ORIGINAL PAPER

E. A. Irlandi

Large- and small-scale effects of habitat structure on rates of predation: how percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve

Abstract Landscape ecology, predominantly a terrestrial discipline, considers the effect of large-scale (tens of meters to kilometers) spatial patterns of habitats on ecological processes such as competition, predation, and flow of energy. In this study, a landscape-ecology approach was applied to a marine soft-sediment environment to examine rates of predation and transfer of secondary production in and around vegetated habitats. Seagrass beds naturally occur in a variety of spatial configurations from patches 1–10s of meters across with interspersed unvegetated sediments (i.e., patchy coverage) to more continuous coverage with little or no bare sediment. I designed experiments to address how percent coverage of seagrass in a 100-m^2 area of seafloor, and the spatial arrangement (degree of patchiness or fragmentation) of an equal area (100 m^2) of vegetation affected predation (lethal) and siphon nipping (sublethal) intensity on an infaunal bivalve, *Mercenaria mercenaria* (hard clam). Measures of seagrass density and biomass with different percent coverage of seagrass were also made. When clams were placed in both the vegetated and unvegetated portions of the seafloor nearly twice as many clams were recovered live with 99% seagrass cover than with 23% seagrass cover, while survivorship was intermediate with 70% cover. Cropping of clam siphons from both the vegetated and unvegetated sediments was also affected by the amount of seagrass cover in a 100-m^2 area of seafloor: mean adjusted siphon weights were approximately 76% heavier from the 99% seagrass cover treatment than from the 70% or 23% cover treatments. Survivorship of clams placed within an equal area of seagrass in very patchy, patchy, and continuous spatial configurations was 40% higher in the continuous seagrass treatment than in either of the two patchy treatments. This study demonstrates that transfer of secondary production in the form of predation and cropping on an infaunal organism is altered as the percent cover of seagrass changes. While large-scale changes in the amount and spatial patterning of vegetation may affect habitat utilization patterns and foraging HGLoopbehavior, increased seagrass density and biomass with increased percent coverage of seagrass limit any conclusions concerning predator foraging behavior and feeding success in response to patch shapes and sizes. Instead, local changes in seagrass characteristics provide the most compelling explanation for the observed results.

Key words Energy flow · Habitat structure · Landscape ecology · *Mercenaria mercenaria* · Scale

Introduction

Landscape ecology, predominantly a terrestrial discipline, includes the study of the effects of large-scale (tens of meters to kilometers) spatial patterning of habitats on biotic and abiotic processes (e.g., Naveh and Lieberman 1984; Forman and Godron 1986; Turner 1989; Zonneveld and Forman 1990). Recent progress in the development of the discipline has been largely theoretical with an emphasis on the effect of spatial pattern on ecological processes such as competition, predation, and flow of nutrients (e.g., Forman and Godron 1981; Franklin and Forman 1987; Forman 1990; Danielson 1991). A landscape-ecology approach to studying ecosystem function has not been widely applied to marine soft sediments (but see Bell and Hicks 1991; Bell et al. 1993, in press). Seagrass beds, however, provide a suitable habitat to experimentally examine the effects of spatial patterning on ecological processes such as predation and trophic transfer of energy through food webs, because they naturally occur in a variety of spatial configurations (den Hartog 1971; Fonseca et al. 1983; Thayer et al. 1984) and represent a benthic community associated with emergent plants similar to terrestrial ecosystems.

During growth and development of seagrass beds, the plants spread via seedling germination and vegetative

E. A. Irlandi
University of North Carolina at Chapel Hill,
Institute of Marine Sciences,
3431 Arendell Street,
Morehead City, NC 28557, USA

propagation resulting in a mosaic of vegetated patches of varying size in a background of unvegetated sediments (Thayer et al. 1984; Duarte and Sand-Jensen 1990). As the beds grow and develop, several biotic and abiotic factors act to influence the ultimate shape of the beds and areal coverage of the vegetation. Rapid current flow and scouring of sediments in high-energy environments are particularly important and may limit development of seagrass beds to patches of seagrass 1–10s of meters across with interspersed bare sediments (i.e, patchy coverage), while in low-energy environments developing patches may eventually coalesce into continuous meadows covering several hectares of seafloor (den Hartog 1971; Fonseca et al. 1983). In some locations, feeding activities of epibenthic predators such as crabs and rays, and anthropogenic impacts such as boat propellers and dredging, can also fragment the vegetation and influence the structure of seagrass beds (Fonseca 1992).

Predation has been studied extensively in subtidal seagrass ecosystems (see Orth et al. 1984; Orth 1992, for reviews), but not at large scales or in the context of landscape ecology. Instead, past research has focused on the small-scale (usually c. 1 m^2) influence of the presence or absence of vegetation (e.g., Reise 1978; Summerson and Peterson 1984) and density of seagrass shoots and below-ground root material on predation (e.g., Coen et al. 1981; Heck and Thoman 1981; Blundon and Kennedy 1982; Peterson 1982). Whether or not predation rates and consumer utilization patterns vary in and around vegetated sediments as the landscape of the seafloor changes from patchy to more continuous seagrass coverage has not been evaluated.

In marine habitats nipping of feeding palps, tails, and siphons of many infaunal invertebrates by bottom-feeding fishes, shrimps, and crabs represents a potential pathway of secondary production to higher trophic levels without necessarily inflicting mortality (e.g., Trevallion et al. 1970; Trevallion 1971; de Vlas 1979; Peterson and Quammen 1982; Woodin 1982). For example, the siphons of estuarine bivalves are consumed in large quantities by the young of many commercially important fish species, suggesting that they may provide a substantial food source to the juvenile fish (Peterson and Quammen 1982; Currin et al. 1984; Hines et al. 1990; Peterson and Skilleter 1994; Skilleter and Peterson 1994). Past studies have suggested that siphon nipping pressures may be less intense within vegetated sediments (Peterson and Quammen 1982; Coen and Heck 1991; Irlandi and Peterson 1991), implying that changes in the amount of seagrass cover in the seafloor may also affect rates of siphon nipping. In addition, comparison of siphon nipping intensity and rates of predation in patchy and more continuous seagrass beds may provide an indirect measure of habitat utilization by demersal organisms and indicate soft-sediment landscapes that promote transfer of secondary production to higher trophic levels.

In this paper I present experiments that tested how large-scale differences in seagrass bed structure affected siphon nipping and predation intensity on an infaunal bi-

valve, *Mercenaria mercenaria* (hard clam). This species of clam lives in both vegetated and unvegetated sediments. Natural densities of clams are higher within vegetated sediments than within unvegetated sediments, and at larger scales densities tend to be greater from seagrass beds with high percent coverage of seagrass than from beds with less seagrass cover (Peterson 1982; Peterson et al. 1984). I designed my experiments to address: (1) how the percent coverage of seagrass in a known area of seafloor (100 m^2) affected siphon nipping and rates of predation on clams from both the vegetated and unvegetated sediments in the seafloor, and (2) how spatial arrangement of an equal area (100 m^2) of vegetation (many small patches, a few moderate-sized patches, or one big continuous patch) affected rates of predation on clams from within the vegetated sediments only. Local grass characteristics (i.e., density and biomass) were also measured.

Methods

Study site

All of the experiments were carried out at a shallow subtidal site, Oscar Shoal, in Back Sound, North Carolina, United States (Fig. 1). Water depth at the site ranged from about 0.1–0.4 m at low tide to 1.2–1.5 m at high tide. Water temperature varies with season in this region: mean monthly temperatures measured at the western end of Back Sound ranged from 4 to 29°C over a 3-year period (Sutherland and Karlson 1977). During these experiments the water temperature was approximately 25–28°C. Salinities are high year round due to relatively low riverine input and high tidal flushing through Beaufort and Barden's Inlets. Salinity in adjacent Bogue Sound, which is connected to Back Sound at the Beaufort Inlet, generally remains >34 ppt in summer and fall and about 32 ppt in winter and spring (H.J. Porter, University of North Carolina-Institute of Marine Sciences, unpublished data).

Mixed-species seagrass beds (*Zostera marina* and *Halodule wrightii*, see below) with varying amounts of vegetation cover grow on the shoal creating three distinct regions with different seafloor landscapes. To quantify the different amounts of seagrass coverage eight 10×10 m plots were staked out in each of the three regions, and the percent coverage of seagrass was determined by scoring the presence or absence of seagrass at 1-m intersections within the plots (n=100 points). One region of the shoal had 99% (±0.31 SE) seagrass cover, the second had 70% (±2.66 SE) cover, and the third had 23% (±1.76 SE) cover.

Seagrass characteristics

Predation in grass beds may be influenced by seagrass characteristics such as shoot density, blade length, and above- and below-ground biomass. To quantify these variables eight replicate 9.8-cm diameter by 15-cm deep cores were taken haphazardly in October 1992 from the grass in the 23% (very patchy), 70% (patchy), and 99% (continuous) seagrass treatments. The grass blades were held upright to avoid cutting them with the core tube. From these cores the number of shoots for each species of seagrass (*Halodule wrightii, Zostera marina*) was counted to determine species composition and the mean of the longest blade per shoot in each core was recorded to the nearest 0.5 cm. Shoots were separated from the root material at the point where the blades attached to the rhizome to determine the above- and below-ground biomass (dry weight to the nearest 0.1 g). A multivariate analysis of variance was performed on the seagrass data obtained form the cores to examine differences in overall seagrass characteristics among treat-

Fig. 1 Map of Back Sound, North Carolina, USA. The *asterisk* indicates the location of the study site, Oscar Shoal
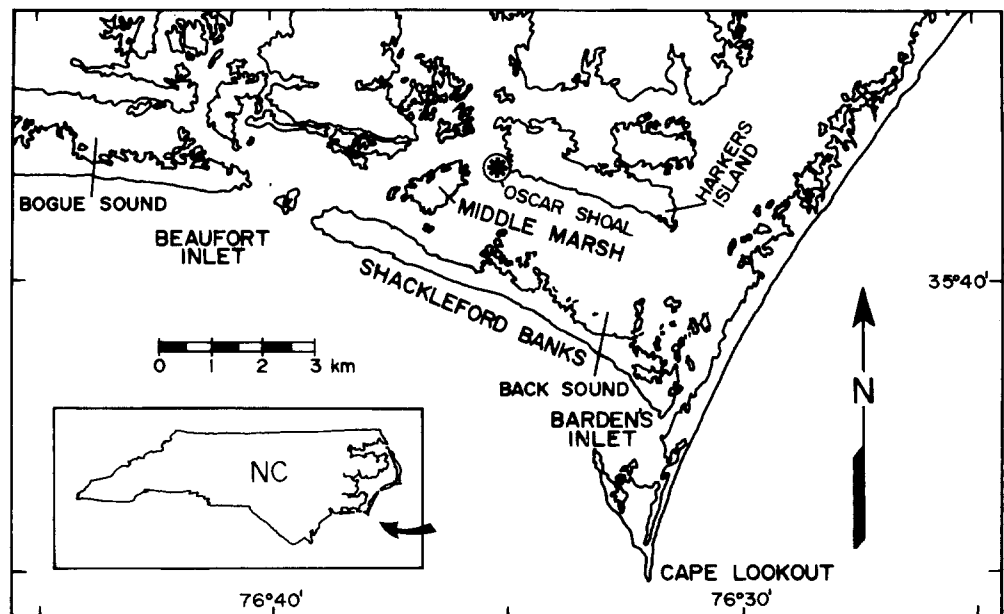
ments. Because individual factors such as shoot density, blade length, and above- and below-ground biomass are known to influence rates of predation the total number of shoots per core, mean blade lengths, and above- and below-ground biomass variables were also analyzed using separate one-way ANOVAs to see if these specific grass characteristics varied among the seagrass treatments used in the experiments. All means were tested for homoscedasticity of error variances (F_{max} test, $\alpha=0.05$) prior to analyses.

Hard clam survivorship

The first experiment assessed how the percent coverage of vegetation in a 100-m^2 area of seafloor affected rates of predation on hard clams from both vegetated and unvegetated sediments. Four 10×10 m plots were established within each of the three separate regions of different seagrass coverage (Fig. 2a). On 4 September 1992, 50 hard clams ranging in size from 20.0 to 27.3 mm in shell length (mean 23.0±0.22 SE, $n=75$) were placed haphazardly in both the seagrass and the sand within each plot. All of the clams used in this and subsequent experiments were obtained from a clam hatchery (Joe Huber, Atlantic, NC) so as to reduce variation in size, genetics, and other characteristics of the experimental animals. Marker-buoys were used to indicate the location of each clam. Markers were constructed by attaching one end of a 40-cm long by 0.5-cm wide polypropylene ribbon to a small float (buoyancy 94 g) and the other end to a 15-cm wire staple. The staples, with their attached floats, were inserted into the seafloor next to each clam. The clams were recovered after 10 days by hand digging a 15-cm circle around the marker buoy.

Clam emigration from the vegetated sediments in each plot was inhibited by the root-rhizome mat, and in unvegetated sediments emigration was almost negligible over these short time intervals. In a test of emigration rates in vegetated and unvegetated sediments, clams ($n=9$) were placed near the center of large (5×5×2 m), predator-free enclosures constructed from 1.27-cm unoriented vexar mesh, one over vegetated sediments and one over unvegetated sediments. In three replicate 10–12 day trials all clams were recovered within 5–10 cm of their starting point in both the vegetated and unvegetated treatments. When predators were present in these same enclosures all clams (dead and live) were recovered from vegetated sediments and only one clam (out of 27) could not be found from the unvegetated treatment over three replicate 10–12 day trials. Based on these results, I assumed that all clams missing from the 10×10 m plots at the end of the

experiment were lost to predation. The proportion of clams recorded as live and dead+missing was determined for each plot. The proportion recovered live was arcsine transformed, and analyzed as the dependent variable in a one-way ANOVA (after confirming homoscedasticity of error variances with an F_{max} test, $\alpha=0.05$) with amount of seagrass cover (99%, 70%, 23%) as the independent variable.

Since rates of predation are often higher in unvegetated than in vegetated sediments, I also separated rates of predation from the seagrass and sand components of the plots and compared them between the 23% and 70% cover treatments (using t-tests) to test: (1) whether clams in unvegetated sediments are eaten more or less as the amount of surrounding seagrass increases; and (2) whether clams in vegetated sediments are eaten more or less as the amount of surrounding sand increases. Question 2 is analogous to the second predation experiment where clams were placed only in the seagrass (see below).

The second experiment tested the effect of spatial configuration of the seagrass on survivorship of an infaunal organism within vegetated sediments. Four replicate plots were established over continuous (99% cover), patchy (70% cover), and very patchy (23% cover) seagrass habitat so that each plot contained the same total area of seagrass (approximately 100 m^2), but with different amounts of interspersed unvegetated sediments (Fig. 2b). The plots over the continuous seagrass remained 10 m on a side, the plots over patchy seagrass were 12 m on a side, and the plots over the patchiest seagrass were 21 m on a side. On 12 October 1992, 50 clams ranging in size from 20.0 to 25.1 mm in shell length (mean 22.4±2.0 SE, $n=60$) were placed haphazardly within the seagrass in each of the plots using buoys as markers (see above). After 10 days, the clams were recovered and the proportion of those recovered live and dead+missing was determined. The proportion recovered live was arcsine transformed, and analyzed (after confirmation of homoscedasticity of error variances with an F_{max} test, $\alpha=0.05$) using a one-way ANOVA with habitat configuration (continuous, patchy, very patchy) as the independent variable.

Siphon nipping

When clams are caged with siphon-nipping fishes, siphon weights adjusted for body weights are significantly lighter than when clams are caged without fish (Irlandi unpublished data). I used this relationship to assess if transfer of secondary production in the form of loss of siphonal tissue varied with percent cover of sea-

grass by examining siphon to body weight regressions from the three percent-cover treatments. On 10 November 1992, 50 clams were placed haphazardly (with marker buoys) in both the vegetated and unvegetated portions of the seafloor in three 10×10 m plots; one of each containing 99% (continuous) seagrass cover, 70% (patchy) cover, and 23% (very patchy) cover (Fig. 2a). The

plots were large enough (10×10 m) for each clam to be considered an independent replicate in the analyses. Fourteen days later all live clams were removed and returned to the laboratory for processing. Animals were killed by steaming and the fused inhalant and exhalant siphons were dissected from the body tissue. Siphon and body tissues were dried at 60°C to a constant weight and weighed to the nearest 0.001 g. ANCOVA was used to determine if siphon weights varied among the different seagrass treatments using body weight as the covariate. Prior to the ANCOVA, slopes of siphon to body weight regressions were determined to be parallel among treatments by testing for a non-significant interaction between the independent variable and the covariate. The assumption of homoscedasticity of regression variances was tested with an F_{max} test ($\alpha=0.05$) on the residual sums of squares from the individual regression lines.

Since cropping intensity may be higher in unvegetated than in vegetated sediments an increase in siphon nipping with less seagrass coverage may be expected given that the number of clams placed in sand increases as the percent coverage of seagrass decreases. I used t-tests analogous to those performed on the predation rates (see above) to examine if siphon nipping pressures for clams within seagrass (or sand) were influenced by the amount of surrounding unvegetated (or vegetated) sediments.

Results

### Seagrass characteristics

A summary of the seagrass data is given in Table 1. The MANOVA indicated a significant overall difference in grass characteristics among the three treatments (Wilks' lambda: $F_{(10,34)}=2.58$; $P=0.019$). The separate one-way ANOVAs using percent coverage of seagrass as the independent variable did not detect any differences among treatments in above-ground biomass or blade lengths ($F_{(2,21)}=0.76$; $P=0.48$ and $F_{(2,21)}=1.09$; $P=0.35$, respectively). Shoot densities, however, were approximately 50–65% more dense in the continuous seagrass cover than in the other two patchier seagrass treatments ($F_{(2,21)}=7.84$; $P=0.003$, Tukey *post hoc* comparisons, Table 1). Below-ground biomass was 72% greater in the
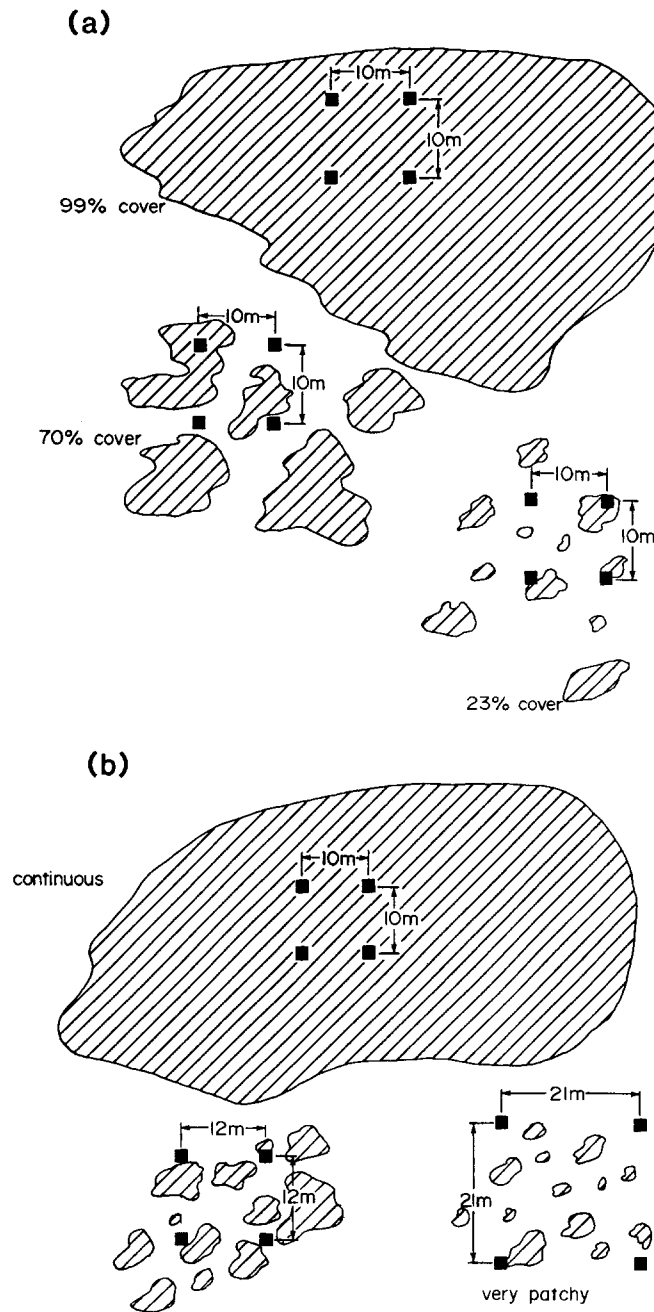
Fig. 2 a Schema of design used in the experiment to test the effect of percent coverage of seagrass in a predetermined area of seafloor (100 m²) on lethal (*n*=4 replicate 10×10 m plots in each of the three regions with different percent coverage of seagrass) and sublethal (*n*=1 plot of each treatment with 50 replicate clams per plot) predation intensity on hard clams. **b** Schema of design used in the experiment to test the effect of different spatial configurations of the same areal extent of seagrass (100 m²) on hard clam survivorship in vegetated sediments (*n*=4 replicate plots per treatment). Note in both 2a and 2b the filled squares represent the corner markers for the plots

Table 1 Summary of seagrass characteristics from eight replicate cores taken from the three different treatments used in the experiments to test the effect of seagrass configuration on lethal and sublethal predation on hard clams. Lengths are given in cm, density in shoots/m², shoot weight=above-ground biomass in g/m², root weight=below-ground biomass in g/m², and species compositions (based on shoot densities) are given in percentages. Numbers in parantheses represent ± 1 SE. Length, density, shoot weight, and root weight values were analyzed in separate one-way ANOVAs to test the effect of seagrass cover on these variables. Like superscript letters denote treatments that were not significantly different from each other in Tukey *post hoc* comparisons

Seagrass data (n=8)	Percent cover		
	23%, Very patchy	70%, Patchy	99%, Continuous
Length	14 (1)	15 (1)	15 (1)
Density	2651 (265)[b]	2917 (265)[b]	4375 (398)[a]
Shoot weight	106 (13)	133 (13)	146 (26)
Root weight	239 (40)[d]	358 (40)[cd]	411 (26)[c]
% *Halodule*	88 (4)	83 (3)	82 (3)
% *Zostera*	12 (4)	17 (3)	18 (3)
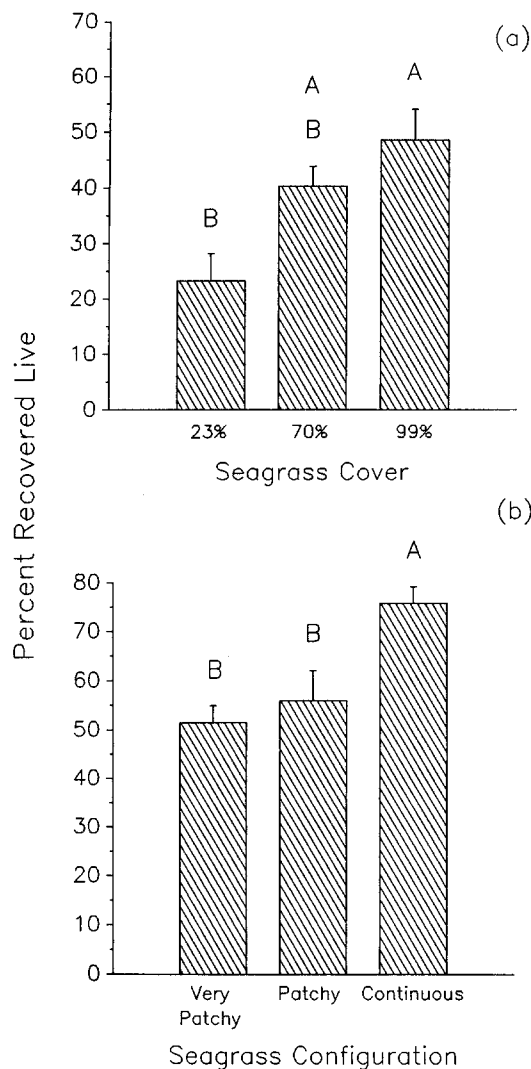
Fig. 3 a Percentage of clams recovered live pooled over both the vegetated and unvegetated sections of the seafloor from the experiment to test the effect of percent coverage of seagrass in a predetermined area of seafloor (100 m^2) on predation intensity on hard clams. ANOVA performed on arcsine-transformed proportions indicated that survivorship was significantly influenced by percent cover of seagrass. b Percentage of clams recovered live from the experiment to test the effect of spatial configuration of an equal area of seagrass cover on hard clam survivorship in vegetated sediments. ANOVA performed on arcsine-transformed proportions indicated that survivorship differed with habitat configuration. For both 3a and 3b, *unlike letters* denote treatments that differed from each other in Tukey *post hoc* comparisons and *error bars* represent +1 SE.

more continuous seagrass cover than in the very patchy cover ($F_{(2,21)}$=6.27; *P*=0.007, Tukey *post hoc* comparisons, Table 1), but did not differ from that of the intermediate seagrass cover treatment.

Hard clam survivorship

In the first experiment, hard clam survivorship averaged over both the vegetated and unvegetated sediments was

Table 2 Breakdown of the mean percentages of clams (out of *n*=50 clams in each of four replicate plots per treatment) that were placed in the grass and in the sand, and the percentage of these clams that were recovered live, in the experiment to test the effect of percent cover of seagrass on hard clam survivorship. Numbers in parantheses represent ± 1 SE. A two-tailed *t*-test was performed to determine if survivorship in unvegetated sediments differed as the amount of surrounding seagrass changed (23% vs. 70% seagrass cover) ($t_{(6)}$=-0.82; *P*=0.44). A similar comparison was made for the percentage of clams recovered live in the vegetated sediments in the 23% and 70% seagrass-cover treatments ($t_{(6)}$=-2.06; *P*=0.09).

	Treatment					
	23% Cover		70% Cover		99% Cover	
	Sand	Grass	Sand	Grass	Sand	Grass
% In each habitat	69 (4)	31 (4)	30 (4)	70 (4)	0 (0)	100 (0)
% Surviving	20 (5)	32 (5)	30 (9)	45 (4)	0 (0)	49 (5)

significantly influenced by the percent cover of seagrass (ANOVA $F_{(2,9)}$=7.41; *P*=0.01). Tukey *post hoc* comparisons indicated that nearly twice as many clams were recovered live from the seagrass and the sand with 99% seagrass cover than with 23% cover, and survivorship with 70% cover was intermediate (Fig. 3a).

In the 70% seagrass cover treatment, on average 30% (±4 SE) of the clams ended up in the unvegetated habitat and 30% (±9 SE) of these were recovered live; while in the 23% seagrass cover treatment 69% (±4 SE) ended up in the sand and of these 20% (±5 SE) were recovered live (Table 2). A two-tailed *t*-test comparing these two means did not detect any significant difference in rates of predation on clams in unvegetated sediments with different amounts of surrounding seagrass ($t_{(6)}$=-0.82; *P*=0.44).

For the clams placed in the vegetation, 70% (±4 SE) of the clams ended up within the seagrass in the 70% cover treatment, and of these, 45% (±4 SE) were recovered live (Table 2); while 31% (±4 SE) of the clams ended up within the seagrass in the 23% cover treatment with 32% (± 5 SE) of them being recovered live (Table 2). A two-tailed *t*-test comparing these mean rates of survivorship did not detect a significant difference between treatments with different amounts of surrounding unvegetated sediments ($t_{(6)}$=-2.06; *P*=0.09).

The second experiment testing the effect of spatial arrangement or configuration of an equal area of seagrass cover demonstrated a significant effect on survivorship of hard clams from the vegetated sediments (ANOVA $F_{(2,9)}$=8.59; *P*=0.008). Tukey *post hoc* comparisons indicated that hard clam survivorship was approximately 40% higher in continuous seagrass than in either of the patchy seagrass configurations (Fig. 3b).

Siphon nipping

The siphon weight for a given body weight of clam pooled over the vegetated and unvegetated portions of
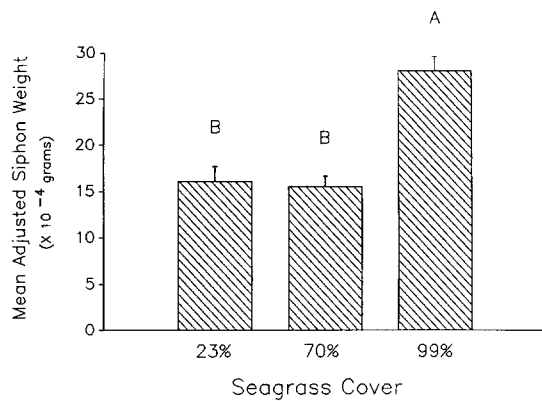
Fig. 4 Adjusted mean siphon weights pooled over clams in both the vegetated and unvegetated portions of the seafloor with different percent coverage of seagrass. ANCOVA indicated a significant effect of percent coverage of seagrass on adjusted mean siphon weights. *Unlike letters* denote treatments that differed from each other in Tukey *post hoc* comparisons. *Error bars* represent +1 SE.

the habitat also varied with the amount of seagrass cover in the landscape (ANOVA $F_{(2,99)}$=12.62; P=0.0001). Tukey *post hoc* comparisons indicated that adjusted mean siphon weights were approximately 76% heavier from the 99% seagrass cover treatment than from the 70% or 23% seagrass cover treatments (Fig. 4). *t*-tests did not detect any significant differences in sublethal predation when comparing adjusted mean siphon weights from clams within grass in the 23% and 70% seagrass cover treatments (mean siphon weights=1.7×10⁻³ g±0.21 SE and 1.6×10⁻³±0.15 SE, respectively; $t_{(43)}$=0.41; P=0.68) or from within unvegetated sediments in both seagrass cover treatments (mean siphon weights=1.3×10⁻³ g±0.15 SE and 1.4×10⁻³±0.17 SE, respectively; $t_{(21)}$=–0.51; P=0.61)

Discussion

This study is novel in that it applies the concepts of landscape ecology, typically a more terrestrial approach, to submerged aquatic vegetation in a marine environment. It explores the influence of seagrass cover on rates of predation at a larger, more realistic scale, that of percent coverage of seagrass in the landscape, rather than just presence or absence of vegetation. My results demonstrate that transfer of secondary production to higher trophic levels in the form of predation and cropping on infaunal organisms increases as the percent coverage of seagrass in the seafloor decreases. The theoretical principles of landscape ecology predict that the large-scale spatial patterning and the size of habitat patches should influence predator foraging behavior. For example, in terrestrial systems the greater edge to interior ratios associated with patchy habitats (e.g., Brittingham and Temple 1983; Andrén et al. 1985; Andrén 1992) and the presence of corridors (e.g., Small and Hunter 1988) fa-

cilitate greater access to prey for mobile predators consuming animals within and among vegetated patches. In this study, rates of predation on clams within vegetated sediments were smallest where edge to interior ratios were smallest [i.e., with 100% (continuous) seagrass cover], but changes in seagrass density and biomass with percent cover of vegetation limit any conclusions concerning predator foraging behavior and feeding success in response to patch shapes and sizes. Instead, local changes in the presence/absence of seagrass and seagrass density and biomass provide the most compelling explanation for the observed results.

The presence of vegetation adds complexity to aquatic habitats and is an important factor controlling rates of predation and animal abundance in marine and freshwater systems (e.g., Heck and Wetstone 1977; Gore et al. 1981; Crowder and Cooper 1982; Orth et al. 1984). In seagrass beds, both the above- and below-ground components of the vegetation provide protection from predation to seagrass inhabitants. A dense cover of seagrass shoots inhibits the mobility of predators as well as interferes with visual detection of prey (e.g., Nelson 1979; Coen et al. 1981; Heck and Thoman 1981) while a thick root-mat prevents digging predators such as crabs and whelks from successfully preying on infaunal organisms (e.g., Blundon and Kennedy 1982; Peterson 1982).

The results from this study were consistent with previous investigations concerning the effect of seagrass density and biomass on rates of predation. Shoot density and below-ground biomass were greater, and more clams were recovered live, from within the vegetation in the continuous seagrass treatment than in the other two patchier treatments. Regression analysis showed that mean clam survivorship was significantly correlated with mean seagrass shoot density for the three treatments (Pearson correlation coefficient r=1.0; P=0.003). There was also a high positive correlation between mean below-ground biomass and mean survivorship (Pearson correlation coefficient r=0.86), but it was not significant (P=0.34).

Many infaunal marine invertebrates that are prey for mobile predators occur in both vegetated and unvegetated sediments. Changes in the percent coverage of seagrass in the seafloor may affect utilization of the habitat and feeding success of consumers, thus affecting rates of predation on these infaunal prey. In this study lethal and sublethal predation, averaged over the vegetated and unvegetated sections of the seafloor, increased as the amount of seagrass decreased. This is not surprising given that predation and siphon cropping may be less intense in vegetated sediments (e.g., Peterson 1982; Coen and Heck 1991; Irlandi and Peterson 1991). Increased survivorship and decreased incidence of siphon nipping with 99% seagrass cover may have occurred because proportionally more clams were placed within the protective cover of vegetation in this treatment than in the 23% and 70% seagrass cover treatments.

If predation and cropping rates were directly proportional to the amount of seagrass one would expect preda-

tion and siphon nipping to be greater in the 23% cover treatment where proportionally fewer clams were placed in the protective cover of vegetation than in the 70% cover treatment. There was a pattern of increased survivorship of clams averaged over both the vegetated and unvegetated sediments within the plots with 70% seagrass cover compared to 23% seagrass cover, but the trend was not significant. Siphon weights averaged over both the seagrass and the sand, however, were very similar from both treatments.

Comparison of the proportion of clams recovered live that were placed in the unvegetated section of the seafloor in the 23% and 70% seagrass cover treatments was an attempt to determine if predation on clams, as a measure of habitat utilization and feeding success independent of seagrass biomass and density, varied as the amount of surrounding vegetation changed. There was some suggestion that very patchy seagrass beds (23% cover) may be used as foraging areas more frequently than patchy seagrass beds (70% cover) given that proportionally more of the clams that were placed within the unvegetated sediments were recovered live as the amount of surrounding seagrass increased, but the difference was not statistically significant. Above- and below-ground biomass and shoot densities of seagrass from the vegetated sediments also did not differ significantly between the 23% and 70% seagrass cover treatments, but proportionally more of the clams that were placed within the vegetation were recovered live as the amount of surrounding unvegetated sediments decreased. This difference also was not detected as significant at the 0.05 level, but the P value was marginal ($P=0.09$). While percent cover and seagrass characteristics were correlated at this site, it is not clear if this is generally the case for all seagrass habitats (Irlandi, personal observation; M.S. Fonseca, unpublished data). Further investigation is needed to determine if seagrass bed shape and size, independent of shoot density and biomass, influence predator foraging behavior and feeding success.

Regardless of the mechanisms producing these patterns in survivorship and siphon nipping (i.e., differences in predator foraging behavior in response to patch shapes and sizes or differences in predator foraging success in response to seagrass density and biomass), these results imply that patchy seagrass beds provide habitats with greater rates of transfer of secondary production to higher trophic levels than more continuous seagrass beds. This information is useful in making management decisions concerning seagrass restoration and preservation (Fonseca et al. 1988; Fonseca 1992; Thayer 1992).

When preserving or restoring a habitat, managers must decide what function the habitat is to serve and what habitat-dependent species are to be maintained and/or preserved. For seagrass beds that support many economically important species, commercial gain may also be a factor involved and managers may strive to maximize production of a particular species. Site selection for restoration and preservation projects may play a role in determining the ecological functioning of the

habitat in that the percent coverage of seagrass may differ under high- and low-energy hydrographic conditions (den Hartog 1971; Fonseca et al. 1983). The results from this study imply that production of hard clams, an economically important bivalve species, will be reduced in patchy seagrass habitats through increased loss of clams due to predation and perhaps decreased net growth rates resulting from loss of siphon tissue. This also means, however, that transfer of secondary production in patchy seagrass beds may support larger numbers of other fishery organisms such as blue crabs (*Callinectes sapidus*) that are common predators on hard clams in estuarine systems (e.g., Blundon and Kennedy 1982; Hines et al. 1990) and bottom feeding fishes such as spot (*Leiostomus xanthurus*) and croaker (*Micropogon undulatus*) that browse bivalve siphons (Currin et al. 1984; Peterson and Skilleter 1994).

Ecologists concerned with habitat preservation and restoration are moving towards a better understanding of how large-scale differences in habitat structure influence biological processes (e.g., Turner 1989). Local variation in habitat characteristics, however, along with large-scale spatial patterning of the habitat, may be directly involved in controlling species interactions such as predation. These results underscore the importance of measuring habitat characteristics at both large and small scales to better understand the influence of habitat structure on ecological processes.

References

Andrén H (1992) Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73: 794–804

Andrén H, Angelstam P, Lindström E, Widén, P (1985) Differences in predation pressure in relation to habitat fragmentation: an experiment. Oikos 45: 273–277

Bell SS, Hicks GRF (1991) Marine landscapes and faunal recruitment: a field test with seagrass and copepods. Mar Ecol Prog Ser 73: 61–88

Bell SS, Hall MO, Fonseca MS (1994) Evaluation of faunal and floral attributes of seagrass beds in high and low energy regimes: a geographic comparison. In: Dyer KR, D'Elia C (eds) Changes in fluxes in estuaries: implications of science to management. Olson and Olson, London, in press

Blundon JA, Kennedy VS (1982) Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. J Exp Mar Biol Ecol 65: 67–81

Brittingham MC, Temple SA (1983) Have cowbirds caused forest songbirds to decline? BioScience 33: 31–35

Coen LD, Heck KL Jr (1991) The interacting effects of siphon nipping and habitat on bivalve (*Mercenaria mercenaria* (L.)) growth in a subtropical seagrass (*Halodule wrightii* Aschers) meadow. J Exp Mar Biol Ecol 145: 1–13

Coen L, Heck KL, Abele LG (1981) Experiments on competition and predation among shrimps of seagrass meadows. Ecology 62: 1484–1493

Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802–1813

Currin BM, Reed JP, Miller JM (1984) Growth, production, food consumption, and mortality of juvenile spot and croaker: a comparison of tidal and nontidal nursery areas. Estuaries 7: 451–459

Danielson BJ (1991) Communities in a landscape: the influence of habitat heterogeneity on the interactions between species. Am Nat 138: 1105–1120

Duarte CM, Sand-Jensen K (1990) Seagrass colonization: patch formation and patch growth in Cymodocea nodosa. Mar Ecol Prog Ser 65: 193–200

Fonseca MS (1992) Restoring seagrass systems in the United States. In: Thayer GW (ed) Restoring the nation's marine environment. Maryland Sea Grant College Park, MD, pp 79–110

Fonseca MS, Zieman JC, Thayer GW, Fisher JS (1983) The role of current velocity in structuring eelgrass (Zostera marina L.) meadows. Est Coast Shelf Sci 17: 367–380

Fonseca MS, Kenworthy WJ, Thayer GW (1988) Restoration and management of seagrass systems: a review. In: Hook DD et al. (eds) The Ecology and management of wetlands, vol. 2. Management, use and value of wetlands. Timber Press, Portland

Forman RTT (1990) Ecologically sustainable landscapes: the role of spatial configuration. In: Zonneveld IS, Forman RTT (eds) Changing landscapes: an ecological perspective. Springer New York, pp 261–280

Forman RTT, Godron M (1981) Patches and structural components for a landscape ecology. BioScience 31: 733–740

Forman RTT, Godron M (1986) Landscape ecology. Wiley, New York

Franklin JF, Forman RTT (1987) Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecol 1: 5–18

Gore RH, Gallagher EE, Scotts LE, Wilson KA (1981) Studies on decapod crustacea from the Indian River region of Florida. I. Community composition, structure, biomass and species-areal relationships of seagrass and drift algae-associated macrocrustaceans. Est Coast Shelf Sci 12: 485–508

Hartog C den (1971) The dynamic aspect in the ecology of seagrass communities. Thalassia Jugos 7: 101–112

Heck KL Jr, Thoman TA (1981) Experiments on predator-prey interactions in vegetated aquatic habitats. J Exp Mar Biol Ecol 53: 125–134

Heck KL Jr, Wetstone GS (1977) Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. J Biogeogr 4: 135–142

Hines AH, Haddon AM, Wiechert LA (1990) Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. Mar Ecol Prog Ser 67: 105–126

Irlandi EA, Peterson CH (1991) Modification of animal habitat by large plants: mechanisms by which seagrass influences clam growth. Oecologia 87: 307–318

Naveh Z, Lieberman AS (1984) Landscape Ecology: Theory and Application. Springer-Verlag, New York

Nelson WG (1979) An analysis of structural pattern in an eelgrass (Zostera marina) amphipod community. J Exp Mar Biol Ecol 39: 231–264

Orth RJ (1992) A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. In: John DM, Hawkins SJ, Price JH (eds) Plant-animal interactions in the marine benthos (The Systematics Association Special Volume 46). Clarendon Press, Oxford, pp 147–164

Orth RJ, Heck KL Jr, Montfrans J van (1984) Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7: 339–350

Peterson CH (1982) Clam predation by whelks (Busycon spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. Mar Biol 66: 159–170

Peterson CH, Quammen ML (1982) Siphon nipping: its importance to small fishes and its impact on growth of the bivalve Protothaca stamina. J Exp Mar Biol Ecol 63: 249–268

Peterson CH, Skilleter GA (1994) Foraging of Macoma balthica on deposited versus suspended foods: the role of siphon-cropping fishes. Oecologia (in press)

Peterson CH, Summerson HC, Duncan PB (1984) The influence of seagrass cover on population structure and individual growth rate of a suspension-feeding bivalve, Mercenaria mercenaria. J Mar Res 42: 123–138

Reise K (1978) Experiments on epibenthic predation in the Wadden Sea. Helgo Wiss Meeresunters 31: 51–101

Skilleter GA , Peterson CH (1994) Foraging of Macoma balthica on deposited versus suspended foods: complex interactions between competition and cropping. Oecologia (in press)

Small MF, Hunter ML (1988) Forest fragmentation and avian nest predation in forested landscapes. Oecologia 76: 62–64

Summerson HC, Peterson CH (1984) Role of predation in organizing benthic communities of a temperate-zone seagrass bed. Mar Ecol Prog Ser 15: 63–77

Sutherland JP, Karlson RH (1977) Development and stability of the fouling community at Beaufort, North Carolina. Ecol Monogr 47: 425–446

Thayer GW (ed) (1992) Restoring the nation's marine environment. Maryland Sea Grant, College Park, MD

Thayer GW, Kenworthy WJ, Fonseca MS (1984) The ecology of eelgrass meadows of the Atlantic coast: a community profile. US Fish and Wildlife Service FWS/OBS-84/02: 1–147

Trevallion A (1971) Studies on Tellina tenius da Costa, III. Aspects of general biology and energy flow. J Exp Mar Biol Ecol 7: 95–122

Trevallion A, Edwards RRC, Steele JH (1970) Dynamics of a benthic bivalve. In: Steele JH (ed) Marine food chains. University of California Press, Berkeley, pp 285–295

Turner MG (1989) Landscape ecology: the effect of pattern on process. Annu Rev Ecol Syst 20: 171–197

Vlas J de (1979) Secondary production by tail regeneration in a tidal flat population of lugworms (Arenicola marina) cropped by flatfish. Neth J Sea Res 13: 362–393

Woodin SA (1982) Browsing: important in marine sedimentary environments? Spionid polychaete examples. J Exp Mar Biol Ecol 60–35–45

Zonneveld IS, Forman RTT (eds) (1990) Changing landscapes: An ecological perspective. Springer, New York