

HABITAT COMPLEXITY AND PATCH CHOICE: SPATIOTEMPORAL DISTRIBUTION OF  
FORAGING SHOREBIRDS ON INTERTIDAL SAND FLATS

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## **ABSTRACT**

BETH MARIE VANDUSEN: Habitat Complexity and Patch Choice: Spatiotemporal  
Distribution of Foraging Shorebirds on Intertidal Sand Flats  
(Under the direction of Charles H. “Pete” Peterson)

This early-winter study correlated patch- and landscape-level factors with spatial and temporal shorebird foraging patterns on four discrete, yet connected, intertidal sand flats in the New River Inlet, North Carolina, USA. Shorebirds were distributed non-randomly among flats, with major differences in abundance and species composition strongly correlated with the benthic macroinvertebrate community. Sediment characteristics added explanatory power; benthic macroinvertebrate community and sediment composition together explained two thirds of the variation in shorebird community patterns. Influence of landscape characteristics such as area-to-edge ratio of the flat and nature of the surrounding habitat (indicative of varying predation risk) likely contributed to the unexplained variation.

Sedimentary influence was exemplified when probing shorebirds avoided a sand flat that contained large amounts of coarse material (gravel, shell). Significantly higher prey (polychaete) densities on this flat suggested that the coarse material acted as a refuge for infaunal prey by deterring probing shorebirds.

To the Author of life...

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## LIST OF ABBREVIATIONS AND SYMBOLS

ANOSIM	Analysis of Similarity
ANOVA	Analysis of Variance
BEST	PRIMER5's <u>B</u> io- <u>E</u> nv + <u>S</u> tepwise procedures combined in PRIMER6
BR	Broad Flat
BVSTEP	PRIMER's Stepwise Procedure
IDW	Inverse-Distance Weighted
IS	Island Flat
LT	Low Tide
LT-1.5	Late Ebb Tide
LT-3	Mid Ebb Tide
MDS	Multidimensional Scaling
SE	Semi-Enclosed Flat
SH	Shell Flat
TC	Tidal Creek Flat
$\rho$	Spearman Correlation Coefficient

## **CHAPTER 1**

### **I. INTRODUCTION**

To stem the decline in shorebird populations around the globe, wildlife managers have employed a number of strategies including habitat creation, restoration, manipulation, and mitigation (e.g. Broome et al. 1998, Sanders 2000, Brusati et al. 2001). As we attempt to protect and enhance populations of species that are in decline, often a result of habitat loss or fragmentation (Reineking & Südbeck 2007), it is imperative that we understand the factors or processes that determine habitat use and value to the target species. Shorebird foraging habitat in general, and intertidal sand flats in particular, provide a window into the challenge of understanding non-random patch use: that is, if flats (patches) in an area are not used equally, then why are some used more than others? What makes one patch more valuable than another, and why does the choice vary among different species of shorebirds?

The processes driving non-random shorebird foraging operate at both local (patch) and landscape levels. At a local scale, patch characteristics determine prey availability, defined by Menge (1972) as the proportion of physically present prey that can be consumed by a predator. While multiple studies have reported a direct correlation between feeding shorebird distribution and abundance and distribution of primary prey (e.g. Goss-Custard 1970, Goss-Custard et al. 1977, Bryant 1979, Colwell & Landrum 1993, Ribeiro et al. 2004), prey abundance is only a part of prey availability— it is the

maximum amount that could be consumed if all prey were accessible. Because the absolute abundance of prey may be less important than the availability of those prey (Ontiveros et al. 2005), any evaluation of prey as a driver of shorebird distributional patterns must go beyond absolute abundance of prey and consider the factors influencing prey availability.

Sediment characteristics directly and indirectly influence availability of prey to foraging shorebirds (Quammen 1982). For birds that forage tactilely, substrates with grain sizes similar to the diameter of prey may impair a bird's ability to detect or capture those prey (Quammen 1982). Additionally, sediment penetrability influences prey availability by affecting bill probing depth and level of resistance encountered by the probing bill (Myers et al. 1980, Kelsey & Hassall 1989). Coarse sediment particles and surface shell hash may prevent probing shorebirds from penetrating the sediment completely, effectively arming the substrate and creating a refuge for prey (Peterson et al. 2006). Sediment composition also affects prey availability indirectly by controlling the rate at which water drains through the substrate. Tidal movement and water drainage rates influence prey surface activity (Vader 1964, Rosa et al. 2007), which is essential for visual foragers such as plovers (Pienkowski 1980).

Tidal flat surface topography also influences prey availability. Tidal flats with more uneven surfaces and scattered microtopographic depressions are left with shallow pools as the tide recedes, creating areas with prolonged surface water-cover and, consequently, prolonged heightened surface activity of certain types of prey (Vader 1964). Conversely, flats with minimal microtopography facilitate foraging by species

such as the semipalmated plover, which intersperses pecks with bursts of running (Nol & Blanken 1999).

Because prey in a given area of an emerging flat are often most active when the water first recedes (Vader 1964), the relationship between flat area and length of the water edge affects the proportion of accessible prey. The more convoluted the water edge, the greater its length and the associated band of surface-active prey. Additionally, water edge length is directly related to how each flat is connected to higher ground. For instance, two square flats with the same area would vary greatly in edge length if one flat were bordered by intertidal marsh on three sides and the other were peninsular, with supratidal land on one side alone.

As flats are imbedded in a matrix of surrounding habitat, it is important to consider landscape-scale characteristics that may influence patch use by foraging shorebirds. In addition to determining water edge length, the surrounding matrix could act as a potential source of hidden predators (as in the case of marsh grass or other vegetation) or, inversely, could provide a predator-free buffer (open water or a wide, vegetation-free backbeach). Dekker and Ydenberg (2004) provide an example of the former: their study shows that dunlins in British Columbia face an increased risk of predation by raptors as the distance to vegetation decreases.

Another landscape-scale characteristic to consider is the extent of patch connectivity and accessibility, which are based on spatial arrangement. For highly mobile shorebirds, exposed flats in close proximity to one another are well connected (Fahrig & Merriam 1985). However, temporal variation in tidal height creates patterns of exposure and

inundation that can vary by flat and affect patch accessibility. Because flats differ in elevation, some flats are accessible for longer periods of time than others. The change in tidal height also creates continual variation in available patch size, and elevational gradients within particular flats affect the rate at which new flat areas are exposed. Consequently, non-random patch use may result from changes in patch accessibility driven by the tidal cycle.

Beyond flat and landscape characteristics, patterns of patch use by foraging shorebirds may be affected by behavioral interactions between birds. Negative interactions (interference competition) could directly affect patch choice by keeping particular individuals or species out of their “preferred” or optimal patches (Vahl et al. 2005); similarly, positive interactions or behavioral patterns such as birds cuing in on other birds (flocking) would lead to non-random distributions (Sridhar et al. 2009).

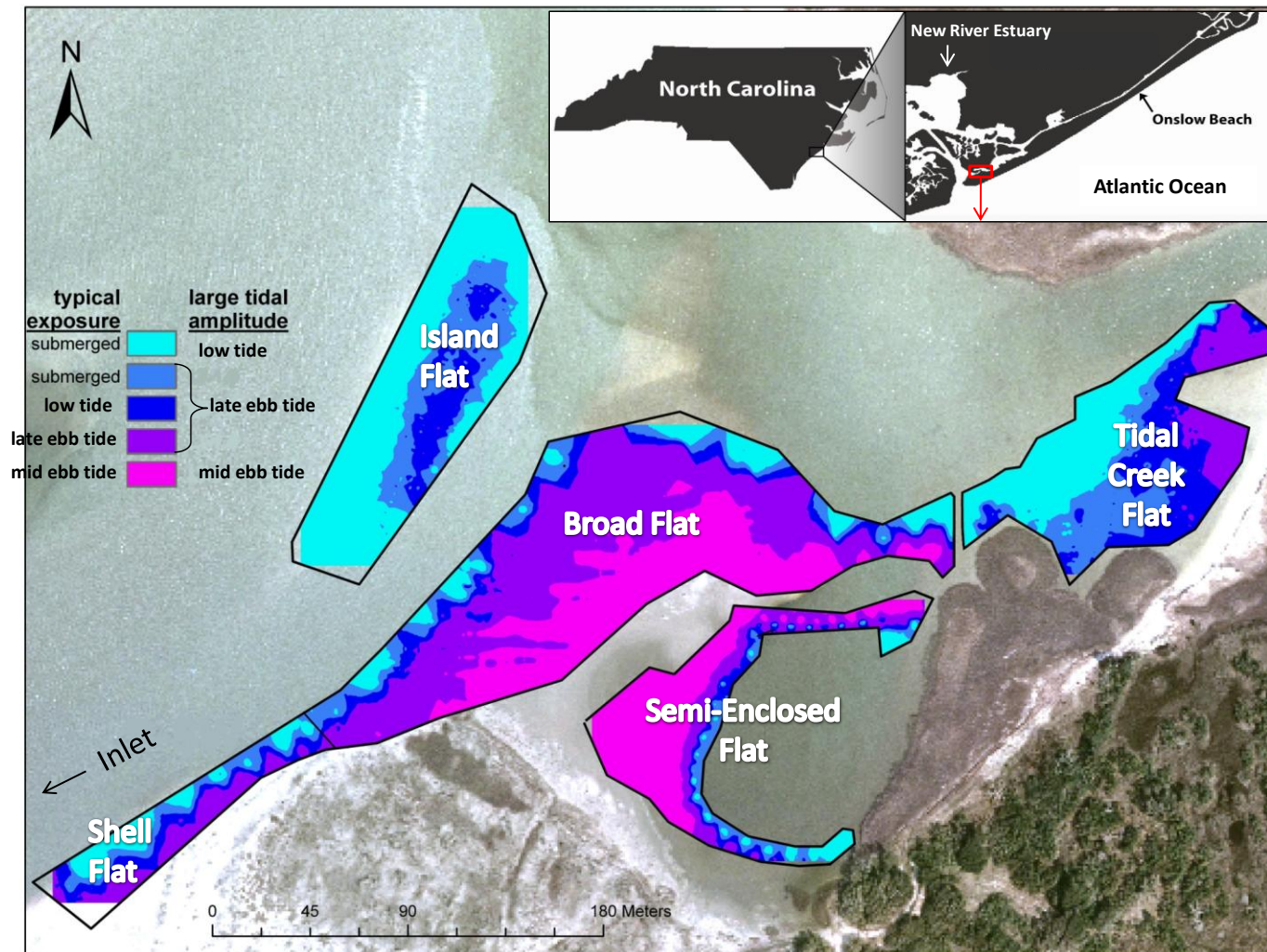
In this study I asked whether wintering shorebirds exhibited different foraging patterns among a group of discrete sand flats located within 250 m of each other inside the New River Inlet (North Carolina, USA), and, if so, which physical or biological characteristics correlated with the observed shorebird foraging patterns. Shorebird observations included both spatial and temporal components, with an emphasis on microhabitat quality and tidally-driven changes in patch size.

## II. MATERIALS AND METHODS

**Study site.** Marine Corps Base Camp Lejeune is located on the North Carolina coast between Cape Lookout and Cape Fear (Fig. 1). Camp Lejeune's 12 km-long, southeast-facing, barrier island Onslow Beach borders the Atlantic Ocean and is bounded on the south by the New River Inlet. My study site, which consisted of four back-barrier intertidal sand flats, was located at the southwest tip of Onslow Beach, adjacent to the inlet. These sand flats experience semi-diurnal tides with mean and spring tidal ranges of 1.3 and 2.0 m, respectively (NOAA 2008).

The exposed flats ranged in area from about 0.5 to 2 ha at the lowest low tides, and were within 5-250 m of each other (Fig. 1). The first flat ("Semi-Enclosed Flat") was the most sheltered of the group; it was bordered on the landward side by marsh and sand spit and it partially circled a large pool of water that was connected to the estuary by a short, narrow (1-2 m wide) tidal stream. The second flat ("Broad Flat") had the greatest intertidal area of the four flats, and was located on the estuary-facing side of the sand spit. The southwest tail of this flat was sampled separately from the rest of the flat because of obvious differences in surface shell cover (hereafter: "Shell Flat"). The third flat, "Island Flat," was a sandy shoal that emerged shortly before low tide and ran parallel to Broad Flat. Located farthest from the inlet, the final flat ("Tidal Creek Flat") bordered a marsh and a tidal creek and was the muddiest of the sand flats. Broad Flat and Semi-Enclosed Flat emerged earliest in the tidal cycle, beginning about three hours before low tide. As the tide continued to ebb, Tidal Creek Flat was exposed next, followed by Island Flat. Tidal amplitudes were fairly consistent over the course of the

**Figure 1. Elevation map of study site.** Crenulations on water edge of Broad and Semi-Enclosed Flats are artifacts of elevation measurement technique.





study, though spring tides in mid December caused earlier exposure of Island Flat and greater total exposed flat areas during that time.

GPS location and elevation data were recorded with a Trimble RTK (Real Time Kinematic) unit on 12 November 2008 and supplemented by additional measurements on 9 February 2009. Survey points were recorded at 0.5 m intervals along transects spaced approximately 10 m apart, perpendicular to the low tide water line of each flat. A total of 4388 points were imported into ArcMap and inverse-distance weighted (IDW) to interpolate elevations for all exposed sand flat surfaces. IDW data were used to calculate surface area exposed for each flat at successive tidal heights (Table 1).

**Table 1. Flat areas (hectares) at observed tidal stages, by tidal range.** Flat surface area at a given tidal stage varied depending on tidal amplitude. Tides on a given observation date were classified as “normal” or “spring” based on exposures recorded in the field; surface areas calculated for each tidal regime listed below. SE = Semi-Enclosed Flat, BR = Broad Flat, SH = Shell Flat, IS = Island Flat, TC = Tidal Creek Flat.

Tidal Stage	Tidal Range	SE	BR	SH	IS	TC	Observation Dates
Mid Ebb	Normal	0.29	0.52	0.01	0	0	Nov 10, 24-26, 28
	Spring	0.29	0.52	0.01	0	0	Dec 13, 15, 16
Late Ebb	Normal	0.40	1.19	0.25	0	0.13	Nov 10, 24-26, 28
	Spring	0.44	1.34	0.30	0.34	0.34	Dec 13, 15, 16
Low Tide	Normal	0.44	1.34	0.30	0.10	0.34	Oct 27-31, Nov 1, 10, 24-26, 28
	Spring	0.54	1.53	0.50	0.74	0.80	Dec 13, 15

**Shorebirds.** Shorebird surveys were conducted on 17 dates between 15 October and 16 December 2008 (Table 1, Appendix A). Observations were conducted at 90-minute intervals beginning three hours before low tide (“mid ebb tide”) -- soon after Semi-Enclosed and Broad Flats first emerged -- and ending at low tide when all flats were fully exposed. Observation dates were chosen based on coordination of the tidal and solar cycles, when a falling tide took place in daylight. Temperature and wind velocity were recorded; all observations were made during non-rainy days when temperature was 8-20 °C (mean 14 °C). During the first week of observations, several wooden stakes were inserted in Broad Flat in order to facilitate tidal height comparisons across dates. Stakes functioned as a point of reference for daily tide line movement; estimates of flat exposure area based on tide line distances from the stakes were made in the field, and later combined with detailed elevation measurements. Shorebird surveys were conducted by walking the length of the sand spit along the vegetation line and counting and identifying all foraging shorebirds on each exposed flat. Because I could see every flat from my sand spit vantage point, I was able to avoid double-counting birds that moved from one flat to another. While little among-flat movement occurred during most of the observations (which usually took about 10 minutes), if birds did move between flats while I was counting I only recorded them at the flat that they were on at the end of my observation. Bird counts for the largest flat were divided into two sections; the small tail on the southwest end of the flat (“Shell Flat”) was observed separately from the main part (“Broad Flat”) because of its differences in surface shell cover and human disturbance (it was frequently occupied by fishermen during

observation periods). Observations were made using 8x40 porro prism binoculars at a minimum distance of about 40 m from foraging birds. This distance was sufficient to avoid disturbing the birds; preliminary observations showed that it is usually possible to get even closer before the birds react and modify natural behavior.

To determine whether shorebird community composition differed among flats (and if an among-site pattern was consistent across time), I used the PERMANOVA routine in PRIMER6 (Anderson et al. 2008) to analyze the shorebird community dataset using a randomized block design (Quinn & Keough 2002), with fixed factor “Flat” and random blocking factor “Date.” Each tidal stage was analyzed separately, and because Shell Flat was disturbed by fishermen on a number of dates, it was excluded from the analysis. A dummy variable was added during the construction of resemblance matrices in order to prevent the loss of “zero” samples (observations with no birds recorded) and associated degrees of freedom (Clarke et al. 2006). Before incorporation into PERMANOVA, shorebird counts were standardized by area (birds per newly exposed hectare). “Newly exposed area” was defined as the area gained by a flat since the previous observation interval; if the flat was not exposed previously then all area that had emerged was used. I chose to standardize the data by newly exposed area because preliminary observations revealed that birds concentrated on areas that were recently emerged rather than foraging across entire flats.

To better visualize among-flat differences in the shorebird community, I created a non-metric multidimensional scaling (MDS) ordination using a Bray-Curtis similarity

matrix constructed from the means of each flat/tidal stage combination. Additionally, I constructed a hierarchical cluster (PRIMER v.6.1.11) of these means.

I also performed a number of univariate analyses in order to gain insight into the multivariate PERMANOVA results. Shorebird univariate analyses compared: (1) abundances, or total birds per flat at particular tidal stages, and (2) separately, bird densities, calculated as number of birds per newly exposed hectare. Once again, I excluded Shell Flat because birds in that area were frequently disturbed by fishermen. To determine if mean abundances and densities differed among the flats, I performed a series of one-way analysis of variances (ANOVAs) followed by Tukey-Kramer HSD post-hoc tests.

**Benthic macrofauna.** Benthic macrofauna were sampled on 12 November 2008. The species abundances recorded on this sampling date were assumed to be representative of abundances across the entire shorebird observation period. It is unlikely that any major recruitment events occurred during this two-month early-winter time period (e.g. Leber 1982, Watzin 1984); additionally, foraging pressure from estuarine predators (fishes, crabs) is lowest during the winter (Grabowski et al. 2005), so benthic species composition and abundance were likely fairly consistent across this short period of time. Flats were sampled for benthic macrofauna at three tidal levels: (1) three hours before low tide (mid ebb tide), (2) 90 minutes before low tide (late ebb tide), and (3) low tide. Flats were sampled only if they were exposed at that tidal stage. Consequently, Tidal Creek Flat was not sampled until late ebb tide and Island Flat was not sampled until low tide. The temporal pattern of flat exposure that occurred on 12

November was typical of exposure patterns observed during much of the shorebird observation period; however, larger tidal amplitudes in mid-December led to several early exposures of Island Flat (at late ebb tide) as well as larger total flat areas.

At each tidal stage the flat surface was divided into microhabitats based on relative local elevation and apparent water content. This resulted in up to three microhabitat levels per flat, with sampling areas classified as “saturated” (damp, but no apparent surface water), “glossy” (water visible at surface level of sediment), or “subtidal” (<3 cm of water cover). Sampling at later tidal stages was focused on newly exposed area, so that a “saturated” sample at late ebb tide was more seaward than a “subtidal” sample taken at mid ebb tide. Because Island and Tidal Creek Flats had lower mean elevations than Broad and Semi-Enclosed Flats, they contained only “glossy” and “subtidal” levels: as a result, no “saturated” samples were taken from these flats. A total of 7 replicate samples, consisting of a core that was 82 cm<sup>2</sup> in surface area and 10 cm deep, were taken at each of the three microhabitat levels at each tidal stage on Semi-Enclosed Flat and at Broad Flat. Additionally, sets of 3 replicate samples were taken at Shell Flat— the area that differed visibly from Broad Flat by its high percentage of surface shell-cover. Tidal Creek Flat was sampled starting at late ebb tide with 8 replicate samples per microhabitat level per tidal stage. As with Broad and Semi-Enclosed Flats, 7 replicate samples per level were taken from Island Flat at low tide.

Though most shorebirds foraging on the sand flats during this period were unable to penetrate the sediment more than 3-4 cm due to their relatively short bill lengths, macrofauna cores were taken to 10 cm depth in order to capture benthic

organisms that would be within range of the longer-billed whimbrel (*Numenius phaeopus*), a shorebird known to winter in the area. By sampling to 10 cm depth, I was also able to capture vertically-moving organisms with burrow depths greater than 4 cm— organisms that would be periodically available to surface-feeding shorebirds, but might be missed by shallower cores.

A total of 199 samples was returned to the laboratory in coolers with ice and were sieved immediately. Contents that remained on the 0.5-mm sieve were preserved in a labeled bottle with 10% buffered formalin with Rose Bengal stain and stored until the organisms could be counted and identified. After identification, organisms were stored in 35% ethanol until they could be dried and weighed ( $\leq 60$  days). Benthic macroinvertebrates were identified to the lowest practical taxonomic level (usually genus or species); some difficult species were aggregated at higher taxonomic levels since considerable redundancy in distribution and behavior of benthic marine macrofauna at lower compared to higher taxonomic levels (i.e. genus/species vs. order/family) has been demonstrated (Warwick 1988, Somerfield & Clarke 1995). All enumerated organisms were dried in a convection oven at 60°C until they reached constant mass (~48 hours). For each sample, dry weights were calculated for taxonomic groups including polychaetes, “amphipods” (actually included all small crustaceans— ~95% amphipods but also some isopods, caprellids, and larval crustaceans), bivalves, and gastropods.

Because the vast majority of benthic invertebrates identified fell into one of four major taxonomic groups (polychaetes, amphipods, bivalves, and gastropods), I used

one-way ANOVAs to test each group for differences in abundance and, separately, biomass among flats at each tidal level. Both the benthic abundance and biomass datasets were  $\log(x+1)$  transformed to validate statistical assumptions of normality and homogeneity of variance.

To determine if benthic community compositions differed among flats, I performed one-way ANOSIMs (analysis of similarity, Clarke & Gorley 2006) based on Bray-Curtis similarity matrices on abundance and biomass datasets ( $\log(x+1)$  transformed), with flat as the independent variable and individual samples as replicates. Additionally, I constructed an MDS ordination based on similarity matrices of flat/tidal stage combination means, and then overlaid it with the results of a hierarchical cluster analysis (PRIMER v.6.1.11) in order to visually emphasize groupings.

**Sediments.** Sediment samples were collected concurrently with benthic macrofauna. A single sediment sample was composed of three pooled 4.8-cm diameter cores taken to 10 cm depth. The three cores were taken haphazardly from the range of microtopographic features on the flat, with specific placement blind to surface sedimentary characteristics. As the tide fell, mid ebb tide and late ebb tide waterlines were marked with flags. All sediment samples were taken at low tide, but replicate sets were taken along each marked waterline so that Broad and Semi-Enclosed Flats had 7 replicate samples from the waterlines of each of the three tidal periods, Shell Flat had 3 replicates, and Tidal Creek Flat had 8 replicates each from the late ebb tide and low tide waterlines. Because Island Flat was only exposed during low tide, 4 replicate samples

were taken from the flat above water, and 4 replicate samples were taken from the shallow (<3 cm deep) subtidal.

In the laboratory, each sediment sample was dried for 24 hours at 120°C and then weighed and passed through a 2-mm sieve in order to remove the largest particles and calculate percent-gravel content. Each remaining sand sample was then thoroughly mixed before a ~5 g sub-sample was run through a CILAS laser particle size analyzer to determine the sample's particle size-class distribution. Grain sizes were binned into six groups based on the Udden-Wentworth scale (silt/ clay: < 63 µm, very fine sand: < 125 µm, fine sand: < 250 µm, medium sand: < 500 µm, coarse/ very coarse sand: < 2000 µm, gravel: ≥ 2000 µm), and percent composition was calculated for each sample. Grain-size group means were compared (1) among flats and (2) among tidal elevations within flats using one-way ANOVAs.

To test for among-flat differences in grain-size distribution, I performed a one-way ANOSIM based on a Euclidean distance resemblance matrix with flat as the independent variable and grain-size distributions from individual samples as replicates. I excluded the size class "fine sand" from the analysis because it was highly negatively correlated with "coarse/ very coarse sand" (-0.898); "coarse/ very coarse sand" acted as a proxy for both size classes. Additionally, I created a similarity matrix from mean grain-size distributions for each flat/tidal stage combination, and used it as the basis for an MDS ordination (Euclidean distance) and hierarchical cluster analysis.

**Integrated Analysis.** The relationship between sediments and benthic community structure was assessed using the BEST procedure in PRIMER6 (Clarke &



Gorley 2006). BEST searches for high rank correlations between a fixed similarity matrix and resemblance matrices produced from a subset of possible explanatory variables that come from a second ('active') similarity matrix. The degree to which the multivariate patterns of the fixed matrix match the patterns of the optimized subset matrix is the degree to which the subset variables "explain" the patterns in the fixed matrix. In this case, the fixed matrix was a Bray-Curtis similarity matrix produced from the benthic abundance dataset. Because benthic and sediment samples were not matched one-to-one in the field, only "glossy" benthic samples were used in the first BEST analysis in an effort to provide the closest match to tide-line sediment samples. In a second analysis, all benthic samples were used. Both benthic and sediment datasets were reduced (by averaging replicates) to 12 matching composite samples— one per tidal stage exposed per flat. The sediment variables in both BEST analyses were the six binned grain sizes listed above; however, because "coarse/ very coarse sand" and "gravel" were highly negatively correlated with "fine sand" ( $<-0.9$ ), I excluded "coarse/ very coarse sand" and "gravel" from the analyses so that "fine sand" acted as a proxy for all three size classes.

The BEST procedure was also used to assess the relationship between flat sediment composition and the shorebird community. In order to match sediments with shorebird samples, the composite sediment samples used in the sediment-benthic BEST analysis described above were replicated until a one-to-one sample correspondence was reached. In this way, each shorebird sample was matched with the sediment profile of a given flat at a given tidal stage. The original shorebird abundance dataset was

standardized by area (birds per newly exposed hectare). Observations from December were excluded because spring tides during that interval changed the distribution of birds on the flats relative to sediment sample locations (e.g., birds foraging at late ebb tide were likely closer to the location of “low tide” sediment samples, resulting in a poor sample match). The composite shorebird dataset was  $\log(x+1)$  transformed, and its Bray-Curtis similarity matrix served as the fixed matrix for the BEST analysis.

The relationship between benthic macrofauna and shorebird communities was assessed using the BEST procedure as well. This analysis was performed using the shorebird and benthic abundance datasets, with the similarity matrix from the shorebird dataset serving as the fixed matrix. Because the sheer number of benthic species (67) made computations cumbersome, I chose to include only those species that were found in five percent or more of the total samples (Table 2). To ensure that the original benthic community patterns were preserved in this 14-species subset, I ran a BEST analysis (BVSTEP: Clarke & Warwick 1998) using the complete benthic species list for the fixed matrix, and the 14-species subset for the active matrix; the resulting high correlation (Spearman correlation coefficient  $\rho = 0.94$ ) confirmed that benthic community patterns were preserved within the species subset. Once I had narrowed down the benthic species list, I performed a BEST analysis using the fixed shorebird Bray-Curtis similarity matrix and the active benthic Bray-Curtis similarity matrix. As with the sediment dataset in the previous analysis, composite benthic samples were replicated until a one-to-one sample correspondence was reached between benthic and shorebird samples. In this

way, each shorebird sample was matched with the benthic community composition of a given flat at a given tidal stage.

A final BEST analysis drew upon all three datasets. The composite sediment and benthic macrofauna datasets were combined on a single spreadsheet to form an active matrix that supplied explanatory variables from both datasets at the same time. Once again, the Bray-Curtis similarity matrix from the shorebird dataset served as the fixed matrix for the BEST analysis.

**Table 2. Benthic macrofauna species found in at least five percent of samples.** This benthic species subset was used in place of the complete 67-species list for all benthic-shorebird BEST procedures.

Higher Taxonomic Classification	Species
Polychaeta	<i>Aricidea fragilis</i>
	<i>Capitella capitata</i>
	<i>Eteone</i> sp.
	<i>Glycera</i> sp.
	<i>Haploscoloplos robustus</i>
	<i>Heteromastus filiformis</i>
	<i>Nereis</i> spp.
	<i>Paraonis</i> sp.
	Unknown
Amphipoda	(All)
Bivalvia	<i>Donax variabilis</i>
	<i>Gemma gemma</i>
	<i>Mercenaria mercenaria</i>
Gastropoda	<i>Nassarius obsoletus</i>

### III. RESULTS

**Shorebirds.** Shorebird communities differed among the flats at each tidal stage, and patterns among flats did not differ significantly across dates (Table 3). The Flat x Date interaction term could not be tested because there was no replication at the level of the sample. A lack of replication at this level means that it is impossible to tell the difference between variation among samples and variation due to the Flat x Date interaction term (Anderson et al. 2008); as a result, the PERMANOVA routine automatically excluded this term. Post hoc pairwise comparisons for Late Ebb and Low Tides were highly significant for every flat pair combination except for Broad Flat and Island Flat, which were not significantly different from each other at either tidal stage (Table 4).

**Table 3. Results of shorebird community PERMANOVA analyses (randomized block design; tidal stages analyzed individually).** NS = not significant ( $\alpha = 0.05$ ). DF = degrees of freedom (Flat, Date, Total).

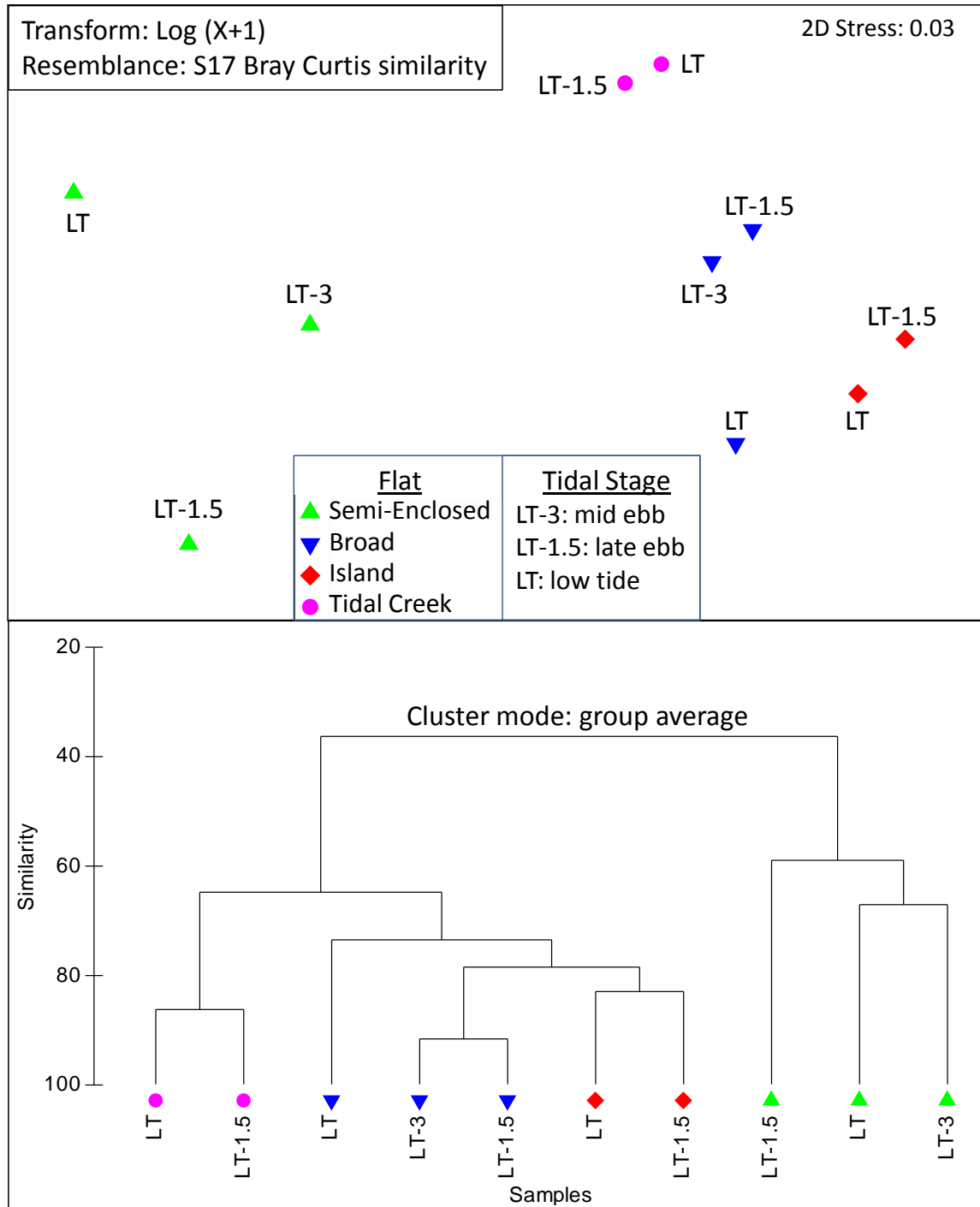
		P (perm)			
Factor:		Flat	Date	Flat x Date	DF
Tidal Stage	Mid Ebb Tide	0.002	NS	excluded	1, 8, 17
	Late Ebb Tide	0.001	NS	excluded	3, 7, 26
	Low Tide	0.001	NS	excluded	3, 10, 43

**Table 4. PERMANOVA pairwise comparisons from analysis of shorebird community dataset.** SE = Semi-Enclosed Flat, BR= Broad Flat, TC = Tidal Creek Flat, I S= Island Flat; Den. df = denominator degrees of freedom, NS = not significant ( $\alpha = 0.05$ ). \*For all Late Ebb Tide Island Flat pairs, P-values were obtained using Monte Carlo sampling.

Late Ebb Tide			Low Tide		
<u>Pair</u>	<u>P (perm)*</u>	<u>Den. df</u>	<u>Pair</u>	<u>P(perm)</u>	<u>Den. df</u>
SE—BR	0.002	7	SE—BR	0.001	10
SE—TC	0.002	7	SE—TC	0.001	10
BR—TC	0.003	7	BR—TC	0.003	10
IS—SE	0.001	2	IS—SE	0.001	10
IS—BR	NS	2	IS—BR	NS	10
IS—TC	0.028	2	IS—TC	0.004	10

An MDS ordination and cluster analysis supported the PERMANOVAs results and provided a pictorial representation of the magnitude of among-flat dissimilarities: an ordination of Semi-Enclosed, Broad, Tidal Creek, and Island Flats (Fig 2) showed clumping by flat, with a clear separation between Semi-Enclosed and the other flats. Additionally, the cluster analysis showed a range in similarity in among-flat community structure, with Broad and Island Flats more similar to each other than to Tidal Creek Flat, and Semi-Enclosed Flat clustering separately from the others.

**Figure 2. Shorebird community non-metric MDS ordination and cluster analysis.**



Univariate analyses showed that shorebird abundances varied significantly among the flats at different tidal stages (Table 5, Fig 3). Mean shorebird abundances were substantially lower at Semi-Enclosed Flat than any other exposed flat at all three tidal stages. When abundances were standardized for newly exposed area, foraging shorebird densities continued to be significantly lower on Semi-Enclosed Flat, but a new pattern of foraging preference emerged. At late ebb tide, mean foraging shorebird density on Tidal Creek Flat was substantially greater than densities observed on Semi-Enclosed or Broad Flats, and when Island Flat was exposed at that tidal stage ( $n = 3$ ), it experienced foraging densities similar to that of Tidal Creek Flat. By low tide, major density disparities had diminished, though Island and Broad Flats continued to be used more heavily than Semi-Enclosed Flat.



**Table 5. Results of shorebird one-way ANOVAs (factor: Flat), by tidal stage.** BR = Broad Flat, IS = Island Flat, SE = Semi-Enclosed Flat, TC = Tidal Creek Flat. For post hoc results, only pairs of means that are significantly different are listed.

**Mean Shorebird Abundances**

<b>Tidal Stage</b>	<b>P-value</b>	<b>F Ratio</b>	<b>DF</b>	<b>Tukey-Kramer post hoc results</b>
Mid Ebb Tide	0.0032	12.60	1, 15	
Late Ebb Tide	< 0 .001	21.78	3, 26	IS > TC > SE; BR = TC > SE
Low Tide	< 0.001	8.44	3, 47	BR = IS = TC > SE

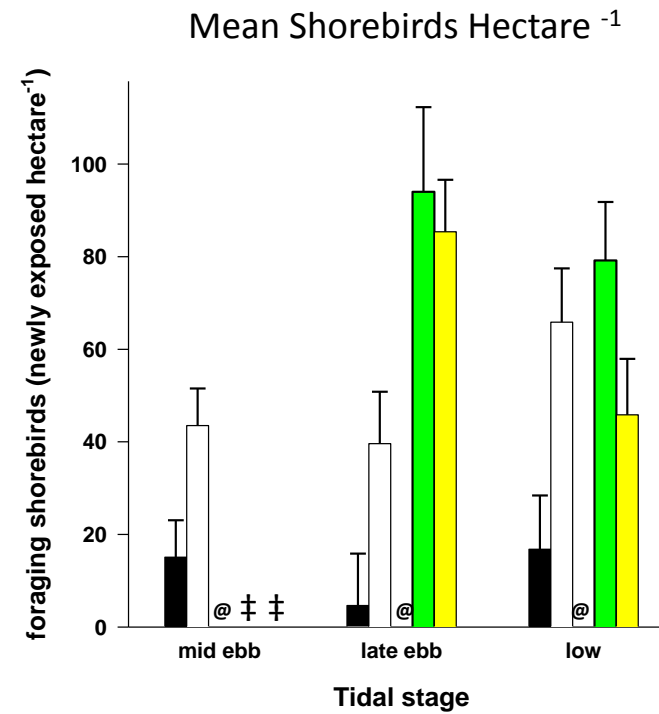
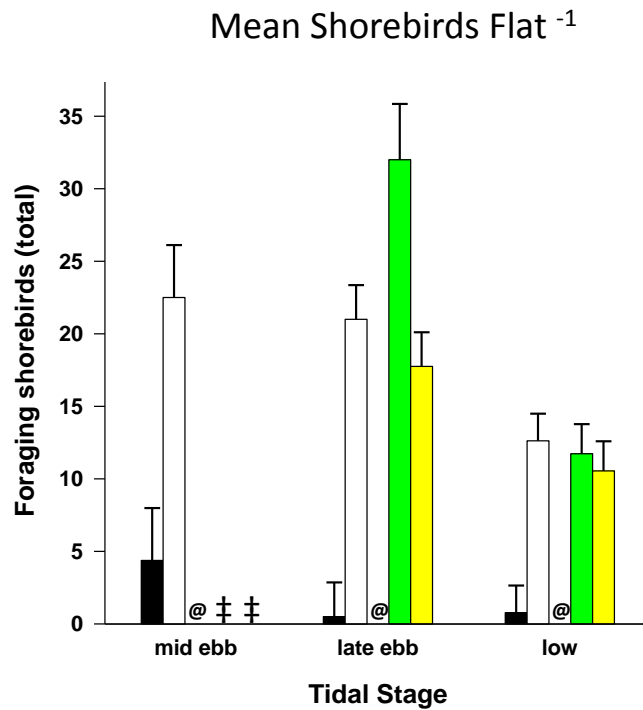
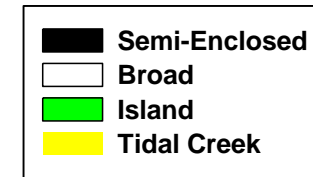
**Mean Shorebird Densities**

<b>Tidal Stage</b>	<b>P-value</b>	<b>F Ratio</b>	<b>DF</b>	<b>Tukey-Kramer post hoc results</b>
Mid Ebb Tide	0.0247	6.32	1, 15	
Late Ebb Tide	< 0.001	10.99	3, 26	TC = IS > SE; TC > BR
Low Tide	0.0038	5.15	3, 48	IS = BR > SE

**Figure 3. Intertidal flat foraging shorebird use: mean abundances and densities by flat and tidal stage.**

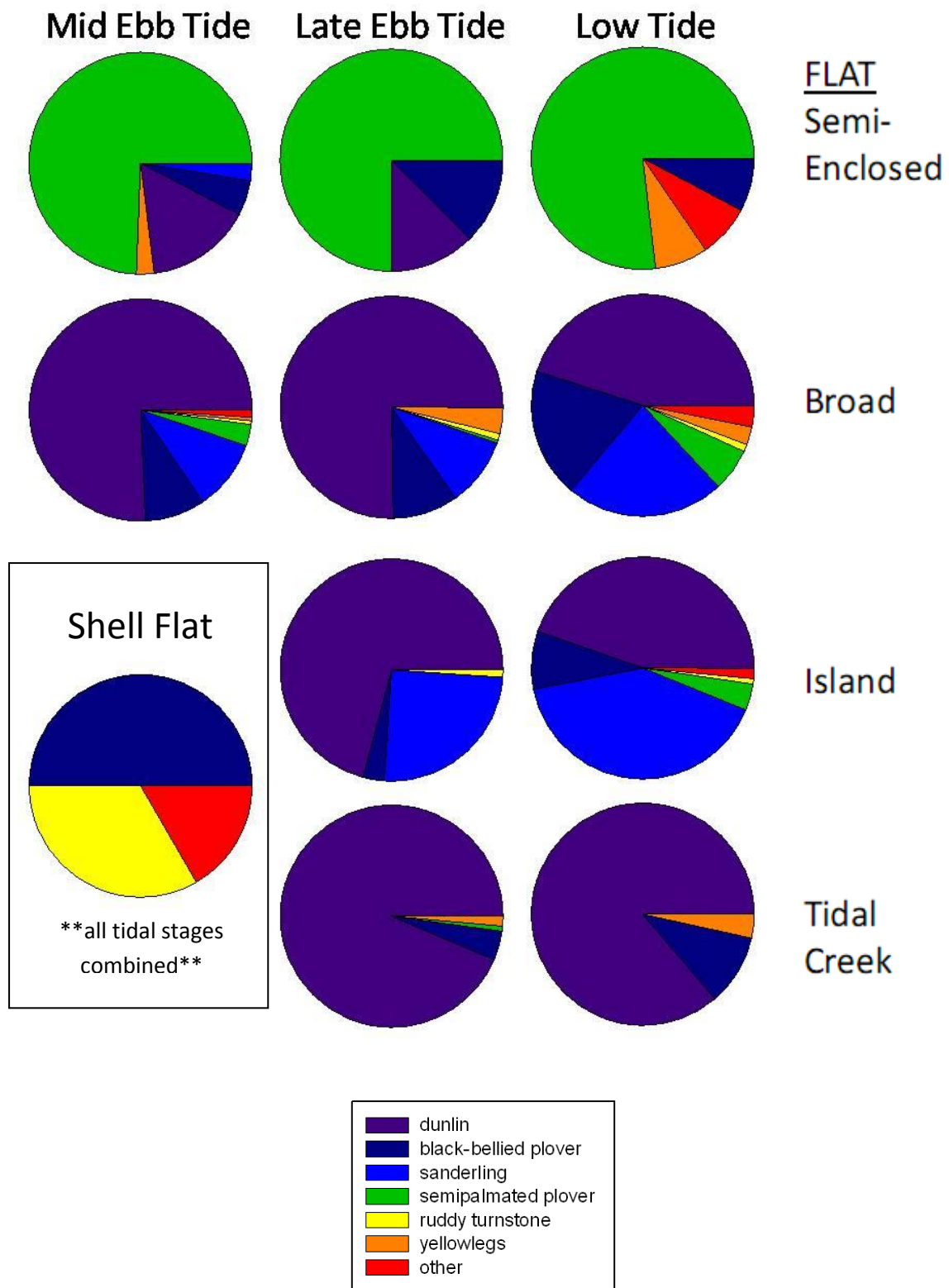
@- Shell Flat excluded from bird abundance and density comparisons because it was frequently disturbed by fishermen.

‡- No Data (flat inundated).



The species composition of foraging shorebirds varied among flats, but varied little within a given flat across tidal stages (Fig 4). Semipalmated plovers (*Charadrius semipalmatus*) made up the majority of birds using Semi-Enclosed Flat but were rarely found on the other flats. Broad and Island Flats had similar overall species compositions, while 80-90% of shorebirds that used Tidal Creek Flat were dunlins (*Calidris alpina*). Dunlins made up about 75% of total birds on Broad Flat at mid ebb and late ebb tides, but their percentage dropped to less than 50% by low tide. This change in percent composition also occurred on Island Flat. Sanderlings (*Calidris alba*) were rarely observed on Semi-Enclosed Flat and never on Tidal Creek Flat, and while few birds were ever observed using Shell Flat, the ones that did were primarily black-bellied plovers (*Pluvialis squatarola*), ruddy turnstones (*Arenaria interpres*), and piping plovers (*Charadrius melodus*). Yellowlegs (*Tringa* spp.) occasionally foraged along the water's edge of most of the flats, but were never observed around Island Flat or Shell Flat.

Figure 4. Shorebird community species compositions by flat and tidal stage, summed across all observation dates.

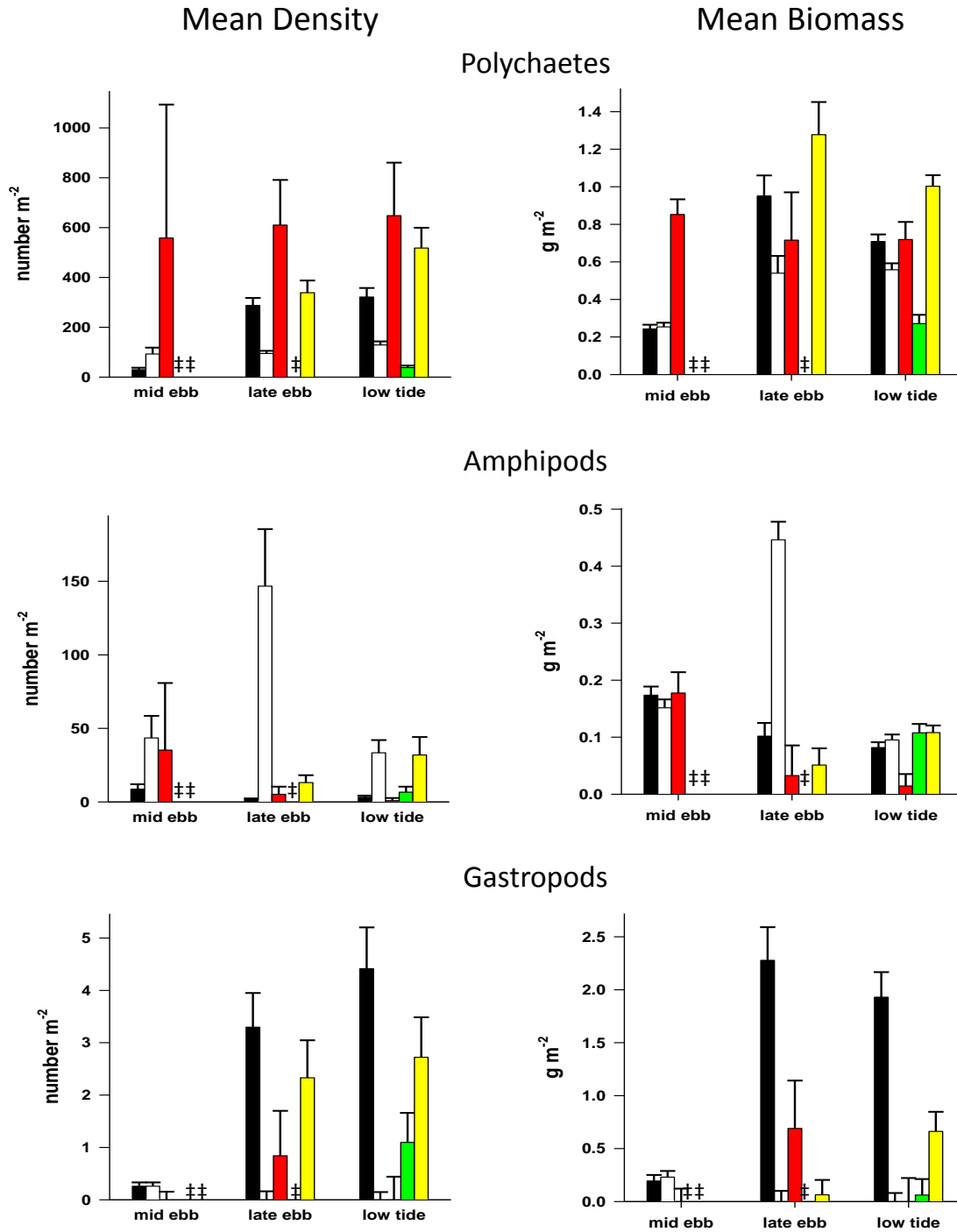
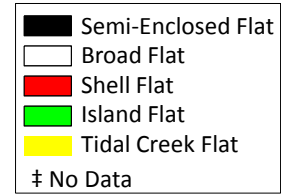


**Benthic macrofauna.** Almost all (98%) of benthic species sampled belonged to one of four taxonomic groups: polychaetes (53%), crustaceans (34%), bivalves (6%) or gastropods (5%) (see Appendix B for complete species list). Although 16 different families of polychaetes were identified, 80% of all polychaetes were either *Nereis* spp. (20%), *Capitella capitata* (17%), *Haploscoloplos robustus* (16%), *Heteromastus filiformis* (14%), *Paraonis* sp. (8%), or *Aricidea fragilis* (5%). Sampled crustaceans were nearly all amphipods (94%), but also contained a few decapods (4% - mostly larval), caprellids, and isopods. Bivalves were mainly *Donax variabilis*, *Gemma gemma*, or *Mercenaria mercenaria*, and primary gastropods were *Nassarius obsoletus* and *Littorina irrorata*.

Shell Flat had significantly higher polychaete densities than other flats at every tidal stage (Fig 5, see Table 6 for ANOVA and Tukey-Kramer post hoc results). Polychaete biomass was greater on Shell Flat than on Semi-Enclosed or Broad Flats at mid ebb tide, but did not differ significantly from other flats at late ebb tide or low tide. Amphipod density and biomass means at Shell Flat were similar to those recorded for Semi-Enclosed and Broad Flats at mid ebb tide, and similar to Semi-Enclosed and Tidal Creek Flats at late ebb tide, although density was significantly less than on Broad Flat. Density and biomass of gastropods and bivalves on Shell flat were not significantly different from other flats at any tidal stage.

**Figure 5. Mean density and biomass of benthic macrofauna groups, by flat and tidal stage.**

‡- No data (flat inundated).



**Table 6. Benthic abundance and biomass one-way ANOVAs (factor: Flat) and post hoc results; ALL FLATS INCLUDED.** Only significant ANOVA results reported ( $\alpha = 0.05$ ). BR = Broad Flat, SE = Semi-Enclosed Flat, SH = Shell Flat, TC = Tidal Creek Flat, IS = Island Flat.

\* Tukey Kramer HSD post hoc results. Only significantly different pairs of means are listed. NSD = no significant differences.

	tidal stage	DENSITY			BIOMASS		
		mid ebb	late ebb	low	mid ebb	late ebb	low
		BR, SE, SH	BR, SE, SH, TC	BR, SE, SH, TC, IS	BR, SE, SH	BR, SE, SH, TC	BR, SE, SH, TC, IS
		2,48	3,62	4,75	2,48	3,62	4,75
POLYCHAETES	F	3.4	3.99	6.69	4.9		
	P-value	0.041	0.012	< 0.001	0.012		
	TK post hoc*	SH>SE	SH>BR	SH=TC=SE>IS	SH>BR=SE		
AMPHIPODS	F		8.04	3.18		2.77	
	P-value		<0.001	0.018		0.049	
	TK post hoc		BR>SH=SE	NSD		NSD	
GASTROPODS	F			2.7		2.96	2.54
	P-value			0.037		0.039	0.047
	TK post hoc			SE>BR		SE>BR	NSD
BIVALVES	F						3.92
	P-value						0.006
	TK post hoc						TC>BR=SE=IS

When Shell Flat was excluded from calculations (Table 7), one-way ANOVAs showed no significant differences in density or biomass of polychaetes, amphipods, gastropods, or bivalves between Semi-Enclosed and Broad Flats at mid ebb tide, though Broad Flat tended to have higher polychaete and amphipod densities at this tidal stage (Fig 5). At late ebb tide, amphipod density was significantly greater on Broad Flat than on the other flats, and gastropod biomass was greater at Semi-Enclosed Flat than at Broad and Tidal Creek Flats. When Island Flat was exposed at low tide, its polychaete density was significantly lower than densities measured at Tidal Creek and Semi-Enclosed Flats, and its polychaete biomass was significantly less than the polychaete biomass at Tidal Creek Flat. Finally, Tidal Creek Flat had significantly greater bivalve biomass than any other flat at that tidal stage.



**Table 7. Benthic abundance and biomass one-way ANOVAs (factor: Flat) and post hoc results; SHELL FLAT EXCLUDED.** Only significant ANOVA results reported ( $\alpha = 0.05$ ). BR = Broad Flat, SE = Semi-Enclosed Flat, TC = Tidal Creek Flat, IS = Island Flat.  
 \* Tukey Kramer HSD post hoc results. Only significantly different pairs of means are listed. NSD = no significant differences.

	tidal stage	DENSITY				BIOMASS		
		mid ebb	late ebb	low		mid ebb	late ebb	low
		BR, SE	BR, SE, TC	BR, SE, TC, IS		BR, SE	BR, SE, TC	BR, SE, TC, IS
			2,54	3,67			2,54	3,67
POLYCHAETES	F		3.67	6.71				3.13
	P-value		0.032	< 0.001				0.031
	TK post hoc*		NSD	TC=SE>IS				TC > IS
AMPHIPODS	F		11.61					
	P-value		<0.001					
	TK post hoc		BR>TC=SE					
GASTROPODS	F						4.59	
	P-value						0.014	
	TK post hoc						SE>TC=BR	
BIVALVES	F							5.47
	P-value							0.002
	TK post hoc							TC > BR=SE=IS

Overall, benthic communities differed among the flats (abundance dataset; ANOSIM, global  $R = 0.158$ ,  $P < 0.001$ ). Individual pairwise comparisons (Table 8) show significant differences between all flat pairs except Semi-Enclosed and Shell Flat, and Semi-Enclosed and Tidal Creek Flat. An MDS ordination (Fig 6) showed some separation among flats, though the benthic community on Shell Flat at mid ebb tide grouped with Broad Flat rather than the later tidal stages on Shell Flat. An ANOSIM of benthic biomass detected no significant difference among flats (global  $R = 0.003$ ,  $P > 0.05$ ), and an MDS ordination of the biomass dataset did not reveal any patterns.

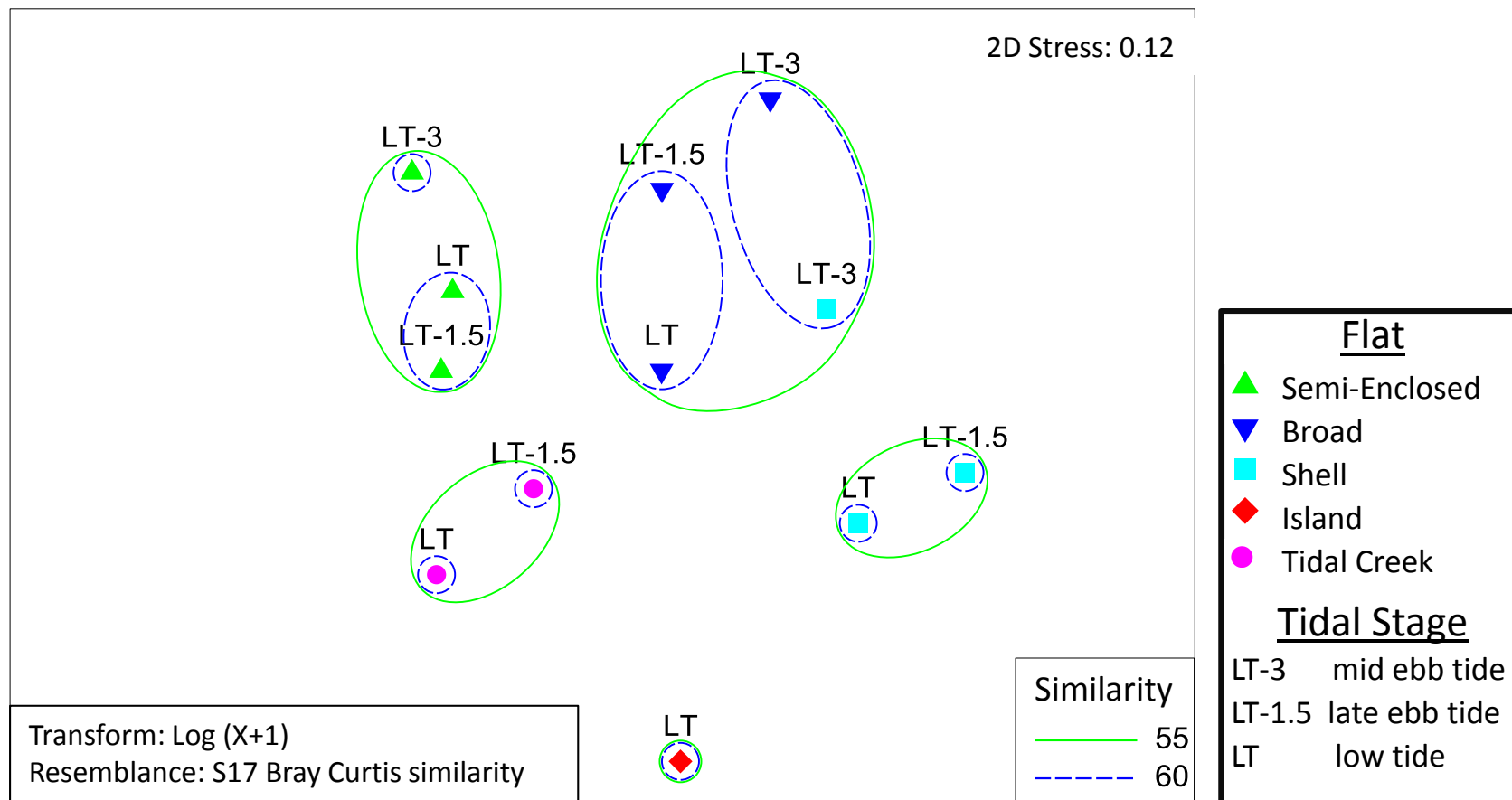
Few differences were found among the microhabitats of individual flats. ANOVA showed microhabitat differences in amphipod abundances on Shell Flat at mid ebb tide ( $F_{2,6} = 6.73$ ,  $P = 0.029$ ), with Tukey-Kramer HSD post hoc tests revealing greater abundances in “saturated” than in “glossy” and “subtidal” microhabitats. Differences in abundance among microhabitats also occurred with polychaetes on Broad and Shell Flats at late ebb tide (ANOVAs: Broad  $F_{2,17} = 3.78$ ,  $P = 0.04$ ; Shell  $F_{2,6} = 7.04$ ,  $P = 0.027$ ); post hoc comparisons showed that abundances were greater in “saturated” than in “subtidal” microhabitats on both flats. The only other observed difference between microhabitats was at Tidal Creek Flat at late ebb tide, where the abundance of gastropods was greater at “subtidal” levels than in “glossy” areas (ANOVA,  $F_{1,14} = 7.0$ ,  $P = 0.019$ ; Tukey-Kramer HSD post hoc).

**Table 8. Benthic community analysis (benthic abundance dataset): post hoc pairwise tests (PRIMER6) following Analysis of Similarity (ANOSIM).**

<b>Groups</b>	<b>R Statistic</b>	<b>Significance Level (%)</b>
Semi-Enclosed, Broad	0.129	0.1
Semi-Enclosed, Shell	0.023	25.5
Semi-Enclosed, Island	0.191	0.1
Semi-Enclosed, Tidal Creek	0.033	10.2
Broad, Shell	0.202	0.1
Broad, Island	0.363	0.1
Broad, Tidal Creek	0.243	0.1
Shell, Island	0.381	0.1
Shell, Tidal Creek	0.316	0.1
Island, Tidal Creek	0.285	0.1

Figure 6. Benthic community MDS ordination with overlaid cluster analysis.

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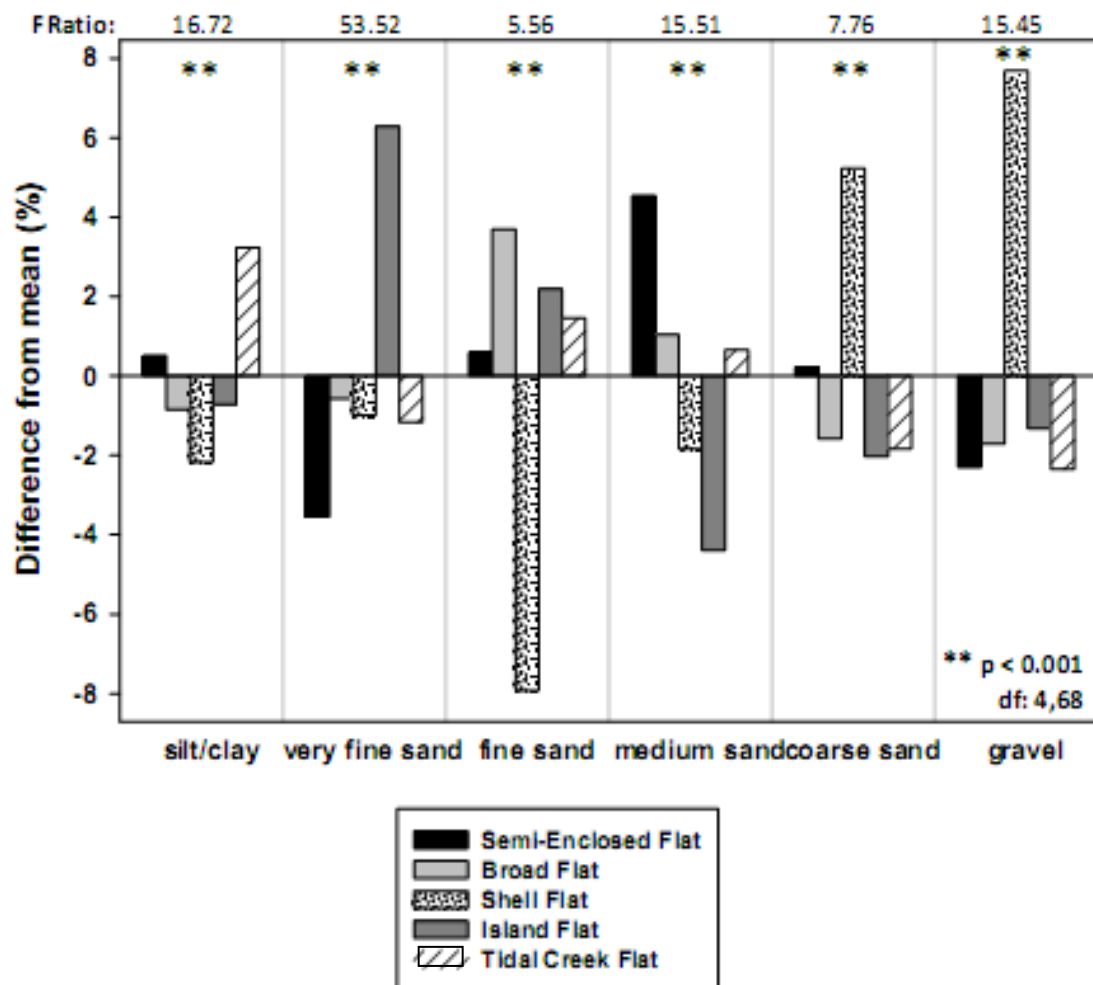


**Sediments.** Overall, the flats differed from each other in specific grain-size classes (Fig 7): Tidal Creek Flat was muddiest with a significantly higher percentage of silt and clay (see post hoc comparisons, Table 9), Island Flat had a higher percentage of very fine sand, Shell Flat was the coarsest by far with a high coarse sand and gravel content, and Semi-Enclosed Flat had significantly more medium sand. Broad Flat had more fine sand than Shell Flat, but when Shell Flat was excluded from the calculations there was no significant difference between Broad Flat and the other flats in fine sand content. Within individual flats, sedimentology was consistent across tidal levels for Semi-Enclosed, Island, and Tidal Creek Flats. However, Broad Flat showed a gradual fining of sediments from mid ebb to low tide with a significant increase in silt/clay percentages (ANOVA:  $F_{2,18} = 8.60$ ,  $P < 0.01$ , Tukey-Kramer HSD) and an increase in the percentage of very fine sand, and Shell Flat showed a marked coarsening of sediments from mid ebb to late ebb and low tide (ANOVAs and Tukey HSD; Coarse/ Very Coarse Sand:  $F_{2,6} = 7.32$ ,  $P = 0.02$ , low tide > mid ebb; Fine Sand:  $F_{2,6} = 13.32$ ,  $P < 0.01$ , mid ebb > late ebb = low tide) .

When grain-size distributions were considered as a whole, there was a significant difference in sediment composition among the flats (ANOSIM: global  $R = 0.454$ ,  $P < 0.001$ ). An MDS ordination of flat grain size distributions (by tidal stage- Fig 8) showed the largest dissimilarities between Shell Flat's late ebb tide and low tide sediments and the sediment compositions of the other flats at every measured tidal stage. In addition to being different from all other flats, Shell Flat's late ebb and low tide sediments separated from each other in the ordination. Mid ebb tide sediments from Shell Flat

clustered with sediments from Broad Flat (all tidal stages); all tidal stages of Semi-Enclosed Flat clustered together, as did Tidal Creek Flat's tidal stages. Island Flat's sediments did not cluster with any other flat.

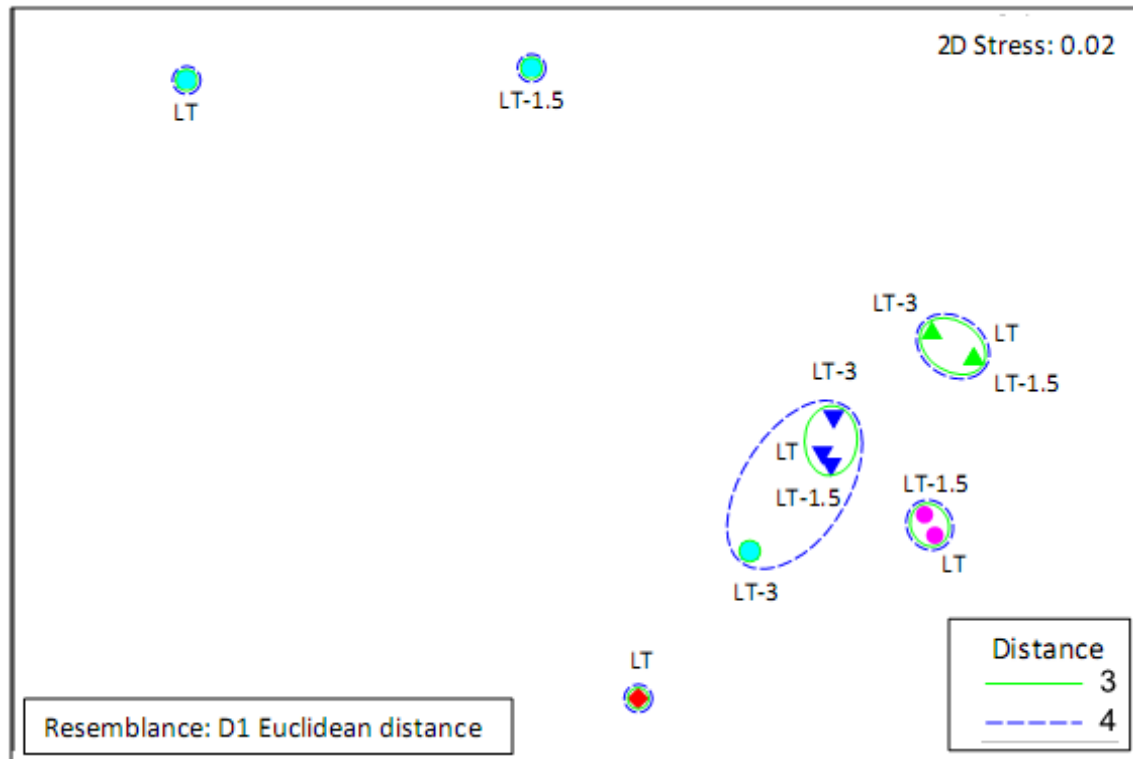
**Figure 7. Flat differences from grain size class means.** Results of one-way ANOVAs (Factor: Flat; conducted separately for each size class) are indicated.



**Table 9. Sediment size classes: Tukey-Kramer HSD post hoc results.** Only significant ( $\alpha = 0.05$ ) pairwise differences are listed. BR = Broad Flat, IS = Island Flat, SE = Semi-Enclosed Flat, SH = Shell Flat, TC = Tidal Creek Flat.

Size Class	Post Hoc Results
Silt/Clay	TC > SE > SH; TC > IS=BR
Very Fine Sand	IS > BR=SH=TC > SE
Fine Sand	BR=IS=TC=SE > SH
Medium Sand	SE > BR=TC > IS; SE > SH
Coarse/ Very Coarse Sand	SH > SE=BR=TC=IS
Gravel	SH > IS=BR=SE=TC

**Figure 8. MDS ordination of flat sedimentary characteristics (by tidal stage), with overlaid cluster analysis.**



Flat	Tidal Stage
▲ Semi-Enclosed	LT-3 mid ebb tide
▼ Broad	LT-1.5 late ebb tide
■ Shell	LT low tide
◆ Island	
● Tidal Creek	



**Integrated analysis.** A BEST analysis between sediments and glossy benthic samples produced a Spearman correlation coefficient ( $\rho$ ) of 0.119 with “silt/clay” and “very fine sand” size classes. However, the analysis between composite samples yielded a much higher optimized correlation ( $\rho = 0.691$ ,  $p < 0.01$ ; variables: “silt/clay”, “very fine sand”). The BEST analysis between sediments and shorebirds had an optimized correlation of  $\rho = 0.528$  ( $p < 0.01$ ) with 2 variables: “medium sand” and “fine sand” (also a proxy for “coarse/very coarse sand” and “gravel”). The benthic-shorebird BEST analysis was optimized with 3 variables (Amphipoda, *Capitella capitata*, *Donax variabilis*.) at  $\rho = 0.612$  ( $p < 0.01$ ). Finally, when all three datasets were used concurrently (correlating sediments and benthic macrofauna with shorebird community patterns), the BEST analysis was optimized at  $\rho = 0.671$  ( $p < 0.01$ ) with 3 variables (*Capitella capitata*, *Donax variabilis*, and “gravel” (= “fine sand” = “coarse/very coarse sand”).

#### IV. DISCUSSION

The non-random distributions of foraging shorebirds observed in this study demonstrate that all sand flats are not perceived and treated equally by foraging birds. In order to understand what makes a flat more useful or valuable to a species of interest, it is important to go beyond patterns of patch use and examine potential drivers of observed patterns.

##### **Patch-Scale Factors**

**Prey abundance and distribution.** Shorebird distribution patterns have been successfully correlated with distribution of primary prey items in other studies (e.g., Goss-Custard 1970, Goss-Custard et al. 1977, Bryant 1979, Colwell & Landrum 1993, Ribeiro et al. 2004, Karpanty et al. 2006). This study supports those findings; the BEST analysis in this study provided an optimized Spearman correlation coefficient of 0.612 which means that benthic community patterns “explain” about three-fifths of the variation in the foraging patterns of the shorebird community. While the abundance and distribution of prey clearly play an important role, the relationship between shorebirds and their food becomes even stronger when sedimentary characteristics are taken into consideration. The BEST analysis that combined sediments and benthos produced a correlation ( $\rho$ ) of 0.671, which means that two-thirds of the variation in shorebird community foraging patterns can be “explained” by the combination of these patch characteristics. This increase in explanatory power may occur because prey availability—as mediated by sedimentary characteristics—is more important than strict

presence/absence (Ontiveros et al. 2005). Below I address potential factors affecting prey availability.

**Sediment characteristics.** Sediment particle sizes affect prey availability through several different mechanisms including interference with effective foraging on infauna (Quammen 1982, Peterson et al. 2006, Finn et al. 2008) and differences in water drainage rates, which influence prey surface activity (Vader 1964). When Quammen (1982) manipulated surface sedimentary characteristics of a mudflat by adding a thin layer of sand to experimental plots, she documented a decrease in overall foraging time spent on the manipulated plots, even though prey abundances remained the same across all areas. The mechanism that she proposed to explain this was that the added sand grains, which were similar in diameter to the diameter of primary prey items (small polychaete and oligochaete worms), interfered with the ability of probing shorebirds to detect, manipulate and capture infaunal prey. Although all of the flats in the current study were sand flats (85-95% sand), the flats varied in percent composition of different sand size classes (Fig 7). The majority of polychaetes found in the flats (including *Capitella* sp., *Haploscoloplos* sp., and *Heteromastus* sp.) had diameters ca. 0.5-1.25 mm, which were similar to the medium and coarse sand size classes (0.25-2 mm). Semi-Enclosed Flat, which consistently had low foraging shorebird densities (and even lower *probing* shorebird densities), had a significantly greater combined percentage of medium and coarse sand grains (27.6%) than Broad, Tidal Creek, and Island Flats (22.4%, 21.7%, and 16.5% respectively). While size class percentages only differed by ~5-10%, the results suggest that Semi-Enclosed Flat may have crossed a particle size “threshold,”

or critical amount of prey-sized particles, that affected the foraging efficiency of probing birds. This may have caused differential rates of prey capture between Semi-Enclosed and the other flats, and contributed to the minimal bird use on that flat.

Even larger sediment particles (gravel, shell hash) interfere with prey detection and capture by impeding sediment penetration by probing birds (Finn et al. 2008). Whereas substrate with a sizeable amount of coarse material may act as a refuge to infaunal prey (Peterson et al. 2006), benthic invertebrates are still vulnerable to visually feeding shorebirds when they are at the surface (Pienkowski 1983). Thus, while tactile foragers experience a decrease in prey capture success, visual foragers are better suited to utilize the habitat than tactile foragers, which may lead to non-random distributions of birds based on foraging guild. In the current study black-bellied plovers, piping plovers, and ruddy turnstones used Shell Flat. Ruddy turnstones forage by flipping shells and coarse material and then looking for prey hidden underneath: a method perfectly suited for the sedimentary characteristics of Shell Flat. Black-bellied and piping plovers are both visual foragers that rely on prey surface activity rather than substrate penetration to locate food items. In contrast, the visibly armored surface of Shell Flat likely deterred probing species such as dunlins, which were never observed on the flat. Even when fisherman-disturbed dates were factored out, Shell Flat supported extremely low numbers of foraging shorebirds (0-2 birds per observation). The species composition of these few birds is consistent with the conclusion that the presence of coarse material deterred the dunlins, which were by far the most abundant shorebird species using the adjacent flats. If this were the case, then the sedimentary characteristics were

responsible for a major reduction in foraging pressure, which could in turn produce the observed increased prey densities on that flat (with polychaetes around four times more abundant at Shell Flat than any other flat).

High polychaete densities could directly or indirectly result from reduced foraging pressure on the flat. If fewer total shorebirds regularly foraged on Shell Flat, the difference in polychaete densities could be the result of prey depletion in the flats that were used more heavily across time. Conversely, polychaete density differences could be the result of non-consumptive effects (Blaustein 1997); heavier foraging by birds on the other flats may have lead the polychaetes in those areas to feed less themselves, thereby lowering growth rates and potentially affecting mortality. Both consumptive and non-consumptive effects could lead to the observed differences in polychaete abundance among the flats.

Prey surface activity, a factor affecting prey availability, is directly influenced by tidal movement (Vader 1964). However, infaunal organisms respond differently to tidally-driven water cover changes. Rosa and colleagues (2007) looked at the response of polychaete *Hediste diversicolor* and bivalve *Scrobicularia plana* to changes in surface water cover and differences in sediment drainage characteristics. They found that these two organisms had very different behavioral responses; whereas *S. plana* surface activity (foraging with siphon) peaked soon after the tidal line receded, the surface activity of *H. diversicolor* was initially low, but increased with time after exposure. *S. plana* maintained higher activity levels in poorly-drained flat areas that retained a thin film of water on the surface; in contrast, *H. diversicolor* was most active on the surface

when sediments were well drained. These differences were reflected in foraging shorebird distributions: birds that fed primarily on *S. plana* focusing their efforts at the tide line and in poorly drained areas with surface water cover, while birds that mainly consumed polychaetes foraged in well-drained areas.

At late ebb tide in this study, dunlin densities were much higher on Tidal Creek Flat than on Semi-Enclosed or Broad Flats. With its higher silt/clay percentages, Tidal Creek Flat was less porous than the other flats, and its poor drainage resulted in the persistence of small pools and areas covered with a thin veneer of water. Because these water-cover characteristics lead to prolonged surface activity in some benthic prey organisms (Vader 1964, Rosa et al. 2007), shorebirds that forage on these macrofauna likely experience increased prey availability in these areas. Dunlins consistently foraged at the tide line and in the “glossy” or “subtidal” (poorly drained) microhabitats. Though I was unable to document what they were eating, there were no significant differences in prey abundance or biomass (polychaetes, amphipods, gastropods, and bivalves) among the flats. These results support the hypothesis that poor water drainage enhanced prey availability on Tidal Creek Flat (due to prey activity levels (Rosa et al. 2007) and/or sediment penetrability (Mouritsen & Jensen 1992)), and that this difference in prey availability contributed to the significant differences in foraging shorebird densities among Tidal Creek, Broad, and Semi-Enclosed Flats at late ebb tide.

The sediment-benthic BEST analysis produced a 69% correlation between “silt/clay” and “very fine sand” size classes and the benthic community. BEST composite samples spanned the entire “newly exposed area” of each flat at each tidal stage, so

samples were matched across a broad area. At this scale, the differences in the benthic community composition can be explained in part by variation in the finer sediments. Interestingly, while benthic community structure is most strongly correlated with “silt/clay” and “very fine sand” content, the bird community is most strongly correlated with all the other grain sizes (the coarser end of the spectrum).

**Flat surface topography.** While flats with heterogeneous topography retain some degree of surface water-cover (and associated enhanced prey availability) where scattered topographic lows occur, minimal microtopography can also be beneficial to certain foraging species. Although Semi-Enclosed Flat exhibited consistently low total shorebird numbers, its high proportion of semipalmated plovers was unique among the flats. Semipalmated plovers forage using a stereotyped run-stop-search technique, which probably results from a limited ability to focus on prey while moving (Turpie 1994). Because their particular foraging method includes bursts of running, semipalmated plovers require open and even substrate (Nol & Blanken 1999). The within-habitat characteristics of Semi-Enclosed Flat may have been more conducive to foraging semipalmated plovers compared to the other flats; the surfaces of Broad and Island Flats were covered with small ripples and ridges, and Tidal Creek Flat had a variety of surface indentations that created a matrix of shallow pools. In contrast, Semi-Enclosed Flat’s sheltered cove probably minimized water flow rates and associated bedform creation, providing the open, even substrate required by semipalmated plovers for efficient foraging.

**Flat geography and geometry.** When Island Flat was exposed at low tide, its foraging shorebird densities were greater than or equal to every other flat even though the densities of key prey items (polychaetes, amphipods) on the flat were significantly lower. This was probably a result of Island Flat's geography; because it was an island, it had roughly double the water-edge length of an equal-sized sand flat extending from land (Fig 1). Edges play an important role for many species of foraging shorebirds including dunlins (Burger et al. 1977, Nehls & Tiedemann 1993, Granadeiro et al. 2006), the most abundant species on the Onslow Beach back-barrier sand flats. Certain benthic prey species are most active at the substrate surface when it is covered with water or when the water first recedes (Vader 1964); thus, enhanced levels of prey activity occur along the tidal margin of an emergent sand flat. Dunlins and other "edge followers" (typically probers— see Granadeiro et al. 2006) closely follow the moving tide line and exert heavy foraging pressure within that margin. Consequently, the area-edge relationship could play a pivotal role in determining the foraging habitat value of a sand flat.



## **Landscape-Scale Factors**

Beyond the area-edge ratio or total edge length, characteristics of the margin itself (defined as the “glossy” area along the water edge), such as width and slope, could be important in determining its relative value compared to other edges available in the landscape. A gently sloping margin results in more “newly exposed area” (and a wider band of active prey) than a steeply sloped margin of the same tide-line length. Following mid ebb tide, the margin of Semi-Enclosed Flat changed drastically in slope (Fig 1). Between mid ebb and low tide very little new area was exposed on the flat, while each of the other flats expanded drastically. Differences in “newly exposed area” per edge length affect the amount of accessible prey on a flat, and, consequently, its value as foraging habitat.

**Surrounding matrix.** In addition to a steep slope, the surrounding habitat matrix may have contributed to the low foraging shorebird densities on Semi-Enclosed Flat at late ebb and low tides. The interior location of the flat meant that it was nearly surrounded by marsh vegetation, so that when the flat area expanded with the falling tide its leading edge moved away from sparse vegetation on one side but got closer to the dense marsh vegetation and tall trees on the opposite side of the small cove (Fig 1). Vegetation proximity plays an important role in shorebird nest site selection (Smart et al. 2006), and may also influence choice of foraging site (Baker 1979, Safran et al. 2000). While studying predation risk to small shorebirds, Dekker and Ydenberg (2004) found that as distance to vegetation decreases, dunlins face an increased risk of predation by raptors. In contrast to Semi-Enclosed Flat, the expanding edge of each of the other flats

moved toward open water or another sand flat, providing increased distance from hidden predators or raptors hunting from perches.

**Connectivity and accessibility.** The Onslow Beach back-barrier sand flats were well interconnected due to their close proximity; shorebirds could move easily among the flats, although movement occurred between some flat pairs more than others (pers. obs.). The shorebird species compositions of Broad and Island Flats were more similar to each other than any other pair of flats, likely a reflection of their respective locations. Their parallel orientation facilitated movement of foraging birds between newly-exposed areas of each flat (pers. obs.), separated only by a narrow (<50 m) channel. Because of their spatial proximity the two flats experienced similar tidal flow rates and directions, which is likely why they had comparable sediment profiles (differing only in very fine and medium sand proportions- see Fig. 7). On Broad Flat dunlins made up about 75% of total foraging shorebirds at mid ebb tide and late ebb tide, but by low tide the percentage dropped to less than 50. This was the only major within-flat change in species composition between tidal stages; notably, this pattern was mirrored on Island Flat.

While the Onslow Beach sand flats were well interconnected, they were not equally accessible. Differences in elevation resulted in different exposure times. Whereas Broad and Semi-Enclosed Flats were exposed (and therefore accessible to foraging birds) for 6+ hours per tidal cycle, Tidal Creek Flat was only exposed for ~4 hours, and Island Flat was only accessible for 2-3 hours. As the lower flats emerged, foraging dunlins moved from the higher flats to the lower flats (pers. obs.). Dunlins

typically started foraging on Broad Flat, then moved en masse to Tidal Creek Flat when it first emerged. They continued foraging there until Island Flat was exposed, at which point many of the dunlins moved to that newly exposed flat. Around low tide dunlins redistributed themselves between Island and Broad Flats; this pattern was especially apparent during spring tides when Island Flat emerged earlier in the tidal cycle. In a study looking at wintering piping plovers near Oregon Inlet (NC, USA), Cohen and colleagues (2008) found that habitat use was strongly linked to the tidal cycle, and that piping plovers moved from ocean and sound beaches to sound islands as island intertidal zones were exposed with the falling tide. The current study also revealed a strong connection between patch use and the tidal cycle, and followed the general trend of bird movement from higher to lower flats; however, because patch types in this study were unreplicated, any inferences related to patch type are limited, and would be strengthened by increasing patch-type replicates in space and time.

## Behavioral Interactions

While it is possible that agonistic behaviors influenced shorebird distributions on the Onslow Beach back-barrier sand flats, it seems unlikely that this played a major role in structuring patterns of patch use. Few negative interactions were observed.

Observations were consistent with species-specific literature (e.g. Warnock & Gill 1996, Nol & Blanken 1999) which report little to no territoriality or other agonistic behavior in non-breeding and/or wintering dunlins, semipalmated plovers, or sanderlings (North Carolina specific: Walters 1984), and non-aggressive intraspecific spacing in black-bellied plovers (Stinson 1980). Only once did I observe a bird being chased from a flat: a semipalmated plover chased a conspecific off of Semi-Enclosed Flat (the bird flew to Broad Flat). However, I frequently observed approximately even spacing between individual feeding black-bellied plovers (>50 m). Though ruddy turnstones are known to interact aggressively with other shorebirds foraging in close proximity (< 1 m) (Metcalf & Furness 1987), I never observed any aggressive interactions between ruddy turnstones and other species on the flats. Ruddy turnstones were one of a few species that used Shell Flat over the course of the two-month observation period; however, they were only observed on the flat on two observation dates. Because they were observed so rarely on the flat, it is highly unlikely that they were behaviorally excluding other species from that polychaete-rich flat. If shorebirds on the flats were not territorial or displaying strong aggressive behavior, it is unlikely that certain flats were avoided due to inter- or intraspecific interactions.

Alternatively, positive interactions between individuals or species could have contributed to the observed non-random distributional patterns. If shorebirds entering the area cued in on other shorebirds already foraging in a particular patch, a non-random aggregation of foraging birds could occur that may have little to do with patch quality. While this may occur on some level, shorebirds are very mobile and can easily move to another patch, and do so when expected benefits exceed benefits of remaining (covered extensively in optimal foraging literature, e.g. Charnov 1976). If anything, when birds cue in on other birds and aggregate in a particular patch, the end effect should be a magnification of shorebird associations with more rewarding foraging habitat.

## Final Thoughts

An underlying assumption of the benthic sampling methods used in this study is that prey abundance and composition remained largely unchanged across the two month bird observation period. While it is unlikely that prey numbers increased during that early-winter period (based on known life histories of local infauna— e.g. Leber 1982, Watzin 1984), it is possible that prey depletion occurred as a result of continuous foraging by shorebirds. Prey depletion by foraging shorebirds has been documented numerous times in soft sediment environments (e.g. Goss-Custard 1977, Schneider 1978, Schneider & Harrington 1981, Sutherland 1982, Quammen 1984). However, greatest prey depletion should occur when birds forage in high densities (Schneider 1985) and/or have higher energy requirements (during pre-migratory fattening, staging, molt, or following a long over-ocean flight) (Myers & McCaffery 1984, Mercier & McNeil 1994). Shorebird densities on the Onslow Beach intertidal flats were relatively low (0-100 birds/ha) compared to densities recorded in studies with measurable prey depletion (e.g. Quammen 1984: 300-400 birds/ha, Mercier & McNeil 1994: 470-1050 birds/ha). In addition, energy requirements of shorebirds in early-winter— the period of this study— are less than at other times of the year (Blem 1980, Kalejta 1992). A number of studies have been unable to detect depletion even when high densities of foraging shorebirds were present (e.g. Duffy et al. 1981, Kaletja 1993). Because both densities and energy requirements of Onslow Beach shorebirds were relatively low, it is unlikely that substantial prey depletion occurred across this study's two-month time period.

The ability of benthic community and sediment characteristics to “explain” two-thirds of the variation in shorebird community foraging patterns suggests that patch-level characteristics play an important role in dictating foraging patterns at this scale. Yet, one third of the total variation is still unaccounted for after these patch-level characteristics have been addressed. Other patch-specific factors not included in the BEST analysis, such as flat microtopography and edge characteristics, may also influence shorebird distributional patterns. Additionally, it is important to consider attributes of the landscape. The surrounding habitat matrix, especially in relation to predation risk from both stealth predators and raptors hunting from perches, likely contributes to some of the unexplained variation. Other landscape-scale factors that have not been considered in this study, including changes or disturbances occurring on other flats in the area, may also contribute to the unexplained variation in shorebird community patterns.

## APPENDIX A: Shorebird Count Data, Not Adjusted for Area.

When Shell Flat is not listed, no birds were observed on the flat. Oct 27 & 28 observations did not include Island or Tidal Creek Flat. BBPL = black-bellied plover, DUNL = dunlin, PIPL = piping plover, RUTU = ruddy turnstone, SAND = sanderling, SEPL = semipalmated plover, WESA = western sandpiper, WILL = willet, YELL = yellowlegs. LT-3 = mid ebb tide, LT-1.5 = late ebb tide, LT = low tide. BR = Broad Flat, SE = Semi-Enclosed Flat, TC = Tidal Creek Flat, IS = Island Flat, SH = Shell Flat.

Date	Tidal Stage	Flat	BBPL	DUNL	PIPL	RUTU	SAND	SEPL	WESA	WILL	YELL
27-Oct	LT	BR	2	7	1	0	3	6	0	0	0
		SE	0	0	0	0	0	1	0	0	0
28-Oct	LT	BR	4	3	0	0	3	3	0	1	0
		SE	0	0	0	0	0	3	0	0	1
29-Oct	LT	BR	3	7	0	0	6	0	0	0	0
		SE	1	0	0	0	0	1	0	0	0
		TC	2	6	0	0	0	0	0	0	1
		IS	1	0	0	0	1	0	0	0	0
30-Oct	LT	BR	2	0	0	0	3	0	1	0	0
		SE	0	0	0	0	0	1	0	0	0
		TC	1	16	0	0	0	0	0	0	1
		IS	1	1	0	0	1	0	0	0	0
31-Oct	LT	BR	2	0	1	0	4	1	0	0	0
		SE	0	0	0	0	0	1	0	0	0
		TC	1	20	0	0	0	0	0	0	1
		IS	1	0	0	0	4	0	0	0	0
1-Nov	LT	BR	3	0	1	0	4	1	0	0	0
		SE	0	0	0	0	0	0	0	0	0
		TC	1	9	0	0	0	0	0	0	0
		IS	2	0	0	0	1	0	0	0	0
10-Nov	LT-3	BR	2	11	0	0	2	3	0	0	0
		SE	1	0	0	0	0	1	0	0	1
		SH	1	0	0	0	0	0	0	0	0
	LT-1.5	BR	3	14	0	0	3	0	0	0	0
		SE	0	0	0	0	0	1	0	0	0
		TC	1	9	0	0	0	0	0	0	1
	LT	BR	2	0	0	0	1	0	0	0	0
		SE	0	0	0	0	0	1	0	0	0
		TC	1	6	0	0	0	0	0	0	1
		IS	1	11	0	0	12	0	0	0	0



Date	Tidal Stage	Flat	BBPL	DUNL	PIPL	RUTU	SAND	SEPL	WESA	WILL	YELL
24-Nov	LT-3	BR	1	24	0	0	1	2	0	1	1
		SE	1	1	0	0	0	4	0	0	0
	LT-1.5	BR	4	26	0	1	4	1	0	0	2
		SE	0	0	0	0	0	0	0	0	0
		TC	0	21	0	0	0	1	0	0	0
	LT	BR	3	11	0	0	3	0	0	0	0
		SE	0	0	0	0	0	0	0	0	0
		TC	1	12	0	0	0	0	0	0	0
		IS	1	1	0	0	0	0	0	1	0
		SH	0	0	0	1	0	0	0	0	0
25-Nov	LT-3	BR	2	11	0	0	2	0	0	0	0
		SE	0	4	0	0	0	7	0	0	0
	LT-1.5	BR	2	17	0	0	3	0	0	0	0
		SE	0	0	0	0	0	0	0	0	0
		TC	1	6	0	0	0	0	0	0	1
	LT	BR	3	2	0	0	3	0	0	0	0
		SE	0	0	0	0	0	0	0	0	0
		TC	0	7	0	0	0	0	0	0	0
		IS	1	7	0	0	0	0	0	0	0
26-Nov	LT-3	BR	3	21	0	1	3	0	0	0	0
		SE	0	0	0	0	0	1	0	0	0
	LT-1.5	BR	3	10	0	0	2	0	0	0	1
		TC	1	10	0	0	0	0	0	0	0
		IS	0	1	0	0	0	0	0	0	0
	LT	BR	3	2	0	0	4	0	0	0	0
		SE	0	0	0	0	0	0	0	0	0
		TC	1	5	0	0	0	0	0	0	0
		IS	1	11	0	0	2	0	0	0	0
28-Nov	LT-3	BR	2	12	0	0	1	0	0	0	0
		SE	0	4	0	0	1	9	0	0	0
	LT-1.5	BR	2	6	0	0	5	0	0	0	0
		SE	1	1	0	0	0	1	0	0	0
		TC	1	19	0	0	0	0	0	0	0
	LT	BR	3	5	1	1	7	1	0	0	0
		SE	0	0	0	0	0	0	0	0	0
		TC	1	0	0	0	0	0	0	0	0
		IS	0	9	0	0	5	0	0	0	0
		SH	0	0	1	1	0	0	0	0	0

Date	Tidal Stage	Flat	BBPL	DUNL	PIPL	RUTU	SAND	SEPL	WESA	WILL	YELL
13-Dec	LT-3	BR	1	0	0	0	2	0	0	0	0
		SE	0	0	0	0	0	0	0	0	0
	LT-1.5	BR	2	13	0	0	3	0	0	0	0
		SE	0	0	0	0	0	0	0	0	0
		TC	1	27	0	0	0	0	0	0	0
	LT	IS	1	30	0	0	8	0	0	0	0
		BR	1	9	0	0	2	0	0	0	0
		SE	0	0	0	0	0	0	0	0	0
		TC	1	20	0	0	0	0	0	0	0
		IS	1	5	0	1	11	5	0	0	0
15-Dec	LT-3	BR	3	40	0	0	4	0	0	0	1
		SE	0	0	0	0	0	0	0	0	0
	LT-1.5	BR	2	25	0	0	1	0	0	0	0
		SE	0	0	0	0	0	0	0	0	0
		TC	0	15	0	0	0	0	0	0	0
		IS	1	11	0	1	11	0	0	0	0
15-Dec	LT	BR	2	20	0	0	3	0	0	0	0
		SE	0	0	0	0	0	0	0	0	0
		TC	1	0	0	0	0	0	0	0	0
		IS	1	13	0	0	16	0	0	0	0
		SH	1	0	1	0	0	0	0	0	0
16-Dec	LT-3	BR	2	18	0	0	3	0	0	0	0
		SE	0	0	0	0	0	0	0	0	0
	LT-1.5	BR	3	9	0	0	1	0	0	0	0
		SE	0	0	0	0	0	0	0	0	0
		TC	1	25	0	0	0	0	0	0	0
		IS	1	27	0	0	5	0	0	0	0

## APPENDIX B. Benthic Species List: Mean Densities<sup>1</sup> by Flat.

### Polychaetes

Family	Species	Semi- Enclosed	Broad	Shell	Island	Tidal Creek
Arenicolidae	<i>Arenicola cristata</i>	0	2.0	0	0	0
Capitellidae	<i>Capitella capitata</i>	48.4	17.7	370.4	18.8	34.3
	<i>Dasybranchus</i> sp.	1.9	0	0	0	0
	<i>Heteromastus filiformis</i>	50.3	5.9	13.6	9.4	247.7
	<i>Notomastus</i> sp.	0	2.0	0	0	0
	Capitellidae- unknown	34.8	0	0	0	0
Cirratulidae	<i>Tharyx</i> sp.	7.7	2.0	4.5	0	15.2
Glyceridae	<i>Glycera</i> sp.	3.9	2.0	27.1	18.8	19.1
	<i>Hemipodus roscus</i>	0	3.9	0	0	0
Goniadidae	<i>Glycinde solitaria</i>	0	0	4.5	0	3.8
	<i>Goniada</i> sp.	0	0	0	9.4	0
Lumbrineridae	<i>Lumbrineris</i> sp.	0	3.9	0	0	0
Maldanidae	<i>Clymenella torquata</i>	0	0	18.1	28.1	0
	<i>Rhodine</i> sp.	0	0	0	0	11.4
Nereididae	<i>Nereis</i> spp.	52.3	145.6	189.7	0	11.4
Oeononidae	<i>Notocirrus spiniferus</i>	7.7	0	0	0	3.8
Onuphidae	<i>Onuphis</i> sp.	0	0	4.5	0	0
Opheliidae	<i>Armandia agilis</i>	1.9	0	0	9.4	3.8
	<i>Ophelia denticulata</i>	3.9	2.0	22.6	0	0
	Opheliidae- unknown	1.9	0	0	0	0
	<i>Travicia</i> sp.	0	0	0	0	3.8
Orbiniidae	<i>Haploscoloplos robustus</i>	54.2	135.7	58.7	0	15.2
	<i>Orbinia americana</i>	1.9	0	0	0	3.8
	<i>Scoloplos</i> sp.	5.8	13.8	0	0	7.6
Paraonidae	<i>Aricidea fragilis</i>	9.7	11.8	27.1	9.4	83.8
	<i>Paraonis</i> sp.	9.7	3.9	176.2	28.1	30.5
Pectinariidae	<i>Pectinaria gouldi</i>	0	2.0	0	0	3.8
Phyllodocidae	<i>Eteone</i> sp.	1.9	9.8	18.1	0	0
	<i>Paranaitis</i> sp.	0	2.0	0	0	3.8
	<i>Phyllodoce</i> sp.	0	0	0	9.4	3.8
Spionidae	<i>Polydora</i> sp.	0	0	13.6	0	0
	Spionidae- unknown	0	0	4.5	0	0
Unknown	unidentified polychaetes	48.4	15.7	18.1	18.8	26.7

<sup>1</sup> organisms per m<sup>2</sup>.

Phylum	ITC <sup>1</sup>	Family	Species	Semi-Enclosed	Broad	Shell	Island	Tidal Creek
Arthropoda	Amphipoda		Amphipoda- all	211.0	464.2	289.1	65.7	122.0
	Caprellidae		Caprellidae- unknown	0	0	0	0	30.5
	Decapoda	Grapsidae	<i>Sesarma reticulatum</i>	0	0	4.5	0	0
		Ocypodidae	<i>Uca pugilator</i>	7.7	0	0	0	0
		Pinnotheridae	<i>Pinnixa</i> sp.	0	5.9	0	0	19.1
		Unknown	Brachyura- unknown	1.9	0	0	9.4	0
			Paguroidea- unknown	0	2.0	4.5	18.8	0
	Isopoda	Anthuridae	<i>Cyathura polita</i>	0	2.0	0	0	0
		Sphaeromatidae	<i>Sphaeroma quadridentatum</i>	0	2.0	4.5	0	0
		Unknown	Isopoda- unknown	0	2.0	0	0	0
Mollusca	Bivalvia	Donacidae	<i>Donax variabilis</i>	1.9	43.3	18.1	37.5	22.9
		Mactridae	<i>Spisula solidissima</i>	3.9	0	0	0	0
		Mytilidae	<i>Brachidontes exustus</i>	0	0	9.0	0	0
		Semelidae	<i>Semele proficua</i>	1.9	0	0	0	0
		Solecurtidae	<i>Tagelus</i> spp.	0	2.0	4.5	0	15.2
		Tellinidae	<i>Tellina</i> spp.	1.9	2.0	0	0	3.8
		Veneridae	<i>Chione</i> sp.	0	2.0	4.5	0	0
			<i>Dosinia</i> spp.	0	0	0	0	7.6
			<i>Gemma gemma</i>	42.6	2.0	0	0	3.8
			<i>Mercenaria mercenaria</i>	9.7	7.9	0	0	11.4
	Gastropoda	Ellobiidae	<i>Melampus bidentatus</i>	0	0	0	18.8	26.7
		Littorinidae	<i>Littorina irrorata</i>	54.2	0	0	0	0
		Nassariidae	<i>Nassarius obsoletus</i>	58.1	0	0	0	15.2
			<i>Nassarius vibex</i>	0	0	9.0	0	0
		Naticidae	<i>Neverita duplicata</i>	0	2.0	0	0	0

<sup>1</sup>Intermediate Taxonomic Classification

Phylum	ITC <sup>1</sup>	Family	Species	Semi-Enclosed	Broad	Shell	Island	Tidal Creek
Hemichordata	Enteropneusta	Harrimaniidae	<i>Saccoglossus kowalevskii</i>	0	3.9	0	9.4	7.6
		Unknown	Enteropneusta- unknown	0	2.0	0	0	0
Nemertea		Lineidae	<i>Micrura leidyia</i>	0	0	0	9.4	0
		Unknown	Nemertea- unknown	1.9	5.9	4.5	28.1	0
Nematoda			Nematoda- unknown	0	2.0	0	0	30.5
Cnidaria	Anthozoa	Edwardsiidae	<i>Edwardsia elegans</i>	0	0	0	9.4	0
Platyhelminthes	Turbellaria	Stylochidae	<i>Coronadena mutabilis</i>	0	0	0	0	3.8
Echinodermata	Holothuroidea		Holothuroidea- unknown	0	2.0	0	0	0

<sup>1</sup>Intermediate Taxonomic Classification

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