

## Balancing the edge effects budget: bay scallop settlement and loss along a seagrass edge

JOHN M. CARROLL,<sup>1,3</sup> BRADLEY T. FURMAN,<sup>1</sup> STEPHEN T. TETTELBACH,<sup>2</sup> AND BRADLEY J. PETERSON<sup>1</sup>

<sup>1</sup>School of Marine and Atmospheric Sciences, Stony Brook University, 239 Montauk Highway, Southampton, New York 11968 USA

<sup>2</sup>Department of Biology, Long Island University, CW Post Campus, Brookville, New York 11548 USA

**Abstract.** Edge effects are a dominant subject in landscape ecology literature, yet they are highly variable and poorly understood. Often, the literature suggests simple models for edge effects—positive (enhancement at the edge), negative (enhancement at the interior), or no effect (neutral)—on a variety of metrics, including abundance, diversity, and mortality. In the marine realm, much of this work has focused on fragmented seagrass habitats due to their importance for a variety of commercially important species. In this study, the settlement, recruitment, and survival of bay scallops was investigated across a variety of seagrass patch treatments. By simultaneously collecting settlers (those viable larvae available to settle and metamorphose) and recruits (those settlers that survive some period of time, in this case, 6 weeks) on the same collectors, we were able to demonstrate a “balance” between positive and negative edge effects, resulting in a net neutral effect. Scallop settlement was significantly enhanced along seagrass edges, regardless of patch type while survival was elevated within patch interiors. However, recruitment (the net result of settlement and post-settlement loss) did not vary significantly from edge to center, representing a neutral effect. Further, results suggest that post-settlement loss, most likely due to predation, appears to be the dominant mechanism structuring scallop abundance, not patterns in settlement. These data illustrate the complexity of edge effects, and suggest that the metric used to investigate the effect (be it abundance, survival, or other metrics) can often influence the magnitude and direction of the perceived effect. Traditionally, high predation along a habitat edge would have indicated an “ecological trap” for the species in question; however, this study demonstrates that, at the population level, an ecological trap may not exist.

**Key words:** *Argopecten irradians; bay scallops; ecological trap; edge effects; landscape; Long Island, New York, USA; predation; seagrass.*

### INTRODUCTION

Understanding the impact of landscape characteristics (e.g., patch size, shape, corridors, and other characteristics) on ecological processes such as recruitment success is increasingly important as anthropogenic habitat fragmentation accelerates. Traditionally, the precepts of landscape ecology have been applied to terrestrial systems despite their clear importance to both aquatic and marine realms (Hinchey et al. 2008). Notable exceptions to this research trend have occurred in the area of seagrass community ecology, where investigators have begun to look at the effects of spatial pattern and configuration on ecosystem function (Robbins and Bell 1994, Irlandi et al. 1995, Eggleston et al. 1998, Hovel and Lipcius 2001, Darcy and Eggleston 2005). Seagrasses are important nearshore habitats that typically support high abundance and diversity of associated organisms (Heck and Orth 1980, Jackson et al. 2001). However, the total areal cover of seagrasses

has declined worldwide due to anthropogenic influences (Orth et al. 2006), and at more local scales, a variety of impacts have created landscape patterns similar to those found in fragmented terrestrial habitats; i.e., mosaics of seagrass patches that vary in size, shape, and degree of isolation (Robbins and Bell 1994), highlighting the importance of examining seagrass landscape characteristics on ecological processes.

The early consensus in landscape ecology was that ecotonal habitats, i.e., transitional zones between two distinct habitats, led to higher species abundances and increased species diversity; however, the modern perception has been that edges are undesirable features, associated with increased predation, decreased habitat quality, and are frequently sites for species invasion (Ries et al. 2004). Understanding the effects that habitat edges have on ecological processes has become an integral part of recent landscape studies. In terrestrial studies, the direction (i.e., positive, negative, neutral) and magnitude of edge effects are often species-specific, and depend on differences in resources/quality between adjacent habitats and interactions between species along habitat edges (Ries et al. 2004, Ries and Sisk 2004). A review by Ries et al. (2004) offered three possible,

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<sup>3</sup>E-mail: johncarroll31@gmail.com

predictable outcomes for a species response to a habitat edge: positive, where the response variable is highest at the edge and decreases with distance from edge; negative, where the response variable is lowest at the edge and increases with distance from edge; and neutral, where the response variable remains constant.

Similar edge effect predictions have also been made for marine seagrass systems, albeit without a potential neutral response (Macreadie et al. 2010a). In a review of seagrass landscape studies, Bostrom et al. (2006) found that species response was not consistent across landscape variables (i.e., size, shape, edge, and other variables) and postulated that seagrass fragmentation might not be detrimental to associated fauna if (1) there are abundant patches with high connectivity, (2) edge effects are not central to the species being studied, and (3) there is unrestricted movement between suitable patches. However, edge effects have been shown to be an important process for many seagrass-associated fauna (Eggleston et al. 1998, Bell et al. 2001, Bologna and Heck 2002, Macreadie et al. 2010a, b, Moore and Hovel 2010, Smith et al. 2011).

As emergent structures, seagrasses dampen water currents, leading to higher deposition of particles along the leading edges of seagrass patches (Peterson et al. 2004). Because bivalve larvae are weak swimmers and can be considered passive particles (Butman 1989, Jonsson et al. 1991), larvae should be expected to settle with higher frequency along seagrass edges. The resulting reduction of recruits into the patch with increasing distance from the edge has been termed a “settlement shadow” (Orth 1992). However, seagrass edges can also have increased predator–prey interactions, leading to mortality (Irlandi et al. 1995, Smith et al. 2008). For individual species, the seagrass edge may create a trade-off of the aforementioned ecological processes (Bologna and Heck 1999). These ecological trade-offs may result in observed net neutral effects across seagrass edges.

Bay scallops (*Argopecten irradians*) are a seagrass-associated bivalve found along the east coast of the United States (Thayer and Stuart 1974). As passive particles, larval bay scallop settlement is strongly influenced by eelgrass structure and hydrodynamics (Eckman 1987). Similar effects of seagrass structure are observed throughout the literature on a variety of species, including jingle shells (*Anomia simplex*; Eckman 1987), clams (Peterson 1986), various mussel species (Bologna and Heck 2000), and other bivalves (Bostrom and Bonsdorff 2000). Bologna and Heck (2000) investigated bivalve settlement to artificial seagrass and found enhanced settlement along the edge, with a relationship between total abundance and the perimeter of the patches, providing evidence of a settlement shadow (Orth 1992). Assuming that scallop larvae are passive particles affected by hydrodynamics and emergent structure, we can predict a similar settlement pattern: higher abundance at the edge of patches, decreasing

toward the center of the largest patches, or a “positive” edge effect (Fig. 1A).

Seagrass edges, however, also alter species interactions, and in particular, predator–prey dynamics. There is evidence to suggest that multiple fauna experience higher predator-induced mortality along seagrass edges than within the patch (Bologna and Heck 1999, Gorman et al. 2009, Smith et al. 2011). Predation is considered a major mechanism structuring scallop abundance (Tettelbach 1986), and predation can be impacted by habitat change or loss (Prescott 1990, Carroll et al. 2010). Additionally, studies have demonstrated decreased scallop survival in both fragmented seagrass landscapes (Irlandi et al. 1995, 1999) and along habitat edges (Bologna and Heck 1999). Based on the available predation data, we can make a second prediction for scallop abundances with lowest numbers along seagrass edges, where predation should be highest, and highest numbers within the seagrass habitat, yielding a “negative” edge effect (Fig. 1B).

Therefore, bay scallops may be considered model invertebrate fauna for landscape ecological studies in the marine environment and, as such, we can predict the outcomes of scallop settlement (where the scallops are settling in the seagrass environment) and recruitment (settling scallops that survive post-settlement processes over a given time period, for this study 6 weeks) against landscape variables such as shape and edge. In this study, we investigate the impacts of landscape parameters (shape, size, within-patch location) on settlement and post-settlement loss of scallops simultaneously, providing empirical evidence that apparent “neutral” responses to habitat edges represent a “balance” between opposing edge effects, and show that predation is the dominant mechanism structuring scallop abundance and is itself not influenced by fragmentation.

## METHODS

### *Study site*

Hallock Bay (HB) is one of the easternmost, enclosed basins in the Peconic Estuary (PE) system. HB is located on the eastern tip of the North Fork of Long Island, New York, USA. It is characterized as a relatively shallow (<2 m mean depth) enclosed basin with seawater exchange through a narrow inlet and, as with other PE basins, the dominant freshwater contribution is through groundwater discharge. It is bracketed to the south and east by Orient Beach State Park, and to the north and west by low-density residential units.

Since the winter of 2007, a scallop restoration site has been established (41°07'41.28" N, 072°16'27.72" W), ~1.5 km from the experimental site (41°08'17.23" N, 072°15'47.96" W; Fig. 1). Over the course of three consecutive winters (2007, 2008, and 2009) ~500 000 scallops have been planted in the spawner sanctuary (~70 000, 169 000, and 240 000, respectively).

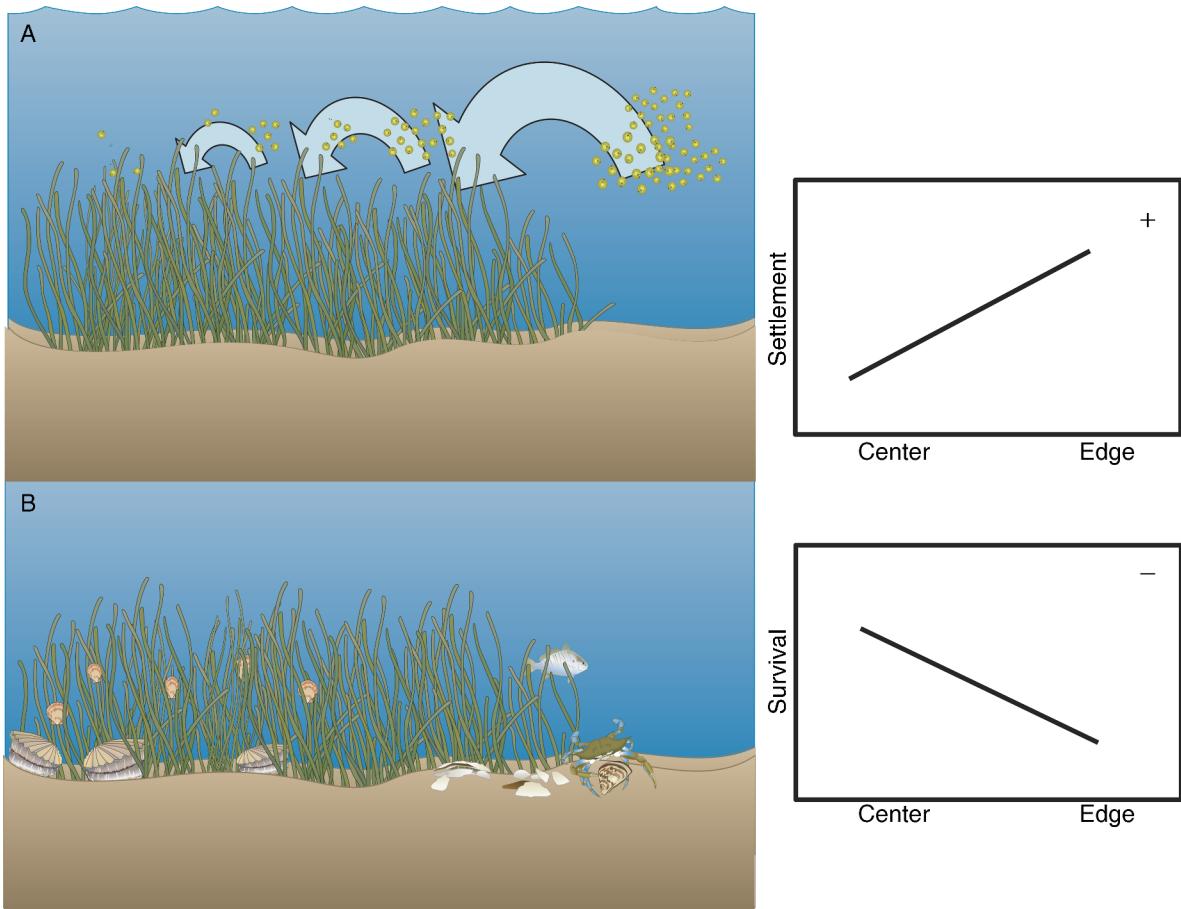


FIG. 1. Conceptual diagram showing (A) the larval shadow, adapted from Orth (1992), and (B) predation across the edge of a seagrass patch to the interior, displaying both positive and negative edge effects.

#### *Artificial seagrass units*

Artificial seagrass units (ASUs) have been used successfully in many studies to examine the impacts of seagrass structure on resident species (Virnstein and Curran 1986, Sogard and Able 1994, Bologna and Heck 2000). In addition, *Argopecten irradians* larvae readily settle on a variety of artificial substrates (Appendix A), with settlement apparently controlled by the availability of surface area (Ambrose and Lin 1991).

Two treatment sizes, “small” ( $8.5 \text{ m}^2$ ) and “large” ( $17 \text{ m}^2$ ), and two shapes, “circular” and a four-pointed star or “stellate” were replicated three times for small shapes, but due to logistical reasons, only twice for large shapes (Appendix B). The shapes were selected with the assumption that linear patches may demonstrate more significant effects than circular ones (Lindenmayer and Fischer 2006) and to maximize differences in the amount of edge and perimeter-to-area ratios (Bologna and Heck 2000). Sizes were chosen so that patches were large enough to have both distinct edge and center habitats ( $>1 \text{ m}$  from the edge; Peterson et al. 2004), as a shortcoming of many previous ASU studies has been

that the size of ASUs was too small to have had discernable edge and center habitats. That is, in previous studies, ASUs were almost entirely edge habitat. Even at this scale of investigation, the  $8.5\text{-m}^2$  stellate shape had only  $0.16 \text{ m}^2$  of center, or core, habitat. We selected the sizes and shapes in order to examine both impacts at the patch scale as well as impacts of within-patch location.

ASUs were constructed by cutting Vexar mesh (InterNet, Anoka, Minnesota, USA) into the desired shapes as a backing for the artificial shoots. Shoots were created by using green polypropylene ribbon tied to the mesh. Blade width, blade number, and canopy height ( $500 \text{ shoots/m}^2$ ; blade width, 5 mm; blade number, 4; canopy height, 35 mm) were within the ranges reported for natural *Zostera* beds within eastern Long Island (Eckman 1987, Pohle et al. 1991). Each ASU was placed onto unvegetated sediment, and anchored using screw anchors at the center of each mat and with a series of rebar stakes along the edges. The experimental units were randomly assigned a position within a  $5 \times 2$  evenly interspersed matrix with a minimum separation distance of 5 m.

### *Recruitment collector construction and sampling*

A series of smaller artificial eelgrass units ( $10 \times 20$  cm) were created in the same manner as the experimental patches, with a total of 10 artificial shoots. In this case, however, the eelgrass units served to collect scallop recruits. Five of the shoots were enclosed within an 800- $\mu\text{m}$  mesh bag secured to the collector with a tie wrap to prevent entry by potential predators, yet allow colonization by scallop larvae. The other five shoots were left exposed to quantify post-settlement loss (i.e., predation or emigration). The collectors were randomly assigned to either the edge or center of each ASU, and were attached to the Vexar via tie wrap so that the leaves of the ASU were under the collectors and were exposed once the collectors were removed. This prevented changes in shoot density on the ASUs from influencing predation, emigration/immigration, and settlement processes.

This design allowed for a predicted recruitment value equivalent to observed “settlement” (individuals within the mesh bag) for comparison with short-term “recruitment” (individuals outside of the mesh bag). For this study, recruitment is defined as those scallops surviving up to 6 weeks post-settlement. Additionally, survival for this study was calculated as the number of recruits divided by the number of settlers for each collector, with the assumption that the loss is due to mortality. While it is possible that scallops can move, several factors indicate the major loss component is due to mortality and emigration can be assumed to be negligible. Typical behavior of post-set scallops (byssal attachment) and ontogenetic changes in behavior where swimming activity increases at intermediate sizes (15–30 mm) as scallop juveniles transition to the bottom (Tettelbach 1991, Garcia-Esquivel and Bricelj 1993) suggest that actively swimming does not readily occur at the sizes encountered. Additionally, it has been shown for other scallop species that swimming is difficult at sizes  $<12$  mm due to hydrodynamic drag and high energy costs (Manuel and Dadswell 1993). Finally, strong tidal currents have been shown to be important for influencing bay scallop movement (Winter and Hamilton 1985, Tettelbach 1986, Powers and Peterson 2000), which do not occur in the study area.

A second series of collectors were designed in the same method; however, holes were cut into the mesh bags for a partial bag treatment. This treatment allowed predators to access the bags while maintaining the potential baffling effects of the fine mesh to estimate whether or not the bags artificially inflate settlement above some level of biotic control. There was no difference between inside and outside of the control bags ( $P = 0.310$ ), indicating that the mesh bags did not artificially inflate settlement. Because there was no difference, raw values for scallops inside the bags were used for statistical analysis with no correction.

Sets of recruitment collectors were deployed and collected every 6 weeks, offset by 3-week intervals, for a

total of four sets of collectors spanning a period of 15 weeks in each of two years. After 6 weeks in the field, each set of collectors was returned to the laboratory for processing. Deployment of recruitment collectors coincided with scallop peak spat settlement, which begins in late May (Tettelbach et al. 1999). Collections were made the second week of July (15 July both years), the first week of August (3 August 2009 and 5 August 2010), the fourth week of August (26 August both years) and the second week of September (17 September 2009 and 16 September 2010). Collectors were separated into exposed and enclosed, and rinsed into an 800- $\mu\text{m}$  sieve with a high-power water hose. Because we could not discern which of the enclosed scallops were attached to the artificial seagrass vs. the mesh bag due to dislodgement during processing, any scallops attached to the outside of the mesh bags were included with those from the “exposed” collectors. All scallop spat  $>1$  mm shell height were enumerated and measured, as were all mud crabs, *Dyspanopeus sayi* found on or within the collectors. In addition, in 2010, all other fauna on the collectors were quantified.

### *Data analysis*

A series of three-way ANOVA tests were used to compare differences in scallop settlement, recruitment, and survival, as well as abundance of mud crabs.

For scallop settlement, “treatment” (T), location (L), and collection (C) were fixed factors; the factor treatment was constructed differently depending on the statistical comparison being considered. When comparing across patch area, treatment had two levels, small and large. When comparing across patch shape, treatment had four levels: large circle (LC), large star (LS), small circle (SC), and small star (SS). Comparisons across perimeter and P:A ratios had three levels: low, intermediate, and high. Location and collection did not vary depending on the test. Location had two levels, either center or edge. Collection had four levels: collections 1, 2, 3, and 4. Analysis of scallop recruitment and abundance of mud crabs were conducted in the same manner. For scallop survival, treatment and location were the same as for settlement; however, collection only had three timepoints as there were rarely new settlers in the fourth collection. When a significant effect of the response variable occurred, a multiple comparisons test (Holm-Sidak test) was used to determine statistically significant differences between treatments. Results were considered statistically significant at an alpha of 0.05.

Point counts of scallop settler and recruit abundances were scaled up to the whole patch for further tests of patch-scale effects. The amount of core habitat was calculated as the area of the ASU  $>1$  m from the edge of the patch. Edge area was calculated as the total ASU area minus the calculated core area (see Appendix B). The mean scallop settler abundance for the whole patch was calculated using the following equation:

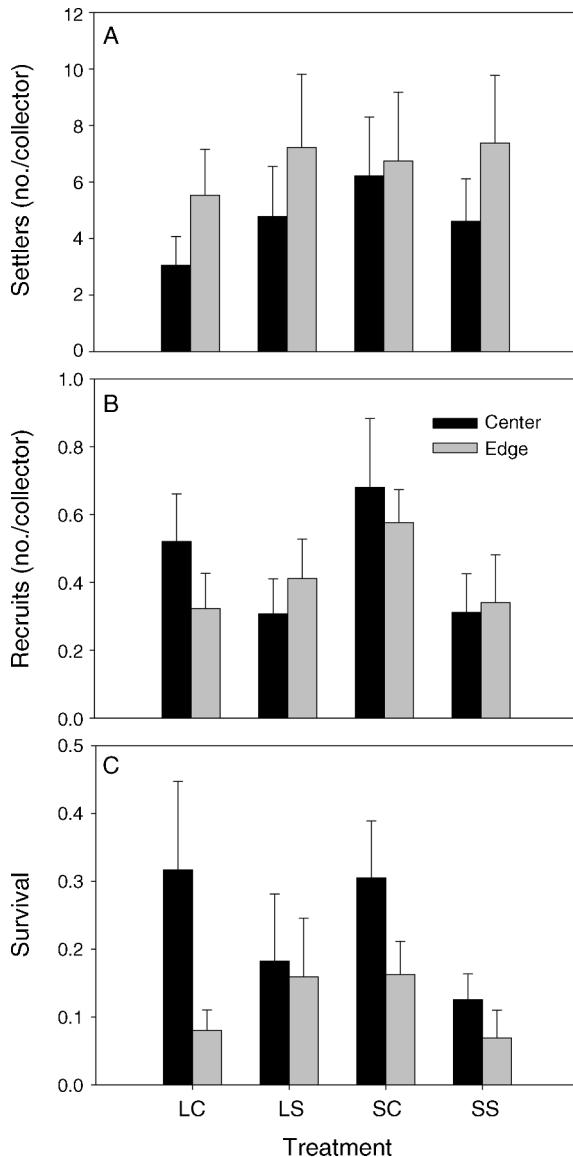


FIG. 2. Densities (mean + SE) of (A) bay scallop (*Argopecten irradians*) settlers, (B) actual recruits, and (C) survival (the ratio of recruits to settlers) per collector as a function of artificial seagrass unit (ASU) treatment in Hallock Bay, Long Island, New York, USA. Black bars represent collectors from the center; gray bars represent collectors from the edge. Key to abbreviations: LC, large circle; LS, large star; SC, small circle; and SS, small star. All collections from both years are pooled for one center and one edge value for each ASU.

$$(\bar{X}_{SE} \times A_E) + (\bar{X}_{SC} \times A_C)$$

where  $\bar{X}_{SE}$  is the mean density of settlers (as determined per collector) along the edge,  $A_E$  is amount of edge area,  $\bar{X}_{SC}$  is the mean number of settlers per collector at the center, and  $A_C$  is the amount of center area. This was repeated for recruits, and extrapolated patch survival was calculated as the number of recruits for each patch divided by the number of settlers.

Finally, a matrix of Pearson's correlations was computed for all measures of patch morphology and both scallop abundance at the collector level and extrapolated patch-scale abundances.

## RESULTS

When predators were excluded, there was no difference in the mean abundance of scallops between patches of different size ( $P = 0.288$ ), perimeter ( $P = 0.560$ ), perimeter : area (P:A;  $P = 0.280$ ), or shape ( $P = 0.489$ ). There were significantly higher scallop abundances along the edges of ASUs ( $6.78 \pm 1.17$  individuals/collector, mean  $\pm$  SE) compared to the interior ( $4.81 \pm 0.86$  individuals/collector;  $P = 0.05$ ; Fig. 2A). There were significant differences for within-patch location (Fig. 2A) and for collection ( $P < 0.001$ ). Peak settlement was observed on the second collection during the first week of August, with  $17.25 \pm 1.88$  scallops/collector, when compared to other collections ( $P < 0.001$  for all comparisons; see Fig. 3A).

On the exposed portion of collectors, where predators were allowed access, patch size ( $P = 0.287$ ) or shape ( $P =$

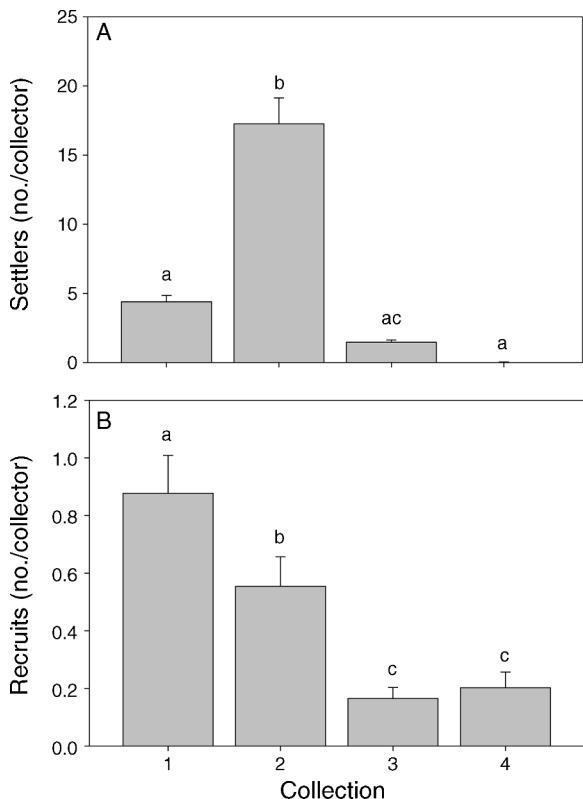


FIG. 3. (A) Settlers per collector (mean + SE) and (B) recruits per collector (mean + SE) across both years and all treatments for each collection. Collection 1 was 15 July for both years, collection 2 was 3 August 2009 and 5 August 2010, collection 3 was 26 August for both years, and collection 4 was 17 September 2009 and 16 September 2010. Different lowercase letters denote statistically significant differences as determined by multiple comparisons tests.

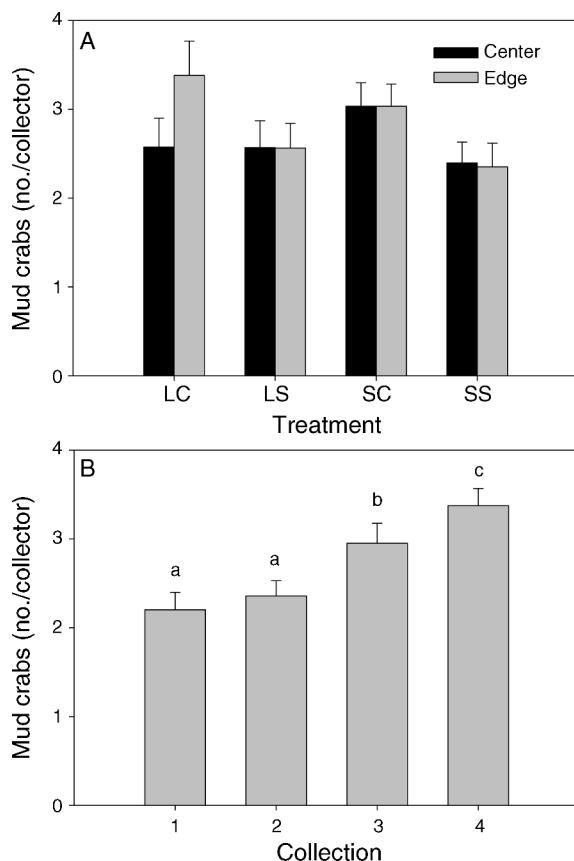


FIG. 4. Densities (mean + SE) of mud crabs per collector (A) at the edge and center of each ASU and (B) across collection periods. For panel (A), black bars represent center collectors, and gray bars represent edge collectors. Crab densities were pooled across all collections in both years to get one center and one edge value for each ASU. For panel (B), crabs were pooled across ASU treatments in both years for one crab density value for each collection. Collection 1 was 15 July for both years, collection 2 was 3 August 2009 and 5 August 2010, collection 3 was 26 August for both years, and collection 4 was 17 September 2009 and 16 September 2010. Different lowercase letters note significant differences from multiple comparisons tests. See Fig. 2 for treatment abbreviations.

0.074) did not have an effect. However, both patch perimeter and P:A ratio had significant impacts on numbers of recruits. Patches with the lowest amount of perimeter ( $P = 0.035$ ) or intermediate P:A ( $P = 0.027$ ) ratios had the highest number of recruits. The small circle patches had both the lowest perimeter and the intermediate P:A ratio. Mean abundances of scallop recruits did not vary from edge to interior ( $P = 0.690$ ; Fig. 2B). Similar to settlement, there was a significant temporal difference among collections ( $P < 0.001$ ); however, unlike patterns in settlement, the peak recruit abundance occurred in July, during the first collection (Fig. 3B).

Scallop survival, estimated as the ratio of recruitment to settlement, did not vary between patches of different size ( $P = 0.810$ ), perimeter ( $P = 0.240$ ), P:A ratio ( $P =$

0.145), or shape ( $P = 0.169$ ). Survival was significantly enhanced at the middle of patches,  $0.229 \pm 0.043$ , when compared to ASU edges  $0.121 \pm 0.027$  ( $P = 0.015$ ; Fig. 2C). Survival also varied over time; it was significantly higher in the first collection ( $0.332 \pm 0.059$ ) than the second ( $0.053 \pm 0.011$ ,  $P < 0.001$ ) and third collections ( $0.153 \pm 0.043$ ,  $P = 0.002$ ). No ratio was determined for the fourth collection, as there was generally no scallop settlement (Fig. 3A; Appendix C). The within-patch location effect was strongest when examined with P:A ratio than other patch treatments.

Mud crabs were the most dominant predator recorded by the collectors. Crab abundance per collector did not differ among treatments ( $P = 0.128$ ) or within-patch location ( $P = 0.746$ ; Fig. 4A). Crab abundance did vary significantly among collections ( $P = 0.001$ ), increasing with time (Fig. 4B).

Core area varied among treatments, being the least on the stellate shapes ( $0.16 \text{ m}^2$  and  $0.5 \text{ m}^2$  for SS and LS, respectively) and the most on circular shapes ( $1.2 \text{ m}^2$  and  $5.5 \text{ m}^2$  for SC and LC, respectively). The series of one-way ANOVAs at this scale of observation yielded only one significant result (Appendix C). Extrapolated recruits were significantly higher on large patches ( $676 \pm 125$  total recruits/ASU) than small patches ( $390 \pm 72$  recruits/ASU,  $P = 0.037$ ) across both years and all collection periods. There was no significant effect of any patch morphometric on total settlers or patch-scale survival. Likewise, the Pearson's correlations yielded only one significant result (Appendix C). The total amount of settlers per patch was significantly related to the amount of perimeter ( $r = 0.959$ ,  $P = 0.041$ ).

## DISCUSSION

A standard interpretation of these results would be as a clear demonstration of a neutral edge effect. Though, in the past, many investigators have suggested such findings to be indicative of experimental error or lack statistical power in discerning true effects (Ries and Sisk 2004). However, using our collection methods, we are able to separate recruitment into its two component processes, namely settlement and post-settlement loss (mainly through mortality) and show for the first time that net neutral edge effects result from a balance of otherwise traditional positive and negative edge effect mechanisms (Fig. 5). To our knowledge, this is the only study to simultaneously investigate settlement and recruitment on the same cohort of individuals within a landscape context and we did so by creating a collector that both protected individuals from predation and allowed natural post-settlement losses to occur. Unfortunately, assessing the generality of these findings is confounded by the difficulty in publishing neutral effects and their misinterpretation as spurious.

Recent literature searches suggest that artificial seagrasses should have exhibited either a positive or negative edge effect on scallop recruitment (Macreadie et al. 2010a), depending on which force was more

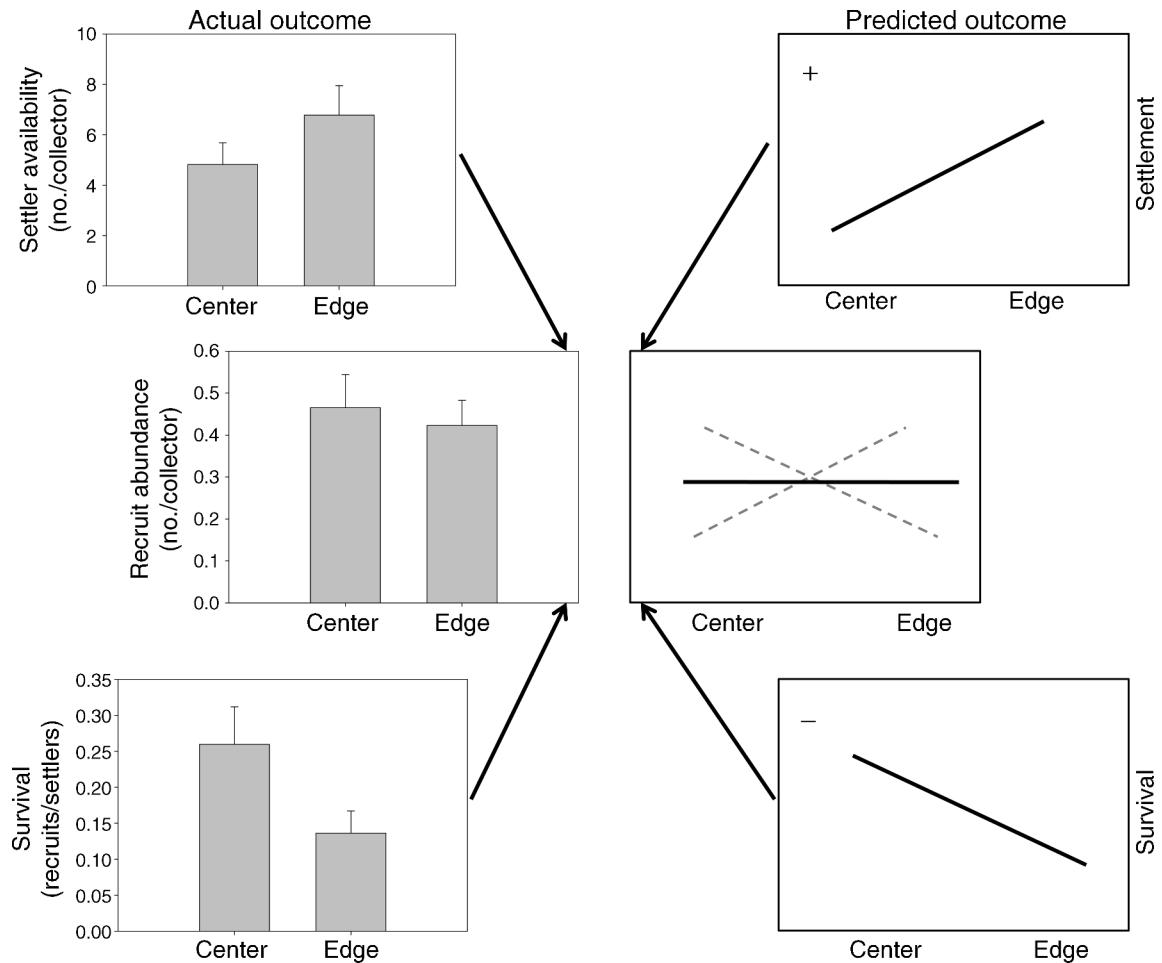


FIG. 5. Actual vs. predicted outcomes for settlement and survival. Settlement (positive edge effect predicted and observed) and survival (negative edge effect predicted and observed) balance each other out, leaving a net neutral edge effect on scallop abundance (not predicted).

important, supply or predation, making a neutral effect essentially a null result. Had this study only investigated scallop abundance, and not also quantified patterns in settlement, the conclusion would have been that there was no effect. Our results suggest that neutral effects are a real phenomenon and should contribute to the understanding of edge effects or at least highlight our incomplete understanding of edge effect budgets.

In this study, the seagrass edge had significant impacts on scallop settlement and survival, affecting the budget of new individuals recruiting to seagrass habitats. Settlement was highest at the patch edges when compared to the interior, regardless of size or shape, and this significant positive effect supports the argument of a settlement shadow, as predicted by Orth (1992) and Bologna and Heck (2000). This settlement enhancement at patch edges adds to the potential pool of recruits to a seagrass meadow. However, survival was lowest at patch edges, a pattern confirmed in other studies (Bologna and Heck 1999, Smith et al. 2011), removing individuals from the potential pool of recruits at the seagrass edge.

This created a “balanced budget” of sorts, the addition of scallops via settlement was neutralized by loss via mortality.

While edge effects on settlement and survival were strong across all treatments, the overall effects of patch morphometrics on response variables were less clear. When examining patch morphology at the collector scale, there was no apparent effect of ASU size, perimeter, P:A, or shape on scallop settlement or survival. However, there was a patch effect at the collector scale of scallop recruitment with significantly higher numbers of recruits per collector on patches with the lowest amount of perimeter and intermediate P:A (SC). Past investigators have suggested that patches with the lowest perimeter should have the lowest densities of bivalves (Bologna and Heck 2000). A similar effect was observed in this study on settlers, not recruits, though our results do highlight the confounding influence of perimeter and P:A.

Fletcher et al. (2007) found that edge effects were either more common in nature than patch-scale effects,

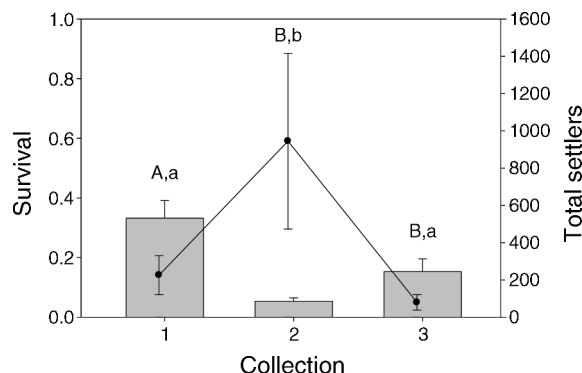


FIG. 6. Survival of bay scallops as estimated by the ratio of actual recruits to settlers (bars, left axis) and mean total settlers for both years (line, right axis) against collection period. Survival estimates were pooled across all collectors for both years to arrive at a single value for each collection ( $\pm$ SE). The values for total settlers are the mean numbers of settlers (only those collected in bags) for all collectors for both years ( $\pm$ SE). Different uppercase letters denote significant differences for survival, while different lowercase letters denote significant differences for settlers as determined by multiple comparisons tests.

easier to detect, or some combination of both. Because the overall amount of edge and core area varied between patches of different sizes and shapes, detecting differences driven by patch morphometrics would have required a sampling method different from our point estimates. We attempted to use our collector counts to scale up to the level of patch. Yet, of 24 statistical tests (12 one-way ANOVAs and 12 Pearson correlations) only two were significant. At the patch level, there were larger total scallop populations on larger patches than smaller patches, despite similar densities throughout. The significant positive relationship between calculated total settlers and perimeter mirrored the positive edge effects we observed on settlement, suggesting that edge effects may have driven patterns in patch morphology (Fletcher et al. 2007).

There were significantly more scallop settlers at the edges of patches than the interiors, and a strong positive correlation between settlement and perimeter for calculated settlers on the patch scale. However, there were no significant effects of within-patch location on recruitment, or significant relationships between patch-scale recruit abundance and perimeter or P:A, suggesting that scallop population abundance across ASUs is not structured by patterns in settlement. Post-settlement processes, such as predatory mortality, are likely the dominant forces structuring scallop abundance on the mats, common for many benthic organisms (Hunt and Scheibling 1997, Scheibling and Robinson 2008, Prado et al. 2009). Numbers of scallops were reduced by 1–2 orders of magnitude from settling densities to actual recruits over a 6-week period. The pattern of settlement within seagrass patches disappeared when exposed to post-settlement loss.

The likely culprit is the xanthid crab, *Dyspanopeus sayi*, the dominant predator within our lagoonal system and an important predator on juvenile bay scallops (Streib et al. 1995). This relatively small species is not likely to be impeded by seagrass structure; they are patch residents (Irlandi et al. 1999) and exhibit enhanced foraging success with increasing seagrass complexity. In this study they were ubiquitous and homogeneously distributed throughout our ASU treatments, demonstrating that densities of these mesopredators (mud crabs) were not impacted by patch area, shape, or within-patch location. It has been shown that small predators can be important consumers of post-set mollusks (Ray-Culp et al. 1999), and given their remarkably high abundance and seagrass climbing abilities (Pohle et al. 1991), these crabs are likely frequently encountered by byssally attached scallops within the canopy.

We must concede, however, that spatial pattern alone cannot inform estimates of predator activity or predation success (scallop survival). Because mud crabs did not exhibit an edge effect, it is possible that other predators foraging along patch edges may have contributed to the observed scallop loss. Potential scallop predators were occasionally recorded in or around the ASUs, including blue crabs, *Callinectes sapidus*, spider crabs, *Libinia dubia*, and juvenile tautog, *Tautoga onitis*. Given the size and motility of these species, it remains possible that collector bias may have under-sampled both their abundance and perceived importance, though the small size of the post-set scallops (<10 mm) and the high densities of mud crabs across all treatments ( $262 \pm 12$  crabs/m<sup>2</sup>) support the notion that mud crabs played a pivotal role in post-settlement mortality.

The difference in survival between collection dates and within-patch location demonstrates a predator response to changes in prey density. There are typically two response categories of predators to changes in prey numbers: an aggregative response or a functional response (Taylor 1984). The lack of spatial patterning attributable to predators in this study was consistent with a functional response (Fig. 6), though as mentioned, our approach to quantifying the predator field inhibits our ability to definitively rule out an aggregative response. Regardless, increasing consumption with increasing scallop supply demonstrates that these predators may not be satiated at current levels of restoration enhanced scallop settlement, at least for the basin studied.

While conditions appear favorable to settlement along seagrass edges, scallops survived poorly at these locations. The balancing of positive and negative edge effects on post-set scallops demonstrates a potential ecological trade-off for scallops at seagrass edges, as shown by others (Bologna and Heck 1999). In addition to being a potential trade-off, it is possible that the competing forces structuring scallop recruitment at seagrass edges represents an ecological trap for scallops.

Terrestrial literature suggests that habitat edges often act as ecological traps (Ries and Fagan 2003), where fauna preferentially settle in a habitat where fitness is reduced (Robertson and Hutto 2006). Robertson and Hutto (2006) asserted that in order to demonstrate the existence of an ecological trap, three criteria must be met: (1) individuals should exhibit preference of one habitat over another, or at least, equal preference, (2) some measure of fitness must be different between habitats, and (3) the fitness outcome for individuals settling in the preferred or equally preferred habitat must be reduced.

Our data appear to fit the criteria laid out by Robertson and Hutto (2006): larvae ‘prefer’ to settle along the edges and survival (a measure of individual fitness) is reduced in edge zones. However, this principle might not be so easily transferred to the marine environment. At the level of the individual, seagrass edges pose a potential trap for settlement-stage bay scallops, yet recruitment data suggest that there is no difference in densities between the seagrass edge and interior. Further, scallop growth is enhanced at seagrass edges relative to patch interiors (Bologna and Heck 1999). Therefore, when considered at the population level, there does not appear to be a detrimental effect of edge-centric settlement.

Ecological traps in the terrestrial realm are often driven by incomplete resource mapping or predator spillover from adjacent habitats (Ries et al. 2004), resulting in reduced numbers in those habitats (Ries and Fagan 2003). Although positive behavioral cues are presented to scallops settling in edge habitats, at larger spatial scales this pattern is regulated by passive processes (local hydrology; Eckman 1987), a complication without a direct terrestrial analogue. In this system, the rate of delivery appeared sufficient to offset a strong negative edge effect. Given that realized recruitment densities did not differ from edge to interior, and the high levels of fragmentation exhibited by local seagrass meadows, we can infer that a large portion of the scallop population may in fact occur within edge habitats. That this takes place despite higher individual mortality, clearly illustrates the need for investigators to more closely examine the implications of ecological traps. Specifically, ecological traps identified at the level of the individual may need to be revisited and reviewed at the population level, as we have demonstrated that population level effects may differ greatly from those recorded at smaller scales.

Likewise, a “soft” or a “hard” edge is likely to affect the degree and strength of both edge effects and ecological traps. In this study a distinct contrast between the seagrass habitat and the surrounding barren substrate was used to detect edge effects. While this hard edge feature is common in eastern Long Island, in other seagrass systems, edges may exhibit reduced shoot densities, lower canopy height, or other measure of complexity, yielding a soft edge or a gradual transition

between habitats, which would increase predator efficiency. We therefore interpret our results as a conservative estimate of post-set scallop mortality. Further, because increasing habitat complexity negatively affects seagrass predators, patches with soft transition zones are more likely to produce ecological traps in seagrass environments, a direct contrast to the terrestrial environment, where studies have demonstrated nest predation to be stronger along edges with sharp contrasts than those with weaker contrasts between the two habitats (Lindenmayer and Fischer 2006).

## CONCLUSIONS

Studies of edge effects, and their driving mechanisms, are abundant in the terrestrial literature, although broad geographic patterns have not emerged (Lindenmayer and Fischer 2006). The composition and configuration of habitats can impact the magnitude and strength of the edge effect, leading to observed variability at local and regional scales. Many factors may contribute to the observed effect such as temporal variability, contrast between adjacent habitats, mechanism for settlement, among others, and the metric used to investigate (abundance, diversity, survival, and other metrics) the edge effect is just as likely to play a role in whether or not an effect is found as the habitat edge itself. In this study, the examined processes (settlement and survival) showed opposite edge effects, yielding a net neutral effect on recruits, suggesting that broad patterns of edge effects may remain similarly elusive in marine “seascapes.”

This is the first study to demonstrate a balanced budget between settlement and post-settlement mortality simultaneously on the same cohort of naturally recruiting individuals, allowing components of the neutral edge response to be teased apart. However, the temporal variability in settlement, recruitment, and survival suggests that at any point in time, there may be an overall positive, negative, or neutral result, indicating that perhaps the best indicator of an edge effect should be examined at longer temporal scales. In addition, the results indicate that while there is an ecological trade-off between settling along a habitat edge and survival at the individual level, there does not appear to be a net negative effect at the population level. Thus, although the terrestrial literature posits that habitat edges in increasingly fragmented landscapes may act as ecological traps, it is possible that habitat fragmentation may not be detrimental to seagrass-associated fauna, as concluded by Bostrom et al. (2006). Rather, the strong positive effect of more individuals along seagrass edges due to typically passive processes of particle (and larval) settlement is likely to be enhanced in fragmented landscapes with more edge habitats. Although survival is lower along the edge, this study suggests that the density of recruits is similar at the edge and interior, and that there might not be a net negative effect of habitat fragmentation on scallop populations.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Underwater photograph of a scallop settler attached to the artificial seagrass (*Ecological Archives* E093-143-A1).

### Appendix B

A table depicting the dimensions of the artificial seagrass units (ASUs) and a figure showing model seagrass patches depicting edge and center habitats (*Ecological Archives* E093-143-A2).

### Appendix C

Tables depicting the results of statistical analysis for scallop settlement, recruitment, and survival (*Ecological Archives* E093-143-A3).