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CONSERVATION ECOLOGY – ORIGINAL RESEARCH

Habitat fragmentation differentially affects trophic levels and alters behavior in a multi-trophic marine system

Elizabeth Rielly-Carroll[1] · **Amy L. Freestone**[2]

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Abstract Seagrass, an important subtidal marine ecosystem, is being lost at a rate of 110 km^2 year^{-1}, leading to fragmented seagrass seascapes. Habitat fragmentation is predicted to affect trophic levels differently, with higher trophic levels being more sensitive, stressing the importance of a multi-trophic perspective. Utilizing the trophic relationship between the blue crab (*Callinectes sapidus*) and hard clam (*Mercenaria mercenaria*), where adult blue crabs prey on juvenile blue crabs, and juvenile blue crabs prey on small hard clams, we examined whether predation rates, abundance, and behavior of predators and prey differed between continuous and fragmented seagrass in a multi-trophic context at two sites in Barnegat Bay, NJ. We tested the hypothesis that fragmented habitats would differentially affect trophic levels within a tri-trophic system, and our results supported this hypothesis. Densities of adult blue crabs were higher in fragmented than continuous habitats. Densities of juvenile blue crabs, the primary predator of hard clams, were lower in fragmented habitats than continuous, potentially due to increased predation by adult blue crabs. Clams experienced lower predation and burrowed to a shallower depth in fragmented habitats than in continuous habitat, likely due in part to the low densities of juvenile blue crabs, their primary predator. Our results suggest that while trophic levels are differentially affected, the impact of habitat fragmentation may be stronger on intermediate rather than top trophic levels in some marine systems.

Keywords Habitat loss · Seagrass · Blue crabs · Fragmentation · Food webs

Introduction

Habitat fragmentation is an important attribute of landscape structure and can shape patterns of species richness (Fahrig 2003), community composition (Crist et al. 2006; Krauss et al. 2010), and ecosystem function (Layman et al. 2007; Waycott et al. 2009). Less is known, however, about how fragmentation may affect interactions among species particularly multi-species interactions and behavioral changes of both predators and prey due to altered trophic relationships (Fahrig 2003). Habitat fragmentation, where large continuous habitat is broken into smaller and more isolated habitat patches, has been shown to alter species relationships including trophic interactions, but often this research focuses on single predator–prey relationships (Crist et al. 2006; Martinson et al. 2012). This approach may overlook important variation in trophic-dependent responses to fragmentation as not all trophic levels are predicted to respond similarly to fragmentation (van Nouhuys 2005). Differences in habitat requirements (Davies et al. 2000), dispersal ability and demography (Kareiva 1987) and behavior (Tigas et al. 2002) may contribute to differing responses to fragmentation among trophic levels.

Most empirical examples examining the effects of fragmentation on species interactions within a multi-trophic

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✉ Elizabeth Rielly-Carroll
erielly@holyfamily.edu

[1] Department of Biology, Holy Family University, 9801 Frankford Avenue, Philadelphia, PA 19114, USA

[2] Department of Biology, Temple University, Philadelphia, PA, USA

context are in terrestrial insect systems, where fragmentation has been shown to lead to declines in predation, herbivory, and parasitism (Tscharntke and Brandl 2004; Valladares et al. 2006; Wimp et al. 2011). The effects of habitat fragmentation on multi-trophic interactions (>two levels) in marine systems are rare (but see Johnson and Heck 2006 for a mesocosm study). Fragmented habitats in marine systems may differ in conditions such as flow (Martinson et al. 2012), sedimentation (Scoffin 1970), and prey refuge (Macreadie et al. 2012), which may differentially affect species' responses in marine ecosystems.

Species losses due to fragmentation have been shown to vary based on trophic position (Zabel and Tscharntke 1998; Krauss et al. 2010), with higher trophic levels being disproportionately impacted (Didham et al. 1998; Roslin et al. 2014; Hovel and Lipcius 2001; Layman et al. 2007). This pattern may be due to the larger space requirements and smaller population size of higher trophic levels (van Nouhuys 2005; Greenleaf et al. 2007; Brückmann et al. 2011). The effects of habitat fragmentation may be especially strong in marine systems where predation by higher trophic levels is a particularly important biotic interaction that can influence prey population sizes, community structures, and ecosystem function (Paine 2002; Shurin et al. 2002; Duffy et al. 2003; Casini et al. 2012). In marine systems, however, higher trophic level species may disperse farther, perhaps providing some buffering capability to the effects of fragmentation (Kinlan and Gaines 2003). Effects on predators may subsequently impact prey either directly or indirectly via trophic cascades (Johnson and Heck 2006). While mesocosm experiments suggest that prey survival can vary with the number of trophic levels present in a fragmented system (Johnson and Heck 2006), no multi-trophic in situ studies have previously been performed that explore the impact of fragmentation on the distribution and abundance of predators and prey.

Predator foraging behavior and predator avoidance behavior of prey may also be altered in fragmented habitats (Bernot and Turner 2001; Dill et al. 2003; Johnson and Heck 2006; Heithaus et al. 2008; Burkholder et al. 2013; Ljungberg et al. 2013). Fragmentation produces edge effects that can result in enhanced encounter frequencies between predators and prey (Fagan et al. 1999; Ries et al. 2004) and subsequent increases in predator foraging rates (Hovel and Regan 2008; Carroll et al. 2012). Fragmentation can also cause a decrease in prey foraging rates due to increased threat of predation (Macreadie et al. 2012) and influence habitat preference (Ljungberg et al. 2013, but see Tait and Hovel 2012), but only a handful of marine studies have examined prey behavior in response to fragmentation.

Identifying the consequences of marine habitat fragmentation is becoming increasingly important. In the past several decades, mangrove losses have reached 35%, while coral reefs have declined by 20% and an additional 20% are now classified as degraded (Millennium Ecosystem Assessment 2005). Seagrass has been disappearing at a rate of 110 km^2 year^{-1} since 1980 (Waycott et al. 2009). While seagrass naturally occurs in a variety of spatial configurations (Boström et al. 2006), current rates of fragmentation are unprecedented and fragmentation is increasing beyond historical levels (Orth et al. 2006), making seagrass an ideal habitat to examine questions regarding the effects of habitat fragmentation. Seagrass is particularly useful for examining how habitat fragmentation may affect patterns of species distributions, behavior, and trophic relationships as it supports a wide variety of flora and fauna, and seagrass-associated food webs are complex and both commercially and ecologically important (Costanza et al. 1997; Christian and Luczkovich 1999; Hemminga and Duarte 2000).

To determine how habitat fragmentation influences multi-trophic food web relationships, predator and prey behavior, and species distributions in marine systems, we utilized the trophic relationship between the adult blue crab (*Callinectes sapidus*), juvenile blue crabs, and the hard clam (*Mercenaria mercenaria*). In this tri-trophic system, adult blue crabs consume juvenile blue crabs; it is estimated that as much as 25% of the adult blue crab diet is other blue crabs (Speir 1999). Juvenile blue crabs preferentially prey upon small-sized hard clams (<15 mm) (Arnold 1984). Seagrass is an important habitat for these species, particularly juvenile blue crabs and hard clams (Heck et al. 2003). Blue crabs have been shown to be more abundant in continuous seagrass habitats than in fragmented habitats (Hovel and Lipcius 2001). Juvenile blue crab survival may be inversely related to patch size in fragmented habitats (Hovel and Lipcius 2001; Hovel and Fonseca 2005), while the effect of fragmentation on basal prey bivalves such as the hard clam can be variable and may be related to predator distributions (Irlandi 1994, 1997).

We tested the hypothesis that fragmented habitats would differentially affect trophic levels within a tri-trophic system. We predicted that adult blue crabs would be less abundant and change their behavior by increasing foraging rates in fragmented habitats due to increased encounter rates. We also predicted that juvenile blue crabs would experience reduced predation rates in fragmented habitats driven by lower densities of adult blue crabs. In response to increased predation rates by juvenile blue crabs, we hypothesized that hard clams would employ stronger anti-predator responses in fragmented habitats.

Materials and methods

In Barnegat Bay-Little Egg Harbor Estuary, New Jersey, 50–88% of seagrass biomass has been lost since the

1980s (Kennish et al. 2009), making the area well suited to examine the impacts of seagrass habitat fragmentation. We selected two sites in Island Beach State Park, a preserved area of Barnegat Bay, New Jersey. At site one, "Seining" (39°51′17.84″N, 74°5′27.69″W), the study area consisted of a 0.60 km^2 continuous meadow of *Zostera marina* and *Ruppia maritima*, the two dominant seagrass species in the estuary. At site two, "Sedge" (39°47′ 24.8064″N, 74°6′ 28.476″W), the study area consisted of a 0.32 km^2 continuous meadow of *Z. marina*. A matrix of fragmented seagrass patches and unvegetated sediment surround each meadow. Patch size in the fragmented seascape ranged from 0.5 to 9.9 m^2 with a mean of 3.02 m^2. At Seining, seagrass shoot density was slightly greater in the seagrass fragments, and averaged 968.48 ± 347.83 shoots m^{-2} in the continuous meadow and 1345.34 ± 546.5 shoots m^{-2} in fragmented habitats. At Sedge, there were no difference in shoot density between habitat types and seagrass density measured 350.63 ± 89.57 shoots m^{-2} in continuous habitats and 299.85 ± 118.84 in fragments. These values are consistent with previous measures of seagrass density in the same location (Kennish et al. 2009), and other estuaries in the Northwest Atlantic (New York State Department of Environmental Conservation 2009). The large differences in densities between sites are likely driven by the presence of *Ruppia* at Seining, which grows more densely than *Zostera*. Barnegat Bay-Little Egg Harbor Estuary is a relatively shallow estuary with a maximum depth of 20 m. At our sites, depth, temperature, and salinity were consistent with depth ranging from 0.5 to 0.9 m, temperature from 21 to 25.3°C, and salinity from 20 to 25 ppt. Vertical clarity (measured with a Secchi disk) usually reached the sediment, and horizontal clarity ranged from 0.5 to 2.1 m. We conducted four field experiments to determine if habitat fragmentation differentially affects predation rates, predator and prey abundances, and prey behavior among three trophic levels. All data were collected between late July and early September 2014. All statistical analyses were performed in JMP® Version 11 (SAS Institute 2000).

Predation rates

To test for effects of fragmentation on predation of juvenile blue crabs we employed a tethering experiment. Tethering is widely used to measure survival rates among treatments, provides an experimental method of assessing predation, and has been used in a variety of marine habitats including seagrass (Heck and Thoman 1981; Bologna and Heck 1999; Hovel and Lipcius 2001, 2002; Peterson et al. 2001). Juvenile blue crabs were collected by seining along 10 m transects with a 1.75 m seine net, in both continuous and fragmented habitats. Seines occurred over six weeks in August and early September. Each day of sampling covered both habitat types at both sites. Crabs were tethered the day of collection. Only intermolt crabs with no missing periopeds between 45 and 75 mm were selected for tethering. The tethering harness was looped under each lateral spine and secured with a drop of cyanoacrylate glue. The harnessed crab was attached to a 30.5 cm stainless steel 15 kg test fishing leader (AUSLINE) which was then affixed to a stake. Harnessed crabs were then haphazardly staked directly in the sediment in either continuous seagrass or a seagrass patch within the fragmented seagrass habitat. For this experiment, and all others, selected seagrass patches within the fragmented habitat were between 10 and 15 m from the continuous seagrass habitat and were between 0.5 and 2 m^2. Within each habitat type, replicates were placed between 2.5 and 5 m away from each other depending on seagrass distribution. Half of all crabs in both habitats were tethered inside plastic 2.5 cm mesh cages (one crab/cage) that eliminated predator access to serve as a control for the effectiveness of the tether apparatus. At Seining, we tethered seven crabs per treatment ($N = 28$). At Sedge, we tethered five crabs per treatment ($N = 20$). We assessed juvenile blue crab survival after 72 h by categorizing crabs as alive or missing. Missing crabs were assumed to be lost to predation as no crabs were lost or separated from their tethers in the control treatments. We used a nominal logistic regression to test for differences in survival rate at each site with factors of habitat type (fixed effect), treatment (fixed effect), and a habitat type by treatment interaction term. For this, and all other experiments, plots in continuous habitat were place within 1 m of habitat edge to control for edge effects that may emerge in fragmented habitats.

To test for the effects of habitat fragmentation on predation of hard clams we used a mark and recapture predator exposure experiment. At Seining, we haphazardly established ten 0.09 m^2 circular plots for each of four treatments ($N = 40$) by lowering landscape edging completely (14 cm depth) into the sediment around the plot. The treatments were (1) predator exposure in fragmented seagrass, (2) predator control in fragmented seagrass, (3) predator exposure in continuous seagrass, and (4) predator control in continuous seagrass. Ten clams were added to each plot. Clams were between 8 and 12 mm, the preferred size for juvenile blue crabs (Arnold 1984), and marked with a small dab of white paint to facilitate recapture. Control treatments were covered with plastic 0.65 cm mesh to exclude predators. At Sedge we utilized the same experimental design; however, each treatment had nine replicates instead of ten. One continuous predator exposure replicate and one fragmented predator control replicate were not recovered at Sedge at the completion of the experiment ($N = 34$). After 10 days we hand dug the plots to a depth of 20 cm and sieved all material (500-micron sieve) to collect remaining clams and recorded seagrass shoot density and patch size.

Adult *Mercenaria mercenaria* have been shown to have a maximum burrowing depth of 20 cm, with juvenile clams, such as those used in this experiment, burrowing to a shallower depth (Eversole 1987; Roberts et al. 1989). Whole live clams were categorized as surviving. Any unburied clams were assumed to be dead and were excluded from analysis. Missing or fragments of clams were categorized as consumed. We used an analysis of variance (ANOVA) with factors of treatment (fixed factor), habitat type (fixed factor), and the interaction term to test for the effect of habitat type and predation on the proportion of clams surviving at each site. Among plots exposed to predators, we used regression to test for a relationship between crab survivorship and patch size and seagrass shoot density.

Predator and prey distribution

To test for differences in the distribution of adult and juvenile blue crabs we recorded number and carapace width for all captured crabs from the standardized 10 m length seines in continuous and fragmented habitats used to catch the crabs for the previously described tethering experiment. We performed thirteen seines per habitat type at Seining ($N = 26$) and fifteen seines per habitat type at Sedge ($N = 30$). Crab abundances were converted to catch per unit effort (CPUE) which represents the number of crabs caught per each seining effort. We used a *t* test to test for differences in number of crabs caught per seining effort and a Welch's test to test for differences in carapace width in continuous and fragmented habitats due to unequal variances in the data.

Behavior

We used tethering experiments to test for differences in hard clam anti-predator behavior (burrowing) across fragmented and continuous habitats using a blocked design. Juvenile hard clams between 8 and 12 mm were tethered to metal landscaping staples (22 cm in length) with 20 cm long monofilament fishing line (13.6 kg test). One end of the line was glued to the valve of the shell using a drop of cyanoacrylate glue. The other end of the line was secured to the landscaping staple. Clams were deployed into paired plots approximately 1 m apart which were each 0.5 m × 0.5 m in area. Each plot received nine clams by securing the metal staple into the sediment; clams were placed on top of the sediment hinge up (living position). All plots were covered in plastic 0.65 cm mesh to prevent predator access. A blue crab actively foraging on hard clams, which we provided as a resource, was placed within a plastic 0.65 cm mesh cage over one plot in each pair to serve as a control. The actively foraging blue crab sends chemical cues signaling the presence of a predator, inducing predator avoidance behavior in the hard clams (burrowing). Hard clams exposed to actively foraging predators burrow significantly deeper than clams excluded from predators (Flynn and Smee 2010). Each block consisted of a set of paired plots in the continuous habitat and a nearby set of paired plots in the fragmented habitat. Within each block, 15–20 m separated paired plots in continuous habitat and fragmented habitat; 25–30 m separated each block. At Seining, we established three blocks ($N = 108$ clams) and at Sedge we established two blocks ($N = 72$ clams). After 10 days we measured the distance on the 20 cm monofilament line that remained exposed above the sediment on each clam after it had burrowed and subtracted it from the total length of the line to determine how far each clam had burrowed. Any missing or dead clams were excluded from analysis. We used a mixed model with factors of site (random effect), block (random effect nested within site), treatment (fixed effect), habitat type (fixed effect), and all interaction terms to test for differences in clam burial depth among continuous and fragmented habitats. Preliminary analyses showed that the effect of "site" accounted for a negligible amount of variation in the model, therefore "site" was removed, and "block" was retained as the only random effect in the model.

We used underwater video to test for differences in predator behavior between continuous and fragmented habitats. In both continuous and fragmented seagrass habitats we haphazardly provided a bait resource (*Brevoortia tyrannus*) in a plastic 2.5 cm mesh envelope staked into the sediment. This allowed active foraging but prevented predators from completely removing the bait. We placed an underwater video camera (GoPro Hero3) approximately 0.25 m away from the prey item. Each filming event was 1–2.5 h, and we recorded nearly 18 h of video. Recording session replicates were deployed on different days but on each day both a continuous and fragmented video were filmed simultaneously (Seining: $N = 6$; Sedge: $N = 8$). The video footage was processed in the laboratory and we recorded the number of blue crab visits to the bait resource per hour, duration of each foraging event, and length of time to first visit. We performed *t* tests to test for differences in number of visits per hour, and length of time to first visit for fragmented and continuous habitats. All video data were square root transformed prior to analysis to adhere to assumptions of normality. We used a Welch's test to test for differences in duration of foraging events due to unequal variances in the data.

Results

We found that the effect of habitat fragmentation on predation rates was dependent on the trophic level of the predator. Predation on juvenile blue crabs was higher in fragmented habitats than continuous habitats at Sedge (Fig. 1, Nominal logistic regression: $R^2 = 0.580$, $\chi^2 = 16.18$, $P < 0.001$; Tethering treatment: $\chi^2 = 11.32$, $P = 0.0008$; habitat type x treatment: $\chi^2 = 5.91$, $P = 0.015$). At Seining, however, predation on juvenile blue crabs was high in both habitat types, and we found no difference in loss of crabs between the two treatments (Fig. 1, Nominal logistic regression: $R^2 = 0.050$, $\chi^2 = 21.15$, $P < 0.001$; Tethering treatment: $\chi^2 = 21.09$, $P < 0.0001$, habitat type × tethering treatment: $\chi^2 = 1.47$, $P = 0.23$). No crabs were lost from control tethers at either site, demonstrating the effectiveness of the tethering method.

In contrast, we found significantly higher predation on hard clams in continuous habitats than in fragmented habitats (Fig. 2, Seining, ANOVA: $R^2_{\text{adj}} = 0.76$, $F_{3/36} = 37.57$, $P < 0.0001$; habitat type: $F_{1/36} = 6.10$, $P = 0.018$; treatment: $F_{1/36} = 101.67$, $P < 0.0001$; habitat type × treatment interaction: $F_{1/36} = 4.68$, $P = 0.037$; Sedge, ANOVA: $R^2_{\text{adj}} = 0.86$, $F_{3/30} = 62.07$, $P < 0.0001$; habitat type: $P = 0.18$; treatment: $F_{1/30} = 183.98$, $P < 0.0001$; habitat type x treatment interaction: $F_{1/30} = 9.003$, $P = 0.0054$). Clams exposed to predators in both the fragmented and continuous habitats experience higher mortality than the predator exclusion controls. However, among clams exposed to predators those in continuous habitat experienced higher mortality than clams in fragmented habitats. Among experimental plots, we found no relationship between survivorship and seagrass density (Seining, Regression: $R^2_{\text{adj}} = -0.02$, $F_{1/18} = 0.51$, $P = 0.48$; Sedge, Regression: $R^2_{\text{adj}} = 0.17$, $F_{1/15} = 4.28$, $P = 0.060$). We also found no relationship between survivorship and patch size in fragmented habitat (both sites, Regression: $R^2_{\text{adj}} = -0.015$, $F_{1/8} = 0.87$, $P = 0.58$).

Habitat fragmentation also affected predator abundance and the size structure of the population. Overall, blue crabs were more abundant in continuous habitats than in fragmented habitats at both sites (Seining, Welch's test: $F_{1/22.3} = 4.360$, $P = 0.0048$; Sedge, t test: $R^2_{\text{adj}} = 0.15$, $F_{1/28} = 5.235$, $P = 0.029$). Adult blue crabs were found in higher densities in fragmented habitats at Seining (Fig. 3a, b, Seining-adult blue crabs: t test, $R^2_{\text{adj}} = 0.13$, $F_{1/24} = 4.90$, $P = 0.036$; Sedge-adult blue crabs: $P = 0.56$). In contrast, juvenile blue crabs were much less abundant in fragmented than continuous habitats (Fig. 3a, b, Seining-juvenile blue crabs: Welch's test: $F_{1/17.2} = 12.30$, $P = 0.0022$; Sedge-juvenile blue crabs: t test, $R^2_{\text{adj}} = 0.10$, $F_{1/28} = 4.48$, $P = 0.0433$).

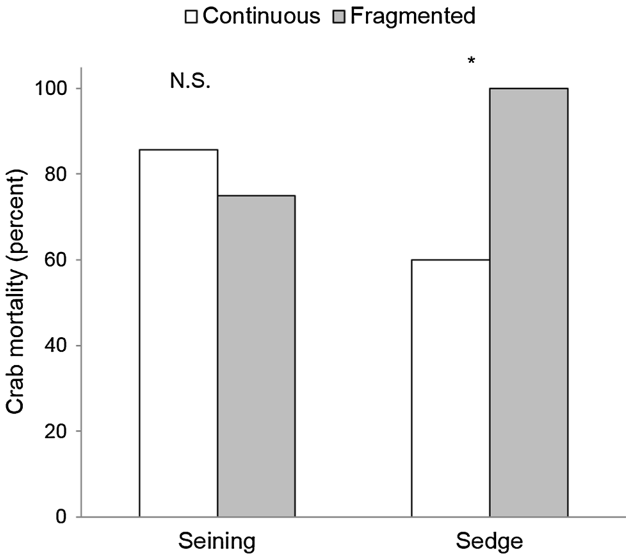

Fig. 1 Juvenile blue crab (*Callinectes sapidus*) mortality at two sites and in two different habitats. Binomial data (survived/consumed) was collected and analyzed to explore the effect of fragmentation on crab mortality. The figure shows the overall percentage of mortality among tethered juvenile blue crabs in continuous habitats (*white bars*) and fragmented habitats (*gray bars*). *Letters* indicate significant differences between treatments, as determined using Nominal Logistic Regression. At Seining the sample size was seven replicates per treatment, and five replicates per treatment at Sedge

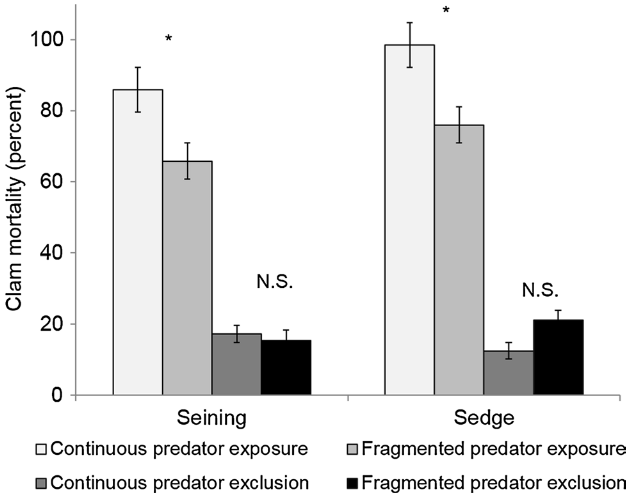

Fig. 2 Hard clam (*Mercenaria mercenaria*) mortality in fragmented and continuous habitats at two sites. Mortality is higher in continuous habitats (*white bars*) than in fragmented habitats (*light gray bars*) when exposed to ambient predation. The continuous and fragmented controls (predator exclusion) are indicated by the *dark gray* and *black bars*, respectively. *Error bars* indicate standard error and *different letters* above *bars* indicate significant differences between treatments, as determined using a Tukey's HSD test. At Seining the standard error is based on sample sizes of ten per group. At Sedge the standard error is based on sample sizes of nine for fragmented predator exposure and continuous control, and eight for fragmented control and continuous predator exposure

Habitat fragmentation changed both prey and predator behavior. Clams burrowed deeper in continuous habitats than fragmented habitat (Fig. 4, mixed model: $R^2_{\text{adj}} = 0.65$, habitat type: $P = 0.16$; treatment: $P = 0.43$; habitat type × treatment: $F_{1/3.4} = 29.31$, $P = 0.0086$). The continuous habitat predation exposure treatment was not different from either of the treatments with actively foraging blue crabs

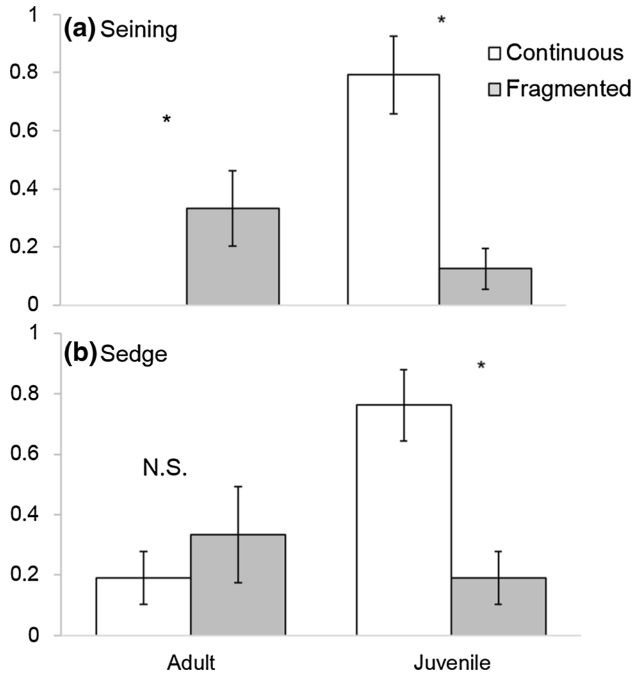

Fig. 3 Blue crab densities in fragmented and continuous habitats at two sites. Adult densities were higher in fragmented (*gray bars*) than continuous habitats (*white bars*) at Seining, and juvenile blue crab densities were higher in continuous habitats than fragmented habitats at both (**a**) Seining and (**b**) Sedge. Crab densities are reported as the number of crabs caught per 10 m seine (Catch Per Unit Effort). *Error bars* indicate standard error, based on sample sizes of 13 per treatment at Seining and 15 per treatment at Sedge. *Different letters* above *bars* indicate significant differences between treatments, as determined using Welch's test for juvenile blue crabs at Seining due to unequal variances and a *t* test for all other comparisons

(experimental control). Clams in the fragmented habitat predation exposure, however, burrowed to a shallower depth than all other treatments. Habitat fragmentation also changed predator behavior. The video observation of predator foraging showed that blue crabs took more time to find the offered prey item in continuous habitats than in fragmented habitats (ESM 1, Fig. 5a, Seining, t test: $R^2_{\text{adj}} = 0.49$, $F_{1/4} = 5.903$, $P = 0.036$; Sedge, t test: $R^2_{\text{adj}} = 0.74$, $F_{1/6} = 17.89$, $P = 0.0055$). Blue crabs also actively foraged longer in continuous habitats than in fragmented habitats (Fig. 5b, Seining, Welch's test: $F_{1/24.6} = 5.384$, $P = 0.029$; Sedge, Welch's test, $F_{1/53.4} = 8.865$, $P = 0.0044$). By contrast, blue crabs had higher number of visits per hour in fragmented habitats (Fig. 5c, Seining, t test: $R^2_{\text{adj}} = 0.74$, $F_{1/4} = 15.36$, $P = 0.017$; Sedge, t test: $R^2_{\text{adj}} = 0.51$, $F_{1/6} = 6.25$, $P = 0.047$).

Discussion

Our results demonstrate that different trophic levels are differentially affected by habitat fragmentation, and suggest that the effect of habitat fragmentation on higher trophic levels may cascade to lower trophic levels. While blue crabs overall were more abundant in continuous habitat compared to fragmented habitat, we found that juvenile and adult blue crabs had distinctly different distributions. Within fragmented habitats, we found higher numbers of adult blue crabs per seine than juvenile blue crabs. By contrast, in continuous habitat we found a greater number of juvenile blue crabs per seine than adult blue crabs (Fig. 3a, b). Additionally, at each site, there were greater numbers of juvenile blue crabs in continuous habitats than fragmented habitats; and adult blue crabs were more abundant in fragmented habitats than in continuous habitats (Fig. 3a, b).

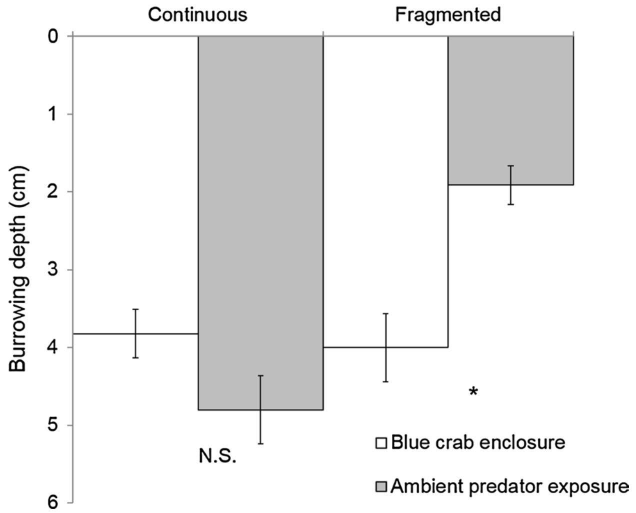

Fig. 4 Hard clam burrowing depth across both sites in two habitat types. Clams exposed to ambient predation burrowed deeper in continuous habitats than in fragmented habitats (pooled data from both sites). *Error bars* indicate standard error based on samples sizes of 45 clams per treatment. *Different letters* below *bars* indicate significant differences between treatments, as determined using a Tukey's HSD test

We then showed that juvenile blue crabs can experience higher predation in fragmented habitats (Fig. 1). High predation on juvenile blue crabs in fragmented habitats is likely driven, at least in part, by the presence of larger adult blue crabs in fragmented habitats. Juvenile blue crabs encounter intense cannibalism by adult blue crabs (Hines and Ruiz 1995), but predation by other species or other juvenile blue crabs (Moksnes et al. 1997) may contribute to these high predation rates as well. Juvenile blue crabs are also thought to utilize depth as a refuge from cannibalism, with higher survivorship of juvenile blue crabs at shallow depths (Dittel et al. 1995; Hines and Ruiz 1995). However, because there was little variability in the depth of fragmented and continuous seagrass habitat at both study sites, it is not likely to be a primary driver of the distribution patterns we observed. Other studies have suggested that blue

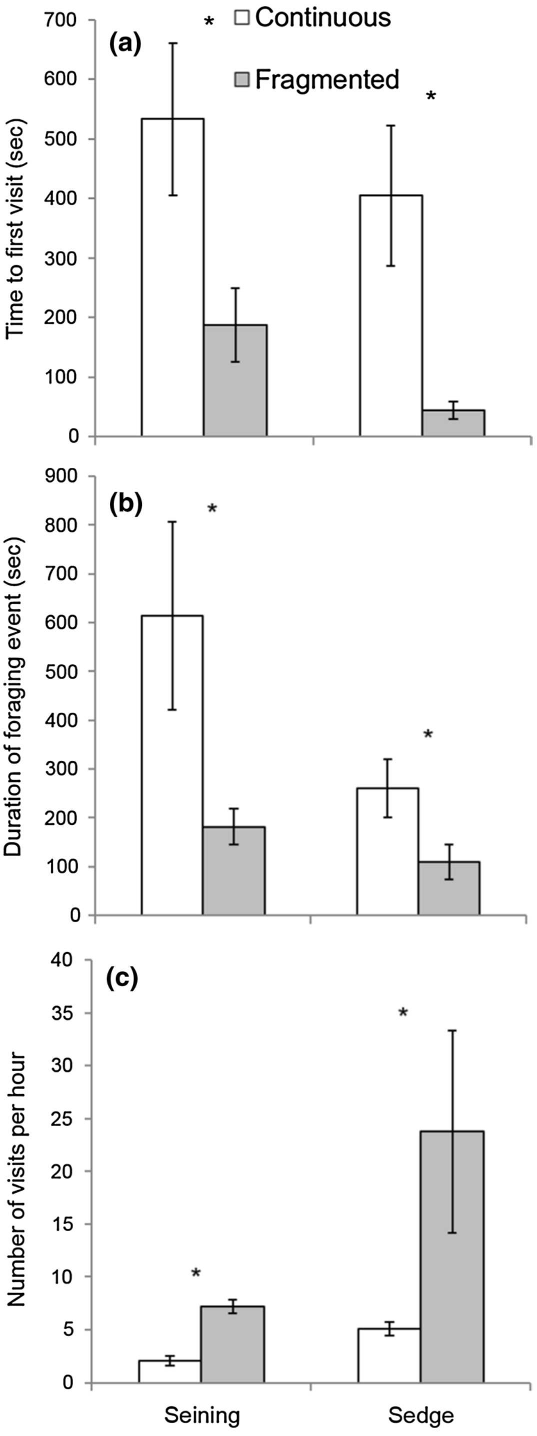

Fig. 5 Blue crab behavior in fragmented and continuous habitats at two sites. Blue crabs took less time to find offered resource (**a**), spent less time foraging (**b**), and had more frequent visits to offered prey item (**c**) in fragmented habitats (*gray bars*) than continuous habitats (*white bars*). Untransformed data are shown. *Error bars* indicate standard error based on sample sizes of four per treatment at Sedge and three per treatment at Seining. *Different letters* above *bars* indicate significant differences between treatments, as determined using a *t* test

crab habitat selection is more related to microhabitat selection rather than depth (Ramach et al. 2009). The abundance of adult blue crabs in fragmented habitats may result from a low refuge value of fragmented habitats for juvenile blue crabs. If fragmented habitats do not serve as a useful prey refuge for juvenile blue crabs, adult blue crabs are more easily able to capture prey (Hovel 2003). A preference for habitat edges may also explain higher abundances of adult blue crabs in fragmented habitats. Marine carnivorous fish have been shown to increase abundance at seagrass edges (Macreadie et al. 2009), though benthic predators such as blue crabs may experience different impacts from fragmentation than fish predators.

Low abundances of juvenile blue crabs in fragmented habitats may explain why hard clams experience lower predation rates in fragmented habitats. Additionally, juvenile blue crabs have been shown to decrease foraging in fragmented habitats due to increased predation risk (Macreadie et al. 2012). The large numbers of juvenile blue crabs in continuous habitats are likely responsible for heavy predation rates on hard clams in continuous habitat (Fig. 2), emphasizing responses to fragmentation may be trophic level specific and cascade from higher trophic levels. Our results suggest that changes in top predator distributions in this multi-trophic relationship is likely to be the underlying driver of lower trophic level abundance patterns in fragmented habitats.

Habitat fragmentation is often studied in tandem with patch size and/or habitat complexity. In seagrass ecosystems, seagrass density and patch size may covary with fragmentation making it difficult to isolate effects of fragmentation per se from impacts of low density or patch size (Canion and Heck 2009). Complex seagrass habitats have been shown to increase survivorship of both juvenile blue crabs and scallops regardless of patch size (Hovel and Lipcius 2001; Hovel and Fonseca 2005; Canion and Heck 2009; Carroll et al. 2012). Because the fragmented seagrass habitat had similar or greater seagrass density than the continuous habitat at our study sites, and clam survivorship was not related to seagrass density or patch size, our results likely reflect differences in distributions and predation driven primarily by fragmentation per se rather than other factors such as patch size and complexity.

Habitat fragmentation also changed behavioral responses in both predators and prey. Hard clams, experiencing greater predation in continuous habitats, employed stronger anti-predator avoidance strategies in continuous habitats by burrowing deeper than in fragmented habitats (Fig. 4). Therefore, deeper burrowing depths are likely to be a response to increased chemical cues from blue crab foraging, and not a direct result of habitat structure.

Chemical cues may have traveled farther than the 1 m separating control and experiment plots; however, the large difference between the experimental plot burrowing depths in continuous versus fragmented habitats suggests this likely did not affect our results. Results from the video analysis support increased foraging of blue crabs in continuous habitats as well. Blue crabs in fragmented habitats find prey items more quickly, have more frequent visits to prey items, but forage for less time (Fig. 5). These changes in blue crab behavior support the prediction that fragmented habitats lead to enhanced encounter rates between predators and prey (Irlandi 1997; Bologna and Heck 1999), and increased predator movement, a probable result of edge effects from habitat fragmentation (Hovel and Regan 2008; Ljungberg et al. 2013). The effect of fragmentation on the abundance and distributions of consumers clearly manifested not only in changes in predation rates among fragmented and continuous habitats, but also in behavioral responses of both predators and prey.

Taken together, these results demonstrate the importance of examining the effects of habitat fragmentation on species distributions and behavior in a multi-trophic context. Habitat fragmentation did not affect all trophic levels similarly, and the effect on a particular trophic level was likely determined by the distribution and behavior of its predator in the seascape. Higher predation rates on intermediate predators (juvenile blue crabs), most likely by top predators (adult blue crabs), in fragmented habitats and lower utilization of fragmented habitats by juvenile blue crabs translated to lower predation on the basal prey (hard clam). Juvenile blue crabs select predator free environments regardless of food availability (Tapia-Lewin and Pardo 2014); therefore, the distribution of their prey item may not be as important as the habitat selection of their top predators. Lower predation rates on basal prey led to weaker predator avoidance behaviors in fragmented habitats. These results support previous studies that suggest the effect of fragmentation on lower trophic levels is determined by the effect of fragmentation on higher trophic levels (van Nouhuys 2005; Krauss et al. 2010; Roslin et al. 2014). While our results focus on benthic marine species, pelagic species such as fish may respond differently to marine fragmentation due to greater dispersal capabilities (Hines et al. 1995); however, many juvenile species of fish heavily rely on seagrass as a nursery area and refuge from predation as well (Beck et al. 2001). In marine systems where predation is a critical biotic interaction, changes in the abundance of predators may have implications for food web stability in fragmented habitats and the potential for trophic cascades.

As habitat and biodiversity loss accelerate, we expect that the abundance and diversity of higher-level consumers will be more affected than lower trophic levels (Estes et al. 2011). Here, we found that while trophic levels are differentially affected by fragmentation, the top predator is seemingly benefiting from the increased vulnerability of its prey in fragmented habitats. Our results suggest that effects on top predators may be more nuanced than others have predicted. Fragmentation can drive changes in abundance, however, which will cascade through trophic levels. Changes in diversity at one trophic level can produce changes in diversity at other trophic levels (Dyer and Letourneau 2003), potentially influencing ecosystem function (Duffy 2003; Tilman et al. 2001). Here, we have shown that changes in the distribution of a top consumer in a system due to habitat fragmentation are likely contributing to changes in predation intensity and behavior of lower trophic levels, suggesting the potential for strong effects of habitat fragmentation not just on higher trophic levels but ecosystem wide.

While our results support predictions found in the terrestrial literature that different trophic levels will be affected differentially by fragmentation, we do not show the expected pattern of top trophic levels disproportionately affected by fragmentation. Marine and terrestrial food webs are different in ways that may influence trophic level responses (Shurin et al. 2006). Predation is thought to be a stronger influence in marine systems than terrestrial, and top–down control on prey can be very strong (Shurin et al. 2002). Therefore, continuous habitat may be more important to intermediate trophic levels, such as the juvenile blue crab, as a refuge. Many marine foundation species such as mangroves, coral reefs, and seagrasses are utilized as a shelter from predation for juvenile invertebrates and fish. Fragmentation and loss of these habitats reduces habitat continuity, complexity (Airoldi et al. 2008), and available refuges for juvenile marine species and may explain why we found fragmentation negatively affected intermediate trophic levels rather than top trophic levels. Our results emphasize the critical importance of marine habitats as nursery areas for many marine species and demonstrate the consequences of continued fragmentation on this essential ecosystem role.

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Author contribution statement EWR and ALF conceived and designed the experiments. EWR performed the experiments and analyzed the data. EWR and ALF wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

References

Airoldi L, Balata D, Beck MW (2008) The gray zone: relationships between habitat loss and marine diversity and their applications in conservation. J Exp Mar Biol Ecol 366:8–15

Arnold WS (1984) The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus rathbun*, on the hard clam, *Mercenaria mercenaria* (Linné). J Exp Mar Biol Ecol 80:207–219

Beck MW, Heck Jr KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Orth RJ (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: a better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. Bioscience 51:633–641

Bernot RJ, Turner AM (2001) Predator identity and trait-mediated indirect effects in a littoral food web. Oecologia 129:139–146

Bologna PAX, Heck KL (1999) Differential predation and growth rates of bay scallops within a seagrass habitat. J Exp Mar Biol Ecol 239:299–314

Boström C, Jackson EL, Simenstad CA (2006) Seagrass landscapes and their effects on associated fauna: a review. Estuar Coast Shelf Sci 68:383–403

Brückmann SV, Krauss J, van Achterberg C, Steffan-Dewenter I (2011) The impact of habitat fragmentation on trophic interactions of the monophagous butterfly *Polyommatus coridon*. J Insect Conserv 15:707–714

Burkholder DA, Heithaus MR, Fourqurean JW, Wirsing A, Dill LM (2013) Patterns of top-down control in a seagrass ecosystem: could a roving apex predator induce a behaviour-mediated trophic cascade? J Anim Ecol 82:1192–1202

Canion CR, Heck Jr KL (2009) Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. Mar Ecol Prog Ser 393:37–46

Carroll J, Furman BT, Tettelbach ST, Peterson BJ (2012) Balancing the edge effects budget: bay scallop settlement and loss along a seagrass edge. Ecology 93:1637–1647

Casini M, Blenckner T, Möllmann C, Gårdmark A, Lindegren M, Llope M, Kornilovs G, Plikshs M, Stenseth NC (2012) Predator transitory spillover induces trophic cascades in ecological sinks. Proc Natl Acad Sci USA 109:8185–8189

Christian RR, Luczkovich JJ (1999) Organizing and understanding a winter's seagrass foodweb network through effective trophic levels. Ecol Model 117:99–124

Costanza R, d'Arge R, Limburg K, Grasso M, de Groot R, Faber S, O'Neill RV, Van den Belt M, Paruelo J, Raskin RG, Hannon B (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260

Crist TO, Pradhan-Devare SV, Summerville KS (2006) Spatial variation in insect community and species responses to habitat loss and plant community composition. Oecologia 147:510–521

Davies KF, Margules CR, Lawrence JF (2000) Which traits of species predict population declines in experimental forest fragments. Ecology 81:1450–1461

Didham RK, Lawton JH, Hammond PM, Eggleton P (1998) Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. Philos Trans R Soc Lond B Biol Sci 353:437–451

Dill LM, Heithaus MR, Walters CJ (2003) Behaviorally mediated indirect interactions in marine communities and their conservation implications. Ecology 84:1151–1157

Dittel AI, Hines AH, Ruiz GM, Ruffin KK (1995) Effects of shallow water refuge on behavior and density-dependent mortality of juvenile blue crabs in Chesapeake Bay. Bull Mar Sci 57:902–916

Duffy JE (2003) Biodiversity loss, trophic skew and ecosystem functioning. Ecol Lett 6:680–687

Duffy JE, Richardson PJ, Canuel EA (2003) Grazer diversity effects on ecosystem functioning in seagrass beds. Ecol Lett 6:637–645

Dyer LA, Letourneau D (2003) Top-down and bottom-up diversity cascades in detrital vs. living food webs. Ecol Lett 6:60–68

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JB, Marquis RJ (2011) Trophic downgrading of planet Earth. Science 333:301–306

Eversole AG (1987) Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Atlantic) Hard Clam. Clemson University, Clemson

Fagan WF, Cantrell RS, Cosner C (1999) How habitat edges change species interactions. Am Nat 153:165–182

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Flynn AM, Smee DL (2010) Behavioral plasticity of the soft-shell clam, *Mya arenaria* (*L.*), in the presence of predators increases survival in the field. J Exp Mar Biol Ecol 383:32–38

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153:589–596

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

Heck KL, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar Ecol Prog Ser 253:123–136

Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. Trends Ecol Evol 23:202–210

Hemminga MA, Duarte CM (2000) Seagrass ecology. Cambridge University Press, Cambridge

Hines AH, Ruiz GM (1995) Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. Bull Mar Sci 57:884–901

Hines AH, Wolcott TG, González-Gurriarán E, González-Escalante JL, Freire J (1995) Movement patterns and migrations in crabs: telemetry of juvenile and adult behaviour in *Callinectes sapidus* and *Maja squinado*. J Mar Biol Assoc UK 75:27–42

Hovel KA (2003) Habitat fragmentation in marine landscapes: relative effects of habitat cover and configuration on juvenile crab survival in California and North Carolina seagrass beds. Biol Conserv 110(3):401–412

Hovel KA, Fonseca MS (2005) Influence of seagrass landscape structure on the juvenile blue crab habitat-survival function. Mar Ecol Prog Ser 300:179–191

Hovel KA, Lipcius RN (2001) Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. Ecology 82:1814–1829

Hovel KA, Lipcius RN (2002) Effects of seagrass habitat fragmentation on juvenile blue crab survival and abundance. J Exp Mar Biol Ecol 271:75–98

Hovel KA, Regan HM (2008) Using an individual-based model to examine the roles of habitat fragmentation and behavior on predator–prey relationships in seagrass landscapes. Landsc Ecol 23:75–89

Irlandi EA (1994) 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. Oecologia 98:176–183

Irlandi EA (1997) Seagrass patch size and survivorship of an infaunal bivalve. Oikos 78:511–518

Johnson MW, Heck KL (2006) Seagrass patch characteristics alter direct and indirect interactions in a tritrophic estuarine food web. Estuar Coasts 29:499–510

Kareiva P (1987) Habitat fragmentation and the stability of predator–prey interactions. Nature 326:388–390

Kennish MJ, Haag SM, Sakowicz GP (2009) Assessment of eutrophication in the Barnegat Bay-Little Egg Harbor system: use of SAV biotic indicators of estuarine condition. N J Environ Digit Lib. doi:10.7282/T3Z60NVX

Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84:2007–2020

Krauss J, Bommarco R, Guardiola M, Heikkinen RK, Helm A, Kuussaari M, Lindborg R (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecol Lett 13:597–605

Layman CA, Quattrochi JP, Peyer CM, Allgeier JE (2007) Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecol Lett 10:937–944

Ljungberg P, Hasper TB, Nilsson PA, Persson A (2013) Effects of small-scale habitat fragmentation on predator–prey interactions in a temperate sea grass system. Mar Biol 160:667–675

Macreadie PI, Hindell JS, Jenkins GP, Connolly RM, Keough MJ (2009) Fish responses to experimental fragmentation of seagrass habitat. Conserv Biol 23:644–652

Macreadie PI, Geraldi NR, Peterson CH (2012) Preference for feeding at habitat edges declines among juvenile blue crabs as oyster reef patchiness increases and predation risk grows. Mar Ecol Prog Ser 466:145–153

Martinson HM, Fagan WF, Denno RF (2012) Critical patch sizes for food-web modules. Ecology 93:1779–1786

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being. World Resources Institute, Washington

Moksnes PO, Lipcius RN, Pihl L, van Montfrans J (1997) Cannibal–prey dynamics in young juveniles and postlarvae of the blue crab. J Exp Mar Biol Ecol 215:157–187

New York State Department of Environmental Conservation (2009) Final report of the New York State seagrass taskforce: recommendations to the New York State Governor and legislature

Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, Heck KL, Hughes AR (2006) A global crisis for seagrass ecosystems. Bioscience 56:987–996

Paine RT (2002) Trophic control of production in a rocky intertidal community. Science 296:736–739

Peterson BJ, Thompson KR, Cowan JH, Heck KL (2001) Comparison of predation pressure in temperate and subtropical seagrass habitats based on chronographic tethering. Mar Ecol Prog Ser 224:77–85

Ramach S, Darnell MZ, Avissar N, Rittschof D (2009) Habitat use and population dynamics of blue crabs, *Callinectes sapidus*, in a high-salinity embayment. J Shellfish Res 28:635–640

Ries L, Fletcher Jr RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu Rev Ecol Evol Syst 35:491–522

Roberts D, Rittschof D, Gerhart DJ, Schmidt AR, Hill LG (1989) Vertical migration of the clam *Mercenaria mercenaria* (*L.*) (*Mollusca: Bivalvia*): environmental correlates and ecological significance. J Exp Mar Biol Ecol 126:271–280

Roslin T, Várkonyi G, Koponen M, Vikberg V, Nieminen M (2014) Species–area relationships across four trophic levels–decreasing island size truncates food chains. Ecography 37:443–453

SAS Institute (2000) JMP®, Version 11, 1989–2007. SAS Institute Inc., Cary

Scoffin TP (1970) The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini lagoon, Bahamas. J Sediment Res 40:249–273

Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, Broitman B, Cooper SD, BS Halpern (2002) A cross-ecosystem comparison of the strength of trophic cascades. Ecol Lett 5:785–791

Shurin JB, Gruner DS, Hillebrand H (2006) All wet or dried up? Real differences between aquatic and terrestrial food webs. Proc R Soc B 273:1–9

Speir H (1999) A review of predation on blue crabs in Chesapeake Bay. Maryland Department of Natural Resources, Annapolis

Tait KJ, Hovel KA (2012) Do predation risk and food availability modify prey and mesopredator microhabitat selection in eelgrass (*Zostera marina*) habitat? J Exp Mar Biol Ecol 426:60–67

Tapia-Lewin S, Pardo LM (2014) Field assessment of the predation risk-food availability trade-off in crab megalopae settlement. PLoS One 9:e95335

Tigas LA, Van Vuren DH, Sauvajot RM (2002) Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biol Conserv 108:299–306

Tilman D, Reich PB, Knops J, Wedin D, Mielke T, Lehman C (2001) Diversity and productivity in a long-term grassland experiment. Science 294:843–845

Tscharntke T, Brandl R (2004) Plant-insect interactions in fragmented landscapes. Annu Rev Entomol 49:405–430

Valladares G, Salvo A, Cagnolo L (2006) Habitat fragmentation effects on trophic processes of insect-plant food webs. Conserv Biol 20:212–217

van Nouhuys S (2005) Effects of habitat fragmentation at different trophic levels in insect communities. Ann Zool Fenn 42:433–447

Waycott M, Duarte CM, Carruthers TJ, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc Natl Acad Sci USA 106:12377–12381

Wimp GM, Murphy SM, Lewis D, Ries L (2011) Do edge responses cascade up or down a multi-trophic food web? Ecol Lett 14:863–870

Zabel J, Tscharntke T (1998) Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially. Oecologia 116:419–425