

# Impact of Armored Shorelines on Shore-Zone Fish Density in a Mid-Atlantic, USA, Estuary: Modulation by Hypoxia and Temperature

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**Abstract** Anthropogenic modifications of estuarine environments, including shoreline hardening and corresponding alteration of water quality, are accelerating worldwide as human population increases in coastal regions. Estuarine fish species inhabiting temperate ecosystems are adapted to extreme variations in environmental conditions including water temperature, salinity, and dissolved oxygen across seasonal, daily, and hourly time scales. The present research utilized quantitative sampling to examine the spatiotemporal distribution of shore-zone estuarine fish species in association with four unique shoreline types across a range of water temperature and dissolved oxygen conditions. Fish were collected from the intertidal and shallow subtidal region of four shoreline types, *Spartina alterniflora* marsh, *Phragmites australis* marsh, riprap, and bulkhead, in the summer and fall of 2009 and 2010. Analyses were performed to (1) compare mean fish density among shoreline types across all water conditions and (2) explore relationships of the complete fish assemblage, three functional species groupings, and two fish species (*Fundulus heteroclitus* and *Menidia menidia*) to unique shoreline/water conditions. Significantly greater mean fish densities were found along *S. alterniflora* shorelines than armored shorelines. Several metrics including fish density, species richness, and occurrence rates suggest *S. alterniflora* shorelines may

serve as a form of refuge habitat during periods of low dissolved oxygen and high temperatures for various species, particularly littoral-demersal species including *F. heteroclitus*. Potential mechanisms that could contribute to a habitat providing refuge during adverse water quality conditions include tempering of the adverse condition (decreased temperatures, increased dissolved oxygen), predation protection, and increased foraging opportunities.

**Keywords** Intertidal · Shoreline hardening · Shoreline armoring · Estuary-dependent · *Spartina* · *Phragmites*

## Introduction

Temperate estuaries worldwide have experienced a decrease in native vegetation within the past several decades, while invasive grass species and several types of shoreline armoring including bulkhead and riprap structures have become more common (Lee et al. 2006; USGS 2011, 2013; Hazelton et al. 2014; Kettenring et al. 2015). These hardened shorelines and invasive grasses have caused changes in the ecological character of the intertidal zone, particularly in urbanized watersheds (Raichel et al. 2003; Bilkovic and Roggero 2008, Peterson and Lowe 2009). Hypoxia resulting from urban and agricultural runoff-driven eutrophication of coastal estuarine ecosystems is increasing in both temporal and spatial scales worldwide, as the past 65 years has seen a rapid acceleration in the number of occurrences of severe hypoxic and anoxic conditions in estuarine environments (Diaz and Rosenberg 1995; Diaz et al. 2004; Diaz and Rosenberg 2008). In conjunction with altered shorelines and increased hypoxia, urbanizing estuaries are likely to experience increased water temperatures over the next 50 years (IPCC 2014).

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Estuaries, with their varied aquatic habitats, serve as critical nursery grounds for the early life stages of many species of fish (Weinstein 1979; Rakocinski et al. 1992; Peterson and Turner 1994; Peterson et al. 2000). Estuary-resident (species that spend their entire life cycle within an estuary), estuary-dependent (species that utilize estuaries for an obligate portion of their life cycle such as spawning), and transient (non-obligate estuarine inhabitants) fishes serve an important role in estuarine food webs and are instrumental in the movement of organic material within and out of estuarine ecosystems (Kneib et al. 1980; Kwak and Zedler 1997; Deegan et al. 2002). Degradation of estuarine habitat is among the most significant threats to fisheries (Burns 1991; Thomas 1995), as over 70% of commercial fishery species (Brouha 1993; Waste 1996) and over 66% of recreational fishery species utilize coastal and estuarine habitats during at least one stage of their life history (Thayer et al. 1996).

Riprap and bulkhead are frequently installed along shorelines in an attempt to reduce erosion and provide storm surge protection for areas of human development. Negative impacts of these structures on populations of fishes, crustaceans, and benthic invertebrates living adjacent to them have been well documented in recent years (Seitz et al. 2006; Strayer et al. 2012; Gittman et al. 2016a, b; Torre and Targett 2016). The work of Bilkovic and Roggero (2008) demonstrated that bulkheads negatively affect the shore-zone environment and related nekton assemblages in large tributaries of Chesapeake Bay.

Disturbance of natural shorelines through the installation of shoreline armoring is one of the primary contributors to the expansion of a non-native genotype of *Phragmites australis* in the mid-Atlantic region (King et al. 2007). *P. australis* invasion has led to a displacement of native macrophyte communities, degradation of wildlife habitat, and alteration of ecosystem processes (Weinstein and Balletto 1999; Windham and Meyerson 2003; Minchinton et al. 2006). Dominant estuarine species such as the mummichog (*Fundulus heteroclitus*) have been shown to be negatively impacted by the spread of *P. australis* that reduces prey density, compared with native marsh, available for resident marsh fishes (Teo and Able 2003a, b; Raichel et al. 2003).

In addition to the physical structure of shore-zones, water quality characteristics including dissolved oxygen (DO) moderate the occurrence and density of estuarine fishes (Boutin and Targett 2013). Hypoxia is any DO below oxygen saturation, and DO <2.3 mg O<sub>2</sub>/l is characterized as severe hypoxia, a condition which is harmful to aquatic fauna (USEPA 2000; Diaz 2001; Tyler et al. 2009). A minimum DO concentration of 4.8 mg O<sub>2</sub>/l is defined as the growth protective criteria for the most sensitive species in the saltwater faunal community in the

mid-Atlantic region (USEPA 2000). Increased nutrient input, particularly nitrogen, from developed watersheds results in excessive algal growth and is commonly associated with severe hypoxia (Nixon 1995; Valiela et al. 1997; Bricker et al. 1999, 2014).

Fish actively search and select the habitat with the relative highest quality available based on habitat functions and considerations of how those functions change over different temporal scales (Rountree and Able 2007). External conditions such as DO, water temperature, salinity, prey availability, and predation risk influence fish behavior and movement; behavioral avoidance strategies in hypoxic waters, in particular, exhibit situational dependence (Kramer 1987; Eby and Crowder 2002). Field studies frequently demonstrate that abundance and diversity of fishes decline as DO decreases (Breitburg et al. 2001; Eby and Crowder 2002; Tyler and Targett 2007). And that fish have been found to migrate away from hypoxic conditions and return immediately following the onset of increased DO (Tyler and Targett 2007). Distribution of fish at an instantaneous point in time in an ecosystem will also reflect temporary searching and imperfect habitat selection. Estuarine ecosystems provide a mosaic of habitat types with different shore-zone structures (vegetated and armored), DO levels, temperatures, and salinities at any given time. Certain habitats may provide better refuge from hypoxia and excessive water temperature by providing less severe DO or temperature conditions, increased predation protection, or increased foraging opportunities, while other habitats may exacerbate physiological stress (Baltz et al. 1993, Szedlmayer and Able 1996, Halpin 2000, Eby and Crowder 2002).

Understanding how the biophysical structure of estuarine shorelines, in association with water quality conditions, affects the functional value and habitat quality of estuaries for shore-zone biota is important in determining anthropogenic impacts on estuarine systems. The present research used quantitative sampling to examine how estuarine shoreline structure in association with diel-cycling DO and water temperature conditions interacts to affect the assemblage structure and density of estuary-resident and estuary-dependent fishes in tidal marsh creeks of the Delaware Coastal Bays. The objectives of this study were to (1) utilize intensive weekly sampling to examine estuarine fish assemblages and density along four different shoreline types (*Spartina alterniflora*, *P. australis*, riprap, and bulkhead) and (2) analyze the interactive impacts of categorical DO and water temperature conditions in association with shoreline type on mean fish density of the whole fish assemblage, three functional groupings of fish species (littoral-demersal, benthivore/piscivore, planktivore), and two highly abundant estuarine species (*F. heteroclitus* and *Menidia menidia*).

## Materials and Methods

### Study Area

The Delaware Coastal Bays are comprised of three major embayments and their respective tributaries and canals (Fig. 1). All three bays are characterized by native fringing *S. alterniflora* (smooth cordgrass) marsh, the invasive *P. australis* (common reed), and increasing human development (Daiber 1969; Tyler 2005; Boutin and Targett 2013).

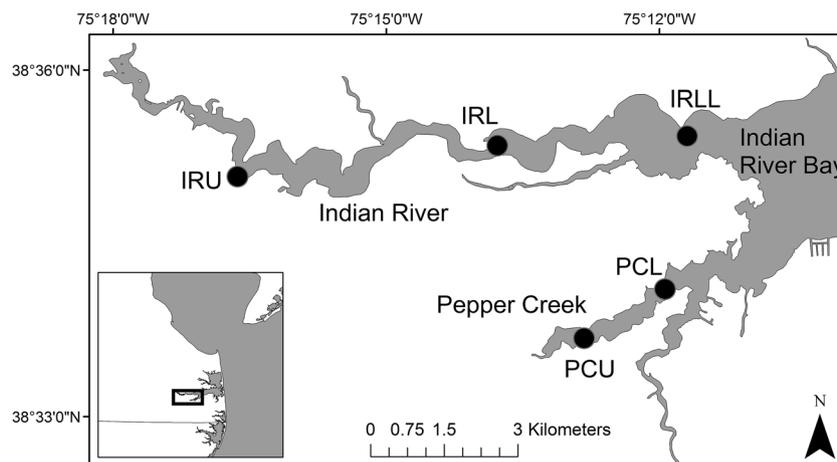
Fish sampling and water quality monitoring were conducted in both Indian River and Pepper Creek (Fig. 1). Both tributaries contain high levels of nutrients, particularly nitrogen (DIBEP 1995; Price 1998; T. Jordan unpublished data), largely due to agricultural and residential runoff within the watershed. Both tributaries exhibit severe diel-cycling hypoxia during summer months (Tyler and Targett 2007, 2009). Fish sampling was conducted in an upper and lower region in each tributary in 2009 and 2010. A third tributary region was sampled near the mouth of Indian River (IRLL) during the summer of 2009 (Fig. 1). Each of the four study shoreline types (bulkhead, riprap, *P. australis*, *S. alterniflora*) was present at each sampling region except lower Pepper Creek (PCL) which did not have a *P. australis* shoreline and IRLL which did not have a riprap shoreline. Within each respective sampling region, all sampled shorelines were located within a 0.75-km stretch of creek including both sides of shore.

### Fish Sampling

Seining was conducted weekly to quantify fish abundance and diversity inhabiting the shore-zone and shallow subtidal region in the five tributary regions from August through October in 2009 ( $n = 67$ ) and May through October in 2010

( $n = 239$ ). Fishes occupying each of the four shoreline types were sampled using a 10-m seine with center bag (2 m high; 5 mm mesh) in 2009 and a 15-m seine with center bag (2 m high; 5 mm mesh) in 2010. Shoreline types sampled were  $\geq 30$  m in length. Individual sections of shoreline where seining occurred are referred to as sampling stations; 23 sampling stations in total were sampled during the summers of 2009 and 2010. Seine hauls sampled areas of  $\sim 21$  and  $\sim 33$  m<sup>2</sup> in 2009 and 2010, respectively. Water depths were taken at the land-water interface and at the maximum offshore sampling distance of the seine haul to calculate volume of water seined and, subsequently, fish density (individuals/m<sup>3</sup>). Because sampling methodologies were identical between nets and years, area and volume swept were accounted for, and as mobility of the fish species sampled is limited, samples between gear and year were pooled for statistical analyses.

Seining was conducted using the following method: One end of the net was placed on shore using a shallow draft boat. The net was unfurled in an arc, 3 m from shore at its maximum extent, along the shoreline. The far end of the net was then brought to shore. A PVC pole was used to startle fish from the area between the net and shoreline toward the net bag. The two ends of the net were walked together along the shoreline and the net was gathered and fish directed into the bag. The net bag was cinched tight in the water and placed in the boat where the sample was removed and placed in a bucket containing tributary water. The sampling station was immediately seined again, using the same method and the same deployment direction. Fish from the second seine haul were placed into a second bucket. As sediment type and subtidal structure can influence species abundance and assemblage structure (Szedlmayer and Able 1996), all sampling stations were located along areas where substrate ranged from sand to mud, with little to no subtidal structure (e.g., woody debris or rock).



**Fig. 1** Indian River and Pepper Creek, tributaries of Indian River Bay, Delaware Coastal Bays, with locations of fish sampling stations in upper Indian River (IRU), lower Indian River (IRL), mouth of Indian River (IRLL) (2009), upper Pepper Creek (PCU), and lower Pepper Creek

(PCL). Multi-parameter sondes were deployed at these locations to continuously measure water temperature, dissolved oxygen (mg/l), and salinity (psu) throughout the study

The catch from both seine hauls was combined to form a single sample. All fish were identified, counted, and released adjacent to the shoreline where they were collected. Riprap and bulkhead sites were sampled within 2 h of high tide. To account for water level and utilization of the marsh surface (Rozas and Minello 1997), *S. alterniflora* marsh and *P. australis* sites were sampled within 2 h of high tide when the water level had just reached the marsh edge.

As each of the four shoreline types examined presents unique sampling environments, species-specific response ratios (Z-scores) were estimated for seine hauls along each shoreline type using Leslie depletion models (Seber 2002). For a concurrent related study, Z-scores were determined for *F. heteroclitus*, *Morone americana*, and *M. menidia* at each of the three shoreline types (marsh, riprap, and bulkhead) (Kornis et al. 2017, supplementary material) using a 20-m beach seine. Proxy Z-score values from these three species were then assigned to each species caught in this study based on similarities in body shape and water column location (Supplement Material A). Z-scores were applied to untransformed abundance data from each sampling event for both the 10- and 15-m bag seines in order to correct for gear bias in capture efficiency specific to each shoreline type.

#### Water Quality Monitoring

YSI model 600XLM multi-parameter sondes were deployed in each of the five study regions (Fig. 1) for continuous monitoring from May through September during 2009 and 2010. Salinity (psu), DO (DO saturation % and mg/l), pH, and water temperature (°C) were recorded at 15-min intervals. Sondes were centrally located among sampling stations within each tributary region and positioned just outside the navigation channel. Each sonde was suspended approximately 15 cm above the substrate using a steel pyramid stanchion.

#### Data Analyses

Mean fish density (individuals/m<sup>3</sup>), corrected for species-specific response ratios, was calculated for all fishes along each shoreline type. For the five species with the greatest mean fish density summed across all four shoreline types, two additional analyses were performed: (1) the percentage of a given species' total catch that was collected at each shoreline type (identifying which shoreline is utilized most frequently by the species) and (2) the percentage of total catch at each shoreline type that each species comprised (identifying species that dominated the collections at the specified shoreline type).

A non-parametric one-way repeated measures ANOVA using a bootstrapping methodology was used to compare fish density by shoreline type across sampling dates. A bootstrapping method was used to account for the unbalanced sampling design. Bootstrapped resampling with replacement

was conducted with 1500 replications. If significant differences were found, Holm-Sidak pairwise multiple comparison post hoc tests were performed (Holm 1979).

Water quality thresholds studied included DO concentrations  $\leq 2.3$  mg O<sub>2</sub>/l and  $\leq 4.8$  mg O<sub>2</sub>/l (inclusive of samples  $\leq 2.3$  mg O<sub>2</sub>/l) and water temperature  $\geq 27$  °C. DO thresholds were based on federal and local EPA guidelines regarding fish growth and health (USEPA 2000). The temperature threshold was based upon analyzing the highest water temperature for which sample sizes remained adequately large on either side of the threshold (one-way and two-way ANOVA analyses of 26 and 28 °C thresholds yielded comparable results). Salinity was not included in data analysis as it was not considered a stressor, with an adverse condition, for estuarine fishes. Mean fish density was calculated for all fish species (total catch) caught across each water condition threshold of interest.

A non-parametric one-way repeated measures ANOVA using a bootstrapping methodology was used to compare fish density across each shoreline type above and below water quality thresholds respectively.

Mean species richness was calculated for each shoreline type and water condition. Mean richness was calculated due to uneven sampling effort across all study factors, making total species richness inappropriate. Presence/absence proportions were calculated across each shoreline type and water condition for *F. heteroclitus* and *M. menidia*. These species were analyzed individually due to their high relative density, different life histories, and potentially differing responses to interaction between shoreline type and water conditions.

Non-parametric two-way ANOVAs were conducted to examine the density of all fishes, three species functional groupings, *F. heteroclitus*, and *M. menidia* across each shoreline (bulkhead, riprap, *S. alterniflora*, *P. australis*) and water condition threshold (2.3 mg O<sub>2</sub>/l, 4.8 mg O<sub>2</sub>/l, 27 °C). For analysis, sample density was categorically assigned to each threshold level (e.g.,  $>2.3$  mg O<sub>2</sub>/l or  $<2.3$  mg O<sub>2</sub>/l). Requisite parametric assumptions of normal distribution, equal variance, and equal sample sizes (sample sizes among all shoreline type/water condition blocks were unequal) were not met by the data, so non-parametric two-way ANOVAs using "aligned rank transformations" (Wobbrock et al. 2011) were used. The aligned rank transformation methodology allows for non-parametric analysis of factorial ANOVAs while calculating interactions. For each main effect or interaction, all responses are "aligned," a process that removes all effects from responses except the one for which alignment is being done. The aligned responses are then assigned ranks like those utilized in other non-parametric ANOVA methodologies. If significant differences were found, the Holm-Sidak method of pairwise multiple comparison post hoc test was performed using the Holm correction to account for repeated tests (Holm 1979). Based on pairwise comparisons, it was possible to determine where significant interactions indicated one

shoreline type served as a “refuge” habitat in comparison with other shorelines. In cases of significant interactions, refuge shoreline types are utilized by fish at higher density rates (or at less reduced density rates) during adverse conditions. Adverse conditions included DO conditions  $\leq 2.3$  and  $\leq 4.8$  mg O<sub>2</sub>/l as well as water temperature  $\geq 27$  °C.

One-way and two-way ANOVA analyses were conducted for all species, for each individual species, and for three functional groups (species assignments to functional groupings are found in Table 2). Functional groupings of fish were created by summing species densities within each sampling event based on functional grouping assignments. Functional groupings were as follows:

- Littoral-demersal—Small-bodied bottom-oriented species that are frequently found in extremely shallow water (<20 cm) and forage on small littoral prey (polychaete worms, small crustaceans, small mollusks, small insects detritus, and plant matter).
- Planktivores—Species that forage on phytoplankton and zooplankton.
- Benthivore/piscivore—Large-bodied bottom-oriented species that forage on a suite of benthic invertebrates and small fishes.

QA/QC was performed on water quality data, DO concentration, and temperature, to remove erroneous data and outliers (primarily due to equipment fouling). Water quality data used for all analyses were taken from the data most immediately prior to the sampling event, either 15 or 30 min depending on data quality. Water quality measurements averaged across the hour, and 4-h period, prior to fish sampling were also analyzed using two-way ANOVA.

All statistical analyses were conducted using R (version 3.2.3).

## Results

### Water Quality

All tributary regions experienced hypoxia below both DO water quality thresholds and water temperatures  $\geq 27$  °C (Table 1). Hypoxic conditions were more frequent and extreme in upper tributary regions. DO during diel cycles ranged from 0 mg O<sub>2</sub>/l (anoxia) to 23.5 mg O<sub>2</sub>/l (super-saturated conditions) among all sampling stations in both years (Table 1). Severe diel-cycling hypoxia, ranging from  $\leq 2.3$  mg O<sub>2</sub>/l to  $\geq 20$  mg O<sub>2</sub>/l within a single diel cycle, began to occur frequently in late May in both 2009 and 2010. In both 2009 and 2010, the upper sampling regions of each tributary experienced the greatest percentage of time in hypoxia (Table 1). Mean monthly water temperature differed by a maximum of 6 °C at any individual sampling location (upper Pepper Creek (PCU), May vs. August) among months. Temperature was commonly higher at the upper region of each tributary. The percentage of temperature measurements  $\geq 27$  °C was also highest in the upper section of each tributary (Table 1).

### Fish Assemblages—Shoreline Comparisons

In total, 43,387 individuals in 20 fish species were collected at the 18 sampling stations over the two-summer study. Species caught included juvenile and adult estuary-resident and estuary-dependent species as well as transient marine fishes (Able and Fahay 1998, 2010; Table 2). Collections were dominated by *F. heteroclitus* (68% of total relative density). The ten species caught in the greatest mean density (Table 2) were found at all sampling locations (PCL, PCU, IRL, upper Indian River (IRU), IRL) in all months except May. The remaining species caught in lower mean density (Table 2) were not collected at all sampling locations or in all months.

**Table 1** Water quality characteristics by tributary region in Indian River and Pepper Creek during August through October 2009 and May through October 2010. See Fig. 1 for sampling station locations and “Materials and Methods” section for timing of water quality readings

| Creek        | Station | Year | Temperature (°C) |                             | DO (mg O <sub>2</sub> /l) |  |  |
|--------------|---------|------|------------------|-----------------------------|---------------------------|--|--|
|              |         |      | Range            | % measurements $\geq 27$ °C | Range                     | % measurements $\leq 4.8$ mg O <sub>2</sub> /l | % measurements $\leq 2.3$ mg O <sub>2</sub> /l |
| Indian River | IRU     | 2009 | 20.1–32.8        | 47                          | 0–18.3                    | 44   | 16   |
|              |         | 2010 | 20.4–35.6        | 52                          | 0–23.0                    | 62   | 28   |
|              | IRL     | 2009 | 19.9–32.2        | 40                          | 0.2–14.5                  | 52   | 14   |
|              |         | 2010 | 21.0–33.8        | 42                          | 0.1–17.6                  | 49   | 16   |
|              | IRLL    | 2009 | 19.9–31.4        | 39                          | 0.1–13.7                  | 49   | 9  |
| Pepper Creek | PCU     | 2009 | 19.1–32.3        | 61                          | 0–23.5                    | 52   | 25   |
|              |         | 2010 | 22.3–33.7        | 67                          | 0–18.4                    | 58   | 22   |
|              | PCL     | 2009 | 19.3–32.0        | 59                          | 0.3–21.0                  | 41   | 8  |
|              |         | 2010 | 22.8–33.9        | 62                          | 0.1–17.9                  | 44   | 14   |

**Table 2** Mean fish density (individuals/m<sup>3</sup> corrected for gear Z-scores) and standard error by shoreline type and species

|   | Life history grouping | Functional grouping | <i>S. alterniflora</i>     | <i>P. australis</i>       | Riprap                     | Bulkhead                  | Percent of catch |
|---|-----------------------|---------------------|----------------------------|---------------------------|----------------------------|---------------------------|------------------|
| All fish species (mean density)                       |                       |                     | 101.28 ± 2.72 <sup>a</sup> | 24.92 ± 0.75 <sup>b</sup> | 17.85 ± 0.35 <sup>b</sup>  | 16.69 ± 0.69 <sup>b</sup> | 100              |
| <i>Fundulus heteroclitus</i> (mummichog)              | R                     | L-D                 | 77.00 ± 9.88 <sup>a</sup>  | 19.31 ± 3.27 <sup>b</sup> | 10.07 ± 1.03 <sup>bc</sup> | 2.63 ± 0.35 <sup>c</sup>  | 67.8             |
| <i>Brevoortia tyrannus</i> (menhaden)                 | D                     | P                   | 11.47 ± 6.93               | 1.14 ± 0.32               | 1.74 ± 0.7                 | 9.40 ± 3.22               | 14.8             |
| <i>Fundulus majalis</i> (striped killifish)           | R                     | L-D                 | 7.48 ± 1.19 <sup>a</sup>   | 1.28 ± 0.24 <sup>ab</sup> | 0.90 ± 0.15 <sup>ab</sup>  | 0.18 ± 0.06 <sup>b</sup>  | 6.1              |
| <i>Menidia menidia</i> (Atlantic silverside)          | D                     | P                   | 1.05 ± 0.19                | 1.99 ± 0.31               | 2.51 ± 0.85                | 2.95 ± 0.78               | 5.3              |
| <i>Bairdiella chrysoura</i> (silver perch)            | R                     | B/P                 | 1.47 ± 0.53                | 0.33 ± 0.05               | 1.02 ± 0.20                | 0.14 ± 0.02               | 1.8              |
| <i>Cyprinodontidae variegatus</i> (sheepshead minnow) | R                     | L-D                 | 1.84 ± 1.39                | 0                         | 0.04 ± 0.01                | <0.01 ± <0.01             | 1.2              |
| <i>Mugil cephalus</i> (striped mullet)                | D                     | P                   | 0.12 ± 0.02                | 0.13 ± 0.04               | 1.00 ± 0.62                | 0.52 ± 0.27               | 1.1              |
| <i>Anchoa mitchilli</i> (bay anchovy)                 | FD                    | P                   | 0.09 ± 0.02                | 0.17 ± 0.08               | 0.29 ± 0.20                | 0.65 ± 0.23               | 0.7              |
| <i>Leiostomus xanthurus</i> (spot)                    | D                     | B/P                 | 0.44 ± 0.17                | 0.26 ± 0.11               | 0.16 ± 0.05                | 0.05 ± 0.01               | 0.6              |
| <i>Cynoscion regalis</i> (weakfish)                   | D                     | B/P                 | 0.04 ± <0.01               | 0.07 ± 0.02               | 0.05 ± 0.02                | 0.02 ± 0.01               | 0.1              |
| <i>Morone saxatilis</i> (striped bass)                | D                     | B/P                 | 0.04 ± <0.01               | 0.07 ± 0.02               | 0.01 ± <0.01               | 0.06 ± 0.01               | 0.1              |
| <i>Gobiosoma bosc</i> (naked goby)                    | FD                    | L-D                 | 0.09 ± 0.02                | 0.06 ± 0.01               | <0.01 ± <0.01              | <0.01 ± <0.01             | 0.1              |
| <i>Paralichthys dentatus</i> (summer flounder)        | D                     | B/P                 | 0.06 ± 0.02                | 0.03 ± <0.01              | 0.01 ± <0.01               | 0.02 ± <0.01              | 0.1              |
| <i>Trinectes maculatus</i> (hogchoker)                | D                     | B/P                 | 0.01 ± <0.01               | 0.05 ± 0.01               | 0.02 ± <0.01               | <0.01 ± <0.01             | <0.1             |
| <i>Caranx hippos</i> (crevalle jack)                  | FD                    | B/P                 | 0.07 ± 0.01                | <0.01 ± <0.01             | 0                          | <0.01 ± <0.01             | <0.1             |
| <i>Mugil curema</i> (white mullet)                    | D                     | P                   | <0.01 ± <0.01              | <0.01 ± <0.01             | <0.01 ± <0.01              | 0.03 ± <0.01              | <0.1             |
| <i>Anguilla rostrata</i> (American eel)               | D                     | B/P                 | <0.01 ± <0.01              | <0.01 ± <0.01             | 0.01 ± <0.01               | <0.01 ± <0.01             | <0.1             |
| <i>Pomatomus saltatrix</i> (bluefish)                 | FD                    | B/P                 | <0.01 ± <0.01              | <0.01 ± <0.01             | <0.01 ± <0.01              | <0.01 ± <0.01             | <0.1             |
| <i>Opsanus tau</i> (oyster toadfish)                  | D                     | B/P                 | 0                          | 0                         | <0.01 ± <0.01              | <0.01 ± <0.01             | <0.1             |
| <i>Menidia beryllina</i> (inland silverside)          | D                     | P                   | 0                          | 0                         | <0.01 ± <0.01              | 0                         | <0.1             |

Superscript letters indicate significant subgroupings based on bootstrapped one-way ANOVAs with Holm-Sidak pairwise comparisons to determine significant subgroupings. Life history groupings indicate species estuary life history relationship. Functional groupings are based on descriptions from Murdy et al. 1997

R-resident, D-obligate dependent, FD-facultative dependent (Able 2005), L-D -littoral-demersal, P-planktivore, B/P-benthivore/piscivore

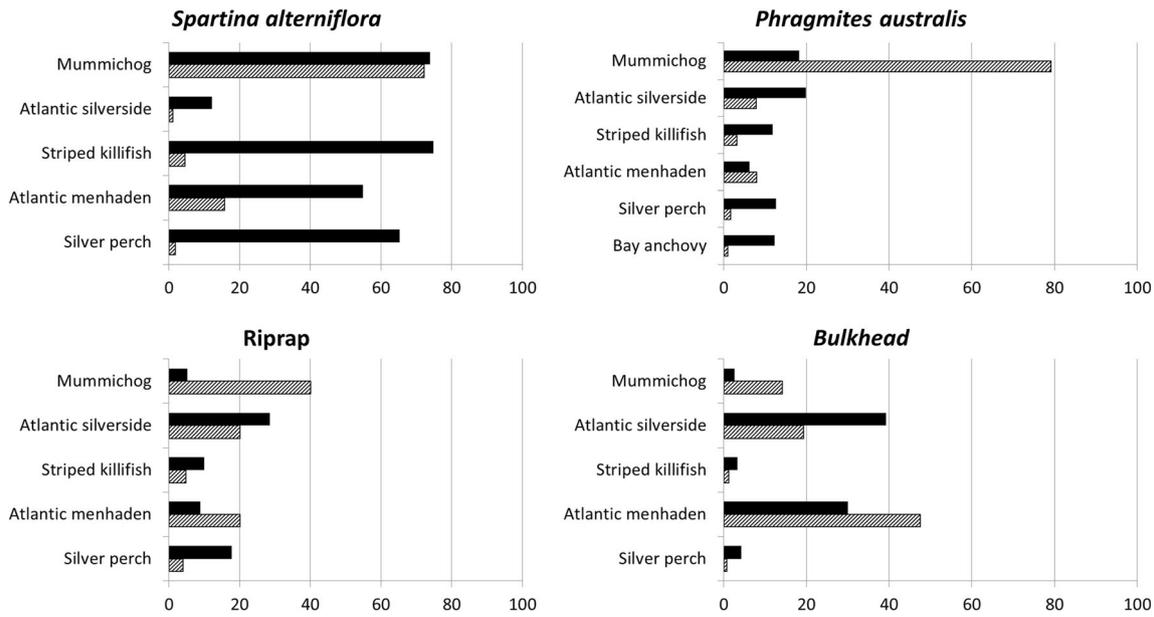
Fish density differed among shoreline types, across all water conditions. Mean fish density was significantly greater (one-way RM ANOVA;  $p < 0.01$ ;  $F = 9.69$ ,  $d.f. = 3$ ) along *S. alterniflora* shorelines than at any other shoreline type (Table 2). Significantly greater densities of *F. heteroclitus* (one-way RM ANOVA;  $p < 0.01$ ;  $F = 10.93$ ;  $d.f. = 3$ ) were caught along *S. alterniflora* and the lowest density was along bulkhead. No significant differences in density among shoreline types were found for *Brevoortia tyrannus*, *Bairdiella chrysoura*, or *M. menidia*. Among the six species caught with greatest mean density, all were found in greater density along *S. alterniflora* shorelines than any other shoreline except for *M. menidia* which was most abundant along bulkhead (Fig. 2). *F. heteroclitus* comprised the greatest proportion of the catch at each shoreline except bulkhead where *B. tyrannus* dominated (Fig. 2).

### Fish Assemblages—Water Quality Threshold/Shoreline Interactions

Significant results were found in non-parametric one-way repeated measures ANOVAs comparing fish density across

shorelines above and below water quality thresholds. In water conditions above 2.3 mg O<sub>2</sub>/l, significantly greater densities were found along *S. alterniflora* shorelines for all species ( $p = 0.015$ ,  $F = 7.44$ ,  $d.f. = 3$ ), littoral-demersal ( $p = 0.074$ ,  $F = 7.03$ ,  $d.f. = 3$ ), and *F. heteroclitus* ( $p = 0.036$ ,  $F = 7.94$ ,  $d.f. = 3$ ) (Fig. 3, Table 3). No significant differences were found among shoreline types in water conditions below 2.3 mg O<sub>2</sub>/l or above 4.8 mg O<sub>2</sub>/l. In water conditions below 4.8 mg O<sub>2</sub>/l, significantly greater mean fish densities were caught along *S. alterniflora* shorelines for all species ( $p = 0.083$ ,  $F = 3.68$ ,  $d.f. = 3$ ), the littoral-demersal species group ( $p = 0.034$ ,  $F = 9.31$ ,  $d.f. = 3$ ), and *F. heteroclitus* ( $p = 0.035$ ,  $F = 9.29$ ,  $d.f. = 3$ ) (Fig. 3, Table 3). In water conditions above 27 °C, significantly greater mean fish densities were caught along *S. alterniflora* shorelines for all species ( $p < 0.01$ ,  $F = 8.26$ ,  $d.f. = 3$ ) and *F. heteroclitus* ( $p = 0.029$ ,  $F = 7.70$ ,  $d.f. = 3$ ) (Fig. 3, Table 3). *S. alterniflora* shorelines were the only shoreline type at which any fish grouping or species was found in significantly greater density in conditions above or below adverse water condition thresholds.

Mean species richness was greater at all shoreline types when DO conditions were above 2.3 mg O<sub>2</sub>/l, although the



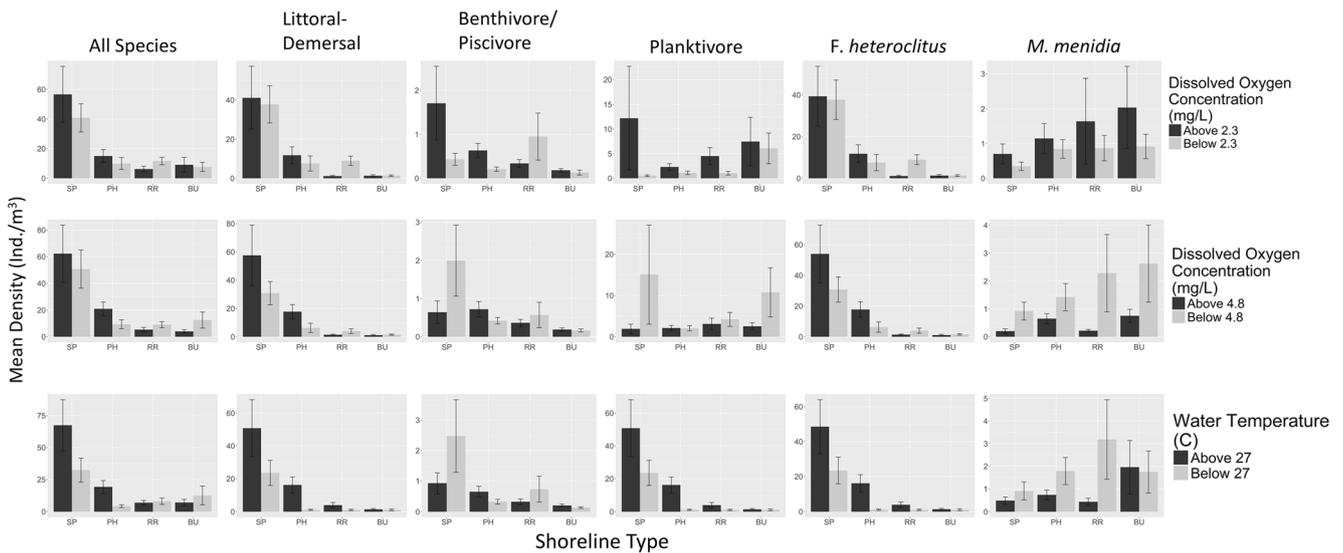
**Fig. 2** Relative mean density (individuals/m<sup>3</sup>) of the most abundant fish species sampled at each shoreline type in Indian River and Pepper Creek, tributaries of the Delaware Coastal Bays, from August through October 2009 and May through October 2010. *Black bars* represent the percentage of a given species’ total catch (across all shoreline types) that was collected at the specified shoreline type; therefore, the *longest black bars* indicate the shoreline at which the species was particularly

abundant (i.e., if a species had equal abundance along all four shoreline types, values for all four *black bars* would be at 25%). *Crosshatched bars* represent the percentage of total catch for a given species at the given shoreline type; thus, the *longest crosshatched bars* indicate species that dominated the collections at the specified shoreline type (i.e., *crosshatched bars* within a panel sum to 100%)

magnitude of difference at each shoreline type was minimal (Fig. 4). *S. alterniflora* shorelines had the lowest reduction in mean species richness from conditions >2.3 mg O<sub>2</sub>/l to ≤2.3 mg O<sub>2</sub>/l, whereas bulkhead shorelines exhibited the greatest decline. Examining the 4.8 mg O<sub>2</sub>/l threshold, *S. alterniflora* and bulkhead shorelines had greater mean

species richness in conditions below the threshold. At the 27 °C water temperature threshold, only *S. alterniflora* shorelines experienced reduced mean species richness at water temperatures above the threshold (Fig. 4).

Species occurrence (presence/absence) rates also differed across water quality threshold and shoreline type (Table 4).



**Fig. 3** Mean catch per unit effort (individuals/m<sup>3</sup>) and standard error by shoreline type and water quality condition for total catch (All Species), the three functional groups as defined in Table 2, *F. heteroclitus*, and

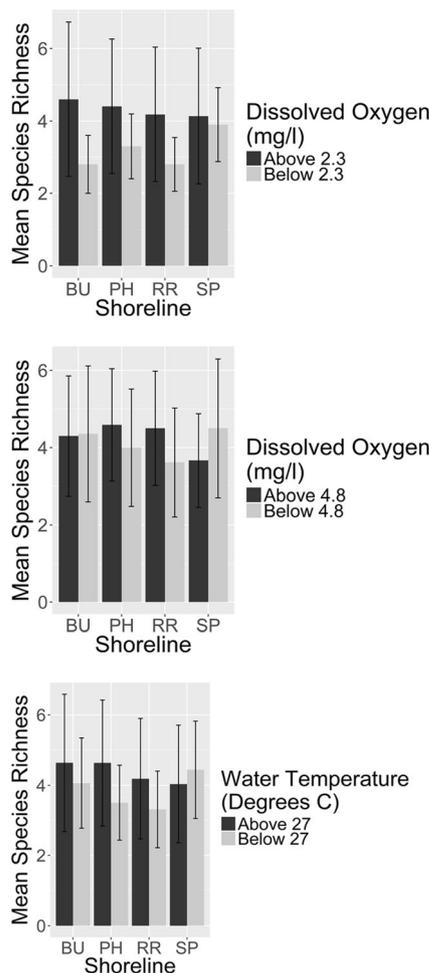
*M. menidia*. Shoreline types are as follows: *Spartina alterniflora*—SP, *Phragmites australis*—PH, riprap—RR, and bulkhead—BU

**Table 3** Shoreline type (*Spartina alterniflora*—SP, *Phragmites australis*—PH, riprap—RR, and bulkhead—BU) with the greatest density caught above and below adverse water conditions, at each water quality threshold. Functional groupings are defined in Table 2. Shoreline codes in bold indicate density at that shoreline was significantly greater

| Grouping/species                             | DO 2.3 mg/l |      | DO 4.8 mg/l |           | Temperature 27 °C |     |
|--|-------------|------|-------------|-----------|-------------------|-----|
|  | >2.3        | <2.3 | >4.8        | <4.8      | >27               | <27 |
| All species                                  | <b>SP</b>   | SP   | SP          | <b>SP</b> | <b>SP</b>         | SP  |
| Littoral-demersal                            | <b>SP</b>   | SP   | SP          | <b>SP</b> | SP                | SP  |
| Benthivore/piscivore                         | SP          | RR   | PH          | SP        | SP                | SP  |
| Planktivore                                  | SP          | BU   | RR          | SP        | SP                | BU  |
| <i>Fundulus heteroclitus</i> (mummichog)     | <b>SP</b>   | SP   | SP          | <b>SP</b> | <b>SP</b>         | SP  |
| <i>Menidia menidia</i> (Atlantic silverside) | BU          | BU   | BU          | BU        | BU                | RR  |

Both *F. heteroclitus* and *M. menidia* were present in more samples, at all shoreline types, when DO during diel cycles remained above 2.3 mg O<sub>2</sub>/l, with the exception of *F. heteroclitus* along bulkhead. Difference in presence/

than at least one other shoreline type at the same threshold condition. Shoreline codes in bold and underlined indicate density at that shoreline was significantly greater than at all other shorelines at the same threshold condition



**Fig. 4** Mean species richness and standard error by shoreline type and water quality threshold. Shoreline types are as follows: *Spartina alterniflora*—SP, *Phragmites australis*—PH, riprap—RR, and bulkhead—BU

absence for *M. menidia* occurred along armored shorelines, where they were present more frequently in higher DO conditions. The smallest differences in presence/absence rates above and below the 2.3 mg O<sub>2</sub>/l threshold occurred at *S. alterniflora* shorelines for *M. menidia* and at riprap for *F. heteroclitus*. At the 4.8 mg O<sub>2</sub>/l threshold, presence/absence rates of *F. heteroclitus* and *M. menidia* varied minimally by shoreline type with little pattern. At the 27 °C water temperature threshold, *F. heteroclitus* were much more commonly present in conditions exceeding the threshold, whereas *M. menidia* varied by shoreline type with little pattern (Table 4).

**Fish Assemblages—Two-Way ANOVA Water Quality Threshold/Shoreline Comparisons**

Results from aligned rank transformation two-way ANOVAs showed density differences across thresholds and species for water conditions present within 15 min prior to fish sampling (Table 5). All significant interactions that were found in two-way ANOVAs determined *S. alterniflora* to be the refuge habitat in comparison with other shoreline types. Density of all species together and for the littoral-demersal species grouping showed no significant interactions among either DO threshold (2.3 or 4.8 mg O<sub>2</sub>/l) and shoreline type. However, a significant interaction between the 27 °C water temperature threshold and shoreline type was found for the density of all species together ( $p = 0.018, df = 3, F = 5.01$ ) and littoral-demersal species ( $p = 0.010, df = 3, F = 5.91$ ). Pairwise comparisons revealed significant interaction between bulkhead and *S. alterniflora* and between riprap and *S. alterniflora*, with *S. alterniflora* being the refuge habitat in each comparison. No significant interaction between the 2.3 mg O<sub>2</sub>/l threshold and shoreline type was found for any species functional group or for either species of interest. No significant interactions among water quality thresholds and shoreline type were found for the planktivore species

**Table 4** Proportion of sampling events at which *F. heteroclitus* and *M. menidia* were present, by shoreline type and at each water quality threshold condition. Water quality thresholds include DO  $\leq 2.3$  mg O<sub>2</sub>/l (DO 2.3), DO  $\leq 4.8$  mg O<sub>2</sub>/l (DO 4.8), and temperature  $\geq 27$  °C (Temp 27)

| Shoreline              | Water threshold | Species                |                   |
|------------------------|-----------------|------------------------|-------------------|
|                        |                 | <i>F. heteroclitus</i> | <i>M. menidia</i> |
| DO 2.3                 |                 |                        |                   |
| <i>S. alterniflora</i> | Above           | 0.76                   | 0.65              |
|                        | Below           | 0.70                   | 0.60              |
| <i>P. australis</i>    | Above           | 0.75                   | 0.91              |
|                        | Below           | 0.60                   | 0.80              |
| Riprap                 | Above           | 0.64                   | 0.85              |
|                        | Below           | 0.60                   | 0.60              |
| Bulkhead               | Above           | 0.62                   | 0.87              |
|                        | Below           | 0.70                   | 0.40              |
| DO 4.8                 |                 |                        |                   |
| <i>S. alterniflora</i> | Above           | 0.72                   | 0.44              |
|                        | Below           | 0.79                   | 0.79              |
| <i>P. australis</i>    | Above           | 0.76                   | 0.94              |
|                        | Below           | 0.71                   | 0.88              |
| Riprap                 | Above           | 0.63                   | 0.75              |
|                        | Below           | 0.65                   | 0.85              |
| Bulkhead               | Above           | 0.65                   | 0.80              |
|                        | Below           | 0.64                   | 0.79              |
| Temp 27                |                 |                        |                   |
| <i>S. alterniflora</i> | Above           | 0.87                   | 0.60              |
|                        | Below           | 0.41                   | 0.75              |
| <i>P. australis</i>    | Above           | 0.85                   | 0.96              |
|                        | Below           | 0.50                   | 0.79              |
| Riprap                 | Above           | 0.70                   | 0.81              |
|                        | Below           | 0.50                   | 0.75              |
| Bulkhead               | Above           | 0.80                   | 0.77              |
|                        | Below           | 0.56                   | 0.88              |

grouping (Table 5). Fishes in the benthivore/piscivore functional grouping had a significant interaction between the 4.8 mg O<sub>2</sub>/l and shoreline type ( $p = 0.014$ ,  $d.f. = 3$ ,  $F = 5.44$ ) and between 27 °C and shoreline type ( $p = 0.031$ ,  $d.f. = 3$ ,  $F = 4.16$ ). In both cases, pairwise comparisons showed significant differences between *P. australis* and *S. alterniflora*, with *S. alterniflora* being the refuge habitat in each comparison. *F. heteroclitus* ( $p = 0.047$ ,  $d.f. = 3$ ,  $F = 3.58$ ) had a significant interaction between the 4.8 mg O<sub>2</sub>/l and shoreline type, but pairwise comparisons did not find significant individual interactions among shoreline types for *F. heteroclitus*, suggesting a weak interaction. Significant interactions between the 27 °C water temperature threshold and shoreline types were found for *F. heteroclitus* ( $p < 0.01$ ,  $d.f. = 3$ ,  $F = 6.98$ ). Pairwise comparisons showed significant interaction between bulkhead and *S. alterniflora*,

with *S. alterniflora* being the refuge habitat. No significant interactions among water quality thresholds and shoreline type were found for *M. menidia* (Table 5).

Water quality conditions occurring at rolling averages for 1 and 4 h prior to sampling were calculated to determine if fish reactions to water quality conditions at longer time frames prior to sampling resulted in stronger interactions than those seen at water quality conditions immediately prior to sampling. Similar results for two-way ANOVAs were found for water conditions averaged across the 1- and 4-h time period prior to fish sampling. Results from Welch's  $t$  tests indicate no significant differences among water quality conditions for DO (15 min vs. ~1 h:  $p = 0.672$ ; 15 min vs. ~4 h:  $p = 0.871$ ) and temperature (15 min vs. ~1 h:  $p = 0.964$ ; 15 min vs. ~4 h:  $p = 0.969$ ) across these time frames.

## Discussion

Estuary-resident fishes spend their entire life cycle within an estuary, utilizing shore-zone habitat for foraging, predator protection, and reproduction (Richards and Castagna 1970; Shenker and Dean 1979; Conover and Ross 1982; Able et al. 2003; Raichel et al. 2003). These species are adapted to the physiological demands of inhabiting temperate estuaries year-round, including those imposed by large fluctuations in temperature, DO, and salinity (Able and Fahay 1998). Likewise, estuary-dependent fish species spend a critical portion of their life cycle (larval and/or juvenile stages) in estuaries, often spanning several seasons (Fay et al. 1983a, b). Estuarine species, which comprise critical links in estuarine and marine food chains worldwide, have been shown to respond to physical changes in shore-zone habitats including shoreline armoring (Kneib 1997; Bilkovic and Roggero 2008). The degree to which these highly adaptable species are able to cope with changes in their environment may be an indicator of how the ecosystem as a whole will respond to shoreline development. Density of estuary-resident and estuary-dependent species (hereafter grouped together as estuarine) can reflect habitat quality (Szedlmayer and Able 1996; Rountree and Able 2007). As estuaries continue to be modified and degraded, additional processes such as competitive release and water quality tolerance (Lowe and Peterson 2014) can also contribute to species presence and density.

Among the most abrupt and permanent changes to estuarine environments are physical changes to marsh habitat as a result of human development, including shoreline armoring. Assessing the density and diversity of estuarine fish assemblages along various shore-zone environments has helped to elucidate the habitat quality provided by different shoreline types (Bilkovic and Roggero 2008; Balouskus and Targett 2016; Gittman et al. 2016a, b; Torre and Targett 2016). These studies, including the present research, have thoroughly

**Table 5** Results of two-way ANOVAs and Holm-Sidak pairwise comparisons of fish density (individuals/m<sup>3</sup>) at pairs of shoreline types across water quality thresholds; for all species, the three functional groups as defined in Table 2, *F. heteroclitus*, and *M. menidia*. Statistical results of two-way ANOVAs comparing conditions above and below the thresholds indicated in the Water quality threshold column are presented in the Interaction *p* value column. Refuge habitat shoreline types are utilized by fish at higher density rates (or at less reduced density rates) during adverse conditions. The bold shoreline type identified within the result matrix

| Species                | Water quality threshold | Interaction <i>p</i> value | SP-PH     | SP-RR     | SP-BU     | PH-RR | PH-BU | RR-BU |
|------------------------|-------------------------|----------------------------|-----------|-----------|-----------|-------|-------|-------|
| All species            | DO 2.3                  | 0.688                      |           |           |           |       |       |       |
|                        | DO 4.8                  | 0.143                      |           |           |           |       |       |       |
|                        | Temp 27                 | 0.018                      | NA        | <b>SP</b> | <b>SP</b> | NA    | NA    | NA    |
| Littoral-demersal      | DO 2.3                  | 0.317                      |           |           |           |       |       |       |
|                        | DO 4.8                  | 0.072                      |           |           |           |       |       |       |
|                        | Temp 27                 | 0.010                      | NA        | <b>SP</b> | <b>SP</b> | NA    | NA    | NA    |
| Planktivore            | DO 2.3                  | 0.780                      |           |           |           |       |       |       |
|                        | DO 4.8                  | 0.137                      |           |           |           |       |       |       |
|                        | Temp 27                 | 0.990                      |           |           |           |       |       |       |
| Benthivore/piscivore   | DO 2.3                  | 0.323                      |           |           |           |       |       |       |
|                        | DO 4.8                  | 0.014                      | <b>SP</b> | NA        | NA        | NA    | NA    | NA    |
|                        | Temp 27                 | 0.031                      | <b>SP</b> | NA        | NA        | NA    | NA    | NA    |
| <i>F. heteroclitus</i> | DO 2.3                  | 0.403                      |           |           |           |       |       |       |
|                        | DO 4.8                  | 0.047                      | NA        | <b>SP</b> | <b>SP</b> | NA    | NA    | NA    |
|                        | Temp 27                 | 0.006                      | NA        | <b>SP</b> | <b>SP</b> | NA    | NA    | NA    |
| <i>M. menidia</i>      | DO 2.3                  | 0.749                      |           |           |           |       |       |       |
|                        | DO 4.8                  | 0.247                      |           |           |           |       |       |       |
|                        | Temp 27                 | 0.742                      |           |           |           |       |       |       |

was identified in the pairwise comparison as being utilized at a significantly ( $<0.05$ ) greater density during adverse conditions defined as DO  $\leq 2.3$  mg O<sub>2</sub>/l (DO 2.3), DO  $\leq 4.8$  mg O<sub>2</sub>/l (DO 4.8), and temperature  $\geq 27$  °C (Temp 27). Shoreline types are as follows: *Spartina alterniflora*—SP, *Phragmites australis*—PH, riprap—RR, and bulkhead—BU. Cells in gray indicate no significant interaction term among water quality threshold and shoreline type for fish density was found. NA (not applicable) indicates a pairwise comparison with no significant interaction

demonstrated the importance of native marsh grasses in serving as critical habitat in estuarine environments and the negative impact of armored shorelines, particularly bulkhead, on fish assemblages. Many other factors influence the occurrence and density of estuarine fishes in an estuary ecosystem including time of year, time of day, and distance from an ocean inlet (Able and Fahay 1998; Chant et al. 2000). Additional factors such as habitat characteristics that vary on hourly and hundred meter scales, like diel-cycling DO conditions and water temperature, have been shown to affect species occurrence and density as well (Blaber and Blaber 1980; Baltz et al. 1993; Tyler and Targett 2007; Stierhoff et al. 2009a). Understanding how both the physical characteristics of estuaries, including shore-zone habitats, and water quality interact to impact habitat quality for estuarine fish is much less well understood and its research may lead to more successful ecosystem management (Baltz et al. 1993).

Fish densities of 70% of all species caught in the present study were greater along vegetated shorelines than along armored shorelines. Across all water quality thresholds examined, *S. alterniflora* shorelines had the greatest total fish densities both above and below each threshold, indicating the native marsh grass is the most utilized habitat regardless of water condition. Species richness decreased at all shoreline types in conditions below the 2.3 mg O<sub>2</sub>/l DO threshold.

However, *S. alterniflora* shorelines exhibited the least decline in species and had the greatest mean species richness in conditions below (but not above) this threshold. Greatest mean species richness in conditions below 4.8 mg O<sub>2</sub>/l was also found at *S. alterniflora*. Additionally, results from two-way ANOVAs indicate a refuge effect provided by *S. alterniflora* compared with armored shorelines during water conditions exceeding 27 °C for all species combined. This collection of results provides strong evidence that *S. alterniflora* provides greater habitat quality than armored shorelines and *P. australis* shores and serves as a refuge habitat by some species during adverse DO and temperature conditions. However, this conclusion is tempered as results from two-way ANOVAs examining interactions between the density of all fishes and DO conditions found no significant interactions, suggesting that neither *S. alterniflora* nor any of the shoreline types examined serve a significant refuge function during adverse DO conditions for the complete estuarine fish assemblage. These varying results imply that while *S. alterniflora* likely serves as a refuge habitat, the relationship between fish habitat use and water quality may be non-linear or not predominated by a threshold effect, particularly in the case of DO for all species. These interactions can be more closely examined by looking at functional species groupings and individual species reactions for adverse water conditions.

Analysis of species functional groupings provides additional strong evidence supporting *S. alterniflora* serving as a refuge habitat during high temperature and low DO conditions. Littoral-demersal species, including *F. heteroclitus*, were found in greater densities at *S. alterniflora* shorelines under all water quality conditions and significantly so in conditions  $<4.8$  mg O<sub>2</sub>/l. The life history characteristics of these species strongly tie them to marsh surface and edge habitats. In contrast, planktivore species utilize open water habitats for feeding and have less interaction with the marsh surface than littoral-demersal or benthivore species (Deegan 1990). However, planktivore species were found in the greatest density along *S. alterniflora* shorelines during adverse conditions  $<4.8$  mg O<sub>2</sub>/l and  $>27$  °C. In seeing interactions not just only in species with strong life history connections with the marsh surface (littoral-demersal) but also in species more directly associated with open water habitats (planktivore), the overall importance of *S. alterniflora* as refuge habitat can be seen. And while the importance of *S. alterniflora* habitats may be stronger for certain species groupings than others, all three functional species groupings utilized *S. alterniflora* in greater densities during adverse water conditions  $<4.8$  mg O<sub>2</sub>/l and  $>27$  °C.

The high relative density of *F. heteroclitus* along all shoreline types was expected given the large populations of this species that inhabit estuarine shores in the mid-Atlantic region of the USA (USFWS 1985; Rountree and Able 1992; Boutin and Targett 2013). *F. heteroclitus* also exhibit high physiological tolerances to changing oxygen and temperature conditions, such as those found in Pepper Creek and Indian River (Tyler et al. 2009) contributing to the species' dominance. These fish are important in salt marsh food webs, where they are instrumental in movement of organic material within and out of salt marsh ecosystems (Kneib 1986, 1997; Kneib and Wagner 1994). *F. heteroclitus* were the species found in greatest density at all shoreline types aside from bulkhead and a majority of all *F. heteroclitus* were caught at *S. alterniflora* shorelines. In addition to greater relative densities of mummichog being found along *S. alterniflora* shorelines than any other shoreline type across all water quality thresholds, the occurrence rate of *F. heteroclitus* in adverse water conditions was greatest at *S. alterniflora* shorelines across all three thresholds. *F. heteroclitus* have a very limited home range, suggesting very discrete relationships to the shoreline they inhabit (Lotrich 1975; Sweeny et al. 1998; Crum et al. 2017). How *F. heteroclitus* density responds to shoreline development and water quality thresholds may serve as a bellwether for other estuarine fauna. The disparity among densities along shoreline types may be due to the species preferential use of marsh pools, ditches, and depressions found on marsh surfaces at high tide. This marsh surface habitat, which is a certain proportion of the *F. heteroclitus* community, will leave for subtidal waters as the tide recedes, is

greatest in *S. alterniflora* marshes (Able and Hagan 2003), and is reduced along *P. australis* marsh due to increased marsh elevation (Weinstein and Balleto 1999; Able and Hagan 2003; Able et al. 2003), and effectively non-existent along hardened shorelines. Weisberg and Lotrich (1982) demonstrated that *F. heteroclitus* require marsh surface habitat to supplement energy consumption. Generally, greater occurrence rates were found along unhardened shorelines regardless of water quality conditions. Significant interactions among shoreline type and water quality in two-way ANOVAs suggest that despite being tolerant of low DO conditions and high temperatures (Abraham 1985; Stierhoff et al. 2003), *F. heteroclitus* exhibit a degree of preferable habitat searching during adverse conditions.

*M. menidia*, a planktivorous species, is among the most abundant forage fish species in US mid-Atlantic estuaries (De Sylva et al. 1962; Richards and Castagna 1970; Able and Fahay 2010; Torre and Targett 2016). The importance of *M. menidia* as a food source for piscivores such as striped bass (*Morone saxatilis*), Atlantic mackerel (*Scomber scombrus*), bluefish (*Pomatomus saltatrix*), and other fishes is well documented (Bayliff 1950; Bigelow and Schroeder 1953; Schaefer 1970; Torre and Targett 2017). The greatest mean density of *M. menidia* was caught at bulkhead shorelines in this study. No shoreline type was dominated by *M. menidia* and only riprap shore-zones had  $>20\%$  of the total catch comprised of this species. Lower mean densities of *M. menidia* were caught in water conditions below the 2.3 mg O<sub>2</sub>/l threshold across all shoreline types suggesting strong avoidance of severe hypoxia. Despite these differences, results from two-way ANOVAs found no significant interactions among shoreline type and water conditions for *M. menidia*. As an estuary-dependent species which utilizes estuarine habitats for spawning in the spring (Balouskus and Targett 2012) and inhabits offshore habitats during autumn and winter seasons (Fay et al. 1983a), it is possible that *M. menidia* utilize open water habitats more frequently and have less direct affinity for specific shoreline structures (either vegetated or armored) when inhabiting estuarine environments. Bulkhead structures have been shown to increase water depth at the land-water interface (Jennings et al. 1999; Peterson et al. 2000; Bilkovic et al. 2006), creating additional open water habitat. Differences between *F. heteroclitus* and *M. menidia* in mean density by shoreline type and responses to both DO and water temperature thresholds effectively show how different species utilize the same available shore-zone habitats in very different ways.

Results of this research show that estuary-resident and estuary-dependent species utilize *S. alterniflora* shorelines at greater density and occurrence rates than invasive *P. australis* or armored shorelines. Species density and richness declined in conditions  $\leq 2.3$  mg O<sub>2</sub>/l. Total fish density, density of littoral-demersal species, and density of *F. heteroclitus* were

greatest at *S. alterniflora* in all water conditions exceeding thresholds. Previous research has shown that fish density is reduced when DO drops below 4.8 mg O<sub>2</sub>/l and is severely reduced when DO drops below 2.3 mg O<sub>2</sub>/l (Eby and Crowder 2002; Tyler and Targett 2007). In the Neuse River Estuary of North Carolina, all ten species of fish studied (including pelagic and demersal estuary-dependent species) avoided areas with DO <2.0 mg O<sub>2</sub>/l (Eby and Crowder 2002). In laboratory studies, fishes (larval, juvenile, and adult) responded to oxygen gradients by moving upwards or laterally away from waters with physiologically stressful or potentially lethal DO concentrations and toward areas of higher DO (Breitburg 2002; Stierhoff et al. 2009b), a strategy that may be difficult for small estuarine fish species to employ over large areas due to low swim speeds and constricted home ranges. Results from this research suggest that the composition and location of the shore-zone fish assemblage in hypoxic estuarine systems may change with hourly changes in DO, and that shoreline structure may interact with diel-cycling hypoxia to effect habitat selection by estuarine fish.

Native *S. alterniflora* shorelines provide the greatest habitat quality in comparison with invasive and armored shorelines for a majority of species caught in this study as exhibited by mean density. This study demonstrates that native *S. alterniflora* shorelines may provide a degree of refuge for benthivore/piscivore species and *F. heteroclitus* during periods of low DO. *S. alterniflora* shorelines were also shown to serve as a refuge habitat during high water temperatures for the complete fish assemblage, benthivore/piscivore species, and littoral-demersal species including *F. heteroclitus*. The mechanisms by which *S. alterniflora* may serve as refuge habitat are varied. Macroalgal growth associated with *S. alterniflora* on the marsh surface and edge may increase DO in the immediate region. The complex physical structure provided by the close stems of *S. alterniflora* may provide predation protection or greater availability of immobile prey species in native marshes may contribute to refuge characteristics. Water/air temperature in the intertidal and shallow subtidal zone has been found to be significantly reduced (~2 °C in the intertidal) in *S. alterniflora* habitats in comparison with hardened shorelines (Balouskus and Targett 2012). Regardless of the exact mechanisms by which *S. alterniflora* serves as refuge habitat, the conservation and management implications are clear and stress the importance of retaining stands of native marsh grasses. When possible, replacement of hardened shoreline with native marsh grasses such as *S. alterniflora* may contribute to the fish assemblage resilience to high temperatures and hypoxic conditions. Where erosion control structures are required, the installation of riprap-sill with native planting on the shoreward side or “living shorelines” may reduce the negative impact of riprap or other armoring on estuarine fish assemblages (Balouskus and Targett 2016, Gittman et al. 2016b).

This study confirmed the contrasting use of armored shorelines, invasive grass marshes, and native *S. alterniflora* marshes by estuarine fish as has been found in prior studies from the Chesapeake Bay (Bilkovic and Roggero 2008; Kornis et al. 2017), Gulf of Mexico (Peterson et al. 2000), Delaware coastal bays (Balouskus and Targett 2016), Hudson River (Strayer et al. 2012), and numerous other locations (Gittman et al. 2016a). New findings from this research have extended these prior studies by examining interactions among shoreline type habitat use and adverse water temperature and DO conditions. Fish density, occurrence rate, and species richness were all found to be affected by interactions among shoreline type and categorical water quality thresholds. These differences suggest variations in habitat quality provided by each shoreline type, exhibited through differences in shoreline-specific density, species richness, and occurrence rates across thresholds of DO and water temperature, suggesting a potentially non-linear or non-threshold relationship between shifting water conditions and relative shoreline habitat quality.

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