



## Foraging effects of cownose rays (*Rhinoptera bonasus*) along barrier islands of the northern Gulf of Mexico

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### ABSTRACT

Large mobile predators are hypothesized to fulfill integral roles in structuring marine foodwebs via predation, yet few investigations have actually examined the foraging behavior and impact of these species on benthic prey. Limited studies from the Cape Lookout system implicate large schooling cownose rays (*Rhinoptera bonasus*) in the devastation of patches of commercially harvested bay scallop via strong density-dependent foraging behavior during migrations through this estuary. However, despite the extensive Atlantic range of *R. bonasus*, the pervasiveness of their patch-depleting foraging behavior and thus impact on shellfisheries remains unknown outside of North Carolina waters. To further understand the potential impacts of cownose rays on benthic prey and the role of bivalve density in eliciting these impacts, we conducted exclusion and manipulation experiments at two sites in the northern Gulf of Mexico frequented by rays during spring migrations. Despite a correlation in ray abundance with haustoriid amphipod (primary natural prey) density at our study sites, we were unable to detect any effect of rays on amphipod densities. In addition, through manipulation of predator access, we determined the main cause of mortality to manipulated patches of hard clams was predation by smaller predators such as *Callinectes sapidus* and not cownose rays. While cownose rays consume hard clam in other parts of their range, we suggest rays along northern Gulf of Mexico barrier islands may prefer foraging on smaller and thinner-shelled bivalves (e.g., *Donax* sp.), as well as more abundant amphipod crustaceans. We caution that these preferences may have reduced our ability to detect effects of rays on manipulated prey, and thus future impact experiments should strongly consider the local diet of these predators and explore novel techniques to estimate effects on small crustaceans. Further synchronized experimentation along basin-wide scales may elucidate the environmental factors that determine the severity of cownose ray foraging impacts across their range.

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### 1. Introduction

In marine ecosystems, dense aggregations of large predators (e.g., schools of fish, pods of marine mammals) move along coastlines, circumnavigate large ocean gyres, and perform pole-ward seasonal movements (Block et al., 2005; Bradbury and Laurel, 2007; Luschi et al., 2003). These large-scale migrations serve multiple species-specific functions, but generally enhance fitness through foraging or reproductive opportunities (Dingle and Drake, 2007). When migratory corridors occur along coastlines, the temporary influx of dense aggregations of large predators may alter local food webs and act as strong agents of connectivity between geographically distant landscapes (Powers et al., in review). Growing evidence suggests that even the ephemeral presence of intermediate or “meso” predators (e.g., rays), which have been released from population control by

apex predators, can have dramatic negative effects on basal resources (Myers et al., 2007). However, despite a clear need for further experimentation with these mesopredators, their foraging effects remain poorly studied across marine ecosystems and thus limit our understanding of the large-scale consequences of top predator declines (Heithaus et al., 2008; Myers et al., 2007).

Unfortunately, working with large mesopredators has numerous logistical restraints. For example, traditional experiments that introduce predators into a caged system have substantial artifacts due to the large and mobile nature of many mesopredator species. Further, because many mesopredators also have complex behaviors and may naturally forage in groups, an adequate appreciation of their foraging ecology and potential effects on prey dynamics require field-based approaches. These shortcomings in studying large predator ecology have undoubtedly limited our knowledge of the potential role of these species in marine ecosystems (Estes and Peterson, 2000). Fortunately, some species of large demersal mesopredators (e.g. molluscivorous fishes) feed on relatively immobile benthic organisms and thus predators can be excluded from foraging areas to examine their potential

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effects on prey. Estimation of the foraging effects of mesopredatory rays (Chondrichthyes: batoidea) is particularly amenable to in situ experimentation due to their general behavior of disturbing sediment and consumption of mollusks. These characteristics of ray foraging leave “traces” of predation (e.g., feeding pits), and have allowed researchers to tractably monitor predation by these species and manipulation of their benthic prey (Hines et al., 1997; Orth, 1975; Reidenauer and Thistle, 1981; Sasko et al., 2006; Smith and Merriner, 1985; VanBlaricom, 1978, 1982).

Select forager response and exclusion experiments on durophagous stingrays (myliobatidae) suggest that these species exhibit density-dependent patch selection when feeding on benthic bivalves (Fegley et al., 2009; Hines et al., 1997; Peterson et al., 2001; Thrush et al., 1991). For example, the New Zealand eagle ray (*Myliobatis tenuicaudatus*) exhibits a predation response that is non-proportional to increasing prey densities; rays ignore patches with low densities of the bivalve *Macomona lilliana* and increase foraging rates once they encounter a threshold of *M. lilliana* patches of 176 clams/m<sup>2</sup> (Hines et al., 1997). Migrating cownose rays (*Rhinoptera bonasus*) in North Carolina may also exhibit density-dependent responses as they appear to select high-density areas of bay scallop but do not appear to vacate the habitats before prey extinction (Peterson et al., 2001; Powers and Gaskill, 2003). The extirpation of bay scallops in patches violates ideal free distribution theory, which would predict that the rays would distribute themselves among other habitats with lower densities of prey before extinguishing the resource (Peterson et al., 2001; Powers and Gaskill, 2003). This behavior also violates the Marginal Value Theorem, as rays most likely reached a non-optimal energy acquisition rate with increased residence time in a patch with relatively depleted resources (Charnov, 1976).

Taken together, studies suggest that ray foraging may be initiated when prey densities exceed a certain threshold; however, no field experiments have experimentally manipulated densities of prey resources available to rays to examine patch selection and overall impact on prey. Moreover, the foraging responses and effects of these species may be site- and/or habitat specific. For example, cownose ray foraging effects have only been studied in a single habitat type (eelgrass, *Zostera marina*) despite evidence that these animals actively forage in other habitats of reduced structural complexity (Ajemian and Powers, 2012; Sasko et al., 2006). To better understand the role of ambient prey density in myliobatid ray foraging behavior and thus the potential impact of these species on shellfish seeding programs, we examined foraging effects and patch preferences of cownose rays in the northern Gulf of Mexico. Cownose rays form large seasonal aggregations along barrier islands of this region (Fig. 1), where they consume large amounts of benthic crustaceans and infaunal bivalves in shallow sandflat habitats (Ajemian and

Powers, 2012). Working at two sites along coastal Alabama, we first examined the effects of cownose rays on natural prey (haustoriid amphipods), and then investigated the potential ray impacts on manipulated densities of a commercially-harvested bivalve species (*Mercenaria* sp.).

## 2. Material and methods

### 2.1. Exclusion-only experiment

To assess impacts of cownose rays on natural prey, we excluded rays from foraging areas in spring 2009. We used the north-facing sandflats of Pelican Island, Alabama as the study site (Fig. 2), where large spring aggregations of cownose ray schools had been previously observed (Ajemian, 2011). Exclusion patches were 2 m × 2 m (4 m<sup>2</sup>) PVC frames, with 1 m pieces of rebar secured throughout the frame vertically. Rebar stakes were separated at a distance of 25 cm throughout the frame edge and within the interior of the plot, and submerged 25 cm into the sediment (75 cm exposed). Control patches of the same dimensions were haphazardly placed nearby >2 m from the exclusions, and marked with 4 rebar stakes at the corners. Exclusion and control patches were replicated (n=6) within two separate sampling blocks situated along Pelican Island. The locations of the patches were completely randomized within each sampling block using Hawth's tools extension for ArcGIS 9.2 (ESRI, Inc.).

The benthos within exclusion and control patches was sampled weekly or biweekly between February and May 2009 using five 15.2 cm diameter (15.0 cm sample depth) hand cores. Within each plot we pooled counts of infaunal invertebrates from the five haphazardly chosen core samples. Gillnet sets (1 h soak) were conducted opportunistically alongside benthic sampling events to assess potential predator abundance. Gillnets were 150 m in length (3 m depth) of



Fig. 1. Photo of a cownose ray shoal in shallow waters off Dauphin Island (Credit: J. Dindo).

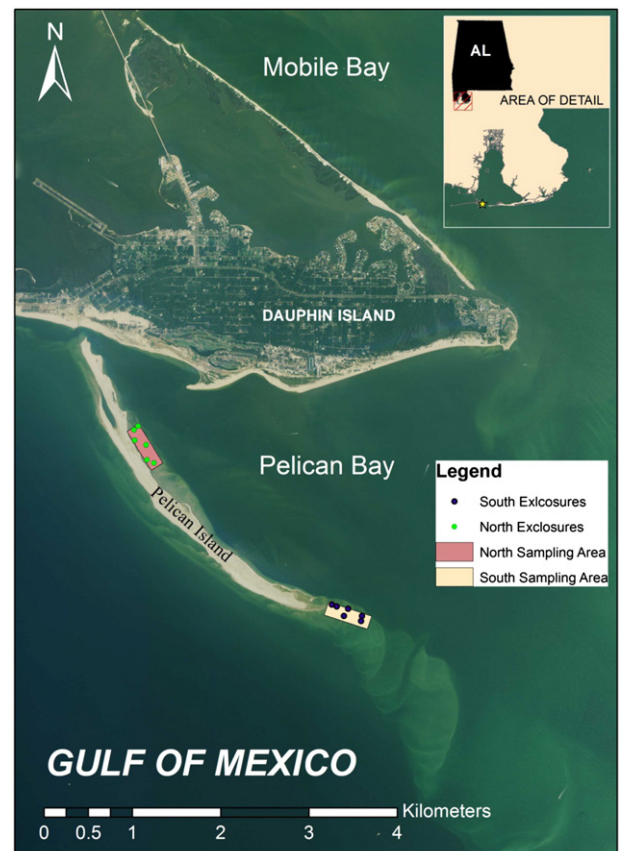


Fig. 2. Map of experimental exclusion locations off Pelican Island sandflats.

15 cm monofilament stretch mesh, deployed perpendicular to the shoreline in water 1–3 m depth.

Three-way mixed model analysis of variance (ANOVA) was used to explore the effects of sampling day (random factor), patch type (exclosure vs. control, fixed factor), and sampling block (north vs. south, random factor) on prey densities. Given the relatively high abundance (>95% of benthic invertebrates by number) and verified consumption of haustoriid amphipods by cownose rays along Pelican Island (Ajemian and Powers, 2012), *Haustorius* sp. was chosen as a representative species for examining foraging effects of rays. For all statistical tests, amphipod densities were square-root transformed to meet normality and homogeneity of variance requirements of ANOVA. Significant factors were further analyzed using Bonferroni pairwise comparisons to identify the source of variation.

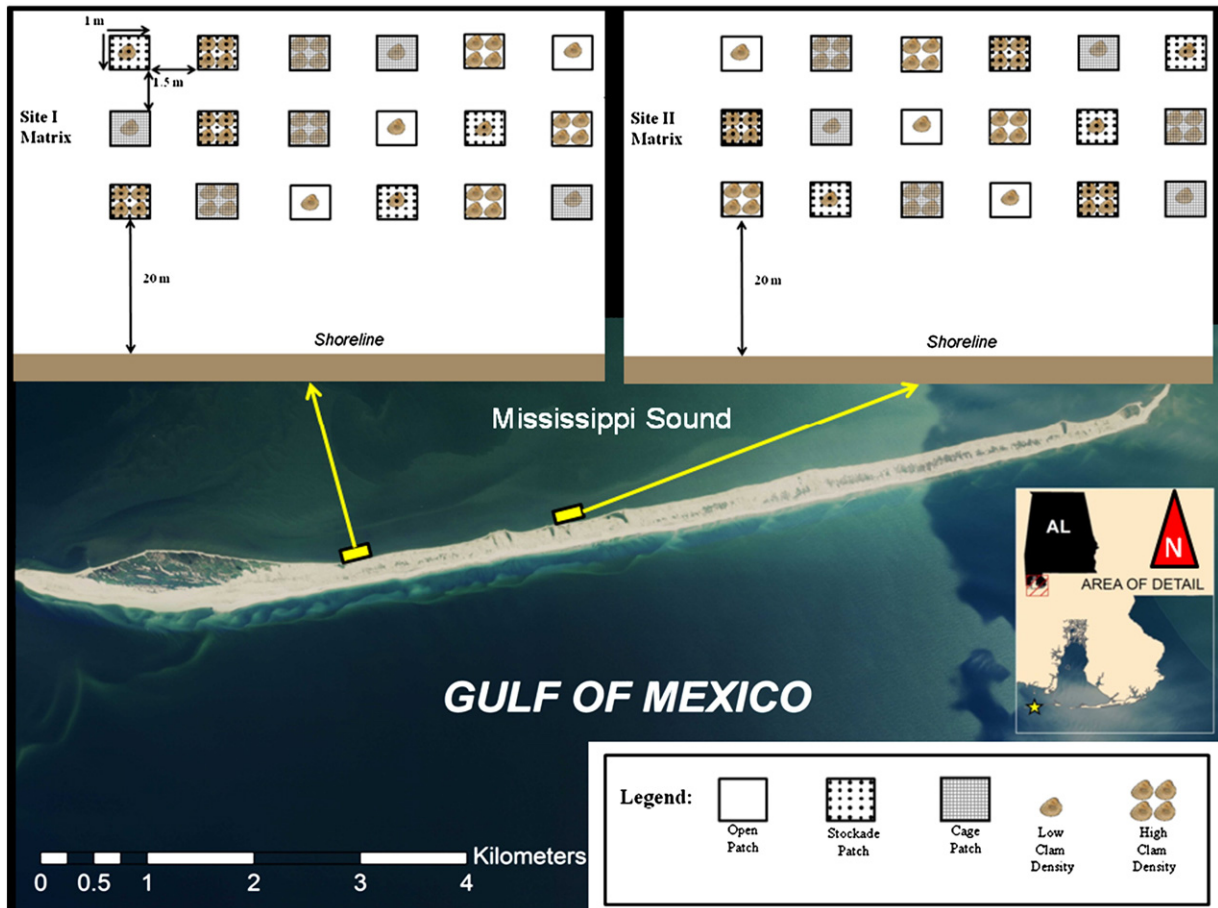
## 2.2. Field manipulation experiment

In a second experiment (2010), we investigated the potential impact and density-dependence of cownose ray foraging on seeded hard clams (*Mercenaria* sp.). The experimental manipulation took place off the west end of Dauphin Island (WEDI), Alabama where large groups of cownose rays were also commonly observed in spring months (Ajemian, 2011). This experimental location had habitat nearly identical to Pelican Island (subtidal sandflats), but was situated further west in Mississippi Sound and thus less influenced by the freshwater outflow of Mobile Bay (Fig. 3). The higher salinity levels were imperative for the hard clams, which prefer a range of 20–30 ppt (Baker et al., 2005). Hard clam was chosen as prey due to its availability in large numbers through local clam seeding programs, relatively large size

(25–35 mm, shell length; 13–18 mm, shell depth), and because cownose rays were previously shown to consume this species elsewhere (Fisher et al., 2011; Smith and Merriner, 1985). Moreover, a recent study demonstrated the potential for hard clam culture in Mississippi Sound (Jackson, 2008).

In winter 2010, we created two  $6 \times 3$  matrices of  $1 \text{ m} \times 1 \text{ m}$  ( $1 \text{ m}^2$ ) patches (18 patches per matrix). Matrices were spaced apart by 2 km along the north-facing shoreline of the west end of Dauphin Island (Fig. 3). Patch depth at low mean water ranged from 0.6 to 0.8 m. Three patch types were used: 1) Cage patch that served as a complete predator exclosure (wire mesh screen with a Vexar top); 2) Stockade patch of rebar stakes to inhibit ray access but allow smaller predators to forage in patches, and 3) Open (control) patch that allowed all predators to access the benthos (simply marked with four rebar stakes at the corners). Each patch had either a low (10 clams/ $\text{m}^2$ ) or high density (40 clams/ $\text{m}^2$ ) of clams, and was replicated three times throughout the matrix (Fig. 3). Treatment distribution was randomized across the  $6 \times 3$  matrix. We ensured one of the six treatments was present in each of the three rows of the matrix to achieve sufficient sample interspersed (Hurlbert, 1984). Patches were separated by a distance of 2 m to ensure migrating adult cownose rays (<1 m disk width) could move freely among patches within the matrix.

Experimental clams were marked with nail polish (two colors, one for tethered and one for untethered clams) to distinguish individuals from immigrating clams. Clams were tethered to a large metal staple (5 clams / staple) using a 20 cm section of monofilament super-glued to the shell (Peterson et al., 2001). Low density patches were composed of 1 staple (5 clams) and 5 untethered marked clams that were distributed haphazardly throughout the patch (10 total



**Fig. 3.** Schematic diagram and map of experimental manipulation sites off the west end of Dauphin Island. Yellow rectangles represent sites of  $6 \times 3$  manipulation grids. Low clam density = 10 clams/ $\text{m}^2$  (5 clams tethered, 5 clams untethered) and high clam density = 40 clams/ $\text{m}^2$  (20 clams tethered, 20 clams untethered). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

clams). High density patches consisted of four metal staples (20 clams) and 20 untethered marked clams (40 total clams). Sites were generally re-visited on a weekly basis over a twelve week period. During each visit, patches were excavated by hand and the total number of marked tethered, marked untethered, chipped and unmarked clams was enumerated. Clam shells that were open were not considered killed by rays, and were removed from patches for subsequent site visits. The presence of chipped or broken marked shells was also noted during each excavation, and fragments were removed from the patch surface. Marked tethered and marked untethered clams were restocked to original densities after each excavation.

Bivalve predation among experimental patches was quantified by calculating the proportional mortality rate (proportion of clams missing, divided by the number of days at liberty) of 1) marked tethered clams, 2) marked untethered clams, 3) the combined total of marked tethered and untethered clams, and 4) the difference between marked tethered and marked untethered clams. Proportional mortality rates were arc-sine square-root transformed to better meet the requirements of ANOVA (Underwood, 1997; Zar, 2010). Three-way mixed-model ANOVAs were used to investigate the effects of patch type (fixed factor), prey density (fixed factor) and sampling week (random factor) on clam mortality rate. All higher order interactions involving sampling week were also considered random factors. Due to the lack of synchronized sampling between the two sites, ANOVAs were run separately on each of the two site matrices (WEDI I, WEDI II). Cage data were not used in the initial analyses due to the high frequency of damaged cages from high winds, and thus mortality rates were initially compared between stockades and control patches. A separate analysis was run for sampling occasions where cages remained present from week-to-week ( $n=3$ ). All post-hoc analyses utilized the Bonferroni method of multiple comparisons. All statistical analyses were performed in XLSTAT 10 (Addinsoft, Inc.).

To examine large mobile invertebrates (teleosts, sharks and rays) abundance and verify consumption of hard clams, gillnets (150 m $\times$ 3 m; 15 cm stretch mesh) were deployed perpendicularly to the shoreline alongside manipulation matrices during each site visit. Stomachs were removed from all potential predatory fishes after individuals experienced an overdose of Tricaine methanesulfonate (MS-222). All prey items were identified to the lowest possible taxonomic level. For each prey item (within each species) we calculated percent frequency of occurrence:  $\%F_a = \frac{100 \times S_a}{S}$  where  $S_a$  is the number of stomachs containing food group  $a$ , and  $S$  is the total number of stomachs containing food (Hyslop, 1980).

### 3. Results

#### 3.1. Field enclosures

The field enclosure experiment found no effects of rays on ambient densities of haustoriid amphipod prey. Off Pelican Island sampling area in 2009, cownose ray densities were observed to decrease nearly 10-fold from the initial sampling date in late-February ( $t=-1$ ; Fig. 4), though rays were still observed foraging near enclosures for the remainder of the period. Ambient amphipod densities similarly dropped after the first sampling date and then remained consistent through the remainder of the study period (Fig. 4). Patch type did not significantly influence amphipod densities ( $F_{1,80}=0.112$ ;  $p=0.738$ ; Table 1) while sampling date ( $F_{4,80}=16.025$ ;  $p<0.0001$ ), block ( $F_{1,80}=6.431$ ;  $p<0.05$ ) and the interaction between sampling date and block ( $F_{2,60}=8.100$ ;  $p=0.001$ ) did (Table 1). Bonferroni pairwise comparisons found amphipod densities were significantly higher at the northern block (1179 individuals/m $^2$ ) than the southern block (450 individuals/m $^2$ ) on trial week 1 ( $p=0.005$ ), though they did not vary significantly between blocks on other dates.

#### 3.2. Field manipulation – open vs. stockade patches

No effect of ray exclusion was found when comparing clam mortality between open and stockade patches even during peak ray abundance. At WEDI I, no patch type or density effects were found among all four clam mortality parameters ( $p>0.05$ ), though trial week significantly influenced mortality rates across all treatments ( $p<0.0001$ ; Table 2A). Mortality rates were significantly higher during week 5 across all treatments, and coincided with a peak in cownose ray abundance (Fig. 5A). Similarly, at WEDI II, trial week was also found to be significant across all four parameters ( $p<0.005$ ), although it was found to significantly interact with patch and density effects for untethered and total clam mortality rates (Table 2). Patch type was significant for untethered clam mortality rate, though this was similarly influenced by both trial week and density. Bonferroni post-hoc analysis found that during trial week 2, untethered clam proportional mortality rate was significantly higher in open patches (0.131/d) than stockade patches (0.062/d) at low clam densities ( $p<0.0001$ ; Fig. 5B). Total clam proportional mortality rate was also highest in week 2 at open patches of low density (0.095/d), and was significantly higher than stockade patches of low density (0.031/d;  $p<0.0001$ ; Fig. 5B).

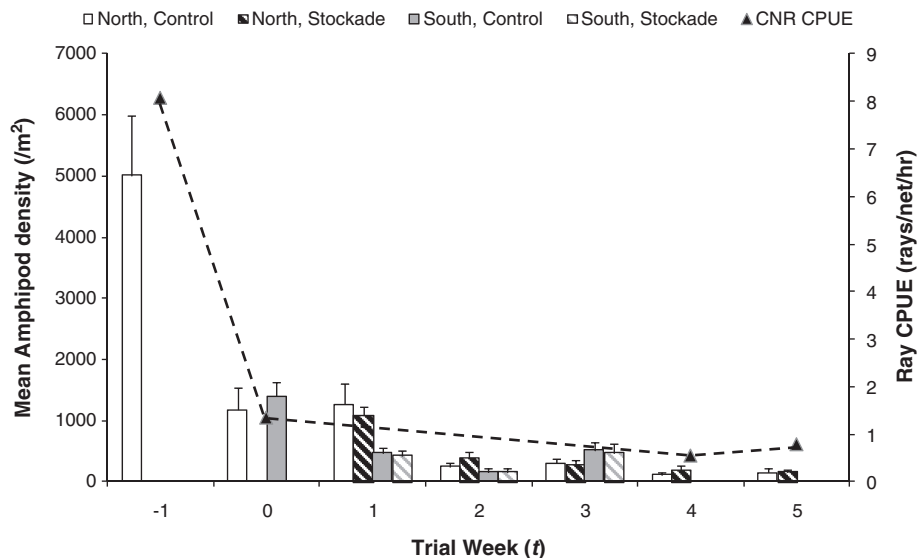


Fig. 4. Bar plot of amphipod densities, grouped by site (north vs. south) and patch type (open control vs. enclosure stockade). Cownose ray (CNR) CPUE is indicated on right axis.

**Table 1**  
Results from 3-way ANOVA on square-root transformed amphipod densities of spring 2009 exclusion-only experiment.

Source	Type	DF	Sum of squares	Mean squares	F	Pr > F
Date	Random	4	3356.387	839.097	16.025	<b>&lt;0.0001</b>
Block	Random	1	336.743	336.743	6.431	<b>0.013</b>
Patch type	Fixed	1	5.879	5.879	0.112	0.738
Date*block	Random	2	848.210	424.105	8.100	<b>0.001</b>
Date*patch type	Random	4	23.329	5.832	0.111	0.978
Block*patch type	Fixed	1	22.971	22.971	0.439	0.510
Date*block*patch type	Random	2	8.761	4.381	0.084	0.920
Error		80	4188.866	52.361		

Bold-faced values significant at  $p < 0.05$ .

**Table 2**  
Results from 3-way ANOVAs on multiple clam mortality variables. A – analysis of Site I mortality comparing stockade and open patches, B – analysis of Site II mortality comparing stockade and open patches, C – analysis of Site I clam mortality during weeks in which all patch types remained present from week to week (3, 5, and 8), D – analysis of Site II clam mortality during weeks in which all patch types remained present from week to week (3, 4, and 8). pTethMR = proportional tethered clam mortality rate; pUntethMR = proportional untethered clam mortality rate, pTotMR = proportional total clam mortality rate (tethered + untethered); pDiffMR = difference in mortality rates between tethered and untethered clams.

Source	Type	DF	pTethMR	pUntethMR	pTotMR	pDiffMR
<b>A)</b>						
Trial week	Random	6	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
Patch type	Fixed	1	0.106	0.614	0.095	0.291
Density	Fixed	1	0.388	0.300	0.184	0.882
Trial week*patch type	Random	6	0.973	0.236	0.614	0.934
Trial week*density	Random	6	0.443	0.462	0.164	0.735
Patch type*density	Fixed	1	0.476	0.208	0.925	0.211
Trial week*patch type*density	Random	6	0.268	0.594	0.222	0.564
Error		56				
<b>B)</b>						
Trial week	Random	6	<b>0.003</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
Patch type	Fixed	1	0.917	<b>0.025</b>	0.171	0.171
Density	Fixed	1	0.770	0.434	0.464	0.464
Trial week*patch type	Random	6	0.959	0.718	0.551	0.551
Trial week*density	Random	6	0.953	0.292	0.301	0.301
Patch type*density	Fixed	1	0.170	<b>0.002</b>	<b>0.004</b>	<b>0.004</b>
Trial week*patch type*density	Random	6	0.040	<b>0.000</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
Error		57				
<b>C)</b>						
Trial week	Random	2	<b>0.002</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.001</b>
Patch type	Fixed	2	<b>0.005</b>	<b>0.005</b>	<b>&lt;0.0001</b>	0.639
Density	Fixed	1	0.784	0.990	0.910	0.803
Trial week*patch type	Random	4	0.875	0.065	0.089	0.752
Trial week*density	Random	2	0.755	0.585	0.814	0.735
Patch type*density	Fixed	2	0.206	0.320	0.102	0.444
Trial week*patch type*density	Random	4	<b>0.031</b>	0.173	<b>0.009</b>	0.428
Error		35				
<b>D)</b>						
Trial week	Random	2	<b>&lt;0.0001</b>	<b>0.024</b>	<b>&lt;0.0001</b>	<b>0.031</b>
Patch type	Fixed	2	<b>0.002</b>	<b>0.005</b>	<b>0.002</b>	<b>0.002</b>
Density	Fixed	1	0.123	0.137	0.074	0.410
Trial week*patch type	Random	4	<b>0.001</b>	0.256	<b>0.040</b>	<b>0.015</b>
Trial week*density	Random	2	0.841	0.694	0.816	0.542
Patch type*density	Fixed	2	0.812	<b>0.002</b>	<b>0.012</b>	<b>0.004</b>
Trial week*patch type*density	Random	4	0.877	0.268	0.386	0.536
Error		36				

Bold-faced values are significant at  $p < 0.05$ .

3.3. Field manipulation – comparisons among all patches

Cage data were compared to other patch types (open, stockade) during weeks 3, 5 and 8 for WEDI I (Fig. 6A) and 3, 4 and 8 for WEDI II (Fig. 6B). Inclusion of cage data did not result in any significant effects of rays on clam mortality rates, however, it did highlight the potential for smaller predators to impact clam mortality during select sampling periods at both sites. At WEDI I, significant trial week and patch effects were found for both tethered and untethered clam mortality rates. Across patches, tethered clam mortality rate was significantly higher during weeks 8 (0.040/d) and 5 (0.040/d) than week 3 (0.014/d;  $p = 0.006$ ), though weeks 5 and 8 were not significantly different from one another ( $p = 0.998$ ). A significant patch type effect was also found at WEDI I ( $F_{2,25} = 6.296$ ;  $p = 0.005$ ) with tethered clam mortality rates significantly higher in open patches (0.043/d) than cage patches (0.014/d;  $p = 0.004$ ). However, tethered clam proportional mortality rates were not significantly different between stockade (0.034/d) and cage patches ( $p = 0.065$ ), or between stockade and open patches ( $p = 0.464$ ). During week 5, stockade (0.079/d) and open (0.075/d) patches of low clam densities were found to have significantly higher total clam mortality rates than cage patches (0.008;  $p < 0.0001$ ), though were not statistically different from one another (Fig. 6A).

At WEDI II, rays similarly had no effects on clam mortality. Significant trial week and patch effects were found across all variables, and interacted significantly with one another for all variables except untethered clam mortality rate. In general, mortality rates were highest during week 8. Although a three-way interaction effect was not found for total clam proportional mortality rates ( $p = 0.386$ ), high density stockade patch mortality rate (0.058/d) was still found to be significantly greater than mortality rates of cage patches of the same density (0.010/d;  $p < 0.0001$ ) on week 8 (Fig. 6B). Trial week and patch type were also observed to influence the difference between tethered and untethered clam mortality rates, where week 8 differences in stockade patches (0.021/d) were significantly higher than what was observed in week 8 cage patches ( $-0.023/d$ ;  $p = 0.042$ ).

Blue crabs appeared to select stockade patches over open patches as evidenced by significant differences between these treatments, though this depended on time. The presence of chipped hard clam shells (i.e., crab predation) was not detectable until week 4 of the experiment (Fig. 7), as indicated by the significant trial week effect on proportional chip rates ( $F_{7,153} = 23.586$ ;  $p < 0.0001$ ). A significant patch type effect was also found for chip rates, with proportional chip rates significantly higher in stockade patches (0.007/d) than open patches (0.003/d;  $p = 0.021$ ).

3.4. Potential predator abundance

Cownose rays were the most common and abundant mobile benthic predator captured next to manipulation plots. Cownose rays were first captured in week 3 when ambient water temperatures first exceeded 14 °C, and abundance peaked during week 5 when temperatures ranged between 17.3 and 18.8 °C. Ray abundance slowly declined during the latter part of the sampling period until no rays were observed in week 8 when temperatures exceeded 25 °C. Cownose ray disk width ranged from 50.0 to 98.6 cm (mean =  $78.7 \pm 1.7$  cm) and were thus too large to fully enter the stockades.

Cownose rays were observed moving into or near manipulation sites between weeks 4 and 8. Other large potential benthic predators sacrificed from gillnet surveys included Atlantic stingrays (*Dasyatis sabina*;  $n = 25$ ), bonnethead sharks (*Sphyrna tiburo*;  $n = 10$ ), southern stingrays (*Dasyatis americana*,  $n = 3$ ) and black drum (*Pogonias cromis*;  $n = 2$ ). Atlantic stingrays ranged from 19.0 to 34.0 cm disk width (mean =  $23.8 \pm 7.1$  cm), and thus may have entered stockades at smaller sizes. Large blue crabs ( $> 10$  cm carapace width) were

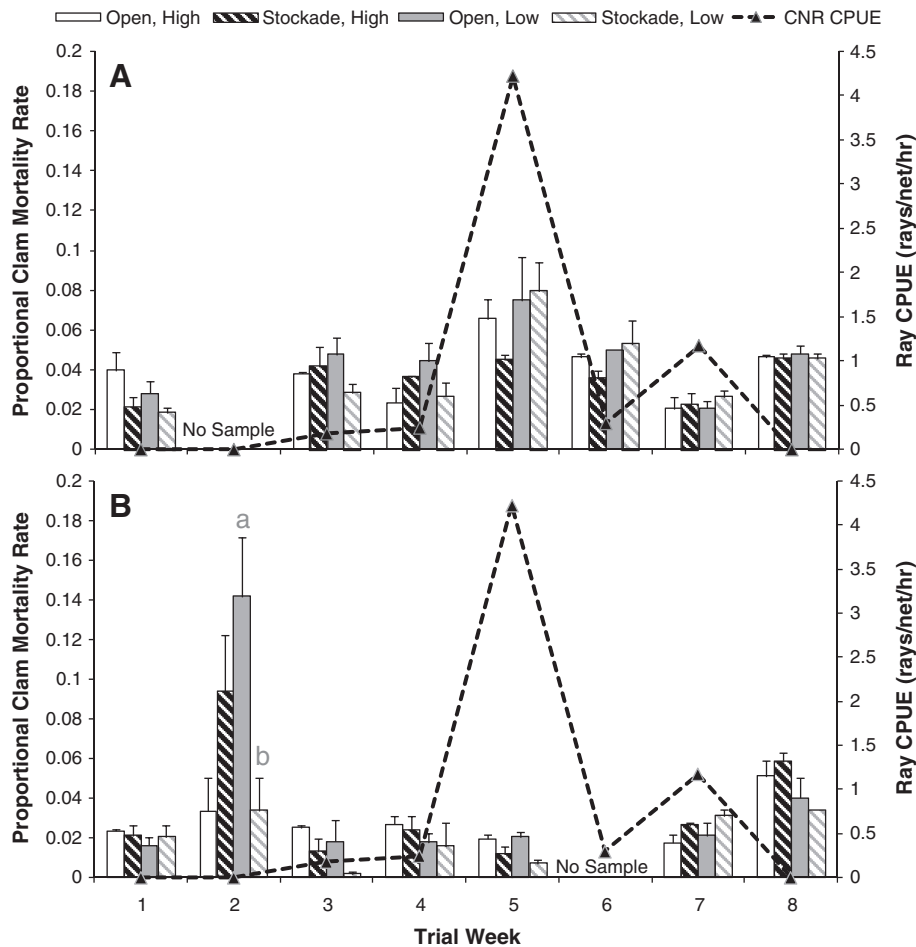


Fig. 5. Eight-week time series of stockade and open patch mortality rates at two sites, WEDI I (A) and WEDI II (B). Lowercase "a" and "b" denote statistically distinct groups.

commonly sighted consuming clams in manipulation patches during weekly excavations, particularly towards the end of the experimental period.

There was no evidence of hard clam consumption by any of the potential mobile fish predators (Table 3). Cownose rays ( $n=27$ ) sacrificed from manipulation sites mainly consumed haustorid amphipods and coquina clams (*Donax* sp.). The diet of Atlantic stingrays was similarly dominated by haustorid amphipods, but also included other small crustaceans such as pea crabs (*Pinnixa* sp.) and ghost shrimp (*Callinassa* sp.). Bonnethead sharks (mean =  $73.8 \pm 2.8$  cm FL) primarily consumed blue crab (*Callinectes sapidus*), though these sharks were only present during the last week of sampling. Southern stingrays were 45.9–57.9 cm DW (mean =  $50.5 \pm 3.5$  cm), but consumed *Callinassa* sp. and amphipods. Black drum captured from this region (70.5–76.2 cm Fork Length) were only observed to consume xanthid crabs.

## 4. Discussion

### 4.1. Impacts of rays on natural prey

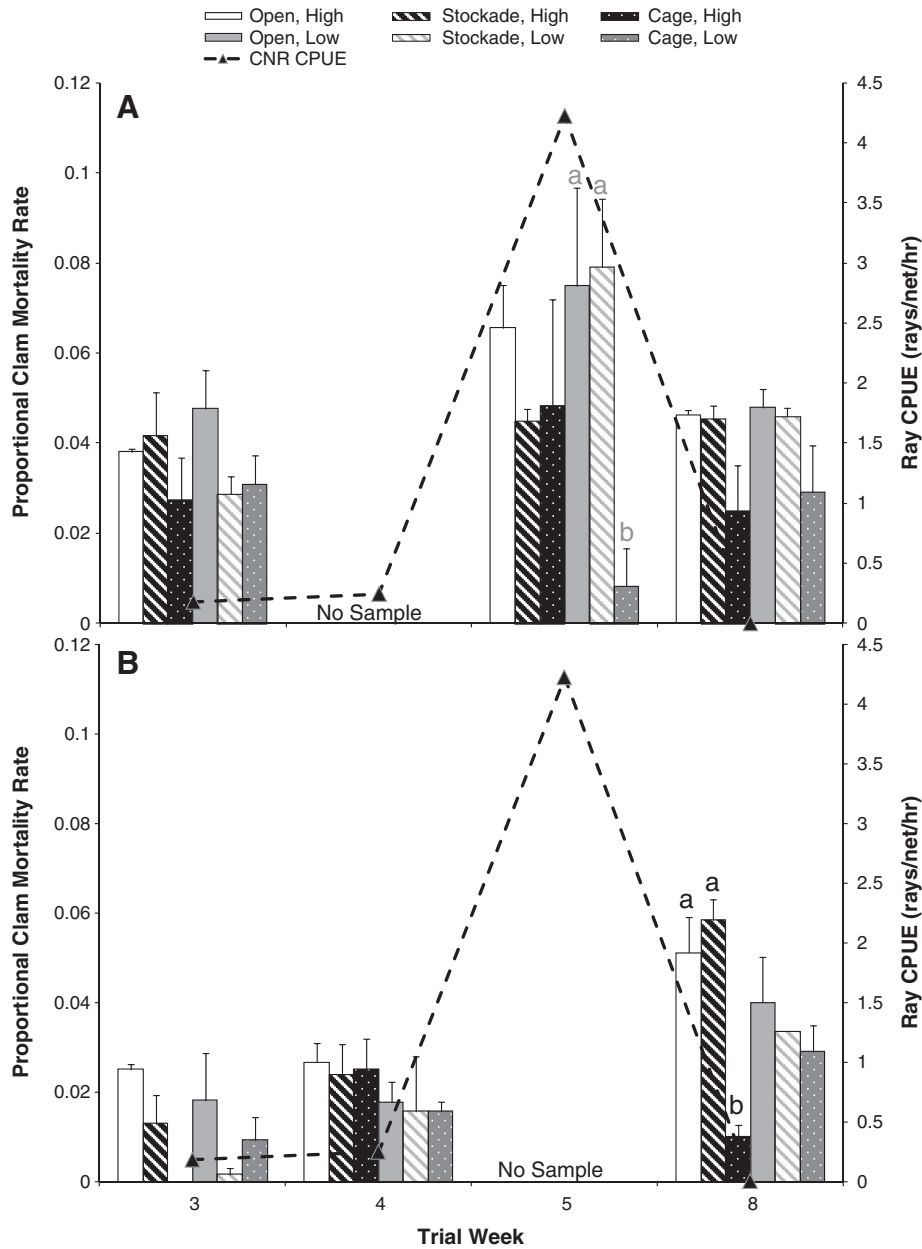
Support for the structuring role of mobile epibenthic predators (including fishes) on benthic prey is pervasive in the scientific literature (Gido, 2003; Micheli, 1997; Peterson, 1979; Quammen, 1982, 1984; Quijón and Snelgrove, 2005; Richards et al., 1999; Sanchez et al., 2006; Summerson and Peterson, 1984; Virtnstein, 1977; Wilson, 1991). In this study, cownose rays were not found to significantly impact densities of haustorid amphipods. Seasonal consumption of amphipods has been noted along Gulf of Mexico barrier islands in several

other fish species, including juvenile kingfish *Menticirrhus* sp. (McMichael and Ross, 1987), black drum *P. cromis* (Overstreet and Heard, 1982) and Florida pompano *Trachinotus carolinus* (Wheeler et al., 2002). Exceedingly high population levels of haustorid amphipods may swamp the effects of seasonal predation events by these migratory benthic predators. As such, impacts on prey may not be detectable from the exclusion of a single predator species.

Impacts of cownose rays on haustorid amphipod densities may not have been detectable due to the dynamic nature of sandflats. The sandflats along Pelican Island were largely unstable with periodic perturbations from wind and waves. This dynamic environment may have replenished episodic excavations (i.e. removals) made by foraging rays with transport of amphipods from surrounding areas into unprotected open patches. Haustorid amphipods, which can also utilize active transport mechanisms (Grant, 1980), may have moved freely between patches, which would have further diluted any predatory effects. Thus, further studies aimed at estimating ray foraging impacts should consider the mobility of the substrate and infauna at experimental patches, as this will likely influence interpretation of predator effects. Due to the small size of haustorid amphipods, it was not logistically feasible to tether individuals to experimental patches.

### 4.2. Impacts of rays on manipulated prey

Even during their peak abundance period, we found no significant foraging effects of cownose rays on hard clams. During the manipulative field experiments, there was only a single sampling week in which proportional clam mortality rate in open patches significantly exceeded proportional clam mortality rate in stockade patches. This



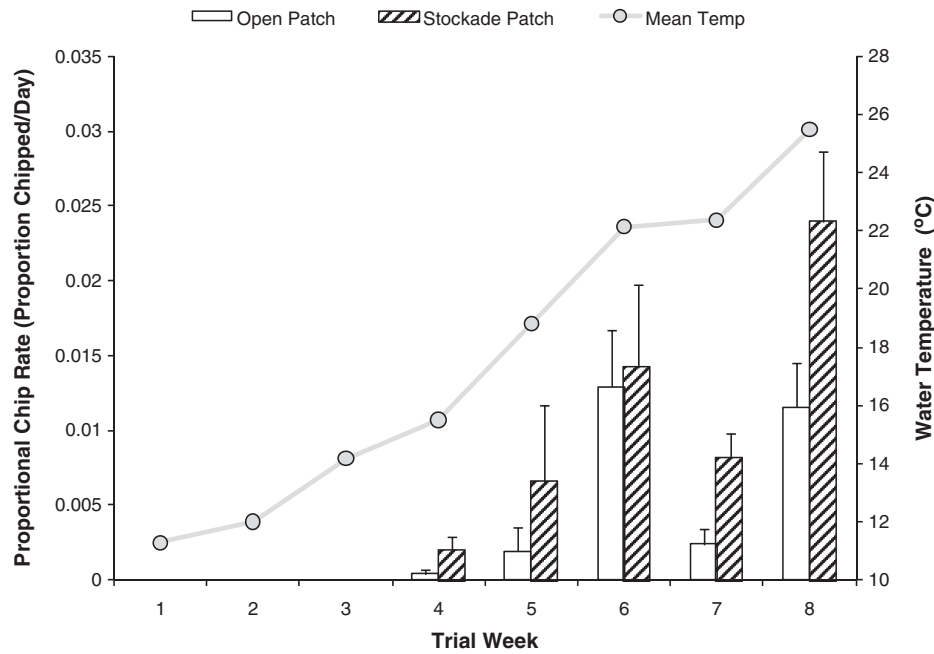
**Fig. 6.** Results from comparisons of total clam mortality among three patch types (open, stockade and cage) at two sites, WEDI I (A) and WEDI II (B). Lowercase letters “a” and “b” denote statistically distinct groups.

occurred during week 2 at WEDI II, but only at low clam density patches (Fig. 5B). Since no cownose rays were captured during trial week 2, and the same patch type effect did not hold for tethered clams, losses of clams were attributed to environmental conditions (e.g., high winds) rather than predation from rays. Thus, cownose rays had no detectable impacts on hard clams throughout the sampling period. The lack of significantly greater predation rates in open patches also suggests that, even if rays did consume a proportion of the clams in open patches, their consumption rates did not exceed those of smaller predators capable of accessing stockade patches.

**4.3. Density-dependent foraging**

Ambient prey density has been shown to affect the foraging behavior of various mobile epibenthic predators in marine communities. Increased preference for high density patches of infauna is

evident in relatively immobile gastropods (Moran, 1985; Peterson, 1982), swimming crabs (Boulding and Hay, 1984; Eggleston, 1990a, b; Lipcius and Hines, 1986; Mansour and Lipcius, 1991; Sponaugle and Lawton, 1990) and even highly mobile rays (Hines et al., 1997; Peterson et al., 2001). At our field manipulation study sites, the ambient bivalve community was dominated by coquinas (i.e., *Donax* spp.), with densities that were maximally 33.3 clams·m<sup>-2</sup>. However, overall mean density of coquinas (across all sites) was 2 clams·m<sup>-2</sup>, and was therefore generally lower than patches stocked with hard clams (10–40 clams·m<sup>-2</sup>). Despite having nearly an order of magnitude lower density than manipulated hard clams, almost 50% of the cownose rays analyzed still consumed coquinas, and all were shown to consume denser (1000 ind·m<sup>-2</sup>) haustoriid amphipods (Table 3). These results may suggest that rays preferred foraging on smaller, thinner-shelled clam species and abundant benthic crustaceans over patchily distributed hard clams. While the hard clams used in this study were within the gape and bite force limits of Chesapeake



**Fig. 7.** Bar plot of proportional chip rates of marked hard clams (bars correspond to primary y-axis, left) between two patch types (open and stockades). Ambient water temperature (line plots) is plotted on the secondary y-axis (right). Data are pooled from both sampling sites.

cownose rays (Fisher et al., 2011) and rank relatively high in terms of caloric value for bivalves (Beukema, 1997), the force required to open the *Mercenaria* spp. shells (13–18 mm, SD) was likely greater than that for smaller coquinas (<5 mm, SD) and haustoriid amphipods in this study and bay scallops consumed in previous work (Peterson et al., 2001). Thus, energetic reward and larger scale density may have played a stronger role than local density in cownose ray foraging behavior.

A study of the related New Zealand eagle ray *M. tenuicaudatus* showed that ray foraging rates did not dramatically increase until a threshold density of 176 clams·m<sup>-2</sup> was reached (Hines et al., 1997); roughly 4× more dense than manipulated hard clam densities in this study. Peterson et al. (2001), on the other hand, noted cownose rays would extinguish bay scallop patches off North Carolina above 10 scallops·m<sup>-2</sup>, though these were much larger in size than the clams used in this study. In Alabama, simultaneous benthic sampling with cownose ray gut content analysis suggests that cownose rays may feed on bivalves even when ambient densities are <10 clams·m<sup>-2</sup> (Ajemian and Powers, 2012). However, all experiments that document

a foraging response or an effect of rays have manipulated patches with prey that are natural to the predator's diet at the field sites. In our manipulation experiments off barrier islands, our goal was to mimic a seeding or bivalve introduction program. Thus, we used a bivalve species (*Mercenaria* sp.) native to Gulf of Mexico waters, but relatively uncommon at our sites. The lack of detectable predation by cownose rays on these manipulated patches of hard clam suggests that either rays were not cueing in on this new food source, or prey was not dense enough to elicit significant foraging responses. These results identify the potential risk of using artificial prey in manipulation experiments where predator effects are being investigated. In addition, these results may also suggest that rays may only have detrimental effects on shellfish when the seed species is locally dominant and naturally being consumed by the rays. We encourage further field experiments that manipulate densities of multiple prey species (natural and introduced) to better comprehend the effects of these large predators.

We used barrier island sandflat habitats to stage our experiments on cownose rays because the highest inshore densities of rays were observed in these environments off the Alabama coast. However,

**Table 3**  
Gut content analysis of potential predators captured in gillnets set alongside field manipulation matrices. Numbers for each prey item represent the frequency of occurrence in the diet.

		Potential predators				
		Cownose ray	Atlantic stingray	Bonnethead shark	Southern stingray	Black drum
		<i>Rhinoptera bonasus</i>	<i>Dasyatis sabina</i>	<i>Sphyrna tiburo</i>	<i>Dasyatis americana</i>	<i>Pogonias cromis</i>
N		27	25	10	3	2
Proportion empty		0.11	–	–	0.33	0.50
<i>Prey category</i>						
Bivalvia	<i>Donax</i> sp.	0.48	–	–	–	–
	Unidentified	0.11	–	–	–	–
Gastropoda	Unidentified	–	–	0.10	–	–
Crustacea	Haustoriidae	1.00	0.88	–	0.50	–
	Alpheidae	–	–	0.10	–	–
	<i>Squilla empusa</i>	–	–	0.10	–	–
	<i>Callinassa</i> sp.	–	0.44	0.20	1.00	–
	<i>Pinnixa</i> sp.	0.41	0.64	–	–	–
	<i>Callinectes sapidus</i>	–	–	0.80	–	–
	Xanthidae	–	–	–	–	1.00
Polychaeta	Unidentified	0.04	0.12	–	–	–



because structure in this habitat type was severely limiting, introducing stockades and cages to a naturally bare bottom may have artificially enhanced densities of small predators such as the blue crab. The added structure may have influenced hydrodynamics (Wilson, 1991) or provided a refuge for blue crabs evading mobile predatory fishes such as bonnethead sharks (Table 3). Preference for stockades by blue crabs was supported by the recovery of large chipped pieces of marked hard clams (Fig. 7), which occurred at significantly higher rates in stockade patches than open patches. The tethered minus untethered clam mortality rate was also significantly higher (i.e., more positive) in stockade patches, indicating a potential preference for tethered clams in these patches. While we do not envision these habitat preferences of blue crabs significantly reduced any effects of rays, the artifacts associated with introducing rebar stockades should be considered in future experimental manipulations, as these can alter the interpretation of predator impacts in environments with low ambient habitat complexity. Interestingly, predators are hypothesized to have greater impact on benthic prey communities in the absence of biogenic structure as these structures can inhibit foraging (Lipcius and Hines, 1986; Peterson, 1982; Sponaugle and Lawton, 1990). However, mobile predators (e.g., blue crab) are known to use structural habitats as migratory corridors, which can actually enhance foraging rates on bivalves (Micheli and Peterson, 1999). The results of these clam tethering experiments suggest that structure can enhance foraging rates of certain predators, particularly in soft-sediment communities.

#### 4.4. Spatial considerations in manipulative experiments

The lack of detectable impacts of cownose rays on manipulated bivalves in Alabama contrasts strongly with similar field experiments conducted off North Carolina. In North Carolina waters, schools of fall-migrating cownose rays have been identified as significant contributors to bay scallop mortality in seagrass beds of Back and Core Sounds, though these effects vary spatially and temporally (Fegley et al., 2009; Peterson et al., 2001). Significant effects of ray predation, however, may have been amplified by the physiography of the Cape Lookout system, where schools of rays are amassed through relatively restricted migratory corridors often <1 km in width. At the study sites off the west end of Dauphin Island in Mississippi Sound, such physiographic bottlenecks did not exist (Fig. 3). Thus, the predatory effects of cownose rays may be diffused by a more expansive migratory corridor along Alabama. Further studies should consider the role of physiography in aggregating populations of migratory predators like cownose rays.

Though cownose rays exhibit relatively high abundances in spring along the Alabama coast, rays can be captured and/or sighted in the region generally between March and November (Ajemian, 2011). Off southwest Florida, cownose rays are year-round residents (Collins et al., 2007b) and probably have limited impacts given their highly variable foraging (Collins et al., 2007a). The more stable environmental regime associated with these lower latitude (i.e., Gulf of Mexico) populations of rays may reduce the need for mass migratory behavior (Dingle and Drake, 2007), which has been otherwise demonstrated for populations of cownose along the temperate Atlantic coast (Blaylock, 1993; Grusha, 2005; Schwartz, 1990; Smith and Merriner, 1987). The lack of large-scale movements may also limit hyperphagia and thus account for the reduced impacts on benthic prey in this region.

#### 4.5. Conclusion

In summary, cownose rays did not influence natural or manipulated benthic prey along barrier island habitats of the northern Gulf of Mexico. The more resident nature and higher diet variability of Gulf of Mexico cownose rays may synergistically limit these impacts on

benthic resources. However, more studies of cownose ray foraging effects are needed in this region and across larger spatial and temporal scales. For example, synchronized exclusion and manipulation experiments over the latitudinal breadth of cownose rays could reveal important spatial and temporal patterns about their regulation of benthic communities. Additional studies should also consider the role of habitat type, particularly complexity, in estimating the predatory effects of these large mobile consumers. Finally, we recommend the development of novel exclusion techniques that do not introduce structural artifacts in low complexity habitats where rays naturally forage.

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