

Causes and consequences of historical multi-trophic diversity change in an intertidal seagrass bed

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Qualitative historical changes in the BMB community

In addition to the quantitative results presented, we also interviewed three persons with long-term, in-depth knowledge of the Bay Mouth Bar (BMB) system: Dr. Robert Paine, who worked extensively at the site in the late 1950s, and who re-visited it in Oct. 2007, Jan. 2009 and Mar. 2010; Doug Gleason, a naturalist and collector for the Gulf Specimen Marine Lab in Panacea, FL, who has visited and periodically collected invertebrates on the bar since the 1970s; and Mary Balthrop, a resident of St. Teresa, FL and recreational naturalist who has regularly observed and visited BMB since 1972.

All persons interviewed described the substantial decline in the area of BMB and in the coverage of formerly extensive *Thalassia* meadows, which is readily apparent in the historical aerial images (Fig. 2) and in other existing historical imagery and maps of the field site (e.g. Olson 1955). All persons agreed that over the last 30 years there has been decline in the number of large bivalves, including *Chione elevata* (cross-barred venus), *Modiolus squamosus* (southern horse mussel), *Mercenaria campechiensis* (southern quahog), *Macrocallista nimbosa* (sunray venus), and *Aquiptecten irradians* (southern bay scallop). Gleason in particular attested to formerly great densities of the mussel *Modiolus*, particularly in *Thalassia* beds. Indeed, *Modiolus* was abundant enough that researchers went to the site to collect this species for lab experiments until as late as the 1980s (Pierce 1970, Nicchitta & Ellington 1983). Balthrop described how bay scallops were once very abundant on the bar, but had declined tremendously, most likely as a result of overharvesting, and no longer supported a recreational fishery.

Paine attested that there has been a conspicuous increase in the number of horse conchs on the bar since 1960, even after taking seasonality into account. He also described the decline in lace murex as conspicuous and substantial: in the 1950's he had recorded observing up to 40 individuals in egg-laying aggregations, and up to 4 individual snails feeding on a single *Chione*. Gleason reported seeing true tulips in *Thalassia* while snorkeling on BMB in the 1970s, and Wells (1970), prior to the closing

of the channel, reported that *F. tulipa* densities on BMB did not appear different from those reported by Paine (1963).

The role of human collection in altering community structure of BMB and in driving down average snail size is unclear. Wells (1970) notes an absence of larger individuals compared to Paine (1963) that he cites may be due to human collection. Horse conchs, true tulips, and lightning whelks are harvested by humans on the Gulf Coast of Florida; however, current population estimates in other seagrass beds in the region suggest that they are not overexploited (Stephenson et al. 2013). Collection of large snails on BMB has been occasionally reported, but never in great intensity. Besides scallops, Balthrop had not observed other bivalve or gastropod species being heavily harvested from the bar, and posits that their decline is probably not due to overcollecting. Gleason also did not believe his occasional collection activities had any noticeable effect on mollusc populations. In our monthly surveys, conducted during the periods when the bar is most accessible, we only rarely observed other people on the bar, and their collections, if any, appeared limited to empty snail shells and the few remaining *Macrocallista nimbosa*. The abundant and conspicuous horse conchs currently on BMB, which are a main target of collectors, also suggests that collection at the site is likely minimal.

Other carnivorous gastropods

Paine (1963) discusses 2 additional carnivorous gastropod species in addition to the 6 species we focus on in this study. These two species were the moon snail (*Neverita duplicata*, formerly *Polinices duplicatus*) and ear shell (*Sinum perspectrum*). In our interview, Paine reported that in his recent visits, these two snails species appeared to have increased on BMB since 1959. These are bivalve-drilling species, which we were not able to effectively survey due to their burrowing behavior and largely subterranean existence. They are likely abundant on the bar, and may also have contributed to declines in bivalves. As competitors to lace murex, these species may also be playing a part in BMB community dynamics, which we were not able to examine in this study. As a preliminary way to assess the abundance of moon snails, we collected all whole (intact), dead *Chione* valves from a subset of the quadrats taken during our summer infaunal survey. We also fed live *Chione* to different snail species in the lab in order to identify the characteristic marks that each leaves on the shell of this clam species. Of the 312 valves collected from BMB, 23% were drilled at the base in the way characteristic of moon snails, 8% were shaved in the way characteristic of lightning whelks, and 3% were drilled close the lip with a more steeply-sided bore hole, which is more characteristic of lace murex and oyster drills (*Urosalpinx*). In contrast, of 92 *Chione* valves collected from 8 quadrats in the area where lace murex were collected for the field experiment, 16% were drilled in the manner of moon snails, 3% were shaved in the manner of lightning whelks, and 11% were drilled in the manner of lace murex and oyster drills.

Gastropod burrowing behavior

Unlike moon snails and ear shells, the 6 large gastropods on which we focused our surveys must move and feed above ground. However, with the exception of horse conchs and lace murex, these snails are known to burrow when inactive. Since current and historical surveys only counted snails that were on the surface of BMB, estimates of snail density are undoubtedly underestimates of true density, and we must assume consistency in burrowing behavior between 1959-1960 and 2012-2013. Since it was not possible to survey buried snails, we attempted to quantify the relative burrowing behavior of each species by recording when living tethered snails in the experiment were found buried vs. on the surface (Fig. S5). The percentage of snails found buried varied substantially between species, with lightning whelks showing the highest rate of burial, and lace murex showing the lowest (after horse conchs, none of which were found buried). Observations we made in the laboratory suggested that burial may act as a defense against predation by horse conchs, which were not able to consume lightning whelks, pear whelks, and banded tulips that had been permitted to bury themselves in sediment (which they did readily) prior to introducing a horse conch. Lace murex did not bury themselves in the laboratory, and were readily captured and consumed by horse conchs. This lack of burrowing behavior by lace murex may partly explain the high susceptibility of this species to horse conch predation in the field.

Preferential habitat use by gastropods

During the monthly field surveys, we recorded the habitat type in which we found each snail as a way to test for preferential habitat use. We also recorded the habitat type present at 306 pre-determined GPS points evenly-spaced across the BMB study area in July 2012 and January 2013. We compared whether the number of each gastropod species we observed in each habitat type during the field surveys differed from the background distribution of habitat types using Chi-Square tests. Habitat types were *Halodule*, *Thalassia*, Mixed *Halodule/Thalassia*, Sand, and Other. The “Other” category was rare, and excluded in Chi-square analysis.

We found that proportion of snails in each habitat differed from the background distribution of habitat types on the sandbar (Chi-Square test, $p < 0.001$; Fig. S6). Horse conchs were found in *Thalassia* more often than expected if snails were randomly distributed, banded tulips were more often found in *Halodule*, and lightning whelks and pear whelks were more often found in sand. Habitat distribution in the winter and summer background surveys did not differ (Chi-square test, $p = 0.33$), although seagrass was much sparser in the winter due to seasonal dieback.

Naturally occurring bivalves in experimental plots

In addition to the tethered clams, we also assessed differences in naturally occurring bivalves in the experimental plots. At the end of the experiment, we excavated two 0.25 x 0.5 m quadrat areas from within each experimental plot. The quadrats were dug to 5 cm depth, and sieved in field through

a 5 mm mesh sieve. Bivalves, small gastropods, and small crabs were collected, and were sorted and identified in the lab. Other animals (e.g. echinoderms, ascidians, tubes of large polychaetes) were enumerated in the field.

Compared to control plots, MLCA-only treatments had no effect on the naturally occurring infaunal community (PERMANOVA; MLCA, $F_{2,33} = 0.649$, $p = 0.892$, $R^2 = 0.057$). The infaunal community was affected only by habitat type (PERMANOVA; habitat, $F_{1,33} = 5.26$, $p = 0.001$, $R^2 = 0.23$), and there was no significant interaction between MLCA and habitat type. Across all experimental treatments (excluding controls to allow for a balanced dataset) infaunal community composition was also only affected by habitat (PERMANOVA, $F_{1,33} = 10.55$, $p = 0.001$, $R^2 = 0.195$). Consumer treatment and predator treatment had no effect on community composition, and there were no significant interactions (all p-values >0.38).

Literature Cited

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Table S1. Diet of gastropods in 1959-1960 (Paine 1963) and in 2012-2013. “Small snails” includes moon snails, turban snails, drills, *Nassarius vibex*, and similar species. “Large snails” includes lightning whelks, pear whelks, banded tulips, true tulips, and lace murex.

	Lightning whelk		Pear whelk		Banded tulip		Horse conch	
	1959-1960	2012-2013	1959-1960	2012-2013	1959-1960	2012-2013	1959-1960	2012-2013
Carrion			5	2	10	9		
Polychaete					31	26		
Barnacle					1	4		
Bivalves								
Clam	163	38	7	5	15	13		
Mussel	5	17			4	24		
Scallop			1	1		1		
Oyster					2	2		
Jingle shell					2	3		
Ark shell	4				1	1		
Pen shell							13	8
Gastropods								
Small snail			1	13	10	8	1	
Large snail			1	3			52	10
Total obs	172	55	15	24	76	91	66	18

Table S2. Most common bivalve species in *Halodule* in 1959-1960 (Paine unpublished data) and in 2013. The 1959-1960 species are unranked. The 2013 species are ranked starting with numerically most abundant. Bolded species not shared between lists.

1959-1960	2013
<i>Stewartia (Lucina) floridana</i>	<i>Anadara transversa</i>
<i>Chione elevata (cancellata)</i>	<i>Chione elevata (cancellata)</i>
<i>Carditamera (Cardita) floridana</i>	<i>Geukensia granosissima</i>
<i>Mactroma fragilis</i>	<i>Mactroma fragilis</i>
<i>Mercenaria campechiensis</i>	<i>Cumingia tellinoides</i>
<i>Macrocallista nimbosa</i>	<i>Angulus texanus</i>
<i>Ensis megistus (minor)</i>	<i>Ensis megistus (minor)</i>
<i>Atrina spp.</i>	<i>Laevicardium mortoni</i>
<i>Tagelus divisus</i>	<i>Tagelus divisus</i>

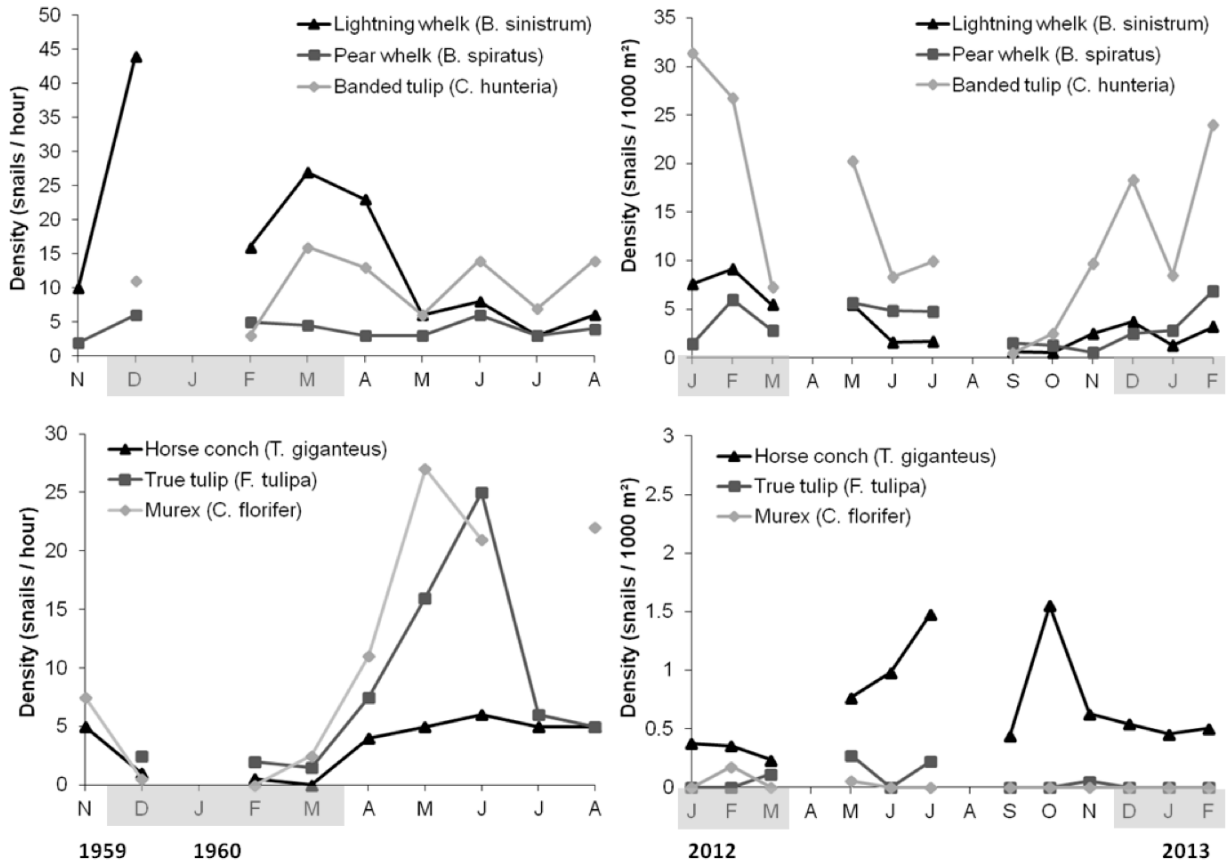


Fig. S1. Time series of gastropod densities on BMB from Paine (1963) and the current study. Shaded months indicate the “winter” season (December-March).

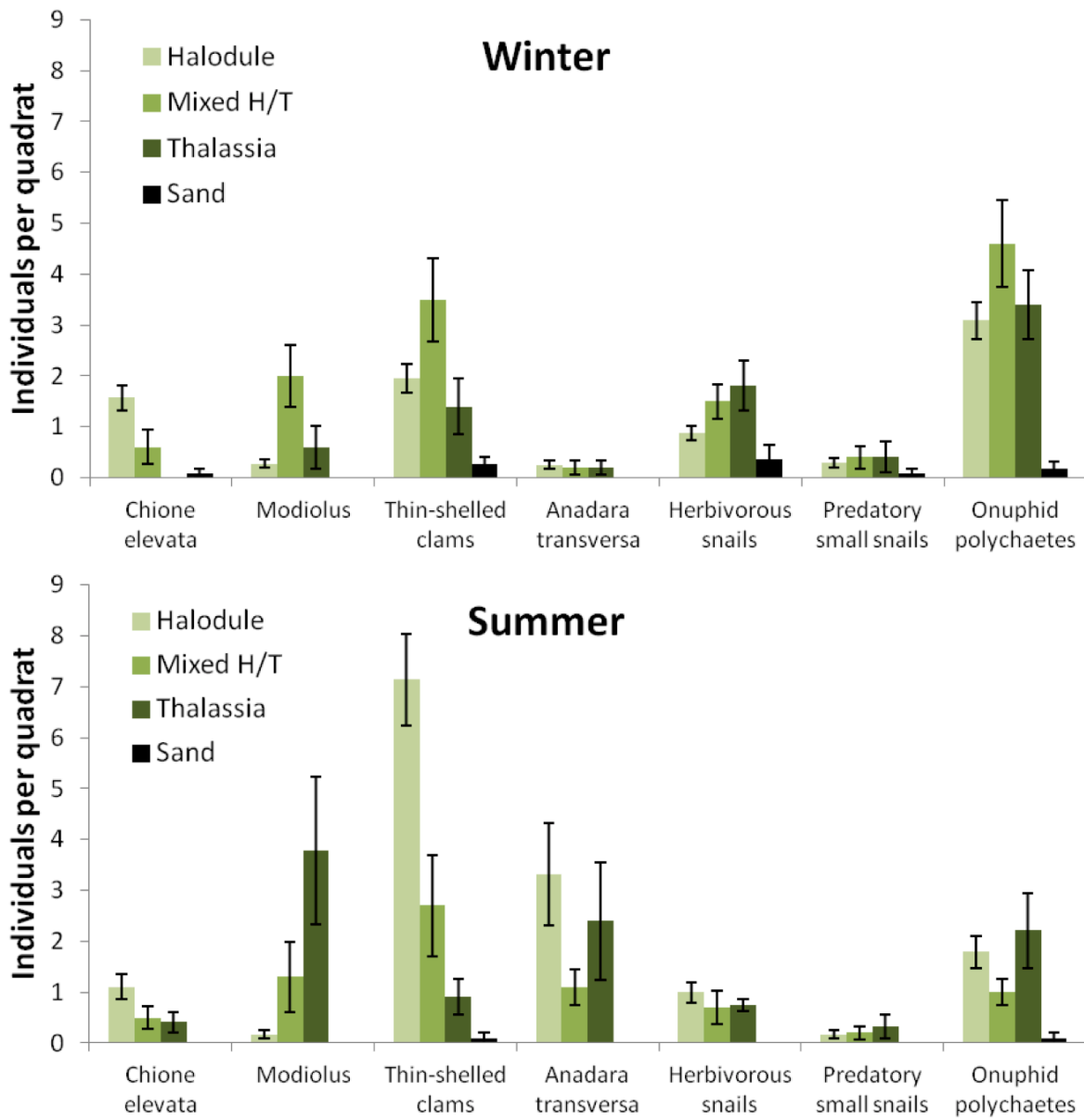


Fig. S2. Abundance of infaunal species and functional groups in different habitat types on BMB in January (winter) and July (summer) 2013. Data are means \pm 1 SE.

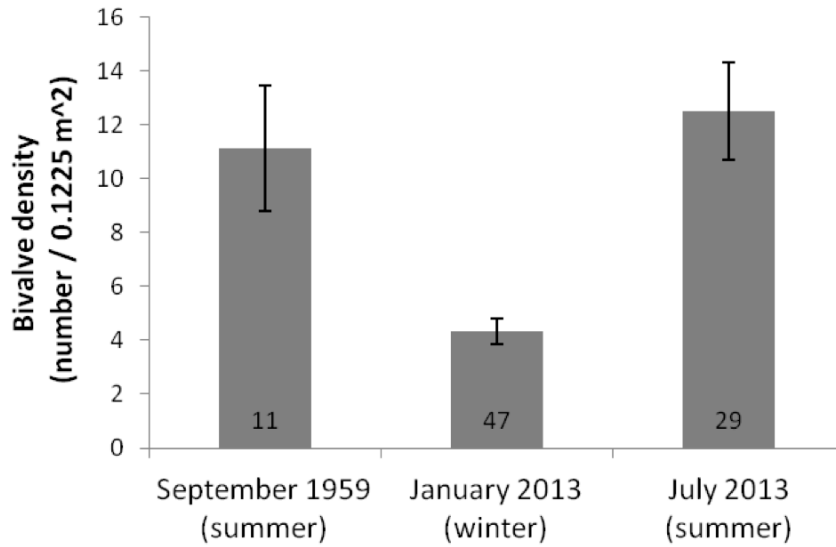


Fig. S3. Density of bivalves in *Halodule* in 1959 (R. Paine *unpublished data*) and in 2013. Bivalve density excluded the mussel *Geukensia granosissima*, which was very patchily distributed. Data are means \pm 1 SE. Numbers on bars are sample sizes (number of quadrats).

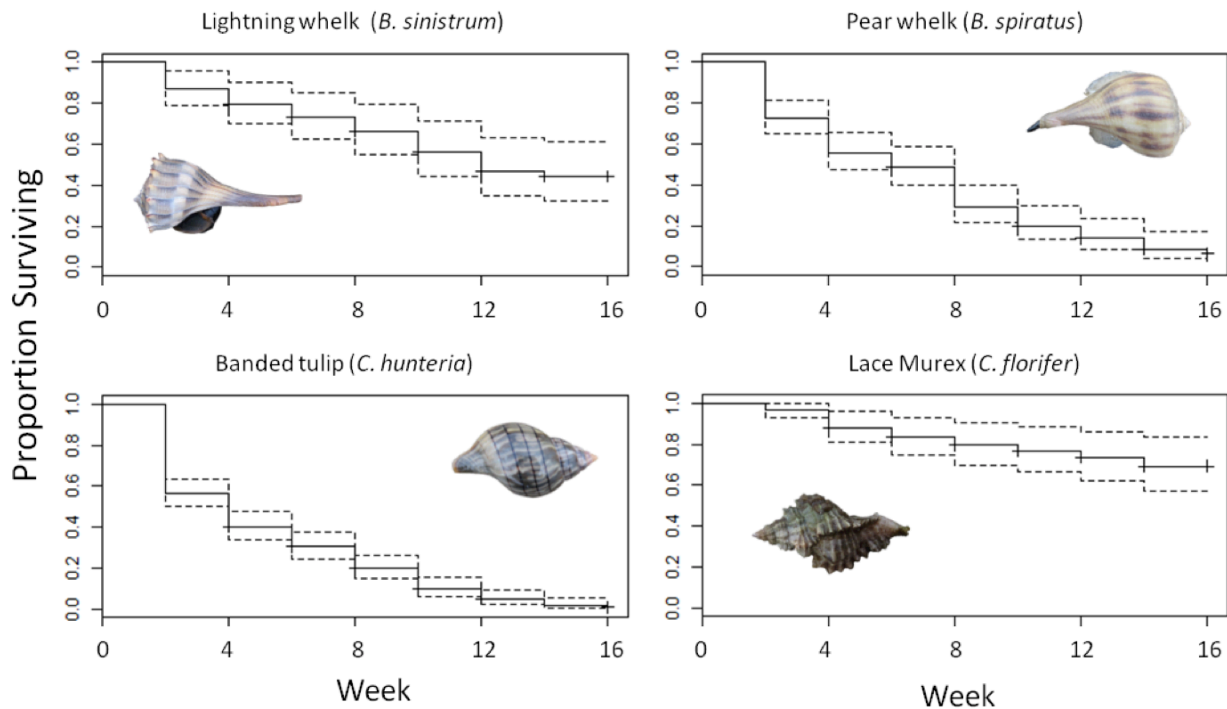


Fig. S4. Survival curves for the four mid-level consumer species used in the field experiment, averaged across all treatments.

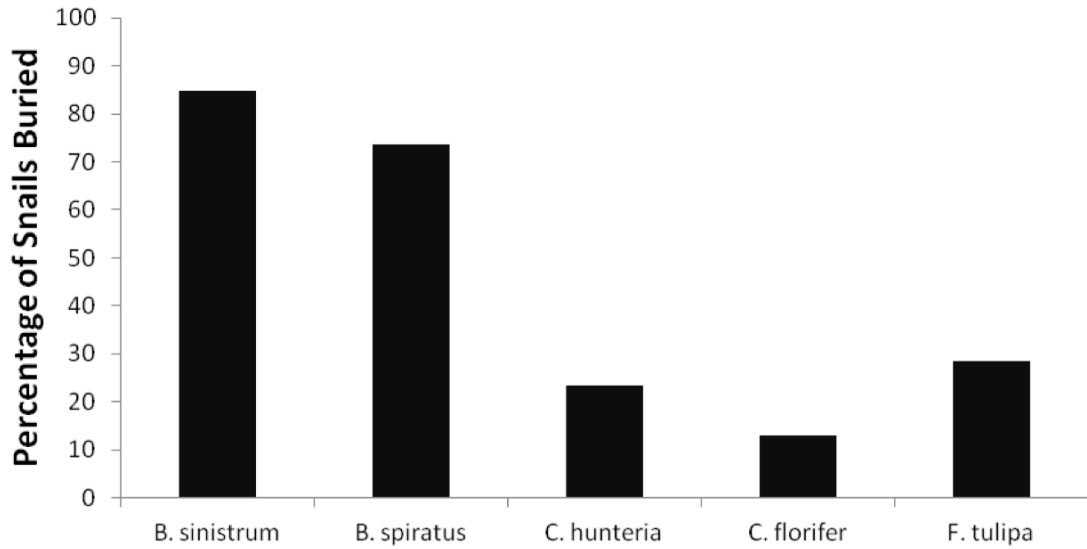


Fig. S5. Percentage of living tethered snails that were found buried during the field experiment. Includes all observations during all checks.

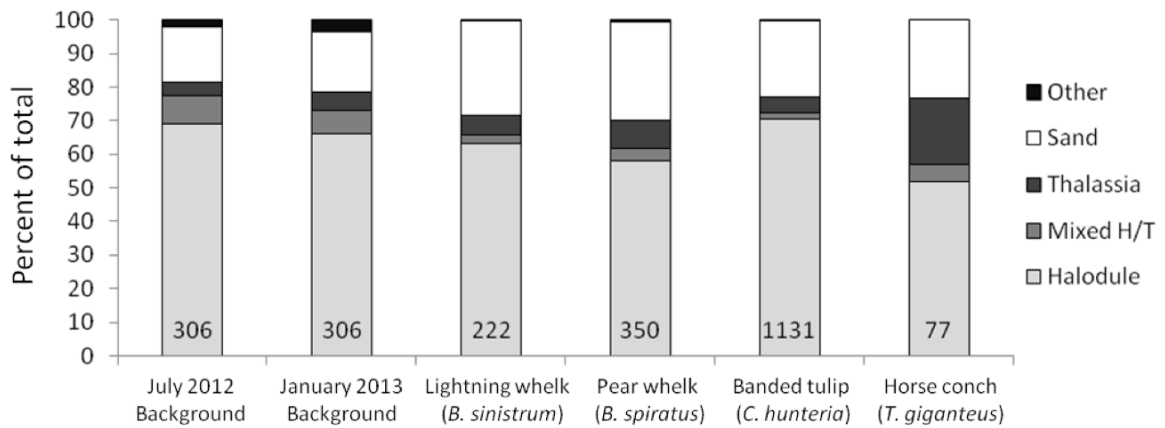


Fig. S6. Habitat types on BMB based on evenly spaced points, and habitat types in which snails were found. Mixed H/T = mixed *Halodule* and *Thalassia*. “Other” includes *Syringodium filiforme*, and mixtures of *Syringodium filiforme* with *Halodule* and/or *Thalassia*.