Both below- and aboveground shoalgrass structure influence whelk predation on hard clams

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ABSTRACT: Seagrass introduces above- and belowground biogenic structure and complexity into otherwise relatively unstructured sand-flat habitat. Observation of burial depths by unmarked and ribbon-tagged knobbed whelks *Busycon carica* in sand and dense and sparse shoalgrass *Halodule wrightii* confirmed that shoalgrass structure inhibits whelk burrowing. Whelks showed a strong preference for sand-flat habitat during spring and summer, creating a partial refuge from whelk predation for hard clams *Mercenaria mercenaria* inside shoalgrass. By early autumn, shoalgrass blades sloughed off, reducing aboveground biomass by over 81%, leading to a massive invasion of seagrass habitat by whelks now exhibiting no habitat preference. The enhanced permeability of the seagrass bed coincided with the large decline in aboveground shoalgrass biomass, a measure of strength of the physical boundary contrast (BC). As shown by tethering whelks in sand, intact shoalgrass, and shoalgrass with aboveground structure removed by clipping, belowground vegetation played a stronger role than aboveground vegetation in limiting the efficiency of predation on hard clams. From summer into autumn, average daily production of empty shells of whelk-consumed hard clams increased, with some evidence of greater increases within seagrass habitat, implying a seasonal breakdown of the refuge function of seagrass. The mechanism by which a strong BC inhibits whelk entry into and use of seagrass habitat is unresolved, perhaps acting as a physical barrier to passage into seagrass or alternatively acting as a behavioral cue indicative of expectation of lower predation efficiency associated with intact but not with clipped seagrass.

KEY WORDS: Habitat structure · Boundary contrast · *Busycon carica* · *Mercenaria mercenaria* · *Halodule wrightii* · Permeability · Temporal refuge · Seagrass

INTRODUCTION

Suitable habitats provide animals with a variety and an abundance of acceptable food resources, living spaces, refuges from predation and unfavorable environmental stresses, and intrinsic advantages over potential competitors. At some spatial scale, all such suitable habitats occur as discontinuous patches, often on relatively small spatial scales at which a mosaic of patch types exists within apparently similar environments (Robbins & Bell 1994, 2000, Vidondo et al. 1997). The degree of isolation between adjoining patches of different habitat types is variable, dependent not only on patch size and relative mobility of the occupants, but also on the permeability of the patch boundary, which can have 'hard edges' inhibiting passage or 'soft edges' allowing ready passage (Wiens et al. 1985, Stamps et al. 1987). The resultant 'boundary contrast' (BC) is defined as the magnitude of difference in structural habitat metrics across patch interfaces (Stamps et al. 1987, Holmquist 1998). The greater the BC, the less permeable is the barrier created by this rapid structural transition at the patch boundary.

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The BC can influence not only rates of emigration and immigration connecting suitable patches of habitat and the surrounding less hospitable areas but also predation pressure and environmental stress on individuals that may tend to accumulate at relatively impassable habitat edges (strong BC). Predator–prey encounter rates are often higher and environmental conditions can be more severe along patch edges than in patch interiors, thereby reducing prey or even predator survival (edge effect: Andren & Angelstam 1988, Saunders et al. 1991, Andren 1992, Irlandi et al. 1995, Fagan et al. 1999). In cases of a weak BC, potential predators and unfavorable environmental conditions may readily penetrate deeply into patches of habitat otherwise favorable for prey species. In contrast, a strong BC may serve as a barrier to permeability of physical environmental stressors and predators, creating functional refuges inside such patches (Holmquist 1998). These boundary effects consequently can modify spatial distributions and population dynamics of patch inhabitants (Wiens 1995, Bender et al. 1998, Hovel & Regan 2008).

During growth and development of seagrass habitat patches, the plants spread via seed release, transport, settlement, and germination as well as via vegetative propagation, typically resulting in a mosaic of vegetated patches of varying sizes within a background of unvegetated sediments (Thayer et al. 1984, Duarte & Sand-Jensen 1990, Bowden et al. 2001). Seagrass patches and unvegetated sediments may even reflect an example of multiple stable or at least persistent states (Peterson 1984) because the higher current flows over unvegetated bottom inhibit seagrass colonization, and the seagrass beds act to slow currents and induce fine sediment and seed deposition, sustaining the seagrass plants and attendant muddier sediments in that location (Fonseca et al. 2007).

Seagrass beds provide 2 different types of structure that is absent from unvegetated sand and mud flats: aboveground shoots and leaves that provide structure in the water column, and roots and rhizomes that bind the sediments below ground and enhance compaction and bottom hardness (Peterson 1982). The aboveground structure provides refuge for nektonic species from visually orienting predators like fishes, and belowground structure provides infaunal invertebrates a refuge from burrowing predators like crabs and whelks (Peterson 1982, see reviews by Orth et al. 1984, Orth 1992). For this new study, we focused novel attention on how the aboveground seagrass structure, which can change seasonally, may also affect the behavior of predatory benthic invertebrates, and we conducted experiments to isolate effects of aboveground from belowground structure on spatio-temporal dynamics of the benthic predation process. We hypothesized that the structural features of dense seagrass create a strong BC at the junction with a sand flat that inhibits permeability of the seagrass edge to burrowing predators. Recognizing that burrowing predators that do penetrate the boundary experience interference from the seagrass structures, including suppressed digging ability (Vince et al. 1976, Brenchley 1982, Peterson 1982, Heck & Wilson 1987, Irlandi 1997), we conducted experimental and observational tests to quantify effects of below- versus aboveground shoalgrass structure on behavior and efficiency of predation by a predatory benthic gastropod on its infaunal bivalve prey. We expect that the strong BC of a dense seagrass bed would also buffer environmental stresses, such as strong current flows, deep into seagrass patches (Irlandi 1996, Peterson et al. 2004).

Our focus on strength of the BC in exploring one possible mechanistic basis for understanding how aboveground habitat structure may contribute to providing a refuge from burrowing benthic predators is related to the widely acknowledged importance of habitat complexity. Functions of habitat complexity have been explored extensively in seagrass beds as a model system amenable to careful observational and experimental hypothesis testing (e.g. Brenchley 1982, Blundon & Kennedy 1982, Peterson 1982, Irlandi 1997, Hovel & Regan 2008). Unfortunately, the current view that belowground structure sufficiently explains how seagrass habitat complexity affords infaunal prey a substantial refuge from burrowing predators fails to explain many anomalous patterns. For example, although higher densities of hard clams *Mercenaria mercenaria* are typically observed in seagrass than in surrounding sand flats (Peterson 1982, 1986, Peterson & Beal 1989), some studies have revealed trivially small differences in density (Peterson et al. 1984, Micheli 1997) or in age and size composition of the clams (Peterson et al. 1984), and at least one study revealed lower clam densities in seagrass than in nearby sand habitat (Nakaoka 2000). Furthermore, the shells of hard clams recently consumed by whelks (as determined from characteristic shell damage: Peterson 1982) are commonly observed inside seagrass beds in late summer (S. Goshima pers. obs.). These observations, apparently inconsistent with the structural refuge hypothesis, may conceivably be reconciled if seasonal changes in aboveground seagrass structure substantially alter the BC and allow whelks to penetrate the seagrass edge and prey more readily

on the hard clams inside. Seagrasses are known to shed their leaves in late summer and autumn in North Carolina (USA), when water temperatures reach high levels (Thayer et al. 1984), raising the possibility that the predation refuge is temporally variable. The build-up of prey densities during the rest of the year could influence whelks to forage in the partially dysfunctional seagrass habitat during autumn, which could conceivably counteract the value of the refuge during the remainder of the year and thereby explain anomalous observations.

Here, we employed the concept of the BC between habitat patches as a means to understand and test whether seasonal change in structural complexity of seagrass affects the ability of whelks to penetrate the habitat edge and successfully prey on hard clams inside. (1) We assessed the possibility of seasonal change in habitat preference of the predatory whelk *Busycon carica*, comparing sand flats to seagrass beds during an intensive observational study. (2) We determined the degree to which differential availability of the *Mercenaria mercenaria* prey versus changing intensity of the habitat structural BC can explain observed habitat preference between seagrass and sand habitats. (3) We tested by field experimentation whether the refuge function of seagrass varies seasonally with changing aboveground habitat structure, which we then relate to the relative magnitude of the BC.

MATERIALS AND METHODS

Study site

All experiments and observations were conducted in low intertidal and shallow subtidal sand and seagrass areas in Pine Knoll Shores, along the southern shoreline of Bogue Sound, North Carolina, USA. Variously sized patches of seagrass occur within the sand flat of Pine Knoll Shores. The seagrass beds are composed largely of shoalgrass *Halodule wrightii*. Where we refer to this species of seagrass, we use shoalgrass in this paper, while we use seagrass to apply to the habitat (of mixed species) more generically. The study area occupied 13 600 m², with seagrass beds and sand flats partially exposed to air only at extreme spring low tides, and additional shallow subtidal sand and seagrass habitat always covered by water. Sediments at the study site were predominantly composed of fine sands with <3% silt–clay by weight (Peterson 1982). Water depths in the predominant central portion of the study area range from

0.1–0.3 m at low tides to 1.1–1.3 m at spring high tides. Salinities exceed 34 psu in summer and autumn and 32 psu in winter and spring in Bogue Sound, except during occasional heavy rainstorms, when values of 26 psu can occur (H. J. Porter unpubl. data). Water temperature varies seasonally, with monthly means ranging from about 4 to 29°C (Sutherland & Karlson 1977).

Study animals

Three whelk species, *Busycon carica*, *B. contrarium*, and *B. canaliculatum*, consume bivalve mollusks in the coastal lagoonal systems of the eastern US (Magalhaes 1948, Peterson 1982, Irlandi 1994, Micheli 1997, Nakaoka 2000). The knobbed whelk *B. carica* is the most abundant at our study site: we encountered a total of 165 whelks during the study period, May to October 1995, of which 150 individuals (91%) were *B. carica*, 14 (~9%) were *B. contrarium*, and only 1 (<1%) was *B. canaliculatum*. We chose the most abundant species, *B. carica*, as our model predator for observations and experiments.

We repeatedly and systematically examined whelks in the field to determine the nature of the prey they were engaged in consuming. We measured shell height (SH) of the whelks, identified prey to species, and measured shell length (SL) of each prey. We chose the most common prey species, the hard clam *Mercenaria mercenaria*, as model prey for the predatory whelk in this study.

The blue crab *Callinectes sapidus* is another important predator on the hard clam in the coastal lagoonal system of the eastern US (Virnstein 1977, Woodin 1978, Blundon & Kennedy 1982, Hines et al. 1990, Micheli 1997). Blue crabs strongly prefer hard clams <35 mm in SL (Peterson 1990, Micheli 1997), and cannot break open hard clams >40 mm in SL (Arnold 1984, Peterson 1990), whereas whelks prefer larger clams from 40 mm up to at least 100 mm in SL (Peterson 1982). Consequently, to isolate impacts of whelk predation separate from blue crabs, we used prey clams between 40 and 80 mm in SL in our manipulative experiments. A full assessment of the role of predation in determining hard clam abundance in vegetated and unvegetated lagoonal habitats would include blue crab predation on smaller, younger individuals, which is also affected by vegetation in several direct and indirect ways (e.g. Micheli 1997, Seitz et al. 2005). All clams used in experiments had been spawned in a local hatchery and then reared in a subtidal sand flat in Pine Knoll Shores for 2 to 4 yr.

Change in aboveground seagrass structure

Seagrass beds, including those in North Carolina, usually show clear seasonal changes in aboveground plant biomass (Thayer et al. 1984, Pangallo & Bell 1988). We measured blade length and aboveground biomass of the shoalgrass *Halodule wrightii* that dominated our study area, sampling on 3 dates in July, September, and October 1995, a sequence likely to bracket the season of rapid loss of seagrass blades (Thayer et al. 1984). We clipped all blades at the sediment surface within 4 randomly chosen 1 m² plots in the seagrass habitat and dried them at 65°C to constant mass as our estimate of aboveground biomass. We also measured length of the longest 30 blades in each sample plot with a ruler, and then the total samples of 120 blades were compared among months.

Whelk predation rates on hard clams among habitats

To test effects of habitat structure on clam predation rate by whelks, we established 4 replicate 1 m² plots in each of 3 types of habitat: (1) seagrass, (2) trimmed seagrass at a location 11.8 m from the nearest sand flat within a relatively large seagrass bed, and (3) on a nearby sand flat within the study area. The trimmed seagrass plots were prepared by clipping with scissors all seagrass blades at the sediment surface within the plots. We planted 20 clams, ranging from 40 to 80 mm in SL and marked by numbered plastic tape (Dymo-tape) on the valves, into each plot on 19 July 1995. Clams were buried by hand in living position in a largely uniform spatial distribution just beneath the sediment surface, and plots were made of the locations of each clam and left for 78 d in the field. We relocated clams by finger-probing the sediments and examined each one on 4 dates about every 20 d, ending on 5 October, recording on each date whether the clam was dead or alive. We recognized experimental clams by the tape, but we also noted that newly dead (within 20 d of the previous examination) were distinguishable from 'older' dead, a distinction that became useful in inferring monthly mortality during regular surveys of the entire study area. At each check, all clams were scored as (1) alive; (2) dead with intact valves (possibly killed by physical stress, disease, or parasitism: Peterson 1982); (3) dead with crushed or chipped valves; (4) dead with valves rasped at the edges; or (5) missing. Mortality in category 3 was attributed to crabs, mainly the blue crab, and in category 4 to

whelks (Peterson 1982, Micheli 1997). Occasionally, whelk predation on smaller *Mercenaria mercenaria* results in fracturing of a valve, but rasping of the margin is also evident, allowing unambiguous attribution to whelk predation (C. H. Peterson pers. obs.). Disturbance associated with finger-probing and subsequent extraction of the clams by hand has potential to loosen sediments sufficiently to render digging by whelks easier and thus enhance observed rates of whelk predation on the clams. However, any such facilitation of whelk predation would be more important in seagrass and trimmed seagrass than in sand because it could loosen the subsurface compaction created by the roots and rhizomes of the seagrass, whereas sand-flat sediments are looser already. Consequently, a potential artifact of disturbance could result in elevation of the estimate of clam predation in seagrass and trimmed seagrass relative to that observed in the sand-flat habitat.

Evidence of hard clam predation by whelks

From July to October 1995, we collected still articulated shells of all dead bivalves seen on the sediment surface. We classified cause of death by the previously explained methods (Peterson 1982, Micheli 1997) based on shell damage: shells rasped on the ventral margin are unambiguously indicative of whelk predation. For those shells categorized as consumed by whelks, we also classified them as either new or old, judging by (1) postmortem cover of attached sessile benthos such as barnacles, bryozoans, or algae either on inside or outside surfaces; (2) pale color of the shell caused by burial in the sediments or by bleaching with sunlight after lying on the sediment surface for a long time; and (3) wear of the shells caused by wave action and sand abrasion. The more fresh-looking clam shells might be expected to have represented more recent deaths, so after our first monthly collection in July to clear off accumulated newly dead shells, we used subsequent monthly collections and counts of newly dead rasped hard clam shells as an index of whelk predation during the preceding month. We also collected and counted old dead shells from our samplings — not to test whether historical predation of some unspecified time interval differed by month but instead to provide the summed data set on all rasped dead shells of hard clams allowing a second test of monthly variation in production of shells rasped and killed by whelks that did not depend on our subjective discrimination between old and new deaths.

Habitat use by whelks

We established 22 transect lines perpendicular to the shoreline spaced at 10 m intervals across the study area and characterized substrate as bare sand or seagrass every 2 m on each line to estimate the proportion of the 2 habitat types in our study area. The resulting 732 points were checked within the 13 600 m^2 study area in early October 1995. We also collected, examined, and returned in-place whelks while walking a set of several haphazardly oriented lines extending across the entire study site on multiple occasions from May through October. We measured SH of each whelk and recorded whether it was in sand or seagrass habitat. In shoalgrass at our study site, blades were short enough and sparse enough that visual surveying at low tide was an accurate method of locating and identifying large benthic organisms at the sediment surface, such as many whelks. When a whelk is buried deeply enough below the sediment surface, it will not be detected. To confirm patterns of seasonal change in habitat selection by whelks at our study site, we established a parallel experiment tagging whelks with floats and documenting habitat occupation (see 'Between-habitat movements'). We compared the area of each habitat type and frequency of whelks found in each habitat type in both data sets (unmarked and tagged whelks) to provide tests of whether the whelks preferentially used either habitat and how use changed from May to August as compared to September and October.

Between-habitat movements of individual whelks

We released and followed marked whelks to record their movements, assessing habitat occupied by each whelk, minimum distance traveled between observations, and movements across habitat boundaries between sand flat and seagrass bed. Ten whelks were marked by attaching a small float made of foam polystyrene (about 5 cm in diameter × 3 cm in thickness) to about 5 m of light-weight monofilament fishing line, which itself was tied to a small rectangular piece of plastic attached to the whelk shell by epoxy resin. They were also marked with individually numbered plastic tape superglued to the shell. The tagged whelks were released haphazardly into habitats that approximated their relative areal cover: 4 into sand flat, 3 into dense seagrass, and 3 into sparse seagrass. From August to October, we searched for floats every day with few exceptions, recorded habitat type for each whelk, inserted a temporary surveying flag at each whelk location and used it to measure straight-line distance from its last recorded position. We successfully followed individual movements of 8 whelks for 5 to 28 d. Replication was reduced by loss of floats. Shoalgrass at our site was sparse enough and the power generated by crawling whelks great enough to prevent entanglement with monofilament lines.

Habitat selection by whelks tethered at habitat boundaries

Tethering of whelks placed at boundaries between sand flat and seagrass (both intact and clipped) habitats was conducted once or twice a month from July through September 1995 to test for active habitat selection in the field. We inserted approximately 2.5 m long PVC poles into the sediments on the habitat boundary, to which we attached light monofilament fishing line, itself glued by epoxy resin to a whelk following the same procedure described for attaching floats to free-ranging whelks. The fishing line could be extended out from the pole to a maximum radius of 1 m, allowing a semicircle of movement range in each of the 2 adjacent habitat types being tested. We established 4 replicates of each of 4 habitat type × prey density treatment contrasts to test the joint effects of both habitat type (sand versus seagrass) and augmented prey density (0 versus 28 m^{-2}) on habitat selection by the whelk. The contrasts were (1) seagrass with 44 hard clams versus sand habitat without clams; (2) seagrass without prey versus sand without prey; (3) trimmed seagrass with 44 clams versus sand without clams; and (4) trimmed seagrass without clams versus sand without clams. Trimming was achieved as described earlier, designed to mimic complete shedding of leaves with full retention of belowground seagrass habitat structure. We did not include any contrasts where clams were placed in sand habitat because our intent was to test whether augmented prey resource in the seagrass habitat of both types could motivate whelks to overcome the impediments of habitat structure. Each whelk was started exactly on the habitat boundary next to the PVC pole, and its position and habitat choice were checked daily for 12 d following initiation of each trial. After recording its position each day, we returned each whelk to its original starting position by the marker pole.

Clam density in both habitat types

We estimated hard clam density and size-frequency distribution both in sand flat and seagrass habitats at our study site in September 1995 to test for habitat-related differences in this season. We completely excavated 8 randomly located 1 m^2 samples from each habitat and sieved them through 5 mm mesh. All hard clams removed from the sieve were brought to the laboratory, and their SL was measured with calipers.

Burrowing depths of clams and whelks

Those hard clams that whelks consume live buried under the sediment surface, requiring whelks to extend their foot and often to burrow into the sediments to access them. Foraging efficiency therefore may depend on both living depths of the clams and burrowing ability of the whelks. We measured burrowing depths of both prey and predator in the field. For the hard clam, we first buried marked clams approximately evenly spaced within both intertidal seagrass and sand-flat plots. Each was marked individually with numbered plastic tape on the valve and was planted by hand in living position just beneath the sediment surface. On 4 September 1995, after 41 d, presumably sufficient time to reposition and achieve natural burrowing depths, we carefully dug out the marked clams by hand at low tide and measured distance from the sediment surface to the top edge of each buried clam by a ruler and their SL with calipers.

In the field, we discovered whelks either on the sediment surface, partially buried, or fully buried. We measured by ruler the burrowing depth of each of 47 free-ranging whelks, defined as the maximum depth from the sediment surface to the lowest point of penetration by the whelk (usually its foot) and measured SH of the whelk with calipers. We also marked 22 whelks by attaching with epoxy resin a highly visible pink plastic ribbon of about 1 m length. The 22 tagged whelks were released haphazardly into habitats that approximated their relative areal cover: 7 into sand flat, 5 into dense seagrass, 8 into sparse seagrass, and 2 in unrecorded habitat. From 2 d after their release inside our study site on 11 September, we regularly searched the study area to find them until 5 October. Whelks were readily detected by the ribbon on the sediment surface even if the marked whelk was completely buried in the sediments. We carefully extended the ribbon vertically

and then dug out each whelk to measure its burrowing depth and recorded the habitat in which it was found. To avoid pseudoreplication in burial depth records from this group of whelks marked with ribbons, we analyzed data from only the first recorded burial depth after release in each habitat where the whelk was discovered. This procedure yielded 31 depth observations from the marked whelks. From these 31 observations of marked and 47 of unmarked whelks, we obtained 78 burrowing depth measurements sorted by habitat.

Whelk feeding rate as a function of habitat

To assess whether habitat influences the feeding rate of whelks on hard clams, we conducted tethering experiments from late July through early September. The goal was to measure actual feeding rates under field conditions because previous feeding rate data came from simplified laboratory environments. Tethering was required to constrain the whelk to remain in the appropriate habitat and to track the whelk continuously so that all consumptions could be detected. We buried 30 hard clams at natural living depths, evenly spaced within a circular plot of 2 m in diameter (9.6 clams m^{-2}), and then we tethered a whelk to a light monofilament line tied to a PVC pole at the center of the circle. Before tethering in the field, whelks were starved for 5 d so as to standardize hunger and feeding motivation. This experiment included 7 replicates in each habitat type: seagrass bed, trimmed seagrass bed, and sand flat. Whelks were allowed to forage for 10 d, during which we visited each replicate plot every day, collected consumed clams that were found at the sediment surface, and noted the position of every whelk to guide our ultimate excavations to locate all consumed clams. Shells of hard clams >40 mm in length are sufficiently massive that physical transport of articulated valves of dead clams is minimal, at least from May through early October on the shallow sand flats and seagrass beds of central Bogue Sound, confirmed by noting the fixed locations of numerous such shells outside our study site. The fetch that could cause shell transport at this site would come from the north, whereas summer winds are southwesterly and the barrier island provides protection from winds out of that direction. No tropical storm occurred during the course of our study, so conditions remained quiescent. Whelk predation was confirmed by detection of rasping on the shell margins of all dead clams.

Statistical analyses

Whelk predation rates, habitat use and habitat selection by the whelks, clam density, clam size, production of articulated shells of dead hard clams, and aboveground seagrass structure were compared among habitats or among months using 1-way or 2-way analysis of variance (ANOVA). Cochran's test or Levene's test was used to ensure that response variables conformed to the ANOVA assumption of homogeneous variances for all statistical tests. Data were log- or square root-transformed when necessary to satisfy the assumption of homoscedasticity. Significant differences among more than 2 means were examined using Tukey's HSD tests. Potential relationships between burrowing depth and shell height in whelks were first examined by linear regression analyses done by habitat. After confirming no detectable relationships, ANOVAs were conducted to compare mean burrowing depths among the habitats. In this case, we adopted the generalized least square (GLS) method on untransformed data for comparisons among habitats and the Tukey test based on a sandwich estimator for multiple comparisons. For the 22 tagged whelks that could be distinguished as individuals, we used only the first recorded burial depth in each habitat, totaling 31 data points. The 47 unmarked whelks whose burrowing depths were also measured could have included multiple measurements of the same individuals but to an unknown degree. Consequently, degrees of freedom could be overestimated in the analyses that used each observation as an independent data point, but we conducted a sensitivity test of how seriously the assumption of independence may have affected the outcome by also including just the first half of the observations. Burrowing depths of hard clams from different habitats were contrasted using analysis of covariance (ANCOVA), in which habitat (sand versus seagrass) was treated as a categorical variable and shell length and burrowing depth were continuous. In the analyses of production of articulated shells of dead hard clams and seagrass blade lengths among months, data were log- and square root-transformed, respectively, to homogenize variances for ANOVA. Proportions of whelks found in the 2 habitats were compared with percentage cover of the habitats in the study area using a binomial test, and the whelk use pattern between habitats was examined using a χ^2-test. Habitat selection between seagrass and sand habitat in the tethering experiment was examined by 2-way ANOVA to test whether seagrass clipping, prey augmentation, or their interaction influenced habitat choice. Then, *t*-tests determined whether frequency of whelk occurrence in the seagrass as opposed to sand-flat habitat differed significantly from the 50% expected in the absence of habitat preference. These analyses of results of habitat choice experiments first converted the results from each individual whelk to a single number, which was the average frequency (and percentage) of the 12 d that the whelk occupied seagrass habitat (trimmed or unmodified) as opposed to sand flat. Replication was provided by the 4 independent trials using different whelks on each date. This procedure avoided pseudoreplication that would exist if each of the 12 observations were treated as replicates.

RESULTS

Changes in aboveground seagrass structure

From July to September and October, the aboveground structure of seagrass habitat greatly declined at our study area. The mean length of the 30 longest blades within each set of 4 randomly chosen 1 m² plots declined progressively from 165 mm in July to 81 mm in September and 66 mm in October (Table 1), which differed by month (1-way nested ANOVA, $F_{2,9} = 21.996$, $p < 0.001$), with significant differences between July and both September and October (Tukey HSD test, $p < 0.005$ in both cases). Mean blade biomass also decreased by 81% from July to September (1-way ANOVA, $F_{1,6} = 329.07$, $p < 0.0001$; Table 1). These declines in aboveground biomass reflect a weakening of the physical BC.

Table 1. *Halodule wrightii.* Monthly changes in blade length and blade biomass (means ± SE) within the study area. Mean blade length was determined from the longest 30 blades in each of four 1 m² plots. It differed significantly by month ($p < 0.001$), with significant differences between July and both September and October ($p < 0.005$ in both cases). Blade biomass also differed significantly between July and September ($p < 0.0001$)

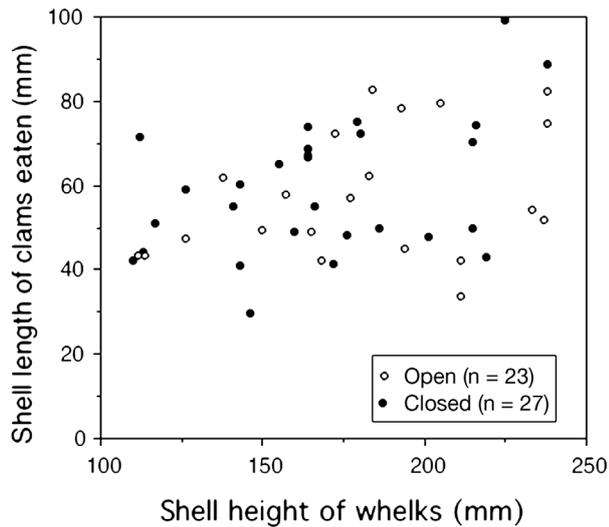| Date	Blade length (mm)	n	Blade biomass (g m⁻²)	n
19 July	165.0 ± 1.7	120	96.2 ± 3.8	4
21 September	81.0 ± 0.9	120	18.8 ± 2.1	4
16 October	66.3 ± 1.1	120	— No data —	

Fig. 1. *Busycon carica* and *Mercenaria mercenaria.* Relationship between shell height of whelks and shell length of clams being consumed by the whelks in the field. Clams not yet forced open (●) and clams already opened (○) by whelks

Fig. 2. *Mercenaria mercenaria.* Survivorship (no. m^{-2} out of 20 plot^{-1}, means ± SE) of marked clams introduced into seagrass, trimmed seagrass, and sand-flat habitats. Survivorship over the complete 78 d experiment varied significantly between sand and both trimmed and intact seagrass plots (p < 0.01), but no significant difference was found between intact and trimmed seagrass treatments (p > 0.9)

Whelk predation rates on hard clams among habitats

The whelks exclusively consumed bivalve mollusks. The most common prey was *Mercenaria mercenaria*: we observed a total of 69 whelk feeding episodes, during which they were consuming *M. mercenaria* 50 times (73%), stout razor *Tagelus plebeius* 13 times (19%), cross-barred venus *Chione elevata* 3 times (4%), and American oyster *Crassostrea virginica* 3 times (4%). In the most commonly attacked prey, the hard clam, whelks preferred larger clams from 40 mm up to at least 100 mm in SL (Fig. 1). Experimental whelks, which were all collected in the study area, ranged from 160 to 240 mm in SH. These size ranges for both prey and predator were the most common and available sizes in the study area (Fig. 1).

Pooled over all 3 habitat treatments, mortality (39 clams recovered as empty shells after 78 d) was dominated by categories attributable to whelk predation: 77% had a characteristically rasped margin. In addition, 10% were missing, which includes inability to relocate live clams but more often reflects mortality by a whelk removing its victim from the plot (implied by experimental results of Peterson 1982); the remaining 13% of the clams originally introduced were found dead without detectable shell damage. Numbers of shells of dead clams found with rasped margins over the full 78 d period varied with habitat (1-way ANOVA, $F_{2,9}$ = 7.952, p <
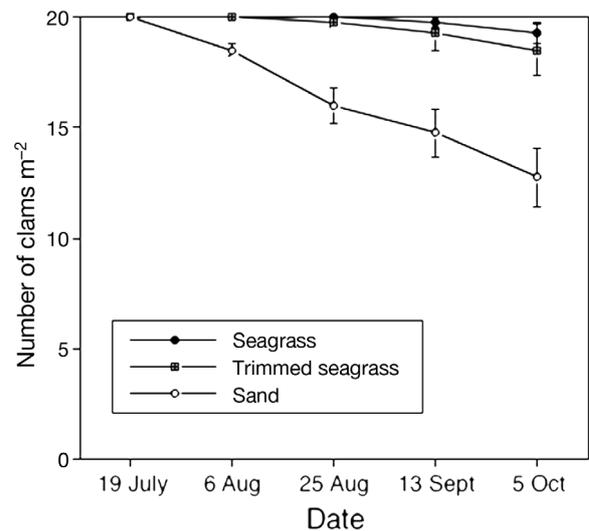
0.05), with 2 out of 80 clams eaten by whelks in seagrass indistinguishable from the 5 clams eaten in trimmed seagrass (Tukey HSD test, p > 0.80) but each far fewer than the 23 clams eaten in the sand habitat (Tukey HSD test, p < 0.05). As a result, survivorship over the full 78 d period varied with habitat (1-way ANOVA, $F_{2,9}$ = 10.925, p < 0.005), with live recovery of 95% in seagrass indistinguishable from the 92.5% in trimmed seagrass (Tukey HSD test, p > 0.90) but both higher than the 64% in unvegetated sand habitat (Tukey HSD test, p < 0.01; Fig. 2). Because this pattern of substantially higher rates of predation by whelks in the sand-flat habitat is the opposite of the direction that would be caused by a disturbance artifact, which would reduce sediment compaction more in the 2 seagrass treatments, the pattern of difference in whelk predation on clams may be a conservative estimate of the protective influence of shoalgrass and its belowground structure. Mortality rates appeared to increase progressively after August in both unmodified seagrass (0% mortality during the period from 19 July to 6 August, 0% from 6 August to 25 August, 1.3% from 25 August to 13 September, and 3.8% from 13 September to 5 October) and trimmed seagrass (0, 1.3, 2.5, and 3.9%, respectively) but not in the sand habitat (7.5, 13.5, 7.8, and 13.6%, respectively), where mortality rate vacillated across the 4 time periods.

Habitat use by the whelk

Of 150 knobbed whelks discovered during visual surveys of the study area over the summer and autumn period, 95 (63 %) were found in sand flat and 55 (37 %) in seagrass habitat. In contrast, our systematic assessment of seagrass cover across the study site revealed that out of 732 observation points, 467 (64 %) fell on seagrass habitat, whereas 265 points (36 %) fell on sand flat. Consequently, the proportion of whelks found in the sand-flat habitat was substantially higher than expected on the basis of percentage cover of sand flat and seagrass patches in the study area (binomial test, $z = 6.826$, $p < 0.01$).

Between-habitat movement of individual whelks

The tagged whelks moved as much as 98 m d^{-1} with a minimum (linear) daily travel distance of 21 ± 9 m (mean ± SE, range: 0–98 m, n = 14 daily observations) in August, 3 ± 1 m (range: 0–21 m, n = 35) in September, and 3 ± 1 m (range: 0–18 m, n = 34) in October. The individual whelks used both seagrass and sand flat, and each moved across both habitat types. Whelks that exhibited active lateral movement during our visual relocations of tagged whelks tended to be those on or near the sediment surface rather than those that were substantially or fully buried. Despite their greater mobility during August, the tagged whelks mainly used sand-flat habitat in August (91 % of all observations), whereas sand-flat use fell in subsequent months to 76 % in September and 38 % in October (Fig. 3A), coincident with the seasonal reduction in strength of the BC. Patterns of habitat use between sand and seagrass varied significantly among months ($\chi^2 = 15.009$, $p < 0.001$).

A similar seasonal switch in habitat use was displayed by the untagged whelks encountered during our field surveys, revealing high use of sand flats (84–87 % of individual whelks) from May through August, declining to 69 % in September and 44 % in October (Fig. 3B); again, significant variation emerged in habitat use among months ($\chi^2 = 15.012$, $p < 0.001$). Although the large seasonal loss of aboveground seagrass structure may imply greater visual capacity to relocate and locate untagged whelks in autumn months, the sparse nature of even intact shoalgrass beds and their short blade lengths allowed unobstructed vision even in spring and summer, so this potential bias is unlikely to contribute substantially to this pattern. The bias would be greater for untagged whelks than for those with
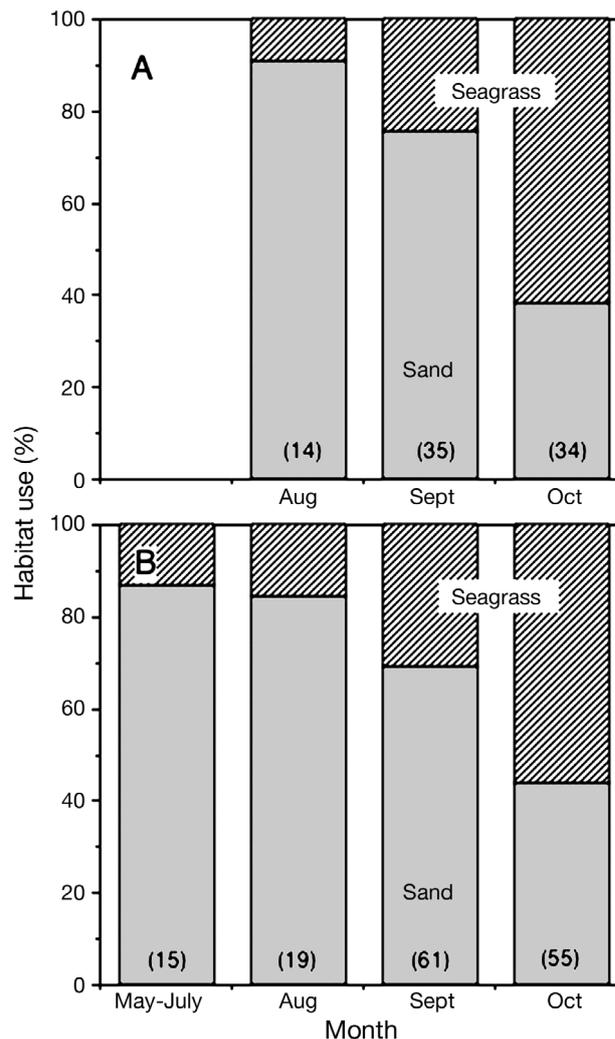

Fig. 3. *Busycon carica.* Temporal patterns of habitat use by whelks as % of all observations in sand vs. seagrass for (A) marked whelks out of 3, 3, and 6 tagged individuals in August, September, and October, respectively, and (B) untagged whelks encountered during surveys of the study area. Sample sizes in parentheses (total numbers of re-sightings of tagged whelks in A, and of encounters with untagged whelks in B). The habitat use pattern between sand and seagrass varied significantly among the months both for tagged and untagged whelks (p < 0.001 for both)

floats, yet the observed declines in sand-flat use were very similar for the 2 sets of whelk observations (Fig. 3), evidence for a trivial bias.

Habitat selection of whelks tethered at habitat boundaries

Centrally tethered whelks were recovered within the seagrass half of the circular experimental plots only 17 % of the time (with prey augmentation) and

10% of the time (without prey augmentation) when seagrass structure was unmodified and thus maintained a strong BC (Fig. 4). Each of these is significantly less than the 50% expected if there were no preference for habitat (with prey augmentation $t = -3.870$, df = 3, $0.02 < p < 0.05$; without prey augmentation: $t = -10.908$, df = 3, $0.001 < p < 0.002$). When seagrass structure was modified by clipping all aboveground vegetation and thus greatly reducing the strength of the BC provided by aboveground habitat structure, whelks occurred within the trimmed seagrass 49% of the time (with prey augmentation) and 39% of the time (without prey augmentation; Fig. 4). Neither of these percentages was detectably different from the 50% expected in the absence of habitat preference (with prey augmentation $t = -0.248$, df = 3, $p > 0.5$; without prey augmentation: $t = -2.799$, df = 3, $p > 0.05$). In a 2-way ANOVA, seagrass habitat condition (intact seagrass with strong BC versus trimmed seagrass with weak or no BC) significantly affected the average propor-
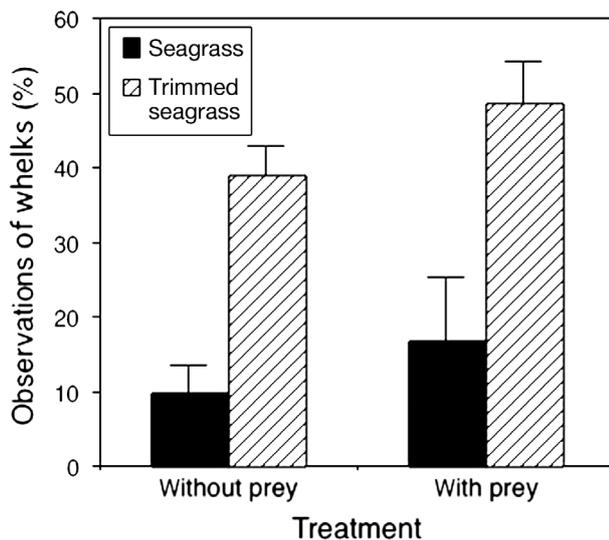
Table 2. *Busycon carica.* Results of a 2-way factorial model 1 analysis of variance testing whether whelk occurrences in the seagrass as opposed to the sand habitat half of circular plots varied as a function of habitat type (intact seagrass versus trimmed seagrass), prey augmentation (without prey addition versus with addition of 28 clams m^{-2}), and the factor interaction

Source of variation	df	Whelk occurrence in seagrass		
		Mean square	*F*	p
Habitat type	1	0.373	28.096	0.0002
Prey	1	0.028	2.132	0.1699
Habitat × Prey	1	0.001	0.056	0.8170
Residual	12	0.013		

tion of whelk occurrences in seagrass as opposed to the sand habitat, while prey augmentation (0 versus 28 hard clams m^{-2}), and the interaction between the 2 factors were non-significant (Table 2). Although the effect of prey augmentation proved non-significant at $p = 0.17$ in the ANOVA (Table 2), more whelks were found in the prey-augmented plots for each seagrass treatment (intact and trimmed) than in the comparable plots without added prey (Fig. 4). Nevertheless, having failed to detect a significant effect of prey augmentation, we combined clam density augmentation treatments to produce pooled estimates of habitat preference, revealing that average frequency of tethered whelk occurrence in intact seagrass was 13%, indicating a preference for sand habitat (*t*-test, $t = 8.124$, df = 7, $p < 0.001$), whereas the analogous average frequency of whelk occurrence in experimentally clipped seagrass was 44%, statistically indistinguishable from 50%, demonstrating no detectable preference between sand and trimmed seagrass habitats ($t = 1.704$, df = 7, $0.1 < p < 0.2$). The p-value of this test is low enough to suggest that there may be some residual contribution of even trimmed seagrass to form a much weaker but nontrivial BC for this treatment.

Fig. 4. *Busycon carica.* Average (+1 SE; n = 4) percent of centrally tethered whelk occurrences in the seagrass half of circular plots containing half seagrass and half sand as a joint function of seagrass condition (intact vs. trimmed of all aboveground materials) and prey augmentation (no addition vs. addition of hard clams at a density of 28 ind. m^{-2}). Seagrass condition had a significant effect on proportional occurrence in seagrass ($p = 0.0002$), but prey augmentation ($p = 0.170$) and the factor interaction did not ($p = 0.817$). Proportional whelk occurrence in intact seagrass as opposed to in an equal area of sand habitat was significantly less than the random expectation of 50% both without ($0.001 < p < 0.002$) and with prey augmentation ($0.02 < p < 0.05$). In contrast, proportional whelk occurrence in trimmed seagrass was not detectably different from the random expectation of 50%, both without ($p > 0.05$) and with ($p > 0.5$) prey augmentation

Clam density by habitat

Average densities of the hard clam in September 1995 were 1.38 ± 0.42 m^{-2} (mean ± SE) in the seagrass and 0.75 ± 0.31 m^{-2} in the sand-flat habitats, based on complete excavation of eight 1 m^2 samples in each habitat. Because of low statistical power, this almost 2-fold difference in hard clam density between habitats was not detectably significant (1-way ANOVA, $F_{1,14} = 1.423$, $p > 0.20$; Fig. 5). Size-frequency distributions imply that all large clams
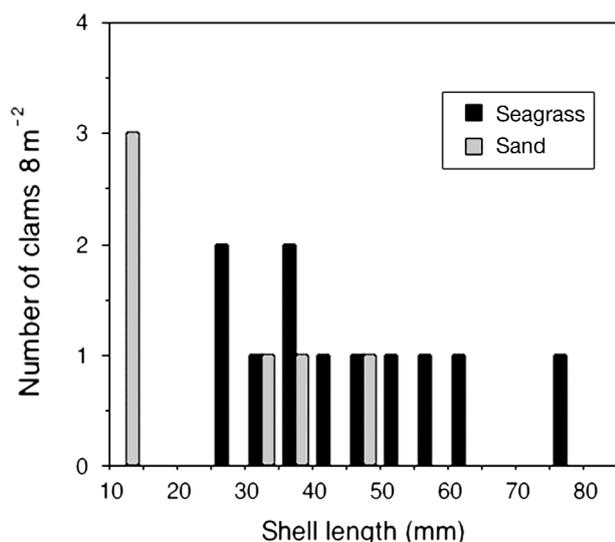
Fig. 5. *Mercenaria mercenaria*. Size-frequency distributions of hard clams collected in September 1995 from 8 randomly located 1 m² plots in each of the sand flat and seagrass bed habitats, using a 5 mm mesh sieve to separate clams from sediments. No significant difference was detected between habitats in clam density (p > 0.2), but mean clam size was greater in seagrass (p < 0.05)
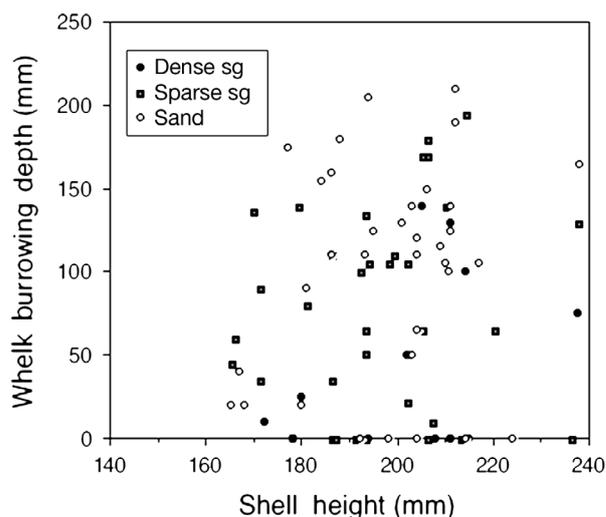

Fig. 6. *Busycon carica*. Relationship between shell height of whelks and their burrowing depths in sand flats, sparsely vegetated or dense shoalgrass beds (sg). Burrowing depths were measured from the sediment surface to the lowest portion of the whelk. No significant correlation existed between whelk shell height and burrowing depth for any of the 3 habitats. Mean burrowing depths differed significantly among the 3 habitat types in a GLS ANOVA (p = 0.015)

(SL >50 mm) were in the seagrass habitat, and mean SL was greater in seagrass (1-way ANOVA, $F_{1,15} = 6.769$, p < 0.05; Fig. 5).

Burrowing depths of clams and whelks

No relationship existed between SL and burial depth of a clam measured to the top edge of the shell in either habitat (seagrass: r = 0.000, n = 28, p > 0.1; sand: r = 0.095, n = 26, p > 0.1). There was also no difference between seagrass and sand-flat habitats in the SL–burrowing depth relationship of clams (ANCOVA, $F_{1,51} = 3.468$, p > 0.05). Thus, hard clams buried to the same relatively constant depth just beneath the sediment surface in both seagrass and sand habitats. Because the lower shell margin is necessarily positioned at deeper depths for larger clams, and because whelks open hard clams by enveloping the clam with their foot and then forcing the lip of their shell aperture between the clam valves, deeper penetration into the sediments is likely required to prey upon larger hard clams.

Whelks burrowed to depths up to 210 mm in the sand flat, up to 195 mm in sparsely vegetated seagrass, and up to 140 mm in dense seagrass (Fig. 6). Burrowing depths in the sand, sparse seagrass, and dense seagrass bed were 100 ± 11 mm (mean ± SE, n = 32), 79 ± 10 mm (n = 35), and 36 ± 15 mm (n = 11),

respectively, which differed by habitat (GLS-test, $F_{2,75} = 4.42$, p = 0.015; Fig. 6). Tukey post hoc contrasts demonstrated a shallower burrowing depth in the dense seagrass than the sparse seagrass (p = 0.048) and sand flat (p = 0.011), but detected no difference between the sparse seagrass and sand (p = 0.173). To assess the sensitivity of this set of results to possible overestimation of degrees of freedom from pseudoreplication (measuring burrowing depth of the same whelk more than once in a given habitat), we reran these analyses using half of our observations, arbitrarily choosing the first half of each habitat's set of observations. This re-analysis produced an unaltered set of demonstrations of statistical significance, implying robustness to even 2-fold overestimation of degrees of freedom.

Whelk feeding rate as a function of habitat

Over the 10 d experiment, each tethered whelk consumed 1 to 7 clams in the sand flat (mean ± SE = 3.0 ± 0.9; n = 7), 0 to 4 in the trimmed seagrass (1.9 ± 0.5; n = 7), and 0 to 2 in the intact seagrass habitat (0.4 ± 0.3; n = 7). Mean numbers of clams consumed differed among habitat types (1-way ANOVA, $F_{2,18} = 4.692$, p = 0.023). Tukey HSD demonstrated significantly higher clam consumption in sand than in the intact seagrass habitat (p = 0.017), but detected no

difference between trimmed and intact seagrass (p = 0.233) or between trimmed seagrass and sand (p = 0.383).

Evidence of hard clam predation by whelks

During a total of 53 surveys of our study area from July through October, we collected 428 still articulated shells of dead bivalves, representing 6 species: 390 hard clams *Mercenaria mercenaria*; 21 Atlantic bay scallops *Argopecten irradians*; 9 stout razors *Tagelus plebeius*; 6 disk shells *Dosinia discus*; 1 cross-barred venus *Chione elevata*; and 1 ark shell *Anadara* sp. Of the 390 pairs of both 'old' and 'new' dead clam shells, 343 (88%) were killed by whelks, as determined by characteristic shell rasping. The vast majority of rasped, empty hard clam shells were discovered within the seagrass habitat. Among old rasped shells, monthly patterns in average numbers of pairs of articulated hard clam shells recovered during systematic surveys of the study area (Fig. 7) revealed highest densities in July, the first month of sampling, although monthly differences were not significant (1-way ANOVA, $F_{3,49} = 0.601$, p = 0.618).
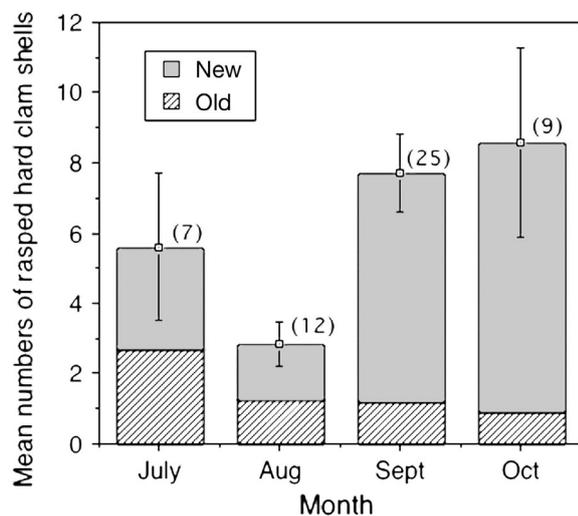

Fig. 7. *Mercenaria mercenaria.* Average daily counts by month of still articulated, rasped shells of dead hard clams from visual searches of the 13 600 m^2 study site. Each shell pair was classified as either recently dead or older based on shell characteristics. Error bars display ± 1 SE around the mean of the sum of old and newly consumed clams, and numbers in parentheses represent the numbers of searches (sample sizes for each mean). Average daily counts of old shells did not vary significantly with month (p = 0.618), while newly dead shells did (p = 0.003), with detectable increases in September and October as compared to August (p < 0.05 in both cases)

In contrast, the average daily counts of newly dead hard clam shells with evidence of whelk predation varied with month (1-way ANOVA, $F_{3,49} = 5.481$, p = 0.003; Fig. 7), revealing a pattern of dramatic increase in September and October (Tukey HSD test, August versus September, p = 0.028; August versus October, p = 0.032). We excluded July from this comparison among months because July differed methodologically from the other 3 months in that no set of daily samplings had taken place during the previous months to remove long-term accumulations of shells that could confound estimation of monthly mortality. When we included both old and new dead shells in our temporal analysis, statistical conclusions remained identical to the analysis of only new dead shells, still showing dramatically higher daily production of rasped empty clam shells in September and October than in August (Fig. 7). Consequently, these differences remain robust to our removal or inclusion of what we interpret as older deaths.

DISCUSSION

Our study provides the first controlled experimental tests of the role of sub-surface seagrass structure in providing a refuge to an infaunal invertebrate from consumption by a burrowing predator and includes novel insight into how the aboveground component of seagrass structure mediates that refuge function by creating a seasonally variable structural BC. To streamline discussion and facilitate conceptual integration of the new information, the extensive and complex results are summarized in Box 1.

In spring and summer, when the BC is strong, knobbed whelks are physically or else behaviorally inhibited from penetration into seagrass habitat, but from late summer into autumn as shoalgrass blades are shed, the BC weakens dramatically and opens the habitat to whelk access. From May into August, only 9% of detected free-ranging whelks fell within the seagrass despite seagrass habitat forming nearly two-thirds of the area of our study site. After massive seasonal sloughing of shoalgrass blades during late summer and early autumn, whelk preference for sand-flat habitat disappeared as they increased their use of seagrass habitat to levels equal to its percent cover in the study area. Consequently, seagrass aboveground structure influences whether whelks penetrate into, occupy, and use prey in seagrass habitat. Nonetheless, the persistent presence during autumn of belowground structure provided by roots and rhizomes continued to reduce whelk digging

Box 1. Data relevant to inferring how below- versus aboveground structures of seagrass habitat influence the spatio-temporally varying predation by knobbed whelks on hard clams from summer to autumn in North Carolina, USA

Seagrass habitat structure dynamics

(1) Mean length of longest shoalgrass blades declined from July to September by 51% and then by 18% from September to October.

(2) Mean aboveground shoalgrass biomass decreased by 81% from July to September, representing a large decline in strength of the physical boundary contrast between sand flat and seagrass habitat.

(3) From mid-August until early October, shed shoalgrass blades without attached roots or rhizomes were evident floating on the water surface.

Effects of seagrass structure on habitat selection by whelks

(4) Although 64% of the study site was shoalgrass covered versus only 36% sand flat, tagged whelks predominantly used sand-flat habitat (91%) in August, but exhibited statistically significant shifts away from sand-flat habitat use to 76% in September and 38% in October, coinciding with the progressively large reductions in boundary contrast as shoalgrass blades were shed.

(5) In monthly surveys of the entire study area, untagged whelks exhibited a statistically significant seasonal shift in habitat occupancy, with sand-flat use of 84 to 87% in May–August to 69% in September and 44% in October, demonstrating mass invasion of shoalgrass in autumn.

(6) In a habitat selection experiment on 4 dates from July to September, 87% of tethered whelks exhibited significant preference of the sand-flat half of the plot over intact shoalgrass, whereas only 56% chose sand over trimmed shoalgrass — a number not significantly different from random expectation, showing that aboveground seagrass structure (and thus the boundary contrast) affects whelk habitat selection.

Effects of seagrass habitat structure on whelk foraging capacity

(7) Burrowing depths of tagged whelks averaged 36 mm in dense shoalgrass, significantly shallower than in sparse shoalgrass (79 mm) and sand habitat (100 mm), which did not differ significantly from one another, suggesting that burrowing efficiency is reduced by belowground structure and possibly also aboveground structure.

(8) Whelks tethered for 10 d in the presence of equally augmented hard clam abundances consumed on average 3.0 clams in sand-flat habitat, significantly more than in unmodified shoalgrass (0.4), with the average consumption of 1.9 in trimmed shoalgrass not significantly different from either other treatment, suggesting that below- and aboveground seagrass structure may each contribute to protection from predation.

Effects of dramatic seasonal loss of aboveground shoalgrass structure on whelk predation on hard clams

(9) In a 78 d experiment from 19 July to 5 October, hard clams 40 to 80 mm in length exhibited 95% survival in shoalgrass and 92.5% in trimmed shoalgrass versus a significantly lower 64% in sand-flat habitat — with 77 to 87% of mortality attributable to whelk predation.

(10) As shoalgrass blades sloughed off, whelks only gradually progressed from the closest sand flat 11.8 m away towards the monitored shoalgrass plots, so distance from source of whelks confounded effects of the weakening boundary contrast in this experiment.

(11) In this same experiment, hard clams in intact and trimmed shoalgrass exhibited gradually rising mortality from late August through early October, while mortality in sand-flat habitat vacillated with no evident autumn increase.

(12) In systematic monthly surveys, numbers of articulated, rasped valves of recently consumed hard clams increased significantly from August to October, with enhancements within shoalgrass habitat, dominating the counts, suggesting that whelk predation was seasonally enhanced as loss of boundary contrast allowed mass invasion of shoalgrass habitat.

Effects of differences in prey availability between habitats

(13) Hard clam density in September averaged 1.38 ind. m^{-2} in shoalgrass versus 0.75 ind. m^{-2} in sand-flat habitat, suggesting greater abundance of the most highly used whelk prey in shoalgrass habitat, although this difference was not statistically significant.

(14) Hard clams were significantly larger in shoalgrass than in sand-flat habitat, implying greater biomass per prey item in shoalgrass habitat.

(15) Although depth of burial of hard clams measured to the uppermost shell margin did not vary with shell length or differ between shoalgrass and sand-flat habitats, whelks would still need to spend more time and energy to penetrate sediments more deeply to capture larger hard clams, whose lower margin necessarily extended more deeply, and thus probably experience more costs to consume the larger clams inside shoalgrass habitat.

(16) In the habitat selection experiment, augmentation of hard clam prey in both unmodified and trimmed shoalgrass plots resulted in higher numbers of whelks choosing to occupy those plots than analogous plots without prey augmentation, suggesting a possible response to chemical attraction, although the pattern was not statistically significant.

depths, thereby still suppressing foraging efficiency of whelks in seagrass even when lacking the vast majority of its aboveground structure. These responses are consistent with prevailing understanding of the dominant role of belowground plant structure in protecting buried prey (e.g. Peterson 1982, 1990, Orth et al. 1984).

Efficiency of predation on hard clams in clipped seagrass appeared greater than in intact seagrass, and when whelk habitat preference for sand flats dis-

appeared in autumn, substantial consumption of hard clams did occur in seagrass, increasing over spring–summer levels inside the study area as many more whelks invaded and used the seagrass habitat to prey upon hard clams (Box 1). Our quantitative characterization of seasonal change in aboveground plant structure, the demonstration of a massive autumn shift in habitat use by knobbed whelks moving into seagrass, and the evidence of increasing predation on infaunal hard clams in seagrass during the autumn period as seagrass habitat was invaded require revision of the prevailing model to add a novel role for aboveground vegetation structure. The refuge function of seagrass habitat is clearly not invariant, as implied by previous characterizations (Blundon & Kennedy 1982, Brenchley 1982, Peterson 1982, Irlandi 1997), but it instead varies seasonally. We apply the BC concept (Stamps et al. 1987, Holmquist 1998) to the observed structural change in aboveground biomass of shoalgrass to help explain the demonstrated shifts in the shoalgrass–knobbed whelk–hard clam relationships during autumn — namely the behavioral abandonment of whelk habitat preference for sand flats during autumn and the whelk penetration into seagrass. Massive invasion of the refuge habitat (seagrass) and increased autumn predation on clams in that habitat may help explain some patterns of anomalous hard clam abundances and size-frequency distributions between sand flat and seagrass habitats (Peterson et al. 1984, Peterson 1986, 2002, Micheli 1997, Nakaoka 2000). However, at our study site, hard clam densities and sizes appeared to remain greater in the seagrass bed (surveyed in September) despite the opening of the barrier to the bed by seasonal blade shedding.

We took advantage of the natural late summer and early autumn sloughing of aboveground seagrass structure as a 'natural experiment'. In manipulative experiments we clipped the aboveground seagrass blades and shoots, allowing us to assess if and how intact seagrass habitat differs from beds lacking most of their aboveground structure in influencing both whelk habitat choice and occupation and whelk predation on hard clams (Box 1). From mid-August to early October, we commonly observed the shed leaves and shoots of shoalgrass floating free on the surface, consistent with a temperature-dependent sloughing of seagrass blades (Thayer et al. 1984, Orth & Moore 1986). Rarely were any roots or rhizomes detected among this floating plant debris, implying sloughing of aboveground material and retention of the buried components, from which regrowth of shoots and leaves later occurs (Pangallo

& Bell 1988). During our systematic samplings of shoalgrass, average length of the longest blades declined from July to September by 51 % and then fell further by 18 % from September to October (Box 1). The observed decline in aboveground biomass was much steeper, declining by 81 % from July to September. Although data on aboveground biomass of shoalgrass were not collected during the October sampling, on the basis of the further 18 % decline in blade length from September to October, we assume that the additional percentage decline in aboveground biomass was at least as large, resulting in an estimated total decline of >84 % in aboveground biomass from mid-July to early October.

The similarity in the seasonal increase in whelk occupation of seagrass habitat by tagged whelks to the seasonal habitat switch by untagged whelks supports our assumption that visual ability to detect whelks did not differ between habitats, allowing us to confidently make use of survey data on untagged whelks. This dramatic change in habitat use by whelks is also evident in the results of our tethering experiment testing between pairs of habitat types: whelks selected sand over seagrass except after seagrass blades were clipped. Trimming away all aboveground structure eliminated the habitat preference, resulting in equal use of sand flat and clipped seagrass. Trimming was carefully done by hand so as to remove no belowground structure. Based on previous unquantified observations of seasonal sloughing of aboveground material by *Halodule wrightii* in Bogue Sound, we had anticipated the dramatic decline in autumn and had chosen a 100 % removal for our trimming treatment, similar to the natural decline in aboveground biomass. Although whelks used trimmed seagrass and no longer preferred sand, trimmed seagrass still appeared to inhibit efficiency of whelk predation on hard clams relative to efficiency documented in sand in experiments involving tethering of whelks in specific habitats (intact shoalgrass, trimmed shoalgrass, and sand). This result also demonstrates the continuing role of belowground vegetation as at least a partial refuge for clams from whelk predation, with belowground structure now experimentally isolated from effects of aboveground material. Our habitat-specific differences in burrowing depths of whelks are consistent with the measurements by Peterson (1982) showing that physical penetrability of surface sediments is much lower in seagrass beds than in adjacent unvegetated sandy bottom. These responses and others (Box 1) to changes in sub-surface structure of seagrass habitat confirm the dominant role of sub-surface seagrass

structure in providing a partial refuge for buried prey from burrowing predators by solidifying the ground and inhibiting digging by the predator to access the prey.

The greatest novelty of our study is the seasonally varying role that aboveground seagrass structure plays in mediating predator–prey interactions between whelks and their hard clam prey. Our 2 experiments and survey observations offer supporting, even if often individually non-significant, indications that whelk predation on hard clams is elevated after loss of aboveground seagrass structure (Box 1). Although results of our 78 d experiment revealed greater whelk predation on hard clams in sand than in intact seagrass habitat, the trimmed seagrass treatment failed to group with the sand-flat results and instead showed low predation more similar to the unmodified seagrass. This result contradicts our conclusion that loss of aboveground seagrass structure enhanced whelk predation on clams. However, because these trimmed plots were established well within a large seagrass bed at locations 11.8 m away from the nearest sand-flat source of whelks, the failure of trimming to induce high rates of whelk predation on clams may reflect a delay to entry provided by a barrier of at least 11.8 m of aboveground seagrass. Indeed, we observed the autumn whelk invasion of the large shoalgrass bed in which these plots were located and could see that they were indeed slow to proceed into the patch interior. Hence, the magnitude of early autumn increase in whelk predation on clams in the monitored patches deep within a large shoalgrass bed is not representative of the large majority of the seagrass beds at the study site, which were much closer to sand-flat sources of whelks.

The temporal pattern of whelk predation on clams in this 78 d experiment provided non-significant indication that from summer to early autumn the rates of whelk predation on hard clams may have increased more in unmodified (although with greatly reduced aboveground biomass, resembling the trimmed treatment) shoalgrass and trimmed shoalgrass than in the sand-flat treatment. This pattern is consistent with the autumn whelk migration from sand-flat habitat into the large shoalgrass bed, providing access to both intact and trimmed seagrass plots. Our whelk tethering experiment showed that predation on hard clams in summer month was significantly greater in sand-flat plots (3.0 clams) than in intact shoalgrass (0.4) and was intermediate in the trimmed shoalgrass (1.9) and closer to the sand-flat rate, although not significantly different from either of the other habitat treatments. Our routine collections of

articulated valves of newly dead hard clams during monthly surveys revealed higher production of rasped shells in September and October than in the preceding summer month of August, with predation especially concentrated within seagrass habitat. The apparent autumn enhancement of whelk predation on hard clams occurred despite the persistent inhibition of burrowing by belowground plant structure and the attendant inefficiency in feeding as compared to feeding in the sand flat, as demonstrated by results of our shoalgrass trimming experiment.

We interpret this change in whelk habitat occupation (Box 1) to reflect the response of whelks to a large seasonal reduction in strength of the otherwise strong BC (Stamps et al. 1987, Holmquist 1998) created by emergent aboveground plant biomass difference at the habitat margin. No other late-summer to autumn change between seagrass and sand-flat habitats seems likely to explain this seasonal shift in whelk use of seagrass habitat. It is possible that a strong BC created by meadows of seagrass leaves and shoots physically blocks whelk entry. Our observations of movements of whelks tagged with floats suggested that whelks made their most extensive lateral movements largely at the sediment surface rather than when buried out of sight and therefore could be responding to physical obstruction of movement by aboveground vegetation.

Alternatively, the decision to enter seagrass habitat may reflect whelk behavioral choices cued by density of aboveground plant structure. Under this mechanism, a strong BC would not actually prevent entry to seagrass habitat but would add energetic costs, such as suppressing movement even once inside the seagrass bed. Our comparisons of predation rate of tethered whelks on hard clams in intact shoalgrass, clipped shoalgrass, and sand provide a non-significant indication that the presence of dense aboveground shoalgrass also plays a role in reducing the efficiency of predation, although less effectively than belowground structure, and so would add energetic costs to whelks foraging for hard clams within intact shoalgrass.

When whelks utilized shoalgrass habitat in autumn, they did not exhibit a detectable preference between shoalgrass and sand flat. Foraging theory would suggest that some benefits of foraging on hard clams should exist within seagrass to overcome the energetic disadvantages associated with inhibited burrowing capacity in the presence of belowground plant structure, as shown by our burrowing depth data, and slower, and thus less efficient, predation rates in the presence of equally enhanced densities

of hard clams, as demonstrated in our tethered whelk experiments (Box 1). Historical prey abundances, largely defined by hard clams from our survey of whelk prey choices, were substantially greater inside North Carolina seagrass beds than on sand flats before overharvesting beginning in the late 1970s (Peterson 1986, 2002, Peterson et al. 1987, 2004), and to a lesser degree, this density difference appears to have persisted into 1995 based on our sampling data. Higher prey densities would be expected to reduce search costs. The average size of hard clams was greater in seagrass than on the sand flat in our study and in Peterson et al. (1984), perhaps providing more energetic reward to whelks per unit effort of search, excavation, and handling.

Whelks are attracted to chemical cues released by hard clams and other invertebrate prey (Powers & Kittinger 2002, Ferner & Weissburg 2005, Ferner et al. 2009), such that a high biomass of hard clams inside seagrass could stimulate entry into this habitat. Our simultaneous manipulation of both hard clam density and aboveground plant biomass demonstrated that abundance of hard clam prey had no detectable direct or interactive effect on habitat choice by whelks, indicating that elevating chemical cues from hard clams may not influence whelk habitat choice on the scale of this experiment. However, these results were somewhat equivocal in that for each habitat treatment, whelk abundances were greater in the plots with augmented numbers of hard clams. Nevertheless, like the physical blocking process, this chemical attraction mechanism and evolutionarily based behavioral explanations for habitat selection all still rely upon the magnitude of the physical BC provided by aboveground seagrass structure to explain the seasonally restricted use of seagrass habitat by whelks.

Although we conducted our research within 1 system, a marine shallow-water environment, involving just 1 species of seagrass and in 1 geographic location, we would expect the processes that we explored to have broad applicability. Many seagrasses shed their aboveground leaves seasonally in response to predictable cycles of environmental stress like high temperatures (Thayer et al. 1984, Duarte & Sand-Jensen 1990) or in response to unpredictable environmental perturbations (Patriquin 1975, Fonseca et al. 1983, Townsend & Fonseca 1998). A review of seasonal changes in 29 eelgrass *Zostera marina* populations from Europe, North America, and Japan covering a latitudinal range of 30 to 56° N showed a highly consistent pattern of a summer maximum in leaf biomass, followed by leaf loss in autumn and a late autumn-to-winter minimum (Olesen & Sand-Jensen 1994). These eelgrass populations exhibited an 8.4-fold increase in median leaf biomass from winter to summer. In Chesapeake Bay, north of our North Carolina study site, Orth & Moore (1986) reported peak leaf biomass of eelgrass in July and August followed by dramatic shedding of older leaves beginning in late August as water temperatures reached 25 to 30°C. Nevertheless, the belowground portions of the plants largely persist (Pangallo & Bell 1988) after blade shedding by heat stress and provide the basis for subsequent regrowth of the aboveground portions of the plants and renewal of their full habitat function and value.

Analogous processes in other habitats with soils, including especially shallow freshwater benthic habitats, as well as terrestrial plant communities and marine benthic environments in deeper water, seem likely. For example, winter die-off of rooted macrophytes in littoral zones of shallow temperate lakes is a widespread phenomenon (Scheffer 1998). Although macrophyte beds in freshwater lakes enhance abundances and use by many benthic invertebrates as contrasted to open patches in littoral habitats (e.g. Beckett et al. 1992), to our knowledge no freshwater studies have tested how above- versus belowground macrophytic vegetation differs in its impacts on interactions between buried prey and excavating predators. A strong BC could influence cross-boundary penetration by mobile animals into a variety of habitats showing seasonal and other variation in biogenic structure (e.g. Wiens 1995, Bender et al. 1998). Even more complex interrelationships between habitat structure and predator behavior may be expected to develop when both above- and belowground biogenic structure exists and can exhibit some decoupled variation.

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