RESEARCH ARTICLE

Ecological trade-offs in seascape ecology: bay scallop survival and growth across a seagrass seascape

John M. Carroll · Bradley J. Peterson

Abstract In marine systems, seagrass meadows, which serve as essential nursery and adult habitat for numerous species, experience fragmentation through both human activity and environmental processes. Results from studies involving seagrass patch size and edge effects on associated fauna have shown that patchy seagrass habitats can be either beneficial or detrimental. One reason for the variable results might be the existence of ecological trade-offs for species that associate with seagrass habitats. Bay scallops, *Argopecten irradians*, are useful model organisms for studying the response of a semi-mobile bivalve to changes in seagrass seascapes—they exhibit a strong habitat association and seagrass offers a predation refuge at a cost of reduced growth. This study investigated the potential ecological survival–growth trade-off for bay scallops living within a seagrass seascape. Scallop growth was consistently fastest in bare sand and slowest at patch centers, and survival showed the opposite trend. Scallops in patch edges displayed intermediate growth and survival. Using models for minimizing mortality (μ) to foraging (f) ratios, the data suggests seagrass edge habitat offered similar value to patch centers. Further, investigations of core-area index suggest that small, complex patches might offer scallops a balance between predation risk and maximized growth. Taken in sum, these results suggest that edge habitats may benefit organisms like bay scallops by maximizing risk versus reward and maximizing edge habitat.

Keywords Bay scallops · Seagrass · Artificial seagrass unit · Ecological trade-off · Mortality to foraging ratio · Edge effects · Seascape ecology

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Introduction

Landscape ecology has begun to answer questions about fragmented and patchy habitats (Turner 2005); however, terrestrial field studies have dominated the discipline. The inclusion of marine settings in landscape ecology has been gradual (Robbins and Bell 1994; Pittman et al. 2011), creating a sub-discipline coined 'seascape ecology'(Bartlett and Carter 1991). While a number of marine habitats have been investigated, seagrass habitats remain well suited for such study (Robbins and Bell 1994) and have received the most attention (Boström et al. 2011). Seagrasses form

critical subtidal habitats for many marine species, and their ecological importance has been widely examined. Seagrass habitats have been experiencing both fragmentation and loss (Orth et al. 2006), which can result from natural processes including growth, hydrodynamics, and animal foraging (Orth 1975; Fonseca and Bell 1998; Hemminga and Duarte 2000). However, due to their existence in shallow, coastal systems, seagrass meadows are also threatened by numerous anthropogenic activities which physically remove and fragment seagrass (Burdick and Short 1999; Bell et al. 2002; Bishop et al. 2005).

As fragmentation increases, the proportion of edge habitat also increases (Murcia 1995; Smith et al. 2008), so understanding edge effects has become an integral part of seascape ecological studies. The early consensus in landscape ecology was that edges were favorable habitats, enhancing species abundance and diversity, but more recently, edges are considered to have detrimental consequences for species found there (Ries et al. 2004; Ries and Sisk 2004; Lindenmayer and Fischer 2006), even being considered 'ecological traps' (Ries and Fagan 2003; Robertson and Hutto 2006). Among the negative consequences are that increased amount of edge habitat is often associated with increased predation and disease, decreased habitat quality, and increased sites for species invasions (Ries et al. 2004). However, the direction (i.e., positive, negative) and magnitude of edge effects is often species-specific, dependent upon differences in resource availability, habitat quality and species interactions along edge zones (Fagan et al. 1999).

Variable responses to seagrass seascapes have been observed in the marine literature. The large versus small habitat patch debate has been considered for decades (McNeill and Fairweather 1993), and studies involving the impacts of patch size and degree of patchiness have yielded positive (Irlandi et al. 1995; Eggleston et al. 1998), negative (Hovel and Lipcius 2001; Hovel 2003) or both positive and negative (Gorman et al. 2009) relationships with faunal abundance and survival. Likewise, seagrass edge studies have demonstrated highly variable survival and growth results (Bologna and Heck 1999; Macreadie et al. 2010; Carroll et al. 2012). Patch shape has received less attention, with studies focusing on faunal abundance and distribution (Tanner 2003; Pittman et al. 2004). A review of seagrass seascape studies found that species responses were not consistent across patch metrics (i.e., size, shape, edge) and postulated that seagrass fragmentation might not be detrimental to associated fauna (Boström et al. 2006).

Despite the variability in results concerning seagrass patch size and edge effects, the assumption is still that continuous meadows are better than small, isolated patches (Uhrin and Holmquist 2003; Tanner 2005). The overwhelming negative perception is likely inextricably linked to predation risk, which may be elevated at patch edges—predators may focus foraging along edges, different predator types may overlap at edges, and the habitat's refuge value may be lower at edges (Smith et al. 2011). Some species show enhanced growth at seagrass edges (Irlandi and Peterson 1991; Bologna and Heck 1999), so the direction of the edge effect is dependent on the process being examined (Carroll et al. 2012). Many species experience a 'food-risk trade-off' when associating with vegetated habitats (Irlandi et al. 1999; Harter and Heck 2006) as individuals try to balance the threat from predators and foraging efficiency (Gilliam and Fraser 1987). To understand what drives the observed variability in responses of mobile organisms to seagrass fragmentation, potential ecological trade-offs need to be more fully explored.

Bay scallops, *Argopecten irradians*, are a rapidly-growing, semi-mobile, filter feeding bivalve with a strong seagrass habitat association (Belding 1910; Thayer and Stuart 1974), and may be useful model organisms for studying seagrass seascapes. Seagrass is a favored substrate for settlement (Eckman 1987) and juveniles bysally attach themselves within the seagrass canopy as a refuge from predators (Pohle et al. 1991). As scallops grow in size, they undergo an ontogenetic shift in habitat, moving from the seagrass canopy to the seafloor as they approach a size refuge from predation (Garcia-Esquivel and Bricelj 1993). The predominant scallop predators in the northeast US are crabs (Tettelbach 1986), and in New York, the dominant scallop predator is likely the xanthid crab, *Dyspanopeus sayi* (Carroll et al. 2012). Studies suggest that seascape configuration can have significant impacts on scallop survival and growth, and illustrate a food-risk type trade-off (Ambrose and Irlandi 1992; Irlandi et al. 1995; Bologna and Heck 1999).

Scallop populations have collapsed throughout their range from Massachusetts to the Gulf of Mexico (Myers et al. 2007; Tettelbach and Smith 2009). Due

to their high commercial value, bay scallops are the target of numerous restoration efforts which have resulted in mixed success (Arnold et al. 2005; Tettelbach and Smith 2009). The variable restoration success may be linked to habitat, as seagrass has also declined considerably throughout the scallops' range (Orth et al. 2006), highlighting the need to understand scallop-seagrass habitat interactions in fragmented environments for management and restoration efforts.

This study quantified the impacts of seagrass patch size, shape and within-patch location on the growth and survival of bay scallops in an experimental field setting. The main objective was to investigate the survival–growth trade-off for bay scallops living in patchy seagrass habitats by focusing on edge effects. We hypothesized that scallops would grow fastest outside of seagrass but experience the highest survival within seagrass. Since scallop abundance tends to be higher at seagrass patch edges (Bologna and Heck 1999), we expected that scallops located here would exhibit intermediate levels of growth and survival, and that predictive models would identify edges as the optimal habitat. This was accomplished by placing hatchery-reared scallops in experimental artificial seagrass units (ASUs) and comparing growth and survival, as well as calculating mortality-to-growth ratios, across positions within a seascape.

Methods

Study site

Hallock Bay (HB) is a small, shallow embayment located at the eastern end of the north fork of Long Island, New York. HB is an enclosed, lagoonal-type estuary, with a narrow inlet for tidal exchange. HB was chosen because it formerly supported both extensive seagrass meadows and a large scallop population. It is currently the site of restoration and monitoring efforts. The site of the field experiments (41°08′17.23″N, 072°15′47.96″W) was located approximately 1.5 km from an on-bottom 'spawner sanctuary' established as part of recent restoration efforts (Tettelbach and Smith 2009). The study site was approximately 50 × 20 m and characterized as having muddy sand sediments with shell hash and relatively little submerged vegetation in the form of macroalgae.
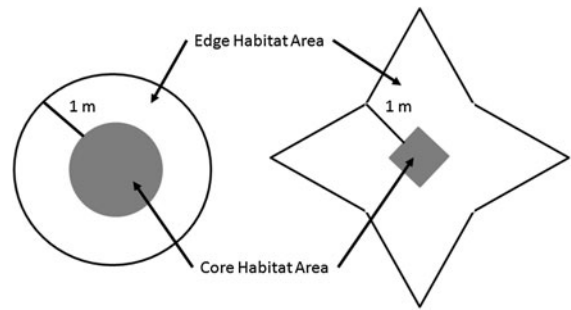

Fig. 1 Conceptual diagram illustrating the calculation of the core area index (CAI, the ratio of core area to total area) for the two shapes of artificial seagrass units (ASUs) utilized in this study, with 1 m being the distance that delineates edge from core habitats regardless of patch size or shape (see Peterson et al. 2004). The *lines* represent the radius (r) for the circles and the length (x) for the square core area at the center of the stars. Core area was calculated as πr^2 for circles and x^2 for the stars

Artificial seagrass units

To assess the impacts of seagrass patch morphology on bay scallop survival and growth, a series of ASUs was constructed which controls confounding variables of natural seagrass such as canopy height and shoot density (Virnstein and Curran 1986; Bologna and Heck 2000; Macreadie et al. 2009). Two treatment sizes, small (8.5 m²) and large (17 m²), and two shapes, a circle and a four-pointed star, were replicated: 3 each for the small shapes, but due to logistical reasons, only 2 each for the large shapes. The shapes were selected to manipulate edge and perimeter to area ratios (Bologna and Heck 2000). Sizes were chosen to allow discernable edge and core (>1 m from the edge) habitats. The 1 m edge habitat has been established in the literature as the distance which hydrodynamic processes are different (Peterson et al. 2004). ASUs of this relatively large size have not typically been used. Details of ASU construction are given in Carroll et al. (2012). In 2007, only small patches were deployed; all size patches were used in 2008 and 2009. In 2007, ASUs were placed randomly in a 3 × 2 array; in both 2008 and 2009, ASUs were deployed in a 5 × 2 array with at least 5 m of unvegetated habitat between the hard edge of each patch. Due to the 2 × 2 shape × size combination, 4 different values for core area index (CAI), the amount of core (>1 m) habitat area relative to the total habitat area, were calculated (Fig. 1; Table 1).

Table 1 Dimensions of artificial seagrass units (ASUs)

	Small		Large	
	Circular	Stellate	Circular	Stellate
Area (m^2)	8.5	8.5	17	17
Perimeter (m)	10.3	14.5	14.5	29
P:A ratio	1.21	1.7	0.85	1.7
CAI	0.180	0.019	0.478	0.033

P:A ratio is the perimeter to area ratio of individual ASUs, and CAI is the core area index

Scallop growth

Hatchery-reared scallops were placed within replicate 38×46 cm, 1 mm mesh predator exclusion devices within ASUs. Sets of 10 individually tagged scallops were measured for shell height, defined as the distance from the umbo to the farthest point from the hinge, to the nearest 0.1 mm, and placed into cages. Replicate cages were placed along the edge and at the center of each ASU (3 at the center and 3 at the edge of each small ASU, 4 at the center and 4 at the edge of each large ASU; $n = 18$ cages for each location at small ASUs and $n = 16$ at each location for large ASUs), another set was placed on barren (unvegetated, muddy sand with some shell hash) substrate within 5 m of the ASU array. Scallops were placed in the field for 12 weeks (Shriver et al. 2002; see online Supplemental Material Table S1 for sizes and dates). At the end of the 12-week periods, scallops were collected, re-measured, and growth rate calculated using the following equation:

$$Growth\,rate = (Final\,shell\,height - initial\,shell\,height)/ \\ number\,of\,days\,deployed \quad (1)$$

Scallops were returned to the lab and dissected for condition analysis, computed using the following dry weight condition index (CI) (Rheault and Rice 1996):

$$CI = (tissue\,dry\,weight/shell\,height) \times 100 \quad (2)$$

Low CI values indicate that energy reserves have been depleted for maintenance under poor environmental conditions (Martinez and Mettifugo 1998).

Chlorophyll and water flow

Since phytoplankton is the primary food source for scallops and can influence growth, in 2008, sets of 60-mL syringes were used by divers to sample water

from within the canopy at the center of a large circle ASU, along the edge, and ~ 10 cm off the bottom above unvegetated sediments as a proxy of food availability. Total chlorophyll a (Chl$a$) was measured by filtering replicate water samples onto GF/F filters, freezing, extracting in acetone, and measuring fluorescence with a Turner fluorometer (Parsons et al. 1984). Samples were collected 4 times in 2008 during the scallop deployment, approximately every 2 weeks (Shriver et al. 2002) from the middle of August to the end of September, from each ASU.

Standard plaster dissolution methods were used as a proxy for differences in flow (Komatsu and Kawai 1992). Plaster of Paris was formed in an ice-cube tray, dried to constant mass, and then sanded so that the mass of each cube was approximately the same. Cubes were weighed and fastened to bricks. Sets of bricks were placed in the field in sand, along the edge and at the center of a large circle. Cubes were recovered after 24 h, dried to constant mass and weighed. Percent loss was calculated for each location.

Scallop survival

In 2008, scallop survival was investigated by tethering juvenile scallops within ASUs, along ASU edges and in barren substrate, as described above. Since scallop size has been demonstrated as the most important factor affecting survival in the field (Tettelbach 1986), only small (18–25 mm) hatchery-reared scallops were used. Sets of 10 scallops were each individually tethered to a 4 m nylon sink line, spaced ~ 40 cm apart (Talman et al. 2004), and placed at the edge and center of each ASU. Tethers were checked for prey survival at 24-h intervals for a period of three consecutive days. All scallops were replaced daily. This experiment was conducted in August and November of 2008, when rates of predation were expected to be different (Carroll et al. 2010). Since no tethers detached from scallops after 72 h in the lab, missing individuals were interpreted as consumed.

Percent mortality was calculated using the following equation:

$$\mu = 1 - \frac{N_t}{N_0} \quad (3)$$

where μ is the calculated rate of mortality, N_t is the number of scallops surviving after one day and N_0 is the number of scallops deployed.

Mortality to growth rate

Species commonly choose among habitats that differ in the net energy received and the risk of death due to predation, which can be represented as a choice model where organisms attempt to minimize the ratio of mortality (μ) to gross foraging rate (f) (Gilliam and Fraser 1987). Bologna and Heck (1999) adapted it for use with scallops by estimating changes in scallop biomass as a proxy for foraging rate. For scallops placed in the ASUs, minimum μ/f was calculated using Eq. 3 above and the following equation:

$$f = Shell\ growthrate\ (\mathrm{mm\ day}^{-1})$$
$$\times \frac{Scallop\ tissue\ dryweight\ (\mathrm{g})}{Shell\ height\ (\mathrm{mm})} \times 1000\ \mathrm{mg/g}$$

$$(4)$$

where f is the calculated average increase in biomass, the growth rate is the difference between the final and initial shell height, and the CI is the relationship between tissue dry weight and shell height (Eq. 2). Minimize μ/f was calculated for scallops in 2008, the only year which both growth and mortality were measured.

The "Minimize μ/f" is a simplified model which only applies if the refuge is safe from predatory mortality, and there are no differences in metabolic costs in each habitat (Gilliam and Fraser 1987). If the mortality rate in the refuge is nonzero, this can be corrected to "Minimize $(\mu - c)/f$," where c is the nonzero mortality rate of the refuge, in this case patch centers, thus representing a reduced "risk" in the non-refuge habitats, i.e., patch edges and bare sand. If the costs associated with the refuge habitat are significantly different than the non-refuge habitat, the model can be corrected as "Minimize $\mu/(f + k)$," where k is the difference between the metabolic costs within the seagrass habitats (either patch centers or edges) and bare sand. The corrected values are then used to compare the "Minimum μ/f" between locations.

Statistical analysis

Due to differences in number of patch treatments among years (2 in 2007, 4 in 2008 and 2009) and since growth and condition may have been confounded by slightly different starting dates and scallop sizes, each year was analyzed separately. In 2007, a two-way ANOVA was used with patch shape (circle vs. star) and within-patch location (center vs. edge) as the explanatory factors. For 2008 and 2009, three-way ANOVAs were used with patch size (small vs. large) as the additional factor. Scallops in unvegetated sediments did not fit into either a patch size or shape factor, and so were analyzed differently. Since circle patches presented the greatest distances from the edge to the center, for each year, one-way ANOVAs were used to compare scallop growth and condition among locations in circular patches to sand.

For tethered scallop survival, each date was analyzed using a separate three-way ANOVA with patch size, shape and within-patch location (center or edge) as fixed factors. Since within patch location was found to have a significant effect, survival of scallops tethered in bare sand was compared to patch centers and edges using a one-way ANOVA. When ANOVAs yielded significant results, the Holm-Sidak test was used for multiple comparisons within each factor.

Chlorophyll a concentration was analyzed using a two-way ANOVA with date collected and location (center, edge, sand) as the explanatory factors. Since plaster dissolution was only measured on one date, a one-way ANOVA was run with location as the factor. In order to investigate the role of chlorophyll or flow on growth, Pearson correlations were used. For chlorophyll, the season averaged chlorophyll for each location was tested against the mean growth rate in 2008 for large circles only (chlorophyll was measured at the center and edges of large circles). Likewise, plaster dissolution was tested against 2008 growth similarly. For patch metrics, CAI was used to test against growth rate and survival at patch centers.

For the "Minimize μ/f" model, experimentally derived values for μ/f at patch centers, edges and sand were compared using a one-way ANOVA. For the correction factors, which were derived from the mean values of the previous analysis, the hypothesis that scallops at patch edges would experience lower values than both patch centers and sand was tested using one-tailed randomization tests (Dahlgren and Eggleston 2000). For the correction factor c, the randomization test compared the experimentally determined difference in μ/f between sand and edge habitats $((\mu - c)/f\mathrm{sand} - (\mu - c)/f\mathrm{edge})$ to a random distribution of values for $(\mu - c)/f\mathrm{sand} - (\mu - c)/f\mathrm{edge}$. The random values for $(\mu - c)/f\mathrm{sand} - (\mu - c)/f\mathrm{edge}$ were generated using experimentally derived mean values

for the correction factor c subtracted from mean values of μ for scallops at patch edges or in sand, and were divided by mean growth rate values (f) for scallops at the edge or in sand, respectively. The randomization procedure was repeated 2,000 times to generate a random distribution of values for ($\mu - c$)/$f$sand − ($\mu - c$)/$f$edge. The null hypothesis was tested as the percentage of the random distribution that was above or below the experimentally determined ($\mu - c$)/ $f$sand − ($\mu - c$)/$f$edge. The null hypothesis was rejected and significance was determined at $\alpha = 0.05$ if 95 % of the randomly generated values were less than the experimentally determined difference. For the correction factor k, the differences between $\mu/(f + k)$center and $\mu/(f + k)$edge were tested as above.

Results

Scallop growth

In 2007, growth was not affected by shape (Fig. 2a), but was affected by location. Scallops located at patch edges grew at a rate of 0.371 ± 0.05 mm day^{-1} (mean ± SE) over the course of 12 weeks, significantly more than scallops in the patch centers, which grew 0.341 ± 0.004 mm day^{-1} SH (two-way ANOVA, $F_{1,36} = 20.550$, $p < 0.001$, Fig. 2b; Table S2). Similarly, the mean CI for scallops at patch edges (1.86 ± 0.04) was significantly enhanced relative to scallops in patch centers (1.60 ± 0.04, $F_{1,36} = 22.828$, $p < 0.001$), but not by shape (Table S2). Growth rate and CI showed significant differences among locations (sand and centers and edges of circle patches, Table 2).

In 2008, growth was not different by size or shape (Fig. 2c, d), but there was a significant interaction between size and shape (three-way ANOVA, $F_{1,52} = 10.474$, $p = 0.002$); in large patches, there were no differences between shapes, although in small patches, growth on circles was greater than growth on stars. There was also a significant effect of within-patch location ($F_{1,52} = 4.333$, $p = 0.042$, Fig. 2e) on scallop growth. CI was not different between size, shape or location (Table S2). When scallops on centers and edges of circle patches were compared to those on sand, growth rate was significantly different (Fig. 3). Likewise, a significant effect of location on condition

was observed (Table 2). While the relationship between growth and CAI was negative, it was not significant (Pearson correlation r = −0.466, $p = 0.534$, Figure S1).

Growth in 2009 was generally lower than the previous two years (Fig. 2). Scallop growth was not different by patch size (two-way ANOVA, $F_{1,51} = 1.187$, $p = 0.281$, Fig. 2f), significant by patch shape ($F_{1,51} = 5.715$, $p = 0.021$, Fig. 2g), and not different by within-patch location ($F_{1,51} = 0.0098$, $p = 0.922$, Fig. 2h). Scallops on star patches grew faster (0.234 ± 0.004 mm day^{-1}) than those on circle patches (0.221 ± 0.003 mm day^{-1}). Scallops on small patches were in marginally better condition than those on large patches ($F_{1,51} = 3.784$, $p = 0.057$), and scallops at edges were in marginally better condition than those in the centers ($F_{1,51} = 3.705$, $p = 0.060$). Patch shape did not affect condition ($F_{1,51} = 1.618$, $p = 0.209$, Table S2). When compared among circle centers, edges and sand, growth rate did not vary significantly, however, CI did show significant differences (Table 2). As in 2008, there was a negative but non-significant relationship between growth rate and CAI (Pearson correlation, r = −0.850, $p = 0.150$).

Chlorophyll and flow

Chlorophyll concentrations varied significantly among sample dates, although the effect depended on location (significant two-way interaction, $F_{6,64} = 12.942$, $p < 0.001$, Fig. S2; Table S3). On 21 August 2008, chlorophyll a concentration was significantly higher at patch centers than either sand ($p < 0.001$) or patch edges ($p = 0.001$). On 03 September, chlorophyll was highest at patch edges than sand and patch centers ($p < 0.001$ for both). There were no differences between the locations for 19 or 30 September. There was a negative, albeit non-significant relationship between chlorophyll a concentration and growth (Pearson correlation, r = −0.466, $p = 0.692$). Plaster dissolution was greatest in unvegetated habitats, losing 12.6 ± 0.2 % of mass in 24 h, significantly higher than both edge and center habitats (7.9 ± 0.6 % and 8.0 ± 0.2 %, respectively, $p < 0.001$ for both). Dissolution did not differ from the patch edge to the patch center ($p = 0.956$). There was also not a significant relationship between dissolution and growth (r = 0.825, $p = 0.393$).
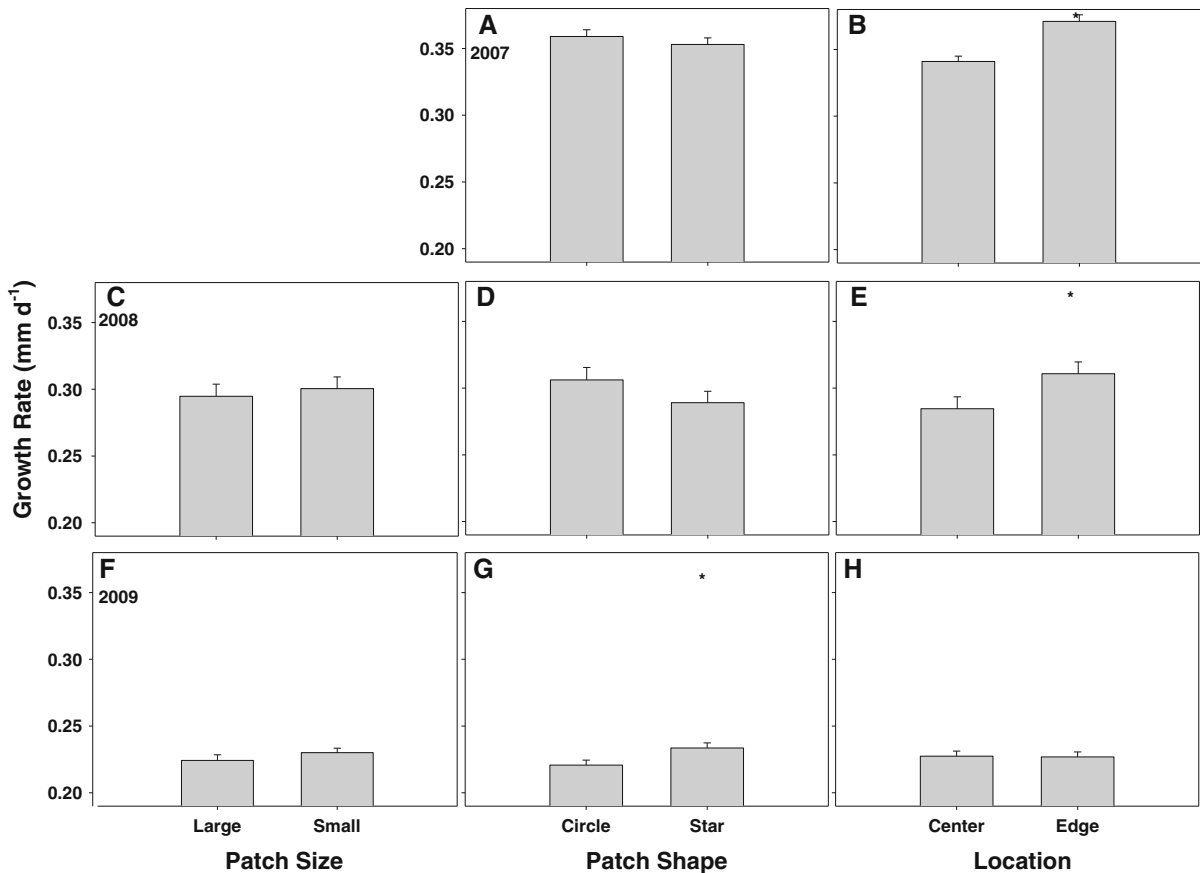
Fig. 2 Shell growth rate (mm day^{-1}) in 2007 for patch shape (**a**), and within-patch location (**b**); in 2008 for patch size (**c**), shape (**d**) and within-patch location (**e**); and in 2009 for patch size (**f**), shape (**g**) and within-patch location (**h**). *Stars* denote when differences were significant. *Error bars* represent standard error

Scallop survival

In August, survival of tethered scallops over 3 days was significantly affected by location (center or edge, three-way ANOVA, $F_{1,32} = 10.034, p = 0.003$, Table S4), but not patch size (large or small) or shape (circle or star). Scallops tethered at patch centers (0.649 ± 0.050) experienced higher survival than those at edges (0.425 ± 0.050). When comparing among seagrass patch centers and edges and sand in August, survival was significantly lower on sand (0.167 ± 0.085) than both seagrass patch centers ($p < 0.001$) and patch edges ($p = 0.036$). There was a significant positive relationship between survival and CAI (Pearson correlation r = 0.989, $p = 0.011$). In November, survival was significantly affected by patch size ($F_{1,32} = 15.306$, $p < 0.001$), shape ($F_{1,32} = 9.893$, $p = 0.004$) and location ($F_{1,32} = 5.598$, $p = 0.024$).

Scallops exhibited higher survival on large (0.570 ± 0.053) versus small patches (0.303 ± 0.043), on circles (0.544 ± 0.047) versus star patches (0.329 ± 0.049), and at patch centers (0.517 ± 0.048) versus patch edges (0.356 ± 0.048). When comparing sand to patch centers and edges in November, survival on sand was 0.025 ± 0.025, which was lower than both centers ($p = 0.002$) and edges ($p = 0.028$). However, there was not a significant correlation between CAI and survival (r = 0.776, $p = 0.224$).

Mortality to growth rate

Scallop shell growth rate in patch centers (0.29 mm day^{-1}) corresponded with an estimated increase in dry tissue weight (dtw) of 5.2 ± 0.2 mg day^{-1}, growth along patch edges (0.31 mm day^{-1}) increased tissue biomass at a rate of 6.0 ±

Table 2 Results of one-way ANOVA and multiple comparisons tests for growth rate (mm day^{-1} ±SE) and condition index (±SE) among the three locations for each year

Years	Location	Growth rate	Result of one-way ANOVA	Multiple comparisons		
				CvE	CvS	EvS
2007	Center	0.338 ± 0.004	$F_{2,19} = 18.474, p < 0.001$	<	<	=
	Edge	0.380 ± 0.008				
	Sand	0.411 ± 0.006				
2008	Center	0.292 ± 0.009	$F_{2,27} = 3.491, p = 0.045$	<	<	=
	Edge	0.326 ± 0.013				
	Sand	0.353 ± 0.015				
2009	Center	0.219 ± 0.006	$F_{2,30} = 1.330, p = 0.280$		NA	
	Edge	0.224 ± 0.005				
	Sand	0.238 ± 0.004				

Year	Location	Condition index	Result of one-way ANOVA	Multiple comparisons		
				CvE	CvS	EvS
2007	Center	1.53 ± 0.03	$F_{2,19} = 49.238, p < 0.001$	<	<	<
	Edge	1.89 ± 0.05				
	Sand	2.43 ± 0.07				
2008	Center	1.77 ± 0.08	$F_{2,27} = 5.234, p = 0.012$	=	<	=
	Edge	1.99 ± 0.05				
	Sand	2.43 ± 0.13				
2009	Center	0.72 ± 0.02	$F_{2,30} = 6.325, p = 0.005$	=	<	<
	Edge	0.77 ± 0.03				
	Sand	0.92 ± 0.03				

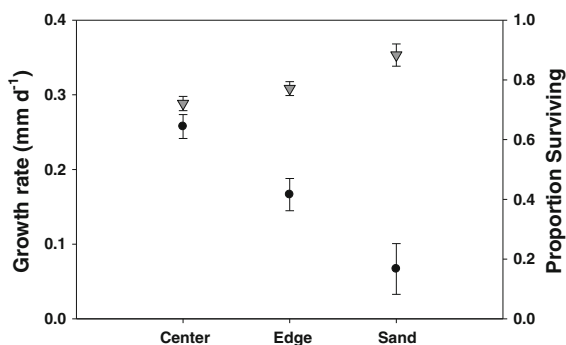For multiple comparisons results, C is center, E is edge and S is sand

Fig. 3 Mean (±SE) growth rate (mm day^{-1}) of scallops located on circle patch centers, circle patch edges, and sand (*gray triangles*) in 2008 and mean (±SE) survival for both months of tethered scallops in 2008 across patch centers, edges and sand (*black circles*), illustrating the growth-risk trade-off. *Error bars* represent standard error

0.2 mg dtw day^{-1}, and on sand, growth (0.35 mm day^{-1}) resulted in a biomass increase of 8.6 ± 0.5 mg dtw day^{-1}. The experimentally determined value of μ/f was lowest at patch centers (0.0764 ± 0.006), intermediate at patch edges (0.0943 ± 0.007) and highest in sand (0.105 ± 0.007), although the differences among the locations were not different (one-way ANOVA, $F_{2,18} = 2.881$, $p = 0.082$, Fig. 4a). When correcting for the mortality that occurs within the refuge, scallops at patch edges experienced minimized $(\mu - c)/f$ (0.024) relative to those on sand (0.052), however, results of the one-tailed randomization test between edges and sand were not significant (Fig. 4b). When correcting for the cost of growth between the habitats, scallops at patch centers had minimized $\mu/(f + k)$ (0.053) relative to

those on patch edges (0.070), but again, the randomization test suggested the difference was not significant (Fig. 4c).

Discussion

Seagrass patch metrics (shape, size, edge) led to variable responses in bay scallops. The position within the seascape impacted both the growth and survival of juvenile bay scallops; however, the processes acted in opposite directions (see Figs. 3, S1). Across all three years of the growth study, there was a significant pattern of fastest growth in unvegetated habitats, intermediate growth at habitat edges, and slowest growth at patch centers, although total growth varied interannually. Scallop condition also demonstrated significant differences among the locations, but this was more variable. These opposed survival trends for tethered scallops which were highest at the centers of

patches to lowest in unvegetated sediments. Such trade-offs can have implications for recovering scallop populations, as seagrass has long been considered the preferred scallop habitat (Belding 1910) and is frequently used to assess habitat suitability in the field.

Other patch metrics tested—size and shape—at times also had an impact on growth, condition and/or survival, although the factor and effect were variable. In 2008, growth was faster in small rather than large circles, and in 2009, there was faster growth on star patches than circles. Both patch scale metrics in 2008 and 2009 may mirror edge effects; small circles have more edge area relative to core area than large circles and star patches have more perimeter and edge area than circles. Similarly, survival in November 2008, exhibited patch scale effects (survival was higher in large vs. small patches and on circle vs. star patches) that were likely linked to edge effects as well. Patch size effects and edge effects may be confounded (Ewers and Didham 2006), and any patterns observed
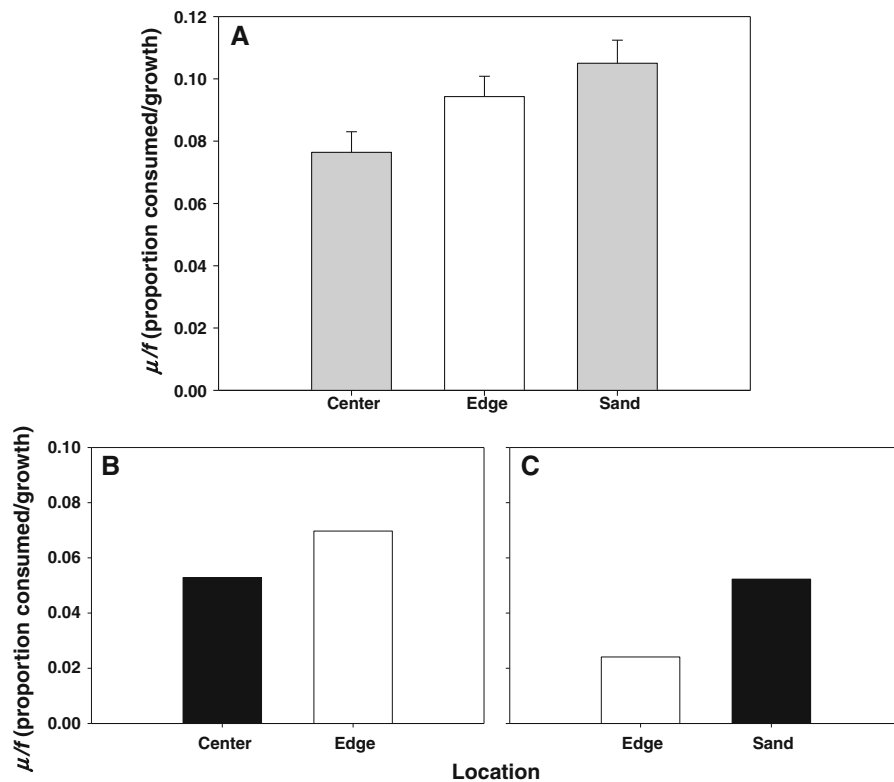

Fig. 4 Mean estimated μ/f (mortality rate/growth rate) of scallops from in each seagrass patch location ($p = 0.082$, **a**). *Error bars* represent standard error. μ/f values are corrected for different metabolic costs of associating with seagrass, $\mu/(f + k)$, where k is the difference in growth between sand and each seagrass habitat (**b**), and corrected for refuge mortality, $(\mu - c)/f$, where c is the mortality in the patch centers (**c**)

by patch morphology may be driven by edge effects 'scaling up' to the patch level (Fletcher et al. 2007; Carroll et al. 2012).

Our results point to an ecological food-risk trade-off across a seagrass edge for scallops, which had been demonstrated previously (Bologna and Heck 1999). The trade-off suggests that the relationship between scallops within seascapes is complex, but does not indicate which habitat should be selected by scallops. Gilliam and Fraser (1987) first introduced a model where individuals seek to minimize the ratio of mortality rate (μ) to foraging rate (f). Fauna are predicted to live in a habitat within which the μ/f ratio is lowest. In the present model, scallops were predicted to minimize the risk of mortality relative to biomass growth. This study found the μ/f ratio to be lowest within the center of seagrass patches due, in most part, to lower predation.

However, the μ/f values of scallops at in all locations were relatively low and were not different from each other. This differed from the pattern in the Bologna and Heck (1999) study, where μ/f was 2–3 times higher at patch edges than bare sand and patch centers, mainly attributable to the 6–70 times higher mortality in this edge zone. In our study, mortality was intermediate along patch edges. While mortality in this study was higher than the Florida study (Bologna and Heck 1999), the differential μ/f pattern may be due to the predators responsible for scallop mortality. The major predator in the Bologna and Heck (1999) study was a large gastropod which the authors suggested was twice as likely to encounter scallop prey along seagrass edges as they move into and out of seagrass patches. Shell damage (cracked, broken shells) for this study was indicative of crab predators, which tend to be ubiquitous throughout the site (Carroll et al. 2012). Regardless, this study supports both the effectiveness of seagrass as a predation refuge (Prescott 1990; Irlandi et al. 1999) and the higher risk associated with edges (Bologna and Heck 1999; Smith et al. 2011).

The lower μ/f in this study compared to Bologna and Heck (1999) is probably attributable to the differences in estimated biomass growth. While we used a different shell-biomass relationship to estimate biomass growth, our estimates are within range of other scallop studies (Bricelj et al. 1987). The growth patterns observed likely served to balance the significant differences in survival among the locations. Scallops on bare sand gained significantly more tissue biomass per day than scallops located within seagrass, despite chlorophyll concentration being similar or lower there. This increased growth was likely driven by the significantly greater flow outside of the seagrass patches, as demonstrated by plaster dissolution. The higher flow could result in a greater flux of food to the scallops on unvegetated bottoms (Cahalan et al. 1989).

It is generally hypothesized that individuals will choose habitats that balance risk of predation and food resources, and that as food availability becomes greater in the riskier habitat, individuals move there (Gilliam and Fraser 1987). However, the μ/f values calculated here do not predict where scallops might optimize the risk of mortality to foraging efficiency. Although μ/f was lowest at patch centers relative to edges and sand, the difference was not significant. The simple "Minimize μ/f" model makes assumptions about mortality and growth (Gilliam and Fraser 1987), and so it was expected that correcting the model should lead to better predictors of habitat choice. By correcting for mortality in the refuge, the new model, "Minimize $(\mu - c)/f$," suggested that scallops along the edge minimized the risk relative to growth compared to those on sandy substrate; the difference between edges and sand more than doubled. However, the one-tailed randomization test did not yield a significant result. When the model was corrected to reflect the biological cost of seagrass association, the new "Minimize $\mu/(f + k)$" model still shows lower values for scallops at patch centers when compared to patch edges (see Fig. 4), although this was also not significant. When used as relative metrics for comparison, the models suggest that scallops would perform better in seagrasses, which can explain why scallops have higher abundances in this 'preferred' habitat. Further, the models can be used to partially explain why mobile species, such as scallops, may remain in settlement habitats (patch edges) even in the face of higher predation—centers may not offer an increased benefit.

Patchy habitats and/or smaller seagrass patches with higher amounts of edge are not likely to be detrimental for scallop populations; scallops seem to balance growth and survival at patch edges. It has been suggested by others that seagrass meadow fragmentation may not adversely affect associated fauna (see review by Boström et al. 2006), although studies have rarely examined the processes leading to these relationships. For scallops, patchy seagrasses may be

better for two reasons. First, having more edge habitat enhances scallop settlement, and despite higher mortality along the edge, numbers of recruits are the same (Carroll et al. 2012) or greater (Bologna and Heck 1999) at patch edges. Second, scallop growth and condition is enhanced at patch edges relative to interiors, and growth and condition of individuals at the center of patches increases as CAI decreases (this study). Survival and growth may intercept each other at low CAI values, suggesting that in smaller and/or more complex patches where edge area is greater than core area, the growth-survival trade-off may be maximized. Similar responses have been observed in patchy versus continuous habitats (Irlandi et al. 1995).

These results, coupled with those from other studies, suggest the terrestrial precepts of patchy landscapes and edge habitats as 'ecological traps' (Ries and Fagan 2003; Robertson and Hutto 2006) might not generally apply to bay scallops. While survival data from this study might support seagrass patch edges as ecological traps—risk of predation is higher—this is not always the case (Peterson et al. 2001; Selgrath et al. 2007). Additionally, when examining metrics of fitness (growth, condition), individuals at seagrass edges actually exhibit greater fitness than their counterparts in patch interiors (Irlandi and Peterson 1991; Bologna and Heck 1999). Reproduction might also be enhanced at patch edges (Bologna and Heck 1999), so at the population level, edges are not likely to have an overall negative impact (Carroll et al. 2012). This suggests that ecological traps may exist solely dependent upon the ecological process being examined, and should be examined at the population level and across multiple processes.

Habitat edges alter species interactions which lead to observed patterns; edges can differentially influence the movement of individuals, induce species mortality, facilitate cross-boundary subsidies, and create opportunities for novel interactions and invasions (Fagan et al. 1999). The direction and magnitude of responses are likely to be both species and process specific, which is a plausible explanation for the variable responses in both terrestrial and marine literature. In this study, the two processes studied acted in opposing directions across a seagrass edge. While the "Minimize μ/f" model was unable to identify any location as the best for scallops, it at least suggested that patch centers and edges do not differ in value. Despite the limitations, specifically that similar experiments were not conducted in natural seagrass patches, it is likely that edge habitats may not have net negative impacts on populations of associated fauna like scallops, and that patchy seagrass habitats might even be beneficial.

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