Diel differences in abundance and diversity of fish species and blue crab (*Callinectes sapidus*) in the sandy beach shore zone of lower Delaware Bay

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Abstract—Diel sampling was conducted during June–September 2013, in the shore zone and adjacent nearshore zone of Delaware Bay, Delaware, to identify day and night changes in nekton density, species richness, and the species assemblage. Mean species richness and total nekton density in the shore zone were higher at night. A detailed examination of abundant species revealed that bay anchovy (*Anchoa mitchilli*), weakfish (*Cynoscion regalis*), spot (*Leiostomus xanthurus*), and blue crab (*Callinectes sapidus*) occurred in higher densities in the shore zone at night than during the day. Bluefish (*Pomatomus saltatrix*) occurred in higher densities during the day. Additionally, small (<20 mm in fork length) Atlantic silverside (*Menidia menidia*) and bay anchovy, were observed in abundance in the shore zone only during daytime. Day and night differences in predator–prey dynamics were likely a primary driver of diel differences in nekton abundances observed in the shore zone. No diel differences in species richness, nekton density, or species assemblage were found in the adjacent nearshore area. Daytime sampling predominates in studies of shore-zone nekton and our results show the value of also sampling at night. Future research should include samples throughout the diel cycle and include tagging and movement data to allow a better understanding of diel dynamics of nekton along sandy beach shores.

Estuarine and ocean shore zones are known to support high nekton densities worldwide (Whitfield, 1999; Félix et al., 2007; Gondolo et al., 2011). Sandy beaches dominate the world's shorelines and are productive habitats serving important functions as nursery areas and migration pathways (McLachlan and Brown, 2006; Marin Jarrin and Shanks, 2011; Rodrigues and Vieira, 2013). Estuaries along the east coast of the U.S. are no exception and support many ecologically and economically important species during one or more of their life stages and are essential for the maintenance of coastal fisheries (Beck et al., 2001; Able et al., 2010).

Nekton assemblages along sandy estuarine beaches and ocean surf zones vary spatially and temporally in response to the dynamic nature of these environments (Layman, 2000; Marin Jarrin and Shanks, 2011). These dynamics include day-night changes which are reflected in the abundance and diel movement of many of the dominant shore zone species (Gibson and Robb, 1996;

Becker and Suthers, 2014; Bennett et al., 2015). Interaction between predator and prey species is a major process driving the distribution of estuarine nekton **as** prey alter their distribution to inhabit shallow water refuge areas (Becker and Suthers, 2014). Despite the importance of diel variation, most studies of sandy beach shore zones have been conducted during the daytime, a period that allows the capture of only a portion of assemblage dynamics (Rountree and Able, 1993; Becker and Suthers, 2014).

Previous studies of diel variation in shore zone nekton assemblages have generally reported increased species richness, catch per unit of effort (CPUE) or density during nighttime (or both) (Horn, 1980; Ross et al., 1987; Layman, 2000; Gaelzer and Zalmon, 2008; Vasconcellos et al., 2010, 2011; Yeoh et al., 2017). There have, however, also been reports of greater species richness or higher densities of shore zone fish species (or both) during the day (Godefroid et al., 1998; Pessanha and Araújo,

2003; Yeoh et al., 2017). In a recent work (Torre and Targett, 2016), we reported habitat-specific differences in the shore zone nekton assemblage between beach and riprap in Delaware Bay and noted diel differences in abundance for some, but not all, species.

We examined differences in abundance and diversity of fishes and blue crab (*Callinectes sapidus*) in the sandy beach shore zone and adjacent nearshore of Delaware Bay. Specifically, total nekton density, species richness, and the density of individual species during the day and night were compared. In addition, sampling occurred concurrently with research that identified feeding patterns of selected dominant species (Torre and Targett, 2017) and this concurrence provided an opportunity to assess the potential role of predator–prey dynamics of the shore zone nekton over the diel temporal range.

Materials and methods

Study area

Delaware Bay is a coastal plain estuary and one of the largest estuaries on the U.S. east coast (Bryant and Pennock, 1988; Pennock and Sharp, 1994). Unvegetated shore zones represent 74% of the bay's shoreline which is characterized by shallow, gradually sloping, sandy or muddy beaches that are often subject to wave erosion (de Sylva et al.[1]; Lathrop et al.[2]). The shore zone and nearshore waters support high densities of small forage and juvenile fish, and are feeding and spawning areas of adult fish (Shuster[3]; de Sylva et al.[1]; Able et al., 2007; Boutin, 2008). The fish fauna of Delaware Bay are dominated by species in the families Engraulidae, Atherinopsidae, Sciaenidae, Moronidae and Clupeidae (de Sylva et al.[1]; Bryant and Pennock, 1988; Torre and Targett, 2016). Blue crab are also abundant in Delaware Bay throughout their life history (Epifanio et al., 1984).
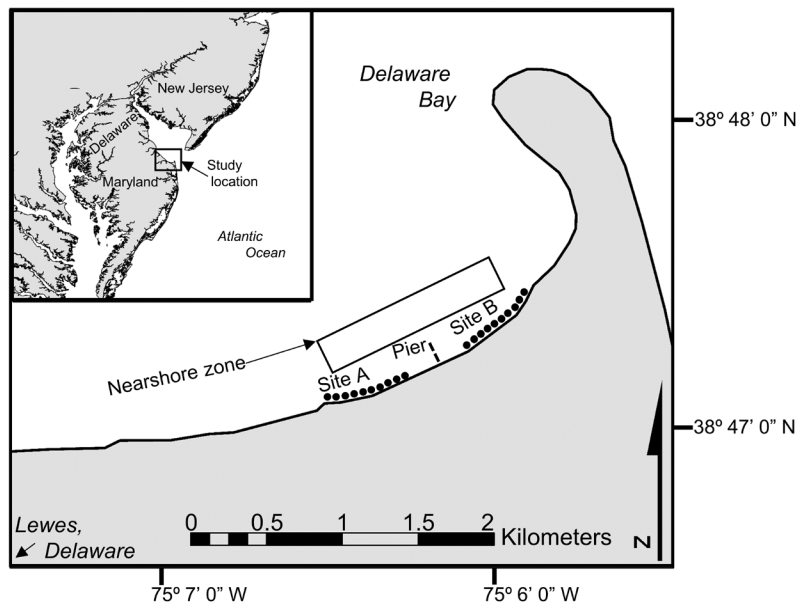

Figure 1

Map of the nearshore zone and the shore zone where sampling occurred during June–September 2013. Nearshore sampling occurred adjacent to the shore zone ~200–500 m from the shoreline. Shore sampling occurred along two ~400 m stretches of Delaware Bay beach. Black circles denote the 10 sampling locations at each shore zone site that were evenly spaced ~20 m from each other. Eight seining hauls (2 during the day and 2 at night) were conducted at 2 randomly chosen locations at site A and at site B each sampling week.

[9]The study area in lower Delaware Bay (Fig. 1) included a gradually sloping beach area and a nearshore habitat composed of course sand and sandbars running parallel to shore ~200–500 m from low tide (tidal range ~1.4 m). Sampling sites were two ~400-m stretches of sandy beach and a single 300-m×1200-m area of nearshore habitat adjacent to the shore zone sites. The 2 stretches of beach (sites A and B; Fig. 1) were separated by a wooden pier, open beneath and perpendicular to the shoreline, and were >100 m from the pier. Each stretch of beach consisted of 10 potential seining locations, with their centers evenly spaced ~40 m apart (Fig. 1).

Macrofauna sampling

Shore zone sampling was conducted with a ~36-m bag seine (1.2 m high; 3.5-mm mesh) every 2 weeks from June through September 2013. Eight seine hauls were taken each sampling week, 2 during daytime and 2 at night, at each of the 2 sites (Fig. 1). Specific seining locations were randomly chosen from the 10 possible at each site (Fig. 1); and if the second location was adjacent to the first, a different one was randomly selected to minimize effects of spatial autocorrelation. Day sampling occurred between 1 h after sunrise and 1 h before sunset, and night sampling between 1 h after sunset

[1] de Sylva, D. P., F. A. Kalber Jr., and C. N. Shuster Jr. 1962. Fishes and ecological conditions in the shore zone of the Delaware River estuary, with notes on other species collected in the deeper water. Univ. Delaware Mar. Lab., Info. Ser. Publ. 5, 164 p. Dep. Biol. Sci., Univ. Delaware, Newark, DE. [Available from website.]

[2] Lathrop, R. G., Jr., M. Allen, and A. Love. 2006. Mapping and assessing critical horseshoe crab spawning habitats of Delaware Bay, 36 p. Cent. Remote Sens. Spatial Anal., Rutgers Univ., New Brunswick, NJ. [Available from website.]

[3] Shuster, C. N., Jr. 1959. A biological evaluation of the Delaware River estuary. Univ. Delaware Mar. Lab., Info. Ser. Publ. 3, 75 p. Dep. Biol. Sci., Univ. Delaware, Newark, DE. [Available from website.]

and 1h before sunrise, during mid-tide and separate 24-h periods. In total, 64 seine-hauls were conducted, 32 during daytime and 32 at night.

Seining covered the intertidal and shallow subtidal area to ~1.5 m depth. The following procedure (after Giordano) was used to quickly enclose the sampling area and minimize loss of large mobile fish: 1) One end of the net was held on the shoreline; 2) the other end was deployed quickly (<45 s) off the bow of a boat, along an elliptical path from that shore point, to enclose the area immediately adjacent to the ~27 m section of shore; 3) both ends of the net were then slowly moved together along the shore; and 4) once the ends were together the net was pulled in, forcing all enclosed fish and crabs into the bag. During nighttime sampling, headlamps were illuminated immediately after step 2 to facilitate the subsequent steps and to observe the catch as it was brought into the net.

The adjacent nearshore area (Fig. 1) was sampled once each month during day and night in July, August, and September. Each sampling effort consisted of 3 tows (10 min at 1–1.5 m/s) in 3–6 m depth with a 6-m otter trawl (10-mm mesh; 5-mm mesh bag liner) during day and night. In total 18 trawl tows were conducted, 9 during the day and 9 at night.

Fish and blue crab were counted and measured to the nearest millimeter (for species with >20 individuals, a random subsample of 20 was measured); fork length (FL) for fish with forked tails, total length (TL) for other species, and carapace width (CW) for blue crab. The area sampled was calculated to convert relative measures of abundance into density. For the shore zone the formula for a half ellipse was used:

$$Area = \frac{1}{2}\pi ab,$$

where a = half the length of the enclosed shoreline; and
$\quad\quad b$ = the distance between shoreline and the apogee of the net.

Values for a and b were measured by setting the seine 5 times during a nonsampling trial and estimated values were a=13.5 m and b=10.0 m. For the nearshore, the following equation was used:

$$Area = wl,$$

where w = the estimated average width of trawl during operation (6 m); and
$\quad\quad l$ = the tow length.

Water temperature and salinity at the time of sampling were measured 0.5 m below the water surface using a dissolved oxygen meter (YSI, Inc.[4], Yellow Springs, OH).

Data analyses

Mean density and species richness of fish and blue crab at both day and night were compared for both shore

zone and nearshore samples. Potential differences in sampling efficiency and species selectivity between the seine net used in shore zone sampling and the otter trawl used in nearshore sampling precluded statistical comparisons between the 2 areas. Two-factor analysis of variance (ANOVA) was used to test for significant (α=0.05) diel and site differences in total nekton density and species richness in the shore zone. Significant diel and site differences in density of individual species that accounted for >1% of the total catch in the shore zone were tested with randomization tests for 2-factor ANOVA (α=0.01). The latter analysis is a nonparametric version of a 2-factor ANOVA that is more robust for the non-normally distributed data and frequent occurrence of zeros (Anderson and Braak, 2003) that resulted from subsetting total nekton density data into individual species. Student's t-tests were used to test for diel differences in total nekton density and species richness in the nearshore. Significant diel differences in the density of individual species that accounted for >1% of the total catch in the nearshore area were tested with a randomization test (α=0.01) in place of Student's t-test for the same reasons noted above (Tebbs and Bower, 2003). Randomization tests were carried out with R software, vers. 2.11.0 (R Core Development Team, 2010), and the critical level of significance was adjusted from α=0.05 to α=0.01 to account for multiple testing.

One-factor ANOVA was used to test for significant (α=0.01) diel differences in the length of species that accounted for >1% of total catch in shore zone and nearshore samples. When unequal variances violated the assumptions of the ANOVA, a Kruskal-Wallis H test was used instead and the critical level of significance was adjusted from α=0.05 to α=0.01 to account for multiple testing.

Differences in species assemblages between day and night in the shore zone and the nearshore were analyzed by using a multivariate approach with nonmetric multidimensional scaling (NMDS) and adonis procedures. The vegan package, vers. 1.13-8, within R software (vers. 2.11.0) was used for this analysis (Oksanen et al., 2008; R Core Development Team, 2010). This approach allows comparison of species assemblages by considering all species present and their abundances. Mean density of each species during day and night was calculated by pooling data from the 2 replicate seine hauls at each site to reduce variability in the analysis. Density data were square root transformed and similarity matrices were constructed for each site with the Bray–Curtis similarity measure. 2D plots depicting similarity of faunal assemblages between day and night were generated from similarity matrices generated with NMDS. Spider diagrams were overlaid upon 2D NMDS plots to show group centroids and spread. Significant variation in species assemblages was tested by using the adonis function in the vegan package (Oksanen et al., 2008). This function performs a permutational multiple analysis of variance (MANOVA) with Bray–Curtis similarity matrices to assign variation in

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[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Frequency of occurrence and mean density (individuals/100 m²), with standard error (SE), of dominant (>1% total catch for diel period) nekton species during day and night in the shore zone of lower Delaware Bay (see Fig. 1) from June through September 2013. Catch data from sites A and B are combined. Significant differences in mean density between day and night are indicated by asterisks according to the criteria: *=$P<0.01$, **=$P<0.005$, ***=$P<0.001$. The critical level of significance was adjusted from $\alpha=0.05$ to $\alpha=0.01$ to account for multiple testing. *P*-values are provided for differences between day and night; values for site interaction effect are not shown because no significant effects were detected. *P*-values are given for species that were not included in a species-specific test (>1% total catch for diel period). Species unique to the shore zone (not observed in the nearshore area) are denoted by ₛ. N/A=no statistical comparison was made because of low abundance.

Species	Total Number	Total % catch	Day Frequency of occurrence	Day Mean density (SE)	Night Frequency of occurrence	Night Mean density (SE)	P-value: day vs. night
All species	6545	100.0	100.00	24.53 (4.63)	100.00	72.22 (11.82)	<0.001 ***
Menidia menidia ₛ	3368	51.3	96.88	17.97 (6.71)	100.00	32.23 (8.76)	0.03
Anchoa mitchilli	2129	32.4	59.38	2.18 (0.58)	96.88	31.05 (9.97)	<0.001 ***
Cynoscion regalis	275	4.2	12.50	0.47	56.25	7.10 (3.27)	<0.001 ***
Pomatomus saltatrix	154	2.3	65.63	2.94 (0.97)	37.50	0.90 (0.13)	<0.001 ***
Brevoortia tyrannus	110	1.7	18.75	8.10 (1.94)	15.63	0.66 (0.11)	0.06
Mugil cephalus ₛ	88	1.3	15.63	5.09 (1.02)	34.38	1.46 (0.20)	0.27
Callinectes sapidus	85	1.3	25.00	0.53 (0.04)	59.38	1.89 (0.37)	<0.001 ***
Leiostomus xanthurus	70	1.1	12.50	0.59 (0.06)	43.75	2.19 (0.59)	<0.001 ***
Trachinotus carolinus	55	0.8	31.25	1.08 (0.12)	25.00	1.89 (0.32)	N/A
Micropogonias undulatus	51	0.8	9.38	0.79 (0.07)	40.63	1.67 (0.61)	N/A
Strongylura marina ₛ	39	0.6	3.13	0.47	34.38	1.63 (0.41)	N/A
Bairdiella chrysoura	35	0.5	15.63	2.64 (0.08)	15.63	0.66 (0.06)	N/A
Menticirrhus saxatilis	34	0.5	18.75	0.86 (0.12)	37.50	0.90 (0.15)	N/A
Paralichthys dentatus	10	0.2	3.13	0.47	21.88	0.61 (0.05)	N/A
Selene vomer	7	0.1	12.50	0.47	9.38	0.47 (0.05)	N/A
Fundulus heteroclitus ₛ	6	0.1	0.00	0.00	9.38	0.94 (<0.01)	N/A
Sphoeroides maculatus ₛ	6	0.1	6.25	0.47	9.38	0.63 (<0.01)	N/A
Fundulus majalis ₛ	4	0.1	6.25	0.71 (0.08)	3.13	0.47 (0.06)	N/A
Pseudopleuronectes americanus	4	0.1	6.25	0.47	6.25	0.47	N/A
Chilomycterus schoepfii	3	0.0	0.00	0.00	9.38	0.47	N/A
Pogonias cromis	3	0.0	6.25	0.47	3.13	0.47	N/A
Astroscopus guttatus ₛ	2	0.0	0.00	0.00	6.25	0.47	N/A
Clupea harengus ₛ	1	0.0	0.00	0.00	3.13	0.47	N/A
Dasyatis americana ₛ	1	0.0	0.00	0.00	3.13	0.47	N/A
Hyporhamphus meeki ₛ	1	0.0	3.13	0.47	0.00	0.00	N/A
Lagodon rhomboides ₛ	1	0.0	0.00	0.00	3.13	0.47	N/A
Ophidion marginatum ₛ	1	0.0	0.00	0.00	0.00	0.47	N/A
Peprilus triacanthus	1	0.0	0.00	0.00	3.13	0.47	N/A
Syngnathus fuscus	1	0.0	3.13	0.47	0.00	0.00	N/A

species assemblage data that was due to explanatory variables (day and night). The number of permutations used was 999.
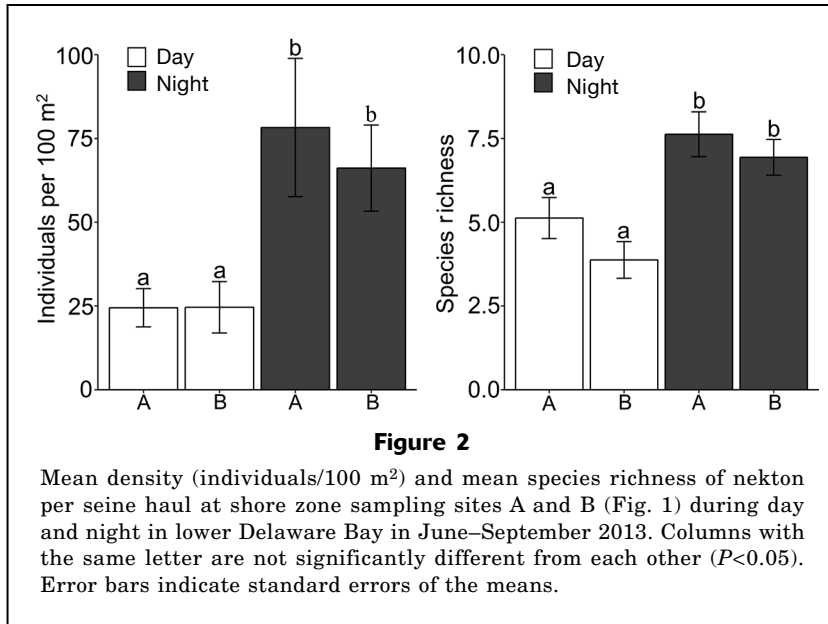
Results

Shore zone and nearshore temperature ranged from ~20.5–25.0°C during June through September 2013. Slightly higher temperatures were measured in the shore zone during the day (20.6–25.0°C) than at night (20.7–23.4°C). Nearshore temperatures were also slightly higher during the day (22.0–23.5°C) than at night (20.0–23.1°C). Salinity values ranged from ~21–29 and were similar between day and night and between the shore zone and nearshore areas.

A total of 9719 fish and blue crab were captured in the shore zone and nearshore area, representing 38 species. The assemblage comprised members of the families Atherinopsidae, Engraulidae, Sciaenidae, Pomatomidae, Clupeidae, Mugilidae, and Portunidae.

Fish density in the shore zone (Table 1) was dominated by Atlantic silverside (*Menidia menidia*, 51%), bay anchovy (*Anchoa mitchilli*, 32%), weakfish (*Cynoscion regalis*, 4%), and bluefish (*Pomatomus saltatrix*, 2%). Total nekton density in the shore zone was

Figure 2

Mean density (individuals/100 m²) and mean species richness of nekton per seine haul at shore zone sampling sites A and B (Fig. 1) during day and night in lower Delaware Bay in June–September 2013. Columns with the same letter are not significantly different from each other (*P*<0.05). Error bars indicate standard errors of the means.

Figure 3

Mean density (individuals/100 m²) of dominant species (>1% of total catch) per seine haul at shore zone sites A and B (Fig. 1) during day and night in lower Delaware Bay in June–September, 2013. Columns with the same letter are not significantly different from each other (*P*<0.05). Error bars indicate standard errors of the means.

94% higher at night than during the day (*P*<0.001) and was similar between the 2 sampling sites (*P*=0.750), with no interaction between time of day and site (*P*=0.829; Table 1, Fig. 2). Diel density differences were also found for a number of dominant shore zone species but there were no significant differences between sites or interaction effects. Bay anchovy, weakfish, spot (*Leiostomus xanthurus*), and blue crab occurred in the shore zone in significantly higher densities at night, whereas bluefish had significantly higher density during the day (Fig. 3). Mean species richness per seine haul in the shore zone was 62% higher (*P*<0.001) at night (7.3 [standard error (SE) 0.8]) than during the day (4.5 [SE 0.8]) and was similar for the 2 sampling sites (*P*=0.108), with no interaction (*P*=0.637; Fig. 2).

In the adjacent nearshore sampling area (Table 2), density was dominated by bay anchovy (73%), spot (11%), and weakfish (9%). Several species were unique to either the shore zone or nearshore sampling areas (Tables 1 and 2). Nearshore fish density was not significantly different during day and night (*P*=0.19, Table 2) and no species-specific differences in day and night densities were found (Table 2). Species richness per tow in the adjacent nearshore sampling area was not statistically different (*P*=0.14) during the night (8.8 [SE 0.9]) and day (6.7 [SE 0.8]).

The size range of dominant species was generally similar during the day and night in the shore zone and nearshore (Table 3), with the exception of the size range of Atlantic menhaden (*Brevoortia tyrannus*, *P*=0.002) and striped mullet (*Mugil cephalus*, *P*<0.001). Larger Atlantic menhaden were present in the shore zone during day and not at night and larger striped mullet were present in the shore zone during the night and not during the day (Table 3). It is noted, however, that only 4 Atlantic menhaden were captured during night sampling.

Ordination of shore zone and nearshore density data by NMDS shows diel differences in the species assemblage in the shore zone but not in the nearshore area (Fig. 4). Permutational MANOVA shows that the diel period significantly explained 17%
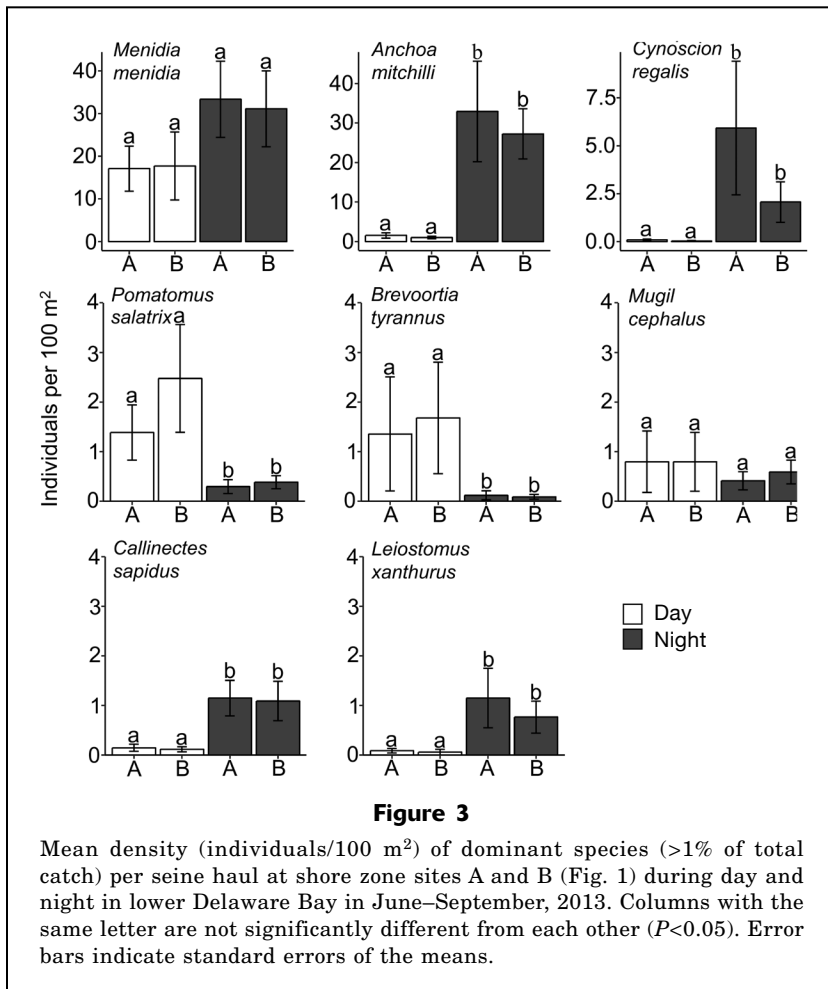
Table 2

Frequency of occurrence and mean density (individuals/100 m^2), with standard error (SE), of dominant (>1% total catch for diel period) nekton taxa during day versus night in the nearshore area of lower Delaware Bay (see Fig. 1) from June through September 2013. Significant differences in mean density between day and night are indicated by asterisks according to the criteria: *=$P<0.01$, **=$P<0.005$, ***=$P<0.001$. The critical level of significance was adjusted from $\alpha=0.05$ to $\alpha=0.01$ to account for multiple testing. Taxa unique to the nearshore area (not observed in the shore zone) are denoted by $_n$. N/A=no statistical comparison was made because of low abundance.

Species (or family)	Total		Day		Night		P-value: day vs. night
	Number	% catch	Frequency of occurrence	Mean density (SE)	Frequency of occurrence	Mean density (SE)	
All taxa	3153	100.00	100.0	4.38 (1.20)	100.0	3.07 (0.65)	0.71
Anchoa mitchilli	2300	72.95	100.0	3.59 (1.26)	100.0	1.86	0.11
Leiostomus xanthurus	346	10.97	77.8	0.41 (0.25)	100.0	0.49	0.28
Cynoscion regalis	285	9.04	66.7	0.28 (0.15)	77.8	0.61	0.11
Peprilus triacanthus	57	1.81	66.7	0.11 (0.04)	55.6	0.12	0.44
Micropogonias undulatus	40	1.27	66.7	0.13 (0.03)	33.3	0.05	0.03
Callinectes sapidus	28	0.89	44.4	0.04 (0.01)	88.9	0.05	N/A
Pomatomus saltatrix	16	0.51	44.4	0.05 (0.01)	55.6	0.03	N/A
Selene vomer	16	0.51	44.4	0.04 (0.01)	33.3	0.06	N/A
Mustelus canis $_n$	13	0.41	33.3	0.02 (<0.01)	66.7	0.03	N/A
Trinectes maculatus $_n$	9	0.29	22.2	0.08 (0.03)	11.1	0.02	N/A
Pogonias cromis	8	0.25	11.1	0.02	33.3	0.05	N/A
Urophycis regia $_n$	8	0.25	22.2	0.05 (0.01)	44.4	0.02	N/A
Bairdiella chrysoura	6	0.19	11.1	0.11	22.2	0.02	N/A
Menticirrhus saxatilis	4	0.13	11.1	0.02	11.1	0.06	N/A
Paralichthys dentatus	3	0.10	0.0	0.00	33.3	0.02	N/A
Gymnuridae $_n$	2	0.06	0.0	0.00	22.2	0.02	N/A
Prionotus carolinus $_n$	2	0.06	0.0	0.00	22.2	0.02	N/A
Syngnathus fuscus	2	0.06	11.1	0.02	11.1	0.02	N/A
Brevoortia tyrannus	1	0.03	11.1	0.02	0.0	0.00	N/A
Chilomycterus schoepfii	1	0.03	0.0	0.00	11.1	0.02	N/A
Pseudopleuronectes americanus	1	0.03	0.0	0.00	11.1	0.02	N/A
Raja eglanteria $_n$	1	0.03	0.0	0.00	11.1	0.02	N/A
Trachinotus carolinus	1	0.03	11.1	0.02	0.0	0.00	N/A

of the variation in species assemblage in the shore zone ($F=5.871$, coefficient of multiple determination [R^2]=0.170, $P<0.001$), whereas site ($F=0.336$, $R^2=0.009$, $P=0.956$) and interaction ($F=0.289$, $R^2=0.008$, $P=0.968$) were not significant. No difference in the species assemblage was identified in relation to day and night in the adjacent nearshore area ($F=1.506$, $R^2=0.086$, $P=0.185$).

Discussion

We observed clear diel differences in nekton assemblage along the sandy beach shore zone in Delaware Bay and greater nekton density and higher species richness at night. Diel patterns were also evident in many of the most abundant species; higher densities were found at night in most cases. Ordination plots revealed distinct day and night groups (see Fig. 4) but showed a large spread within groups, which can be explained by seasonal variation in species assemblages, and which could be reduced with a shorter sampling period. These results expand on those noted by Torre and Targett (2016) and highlight the importance of investigating assemblage dynamics across the diel cycle.

Interaction between predators and prey is a major process driving the distribution of shallow water estuarine nekton (Baker and Sheaves, 2007; Becker and Suthers, 2014; Yeoh et al., 2017). Responding to predation pressure, prey species and small juveniles of larger species alter their distribution to inhabit shallow water refuge areas where low abundance of large, primarily piscivorous fishes is generally thought to decrease predation (Baker and Sheaves, 2007; Becker and Suthers, 2014). Predator–prey interactions are dynamic over the diel cycle because many piscivorous fishes use sight to locate and capture prey (Horodysky et al., 2008; Yeoh et al., 2017). On the basis of this concept and because abiotic conditions were similar for day and night, we believe the diel differences in shore-zone nekton observed in our study are largely driven by day and night differences in predator–prey dynamics.

Table 3

Size range and mean size, with standard error (SE), of dominant (>1% total catch) nekton species during day versus night in the shore zone and nearshore area of lower Delaware Bay (see Fig. 1) during June, July, and August 2013. Size was measured in fork length (FL), total length (TL), or carapace width (CW). Length comparisons (*P*-value column) are from one-factor analysis of variance (ANOVA) or Kruskal-Wallis *H* test, when unequal variances violated assumptions of the ANOVA. The critical level of significance was adjusted from α=0.05 to α=0.01 to account for multiple testing.

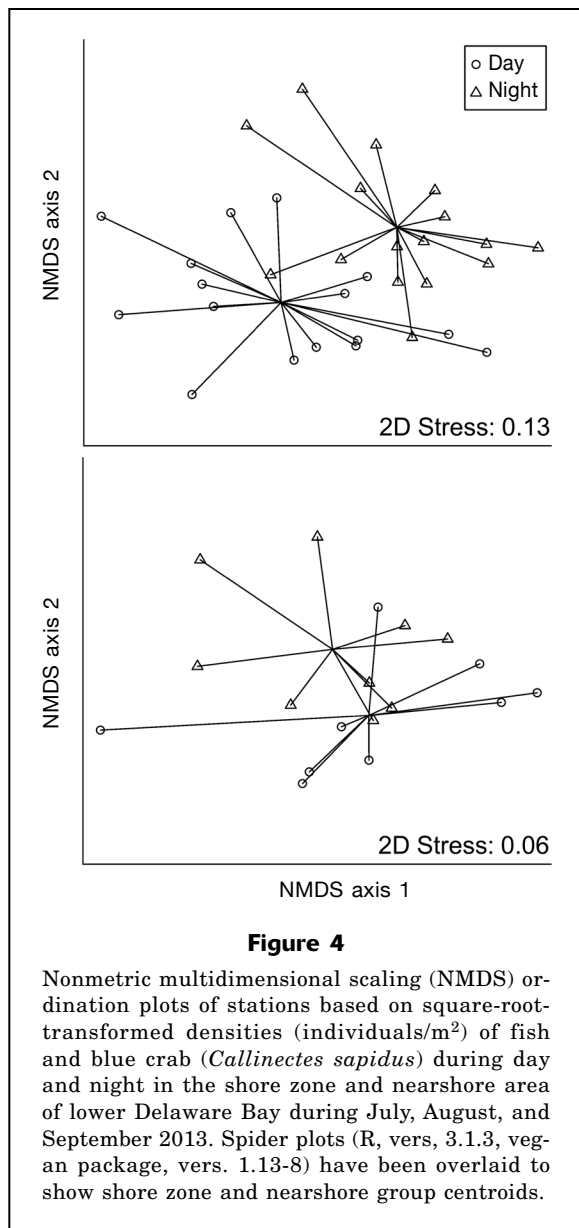| Species	Day		Night		*P*-value: day vs. night
	Size range (mm)	Mean size (SE)	Size range (mm)	Mean size (SE)	
Shore zone					
Anchoa mitchilli	FL: 30–115	60.23 (17.33)	35–94	58.92 (8.00)	0.090
Brevoortia tyrannus	FL: 68–112	84.79 (11.54)	55–89	70.57 (14.06)	0.002**
Callinectes sapidus	CW: 30–170	132.22 (44.38)	15–180	135.5 (27.55)	0.230
Cynoscion regalis	TL: 38–74	52.5 (15.33)	47–294	65.17 (28.14)	0.050
Leiostomus xanthurus	FL: 70–196	111.8 (49.44)	65–219	136.4 (49.01)	0.970
Menidia menidia	FL: 35–125	76.62 (10.76)	34–138	74.03 (11.86)	0.100
Mugil cephalus	FL: 57–187	88.02 (33.81)	65–158	128.15 (25.8)	<0.001***
Pomatomus saltatrix	FL: 24–155	100.82 (23.67)	89–205	123.65 (29.67)	0.030
Nearshore area					
Anchoa mitchilli	FL: 30–111	66.04 (14.08)	26–110	68.36 (11.38)	0.080
Cynoscion regalis	TL: 43–215	141.75 (30.62)	45–232	136.26 (37.37)	0.143
Leiostomus xanthurus	FL: 98–188	142.57 (18.66)	60–193	139.54 (24.05)	0.117
Micropogonias undulatus	TL: 155–227	195.18 (16.34)	147–195	181.86 (16.78)	0.050
Peprilus triacanthus	FL: 32–143	103.53 (31.51)	95–135	115.33 (9.41)	0.060

Concurrent sampling of stomach contents was conducted to identify feeding patterns of selected dominant species (Torre and Targett, 2017), providing an opportunity to consider the potential role of predator–prey dynamics in the diel differences seen in shore-zone nekton. Stomach content data from juvenile bluefish (mean: ~100 mm FL) collected in the shore zone during daytime (Torre and Targett, 2017) showed that they were feeding exclusively on juvenile (<20 mm FL) Atlantic silverside and bay anchovy. Although these prey were too small to be quantitatively sampled by the seine net, we saw large numbers of both species in this size range temporarily retained in the net during daytime sampling, but not at night, despite clear nighttime visibility provided by headlamps. A small number of these fish species were in the net when it was brought onto the beach but were not retained as the net was being moved to where the contents were counted. It is important to note that these small Atlantic silverside and bay anchovy showed a different diel abundance pattern than that of larger individuals (mean: Atlantic silverside, ~75 mm FL; bay anchovy, ~60 mm FL) that were vulnerable to the seine net and which were either not significantly different in abundance during day and during night (Atlantic silverside) or were higher in abundance at night (bay anchovy).

We speculate that the small Atlantic silverside and bay anchovy were abundant in the shore zone during the day because the shallow waters are a relative predation refuge (Torre and Targett, 2017). The bluefish is characterized as a daytime active predator on account of their visual capabilities (Horodysky et al., 2008), and Buckle and Conover (1997) observed that gut fullness of young-of-the-year bluefish in the Hudson River estuary was highest during the day. These small Atlantic silverside and bay anchovy were preyed upon by the small bluefish in the shore zone because bluefish become piscivorous relatively early in life (Scharf et al., 2009); however, predation mortality would still be reduced in comparison with that in adjacent deeper water with higher numbers of larger piscivorous fishes (Baker and Sheaves, 2007). Additionally, Yeoh et al. (2017) reported increased abundance of atherinids (silversides) and other small pelagic fishes in the shore zone during the day.

In contrast, juvenile weakfish were present in greater density in the shore zone at night and stomach content analysis of these individuals (Torre and Targett, 2017) showed that they were feeding almost exclusively on mysid shrimp (*Neomysis americana*). Weakfish are crepuscular and nocturnal predators (Horodysky et al., 2008) and this mysid species is known to undergo migration into surface or shallow waters during night (Hulburt, 1957; Hopkins, 1965). Grecay and Targett (1996) found that although feeding by juvenile weakfish was significantly reduced under dark conditions in the laboratory, fish were able to feed effectively if mysids occurred at sufficiently high density. Therefore, it is possible that weakfish moved into the shore zone at night in response to the higher concentrations of mysid shrimp.

Figure 4

Nonmetric multidimensional scaling (NMDS) ordination plots of stations based on square-root-transformed densities (individuals/m^2) of fish and blue crab (*Callinectes sapidus*) during day and night in the shore zone and nearshore area of lower Delaware Bay during July, August, and September 2013. Spider plots (R, vers, 3.1.3, vegan package, vers. 1.13-8) have been overlaid to show shore zone and nearshore group centroids.

Avian predators may restrict some species to deeper water during the day because birds are higher-order predators in estuarine systems and can exert significant top-down pressure on nekton assemblages (Steinmetz et al., 2003; Yeoh et al., 2017). Bay anchovy are known to exhibit diel vertical movement, inhabiting deeper water during day (Vouglitoisa et al., 1987) and moving upward or into shallow water at night (Hagan and Able, 2008). Although we saw large numbers of small (<20 mm FL) bay anchovy in the shore zone during the day, larger individuals (mean: ~60 mm FL) were more dense in the shore zone at night, possibly as a response to both increased foraging opportunity on mysid shrimp, a staple of their diet (Hartman et al., 2004), and because of reduced avian predation.

Gear avoidance could affect sampling efficiency of mobile fish species (Říha et al., 2008) and contribute to differences in density and species richness between day and night samples. However, the seining methods used in our study were designed to rapidly enclose the sampling area and minimize escape of mobile species (Torre and Targett, 2016, 2017). Furthermore, Říha et al. (2008) reported either similar or higher sampling efficiency during daytime than at night with 10–50 m seine nets. Therefore, it seems unlikely that gear avoidance greatly impacted the observed diel differences in species densities in the shore zone.

As described above, several species were significantly more abundant in the shore zone during either day or night, a finding that would suggest onshore–offshore diel migrations; however, no diel patterns were evident in the adjacent nearshore habitat. Lack of diel changes in the nearshore could be a result of sufficiently different predator-dynamics in the shore zone than in the more extensive and deeper nearshore. Differences in water depth, over a relatively small horizontal distance, create advantages and disadvantages for predators and prey in the shallow shore zone. Prey fishes moving into and out of the shore zone on a diel basis can take advantage of a refuge from predation resulting from the size-specific spatial distribution patterns of piscivorous fish predators (Baker and Sheaves, 2007) and the associated predation constraints imposed on large fishes in very shallow water. There are also diel movements of invertebrate prey, such as mysids, creating potential foraging opportunities for some fish species (Hulburt, 1957; Hopkins, 1965), increased potential vulnerability to avian predation in shallow water (Steinmetz et al., 2003; Yeoh et al., 2017), and the interaction of all these processes with differences in visibility caused by the diel light cycle.

Clear diel differences in the species assemblage in the shore zone and distinct diel patterns in the abundance of several dominant species highlight that day sampling alone does not give a true reflection of the nekton assemblage in the sandy beach shore zone of Delaware Bay. The way we perceive habitat value and its functional role for fishes, including predator–prey interactions, are affected by a reliance on only daytime sampling and observations. Our results show the value of investigating shore-zone nekton dynamics over the diel cycle. Future research should include the following: sampling throughout the diel cycle and incorporating tagging and movement studies (Gibson et al., 2011; Yeoh et al., 2017); and assessment of the influence of lunar, tidal, and seasonal cycles (Gibson et al., 1998) to more fully understand diel movement dynamics of nekton along sandy beach shores.

Acknowledgments

Literature cited

Able, K. W., J. H. Balletto, S. M. Hagan, P. R. Jivoff, and K. Strait.
  2007. Linkages between salt marshes and other nekton habitats in Delaware Bay, USA. Rev. Fish. Sci. 15:1–61. Article

Able, K. W., D. H. Wilber, A. Muzeni-Corino, and D. G. Clarke.
  2010. Spring and summer larval fish assemblages in the surf zone and nearshore off northern New Jersey, USA. Est. Coast. 33:211–222. Article

Anderson, M., and C. T. Braak.
  2003. Permutation tests for multi-factorial analysis of variance. J. Stat. Comput. Sim. 73:85–113. Article

Baker, R., and M. Sheaves.
  2007. Shallow-water refuge paradigm: Conflicting evidence from tethering experiments in a tropical estuary. Mar. Ecol. Prog. Ser. 349:13–22. Article

Beck, M. W., K. L. Heck, K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, et al.
  2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: a better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. BioScience 51:633–641. Article

Becker, A., and I. M. Suthers.
  2014. Predator driven diel variation in abundance and behaviour of fish in deep and shallow habitats of an estuary. Est. Coast. Shelf Sci. 144:82-88. Article

Bennett, R. H., P. D. Cowley, A.-R. Childs, and T. F. Næsje.
  2015. Movements and residency of juvenile white steenbras Lithognathus lithognathus in a range of contrasting estuaries. Est. Coast. Shelf Sci. 152:100–108. Article

Boutin, B. P.
  2008. Tidal tributaries and nearshore areas as nursery habitat for juvenile sciaenid fishes and other estuarine nekton in Delaware Bay and the Delaware coastal bays. Ph.D. diss., 172 p. Univ. Delaware, Newark, DE.

Bryant, T. L., and J. R. Pennock.
  1988. The Delaware estuary: rediscovering a forgotten resource, 144 p. Sea Grant Coll. Program, Univ. Delaware, Newark, DE.

Buckle, J. A., and D. O. Conover.
  1997. Movements, feeding periods, and daily ration of piscivorus young-of-the-year bluefish, Pomatomus salatrix, in the Hudson River estuary. Fish. Bull. 95:665–679.

Epifanio, C. E., C. C. Valenti, and A. E. Pembroke.
  1984. Dispersal and recruitment of blue crab larvae in Delaware Bay, U.S.A. Est. Coast. Shelf Sci. 18:1–12. Article

Félix, F. C., H. L. Spach, P. S. Moro, R. Schwarz Jr., C. Santos, C. W. Hackradt, and M. Hostim-Silva.
  2007. Utilization patterns of surf zone inhabiting fish from beaches in Southern Brazil. Pan-Am. J. Aquat. Sci. 2:27–39.

Gaelzer, L. R., and I. R. Zalmon.
  2008. Diel variation of fish community in sandy beaches of southeastern Brazil. Braz. J. Oceanogr. 56:23–29. Article

Gibson, R. N., and L. Robb.
  1996. Piscine predation on juvenile fishes on a Scottish sandy beach. J. Fish Biol. 49:120–138. Article

Gibson, R. N., L. Pihl, M. T. Burrows, J. Modin, H. Wennhage, and L. A. Nickell.
  1998. Diel movements of juvenile plaice Pleuronectes platessa in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. Mar. Ecol. Prog. Ser. 165:145–159. Article

Gibson, R. N., M. T. Burrows, and L. Robb.
  2011. Field experiments on depth selection by juvenile plaice Pleuronectes platessa. Mar. Ecol. Prog. Ser. 430:197–205. Article

Godefroid, R. S., M. Hofstaetter, and H. L. Spach.
  1998. Moon, tidal and diel influences on catch composition of fishes in the surf zone of Pontal do Sul beach, Paraná. Rev. Bras. Zool. 15:697–701. Article

Gondolo, G. F., G. M. T. Mattox, and P. T. M. Cunningham.
  2011. Ecological aspects of the surf-zone ichthyofauna of Itamambuca Beach, Ubatuba, SP. Biota Neotrop. 11:183–192. Article

Grecay, P. A., and T. E. Targett.
  1996. Effects of turbidity, light level and prey concentration on feeding of juvenile weakfish Cynoscion regalis. Mar. Ecol. Prog. Ser. 131:11–16. Article

Hagan, S. M., and K. W. Able.
  2008. Diel variation in the pelagic fish assemblage in a temperate estuary. Est. Coast. 31:33–42. Article

Hartman, K. J., J. Howell, and J. A. Sweka.
  2004. Diet and daily ration of bay anchovy in the Hudson River, New York. Trans. Am. Fish. Soc. 133:762–771. Article

Hopkins, T. L.
  1965. Mysid shrimp abundance in surface waters of Indian River Inlet, Delaware. Chesapeake Sci. 6:86–91. Article

Horn, M. H.
  1980. Diel and seasonal variation in abundance and diversity of shallow-water fish populations in Morro Bay, California. Fish. Bull. 78:759–770.

Horodysky, A. Z., R. W. Brill, E. J. Warrant, J. a Musick, and R. J. Latour.
  2008. Comparative visual function in five sciaenid fishes inhabiting Chesapeake Bay. J. Exp. Biol. 211:3601–3612. Article

Hulburt, E. M.
  1957. The distribution of Neomysis americana in the estuary of the Delaware River. Limnol. Oceanogr. 2:1–11. Article

Layman, C. A.
  2000. Fish assemblage structure of the shallow ocean surf-zone on the eastern shore of Virginia Barrier Islands. Est. Coast. Shelf Sci. 51:201–213. Article

Marin Jarrin, J. R., and A. L. Shanks.
  2011. Spatio-temporal dynamics of the surf-zone faunal assemblages at a southern Oregon sandy beach. Mar. Ecol. 32:232–242. Article

McLachlan, A., and A. C. Brown.
  2006. The ecology of sandy shores, 2nd dd, 392 p. Academic Press, Amsterdam, Netherlands.
Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, G. L. Simpson, M. H. H. Stevens, and H. Wagner.
  2008. Vegan: community ecology package, vers. 1.13-8. [Available from website.]
Pennock, J. R., and J. H. Sharp.
  1994. Temporal alternation between light- and nutrient-limitation of phytoplankton production in a coastal plain estuary. Mar. Ecol. Prog. Ser. 111:275–288.
Pessanha, A. L. M., and F. G. Araújo.
  2003. Spatial, temporal and diel variations of fish assemblages at two sandy beaches in the Sepetiba Bay, Rio de Janeiro, Brazil. Est. Coast. Shelf Sci. 57:817–828. Article
R Core Development Team.
  2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from website, accessed April 2010.]
Říha, M., J. Kubečka, T. Mrkvička, M. Prchalová, M. Čech, V. Draštík, J. Frouzová, M. Hladík, E. Hohausová, O. Jarolím. et al.
  2008. Dependence of beach seine net efficiency on net length and diel period. Aquat. Living Resour. 21:411–418. Article
Rodrigues, F. L., and J. P. Vieira.
  2013. Surf zone fish abundance and diversity at two sandy beaches separated by long rocky jetties. J. Mar. Biol. Assoc. U.K. 93:867–875. Article
Ross, S. T., R. H. McMichael Jr., and D. L. Ruple.
  1987. Seasonal and diel variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf zone. Est. Coast. Shelf Sci. 25:391–412. Article
Rountree, R. A., and K. W. Able.
  1993. Diel variation in decapod crustacean and fish assemblages in New Jersey polyhaline marsh creeks. Est. Coast. Shelf Sci. 37:181–201. Article
Scharf, F. S., J. A. Buckel, and F. Juanes.
  2009. Contrasting patterns of resource utilization between juvenile estuarine predators: the influence of relative prey size and foraging ability on the ontogeny of piscivory. Can. J. Fish. Aquat. Sci. 66:790–801. Article
Steinmetz, J., S. L. Kohler, and D. A. Soluk.
  2003. Birds are overlooked top predators in aquatic food webs. Ecology 84:1324–1328. Article
Tebbs, J. M., and K. M. Bower.
  2003. Some comments on the robustness of Student t procedures. J. Eng. Educ. 92:91–94. Article
Torre, M. P., and T. E. Targett.
  2016. Nekton assemblages along riprap-altered shorelines in Delaware Bay, USA: comparisons with adjacent beach. Mar. Ecol. Prog. Ser. 548:209–218. Article
  2017. Feeding by bluefish and weakfish along riprap-hardened shorelines: comparisons with adjacent sandy beach in Delaware Bay, USA. Trans. Am. Fish. Soc. 146:341–348. Article
Vasconcellos, R. M., F. G. Araújo, J. N. de Sousa Santos, and M. de Araújo Silva.
  2010. Short-term dynamics in fish assemblage structure on a sheltered sandy beach in Guanabara Bay, Southeastern Brazil. Mar. Ecol. 31:506–519. Article
Vasconcellos, R. M., F. G. Araujo, J. N. de Sousa Santos, and M. de Araújo Silva.
  2011. Diel seasonality in fish biodiversity in a sandy beach in south-eastern Brazil. J. Mar. Biol. Assoc. U.K. 91:1337–1344. Article
Vouglitoisa, J. J., K. W. Able, R. J. Kurtz, and K. A. Tighe.
  1987. Life history and population dynamics of the bay anchovy in New Jersey. Trans. Am. Fish. Soc. 116:141–153. Article
Whitfield, A. K.
  1999. Ichthyofaunal assemblages in estuaries: a South African case study. Rev. Fish Biol. Fish. 9:151–186. Article
Yeoh, D. E., F. J. Valesini, C. S. Hallett, D. A. Abdo, and J. Williams.
  2017. Diel shifts in the structure and function of nearshore estuarine fish communities. J. Fish Biol. 90:1214–1243. Article