

Review of nekton patterns and ecological processes in seagrass landscapes

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Abstract

We reviewed seagrass landscape studies on nekton (fish and larger mobile crustaceans) to summarise: (1) patterns of nekton abundance in relation to patch attributes; and (2) models used to explain processes underpinning observed patterns. The response of nekton to landscape attributes is highly variable. Different taxa showed increasing densities with: increasing and decreasing patch size (12 and 11 taxa, respectively), increasing and decreasing proximity within a patch to edge (9, 14), increasing and decreasing distances from nearest seagrass patch (4, 11), and with patches perpendicular and parallel to currents (1, 2). The majority of taxa (213 out of 281, or 82%) showed no relationships. Landscape scale patterns are important for some species but evidence so far does not demonstrate major landscape effects overall. The lack of pattern might reflect the overriding importance of other factors such as within-patch characteristics, water depth or position within an estuary. It might also result from measurements at the wrong scale. The rigour of surveys can be improved by avoiding confounding of patch attributes by other factors, increasing awareness of statistical power, and more considered survey designs for attributes such as edge effects. The predation model is the most frequently invoked and tested model. Other explanatory models are based on disturbance, rates of encounter, food availability, larval supply, migration and reproductive success, but in many cases are not based on observed patterns. The best experimental work has been done on nekton species for which landscape studies have been built on a detailed understanding of the ecology of the species, such as for blue crabs (*Callinectes sapidus*). As this basic ecological platform is laid for more species, the landscape approach will become increasingly fruitful.

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1. Introduction

Ecological landscapes encompass spatial heterogeneity in habitat types and ecological processes (Turner et al., 2001). Studies of ecological landscapes are at the scale of multiple patches of a habitat, and incorporate patch attributes such as size and shape, and the spatial and/or temporal relationship among habitats. Studies at this scale potentially provide a better understanding of the spatial and temporal habitat requirements for population persistence (Debinski and Holt, 2001)

and, because of the scale at which habitat perturbations by humans often occur, for management of species (Freemark et al., 1995). Increased understanding of how the arrangement and areal extent of habitats influence assemblages of animals can improve conservation efforts and assist in sustainable management of human interactions with ecosystems.

Seagrass meadows support high densities of animals and are considered fundamentally important in providing habitat for commercially or recreationally harvested aquatic animals (Jackson et al., 2001). Seagrass systems are ideal for the application of landscape-scale ideas because of their natural propensity to form variable-sized patches (Robbins and Bell, 1994). Large, continuous beds are also common, but even in

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these situations, patchiness can result from anthropogenic perturbations (Short and Wyllie-Echeverria, 1996; Duarte, 2002).

The first detailed seagrass landscape work was done towards the end of the 1980s, in the USA (e.g. Virnstein and Curran, 1986; Sogard, 1989) and Australia (Bell and Westoby, 1986b,c). During the early 1990s seagrass landscape studies were influenced by terrestrial ecological ideas (Robbins and Bell, 1994). The most conspicuous of these was the application and testing of the SLOSS concept (“Single Large Or Several Small” protected areas) for the protection of biodiversity (McNeill and Fairweather, 1993). Galvanised perhaps by the review of Robbins and Bell (1994) and/or the continued fragmentation of seagrasses resulting from anthropogenic impacts (Short and Wyllie-Echeverria, 1996), there was a surge in the number of studies addressing seagrass landscapes, which culminated in a review of edge effects by Bell et al. (2001). This review again seemed to stimulate interest in the ways in which animals function in seagrass landscapes, and it is time again to reflect upon findings and suggest directions to improve the application of landscape-scale ideas in seagrass systems.

This review focuses on nekton, or animals capable of swimming. The definition of nekton can include or exclude various animal groups, depending on their daily cycle of activity, ontogeny or response to various stimuli (Tibbetts and Connolly, 1998). Our practical definition includes swimming crustaceans (amphipods, isopods, prawns, shrimp and swimming crabs), cephalopods and all fishes. Some of the best designed and analysed seagrass landscape studies (e.g. Irlandi, 1997; Bologna and Heck, 2000; Tanner, 2005) have been on infaunal invertebrates rather than nekton. We have not included these in our analysis of patterns but mention them where they provide insights about conceptual models or improved experimental designs that might be used on nekton.

It is easier to detect patterns in infaunal invertebrates than nekton within seagrass because of the greater mobility of nektonic animals, leading to greater difficulty in sampling and potentially a larger scale at which researchers need to work. Sampling methods for nekton in seagrass and surrounding habitats are clearly critical to the success of landscape studies. Collection techniques for nekton in seagrass have been well described (Rozas and Minello, 1997; Edgar et al., 2001; Guest et al., 2003), but landscape studies often require novel techniques that are effective at scales small enough to sample different microhabitats within patches (Connolly, 1994d). These techniques continue to be refined (e.g. Hovel et al., 2002), and assessments of their efficacy and examination of sampling artefacts (e.g. Hindell and Jenkins, 2005) would be valuable.

Our focus is on seagrass landscape attributes, not within-patch variables such as seagrass shoot length and density or sediment characteristics. Methods for studying within-patch variables are generally well described (e.g. Duarte and Kirkman, 2001), and relationships between nekton and within-patch seagrass variables have been better studied. We have not examined within-patch variables in detail in this review, but urge researchers to continue to assess their effects where it is possible they interact with landscape attributes such as patch size to influence associated faunal assemblages (e.g. Hovel et al., 2002).

The application of landscape ideas in seagrass systems depends on our ability to differentiate ‘patches’ of seagrass from surrounding aquatic habitats. As for other faunal groups (Boström et al., 2006), the decision about what constitutes a patch is an important one for studies of nekton in seagrass landscapes. Typically patches are defined by their edges, where a rapid rate of change in the amount of plant structure is evident (Ries and Sisk, 2004). For nekton studies in seagrass, this has been taken as a change from high to low (or zero) amounts of above-ground seagrass biomass, although the decision rules are typically not reported quantitatively. Landscape studies of nekton are usually at the site scale on the hierarchy of scales shown by Jackson et al. (2001). The most appropriate spatial scale depends on the size and extent of movement of animals, and their perception window (Attrill et al., 2000). It would be helpful for these to be more clearly discussed in landscape-scale studies of nekton.

Work on seagrass patch attributes is less advanced than that on other aspects of nekton in seagrass such as comparisons with adjacent habitats and correlations with seagrass morphology. Numerous studies have documented differences in nekton abundances between seagrass and alternative habitats such as unvegetated sand (Ferrell and Bell, 1991; Connolly, 1994a; Heck et al., 1995; Gray et al., 1996) and algae-covered reefs (Jenkins and Wheatley, 1998). Correlations between seagrass morphology and nekton are reasonably well understood (Orth et al., 1984a,b), especially the effects of shoot density and length (Bell and Westoby, 1986a,b,c). In contrast, few patterns have emerged from research into nekton abundances and landscape attributes of seagrass, either because the influence of patch attributes is weak, or responses of nekton are variable (e.g. over time, or among species). Alternatively, our inability to generalise about relationships between patch attributes and nekton might reflect poor survey design, inappropriate scales, or artefacts associated with sampling. Underwood et al. (2000) highlighted the importance of properly demonstrating patterns before developing explanatory theories or models about processes. Pattern description is, in itself, an hypothesis testing procedure (Underwood et al., 2000), and must be done with enough rigour to properly distinguish a pattern from the null hypothesis of no pattern.

Our objectives in this review were to:

- (1) summarise the patterns in nekton for different seagrass landscape attributes;
- (2) summarise explanatory models espoused to explain patterns and discuss the testing of those models; and
- (3) examine limitations in survey design and suggest improvements for detecting patterns.

2. Patterns in nekton abundance and biomass

We reviewed studies that examined patterns in a measure (abundance, biomass, richness) of nekton with one of four aspects of landscape ecology in seagrass:

- (1) patch size (differences in nekton among patches of different area);

- (2) edge effects (within-patch differences in nekton with proximity to the edge);
- (3) proximity to seagrass (differences in nekton with proximity of patches to other seagrass patches); and
- (4) orientation (differences in nekton depending on whether patch is parallel or perpendicular to currents).

For each study, we scored every reported measure as a positive effect, negative effect or no effect (+, −, 0). Positive effects were those where the measure increased with increasing patch size or with proximity to patch edge (i.e. with decreasing distance from patch edge), or were higher in patches parallel rather than perpendicular to currents (Fig. 1). Only statistically significant results were counted as +ve or −ve effects. Each score was treated independently, even where one measure contributed directly to another (e.g. overall abundance of fish, and abundances of individual species). Some papers reported results for every species, others pooled data into higher-level taxonomic groupings. We treated results from different sampling periods within a study separately, so that values in Table 1 are sums of taxa/time combinations.

2.1. Patch size

Interest in seagrass patch size as a potentially important landscape attribute began with Heck's (1979) demonstration that nekton species richness and abundance were higher in

Panama, where seagrass beds were small and fragmented, than in Florida, where beds were continuous. Heck (1979) did not actually measure patch size, and differences between regions were complicated by variables other than patch size, including latitude and species of seagrass, but the idea was stated and taken up by a succession of scientists. Patch size has now been the most frequently studied landscape attribute (Table 1). Of the 98 fish and invertebrate taxa tested in 8 studies, however, the majority (77%, or 75 out of 98 taxa) have shown no influence of patch size. Of those that showed an effect, the pattern varies; 4 fish taxa had greater densities in larger patches, 7 in smaller patches, while 8 and 4 invertebrate taxa showed +ve and −ve effects, respectively.

Positive and negative relationships have been observed when patch size was analysed as a continuous (Bell and Westoby, 1986c; Bell et al., 2001) and a categorical variable (McNeill and Fairweather, 1993; Eggleston et al., 1998), using natural seagrass (Bell and Westoby, 1986b; Bell et al., 2001) and artificial seagrass units (ASUs) (McNeill and Fairweather, 1993; Eggleston et al., 1998). Where different species of seagrass were sampled as part of a single study, fish and invertebrates responded differently between seagrass species, and different animal species also varied for a single seagrass species (McNeill and Fairweather, 1993).

2.2. Edge

The majority of taxa (85%, or 126 out of 149) showed no effect with distance from the edge of a patch (Table 1). Patterns varied among taxa that showed a significant relationship with distance from edge; 4 fish taxa were more abundant away from the edge but none were more abundant near the edge; for invertebrates, similar numbers of taxa showed a positive (9) and negative (10) relationship (Table 1). Most studies reported only a single sampling event, but where multiple periods were sampled results varied for the same species over time (Hovel and Lipcius, 2002).

Bell et al. (2001) summarised patterns in densities of animals, including nekton, with distance from the edge of seagrass patches. In 5 out of 14 studies animals were more abundant at the edge than interior of seagrass patches (i.e. +ve effect). Three of these studies were on crustacea, and one each was on scallops and fish. Three studies found a −ve relationship, while the remaining studies, and overwhelming majority of species, showed no relationship with distance to edge. All but one of the studies reviewed by Bell et al. (2001), however, used differences in fauna between different-sized seagrass patches as a proxy for edge effects rather than measuring animal abundances at different distances from patch edges. These studies inferred the importance of edge-proximity from any relationship between patch size and animal abundances, based on the assumption that smaller patches have larger perimeter:area (P:A) ratios. This assumption is true only if the shapes of patches are similar, something not measured or reported in these studies. The argument that greater densities of animals in smaller patches is due to higher

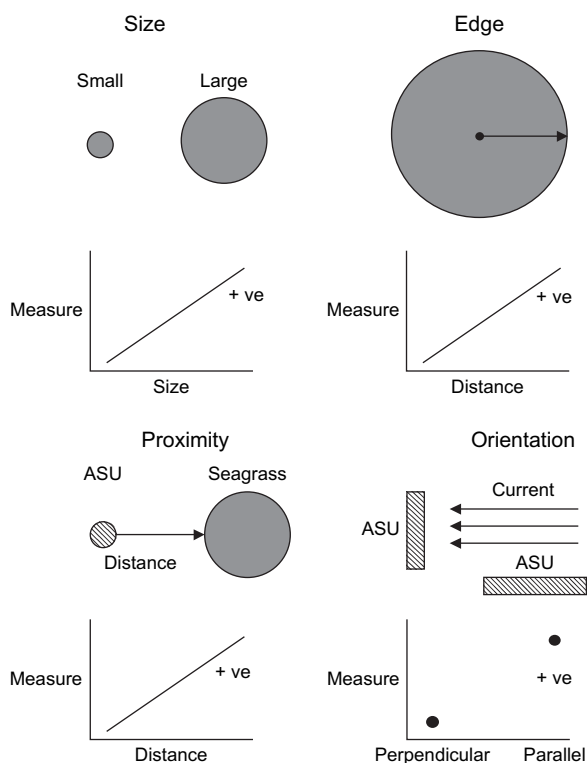


Fig. 1. Diagrammatic representation of direction effects (+ve and −ve) employed in review of studies of nekton and landscape patch attributes. ASU = artificial seagrass unit.

Table 1
Summary of patterns in nekton measures (density or richness) for key patch attributes, by individual studies. Values are the number of taxa/times showing this pattern. +, –, 0 as defined in Fig. 1. Salita et al. (2003) reported differences in multivariate fish assemblages but not individual taxa so is excluded from the table. +/- results are only those reported as statistically significant

Patch attribute	Study	Fish				Invertebrates				Total
		+	–	0	Total	+	–	0	Total	
Size	Bell and Westoby, 1986c	3	1	4	8	1	0	2	3	11
	Bell et al., 2001	0	0	4	4	1	0	7	8	12
	Bell et al., 2002	0	2	12	14	0	0	5	5	19
	Eggleston et al., 1998	–	–	–		1	3	3	7	7
	Eggleston et al., 1999	–	–	–		0	1	4	5	5
	Hovel and Lipcius, 2001	–	–	–		3	0	3	6	6
	Laurel et al., 2003a	1	0	0	1	–	–	–		1
	McNeill and Fairweather, 1993	0	4	19	23	2	0	12	14	37
Total	4	7	39	50	8	4	36	48	98	
Edge	Bologna and Heck, 2002	–	–	–		9	1	15	25	25
	Hovel and Lipcius, 2002	–	–	–		0	1	1	2	2
	Hovel et al., 2002	0	1	31	32	0	0	32	32	64
	Sanchez-Jerez et al., 1999	–	–	–		0	1	9	10	10
	Uhrin and Holmquist, 2003	0	3	9	12	0	7	29	36	48
	Total	0	4	40	44	9	10	86	105	149
Proximity	Hovel and Lipcius, 2001	–	–	–		1	0	0	1	1
	Hovel and Lipcius, 2002	–	–	–		1	1	1	3	3
	Sogard, 1989	1	3	3	7	1	6	1	8	15
	Virnstein and Curran, 1986	–	–	–		0	1	0	1	1
	Total	1	3	3	7	3	8	2	13	20
Orientation	Tanner, 2003	1	1	0	2	1	0	7	10	12
	Total	1	1	0	2	1	0	7	10	12

P:A ratio and therefore an edge effect, is not necessarily correct. Differing faunal abundances with patch size might, for example, result from different abundances across the whole patch rather than at the edge, in which case no edge effect has been demonstrated. Only in one study, on bivalves by Bologna and Heck (1999), did researchers compare the numbers of animals at edges versus interior positions. In a further study, not included in the review by Bell et al. (2001), nekton densities were measured at the edge and interior of a patch (Sanchez-Jerez et al., 1999). Sanchez-Jerez et al. (1999) found that densities of one species of amphipod were greater at the edge than interior, but nine other species showed no significant difference. Four studies (two including fish) that measured nekton abundances at different distances from patch edges have been published since the review of Bell et al. (2001) (Table 1). As in Bell et al. (2001), most taxa (40 of 44 fish, 86 of 105 invertebrates) showed no pattern with edge (Table 1).

2.3. Proximity to natural seagrass

The effects of proximity to natural seagrass patches have been measured using ASUs placed at different distances from seagrass in four studies (Virnstein and Curran, 1986; Sogard, 1989; Hovel and Lipcius, 2001, 2002). Most species (15 out of 20 fish and invertebrates) showed some effect, with the majority (11) more abundant further from natural seagrass (–ve effect) (Table 1). Proximity to natural seagrass patches appears to have a stronger influence on nekton than patch size or proximity to edge within patch. There are similarities

here with the importance of distance from seagrass patches to other physical or biological features, described below.

2.4. Patch orientation

A possibility that the amount of edge facing into the prevailing current might be more important than the total amount of edge in a patch led Tanner (2003) to do the only study of patch orientation and nekton that we could find (Table 1). Tanner (2003) placed rectangular ASUs parallel and perpendicular to tidal currents. Fish abundances were higher in parallel patches (+ve effect) on spring tides (strong currents) and in perpendicular patches on neap tides (weak currents). Amphipods were more abundant in perpendicular patches on spring tides and showed no difference on neap tides, and decapod crustaceans were not different on any tide.

2.5. Patterns with position of seagrass patches

Several studies have examined how nekton abundances vary with position in an estuary or bay. Position has typically been measured as the distance from some physical (estuary mouth, West and King, 1996) or biological (proximity to saltmarsh, Irlandi and Crawford, 1997) feature. Such studies report that a large proportion of taxa show significant differences among positions. It is impossible to assign a direction to such differences, however, since each study uses a different feature from which to measure. Furthermore, negative correlations between features within a single study (e.g. distance

from open water, distance from estuarine habitats such as salt-marsh) prevent a direction being determined reliably. Nevertheless, position within an estuary seems mostly to be quite important (Sogard, 1989; McNeill et al., 1992; Sedberry and Carter, 1993; West and King, 1996; Irlandi and Crawford, 1997; Jenkins et al., 1998; Micheli and Peterson, 1999; Skilleter et al., 2005).

3. Explanatory models of underlying processes

We identified six models used to explain processes generating patterns in nekton abundances and a seventh model based

on abundances of infauna but potentially applicable to nekton (Table 2). For each model, we determined which pattern in animal abundances led researchers to suggest it (Table 2). More than one model was often put forward in a single paper to explain the same pattern. We separated the models depending on whether they were correctly formulated to explain patterns that had been established, or were speculative and unsupported by evidence of nekton patterns. Interestingly, there were similar numbers of these two categories of models. A third category dealing with infauna and sedentary epifauna was also used to highlight models that might be useful in nekton work.

Table 2

Summary of explanatory models for different patterns. A: model suggested for nekton and based directly on observed pattern. B: model suggested for nekton but not strictly based on observed pattern. C: model based on observed pattern for seagrass fauna other than nekton. Numbers in body of table refer to citations at end of table

Model	Pattern	Pattern							
		Size		Edge		Proximity		Orientation	
		+	–	+	–	+	–	+	–
Disturbance	A								
	B	9							
	C	6							
Encounter	A						22, 25		
	B		7, 8, 17						
	C		5						
Food	A						22		
	B	7, 8		21					
	C	15	20		2				
Larval supply	A		17	4			22	23	
	B	7, 1							
	C			5	2				
Migration	A			4			22	22	23
	B	9							
	C	6							
Predation	A	3, 16, 23	16, 23		11, 19				
	B	7, 9, 12	7, 8, 9, 10, 12	21, 4	24		10, 11		
	C	6	13, 14					11, 18	
Reproductive success	A								
	B								
	C				2				
Study									
1	Bell and Westoby, 1986c	10	Hovel and Lipcius, 2001	19	Peterson et al., 2001				
2	Bell et al., 2001	11	Hovel and Lipcius, 2002	20	Reusch and Williams, 1999				
3	Bell et al., 2002	12	Hovel, 2003	21	Sanchez-Jerez et al., 1999				
4	Bologna and Heck, 2002	13	Irlandi, 1997	22	Sogard, 1989				
5	Bologna and Heck, 2000	14	Irlandi et al., 1995	23	Tanner, 2003				
6	Bowden et al., 2001	15	Irlandi et al., 1999	24	Uhrin and Holmquist, 2003				
7	Eggleston et al., 1998	16	Laurel et al., 2003a	25	Virnstein and Curran, 1986				
8	Eggleston et al., 1999	17	McNeill and Fairweather, 1993						
9	Heck, 1979	18	Micheli and Peterson, 1999						

3.1. Disturbance

Environmental disturbance has been proposed as an explanation for higher densities of animals in larger patches (Table 2). This was suggested for nekton by Heck (1979), although his evidence for a patch size effect was weak. On fauna other than nekton, Bowden et al. (2001) suggested the disturbance model to explain their positive relationship between bivalve densities and patch size. The nature of the environmental disturbance is not well defined but is thought to reflect interference by water currents or swell (Bowden et al., 2001). Such environmental variables are difficult to manipulate experimentally and we have found no tests of the disturbance model.

3.2. Encounter

The encounter model is about the rate at which animals encounter seagrass, and it has been suggested to explain higher nekton abundances in smaller patches and in ASUs further from natural seagrass (Table 2). The encounter model can be further refined according to whether the pattern in the measure is generated passively (i.e. larval supply) or actively (i.e. movement of adults).

The passive encounter model has been suggested to explain the higher numbers of settling larvae in smaller ASUs (McNeill and Fairweather, 1993). McNeill and Fairweather (1993) attributed the pattern to the relatively greater perimeter of smaller patches than large so that, per unit area of seagrass bed, more larvae will encounter the small patches. This assumes that encounter rates are determined laterally, by interactions with edge, rather than vertically through interactions between benthic seagrass and pelagic larvae. Note that although the relative amount of edge is clearly important in this model, no edge versus interior pattern would necessarily be detected, since newly settled nekton can redistribute within patches (Bell and Westoby, 1986a; Bell et al., 1987).

After settlement, nekton have increased mobility and dispersal can be considered 'active'. Active encounter has been suggested to explain larger densities of palaemonid shrimp in small ASUs than large (Eggleston et al., 1999). This model is based on the premises that a) animals move amongst beds after settlement, and b) the density in smaller patches will be greater than those in larger patches because of the greater likelihood of interception, per area of habitat, because of the greater P:A ratio in smaller patches compared with large (Eggleston et al., 1999). The active encounter model has also been used to explain higher abundances of adult fish (Sogard, 1989) and amphipods (Virmstein and Curran, 1986) in ASUs distal to natural beds of seagrass. The suggestion is that individuals of nekton species over adjacent unvegetated habitat will seek the nearest seagrass as refuge. Patches distal to other seagrass are surrounded by a greater area of unvegetated habitat, and therefore a larger pool of animals potentially seeking refuge. This explanation rests on the assumption that animals are evenly distributed over unvegetated habitat near and far from natural seagrass beds. This assumption has not been tested in the studies generating the patterns and models, but other studies have

shown that the density of nekton over sand varies strongly with distance from natural seagrass beds (e.g. Ferrell and Bell, 1991). We envisage further testing of this model using ASUs, where small ASUs are placed on their own and alongside large ASUs at each of several distances from natural beds.

3.3. Food

The food model has been used to explain greater densities of nekton in larger patches and along patch edges (Eggleston et al., 1998, 1999; Sanchez-Jerez et al., 1999), although not in studies where underlying patterns in nekton have been properly demonstrated (Table 2). The model predicts greater densities of nekton where food availability (mostly mobile epifauna) is greater. Food availability has been suggested as an explanation for higher fish densities on isolated ASUs (Sogard, 1989). Food availability is also a frequently invoked model in studies of infaunal invertebrates (Irlandi et al., 1999; Reusch and Williams, 1999; Bell et al., 2001), to explain both higher and lower densities of invertebrates with increasing patch size and higher densities in patch interiors.

Food availability has also been considered a driver of nekton abundances outside of the landscape context. Correlations between food availability and fish abundances have been shown at different locations within an embayment (Jenkins and Hamer, 2001), and manipulations of food availability (Levin et al., 1997) have been used to show their importance at small scales near the sand-seagrass edge (Connolly, 1994b,c). Protocols for surveying and manipulating food availability have therefore already been established, and can now be used in landscape studies. In particular, we recommend greater effort in establishing variability in food availability with distance from the edges in different-sized patches. This work needs to be supported by careful descriptions of diets and trophic relationships.

3.4. Predation

The predation model has been the most frequently put forward. It is a remarkably malleable model, with variations suggested to explain +ve and -ve patterns in nekton with patch size, edge and proximity (Table 1). The only cases where predation is correctly formulated as an explanation of nekton patterns, however, are for +ve and -ve relationships with patch size, and for -ve relationships with edge. The explanation for predation reducing nekton abundances in smaller patches is that predators are either more prevalent at edges (and assuming there is more edge to area for small patches, i.e. that shape is unimportant) and/or that predators more easily access the interior of smaller patches. A similar explanation is made for a -ve edge pattern, where lower nekton abundances at patch edges are considered to result from higher rates of predation along the edge.

The predation model has also been the most frequently tested (Table 3), especially with fish (Laurel et al., 2003a) and large crustaceans (Peterson et al., 2001; Hovel and Lipcius, 2001, 2002) using natural seagrass and ASUs. Most

Table 3

Summary of results of studies testing aspects of predation on nekton. Values are the number of variables showing this effect, where +, −, 0 are defined in Fig. 1

Patch attribute	Study	Fish				Invertebrates				Total
		+	−	0	Total	+	−	0	Total	
Size	Hovel and Lipcius, 2001	−	−	−		0	1	2	3	3
	Hovel and Lipcius, 2002	−	−	−		1	1	4	6	6
	Hovel, 2003	−	−	−		1	1	2	4	4
	Laurel et al., 2003a	0	1	0	1	−	−	−		1
	Total	0	1	0	1	2	3	8	13	14
Edge	Peterson et al., 2001	−	−	−		0	1	5	6	6
	Total	−	−	−		0	1	5	6	6
Proximity	Hovel and Lipcius, 2001	−	−	−		0	0	1	1	1
	Hovel and Lipcius, 2002	−	−	−		1	0	1	2	2
	Hovel, 2003	−	−	−		0	0	2	2	2
	Total					1	0	4	5	5

studies testing predation are in two parts: a survey of predator and/or prey abundances in different sized patches or at edge/interior positions, and a mensurative experiment testing predation rates in the same patches or positions (usually attack rates on, or survivorship of, tethered prey). The single study on fish is a good example. Laurel et al. (2003a) used ASUs of different sizes. The use of ASUs avoids the potential confounding of size by differences in seagrass biomass that can happen in natural seagrass patches. For example, in what was an otherwise well-executed experiment by Peterson et al. (2001), differences in survival rates of crustacean prey at edge and interior positions could not be separated from effects on survivorship resulting from the different seagrass biomass at the two positions. Laurel et al. (2003a) showed that although there were more piscivores in larger patches, predation rates on young-of-the-year cod were higher in smaller patches, presumably because of increased predator efficiency in smaller patches. Tethered prey were placed only in the centre of patches, so no information could be gathered about predation rates at edge versus interior positions. One improvement that can be made to such experiments is to compare rates of predation at edge versus interior across patches of different sizes.

3.5. Larval supply

Larval supply has been considered important in shaping patterns of increased nekton densities in smaller patches (McNeill and Fairweather, 1993) and at patch edges (Bologna and Heck, 2002). As water moves from surrounding unvegetated habitat over seagrass, the slower and more turbulent flow could result in deposition of larvae into seagrass (Fonseca et al., 1982; Fonseca and Bell, 1998). This might be expected to be greater at patch edges and therefore also in smaller patches with, depending on shape, higher P:A ratios. The counter argument has also been used, however, that currents will attenuate to an even greater degree over large seagrass beds, resulting in increased deposition and higher densities of larvae in larger patches. Larval supply is another potential explanation for densities of fish in ASUs at different distances from natural seagrass (Sogard, 1989). Tanner (2003) also

suggested that larval supply might have influenced the densities of nekton in patches orientated perpendicular to tidal currents (Table 2).

3.6. Migration

We use the term ‘migration model’ to explain patterns based loosely around movements of adult animals. Aspects of the encounter model also rely on migration of nekton, but the migration model itself is non-specific. It merely states that movements of animals among patches are the reason for higher nekton densities at patch edges (Bologna and Heck, 2002) or at different distances from natural seagrass beds (Sogard, 1989). The migration model needs further refinement before specific procedures to test it can be developed. It is clear, however, that methods for measuring movements of individuals among and within patches will be essential, and since these are not yet available (Pittman and McAlpine, 2001), they will need to be developed and tested.

3.7. Reproductive success

Reproduction has been suggested only to explain differences in the densities of animals between patch edges and interiors. Bell et al. (2001) suggested a model of higher reproductive success in the interior of patches to explain the higher densities of infauna inside patches compared with their edges. Similarly, Bologna and Heck (2000) suggested that the positive association of bivalve recruits with patch size at particular times was due to conspecific aggregation of recruits with adults, which themselves appeared to be more common in the interior than edges of patches. No study has suggested such ideas relating to reproduction for nekton but they might be considered in future.

4. Limitations of survey designs and improved methods for pattern detection

Landscape scale patterns are important for some species. For many other species, patterns with landscape attributes

have not been detected, and their densities are better explained by the position of patches in an estuary or by within-patch attributes such as seagrass density. For these species, the question is whether the lack of pattern at the landscape scale is real, or merely reflects inadequacies in survey design.

A key difficulty in discerning patterns in nekton with seagrass landscapes is that the patch attributes are usually confounded by other variables. The two most pressing concerns are that patch attributes, size in particular, are confounded with position within an estuary and water depth. The effects of position are described above, and effects of depth have also been shown (Bell and Pollard, 1989; Hovel et al., 2002). If patches representing different levels of an attribute (e.g. large and small patches) are spatially segregated, they are likely to be confounded with position or depth (or any of a number of other gradients in estuaries), reducing the chance of demonstrating the importance of the attribute itself. If examining patch size, large and small patches must be interspersed to avoid confounding with other gradients. Where this is impossible, confounding gradients are best avoided by using ASUs and placing them at the same depth (or position) or at all depths (or positions).

There are other difficulties in determining nekton patterns with patch size that might reduce the chance of finding a significant result. Patch size alone might not be influential enough to detect, but it might interact with the shape or orientation of patches. Despite the application of geographic information systems (GIS) and spatial statistics software in mapping seagrass landscapes and describing P:A ratios of patches and other variables indicative of shape (Salita et al., 2003; Jackson and Attrill, 2006), patch shape is rarely measured or accounted for in nekton studies. Even if shape is measured accurately, it does not necessarily avoid the confounding of shape and size. We recommend, therefore, that the procedures demonstrated by Bologna and Heck (2000) in their study of infaunal bivalves be considered in future studies of nekton. They used different-sized replicates of two shapes of ASUs, circular and stellar, to measure how the effects of size (area) and P:A ratio interact. Carefully planned manipulations with other shapes of ASUs will also permit tests of orientation to current such as that demonstrated by Tanner (2003).

The two main issues with ASUs for experimental manipulations of landscape attributes are whether biotic assemblages on ASUs match those of natural seagrass, and the ability to make ASUs large enough to mimic natural beds. Several comparisons of natural and artificial seagrass in temperate and tropical waters have demonstrated that assemblages of algae, invertebrates and fish are similar in the two types of seagrass after several weeks (Bell et al., 1985; Jenkins and Sutherland, 1997; Pinckney and Micheli, 1998; Kenyon et al., 1999; Lee et al., 2001; Upston and Booth, 2003). Although artificial seagrass is made of plastic and can provide no direct nutrition to animals, the microbial and algal assemblages that grow on the plastic presumably form the base of a food web that results in such similar animal assemblages (Upston and Booth, 2003). The required size of ASUs depends on the type of manipulation being attempted. There is no theoretical limit to the size

of ASUs but in practice the largest ASUs to date have had an area of just over 20 m² (Laurel et al., 2003b). Some patterns and models can be tested using ASUs up to this size, but larger ASUs will be needed for tests of attributes such as patch area, and for examining edge effects in larger patches.

The focus of past studies has been a matrix of seagrass patches surrounded by sand. Given that some human-induced perturbations create a matrix of sand halos surrounded by seagrass (Short and Wyllie-Echeverria, 1996), seagrass edges within seagrass beds are also important to understand. We have found no specific study of nekton at these inner edges, although the issue has been partly addressed through recent studies examining heterogeneous seagrass beds (Hovel and Fonseca, 2005) or the total amount of edge in a complex array of patches (Jackson and Attrill, 2006).

Statistical power of tests on nekton abundances is also problematic. Power is the chance of demonstrating a difference where one actually exists (Cohen, 1988), and is the complement of a Type II statistical error (accepting a false null hypothesis). Power is a particular problem in studies of nekton because it is difficult to determine the correct sample size in a survey of different species with (often) very different densities. Schooling species in particular tend to have highly variable densities from sample to sample, ensuring that power remains low. Low power leads to low rates of detection of patterns even where they exist. In addressing this issue, we recommend that the first step is to report power for non-significant results (e.g., Connolly, 1994a). Ultimately, it is possible to adjust the significance level (alpha) so that power is increased in situations where increasing sample size is impossible (Mapstone, 1995).

Another issue potentially masking patterns of nekton abundance is temporal variability. Many studies have sampled at a single time, giving little confidence that patterns (or lack thereof) were representative of other times. Where studies report results at multiple times of the year (e.g. Hovel et al., 2002; Tanner, 2003), most taxa responded differently at different times. A few studies reported sampling at the same time of year in different years (e.g. Bell et al., 2002; Hovel et al., 2002) so that true seasonal differences could be ascertained. Comparisons between day and night patterns can also provide a greater understanding of ecological processes underlying nekton distributions (e.g. Tanner, 2003).

The low detection rate for edge effects may reflect deficiencies in the design of edge surveys than the lack of patterns in nekton abundances. Most early surveys relied on an assumed relationship between patch size and P:A to indicate edge effects (reviewed in Bell et al., 2001), but no inference can necessarily be made about edge patterns based solely on patch size research. Direct measurement of nekton at different distances from patch edges is required. Although targeted edge surveys are increasingly more common and better designed (Table 1, only 1 out of 5 studies was done prior to 2002), there is still room for improvement. We recommend the following key elements:

- (1) Use a design that can both detect a linear gradient of influence (regression model) if it exists *and* test for non-linear

responses such as a categorical, stepped edge influence (i.e. edge versus interior) or some other curvilinear influence (see Tanner, 2005, for an example).

- (2) Finer-grained sampling (samples small and close together) is likely to achieve the objective above. There is a trade-off in the fineness of the resolution, however, since enough animals must also be sampled at each point to give a reliable, repeatable result. Small sampling units may also fail to collect transient nekton.
- (3) Plan for high statistical power to detect likely patterns. The power of regression tests depends solely on sample size and is unaffected by variability (Cohen, 1988), and is therefore easily modelled prior to sampling. Power in analysis of variance (ANOVA) tests (e.g. edge versus interior) depends on sample size and variability among and within samples. Not enough data have been collected on edge effects to model power a priori, so pilot data are needed to ensure adequate power.
- (4) The direction from the centre of patches must be taken into account. This is best done in relation to a depth gradient (e.g. shoreward and seaward, perpendicular to shore) or currents (edge parallel with or perpendicular to tidal currents). Ideally, direction can be treated as another factor and sampled appropriately. If this requires sample numbers beyond the available resources, one can randomise the direction of sampling (and therefore include the variability of direction in the unexplained variance).
- (5) An edge influence must be demonstrated on multiple (replicate) patches. Typically, patch will be a random factor in an ANOVA model, or in an ANCOVA if a regression gradient is being used. Demonstration of an edge effect in a single patch does not constitute a pattern substantial enough to base explanatory theories on.

4.1. Difficulties to overcome in model formulation and testing

In many instances, the predation, disturbance, encounter and food models have been suggested based on the premise that differences between large and small patches are due to differences in their P:A ratio. Patterns that actually support these models, however, are rarely observed. For example, Eggleston et al. (1998) suggested that the higher numbers of blue crab recruits in larger patches were due to the concomitant reduction in predation by shrimps in larger patches because of the lower P:A compared with smaller patches. The model they invoke, however, is refined in a way that no longer fits the observation directly. It is based on a pattern never demonstrated, of lower numbers of animals in the interior of patches than at edges. The pattern could be explained by a positive relationship between numbers of animals and the areal extent of a patch. We recommend that researchers avoid skipping from observing a pattern in nekton between different-sized patches to suggesting a mechanism related to the edges of patches, without evidence to support differences between the edge and interior.

The structure of seagrass beds is strongly influenced by the physical setting of the landscape. One aspect known to be important in some places is hydrodynamic activity. A gradient of increasing hydrodynamic activity was shown to result in seagrass beds ranging from continuous, semi-continuous to widely dispersed, discrete patches (Fonseca and Bell, 1998). Water depth, wave exposure and current speed can be negatively correlated with percent cover and bed P:A ratio (Fonseca and Bell, 1998). Since nekton also respond to changes in depth and hydrodynamic activity (e.g. Hovel et al., 2002; Jackson and Attrill, 2006), the influence of patch attributes might easily be confounded by the direct effects of the physical setting on nekton. Given the difficulty inherent in controlling for physical parameters, the use of ASUs is likely to be the most powerful tool in overcoming potential confounding in experimental tests of processes.

One interesting possibility is that small-scale attributes of seagrass affecting small epifaunal animals might interact with landscape features and indirectly affect the distributions of larger, nektonic animals. For example, predation or food availability differences related to within-patch characteristics such as leaf length might influence epifauna densities, thus affecting nekton distributions. Such ideas are yet to be fully tested but the work on blue crab survival shows that interactions between within-patch and landscape attributes do occur (see below).

5. Conclusions

There has been a marked increase in research of seagrass landscape attributes and nekton in the last four years. Where the work has built on a thorough understanding of the biology of key species, this has led to series of experiments testing processes underlying observed patterns. This is particularly evident in work on the economically important blue crab (*Callinectes sapidus*) in the USA. Blue crab larvae develop in open shelf waters before settling in seagrass beds in shallow waters (Pile et al., 1996). The seagrass provides protection from predation by other invertebrates and fish (Hovel and Lipcius, 2001). Juvenile survival is influenced by within-patch characteristics such as shoot density (Hovel and Lipcius, 2002). Survival is also related to landscape-scale patch attributes such as patch size (Hovel and Lipcius, 2001), but this relationship varies among locations. Survival increases with patch size in North Carolina but decreases with patch size in California (Hovel, 2003). This work has recently been furthered by examining the interaction between within-patch and landscape factors. The relationship between seagrass shoot density and survival depends on the size of patches and whether they provide homogeneous cover or a matrix of seagrass and sand within the patch (Hovel and Fonseca, 2005). Work on other species is still to some extent hampered by the lack of ecological understanding of most organisms in the systems under study. The increased efforts to understand patterns in nekton using seagrass should encourage future workers to explore experimental techniques to better determine

the role that increasingly fragmented seagrass landscapes play in nekton ecology.

The rapid increase in seagrass landscape studies of nekton in recent years has provided a wealth of data on potential patterns and processes. Landscape scale patterns are important for some species but evidence so far does not demonstrate major landscape effects overall. The lack of landscape-level pattern for some species might reflect the overriding importance of other factors, such as water depth and position within an estuary or bay. The great importance of landscape attributes in terrestrial studies (Ries and Sisk, 2004) simply might not apply in marine systems (Hovel et al., 2002). The lack of pattern detected might also result from measurements at the wrong scale. Despite the increasingly numerous and sophisticated surveys of nekton and patch attributes, the rigour of surveys can be further improved by addressing issues of confounding of patch attributes by other factors, increasing awareness of statistical power, and more considered survey designs for attributes such as edge effects.

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