacent watershed for evaluating relationships between watershed metrics of human disturbance and coral condition. Land use/land cover used in the analysis is shown at 2.4 m resolution. (B) Watershed landscape development intensity (LDI) values shown on a green–yellow–red continuum, where green indicates the lowest human disturbance and red indicates the highest. Watershed abbreviations: BI: Buck Island; NC: North Central: NE: Northeast; SC: South Central; SE: Southeast; SW: Southwest; W: West

recorded. Coral size was calculated from measured dimensions as 3-dimensional (3D) colony surface area (SA) rather than traditional projected (planar) 2-dimensional SA, to capture habitat values (Fisher 2007). Three-dimensional coral colony SA was calculated as 3D area = $x \pi r^2$, where $x$ = 1, 2, 3, or 4 depending on species and typical topographic complexity of colonies; flat colonies were assigned a '1' (including *Agaricia agaricites*, *A. fragilis*, *Meandrina meandrites*, *Mycetophyllia ferox*, and *M. lamarckiana*); hemispherical colonies were assigned a '2' (brain and massive corals including *Diploria* spp., *Montastrea cavernosa*, *M. faveolata*, *M. franksii*, and *Porites astreoides*); dome-shaped, lobed, plate, and finger corals were assigned a '3' (*Agaricia tenuifolia*, *Dichocoenia stokesii*, *Montastrea annularis*, and *Porites* spp.); and highly branched corals of the genus *Acropora* were assigned a '4.' This approach to SA estimation was adapted from Dahl (1973) and Acala & Vogt (1997), who also used surface index adjustments to estimate 3D SA. *Dendrogyra cylindricus* was the exception, for which a geometric formula for a cylinder was used to estimate SA ($[2 \pi r h] + [\pi r^2]$). Live colony SA was calculated by multiplying colony size × decimal % live tissue. Coral size and condition metrics were calculated and standardized per $m^2$ of sea floor (Table 1).

Table 1. Coral condition indicators and calculations, based on the USEPA's Stony Coral Rapid Bio-Assessment Protocol (Fisher 2007). Indicators of individual coral colony size and coral cover (*) were calculated based on 3-dimensional (3D) surface area (SA) measurements. LT: Live tissue

| Coral indicator | Calculation |
|---|---|
| Coral density | No. of stony coral colonies/$m^2$ sea floor |
| Average % live tissue | Σ %LT/colonies |
| Taxa richness | No. of taxa/$m^2$ sea floor |
| Average colony SA* | Σ 3D SA/no. of colonies$^{-1}$ |
| Average live colony SA* | Σ live 3D SA/no. of colonies |
| 3D total coral cover* | Σ SA/$m^2$ sea floor |
| 3D live coral cover* | Σ live SA/$m^2$ sea floor |

**Landscape data.** Geospatial data processing and analyses were conducted in ArcGIS (Environmental Systems Resource Institute, ArcMap 9.2). Eleven St. Croix watersheds were delineated with the Arc Hydro tool in ArcMap using digital geospatial data from the National Elevation Dataset (NED; http://nhd.usgs.gov) and National Hydrography Dataset (NHD; http://ned.usgs.gov). Buck Island was included as a watershed for a total of 12 spatial landscape units. St. Croix watershed shapefiles were used to estimate simple landscape watershed metrics such as watershed areal extent, mean watershed elevation data from the NED, total length of streams from the NHD, and human population data (Burke & Maidens 2004). Watershed shapefiles were also used to clip LULC data from 2007 produced by NOAA Coastal Change Analysis Program (www.csc.noaa.gov/digitalcoast/data/ccaphighres/download.html), and to generate percentage of each land cover type including impervious surface and natural land (undeveloped wetlands, forests, and open space). Watershed LDI values were calculated using the method of Brown & Vivas (2005); each land use category was assigned an LDI coefficient based on cumulative, nonrenewable energy input received by each land use type (Table 2). An area-weighted LDI index was then calculated for each watershed as follows: $LDI_{watershed} = (\Sigma\%LU_i \times LDI_i) / 100$, where $\%LU_i$ = percent watershed land area in land use $i$, and $LDI_i$ = LDI coefficient for land use $i$ (Fig. 1, Table 2).

**Correlation and multivariate analyses.** For purposes of relating watershed metrics of human activity to coral condition, sites from both the 2006 and 2007 coral condition surveys were assigned to watersheds based on their proximity to the watershed coastlines. Due to a strong westward ocean current, discharges entering to the north or south coasts will tend to transport sediments and anthropogenic contaminants offshore and to the west (Hubbard 1986); therefore, in 7 cases where stations fell close to a boundary, values were assigned to the eastward watershed (Fig. 1). The average depth of the coral condition stations assigned to each watershed was calculated to assess how variations in sample depths impacted coral condition variability. Similarly, coral condition variability by watershed was evaluated in relation to the average distance of the stations to the midpoint of the watershed shoreline. This was evaluated to assess how distance from land impacted coral condition.

Table 2. Land use/land cover (LULC) classifications from 2.4 m resolution land use raster dataset (NOAA 2009). Landscape development intensity (LDI) coefficients (Brown & Vivas 2005) were assigned to each class. Braces indicate the LULC and LDI that were aggregated to calculate the percentage of St. Croix's landscape (% of landscape) represented by each unique LDI

| NOAA LULC class | LDI coefficient | % of landscape |
|---|---|---|
| Impervious surface | 8.28 | 11.7 |
| Cultivated crops | 4.42 | 0.6 |
| Pasture/hay | 3.03 | 6.4 |
| Grassland/herbaceous | 2.06 | 37.5 |
| Scrub/shrub | 2.06 | |
| Bare land | 1.85 | 12.3 |
| Developed, open space | 1.85 | |
| Deciduous forest | 1.00 | |
| Evergreen forest | 1.00 | |
| Palustrine forested wetland | 1.00 | |
| Palustrine scrub/shrub wetland | 1.00 | |
| Palustrine emergent wetland | 1.00 | 31.5 |
| Estuarine forested wetland | 1.00 | |
| Estuarine scrub/shrub wetland | 1.00 | |
| Estuarine emergent wetland | 1.00 | |
| Unconsolidated shore | 1.00 | |
| Open water | 1.00 | |

Station averages were generated using SAS software (SAS Institute), for coral colony density, percent live tissue, coral colony SA and live colony SA, and totals were tallied for taxa richness, 3D total coral cover, and 3D live coral cover. From these station-level coral indicators, median values were generated from sites assigned to each watershed. Pearson correlation analysis was conducted post hoc to explore relationships between watershed-level median coral indicators and watershed LDI indices, and between coral indicators and watershed percent impervious surface values. Given the exploratory nature of these analyses, we adopted $p < 0.10$ as the significance criterion for these correlations. Linear regression analyses were conducted to examine which of the independent variables (Table 3) explained most of the variability. Correlations among independent variables were assessed by examining Pearson correlation coefficients. Stepwise multiple regression models were developed (S-Plus, Insightful) after screening variables with high correlations to one another to select the most meaningful variables. Selected regression models were evaluated to determine how much of the coral condition variability could be described by these simple landscape metrics.

Table 3. St. Croix watershed characteristics: number of coral survey stations from each year and total number used in analysis, average depth of coral stations, average percent impervious surface and natural land, average elevation, total area, human population density, total stream length, and landscape development intensity (LDI) index. nd: no data available. Watershed abbreviations as in Fig. 1

| Watershed | No. of coral stations 2006 | 2007 | Total | Station depth (m) | % imperv. surface | % natural land | Elevation (m) | Area ($km^2$) | Human population density (no. $km^{-2}$) | Total stream length (km) | LDI index |
|---|---|---|---|---|---|---|---|---|---|---|---|
| W1 | 4 | 6 | 10 | 8.0 | 3.6 | 53.2 | 111.2 | 12.02 | 24.5 | 16.85 | 1.73 |
| W2 | 8 | 0 | 8 | 9.0 | 8.1 | 41.0 | 84.4 | 16.55 | 334.3 | 18.50 | 2.15 |
| SW2 | 0 | 2 | 2 | 5.0 | 10.3 | 30.4 | 52.5 | 27.72 | 136.9 | 32.75 | 2.59 |
| SW1 | 2 | 0 | 2 | 6.2 | 12.3 | 20.5 | 60.9 | 31.82 | 227.1 | 32.36 | 2.55 |
| SC1 | 5 | 5 | 10 | 6.3 | 27.5 | 24.9 | 44.9 | 36.36 | 709.8 | 40.51 | 3.48 |
| SE1 | 11 | 8 | 19 | 5.9 | 3.6 | 10.4 | 46.7 | 22.89 | 162.4 | 29.16 | 2.41 |
| SE2 | 1 | 11 | 12 | 7.9 | 5.1 | 8.2 | 53.5 | 7.21 | 11.4 | 3.90 | 2.29 |
| NE2 | 5 | 6 | 11 | 7.5 | 9.1 | 13.8 | 51.7 | 15.43 | 40.3 | 9.84 | 2.54 |
| NE1 | 10 | 4 | 14 | 7.6 | 18.6 | 33.7 | 51.2 | 16.92 | 201.6 | 11.05 | 2.82 |
| NC1 | 1 | 1 | 2 | 11.4 | 10.4 | 38.6 | 68.1 | 15.95 | 201.4 | 20.63 | 2.35 |
| NC2 | 4 | 2 | 6 | 8.7 | 4.8 | 57.6 | 89.9 | 13.31 | 17.9 | 9.53 | 1.76 |
| BI | 10 | 7 | 17 | 8.7 | 0 | 11.7 | nd | 0.71 | 0 | 0 | 1.94 |

## RESULTS

From 113 stations surveyed in 2006 and 2007, a total of 5791 coral colonies were examined and measured. The number of survey stations associated with each watershed ranged from 0 to 11 in separate years and from 2 to 19 for combined years (Table 3). All except 3 of the watersheds had at least 6 assigned coral survey sites (Table 3, Fig. 1A). Average depth of watershed stations ranged from 5.0 to 11.4 m, and average watershed area ranged from 0.71 to 36.36 $km^2$ (Table 3). Of 39 unique coral taxa, 8 species comprised 88 and 87%, respectively, of total and live 3D coral cover across all stations: (in descending order) *Montastrea annularis*, *M. faveolata*, *M. cavernosa*, *Diploria strigosa*, *Siderastrea siderea*, *Porites porites*, *Acropora palmata*, and *P. astreoides*. Median values for targeted coral indicators were consistently high for both west coast watersheds (W1 and W2), and in most cases for NC2 and Buck Island (BI; Figs. 2 & 3). Of the suite of coral indicators, median percent live tissue varied the least, ranging from 53 to 71% (Fig. 2B). Buck Island stations had the highest medians for average colony surface area and average live colony surface area, indicating the large size of corals observed there as well as relatively large amounts of live tissue per colony (Fig. 3A,B). West coast watersheds and SW1 also had large median coral colony size, and when summed, W1, W2, BI, and NC2 had highest 3D total coral cover and 3D live coral cover (Fig. 3). Watersheds along the south

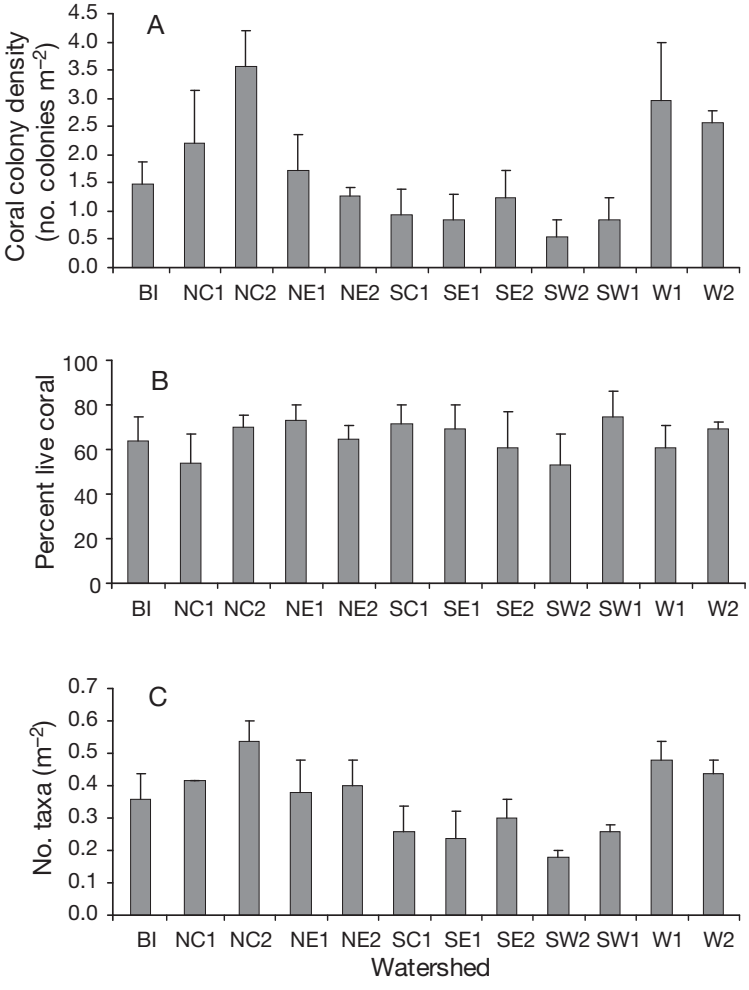


Fig. 2. Median values for (A) coral colony density, (B) percent live coral, and (C) taxa richness, for grouped 2006 and 2007 St. Croix stony coral survey stations assigned to each of 12 watersheds. Error bars are the median absolute deviations. Watershed abbreviations as in Fig. 1

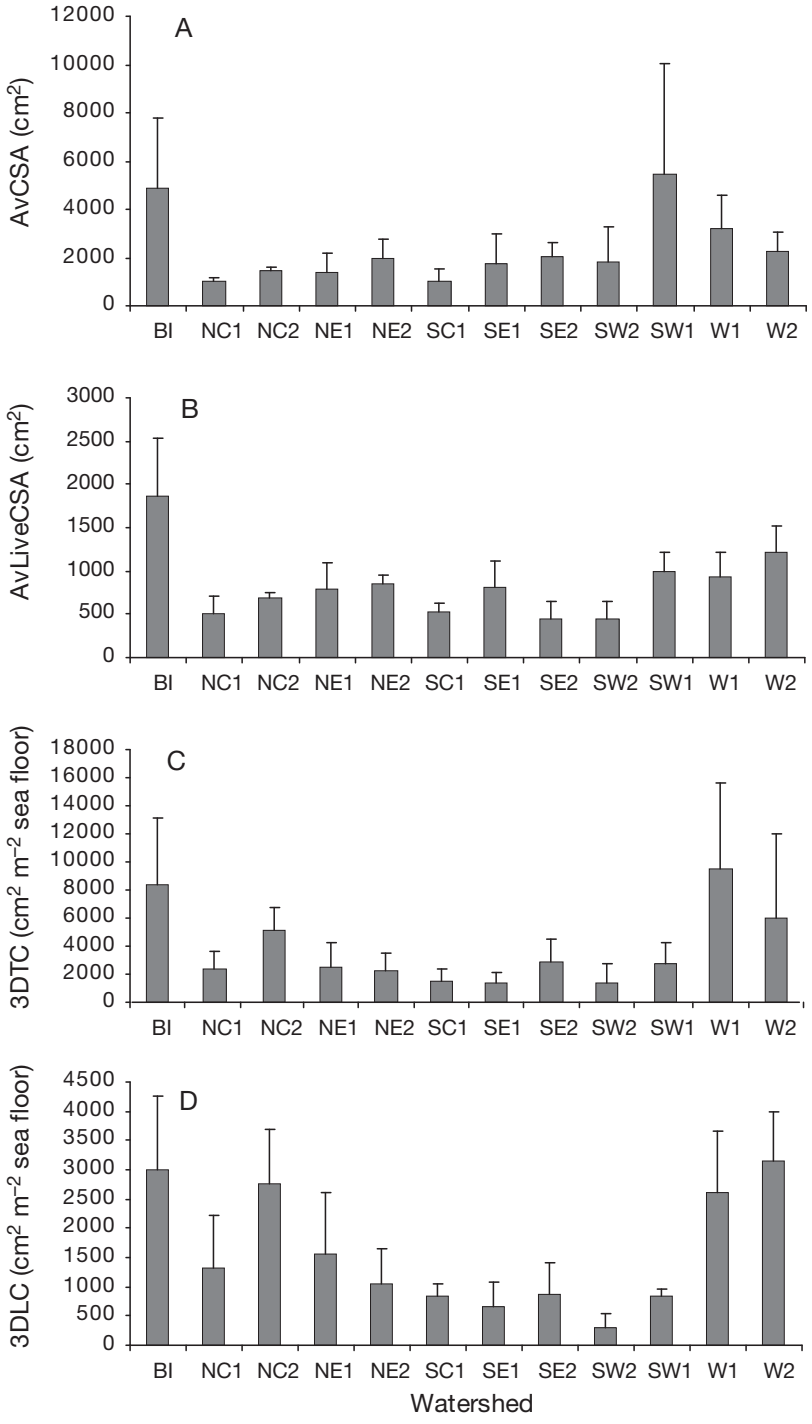


Fig. 3. Median values for (A) average colony surface area (AvCSA), (B) average live colony surface area (AvLiveCSA), (C) 3D total coral cover (3DTC), and (D) 3D live coral cover (3DLC), for grouped 2006 and 2007 St. Croix stony coral survey stations assigned to each of 12 watersheds. Error bars are the median absolute deviations. Watershed abbreviations as in Fig. 1

shore (SW1, SW2, SC1, SE1, and SE2) had the lowest median colony densities and taxa richness (Fig. 2), and except for a high median colony size for SW1, also had smaller colonies and reduced reef area (Fig. 3).

Highest LDI values were calculated for south shore watersheds (in descending order) SC1, SW1, SW2, and north shore watersheds NE1 and NE2 (Table 3, Fig. 1B). While NE1 and NE2 had similar LDIs, they differed in land use, with NE1 having 18.6% impervious surface (including the city of Christiansted) and NE2 only 9.1%. Western watersheds also had relatively low LDIs that were closer in agreement than their respective proportion of impervious surface values (Table 3); W2 contains the city of Frederiksted, which is reflected in the higher proportion of impervious surface compared to W1 (Table 3, Fig. 1). Area-weighted LDI for St. Croix = 2.5, and watershed values ranged from 1.73 to 3.48 (Table 3). The highest LDI coefficient is that for impervious surface, which amounted to 11.3% of island-wide land area and contributed most to high LDI values for south shore watersheds, and for W2 and NE1. Of 2 agriculture land use classes applicable to St. Croix, high-intensity crop cultivation accounted for 0.6% of total land, while pasture use and hay production comprised 6.4% (Table 2). On a watershed level, pasture and hay contributed 25.8% of land use in SE1, 13.7% in SW1, 8.1% in NE2, and 5.2% in NC1 (Fig. 1). Natural lands with lowest LDI coefficients, including forests and wetlands, were in greatest proportion in NC2, W1, W2, NC1, and NE1, where they comprised 34% to 58% of land (Table 3).

Significant negative correlations were found between watershed LDI scores and coral condition data (2006 and 2007 combined) for stony coral density, taxa richness, average colony surface area, average live colony surface area, 3D total coral cover, and 3D live coral cover (Fig. 4). Removal of a single outlying watershed (Fig. 4C) improved the strength of the relationship for average colony surface area. Some of these relationships were found to be significant for 2006 and 2007 data analyzed separately (results not shown). The only coral indicator that showed a positive correlation with watershed LDI was average percent live tissue. Watershed percent impervious surface correlated negatively only with 3D coral cover for combined-year data ($r = -0.57$, $p = 0.055$) and with both 3D total coral cover and 3D live total coral cover for 2006 data ($r = -0.59$, $p = 0.058$; $r = -0.55$, $p = 0.078$, respectively). Within the suite of coral indi-

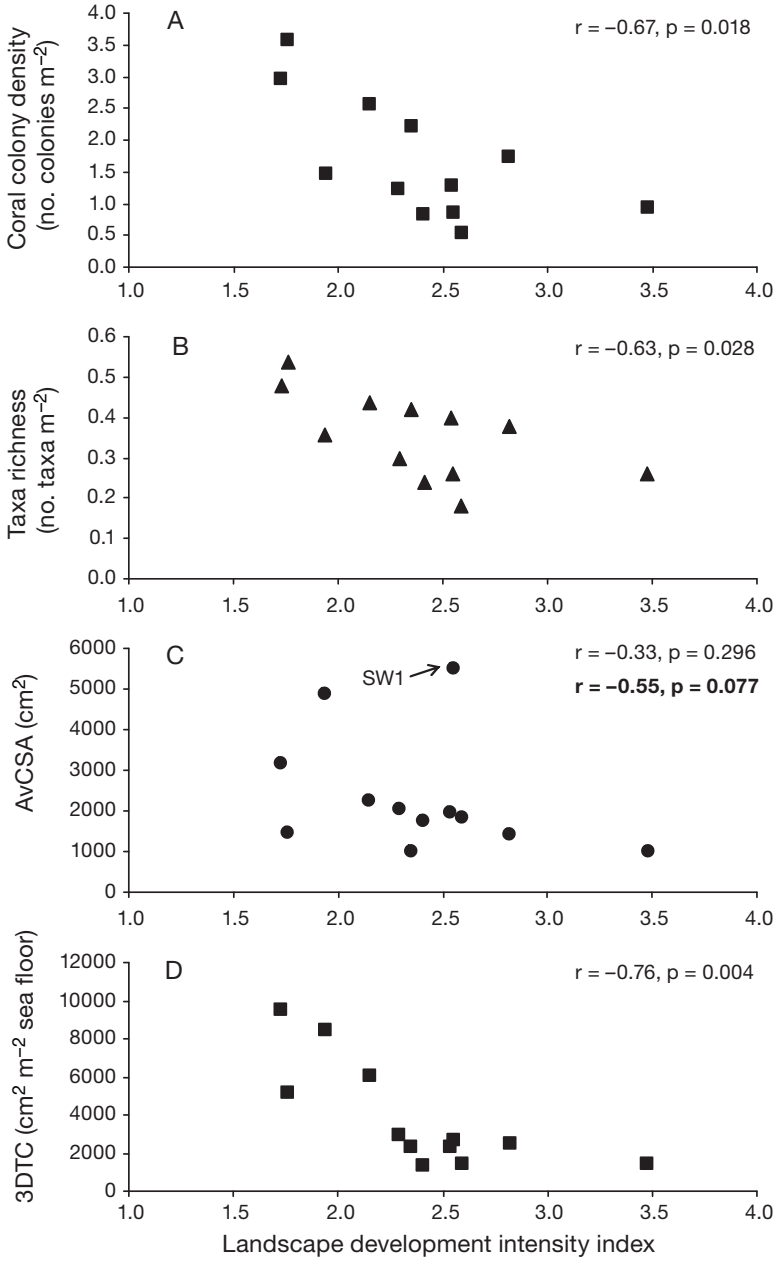


Fig. 4. Relationships between watershed landscape development intensity (LDI) values and (A) coral colony density, (B) taxa richness, (C) average colony surface area (AvCSA), and (D) 3D total coral cover (3DTC). Pearson correlation coefficients are indicated for each with accompanying p values. In (C), the coefficient in **bold** is the result if the outlier (SW1 marked with arrow) is excluded from the correlation analysis

cators, 2 pairs (average colony surface area and average live colony surface area; and 3D total coral cover and 3D live coral cover) were very closely correlated (r = 0.70, p = 0.001; and r = 0.869, p = 0.0002, respectively) because they are based on the same colony measurements adjusted for % live tissue. Because of this, analysis focused on the total size metrics: average colony surface area and 3D total coral cover.

Correlations among landscape variables were examined to identify which variables were most related to the LDI values. LDI values were highly correlated with human population, percent impervious area (used in the calculation of LDI), and watershed area. High correlations were also observed between the watershed percent natural area and average elevation such that higher elevation watersheds had more natural area than low elevation watersheds.

Examination of the correlation structure of the independent variables led to the selection of 3 independent variables to be used in stepwise regression model selection procedures. The 3 variables were watershed LDI, the watershed percent natural area, and average depths of stations associated with an adjacent watershed. The LDI was selected because it was significantly correlated with many coral indicators and because the value represents an index measure of the intensity of human land use. Though the same LULC data were used to calculate both LDI and percent natural area, they were not significantly correlated because of the low LDI coefficient assigned to natural land cover classes. Consequently, the percent natural area variable was retained for the stepwise procedure. The average station depth was chosen as a variable to enter into the stepwise procedure because it was correlated with the average distance to shoreline, and to a large extent represents the degree of marine influence on the samples.

Multiple regression results (Table 4) indicated that LDI, percent natural area, and station depth were good predictors of some coral condition metrics. The LDI alone was selected as the best predictor of 3D total coral cover (Fig. 4D, $r^2 = 0.58$, $p = 0.004$) and 3D live coral cover (data not shown, $r^2 = 0.46$, $p = 0.016$). The LDI, percent natural area, and average station depth were all selected in a multiple regression model that explained 90% of the variability in the coral colony density data (Table 4). Percent natural area and average station depth were selected in a multiple regression model for taxa richness (Table 4). This model explained 74% of the variability in the taxa richness data.

Table 4. Stepwise regression results. LDI: landscape development intensity index, B: coefficient estimate, percent natural:percent of land use classes in a watershed with LDI coefficient = 1.0 (as shown in Table 2)

| Condition indicator | Coefficient | Coefficient value | Coefficent p-value | df | $R^2$ | Regression p-value |
|---|---|---|---|---|---|---|
| Coral density | $B_{LDI}$ | −14.2 | 0.055 | 8 | 0.90 | 0.0002 |
| | $B_{station\ depth}$ | 4.5 | 0.036 | | | |
| | $B_{percent\ natural}$ | 0.9 | 0.001 | | | |
| | $B_0$ | 17.2 | 0.500 | | | |
| Taxa richness | $B_{station\ depth}$ | 0.94 | 0.012 | 9 | 0.74 | 0.0020 |
| | $B_{percent\ natural}$ | 0.08 | 0.031 | | | |
| | $B_0$ | −1.12 | 0.622 | | | |

## DISCUSSION

Empirical evidence from this study supports a relationship between human activity in St. Croix watersheds and the condition of stony corals in adjacent coastal waters. Human activity, measured by the LDI index, was negatively correlated with various indicators of coral condition, including taxa richness, colony size, and colony density. In a similar study at the northern US Virgin Islands (St. Thomas and St. John), proximity to human activity was also linked to adverse change in stony coral condition using an onshore to offshore gradient (Smith et al. 2008). Together, these studies sustain the widely held belief that terrestrial anthropogenic activities adversely impact coral reefs in the near coastal zone (Loya 1976, Hubbard 1986, Richmond 1993, Miller & Cruise 1995, Burke & Maidens 2004, Wolanski et al. 2004, Fabricius 2005, Warne et al. 2005). It is notable that local anthropogenic effects were detected in both studies despite the many regional and global stresses, such as hurricanes (Rogers 1992, Rogers & Beets 2001) and high-temperature events (Hoegh-Guldberg 1999, Miller et al. 2006, Rothenberger et al. 2008, Woody et al. 2008, Miller et al. 2009), which are less discriminate and could mask evidence of local stressors.

The LDI index (Brown & Vivas 2005) integrates impacts from multiple non-renewable energy inputs to the landscape. The index increases where human activities have increased the land area of impervious surfaces, crops, pastures, houses, roads, and industrial infrastructure. The LDI has been previously shown to capture the cumulative impact of human activities in wetlands (Mack 2006, Reiss & Brown 2007). In our study, the majority of watersheds with low LDI values and a high proportion of undeveloped lands were associated with relatively good coral condition in adjacent reefs (Figs. 2 to 4). Other landscape indicators showed significant correlations, including percentage of impervious surface which correlated negatively with 3D total coral cover. Percent impervious surface characterizes the extent of urbanization and industrial development (Grimm et al. 2008), and is highest on the south shore of St. Croix where an oil refinery, a rum distillery, and the island's international airport are located. Since heavy, intermittent precipitation in the Caribbean is common, coral reefs offshore from high impervious surface watersheds receive higher inputs of sediments and chemical contaminants, including polycyclic aromatic hydrocarbons, heavy metals, fertilizers, and pesticides (Rothenberger et al. 2008). Because percent impervious receives the highest LDI coefficient, it correlated strongly with the LDI. Nonetheless, the LDI was more sensitive, correlating negatively with multiple coral parameters.

Two other landscape indicators, percent natural land and station depth, showed positive relationships with coral colony density and taxa richness. This supports the finding that watersheds with a greater proportion of undeveloped lands are associated with healthier coral reefs, perhaps by slowing runoff rate over vegetated land. For example, northwestern St. Croix watersheds (e.g. NC2) are undeveloped, heavily vegetated, and exhibit relatively high coral condition. Significant influence of station depth is consistent with Smith et al. (2008), showing that coral reefs located away from human disturbance are more diverse and provide more reef habitat.

The finding of a negative correlation between the watershed LDI index and coral condition indicators is consistent with expectations that higher human land-use activity adversely affects coral condition. The strength and significance of the relationships from this exploratory examination reveal a strong potential for this approach to demonstrate the cumulative effect of human watershed stressors on coral reef ecosystems. Future applications would be improved by a survey design that balances the number of sites representing each watershed, incorporates landscape weighting factors for runoff potential, and better estimates coastal transport of runoff, particularly near watershed boundaries. Once refined, this tool can inform coastal management decisions that may otherwise be made solely on an economic basis. Its use should support economic development without compromising the ecological integrity of coral reefs and the services they provide.

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