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# Densities of Wintering Scoters in Relation to Benthic Prey Assemblages in a North Atlantic Estuary

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**Abstract.**—During winter, molluscivorous sea ducks often form high density feeding flocks in association with patchily distributed prey, although few studies have documented the substrate and prey characteristics where sea ducks (tribe: Mergini) aggregate and thus what constitutes high-value sea duck foraging habitat. Sea duck surveys were conducted and benthic grab samples collected at sites with different benthic substrate characteristics to compare macroinvertebrate community assemblages in relation to densities of three species of sea ducks: Surf (*Melanitta perspicillata*), Black (*M. americana*), and White-winged (*M. fusca*) scoters (hereafter “scoters” when combined) during winter (2010-2011) in Narragansett Bay, Rhode Island, an urbanized estuary in the Northwest Atlantic. Overall, the highest densities of scoters ( $104 \pm 17$  per  $0.5 \text{ km}^2$ ) were found over sand substrates with homogeneous assemblages of infaunal prey. Significantly lower densities of scoters ( $21 \pm 4$  per  $0.5 \text{ km}^2$ ) were associated with mixed sand-gravel-mud substrates that supported epifaunal assemblages and patchily distributed infauna. Mean energy densities (kcal/g) were higher among infaunal (0.64-4.49) vs. epifaunal (0.17-0.53) prey. Overall biomass ( $\text{g}/\text{m}^2$ ) of polychaetes was higher in mixed substrates, and biomass of infaunal bivalves did not significantly differ among habitat type. However, infaunal prey may have been less accessible to scoters at sites with mixed substrates due to a barrier effect created by high-densities of epifauna with low energetic value. Thus, sand-substrate sites supporting infaunal benthic communities may provide high-quality feeding habitat for scoters wintering in the Northwest Atlantic. Understanding the influences of benthic habitat characteristics and macroinvertebrate prey assemblages on distribution of feeding scoters is particularly important for managing sea ducks in areas with increasing anthropogenic development in the coastal zone. Received 16 November 2012, accepted 13 February 2013.

**Key words.**—benthic community, habitat use, *Melanitta*, Mergini, Narragansett Bay, scoters, winter surveys.

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Prey availability and quality are among the most important habitat characteristics affecting the distribution and abundance of many animals (Pyke *et al.* 1977), including sea ducks (tribe: Mergini) during winter (Guillemette *et al.* 1992; Lewis *et al.* 2008). Winter is energetically demanding for sea ducks, in part due to increased thermoregulatory costs (McKinney and McWilliams 2005), so quality and availability of prey may be particularly important for these species. Decreases in winter food availability have been linked to mass sea duck mortality and decreased reproductive output the following breeding season (Camphuysen *et al.* 2002; Oosterhuis and van Dijk 2002). Sea ducks are characteristically aggregated during nonbreeding periods and may form high-density feeding flocks at sites with relatively

high densities and biomass of prey, including bivalves and other benthic macroinvertebrate taxa (Guillemette *et al.* 1993). Despite the assumed importance of benthic prey to many sea ducks, few studies have explicitly examined how local-scale spatial variation in benthic community composition relates to sea duck abundance (Degraer *et al.* 1999; Larsen and Guillemette 2000; Kirk *et al.* 2008).

The distribution of benthic macroinvertebrates is spatially heterogeneous and driven by dynamic biophysical interactions between the water column and seafloor (Zajac 2008). In shallow, subtidal habitats of western Atlantic estuaries and coastal areas, latitudinal region, salinity, and sediment type have strong influences on the distribution and abundance patterns of benthic macroinvertebrate assem-

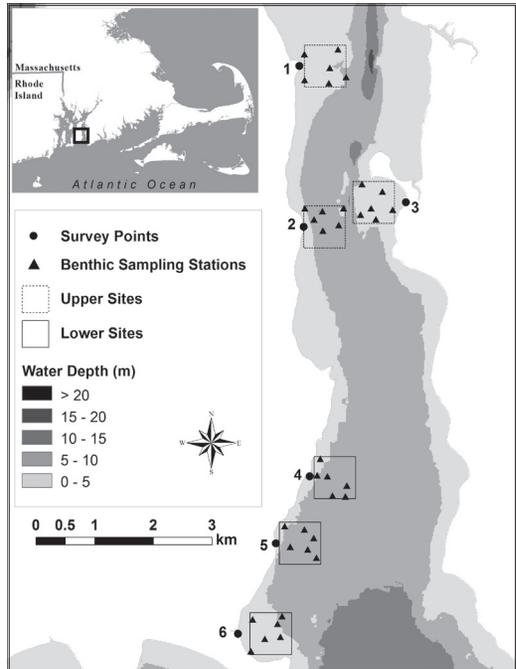
blages. A distinct benthic macroinvertebrate sub-region has been identified from New York Bight to Cape Cod (Hale 2010). Within Narragansett Bay and adjacent Rhode Island Sound, sediment grain size is an important factor affecting variation in benthic species composition, diversity, and abundance (Frithsen 1989; Theroux and Wigley 1998). Individual benthic macroinvertebrates also differ widely in value as potential sea duck prey because of variation in shell mass, size, energy and nutrient content, burial depth, and accessibility (Hamilton *et al.* 1999; Richman and Lovorn 2003). Thus, information on the distribution, abundance, and relative energetic value of potential prey species is important for understanding the ecology of wintering sea ducks.

On the Atlantic coast of North America, sea duck managers have identified a need to better understand sea duck ecology in relation to benthic systems (Sea Duck Joint Venture 2008). Identifying characteristics associated with high-value sea duck foraging habitat is particularly important for monitoring and managing sea duck populations in areas subjected to increasing levels of anthropogenic impacts in the coastal zone (Sea Duck Joint Venture 2008). Within Rhode Island's Narragansett Bay, an urbanized estuary in the Northwest Atlantic, we investigated associations between benthic habitat characteristics, macroinvertebrate community assemblages, and densities of three species of scoters (Surf (*Melanitta perspicillata*), Black (*M. americana*), and White-winged (*M. fusca*) scoters; hereafter "scoters") during winter. Our specific objectives were to: 1) assess scoter densities during winter among sites that differed by substrate type; 2) compare scoter densities among sites as a function of benthic macroinvertebrate community composition; and 3) quantify interspecific variation in energetic value of various species of benthic macroinvertebrates as prey for scoters.

## METHODS

### Study Area and Site Delineation

We conducted fieldwork in the Sakonnet Passage within the eastern portion of Narragansett Bay, Rhode



**Figure 1.** Bathymetry of six land-based survey sites (numbered points), six 0.5 km<sup>2</sup> study plots (boxes), and 36 benthic grab sampling stations (triangles) in the Sakonnet Passage in Narragansett Bay, Rhode Island, sampled during winter of 2010-2011.

Island (Fig. 1). Narragansett Bay is a large estuary (342 km<sup>2</sup>), with semi-diurnal tides (mean range = 1.1 m) and a mean depth of 7.8 m. One of three major north-south passages that divide the bay is the Sakonnet Passage, which covers 61 km<sup>2</sup> and has a mean depth of 6.5 m (Chinman and Nixon 1985). The Sakonnet Passage is mixed primarily by tidal currents averaging 0.5-1.0 knots and has a mean salinity (31‰) similar to the adjacent Rhode Island Sound (Hicks 1959).

Sediment classification in Narragansett Bay is predominantly clayey silt and sand-silt-clay, although the Sakonnet Passage has a unique and abrupt substrate grain size transition zone that occurs approximately mid-way between its northern headwaters and southern entrance to Rhode Island Sound. The northern (upper) reach is mixed silt-clay-gravel (< 25% sand), whereas the southern (lower) reach is predominately (> 75%) well-sorted sand (McMaster 1960). This transition zone provided us a unique opportunity to compare benthic prey communities in relation to sea duck densities among selected sites with different substrate types.

Baseline data from the 2004-2010 Narragansett Bay Winter Waterfowl Survey indicated that a large proportion of scoters in Narragansett Bay used the Sakonnet Passage during winter (U.S. Environmental Protection Agency 2010). To better understand the relationship between scoter densities, benthic substrate classification, and community assemblages of potential benthic

macroinvertebrate prey, we selected six 0.5 km<sup>2</sup> study sites in the Sakonnet Passage that had similar mean water depths (4.8 m; range 3.5-6.6 m) and that were stratified by benthic substrate classification ( $n = 3$  sites from the lower and upper reach, respectively; Fig. 1). We used ArcGIS (Environmental Systems Research Institute 2009) to delineate site boundaries as 0.5 km<sup>2</sup> polygons extending seaward from each land-based survey point and generated six random points (stratified by distance to shore) within each site for benthic macroinvertebrate sampling.

#### Sea Duck Surveys

From 15 December 2010 to 31 March 2011, an observer conducted weekly sea duck counts from fixed, land-based survey points adjacent to each 0.5 km<sup>2</sup> study site ( $n = 6$ ; Fig. 1). Surveys lasted 30 min and were completed within 4 hr following local morning civil twilight (U.S. Naval Observatory 2010). Before each survey was initiated, observers classified overall observation conditions as poor, fair, good, or excellent based on wind speed, visibility, wave height, and precipitation. Observers then used a 20-60 power spotting scope (Swarovski HD-ATS 80) and binoculars to count, by species, all scoters on the water within site plot boundaries, which were visually estimated using established landmarks. Disturbance events were classified as: none, hunting, boat, or other. To quantify foraging behavior, the estimated percentage of scoters observed diving during the entire 30-min survey period was scored as: 1 (0-25%), 2 (26-50%), 3 (51-75%), or 4 (76-100%).

#### Benthic Macroinvertebrate Sampling

We sampled benthic macroinvertebrates at six randomly located stations within each site from 14 October 2010 to 8 April 2011. At each station, we used a 0.04 m<sup>2</sup> Young-modified Van Veen grab affixed with a planar-view camera to collect sediment samples and underwater video of the benthos. Grabs with level sediment to a depth of 7 to 10 cm were considered successful. We collected three replicate, successful grabs per station. We discarded unacceptable grabs (e.g., overfilled or washed out). After collection, we immediately rinsed contents with seawater over a stainless steel No. 12 (1.7 mm mesh size) sieve and packed the samples on ice. This relatively coarse mesh size may have under-sampled the density and biomass of small macrofauna such as amphipods, polychaetes, and isopods (Schlacher and Wooldridge 1996). However, diet studies indicate that while in marine habitats, scoters primarily consume macroinvertebrates exceeding 5 mm in size (Savard *et al.* 1998), so we assumed that the 1.7 mm mesh was adequate for characterizing assemblages of potential prey available to scoters within our study sites. We either stored samples at 4 °C and processed them within 48 hrs, or froze samples at -15 °C for later processing. In the laboratory, we sorted samples by taxa with all individuals identified to species or lowest possible taxon, up to the class level. We pooled the three

replicate grabs (0.04 m<sup>2</sup> each) per sampling station for a representative area of 0.12 m<sup>2</sup>. We multiplied overall abundance of each genera per station by 8.33 to estimate the mean number of individuals per m<sup>2</sup>.

#### Statistical Analyses

*Sea duck densities.* We retained, for subsequent analyses, scoter surveys with observation conditions we classified as excellent, good, or fair and with disturbance events classified as none. We calculated monthly averages of scoters (all species combined) from weekly survey counts conducted at each site from December 2010 to March 2011. The following statistical analyses were conducted using SAS (SAS Institute, Inc. 2008). To determine if scoter abundance significantly differed between upper and lower strata, we used a mixed effects model (Proc GLIMMIX) to fit models with total scoter abundance (monthly averages of all species combined) as the response variable, month and stratum (upper or lower Sakonnet Passage) and the interaction between month and stratum as fixed effects, and site as a random effect. We used an Autoregressive (AR-1) covariance structure to account for correlation of survey data collected at fixed sites over time. We assessed the significance of each fixed effect using Wald Statistics for Type III contrasts.

*Benthic biomass.* We used allometric modeling procedures outlined in McKinney *et al.* (2004) to estimate genus-level dry biomass for genera that comprised > 5% of overall or within-stratum benthic macroinvertebrate abundance. For each grab sample, we measured length and dry mass of shell and tissue from at least 10 randomly selected individuals representing each genus. We collected length measurements with digital calipers to nearest 0.01 mm along the longest body axis. After drying at 60 °C for 48 hr, we measured mass using a Mettler scale with an accuracy of 0.0001 g. For molluscs, we removed soft tissue from shell parts and weighed separately. We measured whole animal mass for amphipods and polychaetes.

We fit linear and non-linear regression models to explain the relationship between dry biomass and length. For all taxa, power models ( $y = ax^b$ ) provided the best fit (highest  $r^2$  coefficient) for explaining the relationship between length ( $x$ ) and whole animal (shell + tissue for molluscs) dry mass ( $y$ ). We used these models to estimate biomass at each sampling station using the average shell length of 10 randomly selected individuals per genus. For amphipods, we estimated dry biomass using an overall average dry mass value of individuals ( $n = 100$ ) collected from Narragansett Bay (U.S. Environmental Protection Agency, unpubl. data; Appendix). We combined marine worms of the genera *Nereis*, *Nephtys*, and *Glycera* at the suborder level *Phyllodoceida*. Because biomass data were not normally distributed, we compared biomass of benthic prey between upper and lower strata using Wilcoxon rank-sum tests. Specifically, we tested for differences in biomass of infaunal bivalves and polychaetes as previous research has shown that these

prey categories comprise relatively high proportions of scoter diets (e.g., Stott and Olsen 1973; Fox 2003; Anderson *et al.* 2008).

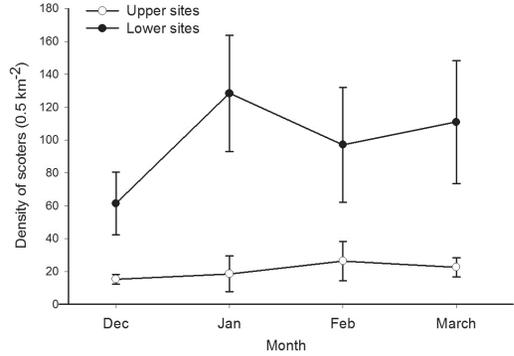
We estimated percent shell mass for each molluscan genus by calculating: mass of shell / (mass of tissue + shell). We used the following published soft-tissue energy equivalents to estimate overall energy density of biomass-modeled benthic macroinvertebrates in kilocalories (kcal) per unit overall dry mass: McKinney *et al.* (2004) for bivalves and gastropods, and McKinney *et al.* (2004) or Steimle and Terranova (1985) for polychaetes and molluscs. We compared energy densities across molluscan genera with varying proportions of shell biomass using paired Wilcoxon tests with Bonferroni-adjusted significance values.

*Benthic community multivariate analyses.* We used Plymouth Routines in Multivariate Research software to analyze benthic community structure between strata on 4<sup>th</sup>-root transformed biomass data (PRIMER; Clarke and Gorley 2006). This transformation is conventional for analysis of such benthic data to reduce the influence of the most dominant taxa (Clarke and Gorley 2006). We calculated resemblance between sampling stations using the Bray-Curtis similarity coefficient. From the Bray-Curtis similarity matrix, we created a dendrogram using the group-average linkage method. Non-metric multi-dimensional scaling (MDS) ordination was used to graphically display, in two-dimensional space, relative Bray-Curtis dissimilarity distances between sampling stations, with contour lines delineating sampling stations with Bray-Curtis similarity values  $\geq 0.5$ . We used the ANOSIM (analysis of similarities) procedure to test the *a priori* null hypothesis of no assemblage differences between sampling stations stratified by position. We then used the SIMPER (similarity percentages) sub-routine to quantify the contribution of each genus to the within-group similarity of upper vs. lower strata (Clarke and Gorley 2006).

## RESULTS

### Densities of Scoters

We observed significantly higher average densities of scoters within lower vs. upper Sakonnet Passage sites ( $F_{1,16} = 5.47$ ;  $P = 0.03$ ) with no evident monthly variation during winter ( $F_{3,16} = 1.31$ ;  $P = 0.30$ ; Fig. 2). Scoter density (mean  $\pm$  SE) individuals  $0.5 \text{ km}^{-2}$ ) within upper sites was  $20.64 \pm 4.04$  (range 2-115; 84% Surf, 10% White-winged, 6% Black scoters). Scoter density within lower sites averaged  $104.38 \pm 17.42$  (range 8 - 500; 69% Surf, 0% White-winged, and 31% Black scoters). Over 50% of scoters observed were diving during each survey across strata, suggesting that all sites were used as feeding habitat.



**Figure 2.** Seasonal variation in scoter densities (mean  $\pm$  SE birds  $0.5 \text{ km}^{-2}$ ) at upper and lower sites in the Sakonnet Passage in Narragansett Bay, Rhode Island, based on surveys conducted weekly at each site from 15 December 2010 to 31 March 2011. Counts of Surf, Black, and White-winged scoters are pooled for this analysis.

### Densities and Biomass of Benthic Macroinvertebrates

Benthic macrofaunal abundance (individuals  $\text{m}^{-2}$ ) at upper sites was dominated by epifaunal common slipper snails (*Crepidula fornicata*) and common jingleshells (*Anomia simplex*) (Table 1). These high density *Crepidula-Anomia* beds covered 66% ( $n = 12$ ) of the sampling stations at upper sites. The remaining 34% of upper-site sampling stations contained relatively high densities of infaunal *Tellinid* bivalves. Benthic macrofaunal abundance (individuals  $\text{m}^{-2}$ ) at lower sites was dominated by relatively homogeneously distributed, tube-dwelling *Ampeliscid* amphipods, gastropods of the genus *Ilyanassa*, and *Tellinid* bivalves (Table 1). Overall, benthic biomass ( $\text{g m}^{-2}$ ) of *Phyllodocid* polychaetes was higher in upper vs. lower strata ( $Z = 2.073$ ,  $P = 0.038$ ; Fig. 3). Biomass of infaunal bivalves did not differ between strata ( $Z = -1.191$ ,  $P = 0.234$ ).

### Food Value of Benthic Macroinvertebrates

Energy density was inversely related to proportion of shell biomass (Table 2). Shell-less marine worms of the order *Phyllodocida* had the highest overall energy density (4.49 kcal/g), followed by *Ampeliscid* amphipods (2.51 kcal/g) and the relatively

**Table 1.** Mean ( $\pm$  SE) dry biomass ( $\text{g m}^{-2}$ ), density (individuals  $\text{m}^{-2}$ ), frequency of occurrence (percent of grabs present), and overall range of lengths (mm) of benthic macroinvertebrate taxa comprising  $> 5\%$  of overall abundance of benthic macroinvertebrates collected from upper and lower sites in the Sakonnet Passage, Narragansett Bay, Rhode Island, during the winter of 2010-2011.

Taxa <sup>a</sup>	Biomass	Density	Frequency	Length
<b>Upper Sites</b>				
<i>Crepidula</i>	863.83 $\pm$ 267.48	2,071 $\pm$ 539	94	10-23
<i>Anomia</i>	127.13 $\pm$ 37.33	186 $\pm$ 50	83	11-27
<i>Ilyanassa</i>	5.97 $\pm$ 1.29	39 $\pm$ 11	72	6-26
<i>Pagurus</i>	5.68 $\pm$ 1.45	11 $\pm$ 3	67	5-17
<i>Phyllodocida</i> <sup>b</sup>	3.13 $\pm$ 1.02	34 $\pm$ 8	94	27-207
<i>Tagelus</i>	1.86 $\pm$ 1.50	30 $\pm$ 23	17	9-23
<i>Tellina</i>	1.41 $\pm$ 0.80	51 $\pm$ 24	61	5-12
<i>Ensis</i>	0.81 $\pm$ 0.43	2 $\pm$ 1	22	27-45
<i>Ampelisca</i>	0.01 $\pm$ 0.01	44 $\pm$ 30	22	2-6 <sup>c</sup>
<b>Lower Sites</b>				
<i>Pagurus</i>	8.79 $\pm$ 3.36	10 $\pm$ 3	50	8-16
<i>Ilyanassa</i>	6.72 $\pm$ 2.43	45 $\pm$ 16	89	7-15
<i>Phyllodocida</i> <sup>b</sup>	0.91 $\pm$ 0.28	26 $\pm$ 5	89	16-63
<i>Ensis</i>	0.81 $\pm$ 0.19	15 $\pm$ 3	72	12-34
<i>Mulinia</i>	0.76 $\pm$ 0.39	7 $\pm$ 3	39	6-17
<i>Tellina</i>	0.57 $\pm$ 0.12	41 $\pm$ 8	83	5-10
<i>Ampelisca</i>	0.09 $\pm$ 0.02	495 $\pm$ 110	83	2-6 <sup>c</sup>

<sup>a</sup>The remaining 5% of overall biomass of benthic macroinvertebrates was composed of the following taxa: *Acmaea*, *Anachis*, *Anadara*, *Asterias*, *Busycon*, *Cancer*, *Carcinus*, *Diopatra*, *Epitonium*, *Gemma*, *Haminoea*, *Isopoda*, *Littorina*, *Mercenaria*, *Mitrella*, *Nucula*, *Ovalipes*, *Palaemonetes*, *Pandalus*, *Panopeus*, *Pectinaria*, *Sabellaria*, *Spiochaetopterus*, *Turbonilla*, and *Yoldia*.

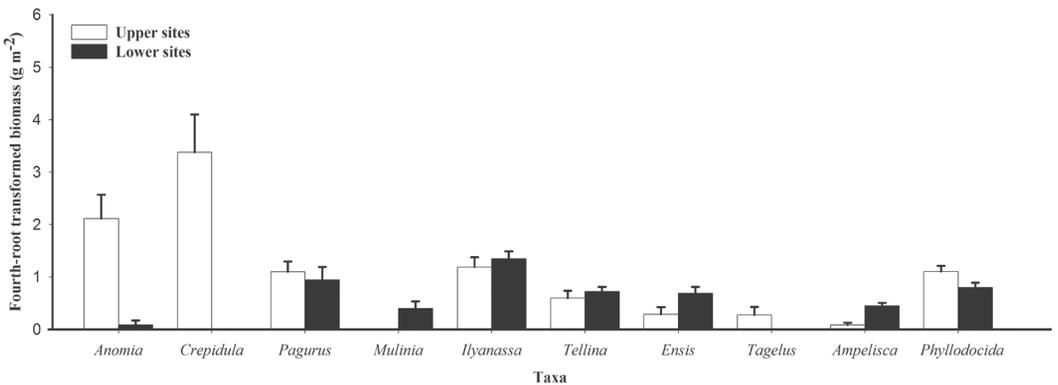
<sup>b</sup>Includes polychaetes of the genera *Nereis*, *Nephtys*, and *Glycera*.

<sup>c</sup>Length range derived from *Ampelisca* sampled throughout Narragansett Bay, RI (U.S. Environmental Protection Agency, unpubl. data).

low shell mass ( $< 75\%$ ) infaunal bivalves of the genera *Tagelus* and *Ensis* (1.20 and 1.12 kcal/g, respectively). The genera with the highest shell mass, *Anomia* (96%) and *Crepidula* (93%), had the lowest overall energy densities (0.17 and 0.26 kcal/g, respectively).

### Multivariate Benthic Community Analyses

An Analysis of Similarities Test (ANO-SIM) indicated a significant difference in benthic macroinvertebrate community composition between upper vs. lower sites (global  $R = 0.406$ ,  $P < 0.01$ ). The upper stations



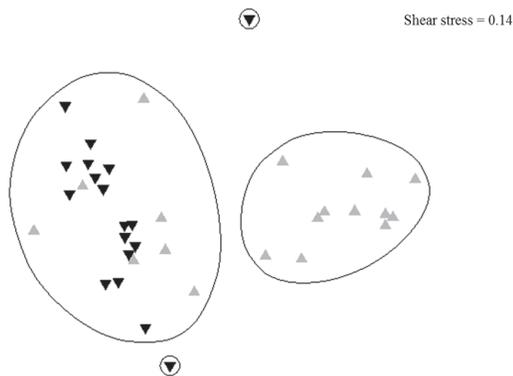
**Figure 3.** Fourth-root transformed mean ( $\pm$  SE) biomass ( $\text{g m}^{-2}$ ) of benthic macroinvertebrate taxa by stratum (upper vs. lower sites), arranged along a continuum of low to high energy densities (including shell).

**Table 2.** Food value of benthic macroinvertebrate genera collected in Narragansett Bay, Rhode Island. Food value relates to ease of capture and nutritional quality which here includes: prey mobility, exposure (infauna or epifauna), percent shell mass (dry mass of shell/dry mass of shell and tissue), and overall mean ( $\pm$  SE) energy density (kcal/g dry mass of whole animal). Taxa are arranged on a continuum of high to low energy densities. Molluscan genera connected by a vertical line did not significantly differ in energy density ( $P < 0.002$ , Wilcoxon, Bonferroni corrected).

Genera	Mobility and Exposure	Shell Mass (%)	Energy Density
<i>Phyllodocida</i>	Highly mobile marine worm	—	4.49
<i>Ampelisca</i>	Tube-dwelling amphipod	—	2.51
<i>Tagelus</i>	Sessile infaunal bivalve	72.38 $\pm$ 2.26	1.20 $\pm$ 0.10
<i>Ensis</i>	Sessile infaunal bivalve	74.36 $\pm$ 2.69	1.12 $\pm$ 0.12
<i>Tellina</i>	Sessile infaunal bivalve	81.61 $\pm$ 0.76	0.80 $\pm$ 0.03
<i>Mulinia</i>	Sessile infaunal bivalve	84.80 $\pm$ 0.89	0.64 $\pm$ 0.04
<i>Ilyanassa</i>	Epifaunal gastropod	84.42 $\pm$ 0.74	0.53 $\pm$ 0.03
<i>Pagurus</i>	Highly mobile epifaunal crustacean	90.16 $\pm$ 2.15	0.30 $\pm$ 0.06
<i>Crepidula</i>	Sessile epifaunal gastropod	92.54 $\pm$ 0.45	0.26 $\pm$ 0.02
<i>Anomia</i>	Sessile epifaunal gastropod	96.05 $\pm$ 0.52	0.17 $\pm$ 0.02

show relatively scattered (variable) benthic macroinvertebrate composition compared to the more clustered (homogeneous) benthic macroinvertebrate composition among the lower sampling stations (Fig. 4).

The MDS ordination delineated two major clusters of sampling stations. Sampling stations comprising each cluster shared at least 50% Bray-Curtis similarity in benthic macroinvertebrate biomass composition. One cluster contained the majority ( $n = 16$ ) of lower sampling stations and a lesser number ( $n = 7$ ) of upper sampling stations.



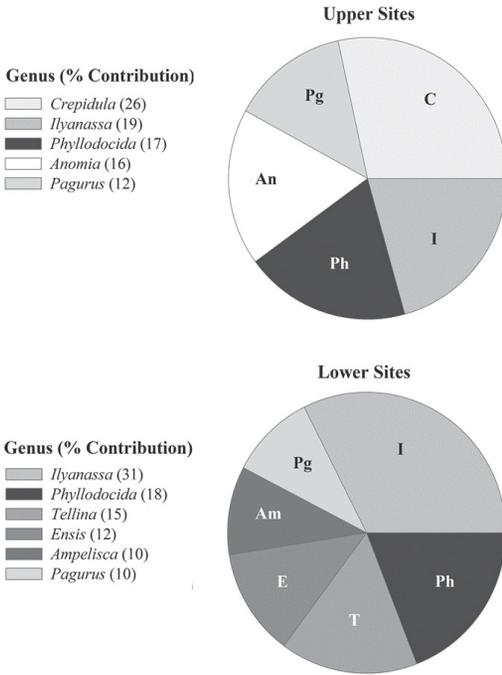
**Figure 4.** Non-metric multidimensional scaling ordination plot of fourth-root transformed benthic macroinvertebrate biomass data, showing relative Bray-Curtis similarities between upper and lower sampling stations (light gray upward and black downward facing triangles, respectively; stress = 0.14) in the Sakonnet Passage in Narragansett Bay, Rhode Island. Contour lines delineate stations with Bray-Curtis similarity values  $\geq 0.50$ .

Benthic macroinvertebrates comprising this cluster were largely represented by the taxa *Ilyanassa*, *Phyllodocida*, *Tellina*, and *Ensis*. The other cluster contained the majority ( $n = 11$ ) of upper sampling stations and was dominated by large proportions of low energy density genera such as *Crepidula* and *Anomia*.

The SIMPER sub-routine indicated that overall similarity in benthic macroinvertebrate taxa was greater among the lower (61%) vs. upper (49%) sampling stations, indicating that benthic communities at upper sites were more variable in composition of macroinvertebrate taxa. Benthic macroinvertebrates that were consistently found within the lower sites included relatively high-energy potential prey items such as *Ilyanassa*, *Phyllodocida*, *Tellina*, and *Ensis* (Fig. 5). Low-energy epifauna of the genera *Crepidula*, *Anomia*, and *Pagurus* contributed to over 50% of the benthic community composition within the upper sites.

## DISCUSSION

Overall, we found the highest mean densities of scoters (approximately 200 km<sup>-2</sup>) in the lower vs. upper Sakonnet Passage. McKinney (2004) estimated that the mean density of winter waterfowl (all species combined) in Narragansett Bay was 39 individuals km<sup>-2</sup>, which was similar to the mean density of scoters (41 km<sup>-2</sup>) that we detected in the upper



**Figure 5.** Contribution (%) of benthic taxa to the average Bray-Curtis similarity between sampling stations stratified by position (upper vs. lower) in the Sakonnet Passage in Narragansett Bay, Rhode Island. Taxa are shaded along a gradient of lowest energy density (light) to highest energy density (dark) and are denoted within each slice by the following letters: Ph (*Phyllodocida*), Am (*Ampelisca*), E (*Ensis*), T (*Tellina*), I (*Ilyanassa*), Pg (*Pagurus*), C (*Crepidula*), An (*Anomia*).

Sakonnet Passage. Scoters are likely attracted to the lower Sakonnet Passage by favorable abiotic and biotic habitat conditions. A previous study found that in Narragansett Bay, the abundance of open-water habitat species (including Surf, Black, and White-winged scoters) decreased with increasing residential development along adjacent shorelines and that sites used by wintering waterfowl in the Sakonnet had less shoreline development than sites located elsewhere in the bay (McKinney *et al.* 2006).

Past research has shown that substrate type influences benthic community structure in marine environments (e.g., Zajac *et al.* 2000). The lower Sakonnet Passage is unusual, compared to most of Narragansett Bay, in that the dominant benthic sediment type was well-sorted sand that is more characteristic of benthic habitats within

nearshore Rhode Island Sound (McMaster 1960). Conversely, benthic habitats in the upper Sakonnet are a mosaic of silt, clay, and gravel sediments. These mixed sediments are more typical of sediment composition found throughout Narragansett Bay (McMaster 1960). We found in this study that differences in sediment characteristics in the lower vs. upper Sakonnet were associated with distinct assemblages of benthic macroinvertebrate taxa. Sandy substrates in the lower Sakonnet supported dense beds of *Ampeliscid* amphipods, as well as relatively high biomass of *Ilyanassa* whelks, and the infaunal bivalves *Tellina* and *Ensis*. At upper Sakonnet Passage sites over mixed gravel, sand, or mud substrates, epifaunal beds of *Crepidula fornicata* dominated the biomass and we found significantly higher biomass of *Phyllodocid* worms relative to lower sites. Stickney and Stringer (1957) also found increased densities and larger sizes of *Nereis* polychaetes occurring within *Crepidula* beds in Narragansett Bay.

High-density populations of *Ampeliscid* amphipods or *Crepidula* create distinct habitats by directly modifying the sediment and distribution of benthic fauna (French *et al.* 1992). High densities of *Ampeliscid* amphipods alter the surficial sediment layer through tube-building, which may enhance growing conditions for infaunal bivalves (MacKenzie *et al.* 2006). Dense *Crepidula* beds form biogenetic reefs that increase habitat complexity and provide refuge for other species of benthic invertebrates (Lindsey *et al.* 2006). Thus, benthic community structure within estuarine systems appears to be largely influenced by interactions between benthic substrate type and dominant macroinvertebrate species.

Energy density of potential prey items within the upper and lower Sakonnet benthic communities differed among taxa and, for hard-bodied organisms, was inversely related to mean amount of shell mass. *Anomia* and *Crepidula* had the highest overall shell mass and lowest overall energy densities of all taxa we sampled. Among molluscs, razor clams (i.e., *Tagelus*, *Ensis*) and *Tellins* had the lowest shell mass and highest energy density.

Sea ducks select prey items with the highest tissue to shell ratio when offered bivalves varying by length and shell morphology (Bustnes 1998), and this prey selection strategy would provide sea ducks in our study area with more energy-dense prey. Minimizing amounts of ingested shell may also reduce the energy required to crush and process indigestible materials (Richman and Lovvorn 2003).

Soft-bodied organisms such as *Ampelisca* and *Phyllodoce* marine worms provided the highest energy per unit mass of all the taxa that we sampled, although their contribution to diets of sea ducks depends in part on body size. For example, small, mobile prey, such as amphipods, may not provide a sufficient amount of predictable biomass for large-bodied sea ducks during winter (Goudie and Ankney 1986). Larger-bodied White-winged Scoters tend to consume more hard-shelled prey, whereas smaller-bodied Surf Scoters usually consume a mixture of bivalves and soft-bodied prey (Anderson *et al.* 2008). Black Scoters, the smallest of the three species, consume bivalves, polychaetes, and amphipods in marine environments (Bordage and Savard 1995). The range of size and energy densities of prey available in the Sakonnet Passage may allow for resource partitioning among the different-sized scoter species feeding within mixed flocks (Richman and Lovvorn 2009).

Flocking behavior of wintering sea ducks helps them to locate high-quality feeding sites (Guillemette *et al.* 1993) that are temporally and spatially variable (Larsen and Guillemette 2000). The highest densities of scoters in our study were associated with sand substrates that supported homogeneous distributions of benthic macroinvertebrate taxa with relatively high energy per unit mass. Smaller flocks of scoters were associated with mixed-substrate habitats that supported benthic communities composed of taxa with heterogeneous energy densities (i.e., 66% low-value epifaunal *Crepidula* beds, 33% high-density, energetically valuable infauna) and accessibility. Our survey data showed relatively consistent numbers of birds within each stratum during winter, although sites

with spatially variable prey supported lower densities of birds.

Our findings indicate that nearshore, sandy habitats support relatively high-value benthic prey communities that likely provide high-quality foraging habitat for scoters on southern New England wintering grounds. Stott and Olsen (1973) found that in northern New England, Surf Scoters also selected sites with sandy substrates, where they fed primarily on Arctic wedge clams (*Mesodesma arctatum*) and Atlantic razor clams (*Siliqua costata*). The razor clam (*Ensis directus*) is invasive to sand-flat habitats in Western Europe, where it has become an important prey item for scoters (Tulp *et al.* 2010). Scoters in Western Europe have also been associated with high densities of *Tellinid* bivalves in shallow (< 10 m), sandy habitats (Degraer *et al.* 1999). Overall biomass of infaunal bivalves was not significantly different between upper vs. lower Sakonnet Passage sites. However, *Ensis* and *Tellins* were evenly distributed at sites in the Sakonnet Passage with relatively high densities of scoters. Conversely, we found highly heterogeneous distributions of *Tellins* and razor clams of the genus *Tagelus* at sites with relatively low densities of scoters. The majority of sampling stations at sites with low scoter use were dominated by high densities of *Crepidula*, which formed pavement-like beds over the substrate that may have prevented scoters from accessing infaunal prey in these areas (Witman 1985). Diet analyses from sea ducks collected throughout the U.S. Atlantic coast indicate that scoters do not typically consume *Crepidula fornicata* (P. Osenton, unpubl. data). Thus, in the Sakonnet Passage, more scoters are attracted to sand-substrate habitats that support homogeneous distributions of infaunal bivalves relative to mixed-substrate habitats with variably distributed infaunal and epifaunal prey. It may also be easier for scoters to detect and sift prey items from clean, sandy substrates relative to finer substrates with higher organic content (Fox 2003).

During the non-breeding season, scoters forage over both hard and soft substrate benthic habitats (Perry *et al.* 2007). More

information on associations between scoters and hard substrate prey communities, such as blue mussels (*Mytilus edulis*), is needed to better understand foraging dynamics of scoters in southern New England. Although blue mussels are a predominant prey species for scoters wintering on the Canadian Atlantic coast (Goudie and Ankney 1986), the abundance and stability of blue mussel populations in southern New England may be constrained by lack of suitable hard substrate and increased heat stress at this southern limit of the species range (Tam and Scrosati 2011). In Narragansett Bay, blue mussels form temporally variable and patchily distributed epifaunal reefs (French *et al.* 1992). Therefore, infaunal bivalves occupying sandy substrates may provide a more stable source of prey capable of supporting a local population of scoters throughout winter, whereas mussel-dominated habitats over hard substrate may be more susceptible to depletion by foraging scoters (Kirk *et al.* 2008). In summary, certain types of benthic sediments are associated with different macroinvertebrate prey communities in southern New England that in turn determine the distribution of wintering scoters, and this information is useful in predicting how offshore development may affect these components of the ecosystem.

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**Appendix. Length range, total mean dry animal mass (g), and allometric power model parameters for estimating total dry mass (g) from length for the most abundant benthic macroinvertebrate genera collected in the Sakonnet Passage in Narragansett Bay, Rhode Island, during the winter of 2010-2011. Equations are in the form of  $y = ax^b$  where  $x$  is the shell length (total length for polychaetes) in mm,  $a$  is the length coefficient and  $b$  is the shell length exponent, and  $y$  is the predicted whole animal dry mass (g).**

Taxon	Shell Length (mm)	Whole Dry Mass (g)	$n$	A	b	SE for Predicted Mass (g)	$r^2$
<i>Pagurus</i>	13-28	1.8018 ± 0.31	10	0.00326	2.1242	0.31	0.94
<i>Mulinia</i>	4-19	0.1551 ± 0.05	10	0.00011	2.8244	0.05	0.99
<i>Tellina</i>	9-15	0.0453 ± 0.02	10	7.2 E-05	2.6078	0.01	0.84
<i>Ensis</i>	20-39	0.1307 ± 0.03	8	7.7 E-08	4.1392	0.03	0.99
<i>Tagelus</i>	14-20	0.0962 ± 0.01	9	4.7 E-06	3.4392	0.01	0.81
<i>Anomia</i>	15-32	0.7509 ± 0.12	10	0.00127	1.9944	0.12	0.76
<i>Ilyanassa</i>	12-18	0.4526 ± 0.03	11	0.00095	2.2298	0.04	0.92
<i>Crepidula</i>	9-28	0.5475 ± 0.20	10	5.8 E-07	4.5071	0.20	0.97
<i>Phyllodoce</i>	22-184	0.1604 ± 0.06	13	1.3 E-05	2.1098	0.06	0.93
<i>Ampelisca</i>	2-6	0.0002 ± 1.0 E-4 <sup>a</sup>	100	—	—	—	—

<sup>a</sup>Derived from dry-mass average of individuals collected within Narragansett Bay, RI.