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-

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 Dredging Mooring Overfishing	Construction Sea level rise Die-back Invasive species	Acidification Eutrophication Climate change Overfishing	Overfishing Disease Sedimentation Eutrophication	Mariculture Construction Forestry Sea level rise
Ecosystem goods and services	Biodiversity Food Export of materials Ecotourism Stabilization Carbon and nutrient sequestration	Biodiversity Food Export of materials Ecotourism Stabilization Contaminant and nutrient interception	Biodiversity Food/Fisheries Ecotourism Stabilization Carbon sequestration	Food Biodiversity Stabilization Filtering Carbon and nutrient sequestration	Food Timber Biodiversity Ecotourism Stabilization 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

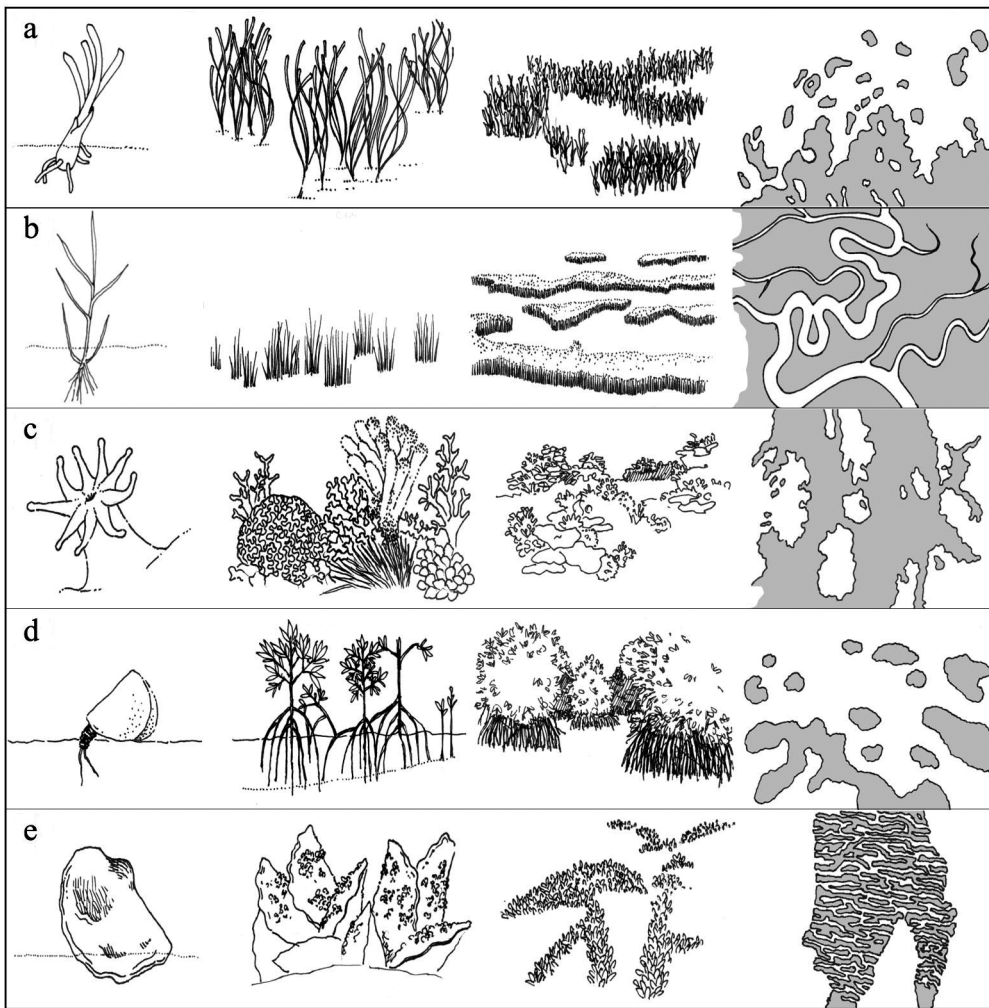| Disturbance type	Fragmentation mechanism	Seagrass meadow	Salt marsh	Coral reef	Mangrove forest	Oyster reef	Sum
Physical	Storm events/sand scour	+	+	+	+	+	5
	Tsunami	+	+	+	+	+	5
	Construction	+	+	+	+	+	5
	Dredging	+	+			+	3
	Hydrologic alterations		+		+	+	3
	Siltation/sedimentation	+		+		+	3
	Propeller 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 multi-scale, 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 dynam-

ics, 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.isi-knowledge.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
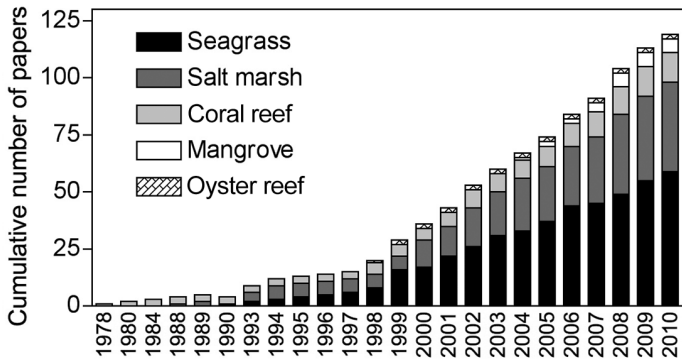
Fig. 2. Cumulative number of studies in coastal biogenic ecosystems applying landscape ecological principles to explain faunal responses

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.
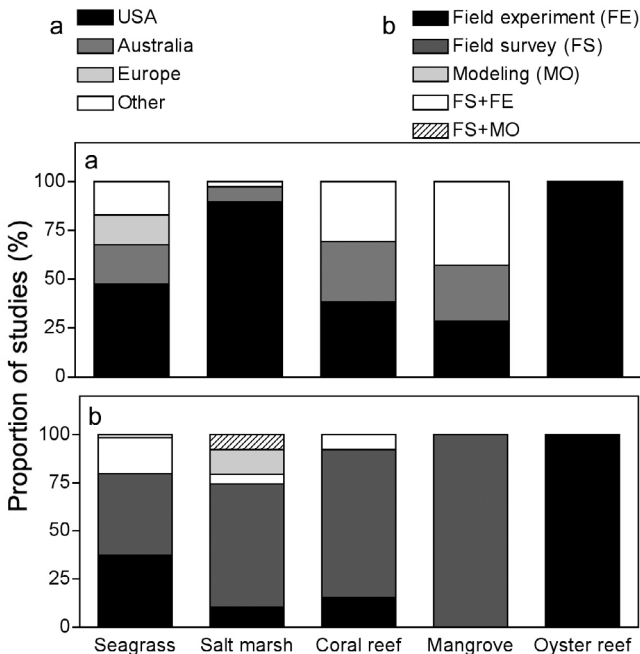

Fig. 3. (a) Geographical regions and (b) methodological approaches covered in the seascape literature (1978–2010, Appendix 1) linking seascape metrics to faunal response variables

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, Meyneke 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-
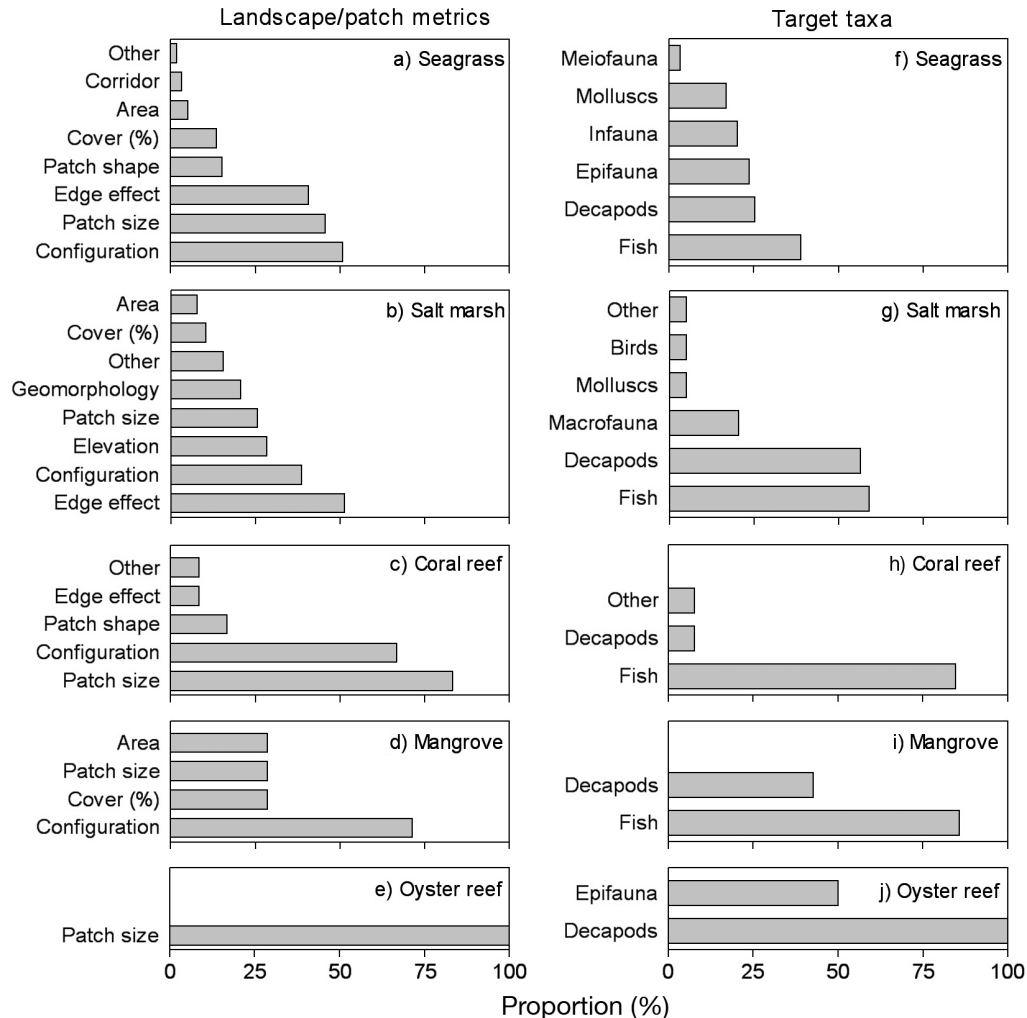
Fig. 4. Summary of (a−e) spatial pattern metrics applied to explain (f−j) target faunal groups in the 5 biogenic ecosystems studied. Patch size includes studies reporting habitat area measurements. Configuration refers to various landscape indices used to quantify the component habitat, e.g. number of 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-
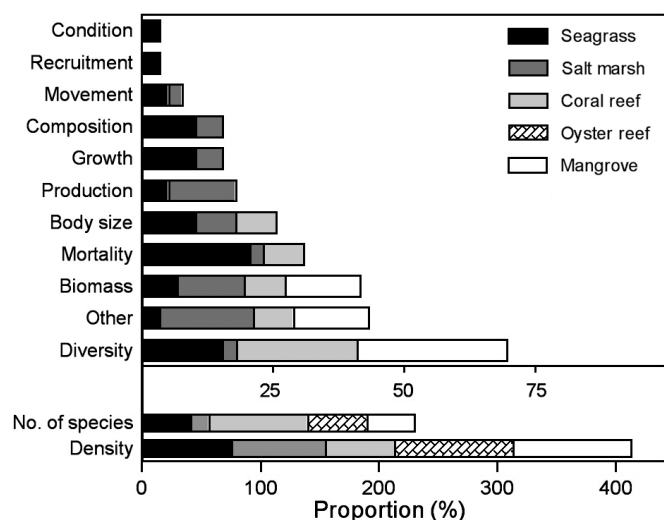
Fig. 5. Faunal response variables measured to investigate the influence of landscape or patch features on the 5 biogenic ecosystems. Density: number of individuals or abundance. No. of species: number of taxa or species recorded. Diversity: calculated diversity indices for faunal assemblages, e.g. Shannon-Wiener 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)
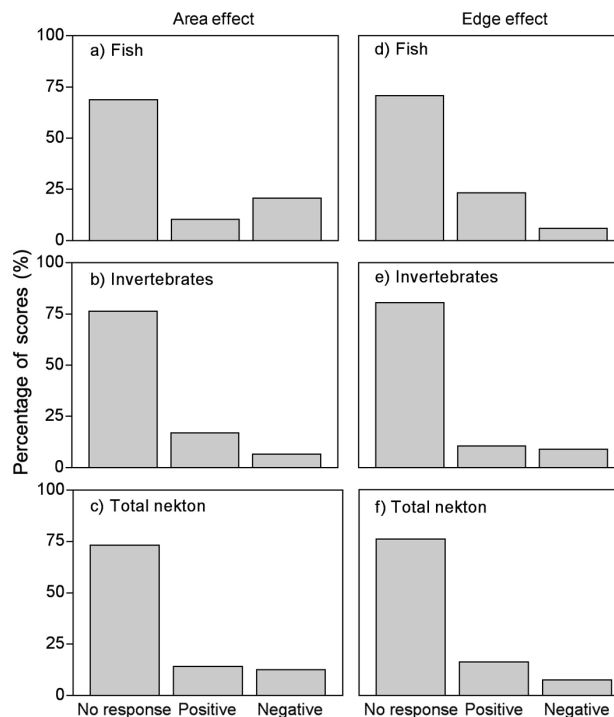

Fig. 6. Summary of (a,d) fish and (b,e) invertebrate as well as (c,f) total nekton responses to area (patch size) and edge effects (edge–interior comparisons) in seagrass seascapes. Only statistically significant responses in species density or richness are included. For details, see 'Materials and methods' 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 (diam-

eter >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 ben-

efit 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)

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					