

LANDSCAPE ASPECTS OF OYSTER REEFS: FRAGMENTATION AND HABITAT
UTILIZATION

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ABSTRACT

The functional value of oyster reefs is recognized in many estuarine systems, with increasing interest in oyster reef restoration for ecological function rather than for fishery production. Reefs provide structure and refuge for juvenile fish and crustaceans, and may be a locus for predator foraging. However, reef morphology influences the relative value of refuge and forage functions, and reef utilization by benthic, epibenthic, and nektonic organisms. Reef fragmentation will increase the edge to interior ratio, and may enhance use by organisms that favor edge regions, or decrease use by species requiring more interior habitat. The influence of fragmentation was examined using created intertidal oyster reefs and natural reef patches in southeastern North Carolina. Created reef treatments included a uniform circular reef, a small fragmented reef, a large fragmented reef, and reference natural reef and mudflat areas. In addition, uniform and fragmented patch reefs in two nearby tidal creeks were also sampled. All treatments were sampled immediately after construction in June 2002, and then quarterly over two years, targeting infauna, epifauna, and nekton. Effects of fragmentation on infauna were variable, with a combination of positive and negative species-specific responses. However, preferential use of large fragmented reefs over small fragmented reefs was observed for *Lagodon rhomboides*, *Panopeus herbstii*, and *Geukensia demissa*, suggesting that the small fragmented reefs were most likely below the patch size threshold at which edge effects become beneficial. Implications are that oyster reef fragmentation may be an important factor for restoration managers to consider when designing reefs in which increased habitat utilization is a primary goal. Although a degree of fragmentation may be beneficial for some species, once

fragmentation leads to a loss of reef area below critical thresholds, degradation effects on habitat utilization could be great.

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INTRODUCTION

Habitat fragmentation is a process that involves the reduction of continuous areas of habitat to smaller patches; thereby resulting in loss of interior habitat and gains in edge habitat (Villard et al. 1999, Forman 1995). These changes are thought to influence the survival and persistence of various species in both terrestrial (e.g. Karieva 1987, Robinson et al. 1995) and marine (e.g. Irlandi 1994, Bell et al. 2001, Hovel 2003) environments. The responses of fauna to fragmentation will depend on whether species preferentially utilize the ecotone along patch edges, if they have fidelity to the interior sections of the habitat (Bender et al. 1998), or whether the interior areas present unique habitat attributes. The evaluation of edge as a distinct habitat type (depending on the species and the habitat) has become an important issue in conservation biology (e.g. Saunders et al. 1991), especially since fragmentation often results from or is allocated by anthropogenic activities. At the center of this controversial issue is the SLOSS (Single Large Or Several Small) debate. In terrestrial systems, the equilibrium theory of island biogeography (MacArthur and Wilson 1967) and the species-area relationship have been used extensively in reserve design. Both favor a single large patch over several small patches, other factors being equal. However, with the recent shift towards metapopulation theory and recognition of edge effects, the idea that a single large reserve is more advantageous to species' preservation has been questioned for certain species types and ecosystems. The generality of this edge effect, however, is hotly debated because results vary tremendously among different systems (Donovan et al. 1997). For example, Tschardtke et al. (2002) found that the percentage and abundance of polyphagous butterfly species were higher in smaller grassland fragments than in larger ones. Some species of songbirds, however, presented a negative correlation between the degree of fragmentation and bird density or fecundity (Donovan and Flather 2002).

Metapopulation concepts may be particularly applicable in marine systems, where dispersal mechanisms connect otherwise segregated populations or subpopulations (Eggleston 1999). The vast majority of fragmentation studies in the marine realm have focused on seagrass beds (e.g. McNeill and Fairweather 1993, Eggleston et al. 1998, Irlandi et al. 1999, Bell et al. 2001, Hovel and Lipcius 2002, Hovel 2003) and salt marshes (Peterson and Turner 1994, Zimmerman et al. 1984). Submerged aquatic vegetation (SAV) has long been recognized as a nursery habitat for many species, forming structural habitats in otherwise unstructured soft bottoms (Hovel 2003). Recent studies suggest that many small seagrass patches may increase the overall probability of encounter by larvae (e.g. blue crabs and grass shrimp) thereby increasing overall recruitment per unit area of habitat when compared to larger, uniform patches (Eggleston et al. 1998). There may be minimum area requirements but some degree of fragmentation may increase aspects of habitat function, suggesting a need to incorporate species-specific responses to habitat structure at multiple scales (Hovel 2003).

Another potentially important structural habitat in intertidal and subtidal temperate coastal systems is oyster reefs. Throughout its geographic range, the American oyster, *Crassostrea virginica*, provides subtidal and intertidal reef structure that supports a number of other organisms generally not found in surrounding soft-bottom habitats (Dame 1979, Zimmerman et al. 1989, Coen et al. 1999, Posey et al. 1999). Although *C. virginica* has long been recognized as an important economic estuarine species due to its direct fisheries value, the ecological value of the habitat oysters create and the influence of oysters on estuarine function is often overlooked (Lenihan and Peterson 1998, Meyer and Townsend 2000), and only recently have resource managers begun to look at oyster reefs as critical estuarine habitat. Oysters provide several critical ecosystem functions: reduced water turbidity through active filtration

(Newell 1988, Cressman et al. 2003, Nelson et al. 2004) and decreased water flow (Dame et al. 1984), stabilization of substrate, erosion reduction (Meyer et al. 1997), and provision of habitat for many other marine organisms (Coen et al. 1999).

Oysters provide three-dimensional structure and hard substrate in an otherwise 2-dimensional soft substrate environment. The shell matrix provides refuge for epifauna and a number of fish, crabs, shrimps, and other small crustaceans (Larsen 1985, Meyer 1994, Coen et al. 1999). Enhanced densities of grass shrimp, xanthid crabs, blue crabs, and benthic fishes have been associated with oyster reefs (Meyer and Townsend 2000) compared to open sand areas. Many commercially important species such as blue crabs, penaeid shrimp, striped bass, sheepshead, and flounder utilize intertidal oyster reefs as transients, coming and going with the tide (Posey et al. 1999, Coen et al. 1999). The presence of oyster reefs may also have significant impacts on adjacent soft substrate habitats, related to both concentration of epifauna and nekton and physical effects, though infaunal response to reefs have been variable (Larsen 1985, Powell 1994). Ecosystem functions of oyster reefs also vary with location, e.g. subtidal vs. intertidal reefs, or geographic location. Subtidal reefs can be inhabited during all periods of the tidal cycle, thus supporting more resident species such as blennies and gobies, which may be absent from intertidal reefs. However, oyster reefs are predominantly intertidal structures from southeastern North Carolina to Florida. Fishes inhabiting intertidal reefs must come and go with the tides, and resident epifauna inhabiting these reefs must be able to handle frequent exposure to air. In addition, edge effects may be more pronounced in intertidal reefs because of interactions between reef structure and flow.

However, over the past century fishery landings of *Crassostrea virginica* have declined by up to 90% in most of the Atlantic coastal states (MacKenzie 1996), especially the mid

Atlantic (Hargis and Haven 1988) and Pamlico Sound (Frankenberg 1995). The existence of multiple causes for the oyster's decline (disease, over-fishing, pollution, etc.) has complicated the management of this keystone species (Lenihan and Peterson 1998) and led to reduction of extensive reef systems in favor of smaller, fragmented reefs. Substantial state and federal resources have been allocated in attempts to restore the oyster fishery to pre-existing levels, including the creation of both subtidal and intertidal oyster reefs in many of the Atlantic coast's estuaries (Ortega and Sutherland 1992, Luckenbach et al. 1996, Coen et al. 1997).

The consequences of increasing the edge to interior ratio in oyster reef systems may be particularly important since the increased degradation of reefs has caused a shift towards smaller, fragmented reef patches, rather than the large, extensive reef systems of earlier times.

Considering the habitat value that oyster reefs provide, surprisingly little effort has been made towards investigating the potential effects of habitat fragmentation, with the exception of recent work by Eggleston et al. (1998) and Eggleston (1999) showing that macrofauna were more sensitive to patchiness in oyster shell than in seagrass or mixed habitats. The effects of reef fragmentation on adjacent soft substrate fauna have not been investigated. Fragmentation may alter between-habitat connections through changes in the proportion of critical edge and transitional habitat. Increased oyster patchiness would increase connectedness with adjacent soft sediment habitats, with possible increases in infauna related to organic enhancement or decreases related to off reef predation by reef associated fish and crabs (Posey and Ambrose 1994, Posey and Hines 1991).

Eggleston (1999) suggested that there is a parabolic relationship between habitat fragmentation and biodiversity, with the highest biodiversity occurring at intermediate levels of habitat fragmentation. If this is true, then oyster density and species diversity per unit area may

be higher in smaller patches above some minimum critical size. This may be similar to the “edge effect” seen in salt marshes, where transient fish and decapod species utilize only the first 3 m of marsh surface and do not penetrate into the flooded interior marsh surface (Peterson and Turner 1994).

In this study, a comparison of intertidal fragmented reefs of varying patch size and uniform reefs will be made, using both natural and created reefs, to assess the degree of habitat utilization by various species of benthic, epi-benthic, and nektonic organisms. The hypothesis that habitat fragmentation, but not habitat loss, will result in increased utilization of the oyster reef patches by other marine organisms will be tested.

METHODOLOGY

A combination of created reefs with defined edge to interior characteristics and natural reefs of varying edge morphology (patch size and proximity) were used to evaluate the habitat functions of intertidal oyster reefs. Whereas created reefs provide a controlled assessment of the local effects of fragmentation, natural reefs present a broader understanding of reef utilization as they incorporate other potential landscape factors, such as surrounding habitats and sediment variability.

As part of a larger study examining landscape relations for oyster reef function, construction of experimental oyster reefs was begun in March 2002 on an open mud flat located near the mouth of Hewletts Creek (Masonboro Sound) in southeastern North Carolina (Fig. 1). This area is over 75% intertidal and lacks any submerged aquatic vegetation. Naturally occurring reefs located near the area are intertidal, and consist of either patches or fringing reefs, many with a 3-5m patch diameter. The specific sites did not support reefs at the time of

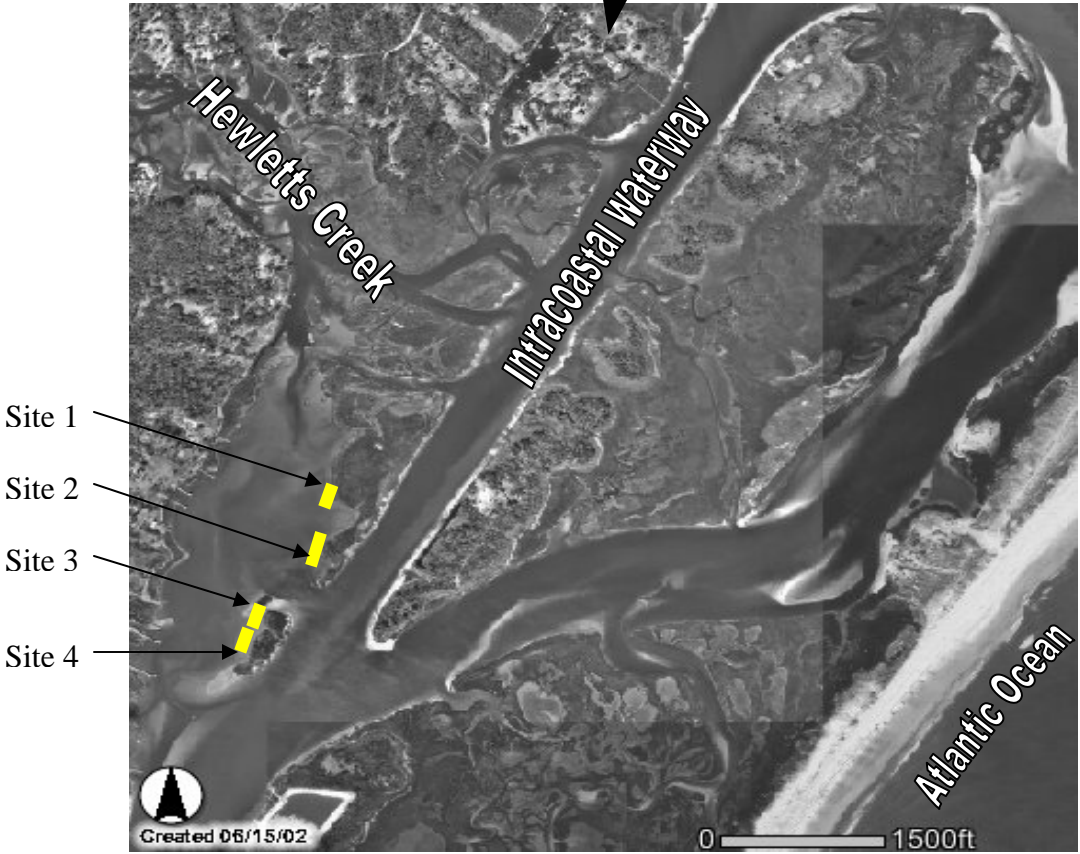
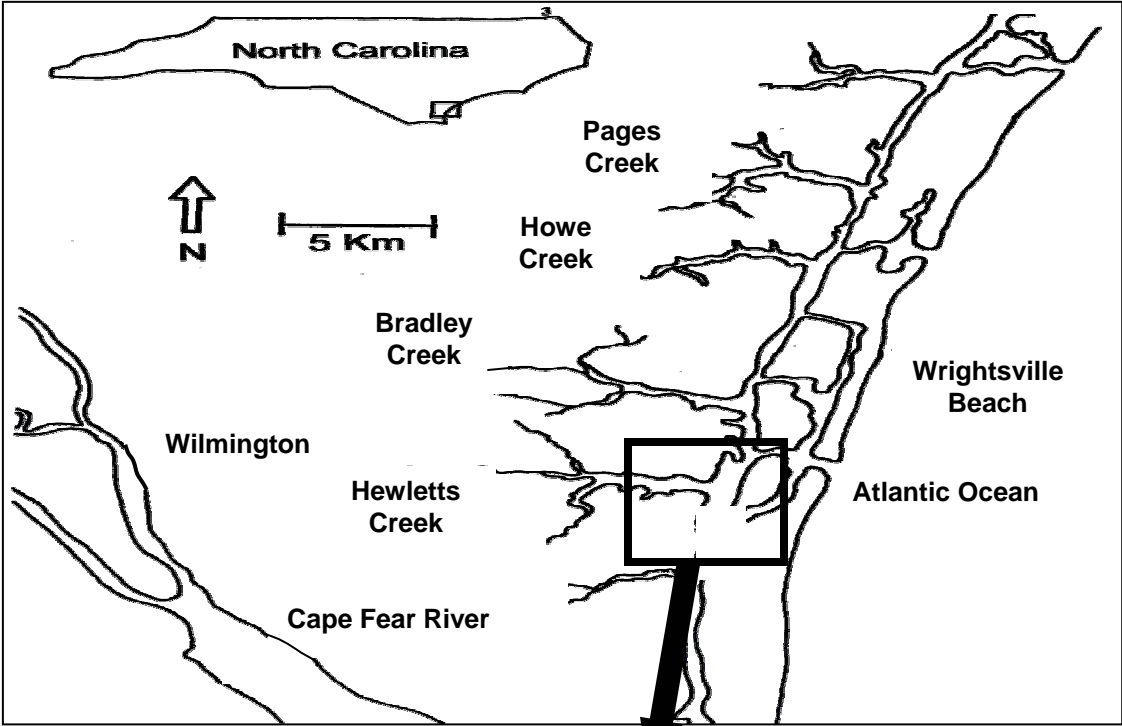


Figure 1: Study site: Southeastern North Carolina watersheds (top) and Hewletts Creek watershed and specific site locations (bottom, sites 1-4).

construction, but have been shown to support them when suitable substrate is made available (Alphin and Posey, unpublished data).

Four sites within the study area were chosen, all with similar topography, tidal range, salinity, and sediment characteristics. At each site, three reef treatments were constructed for this study of fragmentation effects using clean cultch purchased from a nearby oyster shucking facility, placing shell to form a 6" base. Live, single seed oysters obtained from a commercial aquaculture operation were then added in equal numbers to each reef. To add additional vertical complexity, which has been shown to be important for utilization by various organisms (Posey and Alphin, unpublished data 2004), culms (clusters of oysters growing in the vertical direction) were transferred from natural reefs located within nearby Hewletts Creek. All culms were defaunated prior to placing them on the created reefs so as to avoid the transfer of any resident organisms. Defaunation was accomplished by removing the culms from existing reefs and placing them on a nearby marsh, well above mean high tide level. After two weeks of exposure and following inspection for live organisms, the culms were then arranged on the created reefs.

Three treatments were constructed at each site: one uniform, circular reef (diameter of 3.6 m, area 10.18 m²), one small fragmented reef, and one large fragmented reef (Fig. 2A). This allowed for the examination of the importance of patch size to faunal utilization. Both fragmented treatments were constructed of four circular patches of equal area. This created open channels between patches and increased the amount of edge within the encompassed treatment area. The small fragmented reefs have an overall area (both shell and open space) equal to the shell coverage of the uniform treatments (encompassing circle around patches with a diameter of 3.6 m, area of 10.18 m²; each patch has a diameter of 1.28 m, area of 1.28 m²), while the larger fragmented reefs have an area of actual shell consistent with the uniform treatments

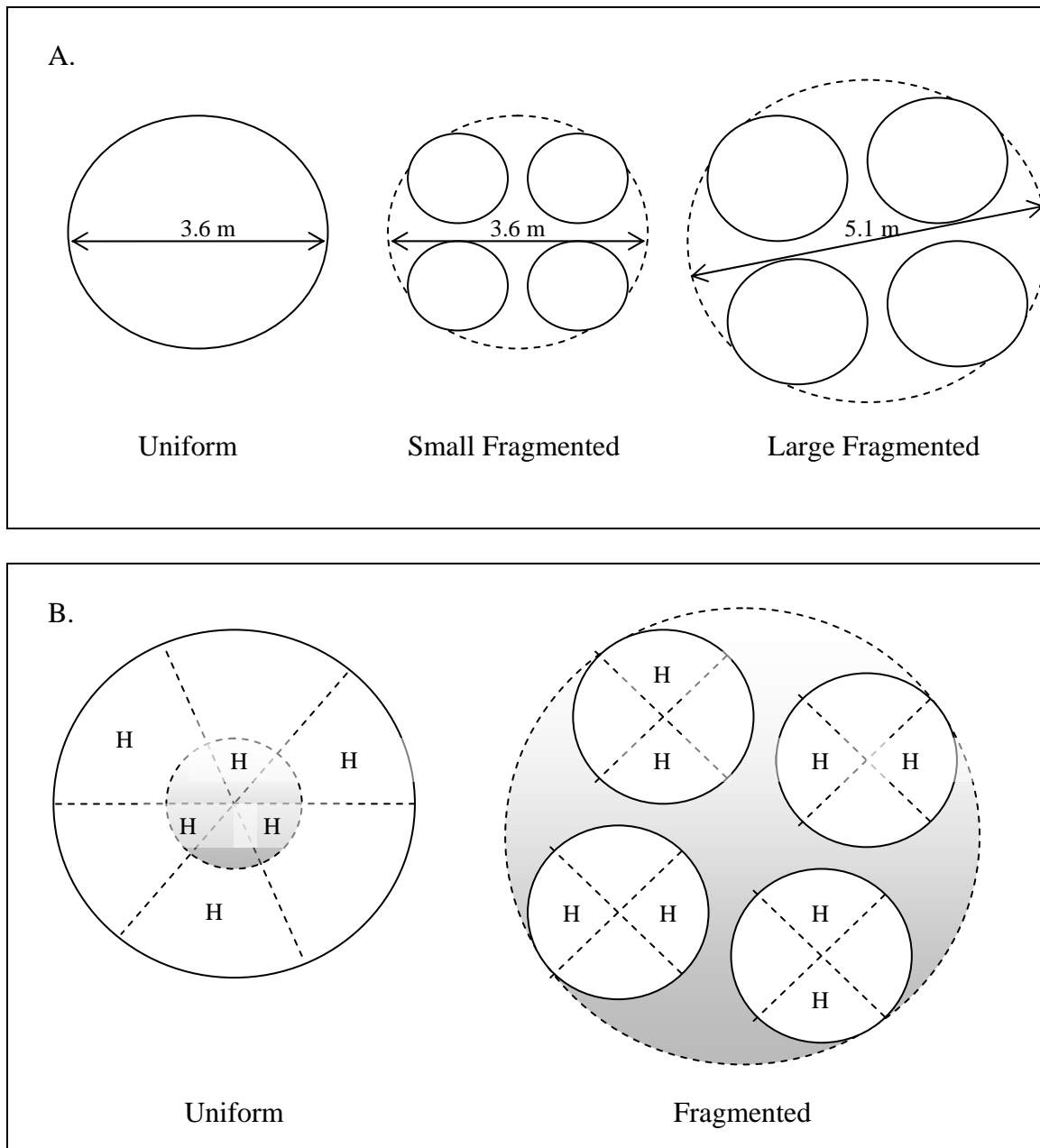


Figure 2. An illustration of reef parameters for the three treatments used in this study (A) and a schematic of locations of high and low relief areas within treatments (B). H indicates areas of high vertical relief consisting of culms. Those areas not containing an H do not contain culms, and are thus categorized as low vertical relief.

(encompassing circle around patches with a diameter of 5.1 m, area of 20.4 m²; each patch has a diameter of 1.8 m, area of 2.6 m²). This tested the relative importance of habitat loss in addition to increasing the edge to interior ratio. All treatments had vertical culms (high relief) on half of the patch area, and single oysters (low relief) on the other half, to increase surface heterogeneity of the reefs which may maximize faunal use (Figure 2B). All treatments were placed at least 10 m apart so as to reduce potential interactions among reef treatments.

For all sampling, each treatment (uniform, small fragmented, large fragmented) was sampled for all four sites (all treatments within a site being sampled on the same day), along with the open sand reference area at each site. Four nearby uniform natural reefs (referred to throughout this study as reference reefs) of similar size also were sampled. Beginning in spring 2003, natural uniform and fragmented reefs within Hewletts Creek and Pages Creek were sampled to evaluate the effects of natural reef fragmentation and whether the created reefs functioned similarly to natural reefs. The natural uniform and fragmented reefs were of similar size to the experimental reefs. To assess usage by different organisms (including nektonic, epibenthic, benthic, and infaunal species), several sampling methods were employed, including Breder traps, shell excavations, gill nets, and sediment cores.

Breder traps (Breder 1960) were used in order to assess the abundances of mobile epibenthic fauna, targeting juvenile fish and crustaceans. Traps were constructed of clear acrylic (31 cm X 15 cm X 16 cm), with wings of clear acrylic that guide the organisms into the trap. Three traps were placed within the low relief sections, abutting the high relief, securing the traps with tent stakes driven into the substrate. The orientation of the trap opening was varied with respect to tidal flow so as to maximize possible catches. For fragmented reefs, one trap was placed within the channel between the patches with the wing opening away from the marsh

towards the open mudflat. The remaining two traps were placed on two different patches of the fragmented reefs, opposite one another and parallel to the marsh (Figure 3). Traps placed on the uniform treatments mimicked this arrangement, with one trap placed along the edge rather than in a channel area (which does not exist for uniform reefs). Traps placed on the mudflat sites and natural reefs (both uniform and fragmented) had similar 90° orientation placements. Traps were placed on the treatments at low tide and left in place for two hours after flood tide submergence, a time period based on prior Breder trap studies (Innes 1992, Townsend 1991). Upon retrieval, organisms were identified and measured. Breder trap sampling for experimental reefs began in late June 2002 after the reefs had time to establish themselves following completion of construction in early May. Repeated sampling occurred in September-October 2002, March-April 2003, June-July 2003, and September-October 2003, for a total of 5 seasons of data collection. The natural reefs located in Hewletts and Pages Creeks were sampled beginning March-April of 2003, with seasonal sampling through September-October 2004. Natural reefs were chosen based on similar site characteristics and reef configurations to those of the experimental reefs. Breder trap sampling was not conducted in mid winter because of low nekton abundances at that time.

As a companion method to Breder traps, gill nets were used in order to assess use of the reefs by larger transient, nektonic species. Gill nets (5.5 m X 1.2 m) were placed across the reefs (parallel to shore), using graded mesh size panels of 1.27 cm, 2.54 cm, and 5.08 cm stretch mesh, similar in size to those used in previous studies (Harding and Mann 2001, Lenihan et al. 2001). One net was placed across each treatment at low tide and allowed to fish for two hours after flood tide submergence. Organisms caught were identified, measured, and released.

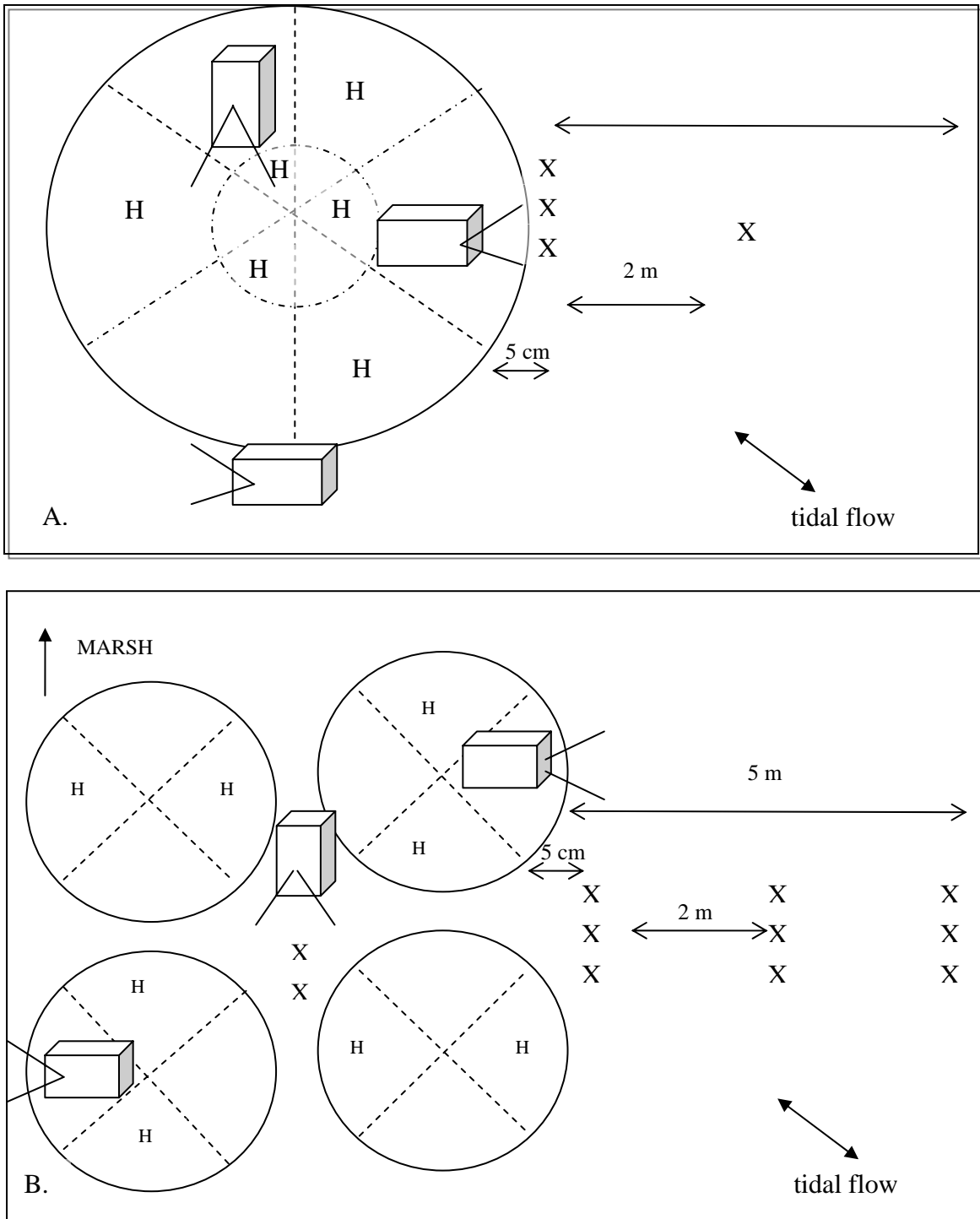


Figure 3. A diagram illustrating sampling configurations for both Breder traps and cores for uniform (A) and for fragmented (B) treatments. Trap placement is indicated by trap diagrams, core placement by “X”s. “H” indicates high relief areas. Orientation of traps away from the marsh reduced the chances of catching organisms coming off of the marsh. Cores located at 5m were only taken in July of 2003.

Sampling was conducted in June-July 2002, September-October 2002, March-April 2003, June-July 2003, and September-October 2003, resulting in 5 seasons of data collection. Natural reefs within the tidal creeks were not sampled due to time constraints. Due to low catches, gill net data was not statistically analyzed, and will only be discussed in a qualitative manner.

Excavations of all reefs were performed while reefs were exposed at low tide at each treatment using 20 cm X 20 cm quadrats in order to target benthic and epi-benthic invertebrates, such as crabs and errant polychaetes. Three excavations were performed for each treatment: one quadrat was placed in high relief, one in low relief, and a third placed half in high relief and half in low. After randomly establishing the location of the quadrat within each of the relief types, all shell located within the quadrat (including live oysters) was placed on a 2 mm sieve screen and washed clean of mud and debris. All retained organisms were identified and measured.

Excavation sampling began in June-July 2002, and was repeated quarterly through spring 2004, resulting in 8 seasons of data collection. Sampling of the natural reefs within the tidal creeks began in January 2003 and continued quarterly through January 2004, resulting in 5 seasons of data collection. Beginning January 2003, biomass of all organisms recovered during excavations was determined through standard ash-free-dry-weight techniques. With the exceptions of polychaetes and amphipods, which were identified to family, all organisms brought back were identified to species for biomass determination. Total biomass was determined for each species/family per treatment.

Infaunal cores (15 cm deep) were taken adjacent to all created reefs in July 2002 after reef establishment. For uniform treatments, three cores were taken at each reef's edge, and 2 m out from the reef (Figure 3). For fragmented treatments, similar locations were sampled with 2 additional cores taken within the channels between the patches. Three cores were also taken on

the mudflat reference area at each site. Sampling was repeated in July 2003, with three additional cores taken 5m out from each reef's edge in order to better assess potential distance from reef effects on infaunal abundances. Each core was preserved in 10% buffered formalin with 0.009 g/L rose bengal dye for at least 48 hours and then transferred to 50% isopropyl. Following identifications to the genus or species level, the biomass of each sample was obtained as described earlier and recorded for analysis.

Analysis of Variance (ANOVA) was used to compare the abundances and mean sizes of dominant species caught among different treatments for both Breder trap and excavation data, as well as for total biomass of dominant species caught in excavations. Species comprising >1% of total catches were considered dominant. Abundance data were log transformed to meet assumptions of homogeneity of variance (F-max test); mean size data did not need to be transferred to meet assumptions. Because of expected non-independence in sizes of fish within a trap, mean size was averaged per trap before analysis. A 3-way ANOVA was run using the SAS PROC GLM procedure with season, treatment, and site (blocked variable) as main effects, along with interactions for season and treatment. For natural reefs located in Hewletts and Pages Creeks, separate 2-way ANOVAs were run for each creek with treatment and season as main effects because of differences in reef topography and creek community structure. The Student-Newman-Keul (SNK) test was used to conduct pair-wise comparisons among treatments when ANOVA indicated a significant effect. Diversity of epifauna and nekton was calculated using the Shannon-Weiner Index. Both diversity and species richness were calculated on a per reef/per time basis.

For infaunal abundances and total infaunal biomass, a 4-way ANOVA (log-transformed) was run for reef treatments (uniform, small fragmented, large fragmented) using the SAS PROC

GLM procedures with year, treatment, distance from reef, and site (blocked variable) as main effects, including interactive effects among year, treatment, and distance. Because distance was not a factor for mudflat sites, a separate 3-way ANOVA with year, treatment, and site was run for reef and mudflat data regardless of distance. The Student-Newman-Keul (SNK) test was used to conduct comparisons among treatments when ANOVA indicated a significant effect. Diversity was calculated using the Shannon-Weiner Index. Both diversity and species richness were calculated on a per reef/per time basis.

RESULTS

Breder Trap Abundances

Abundances were grouped by season: spring, summer, and fall. Both summer and fall included two years of data, whereas spring data were collected in 2003 only. Overall dominant species (those comprising >1% of total catches) were *Clibanarius vittatus* (striped hermit crab), *Eucinostomus lefroyi* (mottled mojarra), *Fundulus heteroclitus* (mummichog), *Ilyanassa obsoleta* (mud snail), *Lagodon rhomboides* (pinfish), *Leiostomus xanthurus* (spot), *Micropogonias undulatus* (croaker), *Mugil cephalus* (striped mullet), *Palaemonetes vulgaris* (grass shrimp), *Paralichthys dentatus* (summer flounder), *Penaeus aztecus* (brown shrimp), and an unidentified larval fish. Of these, pinfish (*Lagodon rhomboides*) mummichogs (*Fundulus heteroclitus*), and spot (*Leiostomus xanthurus*) were by far the most common species caught, comprising 98% of total catches during summer sampling periods.

Mean total abundances on created reefs (Table 1) differed by season, with highest

catches in spring and lowest in fall ($F=30.82$, $p=0.001$). Although there was a small season-treatment interaction ($F=2.65$, $p=0.02$), treatment alone was not significant ($F=0.29$, $p=0.83$), nor did analysis of treatment by season indicate a significant effect. There were also no differences in mean total abundances between sites ($F=1.14$, $p=0.34$).

Lagodon rhomboides dominated catches during all seasons, with higher abundances in spring and lowest in fall ($F=30.92$, $p=0.0001$). An interaction occurred between treatment and season ($F=2.60$, $p=0.026$), and a season by season comparison of treatments (Table 2) revealed a marginally significant difference between treatments during spring ($F=3.36$, $p=0.06$), as well as a treatment effect for summer ($F=3.62$, $p=0.027$). There was no significant difference among treatments in fall, reflecting low numbers at this time. During spring, pinfish were most common on the open mud flat and least on the large fragmented and natural reef treatments (Figure 4). Summer patterns contrasted with spring, with significantly higher abundances on the large fragmented and uniform treatments.

The only other significant treatment effect occurred with the mud snail *Ilyanassa obsoleta*, which was more common on the uniform reef treatment during spring ($F=2.85$, $p=0.044$). There was also a treatment-season interaction ($F=2.28$, $p=0.047$).

Seasonal differences in abundance (Table 1) were also observed for *Fundulus heteroclitus* ($F=8.84$, $p=0.0004$), *Leiostomus xanthurus* ($F=23.7$, $p=0.0001$), and *Micropogonias undulatus* ($F=0.73$, $p=0.0001$). *Fundulus heteroclitus* was more common during spring and summer than in fall (see Figure 4). *Leiostomus xanthurus* abundances were highest during spring, while croaker (*Micropogonias undulatus*), were only caught during spring. Although not significant, there was a general trend among treatments for *Fundulus heteroclitus*, *Leiostomus xanthurus*, and *Micropogonias undulatus* during spring and fall, and for pinfish during summer,

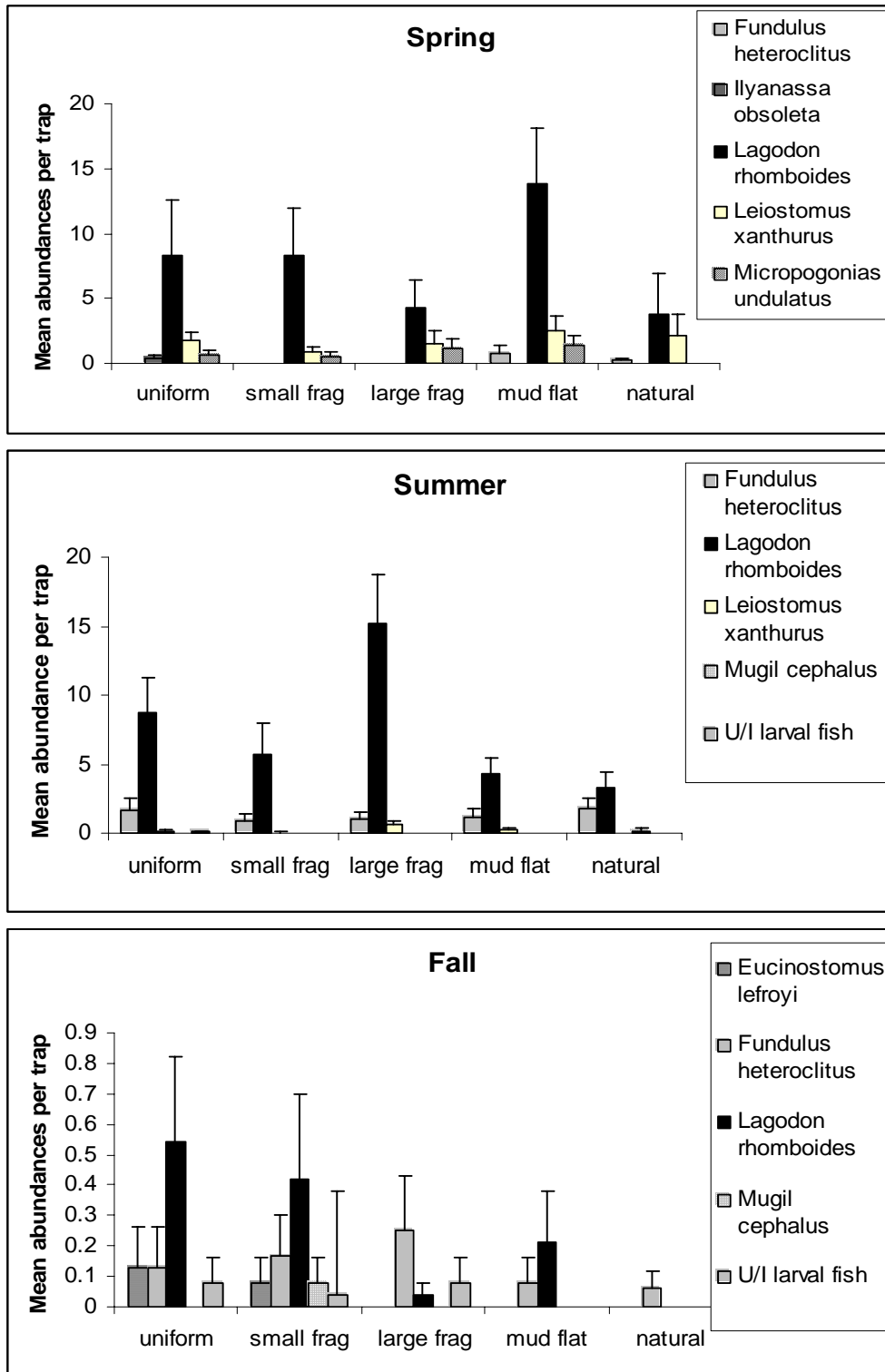
Table 1. 3-way ANOVA results for the fish community sampled with Breder traps from the experimental and reference reefs. Shown are F-values and (p-values). Values with asterisks indicate a significant relationship ($p < 0.05$). Where significant effects are present, SNK rankings are shown in decreasing order, with treatments differing indicated with different superscript letters. UN=uniform, FS=small fragmented, FL= large fragmented, MD=mudflat, SPR=spring, SUM=summer, and FAL=fall.

Species	Treatment	Season	Treatment*Season	Site
<i>Clibanarius vittatus</i>	0.83 (0.481)	2.45 (0.094)	1.00 (0.434)	1.35 (0.272)
<i>Eucinostomus lefroyi</i>	0.13 (0.733)	1.50 (0.270)	0.51 (0.796)	2.00 (0.122)
<i>Fundulus heteroclitus</i>	0.25 (0.865)	8.84* (0.0004)* SUM ^a , SPR ^b , FAL ^b	0.71 (0.646)	3.93* (0.012)*
<i>Ilyanassa obsoleta</i>	2.85* (0.044)* UN ^a , FL ^a , FS ^a , MD ^a	2.28 (0.110)	2.28* (0.047)*	1.14 (0.340)
<i>Lagodon rhomboides</i>	0.42 (0.743)	30.92* (0.0001)* SUM ^a , SPR ^a , FAL ^b	2.60* (0.026)*	2.21 (0.095)
<i>Leiostomus xanthurus</i>	0.89 (0.449)	23.70* (0.0001)* SPR ^a , SUM ^b , FAL ^b	0.84 (0.545)	1.09 (0.359)
<i>Micropogonias undulatus</i>	0.73 (0.449)	19.23* (0.0001)* SPR ^a , FAL ^b , SUM ^b	0.59 (0.740)	4.16* (0.009)*
<i>Mugil cephalus</i>	0.61 (0.613)	0.73 (0.487)	0.73 (0.629)	0.97 (0.412)
<i>Palaeomonetes vulgaris</i>	0.61 (0.613)	0.73 (0.487)	0.73 (0.629)	0.97 (0.412)
<i>Paralichthys dentatus</i>	1.05 (0.378)	0.55 (0.579)	1.85 (0.102)	1.03 (0.385)
<i>Penaeus aztecus</i>	1.07 (0.368)	0.58 (0.562)	0.45 (0.846)	0.20 (0.896)
U/I larval fish	0.53 (0.661)	1.86 (0.165)	0.75 (0.614)	0.51 (0.676)
Mean total abundance	0.29 (0.831)	30.82* (0.0001)* SUM ^a , SPR ^a , FAL ^b	2.65* (0.023)*	1.14 (0.340)

Table 2. By-season treatment effects for pinfish (*Lagodon rhomboides*). Shown are F-values and (p-values). Values with asterisks indicate a significant relationship ($p < 0.05$). When significant effects are present, SNK rankings are shown in decreasing order, with treatments differing indicated with different superscript letters. UN=uniform, FS=small fragmented, FL= large fragmented, and MD=mudflat.

Season	Treatment	Site
Spring	3.37 (0.068)	26.86* (0.0001)*
Summer	3.62* (0.027)* FL ^a , UN ^a , MD ^a , FS ^b	0.52 (0.674)
Fall	1.23 (0.320)	0.29 (0.833)

Figure 4. Mean abundances (+ SE) of organisms caught in Breder traps during spring, summer, and fall sampling. Each number represents the mean number of organisms per trap for all four sites.



in which abundances were higher on the large fragmented treatments relative to the small fragmented treatments, with intermediate abundances on uniform reefs. Differences among sites were present for *Fundulus heteroclitus* (Table 1, $F=3.93$, $p=0.012$) and *Micropogonias undulatus* ($F=4.16$, $p=0.009$).

Abundances of nekton caught in Breder traps for natural reefs in Hewletts and Pages Creeks were much lower than those of the created and reference reefs. Dominant species were *Fundulus heteroclitus*, *Lagodon rhomboides*, *Leiostomus xanthurus*, and *Penaeus aztecus*. There were no significant treatment effects in either creek (Table 3), although seasonal differences for *Lagodon rhomboides* ($F=5.65$, $p=0.030$) and mean total abundance ($F=17.28$, $p=0.001$) were observed in Hewletts Creek. Seasonal patterns for pinfish within Hewletts Creek were similar to those of the created reefs, with highest abundances observed in spring (Figure 5). There were no significant seasonal differences for natural reefs in Pages Creek, as catches were extremely low.

Total Length of Fish Caught in Breder Traps

The mean total length of *Fundulus heteroclitus* caught in Breder traps among created reefs showed significant effects for treatment (Table 4), with larger fish caught in small fragmented treatments compared to mud flat or large fragmented treatments (Figure 6, $F=4.21$, $p=0.023$). Mummichogs also exhibited effects of season ($F=12.05$, $p=0.0006$), with larger fish caught in summer than fall. There was a slight treatment-season interaction ($F=3.04$, $p=0.041$). Site differences were not significant for *Fundulus heteroclitus* size. The total length of *Lagodon rhomboides* caught in Breder traps differed only with season, with largest fish caught in fall and smallest fish caught in spring ($F=85.09$, $p=0.0001$, Figure 7). Season was also highly significant for the total length of *Leiostomus xanthurus* ($F=141.46$, $p=0.0001$), with mean length during

Table 3. 2-way ANOVA results for the fish community on natural reefs in Hewletts and Pages Creeks collected using Breder traps. Shown are F-values and (p-values) with significant differences indicated by an asterisk. When significant effects are present, SNK rankings are shown in decreasing order. SPR=spring, SUM=summer, and FAL=fall.

Species	Treatment	Season
Hewletts Creek		
<i>Fundulus heteroclitus</i>	0.43 (0.533)	2.34 (0.159)
<i>Lagodon rhomboides</i>	0.08 (0.788)	5.65* (0.030)* SPR ^a , FAL ^b , SUM ^b
<i>Leiostomus xanthurus</i>	0.25 (0.631)	2.25 (0.168)
<i>Penaeus aztecus</i>	1.00 (0.347)	1.00 (0.410)
Mean total abundance	0.67 (0.272)	17.28* (0.001)* SPR ^a , FAL ^b , SUM ^b
Pages Creek		
<i>Fundulus heteroclitus</i>	0.34 (0.574)	1.76 (0.232)
<i>Lagodon rhomboides</i>	2.74 (0.136)	3.54 (0.079)
Mean total abundance	1.39 (0.272)	2.97 (0.109)

Figure 5. Mean abundances (+ SE) of organisms caught in Breder traps for uniform and fragmented natural reefs in Hewletts and Pages Creeks during spring, summer, and fall sampling. HC= Hewletts Creek, PC=Pages Creek.

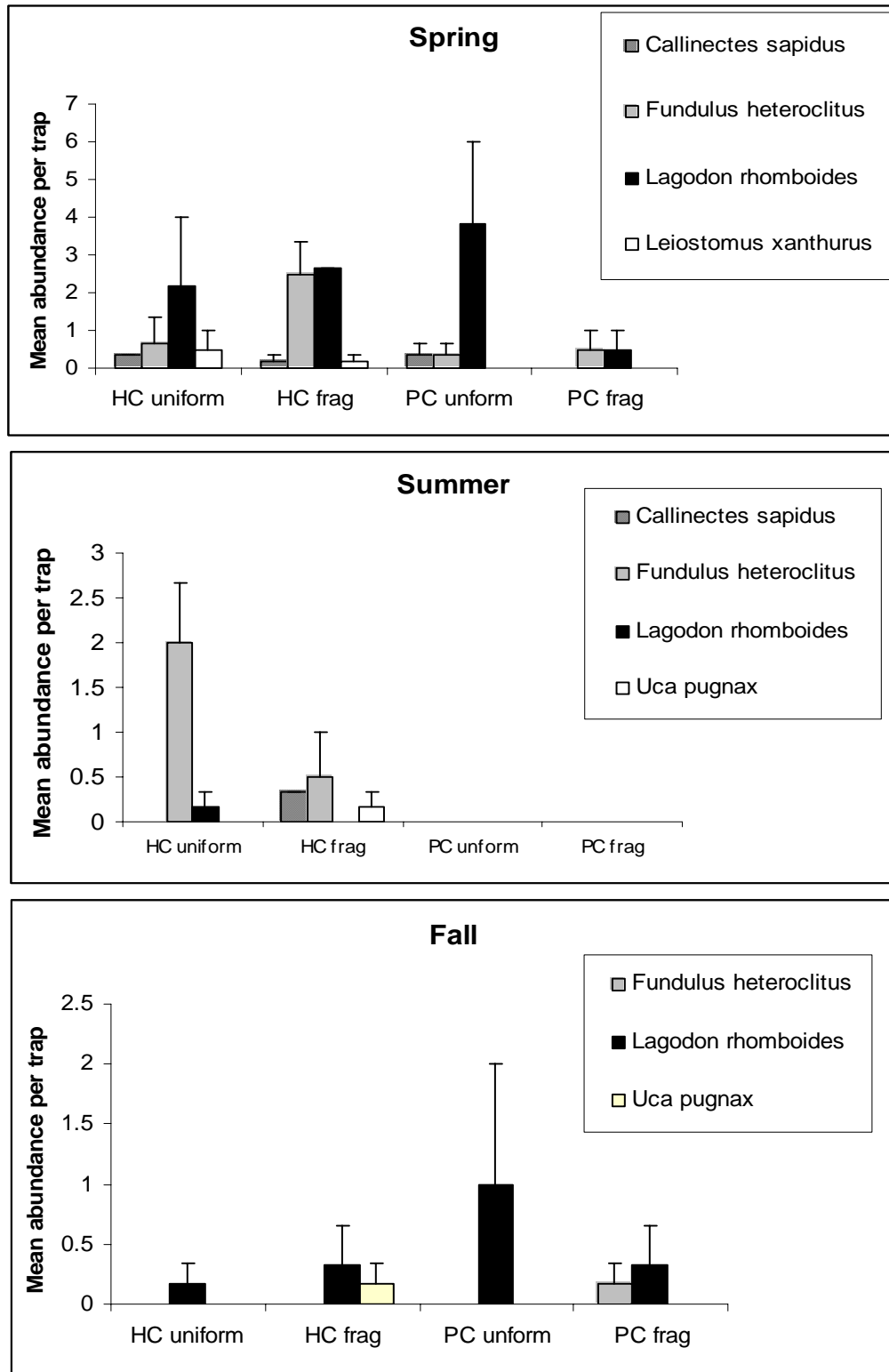


Table 4. ANOVA results for mean total length of dominant species caught in Breder traps. Natural reefs in Hewletts and Pages Creeks were run separately by creek using 2-way ANOVAs. Shown are F-values and (p-values) with significant differences indicated by an asterisk. When significant effects are present, SNK rankings are shown in decreasing order, with treatments differing indicated with different superscript letters. UN=uniform, FS=small fragmented, FL=large fragmented, MD=mudflat, NA= natural, SPR=spring, SUM=summer, and FAL=fall.

Species	Treatment	Season	Treatment*Season	Site
Experimental Set				
<i>Fundulus heteroclitus</i>	4.21* (0.023)*	12.05* (0.0006)*	3.04* (0.041)*	0.75 (0.620)
	FS ^a , NA ^a , UN ^a , FL ^a , MD ^a	SUM ^a , SPR ^a , FAL ^b		
<i>Lagodon rhomboides</i>	1.83 (0.157)	85.09* (0.0001)*	1.56 (0.175)	0.83 (0.551)
		FAL ^a , SUM ^b , SPR ^c		
<i>Leiostomus xanthurus</i>	2.24 (0.133)	141.46* (0.0001)*	0.92 (0.460)	2.88* (0.052)*
		SUM ^a , SPR ^b , FAL ^c		
Hewletts Creek				
<i>Lagodon rhomboides</i>	2.50 (0.212)	9.38* (0.051)*	N/A	N/A
		FAL ^a , SUM ^a , SPR ^a		
Pages Creek				
<i>Lagodon rhomboides</i>	0.01 (0.916)	104.23* (0.010)*	N/A	N/A
		FAL ^a , SPR ^b , SUM ^c		

Figure 6. Mean total lengths (+ SE) for *Fundulus heteroclitus* caught in Breder traps during all sampling periods for experimental reefs. The numbers over the bars indicate the number of traps from which mean total lengths were calculated.

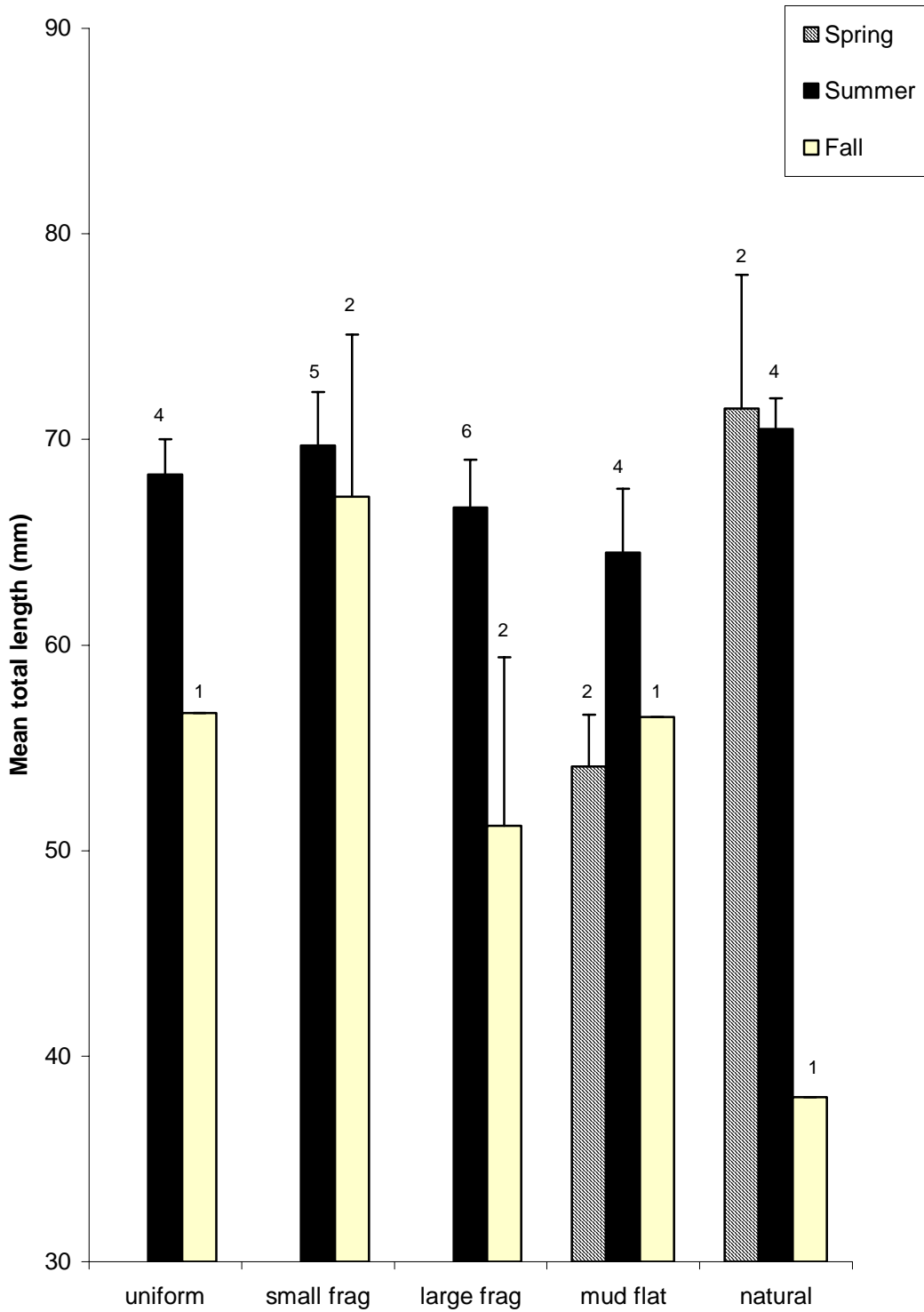
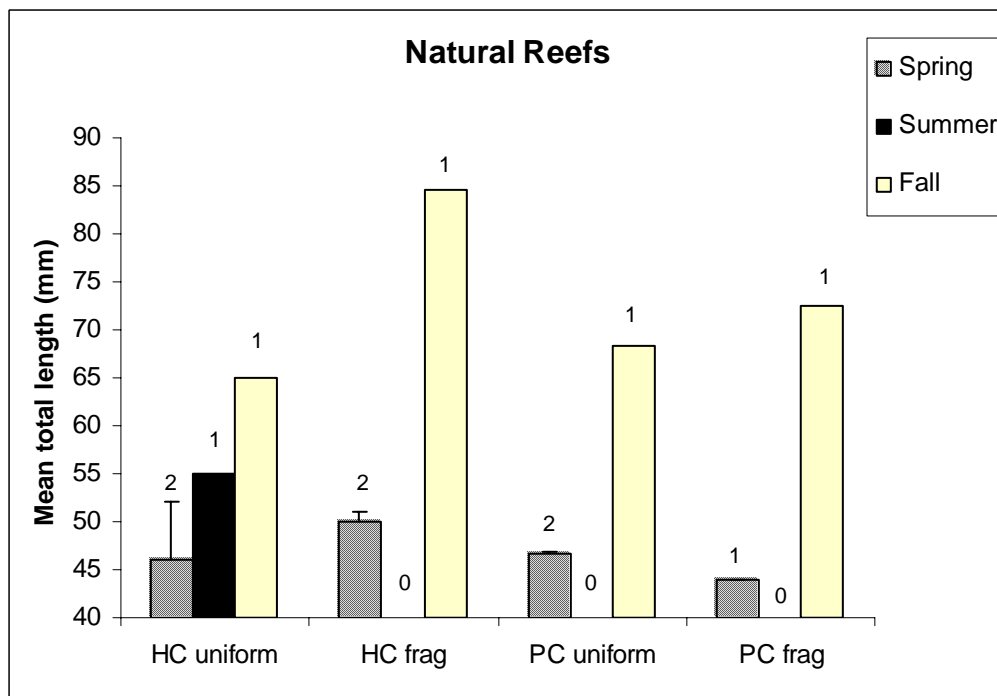
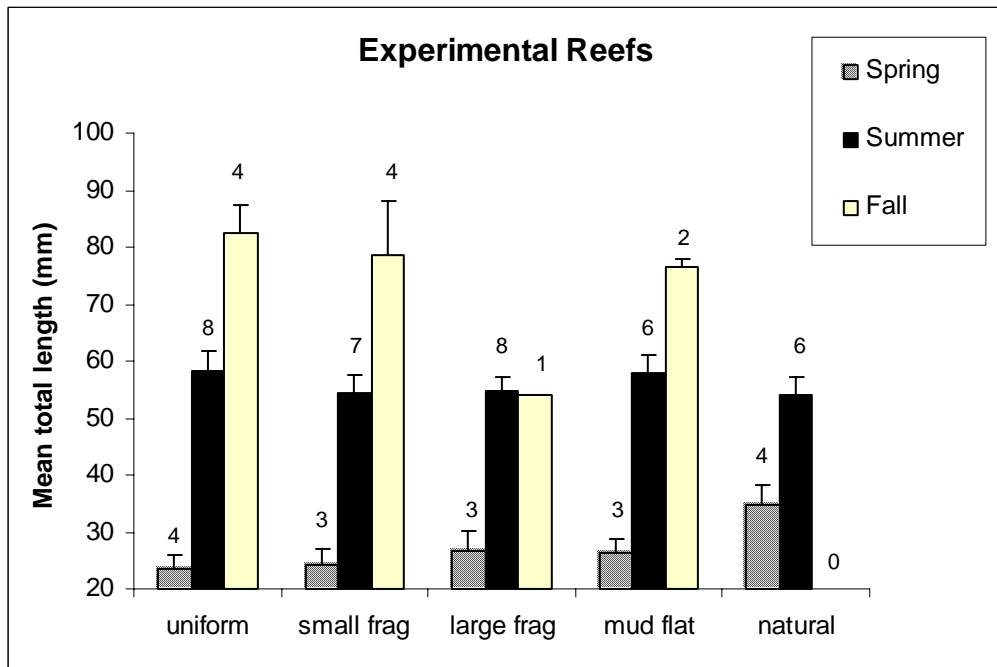


Figure 7. Mean total lengths (+ SE) for *Lagodon rhomboides* caught in Breder traps during all sampling periods. The numbers over the bars indicate the number of traps from which mean total lengths were calculated.



spring less than that of summer (Figure 8). Spot also showed a marginal site effect ($F=2.88$, $P=0.052$).

Within the tidal creeks, catches were sufficient to evaluate size differences only for *Lagodon rhomboides* (Figure 7). Treatment had no effect on TL in either creek, but season differences occurred in both creeks (Hewletts Creek: $F=9.38$, $p=0.051$, Pages Creek $F=104.23$, $p=0.010$). Largest fish were caught during fall and smallest during spring.

Diversity and Species Richness from Breder Traps

Diversity, as calculated by the Shannon-Weiner Index, for the experimental reefs (all created reef treatments, the mud flat, and reference reefs) was highest during spring (Figure 9). During spring and summer, highest diversity was seen on reference reefs and small fragmented reefs, while fall showed higher diversity on created reefs than on natural reefs. For natural reefs within the tidal creeks, diversity was highest during spring for Hewletts Creek and fall for Pages Creek. For both, diversity was lowest during summer.

Species richness was also generally highest during spring (Figure 10), with lowest species richness in fall. During spring and fall, highest species richness was found on small fragmented treatments, whereas the large fragmented treatments exhibited higher values during summer.

Gill Net Abundances

Abundances of nekton caught in gill nets were extremely low throughout the study, thus results will only be discussed qualitatively. Summer 2002 catches were near 0. In the following fall, catches were dominated by *Leiostomus xanthurus*, *Lagodon rhomboides*, and *Eucinostomus*

Figure 8. Mean total lengths (+ SE) for *Leiostomus xanthurus* caught in Breder traps during all sampling periods for experimental reefs. The numbers over the bars indicate the number of traps from which mean total lengths were calculated.

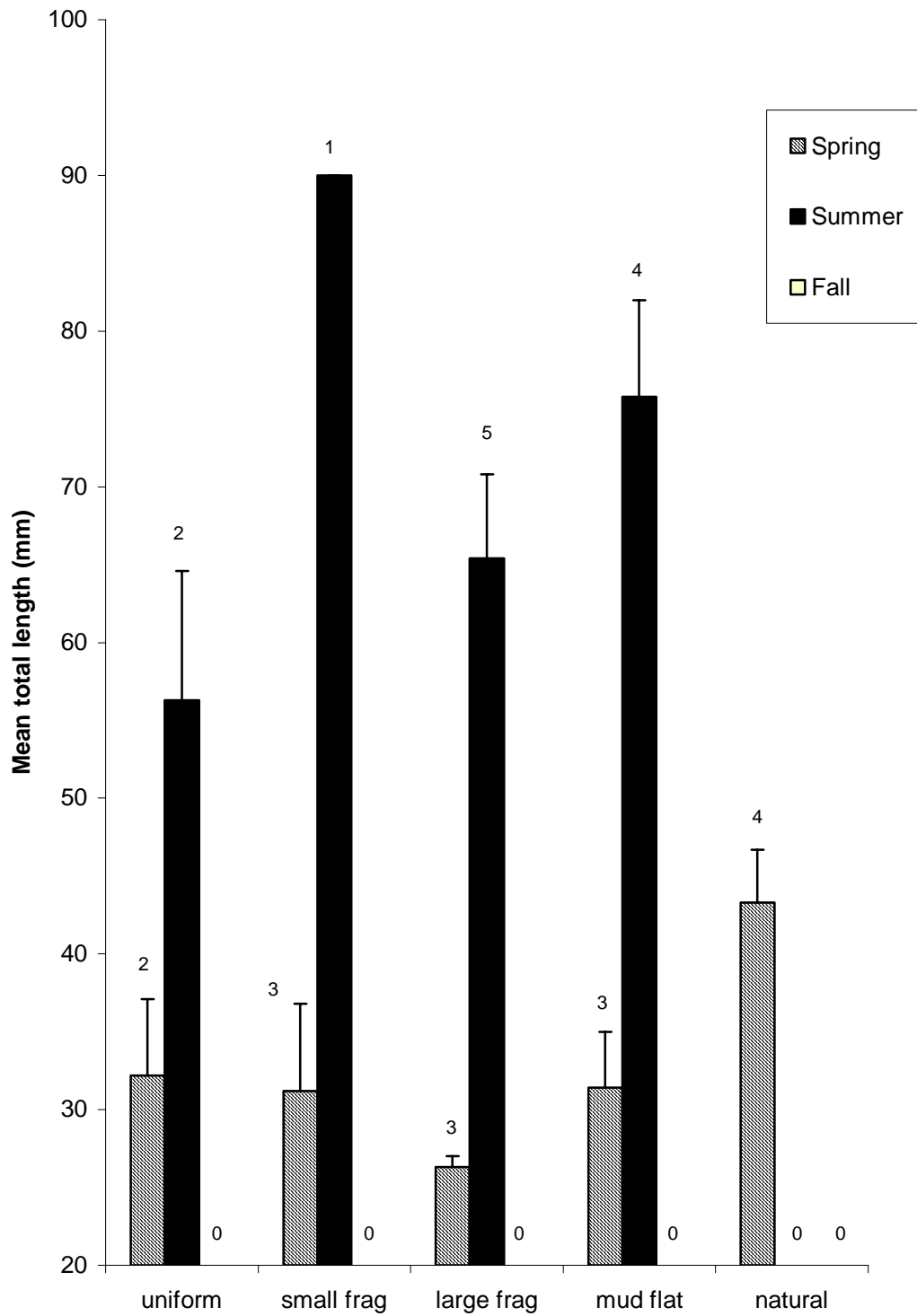


Figure 9. Diversity (Shannon-Weiner Index) of organisms caught in Breder traps for all treatments for all sampling periods. HC = Hewletts Creek natural reefs, PC = Pages Creek natural reefs.

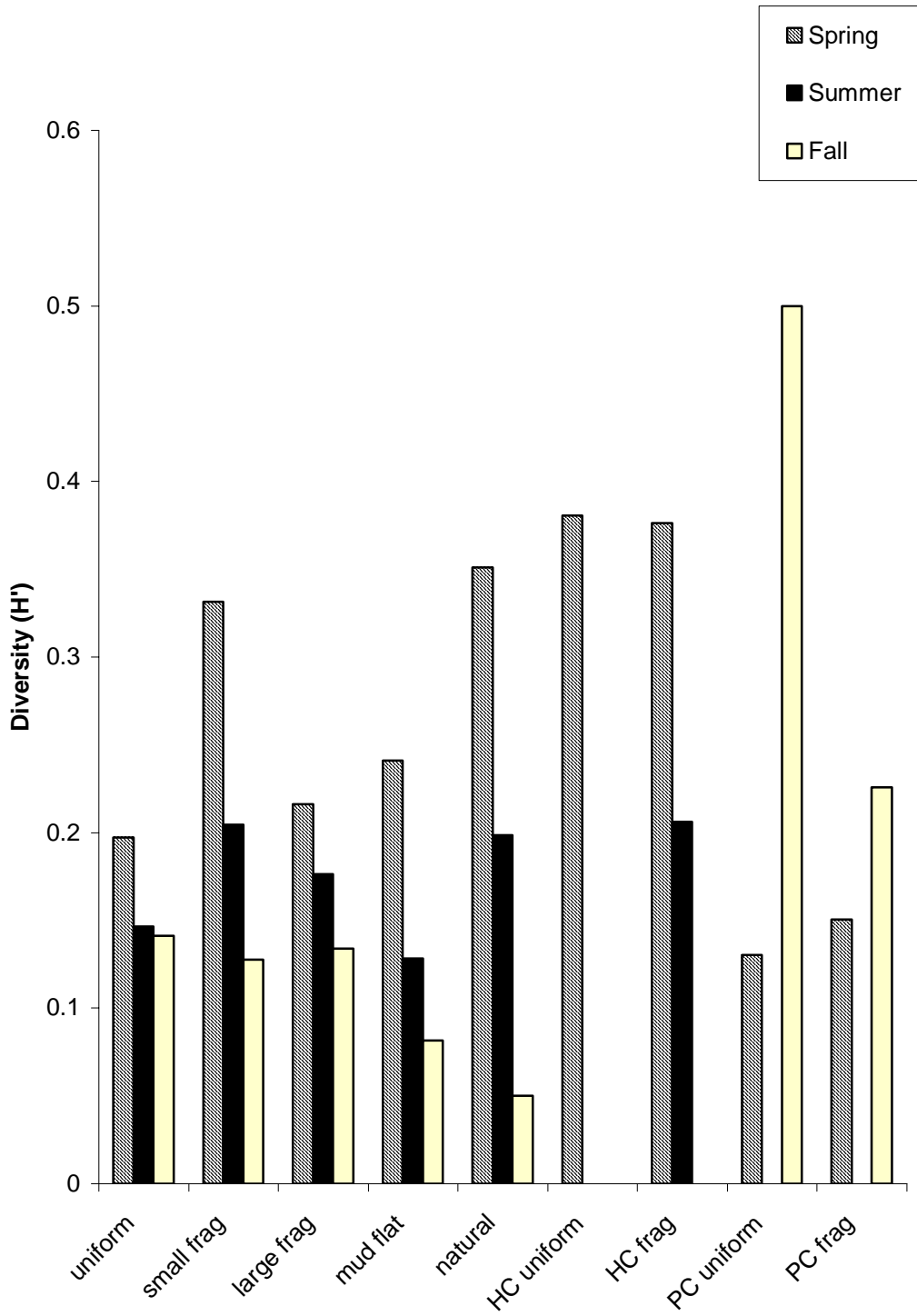
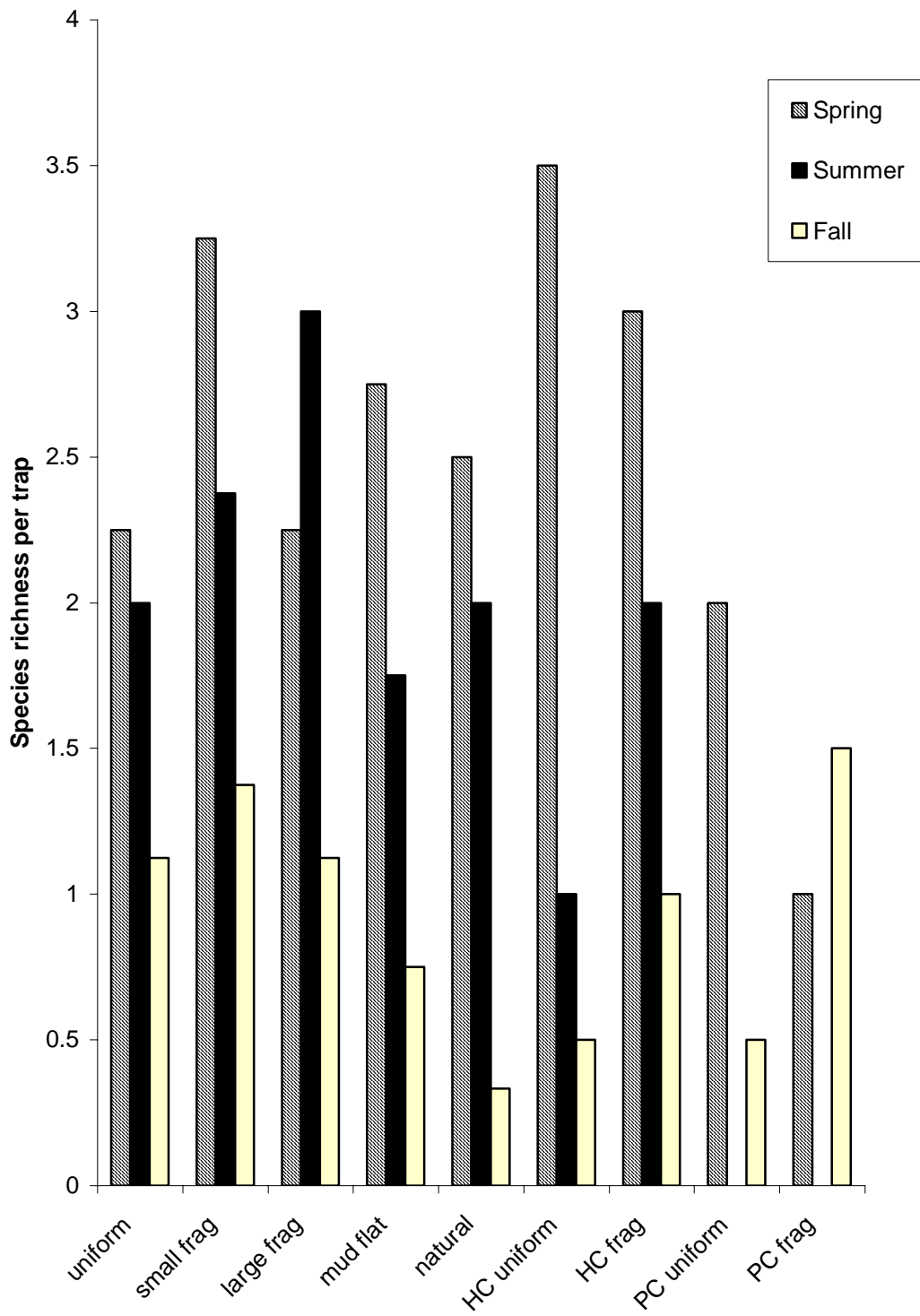


Figure 10. Species richness of organisms caught in Breder traps on all treatments during all sampling periods. HC = Hewletts Creek natural reefs, PC = Pages Creek natural reefs.



lefroyi (Figure 11). Pinfish were most abundant on both small and large fragmented treatments. *Eucinostomus lefroyi* abundances were also highest on the large fragmented treatments, followed by the mud flat and channel.

Spring 2003 sampling produced near 0 catches, although fish were caught the following summer. Dominant species for summer 2003 were menhaden, *Brevoortia tyrannus*, pinfish, *Lagodon rhomboides*, and striped mullet, *Mugil cephalus*. Abundances of menhaden were highest in the channel, with catches also occurring on the uniform and mudflat treatments. Pinfish were caught in the channel and in the large fragmented reefs. Striped mullet were most common on reference reefs, but were absent on small fragmented reefs. Only one fish was caught during fall 2003, a pinfish (on a large fragmented reef).

Excavation Abundances

Abundances were grouped by season: spring, summer, fall, and winter, with 2 years of data per season. Dominant species of epifauna (those comprising >1% of total composition) were Amphipoda, an unidentified anemone, *Eurypanopeus depressus* (flat mud crab), *Geukensia demissa* (Atlantic ribbed mussel), *Menippe mercenaria* (stone crab), *Palaemonetes pugio* (grass shrimp), *Panopeus herbstii* (common mud crab), polychaetes, *Rhithropanopeus harrisi* (white-fingered mud crab) *Urosalpinx cinerea* (oyster drill) and *Uca pugnax* (mud fiddler crab). Of these, *Eurypanopeus depressus*, *Geukensia demissa*, *Panopeus herbstii*, polychaetes, and *Urosalpinx cinerea* were by far the most common, comprising 80% of total catches during summer sampling periods.

Mean total abundances of all organisms in the experimental and reference reefs showed both season and treatment effects (Table 5). Abundances were higher in created reefs than in

Figure 11. Mean abundances of fish caught in gill nets during fall 2002 and summer 2003.

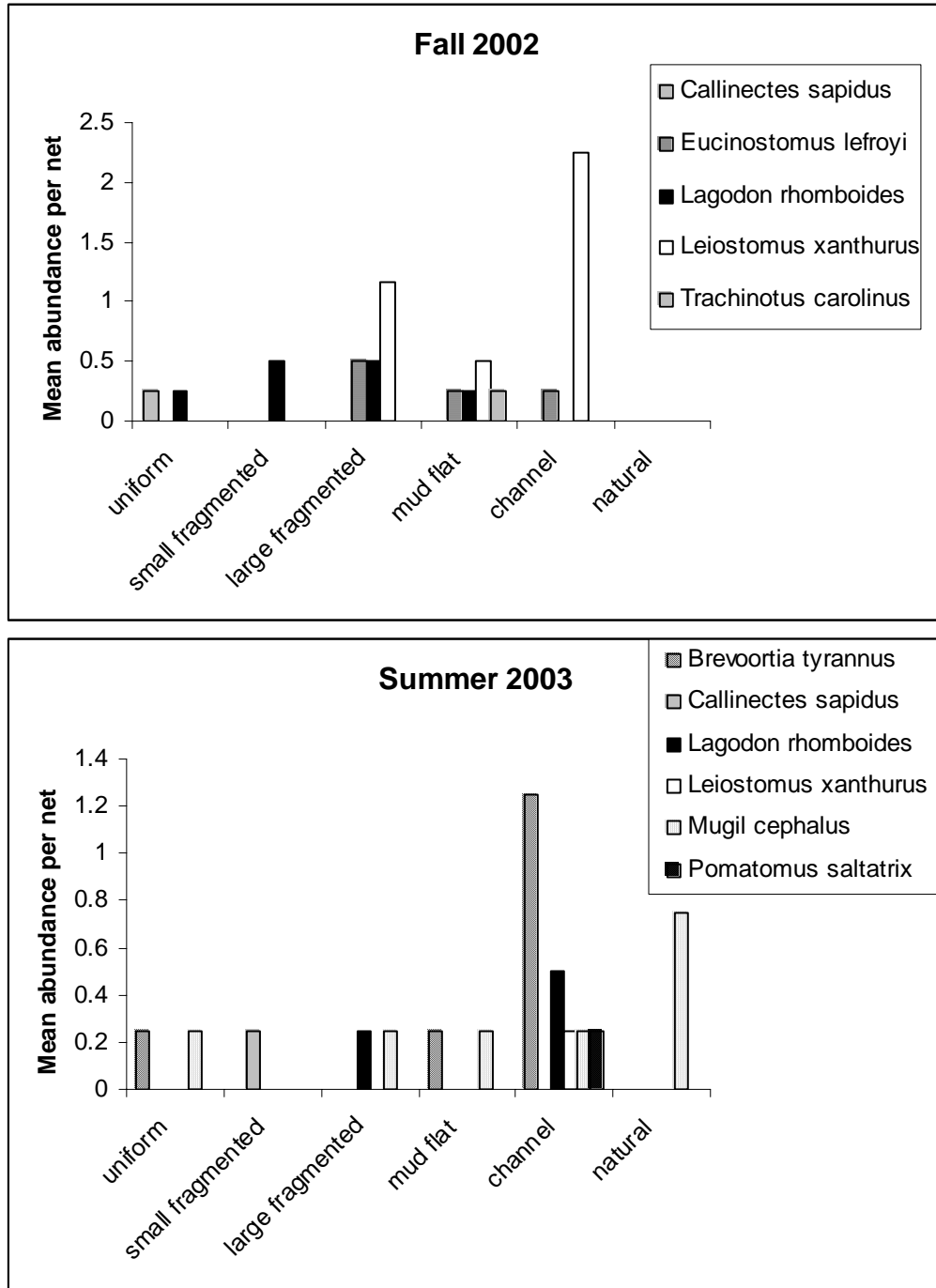


Table 5. 3-way ANOVA results for the epibenthic community collected from excavations of experimental treatments. Shown are F-values and (p-values) with significant effects (p<0.05) indicated by an asterisk. When significant effects are present, SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values. UN=uniform, FS=small fragmented, FL= large fragmented, MD=mudflat, NT= natural, SPR=spring, SUM=summer, FAL=fall, and WIN=winter.

Species	Treatment	Season	Site	Season*Treatment
Amphipoda	10.59* (0.0001)* NT ^a , FS ^a , UN ^a , FL ^a , MD ^b	17.19* (0.0001)* SPR ^a , WIN ^b , SUM ^b , FAL ^c	1.50 (0.182)	1.52 (0.124)
anemone	0.55 (0.651)	1.91 (0.131)	0.68 (0.669)	0.62 (0.824)
<i>Eurypanopeus depressus</i>	7.24* (0.0002)* UN ^a , NT ^a , FL ^a , FS ^a , MD ^b	1.41 (0.242)	2.12* (0.055)*	0.70 (0.746)
<i>Geukensia demissa</i>	8.13* (0.0001)* UN ^a , FL ^a , FS ^a , NT ^b , MD ^b	1.81 (0.149)	0.17 (0.985)	0.69 (0.759)
<i>Menippe mercenaria</i>	1.55 (0.205)	2.82* (0.042)* SUM ^a , FAL ^a , SPR ^a , WIN ^a	1.71 (0.123)	1.00 (0.453)
<i>Palaemonetes pugio</i>	2.96* (0.035)* FS ^a , NT ^a , UN ^a , FL ^a , MD ^a	1.58 (0.197)	0.72 (0.631)	1.08 (0.384)
<i>Panopeus herbstii</i>	33.15* (0.0001)* UN ^a , FL ^{ab} , FS ^b , NT ^b , MD ^c	3.81* (0.012)*	0.18 (0.982)	1.12 (0.353)
polychaete	14.46* (0.0001)* UN ^a , FS ^a , FL ^a , NT ^a , MD ^b	5.51* (0.001)*	1.74 (0.116)	1.86* (0.046)*
<i>Urosalpinx cinerea</i>	6.78* (0.0003)* FS ^a , UN ^a , FL ^a , NT ^a , MD ^b	11.49* (0.0001)*	0.23 (0.965)	1.41 (0.170)
Mean total abundance	63.68* (0.0001)* FS ^a , UN ^a , FL ^{ab} , NT ^b , MD ^c	13.86* (0.0001)* SPR ^a , WIN ^b , FAL ^b , SUM ^c	0.39 (0.884)	1.03 (0.422)

reference reefs, with all reef treatments showing higher abundances than on the mud flat (F=63.68, p=0.0001).

Treatment effects were seen for Amphipoda (F=10.59, p=0.0001), *Eurypanopeus depressus* (F=7.24, p=0.0002), *Geukensia demissa* (F=8.13, p=0.0001), *Palaemonetes pugio* (F=2.96, p=0.035), *Panopeus herbstii* (F=33.15, p=0.0001), polychaetes (F=14.46, p=0.0001), and *Urosalpinx cinerea* (F=6.78, p=0.0003). For these species, the mean abundance per 400 cm² was lower for the mudflat than for all other treatments. *Geukensia demissa* were also significantly more abundant on created reefs than on the natural reefs. *Panopeus herbstii* was significantly more abundant on the uniform and large fragmented reefs than on any other treatment.

Seasonal differences in abundance occurred for Amphipoda (F=17.19, p=0.0001), *Menippe mercenaria* (F=2.28, p=0.042), *Panopeus herbstii* (F=3.81, p=0.012), polychaetes (F=5.51, p=0.001), and *Urosalpinx cinerea* (F=11.49, p=0.0001). Mean abundances of amphipods were higher for spring and winter than summer or fall (Figure 12). *Menippe mercenaria* was only present during summer and fall seasons. Abundances of *Panopeus herbstii* were significantly lower in winter than in any other seasons and highest during summer (Figure 12). Polychaetes found during excavations showed significantly lower abundances in fall when compared to all other seasons. There was also a slight season-treatment interaction for polychaetes (F=1.86, p=0.046). Oyster drills (*Urosalpinx cinerea*) exhibited lower abundances in summer than for any other season.

Amphipod abundances on natural reefs in Hewletts Creek also showed a seasonal effect, as well as a treatment effect (Table 6). They were far more abundant during spring sampling (Figure 13). No other treatment effects were observed within the natural reefs in tidal creeks,

Figure 12. Mean abundances (+ SE) of organisms caught in excavations during all seasons for experimental reefs.

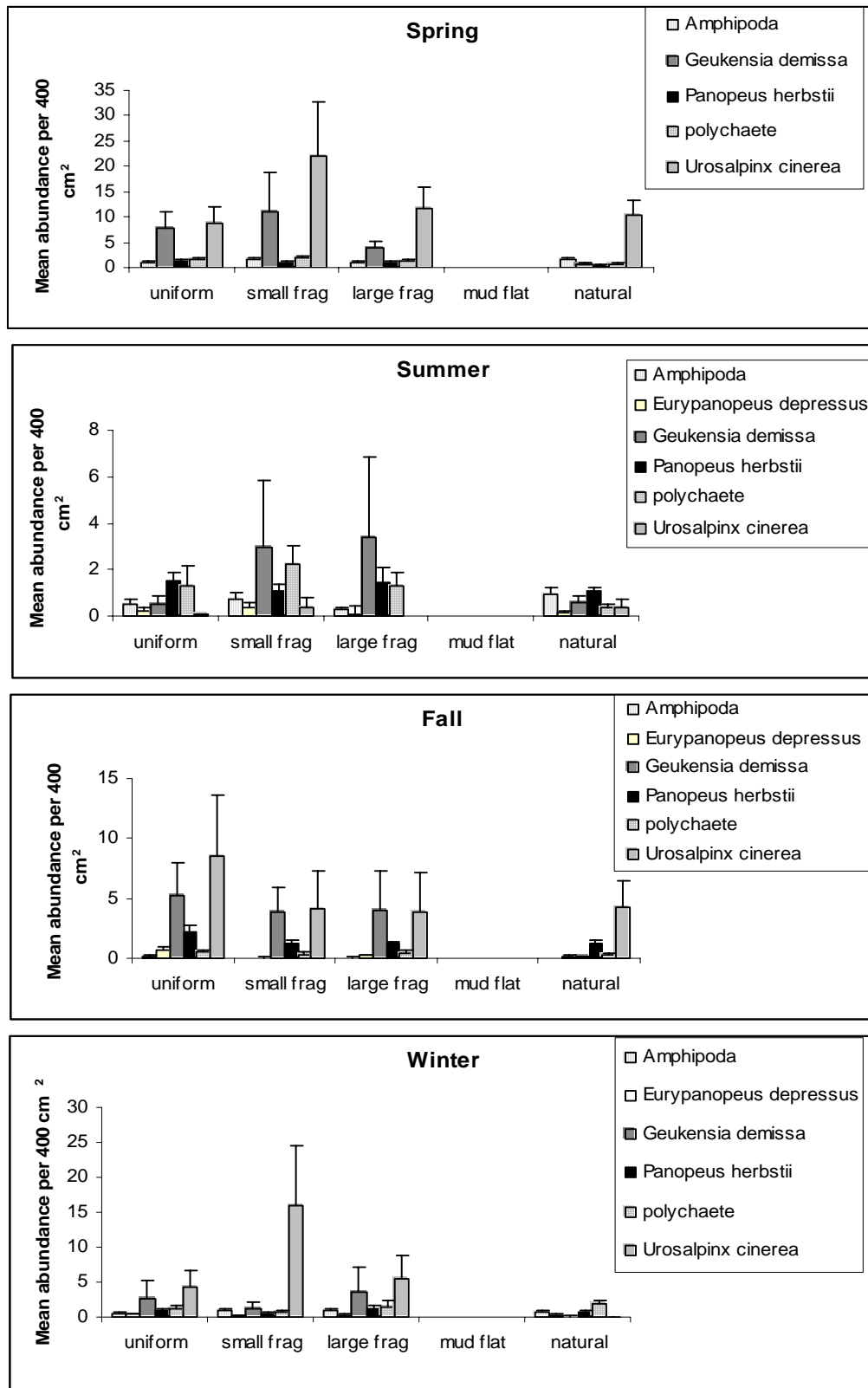
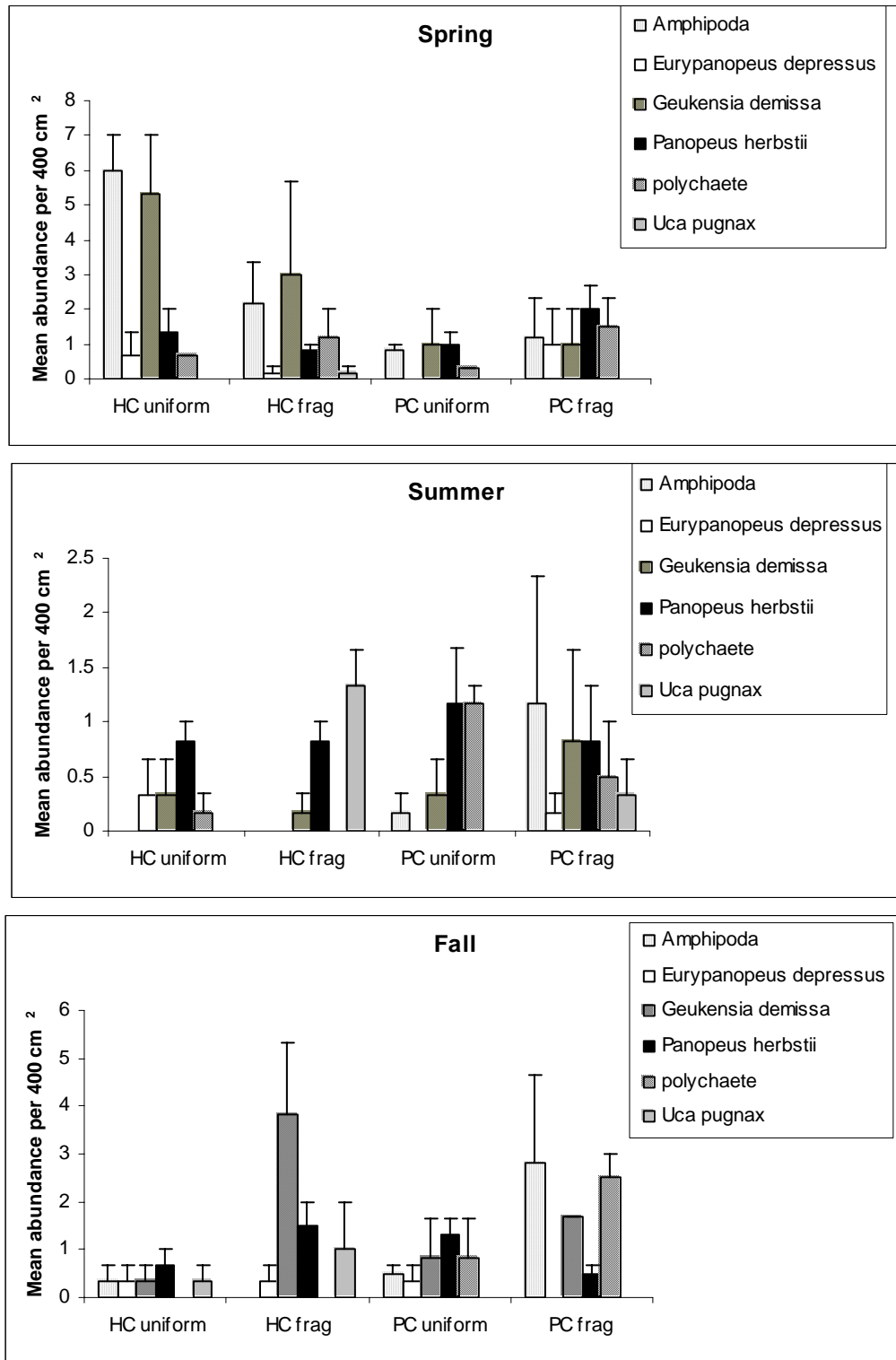


Table 6. 2-way ANOVA results for the epibenthic community collected from excavations on natural reefs in Hewletts and Pages Creeks. Shown are F-values and (p-values) with significant ($p < 0.05$) comparisons indicated by an asterisk. When significant effects are present, SNK rankings are shown in decreasing order, with different superscripts indicate statistically different values. UN=uniform, FR=fragmented, SPR=spring, SUM=summer, and FAL=fall.

Species	Treatment	Season	Site
Hewletts Creek			
Amphipoda	5.16* (0.057)* UN ^a , FR ^a	21.21* (0.001)* SPR ^a , FAL ^b , SUM ^b	1.66 (0.238)
<i>Eurypanopeus depressus</i>	0.74 (0.419)	0.19 (0.830)	0.74 (0.419)
<i>Geukensia demissa</i>	0.62 (0.457)	3.07 (0.110)	3.14 (0.119)
<i>Panopeus herbstii</i>	0.14 (0.720)	0.49 (0.630)	0.71 (0.427)
polychaete	0.37 (0.560)	14.23* (0.003)* SPR ^a , SUM ^b , FAL ^b	0.17 (0.691)
<i>Rhithropanopeus harrisi</i>	0.00 (1.000)	0.50 (0.627)	2.00 (0.200)
<i>Uca pugnax</i>	0.04 (0.851)	0.67 (0.543)	0.58 (0.472)
<i>Urosalpinx cinerea</i>	0.11 (0.748)	2.18 (0.183)	0.11 (0.748)
Total abundance	0.06 (0.819)	5.31* (0.040)* SPR ^a , FAL ^{ab} , SUM ^b	3.13 (0.120)
Pages Creek			
Amphipoda	1.04 (0.342)	0.20 (0.824)	0.16 (0.704)
<i>Eurypanopeus depressus</i>	0.67 (0.441)	0.43 (0.667)	2.55 (0.155)
<i>Geukensia demissa</i>	0.64 (0.451)	0.98 (0.422)	3.11 (0.121)
<i>Menippe mercenaria</i>	1.97 (0.203)	0.52 (0.618)	0.03 (0.338)
<i>Palaemonetes pugio</i>	1.00 (0.351)	1.00 (0.415)	1.00 (0.351)
<i>Panopeus herbstii</i>	0.14 (0.722)	0.72 (0.521)	1.48 (0.264)
polychaete	0.71 (0.428)	0.72 (0.519)	0.35 (0.571)
<i>Uca pugnax</i>	1.00 (0.351)	1.00 (0.415)	1.00 (0.351)
<i>Urosalpinx cinerea</i>	0.40 (0.546)	1.80 (0.234)	1.06 (0.338)

Total abundance	0.11 (0.756)	1.70 (0.251)	2.39 (0.166)
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Figure 13. Mean abundances of organisms (+ SE) caught during excavations on uniform and fragmented natural reefs in Hewletts and Pages Creeks during spring, summer, and fall sampling.



and the only other seasonal difference in abundance occurred for polychaetes in Hewletts Creek (more abundant in during spring). There were no significant differences in any other species found in Hewletts Creek for season or treatment.

Mean Carapace Widths of Crabs from Excavations

For the experimental treatments (all created treatments, the mud flat, and natural reefs at the mouth of Hewletts Creek), crabs *Eurypanopeus depressus*, *Menippe mercenaria*, and *Panopeus herbstii* were found with enough frequency during excavations to analyze differences in carapace width among treatments, seasons, and sites (Table 7). The only significant difference occurred for *Eurypanopeus depressus*, which was smaller during spring than in any other season ($F=4.49$, $p=0.010$).

On natural reefs within the tidal creeks, only *Panopeus herbstii* was abundant enough to be analyzed for differences in carapace width. Crabs caught on reefs in Hewletts Creek showed no differences in size related to treatment, season, or site. In Pages Creek, however, there was a seasonal effect observed, with larger crabs collected in spring compared to summer or fall ($F=12.47$, $p=0.005$).

Diversity and Species Richness of Epifauna

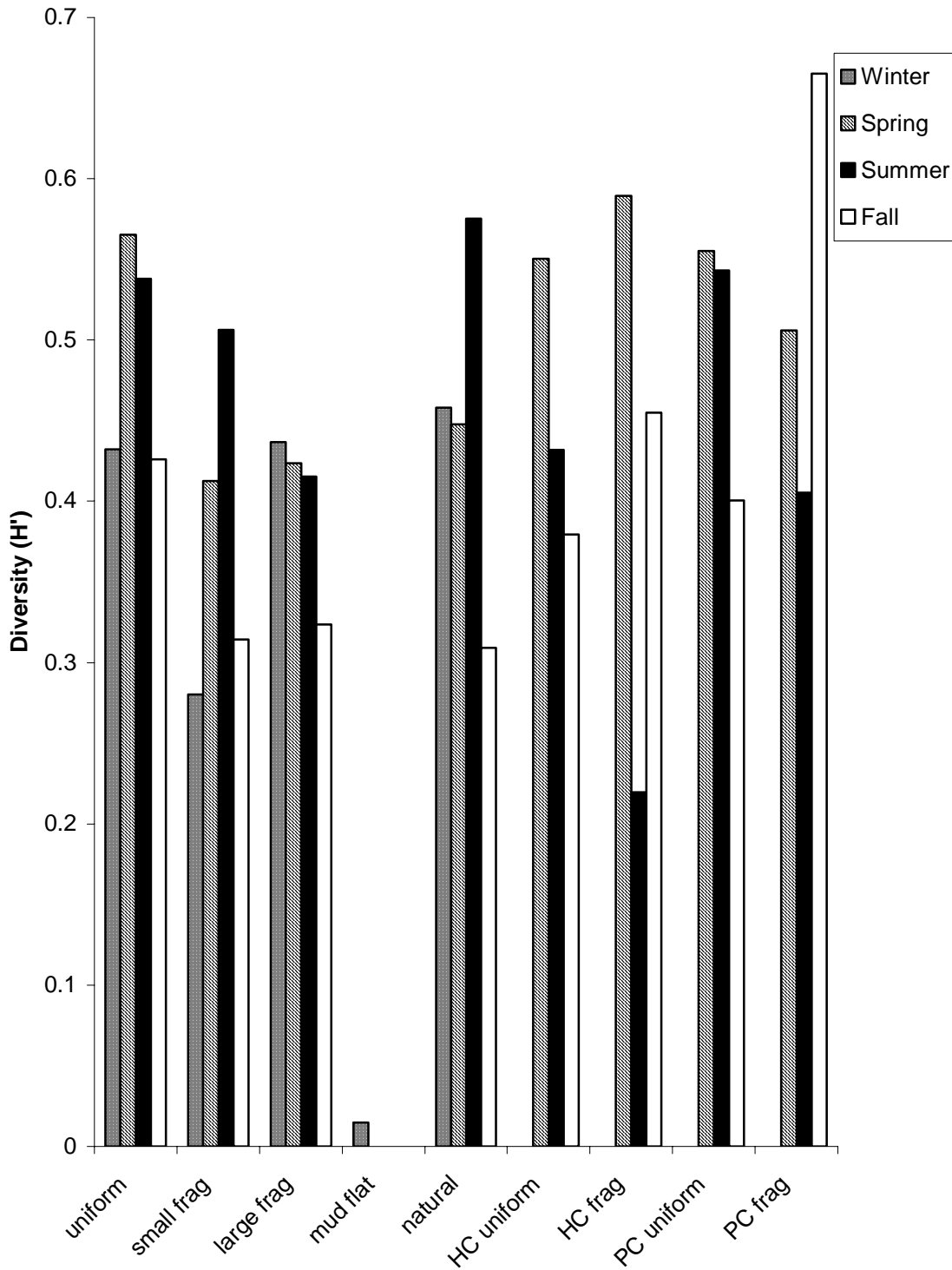
Diversity among the experimental treatments and reference reefs (Figure 14) was lowest overall during fall. Diversity was also highest on uniform treatments during spring, compared to other treatments that season. Summer sampling showed highest diversity on the reference reefs, whereas winter values were similar across uniform, large fragmented, and natural treatments.

Overall diversity within tidal creek natural reefs was similar to experimental treatments.

Table 7. 2-way and 3-way ANOVA results for the carapace widths of crabs found in excavations for all treatments. Natural reefs within Hewletts and Pages Creeks were tested separately by creek. Shown are F-values and (p-values) with significant ($p < 0.05$) comparisons indicated by an asterisk. When significant effects are present, SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values. SPR=spring, SUM=summer, FAL=fall, and WIN=winter.

Species	Treatment	Season	Site	Treatment*Season
Experimental Set				
<i>Eurypanopeus depressus</i>	2.33 (0.115)	4.49* (0.010)* SUM ^a , FAL ^a , WIN ^{ab} , SPR ^b	2.28 (0.072)	1.85 (0.100)
<i>Menippe mercenaria</i>	5.24 (0.295)	4.25 (0.288)	1.71 (0.416)	8.73 (0.208)
<i>Panopeus herbstii</i>	1.15 (0.320)	0.49 (0.691)	0.88 (0.512)	0.38 (0.940)
Hewletts Creek				
<i>Panopeus herbstii</i>	0.09 (0.776)	1.58 (0.272)	1.90 (0.211)	N/A N/A
Pages Creek				
<i>Panopeus herbstii</i>	2.29 (0.174)	12.47* (0.005)* SPR ^a , FAL ^b , SUM ^b	2.59 (0.151)	N/A N/A

Figure 14. Diversity of species (Shannon-Weiner Diversity Index) found in excavations. HC = Hewletts Creek natural reefs, PC = Pages Creek natural reefs.



Spring showed highest diversity for most treatments, while summer diversity was lower in both creeks. With the exception of fragmented reefs in Pages Creek, fall values were also lower than spring.

Species richness was highest during spring for all reefs. For the experimental treatments (Figure 15), lowest values were seen during fall, with intermediate values in summer and winter. In the tidal creeks, oyster reefs supported more species per 400 cm² during fall than summer. In all cases, both diversity and species richness on the mud flat was dramatically less than seen on oyster reefs, either created or natural.

Biomass of Epifauna

Sixteen species in excavations comprised >1% of the total biomass, however only a few occurred with enough frequency to be analyzed for differences in biomass over treatments, seasons, and sites. For the experimental and reference treatments, those species were *Eurypanopeus depressus*, *Geukensia demissa*, *Panopeus herbstii*, and *Urosalpinx cinerea*. The only treatment effects seen were for *Geukensia demissa* (F=5.57, p=0.008) and *Urosalpinx cinerea* (F=64.72, p=0.0001). *Geukensia demissa* taken from large fragmented treatments had significantly greater biomass than those from the small fragmented and uniform treatments, all of which were greater biomass than mussels from the reference reefs (Table 8). *Urosalpinx cinerea*, on the other hand, exhibited higher biomass on small fragmented treatments than on any other. Treatment did not significantly affect the biomass of organisms caught in excavations from natural reefs in either tidal creek.

Seasonal differences in biomass were also present for ribbed mussels (marginal significance: F=2.72, p=0.059) and oyster drills (F=43.46, p=0.0001) within the experimental

Figure 15. Species richness for organisms caught during excavations. HC = Hewletts Creek natural reefs, PC = Pages Creek natural reefs.

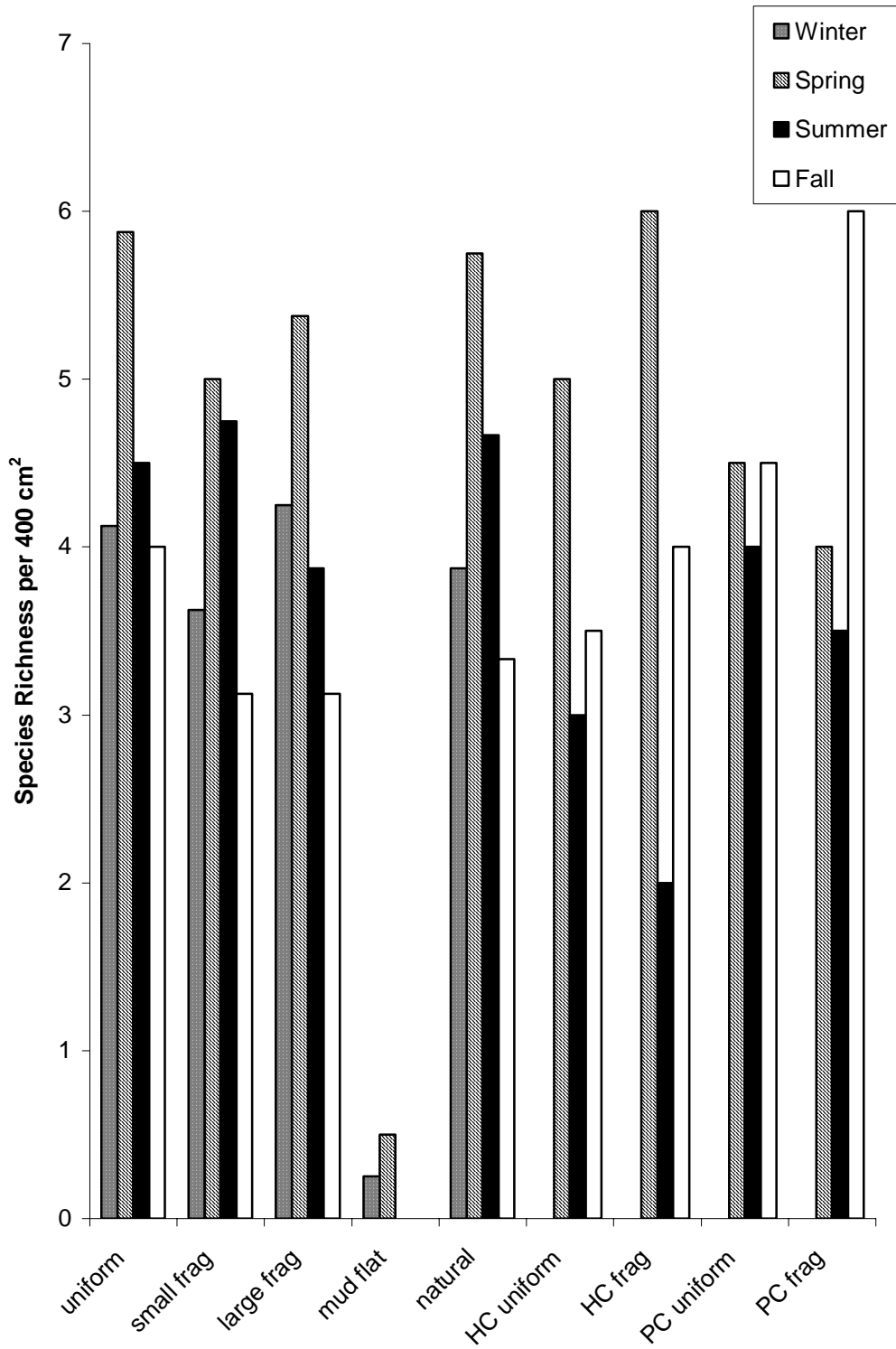


Table 8. 2-way and 3-way ANOVA results for the biomass of epifauna found during excavations. Natural reefs in Hewletts and Pages Creeks are analyzed separately by creek. Shown are F-values and (p-values) with significant (p<0.05) comparisons indicated by an asterisk. When significant effects are present, SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values. UN=uniform, FS=small fragmented, FL= large fragmented, MD=mudflat, NT= natural, SPR=spring, SUM=summer, FAL=fall, and WIN=winter.

Species	Treatment	Season	Site	Season*Treatment
Experimental Set				
<i>Eurypanopeus depressus</i>	2.62 (0.093)	0.28 (0.841)	0.44 (0.815)	0.16 (0.995)
<i>Geukensia demissa</i>	5.57* (0.008)*	2.72* (0.059)*	0.54 (0.775)	1.20 (0.329)
	FL ^a , FS ^b , UN ^b , NT ^c	WIN ^a , FAL ^a , SPR ^a , SUM ^a		
<i>Panopeus herbstii</i>	0.42 (0.661)	1.32 (0.281)	1.07 (0.393)	0.38 (0.937)
<i>Urosalpinx cinerea</i>	64.72* (0.0001)*	43.46* (0.0001)*	1.41 (0.248)	36.22* (0.0001)*
	FS ^a , NT ^b , FL ^b , UN ^b	SUM ^a , SPR ^b , FAL ^b , WIN ^b		
Hewletts Creek				
<i>Geukensia demissa</i>	0.23 (0.655)	0.76 (0.525)	0.03 (0.873)	N/A N/A
<i>Panopeus herbstii</i>	0.59 (0.468)	0.81 (0.485)	1.23 (0.305)	N/A N/A
Pages Creek				
<i>Geukensia demissa</i>	11.40 (0.078)	12.01 (0.077)	1.92 (0.300)	N/A N/A
<i>Panopeus herbstii</i>	0.01 (0.922)	7.90* (0.016)*	4.33 (0.076)	N/A N/A
		SPR ^a , SUM ^b , FAL ^b		
<i>Urosalpinx cinerea</i>	4.77 (0.273)	2.02 (0.390)	5.54 (0.256)	N/A N/A

treatments, as well as for *Panopeus herbstii* ($F=7.90$, $p=0.016$) from reefs in Pages Creek.

Biomass of ribbed mussels was higher during winter and spring than in summer and fall (Figure 16). There was significant treatment-site interaction for this species, in which higher abundances were seen for the small fragmented treatments during summer. *Panopeus herbstii* found on reefs in Pages Creek had higher mean biomass during spring (Figure 17).

Infaunal Abundances

The average number of organisms found in sediment cores (Figure 18) was significantly higher in July 2002 than in July 2003 ($F=9.49$, $p=0.003$, Table 9). Although there were differences in total abundance among sites, there were no significant treatment or distance effects for total infaunal abundance. *Gemma* ($F=13.51$, $p=0.0005$) and *Tharyx* ($F=5.81$, $p=0.019$) were also more prevalent in 2002 than 2003, whereas *Leitoscoloplos* ($F=6.65$, $p=0.012$) and *Mediomastus* ($F=10.65$, $p=0.002$) abundances increased as the reefs developed, with significantly higher numbers found during the second year of sampling. *Gemma* (Figure 19) exhibited differences among treatments, with higher densities in the mud flat than near reefs. There were also higher abundances found near large fragmented reefs than near their small fragmented counterparts ($F=6.03$, $p=0.004$). When years were analyzed separately (Tables 10-11), this difference in abundance can be seen during 2003 ($F=4.27$, $p=0.023$), after the reefs have fully developed, but is not present in 2002. Abundance of *Gemma* did not vary with distance away from a reef, with similar numbers found at 5 cm, 200 cm, and 500 cm away from the reef. These abundances were also similar to those found within the channels between patches of the fragmented treatments.

The only other treatment effect observed was for *Tharyx* in 2003 ($F=4.09$, $p=0.027$),

Figure 16. Average biomass of organisms (+ SE) found during excavations on the experimental treatments during spring, summer, fall, and winter sampling. The numbers over the bars indicate the number of treatments from which mean total biomass was calculated.

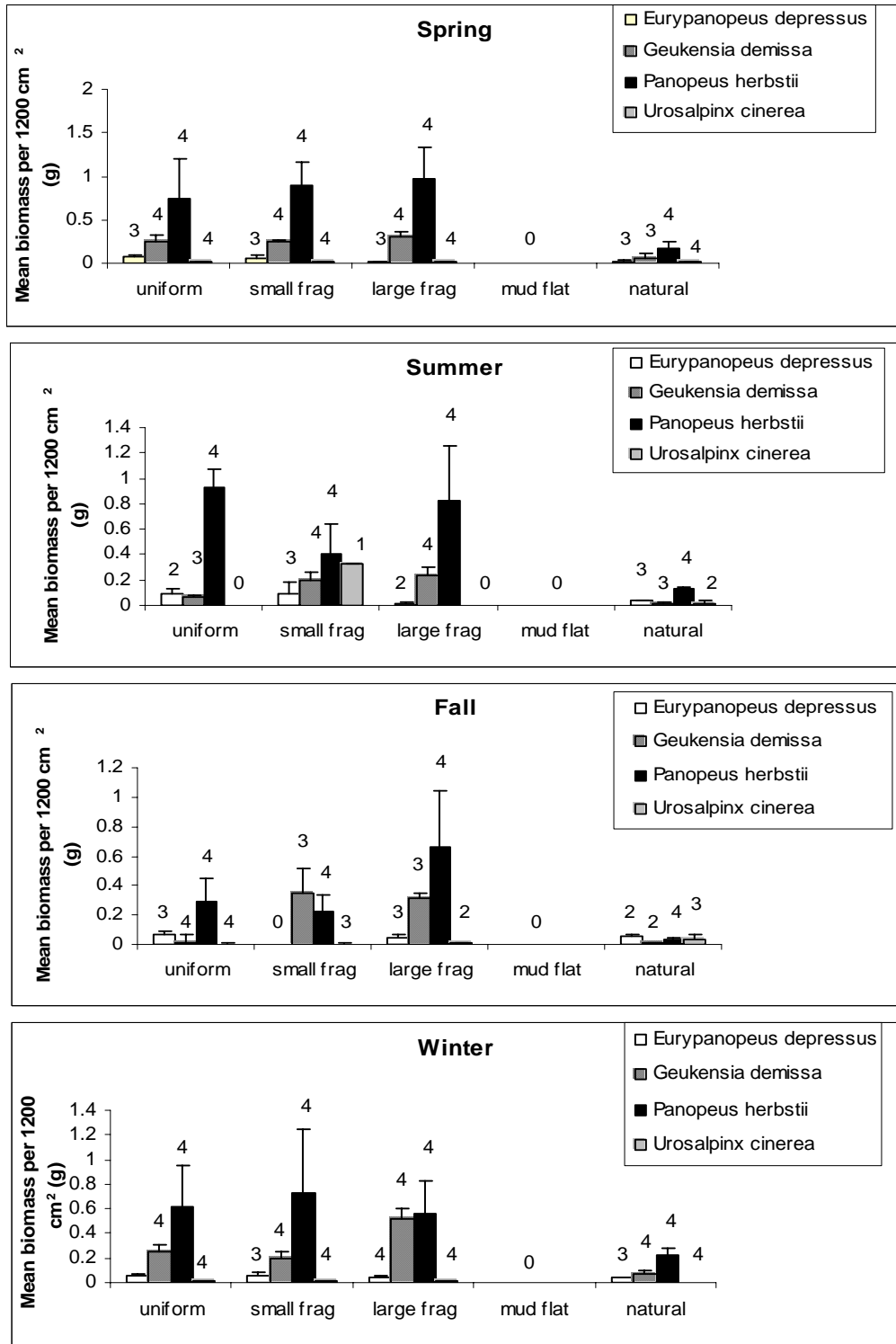


Figure 17. Average biomass (+ SE) of *Panopeus herbstii* caught during excavations of natural reefs in Pages Creek. The numbers over the bars indicate the number of treatments from which mean total biomass was calculated.

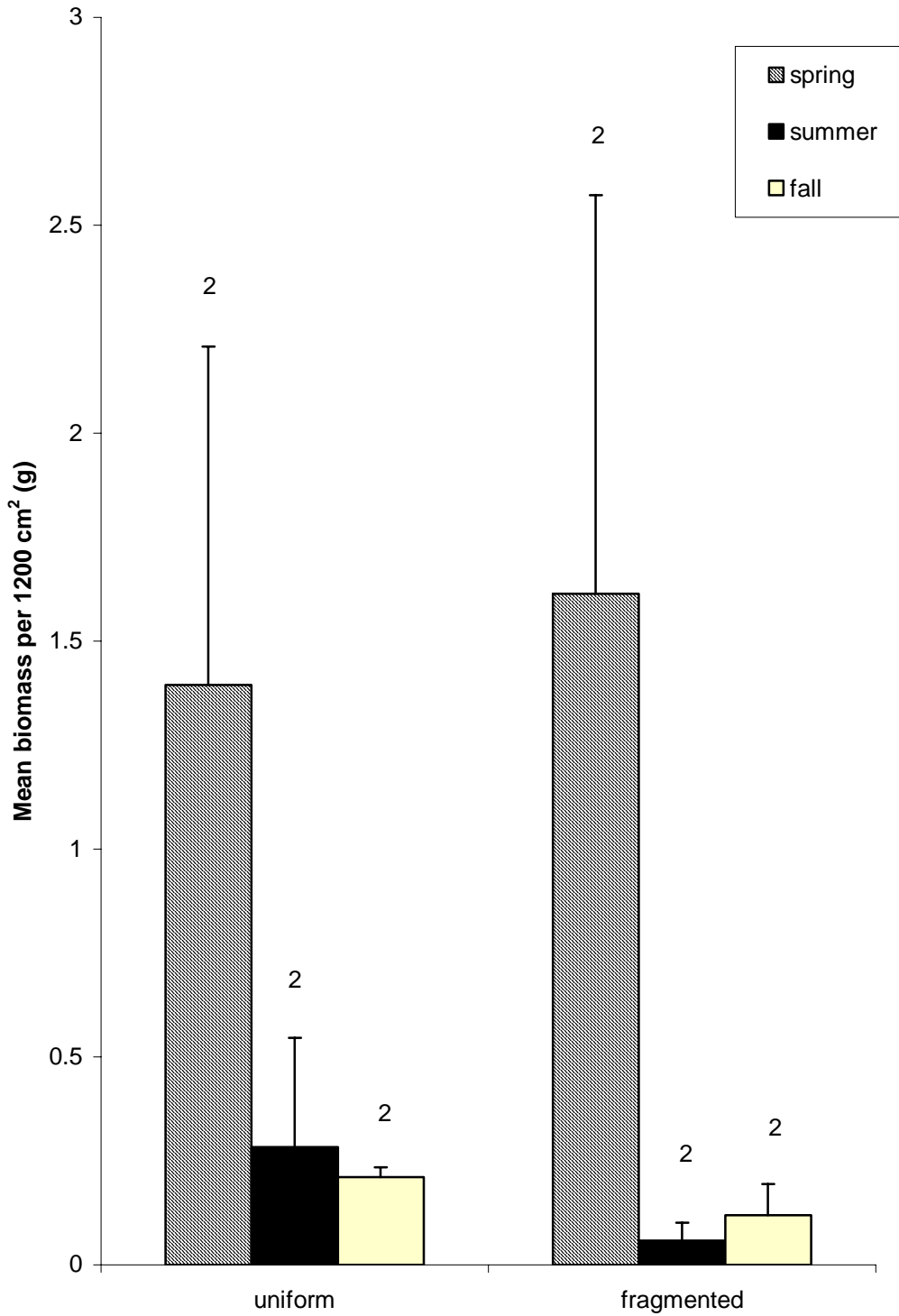


Figure 18. Mean total abundances (+ SE) of all infaunal organisms found in cores during July 2002 and July 2003. UNIF= uniform, FRSM=small fragmented, FRLG=large fragmented, MUDF=mudflat, 5=distance of 5 cm, 200=distance of 200 cm, 500=distance of 500 cm, CHAN=in channel between reef patches.

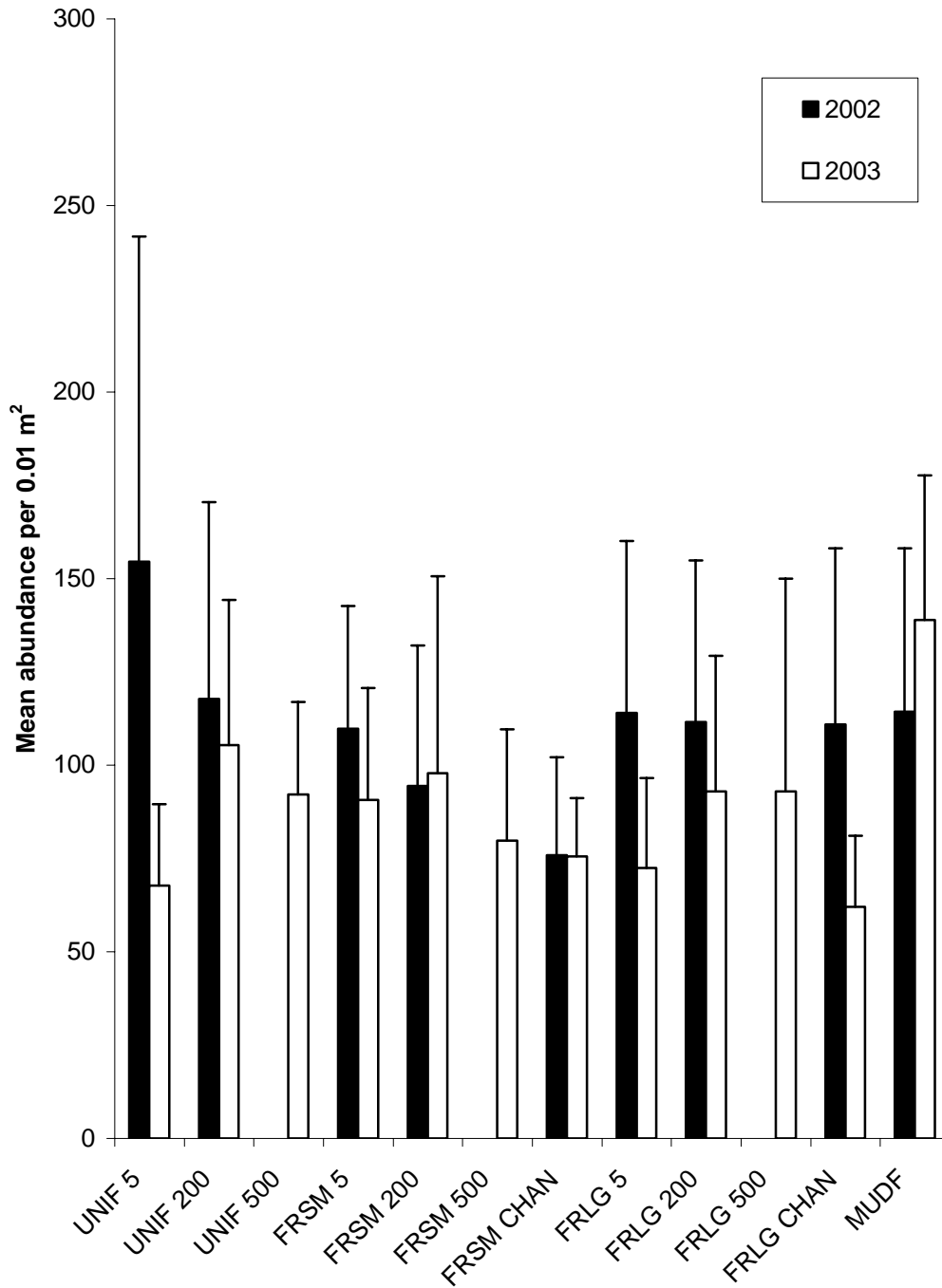


Table 9. Results from the 4-way ANOVA for the effects of treatment, distance from reef, year, and possible interactions on infaunal abundances on all created reef treatments. Shown are F-values and (p-values) with significant (p<0.05) comparisons indicated by an asterisk. When significant effects are present, SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values. UN=uniform, FS=small fragmented, FL= large fragmented, CH= in channel between reef patches.

Species	Treatment	Distance	Year	Yr*Treat	Site	Treat*Dis
<i>Aricidea</i>	1.41 (0.253)	0.67 (0.573)	0.05 (0.831)	1.07 (0.348)	18.61* (0.0001)*	0.15 (0.979)
<i>Driloneris</i>	1.38 (0.261)	0.21 (0.892)	0.66 (0.421)	0.76 (0.471)	2.55 (0.064)	0.73 (0.604)
<i>Gemma</i>	6.03* (0.004)*	1.99 (0.125)	13.51* (0.0005)*	0.26 (0.772)	662.47* (0.0001)*	0.75 (0.587)
<i>Leitoscoloplos</i>	1.77 (0.180)	3.60* (0.019)*	6.65* (0.012)*	0.18 (0.838)	19.95* (0.0001)*	2.66* (0.031)*
<i>Mediomastus</i>	0.92 (0.404)	2.41 (0.076)	10.65* (0.002)*	0.04 (0.956)	10.31* (0.0001)*	0.59 (0.704)
<i>Nereis falsa</i>	0.71 (0.494)	5.89* (0.001)*	3.48 (0.067)	0.97 (0.387)	6.07* (0.001)*	0.50 (0.777)
<i>Oligochaete</i>	1.58 (0.214)	0.24 (0.869)	2.50 (0.119)	0.99 (0.379)	6.41* (0.0008)*	0.85 (0.518)
<i>Streblospio</i>	2.55 (0.087)	1.33 (0.273)	2.10 (0.153)	0.18 (0.835)	5.88* (0.001)*	1.22 (0.309)
<i>Syllid</i>	0.45 (0.640)	2.46 (0.071)	2.53 (0.117)	0.47 (0.629)	6.57* (0.0007)*	0.87 (0.508)
<i>Tharyx</i>	2.16 (0.124)	0.11 (0.952)	5.81* (0.019)*	0.55 (0.578)	0.47 (0.702)	0.82 (0.537)
Total	0.99 (0.378)	0.17 (0.914)	9.41* (0.003)*	0.93 (0.400)	13.78* (0.0001)*	1.09 (0.376)

Figure 19. Mean abundances (+ SE) of dominant taxa found in sediment cores in July 2002 and July 2003 across treatments and varying distance. Cores taken in 2002 are indicated by black bars, and white bars indicate cores taken in 2003. UNIF= uniform, FRSM=small fragmented, FRLG=large fragmented, MUDF=mudflat, 5=distance of 5 cm, 200=distance of 200 cm, 500=distance of 500 cm, CHAN=in channel between reef patches.

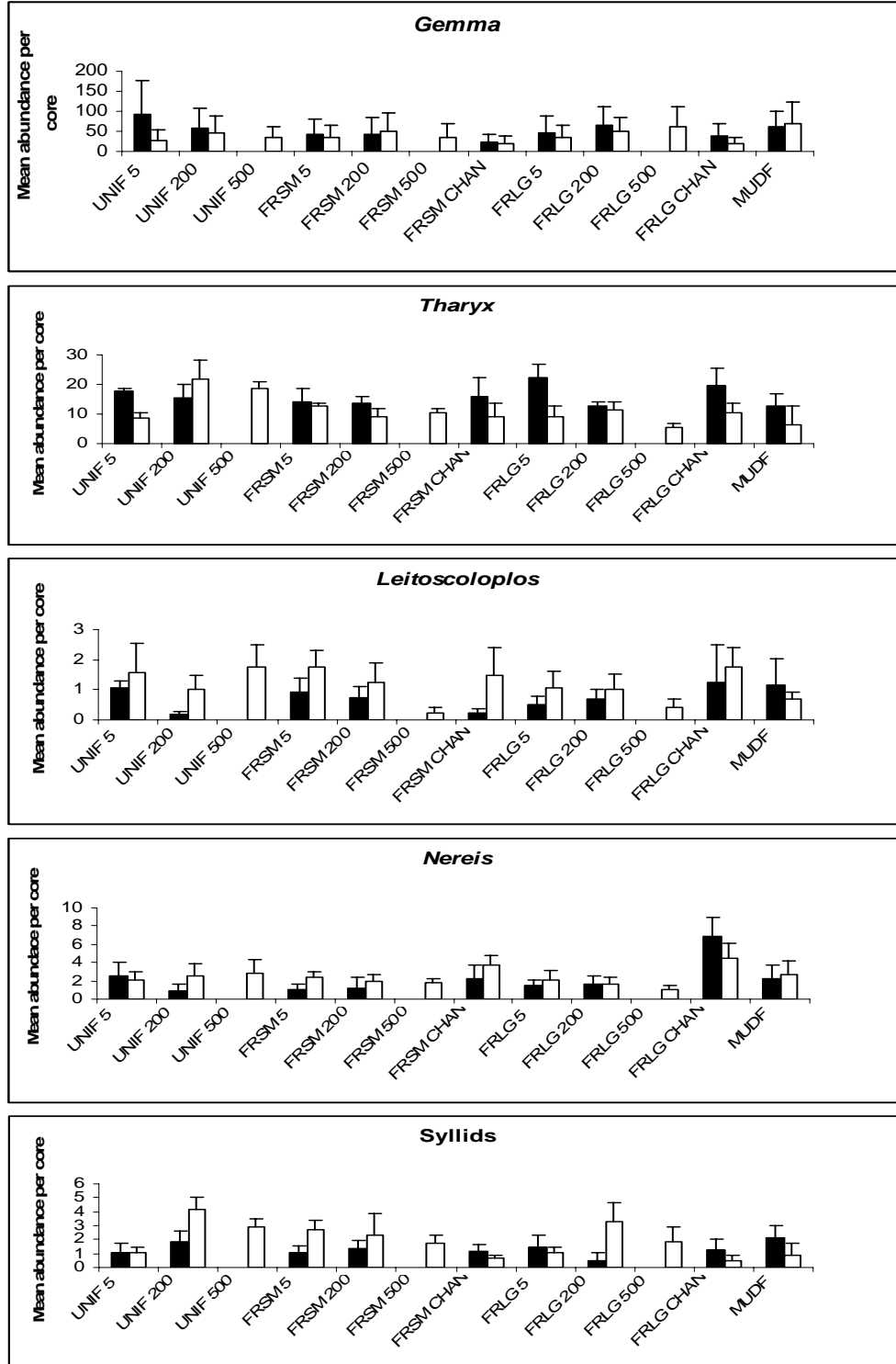


Table 10. Results from a 3-way ANOVA for the effects of treatment, distance from reef, site, and possible interactions on infaunal abundances on all created reef treatments during July 2002. Shown are F-values and (p-values) with significant (p<0.05) comparisons indicated by an asterisk. When significant effects are present, SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values. UN=uniform, FS=small fragmented, FL= large fragmented, CH= in channel between reef patches.

Species	Treatment	Distance	Treatment*Distance	Site
<i>Aricidea</i>	2.15 (0.142)	0.33 (0.721)	0.02 (0.997)	10.41* (0.0002)*
<i>Driloneris</i>	0.79 (0.468)	0.03 (0.971)	0.74 (0.540)	1.42 (0.265)
<i>Gemma</i>	2.79 (0.084)	1.97 (0.164)	1.89 (0.162)	433.57* (0.0001)*
<i>Leitoscoloplos</i>	0.58 (0.567)	1.25 (0.308)	4.31* (0.016)*	10.61* (0.0002)*
<i>Mediomastus</i>	0.19 (0.828)	0.47 (0.632)	0.38 (0.768)	10.15* (0.0002)*
<i>Nereis falsa</i>	1.19 (0.324)	2.70 (0.091)	0.57 (0.643)	1.50 (0.244)
oligochaete	0.29 (0.750)	0.16 (0.850)	0.31 (0.820)	13.46* (0.0001)*
<i>Streblospio</i>	0.51 (0.610)	1.42 (0.263)	0.26 (0.850)	1.18 (0.342)
Syllid	0.03 (0.970)	0.20 (0.817)	0.21 (0.889)	4.08* (0.020)*
<i>Tharyx</i>	0.77 (0.477)	0.23 (0.799)	0.37 (0.779)	1.43 (0.263)
Total	0.42 (0.659)	0.65 (0.533)	0.74 (0.539)	10.44* (0.0002)*

Table 11. Results from a 3-way ANOVA for the effects of treatment, distance from reef, site, and possible interactions on infaunal abundances on all created reef treatments during July 2003. Shown are F-values and (p-values) with significant (p<0.05) comparisons indicated by an asterisk. When significant effects are present, SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values. UN=uniform, FS=small fragmented, FL= large fragmented, CH=in channel between reef patches.

Species	Treatment	Distance	Treatment*Distance	Site
<i>Aricidea</i>	0.23 (0.799)	0.53 (0.668)	0.23 (0.945)	7.02* (0.001)*
<i>Driloneris</i>	0.16 (0.851)	0.21 (0.890)	0.36 (0.872)	1.74 (0.180)
<i>Gemma</i>	4.27* (0.023)* FL ^a , UN ^{ab} , FS ^b	1.16 (0.341)	0.22 (0.951)	341.37* (0.0001)*
<i>Leitoscoloplos</i>	0.84 (0.443)	2.30 (0.097)	1.08 (0.393)	10.50* (0.0001)*
<i>Mediomastus</i>	0.73 (0.493)	1.88 (0.153)	0.57 (0.723)	2.82* (0.056)*
<i>Nereis falsa</i>	0.62 (0.544)	3.69* (0.023)* CH ^a , 5 ^b , 200 ^b , 500 ^b	0.35 (0.877)	4.60* (0.009)*
Oligochaete	2.95 (0.068)	0.64 (0.594)	0.96 (0.458)	2.24 (0.104)
<i>Streblospio</i>	2.36 (0.112)	0.40 (0.754)	1.25 (0.311)	5.03* (0.006)*
Syllid	0.81 (0.456)	3.91* (0.018)* 200 ^a , 500 ^a , 5 ^{ab} , CH ^b	1.27 (0.303)	4.60* (0.009)*
<i>Tharyx</i>	4.09* (0.027)* UN ^a , FS ^b , FL ^b	0.52 (0.672)	2.41 (0.060)	3.86* (0.019)*
Total	1.92 (0.164)	0.56 (0.647)	1.37 (0.265)	6.08* (0.002)*

which was more abundant near uniform reefs than near fragmented ones. This difference was driven by a dramatic decrease in abundance from 2002 to 2003 found in cores taken within the channel between reef patches (Figure 19).

Leitoscoloplos and *Nereis falsa* both showed effects of distance on abundance, as did syllids (in 2003 only). Although not distinguished in the SNK test, there were significantly higher abundances of *Leitoscoloplos* found in channels of the fragmented treatments and at the 5 cm distance from the reef than at 200 and 500 cm distances from the reefs ($F=6=3.60$, $p=0.019$, Table 11). There was also a treatment-distance interaction detected for this species ($F=2.66$, $p=0.031$). Cores taken inside the channels created by the fragmented patches also had significantly higher abundances of the polychaete *Nereis falsa* than for any other distance ($F=3.69$, $p=0.023$). This difference can only be seen in 2003. In contrast, syllids were actually *less* abundant in channel cores than in cores taken at all other locations in 2003 ($F=3.91$, $p=0.018$), even with their general increase in abundance through this study.

Diversity and Species Richness of Infauna

Overall diversity of infauna was higher in 2002 than in 2003. Cores taken near small fragmented reefs had the highest diversity overall during both years. Diversity of infauna near large fragmented reefs was highest during the first year, and then dropped dramatically the following year. A similar pattern was seen for the mud flat, with higher values in 2002. Overall, the mud flat exhibited the lowest diversity of all treatments.

The diversity of infauna found in cores at specific distances away from the reefs varied slightly (Figure 20). In 2002, diversity was higher at 200 cm from the uniform and small fragmented reefs than at 5cm from the reefs' edges. The large fragmented treatments exhibited a

different pattern, with highest diversity within the channels. In 2003, diversity was relatively similar across all distances for the uniform and small fragmented reefs. Large fragmented reefs, however, exhibited far lower values than their counterparts, with the exception of cores taken within channels. Diversity was particularly low in cores taken 500 cm from large fragmented treatments.

Overall species richness was remarkably similar between all treatments, during 2002. In 2003, species richness was lower overall, but especially low for infauna found near large fragmented reefs compared to other treatments, with the highest number of species found on the mudflat, away from the reefs. Species richness varied somewhat with distance. In 2002, richness was lower within channels of fragmented treatments than at 5 and 200 cm distances (Figure 21). This difference is also present in 2003, although not as pronounced for the small fragmented reefs as for large.

Infaunal Biomass

Biomass averages of infauna from 2002 samples did not differ significantly from that of 2003 (Table 12). There were no overall effects seen for treatment or distance. However, when years were analyzed separately, there were significant differences in infaunal biomass during 2003. Uniform and small fragmented reefs had average infaunal biomasses that were twice that of the large fragmented reefs ($F=4.06$, $p=0.020$, Figure 22). In addition, infaunal biomass found in cores from channels were greater than the biomass of infauna at any other distance ($F=2.68$, $p=0.051$).

Figure 20. Diversity of infauna found in cores for all treatments and distances. UNIF= uniform, FRSM=small fragmented, FRLG=large fragmented, MUDF=mudflat, 5=distance of 5 cm, 200=distance of 200 cm, 500=distance of 500 cm, CHAN=in channel between reef patches.

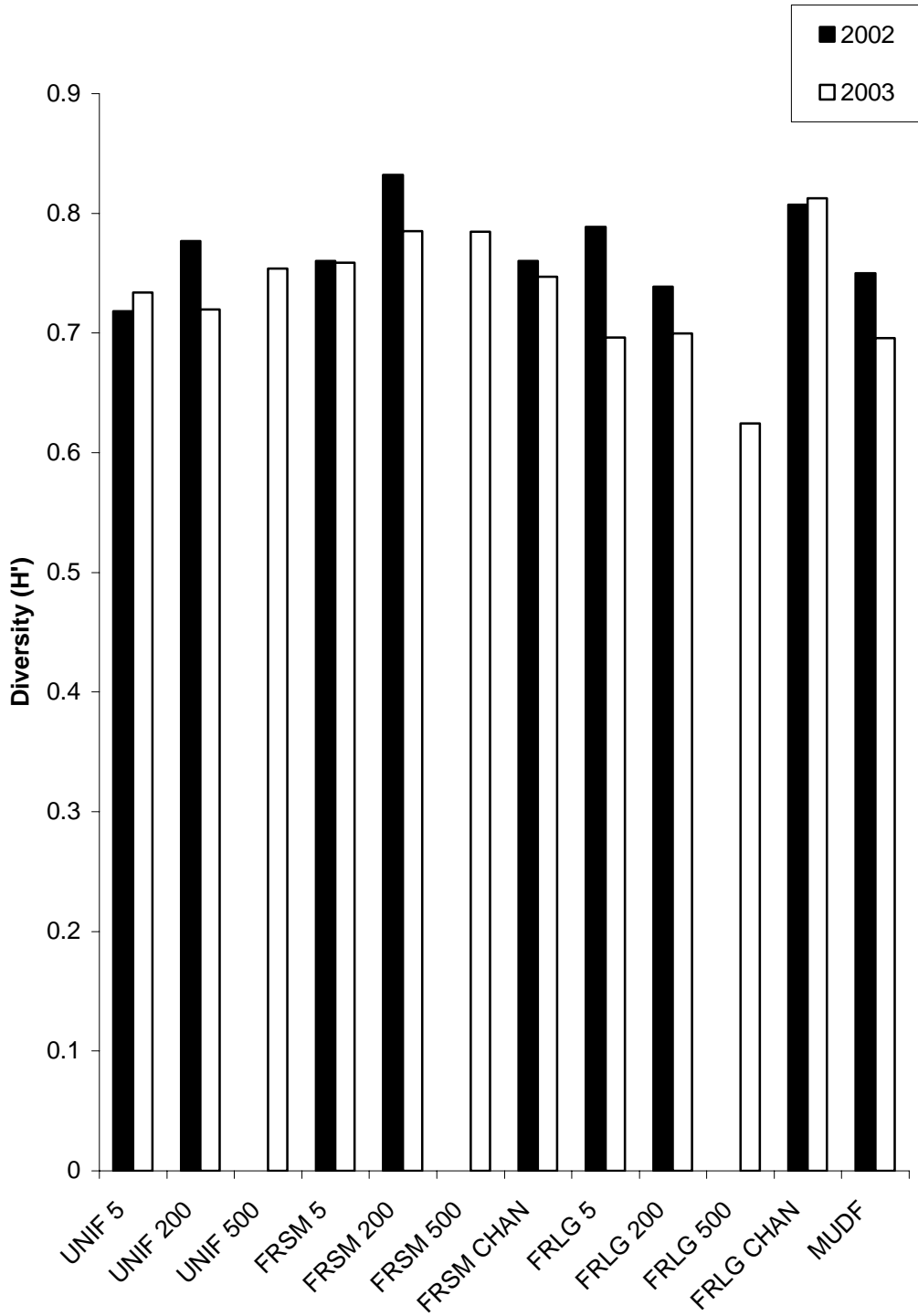


Figure 21. Species richness of infauna found in cores for all treatments and distances. UNIF= uniform, FRSM=small fragmented, FRLG=large fragmented, MUDF=mudflat, 5=distance of 5 cm, 200=distance of 200 cm, 500=distance of 500 cm, and CHAN=in channel between reef patches.

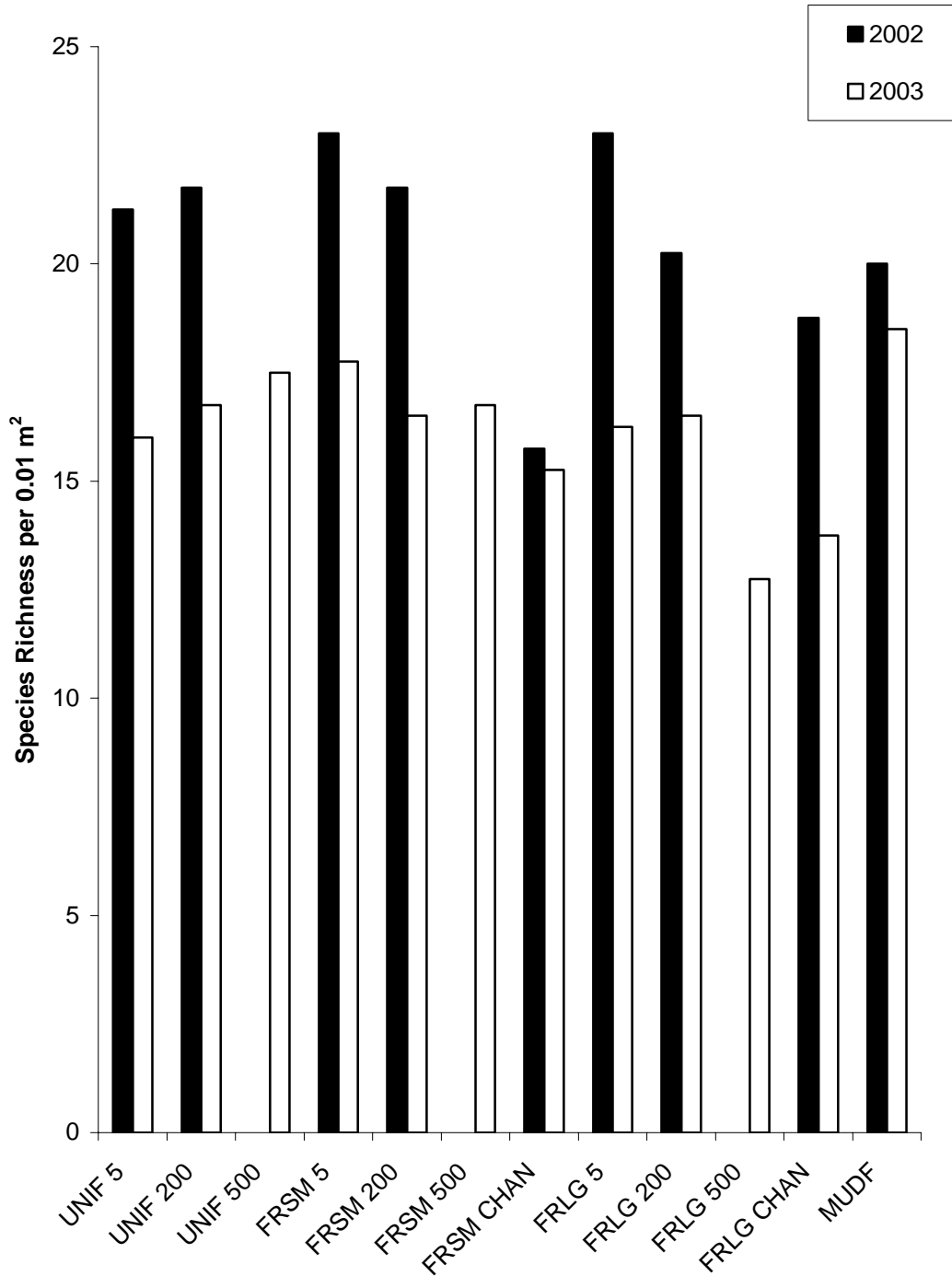
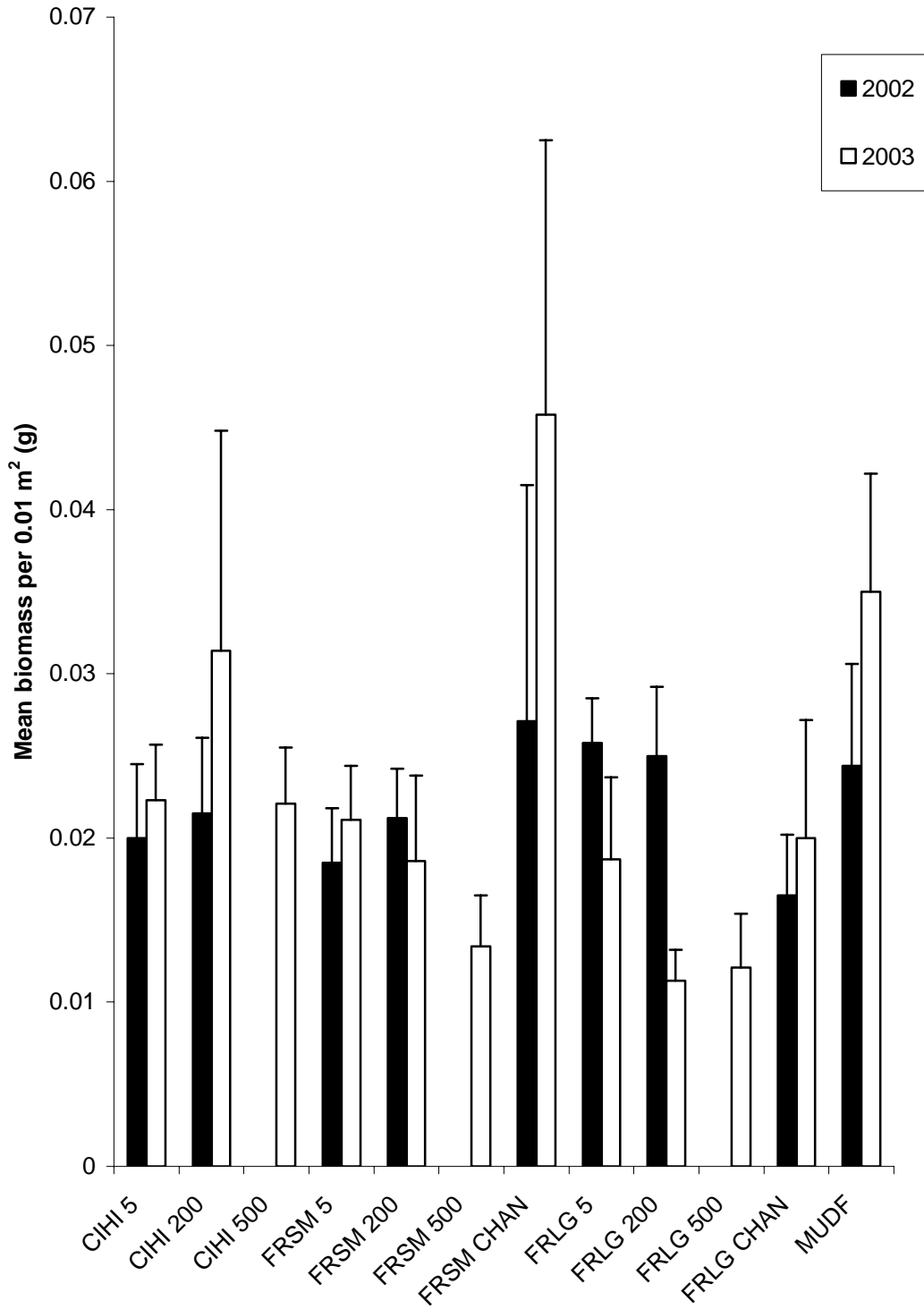


Table 12. 4-way ANOVA results for the effects of treatment, distance, year, site, and all possible interactions on the overall biomass of infauna for created reef treatments. Shown are F-values and (p-values) with significant ($p < 0.05$) comparisons indicated by an asterisk.

Treatment	Distance	Year	Year*Treat	Site	Treat*Distance
1.30 (0.274)	2.14 (0.097)	0.14 (0.705)	2.02 (0.135)	5.43* (0.001)*	1.60 (0.163)

Figure 22. Overall infaunal biomass from July 2002 and July 2003. UNIF= uniform, FRSM=small fragmented, FRLG=large fragmented, MUDF=mudflat, 5=distance of 5 cm, 200=distance of 200 cm, 500=distance of 500 cm, CHAN=in channel between reef patches.



DISCUSSION

As predicted by results of previous studies (Coen et al. 1999, Posey et al. 1999), greater utilization of oyster reefs compared to open mudflat was observed for many species of epifauna, including amphipods, *Eurypanopeus depressus*, *Geukensia demissa*, *Palaemonetes pugio*, *Panopeus herbstii*, and *Urosalpinx cinerea*, as well as the total overall abundances of organisms collected from oyster shell excavations. In addition, diversity and species richness of organisms collected using Breder trap and excavation methods was similar for created and natural reefs, indicating that artificial reefs provide a similar ecological function as their natural counterparts. Although abundances of fishes caught in Breder traps and gill nets were similar between created and natural reefs, they did not exhibit significantly higher abundances over oyster reefs compared to open mudflat, possibly reflecting the necessity of passing over mudflat areas as the tide floods intertidal regions and variable catches, spatially and temporally. However, utilization of oyster reefs themselves was affected by reef fragmentation.

This can be seen for *Lagodon rhomboides*, which was by far the most common species caught in Breder traps. During both summer sampling periods, utilization of large fragmented reefs was significantly higher than that of uniform reefs. This suggests that reef fragmentation (at least at the larger scale) is providing some benefit to the fish during this time. For example, the increased edge to interior ratio could be providing the fish more access to invertebrates inhabiting the reefs, thus increasing access to food sources. Juvenile pinfish feed on encrusting algae (frequently seen on oyster reefs) and invertebrates found in and around oyster reefs (Lehnert and Allen 2002). Gut content analysis has also revealed grass shrimp, amphipods, and mud crabs *Panopeus herbstii* and *Eurypanopeus depressus*, in the stomachs of pinfish < 150 mm in length (Lenihan et al. 2001). All of the aforementioned species were abundant in the reefs

sampled in this study. Fragmentation might also be providing pinfish with some relief from predation pressures, in that channels created by reef patches could provide possible escape routes or hiding places. Indeed, it has been suggested that habitat heterogeneity may modify the outcomes of biological interactions such as competition and predation (Coen et al. 1981). Hettler (1989) found higher abundances of pinfish in a marsh bordered by deep channels with shell debris than in marshes bordered by bare sand. The channels created by fragmented reefs in this study may have a similar function.

Although spring sampling did not produce any significant differences in pinfish abundances, this is when pinfish were at their smallest (average size was 27.1 mm TL). It may be that the reef structure itself was overwhelmingly large relative to their size, thus they may not have perceived any differences in reef morphology. The scales over which habitat structure occur influence how organisms respond to the environment (Irlandi and Crawford 1997). For small juveniles, the scale of fragmentation may have been too large to have an affect on pinfish utilization. The pattern of preferential use of large fragmented treatments by pinfish again disappears in fall. However, catches were lower during fall than any other season, reflecting movement of larger pinfish out of the estuary.

Gill nets were used during this study in hopes of further evaluating reef utilization by larger nektonic individuals, as Breder traps generally target juveniles and are species-selective (Rozas and Minello 1997). However, gill nets exhibited much lower catches relative to Breder traps. Catches were highest in fall of 2002, when there was again a slight trend for pinfish to have higher abundances on fragmented reefs than on uniform reefs. *Leistomus xanthurus* also exhibits this same trend during fall gill net sampling. Although gill nets of similar length and mesh sizes were useful in previous studies to catch larger individuals (> 100 mm) of species

such as croaker, menhaden, bluefish, spot, striped bass, flounder, and weakfish (Harding and Mann 2001, Lenihan et al. 2001), catches in the present study were too low to be conclusive. The study sites used by Harding and Mann (2001) had a maximum tidal current of 0.12 m/s (Chen et al. 1977), and saw significantly higher catches from dusk to dawn. The study sites located in Masonboro Sound, on the other hand, had average flow rates of 0.02 m/s, and nets were put out only during the daytime in the present study.

Small fragmented treatments did not have similar faunal distribution patterns as the large fragmented treatments. Lower abundances on smaller fragmented reefs were common for many species, including *Lagodon rhomboides* (Breder traps and gill nets), *Fundulus heteroclitus* (Breder traps), *Leiostomus xanthurus* (gill nets), *Panopeus herbstii* (excavations), and *Geukensia demissa* (biomass from excavations) which all had lower numbers on small fragmented treatments compared to either larger fragmented or uniform treatments. Fragmentation is believed to be advantageous to species that prefer edge to interior habitat, but only after a minimum, or threshold, patch size is reached. I propose that the small fragmented reefs used in this study are an example of patch sizes below this threshold. The small fragmented treatments represent a situation of habitat degradation in addition to habitat fragmentation, in that the overall area of shell cover was half that of the uniform or large fragmented treatments. Some models for terrestrial systems predict that changes in habitat configuration should begin to influence faunal abundance at a threshold level of 30-50% habitat loss (Andr n 1994, Fahrig 1998). An analogous minimum patch requirement may explain lower abundances of fishes and certain eipfauna on small fragmented treatments compared to fragmented reefs with larger patch sizes. Highest biodiversity has been predicted to occur at intermediate levels of habitat fragmentation (Eggleston 1999), analogous to the intermediate disturbance hypothesis (Connell

1978). Although not significant, *Fundulus heteroclitus* caught in Breder traps during fall showed a similar pattern to that of *Lagodon rhomboides*, in which there was a general trend of higher abundances on large fragmented reefs than on small fragmented treatments, with intermediate abundances on uniform reefs. It is curious that this trend was *not* seen during summer sampling periods, when pinfish showed preference for large fragmented treatments. However, mummichogs were significantly larger during summer ($F=12.05$, $p=0.0006$) than in any other season. As seen for pinfish, during the season in which largest fish are caught, there was no trend towards preferential use of the large fragmented treatments. The larger *Fundulus heteroclitus* preferred the small fragmented treatments to the large ($F=4.21$, $p=0.023$). It is possible that the benefits of fragmentation may be a function of size/age. The responses of larger pinfish and mummichogs might also be indicative of a change in the definition of refuge habitat for these species as they get larger.

Effects of fragmentation on epifauna in this study varied. Although amphipods, *Eurypanopeus depressus*, *Geukensia demissa*, *Palaemonetes pugio*, *Panopeus herbstii*, polychaetes, and *Urosalpinx cinerea* were all more common on oyster reefs than on nearby mud flats, only abundances of *Geukensia demissa*, *Palaemonetes pugio*, *Panopeus herbstii*, and *Urosalpinx cinerea* seemed to be affected by habitat fragmentation and habitat loss. Significantly higher abundances of *Panopeus herbstii* were found on large fragmented and uniform reefs than on small fragmented reefs, once again suggesting that the small fragmented reefs are below the threshold for which fragmentation is advantageous. The common mud crab's distribution may reflect indirect effects of food availability. The Atlantic ribbed mussel *Geukensia demissa*, a common food source for *Panopeus herbstii* (Seed 1980), had a greater total biomass on large fragmented reefs than on small fragmented reefs. Presence of prey may

also have affected blue crabs, *Callinectes sapidus*, which, when encountered, occurred only on large fragmented treatments. Blue crabs, like mud crabs, are known to feed extensively on *Geukensia demissa* (Seed 1980). Both mud crabs and blue crabs also prey upon juvenile oysters (Grabowski 2004), which may have been more abundant on large fragmented treatments, given the larger area of shell cover to that of small fragmented reefs.

In contrast to *Panopeus herbstii*, abundances of the flat mud crab *Eurypanopeus depressus* were not affected by oyster reef fragmentation. However, the diet of the flat mud crab is very different from that of the common mud crab. *Eurypanopeus* are smaller on average than *Panopeus*, and have a less restrictive, more omnivorous diet, consuming primarily algae, detritus, and - to a lesser degree - polychaetes, and amphipods (McDonald 1982). Neither polychaetes nor amphipods found during excavations differed among fragmentation treatments, and algal mats seen during spring and winter sampling covered more area on average (personal observation) on uniform reefs. In addition, *E. depressus* primarily occupy habitats created by oyster clusters, and are often absent from reefs that have little or no cluster material (Meyer 1994). Thus, continuous reefs of high vertical complexity (i.e. the uniform treatments) may be more beneficial for this particular species.

Urosalpinx cinerea and *Palaemonetes pugio* were the only species of epifauna found to have a positive correlation with the small fragmented treatments. There were significantly greater values for both abundance and biomass of oyster drills on small fragmented reefs. Decreased utilization of small fragmented reefs by predators (pinfish and common mud crabs) may have released the oyster drills from predation pressure, allowing for the increase in biomass. In addition, the oyster drills, responding to reduced predation levels, may further contribute to the degradation of the reef by consuming higher numbers of juvenile oysters.

Predation effects also may be important to understanding infaunal abundances among treatments and distances from reefs. Some reef-associated predators on offshore hard-bottom reefs use the reef primarily as refuge, and depend on the surrounding mud flat for food, causing abundance halos around the reef (Posey and Ambrose 1994). The same may be true for oyster reefs. Total abundances of infauna observed in this study were significantly higher in 2002 than in 2003 ($F=9.49$, $p=0.003$), suggesting that predators (e.g. decapod crustaceans and epibenthic fishes) drawn to the oyster reefs may have decreased the numbers of infauna. This may have been particularly true for the bivalve *Gemma gemma* and the polychaete *Tharyx*. Both species showed lower abundances during the second year of sampling compared to the first. During first year sampling, the abundances of *Gemma* and *Tharyx* were consistent across all treatments and distances from the reefs. However, during the second year, significantly more gem clams were found on the open mud flat than in cores taken near reefs. In addition, higher abundances of *Tharyx* were found near uniform reefs than near fragmented reefs, consistent with observations of greater predator abundances near fragmented reefs (pinfish and common mud crabs). Total infaunal biomass in 2003 was much lower in cores near large fragmented reefs than near uniform or small fragmented reefs. Although higher abundances of *Gemma* were found near large fragmented reefs than near small, this may have been due to increased predation near small fragmented reefs by the grass shrimp, *Palaemonetes pugio*, which showed a slight preference for the small fragmented treatments.

Although no halo was observed (i.e. infaunal abundances at 5 cm were not less than abundances at 500 cm), this may be due to the intertidal nature of the study sites. Key nektonic predators such as pinfish are transient species, forced to leave the reefs at low tide. Thus, predation on infauna surrounding the reefs is not constant, and may be less than that observed

near subtidal reef structures. In addition, larger nekton may have perceived an entire site as one large reef assemblage, thus 500 cm may not have been a sufficient distance to see a decrease in infaunal abundances at these locations.

On the other hand, reef morphology may also affect microphytobenthos biomass and nutrient levels, which may in turn impact infaunal communities. The presence of several smaller reef patches may have an overall enhancement effect on adjacent microphytobenthos communities compared to one large reef of similar area. Molesky (2003) observed an increase in organic content in convolutions of created oyster reefs. A similar effect may occur within the channels created by fragmented reefs. This increase may then enhance the local infaunal community. In this study, the polychaetes *Leitoscoloplos* and *Nereis falsa* both showed effects of distance from reef on abundance. Cores taken inside fragmented channels had higher abundances than cores taken at 5 cm, 200 cm, and 500 cm from the reef's edge. This pattern may be an indirect effect of fragmentation, in that fragmentation may affect the organic content and grain size of sediment, as well as increase nutrients and microphytobenthos biomass within the channels, due to current flow effects, which in turn might have increased the numbers of polychaetes in the area.

This study provides additional evidence for the utilization of oyster reefs as habitat by many different marine organisms. Although fragmentation of oyster reefs did not affect nekton, epifauna, and infauna uniformly, this study does present evidence that it influences the abundance and biomass of several species. Both direct and indirect effects of fragmentation were seen. More importantly, there is evidence for a patch-size threshold, beneath which negative effects on abundances are seen. Impacts of patch-size may only be detected in large patches where different core and edge micro-habitats can be established (Bell et al. 2001). A

review by Andr en (1994) of studies on birds and mammals states that when <30% of the original habitat remains in the landscape, species richness declines dramatically, but the exact percentage would depend on original landscape characteristics. This study presents evidence of a similar threshold, in that a 50% reduction in habitat caused a decline in abundances of many species. This loss of habitat also caused an increase in abundance and biomass of the oyster drill *Urosalpinx cinerea*, which may then further contribute to reef degradation through predation of the oysters themselves.

As oyster reef degradation caused by overfishing, pollution, and disease continues, naturally occurring reefs grow closer and closer to this threshold. With the decline in natural oyster reefs, there has been increasing efforts made to improve the success rate of artificial oyster reef restoration. Past efforts have focused on the construction of large, expansive reefs with rather low edge to interior ratios. However, in recent years restoration of subtidal oyster reefs within the Chesapeake Bay has been guided towards multiple small reef patches within close proximity of one another (Luckenbach, personal communication), as this landscape may be advantageous over the large, expansive reefs favored in the past. The results of this study support this idea, and suggest that reef fragmentation is also beneficial when restoring intertidal oyster reefs. Fragmentation may be particularly useful if increasing faunal abundances of organisms which utilize reefs as habitat is a desired goal of the restoration. Similar to designing a salt marsh with many small channels through it to provide more access to edge habitat, fragmentation of intertidal oyster reefs (with patch sizes above a certain threshold) may be a beneficial option for restoration managers to consider.

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