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FISHES OF A TEMPERATE ESTUARY: ECOLOGY AND RESPONSE TO AN
URBANIZED WATERSHED

By

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ABSTRACT OF THE DISSERTATION

Fishes of a Temperate Estuary: Ecology and Response to an Urbanized Watershed

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Anthropogenic activities have left no part of the global ecosystem untouched; not even the highest mountain peaks or deepest ocean trenches. Of the many ways anthropogenic activities can alter the ecosystem, urbanization (anthropogenic land development) is perhaps one of the most profound ways by which humans physically transform the environment.

The urbanization of coastal watersheds has been occurring for centuries and continues today. Nearly 40% of the United States' population resides within coastal counties, and this percentage is projected to increase due to continued coastal migration and the exponentially growing human population. Unfortunately, the impact of this watershed urbanization on coastal fauna is still not well understood. The understudied fauna includes estuarine fishes, which use these areas as nurseries and are essential to sustaining healthy fish populations. In this dissertation, natural and anthropogenic influences on fish assemblage structure (species composition, abundance, diversity) were

studied to determine how watershed urbanization affected the fishes in Barnegat Bay, a temperate lagoonal estuary located in New Jersey, U.S.A.

In the first and second chapters, changes in fish assemblage structure in relation to temporal and subhabitat influences were studied to understand the assemblage response to natural variation prior to evaluating the influence of urbanization on assemblage structure. In Chapter I, the long-term response of fishes to the passage of Hurricane Sandy was assessed. Fish assemblage structure remained relatively stable over the three year study period, which encompassed the large episodic disturbance of Hurricane Sandy. The ability of fish to relocate from areas of temporarily unsuitable habitat and annual new recruitment of fishes to the bay likely contributed to the observed stability in the fish assemblage. In Chapter II, fish usage of the dominant subtidal habitats (marsh creeks, sand, submerged aquatic vegetation) within Barnegat Bay were documented. Fishes used all habitats sampled demonstrating the importance of the habitat mosaic within Barnegat Bay. Further, the assemblages in marsh creeks were often as abundant and diverse as those in submerged aquatic vegetation, highlighting the importance of marsh creeks as important fish habitat in addition to submerged aquatic vegetation habitat.

In the third and fourth chapters, the influence of urbanization on fishes in Barnegat Bay was assessed at varying spatial scales. In Chapter III, structural characteristics of the fish assemblages along the large watershed-wide urbanization gradient, which increases from the southern to the northern portion of the bay's watershed, were evaluated. Structural differences in fish assemblages that could be solely attributed to the large-scale urbanization gradient in the watershed were not readily apparent, likely due to a lack of cumulative impacts at this large scale. In Chapter IV, fish

assemblages inhabiting unaltered marsh creeks and lagoon housing complexes with heavily armored shorelines were compared. At this smaller scale, differences in fish assemblage structure between unaltered and armored habitats were evident, with species that relied on the salt marsh and shallow waters being less abundant in the lagoon complexes. These findings suggest urbanization in the Barnegat Bay watershed has caused localized changes in fish assemblages which have not accumulated to assemblage impacts on a large-scale, but could do so if urbanization in the bay's watershed continues unabated.

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INTRODUCTION

Estuaries offer ecologically important habitat for various species of fish (Able 2005) and invertebrates (Minello et al. 2003) and provide essential ecosystem services such as disturbance regulation, recreation, and food production (Costanza et al. 1997). Consequently, the watersheds surrounding estuaries are often densely populated leading to human driven degradation of these coastal ecosystems (Lotze et al. 2006; Halpern et al. 2008). The urbanization (anthropogenic land development) of these coastal ecosystems through processes such as marsh infilling, dredging, bulkheading, and lagoon construction alters the physical parameters of the environment and destroys valuable habitat (Sugihara et al. 1979). Additionally, as land is urbanized, the extent of impervious surfaces increases resulting in changes to coastal water quality (Seilheimer et al. 2007).

The impact of anthropogenic development on estuarine fauna has been studied; however, Brown et al. (2009) cautioned generalizing responses to urbanization across systems due to differences in intrinsic variation. Additionally, quantifying human impacts within highly variable estuarine systems can be difficult since organisms may respond similarly to anthropogenic and natural stressors. Elliott and Quintino (2007) refer to this conundrum as the Estuarine Quality Paradox and stress the importance of understanding natural system variation and the use of structural (e.g. species composition, abundance, diversity) and functional (e.g. trophic relationships, production indices) characteristics when assessing human impacts on estuarine fauna. Scale is also an essential consideration when evaluating anthropogenic influences on fauna (Peterson and Lowe 2009; Nicholas et al. 2010; Hughes et al. 2014). For example, studies on salt marsh fish assemblages in Louisiana after the BP Oil Spill indicated no obvious differences in

assemblage structure between oiled and unoiled marshes (Able et al. 2015); however, at the individual fish level physiological impacts were observed (Whitehead et al. 2012).

Within estuarine systems, fish are particularly important because they serve as a key link in the food web, transferring energy from primary producers to marine mammals and to humans. Fish are a vital resource to human society. Over 3 billion people rely on fish for nearly a quarter of their animal protein intake and the fishing industry supports over 60 million jobs worldwide (Food and Agriculture Organization 2018). In addition to fishing pressures, fishes are impacted by other human driven processes, such as urbanization, and are valuable tools for assessing the extent of potential impacts (Izzo et al. 2016). Various studies have recognized the impacts of urbanization on structural (Able et al. 1998; Hendon et al. 2000; Peterson et al. 2000; Bilkovic and Roggero 2008; Partyka and Peterson 2008; Balouskus and Targett 2016) and functional (Able et al. 1999; Wedge et al. 2015; Hall-Scharf et al. 2016) characteristics of fish assemblages.

The overall goal of this dissertation was to provide the first assessment of the response of fishes in Barnegat Bay, New Jersey, U.S.A to the urbanization within the surrounding watershed. In recent decades the watershed has seen increased human population growth (Kauffman and Cruz-Ortiz 2012) resulting in an increase of urbanized land; however, no studies have been conducted to assess the potential response of fishes to this increasing urbanization despite the importance of fish to the New Jersey economy. In 2016, the New Jersey fishing industry generated \$8 billion and supported 52,000 jobs (National Marine Fisheries Service 2018), making it essential to understand how urbanization impacts this critical fisheries resource. In addition, although there have been previous assessments of the fishes inhabiting the bay (Marcellus 1972; Tatham et al.

1977; Danila et al. 1979; Vouglitois 1983; Tatham et al. 1984; Vouglitois et al. 1987; Jivoff and Able 2001), none have surveyed the fishes throughout the entire bay and without a thorough understanding of the natural processes influencing the distribution of fishes, it is difficult to assess the impact of anthropogenic activities (Izzo et al. 2016). Therefore, the first and second chapters of this dissertation will investigate fish assemblage structure throughout the entire bay in relation to natural processes and the third and fourth chapters will then evaluate fish assemblage structure in relation to urbanization at two different spatial scales.

In Chapter I, the long-term response of fishes to the passage of Hurricane Sandy was assessed. In 2012, Hurricane Sandy made landfall just south of Barnegat Bay during a three-year sampling program. Given the impracticality of pre-planning long-term ecological studies involving hurricanes, previous investigations of fish responses to hurricane passage have often been over short temporal durations and generally lack a pre-storm baseline. The yearly Barnegat Bay sampling that bracketed Hurricane Sandy provided a unique opportunity to study the potential long-term impacts of hurricanes on fish assemblage structure. Understanding the ecological impact of hurricanes is important as climate change may influence the severity, frequency, and path of these storms (Mann and Emanuel 2006, Knutson et al. 2010, Grossmann and Morgan 2011, Colbert et al. 2013, Walsh et al. 2016). This chapter is published in *Marine Ecology Progress Series* (Valenti et al. 2020).

In Chapter II, fish usage of the habitat mosaic within Barnegat Bay was documented. Research on fish usage of subtidal estuarine habitats has focused disproportionately on submerged aquatic vegetation (Beck et al. 2001; Hyndes et al.

2018). In this chapter, structural characteristics of the fish assemblages inhabiting all dominant habitat types (upper creek, creek mouth, sand, submerged aquatic vegetation) in Barnegat Bay were compared. Understanding the patterns and complexities of fish habitat usage within entire estuarine seascapes is vital to habitat and fisheries conservation efforts (Pérez-Ruzafa et al. 2019).

Chapter III focused on the influence of urbanization at the large, bay-wide spatial scale. Structural characteristics of fish assemblages along the gradient of urbanization that increases from the southern to northern portion of the bay's watershed were evaluated. Many studies of urbanization effects on estuarine fishes have focused on smaller spatial scales (Balouskus and Targett 2016; Gittman et al. 2016), yet studies at larger, watershed-wide scales are rare. Large scale studies such as this are important for investigating the potential manifestation of cumulative anthropogenic impacts (Peterson and Lowe 2009). This chapter is published in the *Journal of Coastal Research* (Valenti et al. 2017).

In Chapter IV, the influence of urbanization on a smaller, more local spatial scale was evaluated. The structural response of deep-water (>1 m) fish assemblages to shoreline armoring was assessed by comparing fish assemblages inhabiting unaltered marsh creeks to those within lagoon housing complexes. Between 36 – 45% of Barnegat Bay's shoreline is armored with bulkhead (Kennish 2001, Lathrop and Bognar 2001). Although many of the marsh creeks in Barnegat Bay have armored shorelines, the potential impact of these alterations on the local fish assemblages has not been studied. Additionally, although many studies have investigated the impacts of shoreline armoring on fish assemblages inhabiting intertidal and shallow subtidal (<1 m) waters (Peterson et

al. 2000; Balouskus and Targett 2016), little information is available about the impact on fishes in deeper-water habitat further from the shore.

References

- Able, K.W. 2005. A re-examination of fish estuarine dependence: Evidence for connectivity between estuarine and ocean habitats. *Estuarine, Coastal and Shelf Science* 64: 5–17.
- Able, K.W., P.C. López-Duarte, F.J. Fodrie, O.P. Jensen, C.W. Martin, B.J. Roberts, J. Valenti, K. O'Connor, and S.C. Halbert. 2015. Fish assemblages in Louisiana salt marshes: Effects of the Macondo oil spill. *Estuaries and Coasts* 38: 1385–1398.
- Able, K.W., J.P. Manderson, and A.L. Studholme. 1998. The distribution of shallow water juvenile fishes in an urban estuary: The effects of manmade structures in the lower Hudson River. *Estuaries* 21: 731–744.
- Able, K.W., J.P. Manderson, and A.L. Studholme. 1999. Habitat quality for shallow water fishes in an urban estuary: The effects of man-made structures on growth. *Marine Ecology Progress Series* 187: 227–235.
- Balouskus, R.G., and T.E. Targett. 2016. Fish and blue crab density along a riprap-sill-hardened shoreline: Comparisons with Spartina marsh and riprap. *Transactions of the American Fisheries Society* 145: 766–773.
- Beck, M.W., K.L. Heck., K.W. Able, D.L. Childers, D.B. Eggleston, B.M. Gillanders, B. Halpern, et al. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* 51: 633–641.
- Bilkovic, D.M., and M.M. Roggero. 2008. Effects of coastal development on nearshore estuarine nekton communities. *Marine Ecology Progress Series* 358: 27–39.
- Brown, L.R., M.B. Gregory, and J.T. May. 2009. Relation of urbanization to stream fish assemblages and species traits in nine metropolitan areas of the United States. *Urban Ecosystems* 12: 391–416.
- Colbert, A.J., B.J. Soden, G.A. Vecchi, and B.P. Kirtman. 2013. The impact of anthropogenic climate change on North Atlantic tropical cyclone tracks. *Journal of Climate* 26: 4088–4095.
- Costanza, R., R. D'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, et al. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260.
- Danila, D.J., C.B. Milstein, and Associates. 1979. Ecological studies for the Oyster Creek Generating Station, progress report for the period September 1977-August 1978: Finfish, shellfish, and plankton. Ithaca: Ichthyological Associates.

- Elliott, M., and V. Quintino. 2007. The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Marine Pollution Bulletin* 54: 640–645.
- Food and Agriculture Organization. 2018. The state of world fisheries and aquaculture 2018 - meeting the sustainable development goals. Rome: Food and Agriculture Organization. License: CC BY-NC-SA 3.0 IGO.
- Gittman, R.K., C.H. Peterson, C.A. Currin, F.J. Fodrie, M.F. Piehler, and J.F. Bruno. 2016. Living shorelines can enhance the nursery role of threatened estuarine habitats. *Ecological Applications* 26: 249–263.
- Grossmann, I., and M.G. Morgan. 2011. Tropical cyclones, climate change, and scientific uncertainty: What do we know, what does it mean, and what should be done? *Climatic Change* 108: 543–579.
- Hall-Scharf, B.J., T.S. Switzer, and C.D. Stallings. 2016. Ontogenetic and long-term diet shifts of a generalist juvenile predatory fish in an urban estuary undergoing dramatic changes in habitat availability. *Transactions of the American Fisheries Society* 145: 502–520.
- Halpern, B.S., S. Walbridge, K.A. Selkoe, C.V. Kappel, F. Micheli, C. D'Agrosa, J.F. Bruno, et al. 2008. A global map of human impact on marine ecosystems. *Science* 319: 948–952.
- Hendon, J.R., M.S. Peterson, and B.H. Comyns. 2000. Spatio-temporal distribution of larval *Gobiosoma bosc* in waters adjacent to natural and altered marsh-edge habitats of Mississippi coastal waters. *Bulletin of Marine Science* 66: 143–156.
- Hughes, R.M., S. Dunham, K.G. Maas-Hebner, J.A. Yeakley, C. Schreck, M. Harte, N. Molina, C.C. Shock, V.W. Kaczynski, and J. Schaeffer. 2014. A review of urban water body challenges and approaches: (1) Rehabilitation and remediation. *Fisheries* 39: 18–29.
- Hyndes, G.A., P. Francour, P. Guidetti, K.L. Heck, and G. Jenkins. 2018. The roles of seagrasses in structuring associated fish assemblages and fisheries. In *Seagrasses of Australia: Structure, ecology and conservation*, ed. A.W.D. Larkum, G.A. Kendrick, and P.J. Ralph, 589–627. Cham: Springer Nature.
- Izzo, C., Z.A. Doubleday, G.L. Grammer, K.L. Gilmore, H.K. Alleway, T.C. Barnes, M.C.F. Disspain, A.J. Giraldo, N. Mazloumi, and B.M. Gillanders. 2016. Fish as proxies of ecological and environmental change. *Reviews in Fish Biology and Fisheries* 26: 265–286.
- Jivoff, P., and K.W. Able. 2001. Characterization of the fish and selected decapods in Little Egg Harbor. *Journal of Coastal Research* 32: 178–196.
- Kauffman, G.J., and C. Cruz-Ortiz. 2012. Economic value of the Barnegat Bay watershed. Newark: University of Delaware.
- Kennish, M.J. 2001. Physical description of the Barnegat Bay-Little Egg Harbor estuarine system. *Journal of Coastal Research* 32: 13–27.

- Knutson, T.R., J.L. McBride, J. Chan, K. Emanuel, G. Holland, C. Landsea, I. Held, J.P. Kossin, A.K. Srivastava, and M. Sugi. 2010. Tropical cyclones and climate change. *Nature Geoscience* 3: 157–163.
- Lathrop, R.G., and J.A. Bognar. 2001. Habitat loss and alteration in the Barnegat Bay region. *Journal of Coastal Research* 32: 212–228.
- Lotze, H.K., H.S. Lenihan, B.J. Bourque, R.H. Bradbury, G. Cooke, M.C. Kay, S.M. Kidwell, M.X. Kirby, C.H. Peterson, and J.B.C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312: 1806–1809.
- Mann, M.E., and K.A. Emanuel. 2006. Atlantic Hurricane trends linked to climate change. *Eos, Transactions American Geophysical Union* 87: 233–235.
- Marcellus, K.L. 1972. Fishes of Barnegat Bay, New Jersey, with particular reference to seasonal influences and possible effects of thermal discharges. New Brunswick: Rutgers University.
- Minello, T.J., K.W. Able, M.P. Weinstein, and C.G. Hays. 2003. Salt marshes as nurseries for nekton: Testing hypothesis on density, growth and survival through meta-analysis. *Marine Ecology Progress Series* 246: 39–59.
- National Marine Fisheries Service. 2018. Fisheries economics of the United States, 2016. U.S. Department of Commerce, National Oceanic and Atmospheric Administration Technical Memo: NMFS-F/SPO-187.
- Nicholas, D., J. Lobry, M. Lepage, B. Sautour, O. Le Pape, H. Cabral, A. Uriarte, and P. Boët. 2010. Fish under influence: A macroecological analysis of relations between fish species richness and environmental gradients among European tidal estuaries. *Estuarine, Coastal and Shelf Science* 86: 137–147.
- Partyka, M.L., and M.S. Peterson. 2008. Habitat quality and salt-marsh species assemblages along an anthropogenic estuarine landscape. *Journal of Coastal Research* 24: 1570–1581.
- Pérez-Ruzafa, A., I.M. Pérez-Ruzafa, A. Newton, and C. Marcos. 2019. Coastal lagoons: Environmental variability, ecosystem complexity, and goods and services uniformity. In *Coasts and estuaries: The future*, ed. E. Wolanski, J.W. Day, M. Elliott, and R. Ramachandran, 253–276. Amsterdam: Elsevier.
- Peterson, M.S., B.H. Comyns, J.R. Hendon, P.J. Bond, and G.A. Duff. 2000. Habitat use by early life-history stages of fishes and crustaceans along a changing estuarine landscape: Differences between natural and altered shoreline sites. *Wetlands Ecology and Management* 8: 209–219.
- Peterson, M.S., and M.R. Lowe. 2009. Implications of cumulative impacts to estuarine and marine habitat quality for fish and invertebrate resources. *Reviews in Fisheries Science* 17: 505–523.
- Seilheimer, T.S., A. Wei, P. Chow-Fraser, and N. Eyles. 2007. Impact of urbanization on the water quality, fish habitat, and fish community of a Lake Ontario marsh,

- Frenchman's Bay. *Urban Ecosystems* 10: 299–319.
- Sugihara, T., C. Yearsley, J.B. Durand, and N.P. Psuty. 1979. Comparison of natural and altered estuarine systems: Analysis. New Brunswick: Center for Coastal and Environmental Studies.
- Tatham, T.R., D.J. Danila, and D.L. Thomas. 1984. Fishes of Barnegat Bay. In *Ecology of Barnegat Bay, New Jersey*, ed. M.J. Kennish and R.A. Lutz, 241–280. New York: Springer-Verlag.
- Tatham, T.R., D.J. Danila, D.L. Thomas, and Associates. 1977. Ecological studies for the Oyster Creek Generating Station: Volume one fin- and shellfish. Forked River: Ichthyological Associates.
- Valenti, J.L., T.M. Grothues, and K.W. Able. 2017. Estuarine fish communities along a spatial urbanization gradient. In: *A comprehensive assessment of Barnegat Bay–Little Egg Harbor, New Jersey*, ed. G.A. Buchanan, T.J. Belton, and B. Paudel, *Journal of Coastal Research* Special Issue No. 78: 254–268.
- Valenti, J.L., T.M. Grothues, and K.W. Able. 2020. Juvenile fish assemblage recruitment dynamics in a mid-Atlantic estuary: Before and after Hurricane Sandy. *Marine Ecology Progress Series* 641: 177–193.
- Voughlitois, J.J. 1983. The ichthyofauna of Barnegat Bay, New Jersey: Relationships between long-term temperature fluctuations and the population dynamics and life history of estuarine fishes during a five year period, 1976-1980. New Brunswick: Rutgers University.
- Voughlitois, 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. *Transactions of the American Fisheries Society* 116: 141–153.
- Walsh, K.J.E., J.L. McBride, P.J. Klotzbach, S. Balachandran, S.J. Camargo, G. Holland, T.R. Knutson, et al. 2016. Tropical cyclones and climate change. *Wiley Interdisciplinary Reviews: Climate Change* 7: 65–89.
- Wedge, M., C.J. Anderson, and D. DeVries. 2015. Evaluating the effects of urban land use on the condition of resident salt marsh fish. *Estuaries and Coasts* 38: 2355–2365.
- Whitehead, A., B. Dubansky, C. Bodinier, T.I. Garcia, S. Miles, C. Pilley, V. Raghunathan, et al. 2012. Genomic and physiological footprint of the Deepwater Horizon oil spill on resident marsh fishes. *Proceedings of the National Academy of Sciences* 109: 20298–20302.

CHAPTER I

Juvenile Fish Assemblage Recruitment Dynamics in a Mid-Atlantic Estuary: Before and After Hurricane Sandy

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Abstract

Hurricanes can have long-term effects on estuarine fauna. Understanding these effects is important as climate change may influence the severity and frequency of these storms. On 29 October 2012, Hurricane Sandy, a large storm spanning roughly 1850 km in diameter, made landfall in Brigantine, New Jersey (U.S.A.) approximately 20 km south of Barnegat Bay during an ongoing study of the bay's ichthyofauna, providing an opportunity to observe fish recruitment dynamics coincident with hurricane passage. The objective of this study was to measure variance in the Barnegat Bay pre-Sandy fish assemblage relative to that of one and two years after the storm. Barnegat Bay fishes were surveyed with an extensive otter trawl study in April, June, August, and October of

2012 (pre-Sandy), 2013 (one year post-Sandy), and 2014 (two years post-Sandy). Species composition of the fish assemblage was similar across years. Analyzed structural characteristics (abundance, diversity, richness) of the fish assemblage were occasionally more likely to occur or were larger pre-Sandy and two years post-Sandy relative to one year post-Sandy, but this trend was inconsistent across seasons and between structural characteristics. Furthermore, odds of occurrence and length frequency distributions for many resident species and sentinel fall/winter spawners did not indicate that variance could be definitively explained as a hurricane effect. The capability of fish to relocate from areas of temporarily unsuitable habitat and annual new recruitment of larvae and juveniles to the bay likely contributed to the observed stability in the fish assemblage.

Introduction

On 29 October 2012, Hurricane Sandy, also known as Post-tropical Cyclone Sandy and Superstorm Sandy, made landfall in Brigantine, New Jersey (U.S.A.). Prior to landfall, Hurricane Sandy transitioned to post-tropical cyclone status and drastically increased in size by merging with an early winter storm system – hence the ‘Superstorm’ designation (Halverson & Rabenhorst 2013, National Oceanic and Atmospheric Administration 2013). The immense diameter of the storm (1850 km) and eastward approach to the coastline, combined with a spring high tide, produced record breaking maximum water levels (Hall & Sobel 2013, Forbes et al. 2014) which surpassed two and a half meters in some New Jersey coastal bays (U.S. Geological Survey 2019) and resulted in multiple temporary breaches of the barrier islands (Blake et al. 2013, Parrish et al. 2016). The magnitude of this storm surge caused severe dune erosion (Coastal

Research Center 2012, Miselis et al. 2016), extensive damage to coastal property (Blake et al. 2013), and large quantities of natural and manmade debris to wash into coastal waters (Bilinski et al. 2015).

Episodic events, such as hurricanes, can have short-term and long-term effects on marine (Kaufman 1983, Fenner 1991, Heupel et al. 2003, Udyawer et al. 2013, Meléndez-Vazquez et al. 2019) and estuarine fauna (Boesch et al. 1976, Roman et al. 2005, Paperno et al. 2006, Stevens et al. 2006, Biggs et al. 2018, Massie et al. 2019). In the short-term aftermath of Hurricanes Agnes and Isabel, juvenile freshwater and estuarine fishes within the Chesapeake Bay and tributaries shifted downstream due to a large volume of freshwater inflow and subsequent reductions in salinity (Hoagman & Wilson 1977, Ritchie Jr. 1977, Houde et al. 2005). Following the passage of Hurricane Hugo, hypoxic conditions in the Ashley River and nearby marsh creeks (South Carolina) resulted in massive fish kills (Knott & Martore 1991). However, in Barnegat Bay (New Jersey) low salinity and dissolved oxygen (DO) conditions during and after the short duration of Hurricane Sandy were absent (Taghon et al. 2017) and qualitative observations immediately after the storm failed to identify population level impacts or instances of mass fish mortality (Bilinski et al. 2015). Delayed-onset, long-term hurricane effects on the fish assemblage dynamics in this estuarine system, emerging from the modification or destruction of essential habitat, alteration of estuarine larval supply, or a combination of these or other processes that have the potential to influence fish distributions over extended time scales, are unknown.

While previous observations of fish response to hurricane passage has been on the scale of days to weeks, interannual trends associated with these events are rarely

documented. Investigation of this time scale for estuaries is critical given that they serve as nursery habitat for ecologically and economically relevant fishes and invertebrates (McHugh 1976, Potter et al. 1990, Able & Fahay 1998, 2010, Beck et al. 2001, Wasserman & Strydom 2011, Tournois et al. 2017). Shallow lagoonal estuaries (e.g. Barnegat Bay) are particularly vulnerable to perturbations from episodic storm events, which often produce extensive storm surge, sediment deposition, and shoreline erosion (Kennish & Paerl 2010) and in turn may influence the recruitment of larval and juvenile fishes to these estuaries and resulting fish assemblages. Understanding the ecological impact of episodic tropical cyclones within lagoonal estuaries is becoming increasingly important as climate change may influence the severity, frequency, and path of these storms (Mann & Emanuel 2006, Knutson et al. 2010, Grossmann & Morgan 2011, Colbert et al. 2013, Walsh et al. 2016).

Given that controlled experiments on the effects of such large spatial scale disturbance events are nearly impossible to arrange, we capitalized on a unique opportunity to track structural characteristics (abundance, diversity, richness, composition) of the estuarine fish assemblage inhabiting Barnegat Bay through and beyond such an event as a baseline measure of assemblage variance and trajectory. In this we followed recommendations for an increased application of observational approaches to marine ecology by using generalized linear regression models to partition variance rather than testing significance (Bolker et al. 2009, Beninger et al. 2012, Boldina & Beninger 2016).

Methods

Study Area

Barnegat Bay is a shallow (mean water depth < 2 m) lagoon-type (Kennish & Paerl 2010, Whitfield & Elliott 2011) estuary that extends nearly 70 km along the coast of New Jersey (Fig. 1). The bay is directly connected to the Atlantic Ocean via the Little Egg and Barnegat inlets and indirectly connected to the ocean via the Point Pleasant Canal. The canal joins the northern bay and the Manasquan River, which ultimately drains into the ocean. Freshwater input to the system is dominated by tributaries located along the western shore of the bay (Kennish 2001). Throughout most of Barnegat Bay the water column is well mixed, but in deeper waters (e.g. the Intracoastal Waterway) two-layered flow is apparent (Chizmadia et al. 1984). The modeled estuarine residence time ranges from 0 – 50 days and is sensitive to wind speed, tides, time of year, and location within the bay (Defne & Ganju 2015).

Hurricane Sandy

On 29 October 2012, Hurricane Sandy made landfall less than 20 km from the southern end of Barnegat Bay (Fig. 1) (Halverson & Rabenhorst 2013, National Oceanic and Atmospheric Administration 2013). The landfall location and the storm's perpendicular approach to the coastline placed Barnegat Bay on the right side of the storm track where winds are often strongest (Hall & Sobel 2013, Halverson & Rabenhorst 2013), causing this region to be one of the most severely impacted by the storm (Bilinski et al. 2015).

Storm surge magnitude within the bay varied regionally with maximum recorded water levels reaching 2.1 m (relative to NAVD 88) in the northern bay, 1.7 m in the

central bay, and 2.0 m in the southern bay (U.S. Geological Survey 2019). These maximum water levels observed in Barnegat Bay during Sandy were comparable to observed tidal heights from previous storms that have impacted the New Jersey coastline (Able 2015, Psuty & Ofiara 2002). During the storm, a new inlet on the barrier island was temporarily formed at Mantoloking and closed by 4 November 2012 (Federal Emergency Management Agency 2013, Aretxabaleta et al. 2014). The ocean temporarily breached the barrier island at various other locations including at Holgate on the southernmost end of Long Beach Island (Bishop et al. 2016).

Sampling Protocol

Otter trawl sampling occurred in April (spring), June (early summer), August (late summer), and October (fall) in each of three years (2012 – 2014). October 2012 sampling was completed before Hurricane Sandy made landfall in New Jersey and the next sampling event following Hurricane Sandy was six months later in April of 2013. Therefore, 2012 represents pre-Sandy samples and 2013 and 2014 represent roughly six months to one year and one and a half to two years post-Sandy samples, respectively. For brevity, the 2013 and 2014 samples will be referred to as “one year post-Sandy” and “two years post-Sandy”, respectively.

Sampling consisted of three 120-second otter trawl net tows (4.9 m headrope, 19 mm mesh wings, 6.3 mm mesh codend liner) at each of 49 sites, spanning the length of the bay, during every sampling event (Fig. 1, Table 1). Trawls of this size selectively target smaller fishes (< 200 mm) (Olin & Malinen 2003), which in Barnegat Bay mainly encompasses juvenile fishes, but also includes species with smaller adult stages (Able &

Fahay 2010). Sampling sites were selected based on previous studies (e.g. Sugihara et al. 1979, Jivoff and Able 2001, Valenti et al. 2017) and reconnaissance sampling. From each tow all fishes were identified and counted, and the lengths (total or fork length in mm, depending on species) of the first 20 individuals of each species were recorded. Environmental parameters (water temperature, salinity, DO, pH) were measured (using a handheld Yellow Springs Instrument) and the water depth was recorded every time a site was sampled. Due to the immense size of the hurricane (spanned from Florida to Maine) (Forbes et al. 2014), control sites (i.e. those unaffected by the hurricane) were not available for inclusion in this study.

Data Analysis

Abundance

Overall Catch-per-unit-effort

Prior to analysis, the abundance data from the three replicate trawl tows at each site were combined, regardless of species, and standardized to overall catch-per-unit-effort (CPUE) (number fish s^{-1}). Only data on fish that could be identified to species were used in this and all other analyses in this study. Due to the large number of zero-catch sampling events in the data set (97 out of 578 events, i.e. 17%), a Bernoulli and gamma hurdle model, commonly referred to as the zero-altered gamma (ZAG) model, was fit to the overall CPUE data. This model assumes two processes govern the data; one determines if fish will be present or absent (i.e. $CPUE > 0$ or $CPUE = 0$) (Bernoulli part of the model) and the second influences the CPUE magnitude, given that fish are present (i.e. $CPUE > 0$) (gamma part of the model) (Zuur & Ieno 2016). For the Bernoulli part of

the model, the overall CPUE data were converted to presence or absence data and used as the response variable. For the gamma part of the model, only sampling observations with non-zero overall CPUE values were used for the response variable and all regression parameters had at least 20 observations (Zuur & Ieno 2016). Year and month were categorical covariates in both the Bernoulli and gamma models, but the interaction term was only included in the gamma model based on model selection using Akaike information criterion (AIC) (Burnham & Anderson 2004). A site random effect was included in both the Bernoulli and gamma models. The overall CPUE ZAG Generalized Linear Mixed Model (GLMM), and all other GLMMs in this study, were run using the lme4 package (version 1.1-21) (Bates et al. 2015) in RStudio (version 1.2.1335) (RStudio Team 2018). All other analyses in this study were also performed in RStudio.

Species-Specific Catch-per-unit-effort

In addition to overall CPUE, the species-specific CPUEs of the 12 most abundant species collected were analyzed. These 12 species were characterized based on their estuarine usage, year classes represented in the samples, and spawning duration. Since responses to hurricanes are variable, a consistent response from species with similar characteristics would assist in discerning hurricane effects from typical interannual variability. The species-specific CPUE data were converted to presence or absence data and used as the response variable in species-specific Bernoulli GLMMs. For all models, year and month were categorical covariates, site was included as a random effect, and the interaction term was not included based on model selection using AIC. Yearly length frequency plots, coded by month, were also created for these 12 species using ggplot2

(version 3.1.1) (Wickham 2016), gridExtra (version 2.3) (Auguie 2017), and gtable (version 0.3.0) (Wickham & Pedersen 2019).

Post-hoc analyses compared variables of interest in the overall CPUE hurdle model and species-specific CPUE models using the emmeans package (version 1.3.5) (Lenth 2019). Reported ratios and confidence limits from the Bernoulli and gamma GLMMs were back-transformed from the logit and log scales, respectively; however, Z-tests were performed on the logit and log scales (Bolker et al. 2009). Confidence intervals and p-values were adjusted for multiple comparisons using Tukey's honest significant difference method.

Diversity

The species-specific CPUE data were used to calculate Shannon diversity, with the vegan package (version 2.5-4) (Oksanen et al. 2019), for each sampling event that collected at least one individual (diversity values are only statistically defined for samples with one or more individuals) (Stevens 2009). This resulted in 481 observations that were used in the diversity analysis (97 out of 578 events collected no fish). Given the large number of zero diversity sampling events (i.e. those where only one species was collected) in the data set (96 out of 481 events, i.e. 20%), a ZAG model was fit to the diversity data. Like the CPUE model, this model assumes two processes govern the data; one determines if diversity will be present or absent (i.e. $\text{diversity} > 0$ or $\text{diversity} = 0$) (Bernoulli part of the model) and the second influences the magnitude of diversity, given that diversity is present (i.e. $\text{diversity} > 0$) (gamma part of the model). For the Bernoulli part of the model, the diversity data were converted to presence or absence data and used

as the response variable. For the gamma part of the model, only sampling observations with non-zero diversity values were used for the response variable and all regression parameters had at least 13 observations. For both parts of the model, year, month, and the interaction term were categorical covariates and site was included as a random effect.

Richness

Richness, the number of species collected, was also assessed as an indicator of assemblage biodiversity. Richness was standardized by totaling the number of different species collected in the replicate trawl tows at each site and dividing by the number of tows performed (number species collected tow⁻¹). Due to the large number of zero-catch sampling events in the data set (17%), a ZAG model was fit to the standardized richness data in the same manner as for CPUE and diversity. For the gamma part of the model, all regression parameters had at least 20 observations. Year and month were categorical covariates in both the Bernoulli and gamma models, but the interaction term was only included in the gamma model based on model selection using AIC. A site random effect was included in both the Bernoulli and gamma models. Post-hoc analyses compared variables of interest in the diversity and richness models following the protocol previously described for the CPUE models.

Assemblage Composition

Non-metric multidimensional scaling (NMDS), a robust, unconstrained ordination technique (Minchin 1987), was used to visualize latent dissimilarities in assemblage composition across the years and months sampled. The abundance data from sites with

the same habitat characteristics sampled within the same year and month were combined and standardized to CPUE resulting in 48 sampling observations. These CPUE values were then root-root transformed and dissimilarities were calculated on the Bray-Curtis index and projected as NMDS with the vegan package. An interpretable, convergent NMDS solution was reached using three dimensions (i.e. $k = 3$) (Clarke 1993) and the results of the first two dimensions were displayed as sample and species plots. The axes in the sample plot were centered, rotated so the variance of the observations was maximized along the first axis, and scaled so that one unit change indicates a halving of assemblage similarity between sampling observations. Species locations in the species plot are weighted averages based on the CPUE data.

Results

Environmental Parameters

The measured environmental parameters were fairly consistent across years and seasons, with the exception of seasonal shifts in water temperature and DO (Table 1). Water temperature increased from April to August and began to decrease in October. DO followed the opposite trend, decreasing from April to August and increasing slightly in October.

Abundance

Overall Catch-per-unit-effort

Nearly 34,000 fish were collected during the three years of sampling. Over 50% of those individuals were caught during 2014 and nearly 85% were captured during the

late summer and fall months of all years (Table 2). The odds of collecting fish in any given trawl tow (CPUE occurrence odds) ranged from roughly equal to slightly higher pre-Sandy (2012) than one year post-Sandy (2013) (Odds Ratio [OR] = 1.881, 95% Confidence Interval [CI]: 0.946 – 3.740, $p = 0.079$) and were consistently lower one year post-Sandy relative to two years post-Sandy (2014) (OR = 0.342, CI: 0.164 – 0.714, $p = 0.002$) (Table S1). CPUE occurrence odds pre-Sandy compared to two years post-Sandy were variable and showed no consistent trend (OR = 0.643, CI: 0.296 – 1.396, $p = 0.376$).

Within the month of April, CPUE was larger pre-Sandy compared to one year post-Sandy (Ratio [R] = 3.526, CI: 1.507 – 8.250, $p = 0.002$) or two years post-Sandy (R = 2.837, CI: 1.340 – 6.008, $p = 0.003$) (Table S1). Comparison of April CPUE values between one year post-Sandy and two years post-Sandy yielded no definitive trend between years (R = 0.805, CI: 0.361 – 1.793, $p = 0.800$). The June CPUE values for pre-Sandy ($p < 0.001$) and two years post-Sandy ($p < 0.001$) were consistently larger than one year post-Sandy CPUE values. In August, one year post-Sandy CPUE was smaller than the CPUE two years post-Sandy (R = 0.502, CI: 0.271 – 0.931, $p = 0.024$). Two years post-Sandy October CPUE was notably larger relative to pre-Sandy ($p < 0.001$) or one year post-Sandy CPUE ($p < 0.001$). No trend was observed in the October pre-Sandy and one year post-Sandy CPUE comparison (R = 1.572, CI: 0.804 – 3.073, $p = 0.253$) (Table S1).

Species-Specific Catch-per-unit-effort

The 12 most abundant species collected accounted for 97% of the total catch. Bay anchovy *Anchoa mitchilli* was the most abundant species collected overall, accounting for

approximately 57% of the total catch and dominating catches in every year, regardless of month, with the exception of April 2013 and April 2014 when Atlantic herring *Clupea harengus* and naked goby *Gobiosoma bosc* were the most abundant species collected, respectively. After *A. mitchilli*, Atlantic silverside *Menidia menidia* (17%), fourspine stickleback *Apeltes quadracus* (6%), and northern pipefish *Syngnathus fuscus* (4%) were the next most abundant species collected (Table 3).

No consistent trends in annual CPUE occurrence odds were observed for species with similar estuarine usage, year classes represented, or spawning durations (Table 4). Young-of-year (YOY) were collected for all of the twelve most abundant species and most of these species had odds of occurrence that were influenced by year; although the odds of occurrence for *A. mitchilli* and Atlantic menhaden *Brevoortia tyrannus* were fairly uniform across years. *G. bosc*, *M. menidia*, Atlantic croaker *Micropogonias undulatus*, oyster toadfish *Opsanus tau*, summer flounder *Paralichthys dentatus*, and winter flounder *Pseudopleuronectes americanus* had higher CPUE occurrence odds two years post-Sandy (2014) relative to pre-Sandy (2012) or one year post-Sandy (2013) and inconsistent CPUE occurrence odds pre-Sandy relative to one year post-Sandy. The odds of occurrence for *A. quadracus* and silver perch *Bairdiella chrysoura* were higher pre-Sandy and two years post-Sandy compared to one year post-Sandy with no consistent trend between pre-Sandy and two years post-Sandy odds. Spot *Leiostomus xanthurus* and *S. fuscus* CPUE occurrence odds varied for all years, with the exception of *L. xanthurus* odds one year post-Sandy compared to two years post-Sandy (Table 4). Trends in seasonal CPUE occurrence odds were observed for many species, but these trends varied

for species with similar estuarine usage, year classes represented, and spawning durations (Table S2).

No consistent patterns in annual length frequency distributions were observed for species characterized as estuarine residents or transients or species with similar year classes represented or spawning duration (Fig. 2, 3, & 4). For *G. bosc*, *A. mitchilli*, *P. dentatus*, and *S. fuscus*, length frequency distribution patterns were similar among years (Fig. 2B, 3A, 3D, & 4D, respectively). One year post-Sandy *A. quadracus* CPUE was low relative to pre-Sandy and two years post-Sandy abundances, especially in August and October when no individuals were collected (Table 3); this absence of individuals is reflected in the punctuated length frequency distribution one year post-Sandy (Fig. 2A). *O. tau* and *P. americanus* less than 50 mm were absent or less abundant pre-Sandy and one year post-Sandy compared to two years post-Sandy (Fig. 2C & D, respectively). Individuals of *B. chrysoura* larger than 90 mm were rare in one year post-Sandy samples (Fig. 3B). Although *M. undulatus* was most abundant two years post-Sandy (Table 3), individuals larger than 60 mm, which were collected pre-Sandy and one year post-Sandy in August and October, were absent (Fig. 3C). *B. tyrannus* length frequency distributions were fairly similar across years, but individuals smaller than 35 mm were absent pre-Sandy while individuals larger than 130 mm were absent two years post-Sandy (Fig. 4A). *L. xanthurus* had highly variable length frequency distributions among years (Fig. 4B). Length frequency distributions for *M. menidia* one year post-Sandy and two years post-Sandy were similar; however, in pre-Sandy samples, individuals less than 30 mm were absent (Fig. 4C).

Diversity

The odds of observing diversity (diversity occurrence odds) did not vary annually within April or June, but did vary annually in August and October (Table S3). In August and October, the odds of diversity occurrence were consistently higher pre-Sandy (2012) and two years post-Sandy (2014) compared to one year post-Sandy (2013). No trend was observed when pre-Sandy and two years post-Sandy August diversity occurrence odds were compared (OR = 1.956, CI: 0.241 – 15.876, $p = 0.733$). In October, diversity occurrence odds ranged from much lower to roughly equal pre-Sandy (2012) relative to two years post-Sandy (OR = 0.086, CI: 0.007 – 1.097, $p = 0.062$). The magnitude of diversity observed did not vary annually within April, June, or October, but varied annually in August where diversity was larger pre-Sandy ($p = 0.012$) and two years post-Sandy ($p = 0.001$) compared to one year post-Sandy (Table S3).

Richness

Collections included individuals of 72 different species (Table 3) with the highest richness occurring in the months of August and October (Table 2). In each year there were a number of unique species collected (i.e. those only collected in that year). Five unique species were collected pre-Sandy. One year post-Sandy and two years post-Sandy five and fourteen unique species were collected, respectively (Table 3).

Due to the nature of presence and absence data, the odds of observing richness (richness occurrence odds) in any given trawl tow (Table S4) are identical to the CPUE occurrence odds, which were previously described in the “Overall Catch-per-unit-effort” section and therefore the results are not repeated here. The magnitude of the observed

richness varied annually within all months except April (Table S4). In June and October, richness was smaller pre-Sandy and one year post-Sandy relative to two years post-Sandy; however, in June there was no consistent trend in richness for the pre-Sandy and one year post-Sandy comparison ($R = 1.020$, CI: $0.779 - 1.335$, $p = 0.984$), whereas in October pre-Sandy richness was larger than one year post-Sandy richness ($R = 1.387$, CI: $1.052 - 1.827$, $p = 0.015$). August richness was consistently smaller one year post-Sandy compared to pre-Sandy ($p < 0.001$) or two years post-Sandy ($p < 0.001$), with no consistent trend between pre-Sandy or two years post-Sandy richness ($R = 0.833$, CI: $0.645 - 1.075$, $p = 0.213$) (Table S4).

Assemblage Composition

The fish fauna inhabiting Barnegat Bay encompassed various estuarine resident (e.g. *G. bosc*) and transient (e.g. *P. dentatus*) species and included southern stray (e.g. crevalle jack *Caranx hippos*) and shelf stray (e.g. butterfish *Peprilus triacanthus*) species (Table 3). The first two axes of the NMDS analysis indicated overall similarity in annual assemblage composition, with only slight separation of 2014 samples (two years post-Sandy) from 2012 (pre-Sandy) and 2013 (one year post-Sandy) samples along the second axis; however, seasonal shifts in assemblage composition were evident along the first axis (Fig. 5). The third axis did not add any additional information to the interpretation and therefore is not discussed.

Discussion

Recruitment dynamics of the fish assemblage inhabiting Barnegat Bay, as measured by select structural characteristics (CPUE, diversity, richness, composition), remained relatively stable over a three year period encompassing the large episodic disturbance of Hurricane Sandy. Although the analyzed structural characteristics occasionally had higher odds of occurrence or were larger pre-Sandy (2012) and two years post-Sandy (2014) relative to one year post-Sandy (2013), this trend was not consistent across seasons or between structural characteristics making it difficult to attribute these differences in assemblage dynamics solely to Hurricane Sandy. However, Meléndez-Vazquez et al. (2019) documented a similar high-low-high or “boomerang” pattern in fish assemblage dynamics following Hurricane Maria, suggesting that the interannual trends observed in this study may be in part related to hurricane passage, although this is challenging to conclude, especially given that the ecological mechanism driving this disturbance induced “boomerang” pattern is unknown (Miller et al. 2011, Hall et al. 2012, Fox 2013). The apparent absence of a pronounced hurricane effect one to two years after the event was also evident in the Barnegat Bay benthic community. Comparison of the benthic community three and a half months prior and eight months after Sandy yielded minimal noticeable differences in benthic community dynamics (Taghon et al. 2017). This is particularly relevant because many fish species collected in this study rely on benthic food sources (Festa 1979).

The absence of a pronounced hurricane effect and the observed stability in fish assemblage dynamics likely emerged from many interacting factors. Estuaries worldwide are known for supporting relatively stable fish assemblages; although species abundances may fluctuate annually, species composition is fairly consistent across years (Jackson &

Jones 1999, Garcia et al. 2001, Griffiths 2001, James et al. 2008). Annual stability in species composition has been observed for fish larval supply to Barnegat Bay (Witting et al. 1999, Able et al. 2017) and in the juvenile fish assemblage inhabiting the bay (this study). The inherent stability of the Barnegat Bay fish assemblage may help diminish the potential for structural changes to the fish assemblage, external to typical interannual variability, following episodic storm events, such as Hurricane Sandy.

Further, fish are often capable of relocating from areas of unsuitable habitat, and have been documented doing so in reference to changes in salinity, DO, and barometric pressure caused by storms (Heupel et al. 2003, Houde et al. 2005, Udyawer et al. 2013, Massie et al. 2019), as seen for summer flounder *Paralichthys dentatus* in adjacent Great Bay (Sackett et al. 2007). In some cases this relocation can occur for prolonged periods of time until water quality approximates pre-storm conditions (Knott & Martore 1991). In Barnegat Bay, although temporary movements and distribution shifts of fishes in the days immediately following the storm probably occurred, the absence of low salinity and DO conditions during and after Hurricane Sandy (Taghon et al. 2017), and the well-mixed nature of this shallow lagoonal estuary (Chizmadia et al. 1984, Defne & Ganju 2015), likely precluded any prolonged distribution shifts related to alterations in water quality. Moreover, the fact that Sandy occurred during the fall, in a period of declining temperature, made it less likely that abrupt changes in temperature and low DO could occur.

This lack of a shift in salinity and DO following Hurricane Sandy contrasts with observations following hurricanes that impacted other U.S. east coast lagoonal estuaries. Pamlico Sound (North Carolina), the largest lagoonal estuary in the United States (Paerl

et al. 2006), has been affected by a multitude of hurricanes over the past few decades, with many storms resulting in salinity and DO shifts that consequently affected fish assemblages (Paerl et al. 2001, Adams et al. 2003, Burkholder et al. 2004). Potential drivers of the differing hurricane responses between these two lagoonal estuaries include the timing of the storms and larger freshwater influence, greater water depths on average, and a longer residence time in Pamlico Sound compared to Barnegat Bay (Paerl et al. 2001, Paerl et al. 2010). Great South Bay (New York) was also impacted by Hurricane Sandy, resulting in a permanently open breach through Fire Island (Aretxabaleta et al. 2014). This increased connectivity between Great South Bay and the ocean has resulted in altered water quality parameters and fish assemblage dynamics (Tinoco 2017, Olin et al. 2019). The differing hurricane effects in these studies suggest that estuarine and faunal responses to hurricanes are highly variable and depend heavily on the storm (e.g. path, wind speeds), estuary (e.g. freshwater input, potential for barrier island breaches), and watershed (e.g. urban versus rural) characteristics (Mallin & Corbett 2006).

In addition to intermittent movements related to habitat quality, many of the fishes inhabiting Barnegat Bay also undergo annual seasonal migrations (as observed in this study), entering or recruiting as larvae to the estuary as the water warms during the spring and leaving as the water cools in the fall (Able & Fahay 2010). Since Hurricane Sandy made landfall late in October, many estuarine transient species had likely already migrated into the ocean, reducing the number of individuals enduring the full force of the storm while confined to this extremely shallow, estuarine habitat. However, estuarine resident species (e.g. naked goby *Gobiosoma bosc*, oyster toadfish *Opsanus tau*, winter flounder *Pseudopleuronectes americanus*) did not appear differentially affected by the

storm compared to estuarine transients (e.g. Atlantic silverside *Menidia menidia*, northern pipefish *Syngnathus fuscus*), potentially due to the inherent adaptability of estuarine species to environmental perturbations (Elliott & Quintino 2007).

Although many transient species likely migrated from the estuary, in a seasonal pattern (Able & Fahay 2010), prior to the storm, hurricanes have the potential to influence estuarine larval supply by temporarily altering hydrodynamics (Hoagman & Merriner 1977), as was observed for New Jersey coastal ocean circulation during Sandy (Miles et al. 2017), which could result in subsequent recruitment effects. With regards to Hurricane Sandy, larval supply of species that spawn in fall/early winter, such as the estuarine transients bay anchovy *Anchoa mitchilli*, Atlantic menhaden *Brevoortia tyrannus*, spot *Leiostomus xanthurus*, Atlantic croaker *Micropogonias undulatus*, and *P. dentatus* (Able & Fahay 1998, Able & Fahay 2010), were most likely to be affected by the storm. However, abundances of larvae in Barnegat Bay typically exhibit some interannual variation (Witting et al. 1999, Able et al. 2017) and hurricane induced alterations in larval supply do not necessarily directly translate to observable changes in juvenile recruitment, at least not in the larger Chesapeake Bay (Montane et al. 2005). Effects of Hurricane Sandy on *A. mitchilli*, *B. tyrannus*, *M. undulatus*, and *P. dentatus* recruitment dynamics were not evident as YOY of these species were present in samples one year post-Sandy, and CPUE occurrence odds and length frequency distributions for these species one year post-Sandy relative to pre-Sandy and two years post-Sandy did not indicate the existence of a defined hurricane effect. *L. xanthurus* had variable yearly length frequency distributions and higher CPUE occurrence odds pre-Sandy relative to one and two years post-Sandy, but large annual fluctuations in *L. xanthurus* larval and

juvenile abundances within New Jersey estuaries is normal (Able & Fahay 1998, Able & Fahay 2010, Able et al. 2017).

Silver perch *Bairdiella chrysoura* and fourspine stickleback *Apeltes quadracus* had lower odds of occurrence one year post-Sandy compared to pre-Sandy and two years post-Sandy. Similarly to *L. xanthurus*, *B. chrysoura* exhibit large annual fluctuations in larval (Able & Fahay 1998, Able et al. 2017) and juvenile (Able & Fahay 2010) abundances within New Jersey estuaries, so the lower odds of occurrence observed one year post-Sandy may not be attributable to the hurricane. *A. quadracus* are estuarine residents that spawn in the late spring/early summer (Able & Fahay 2010); the cause of the lower CPUE occurrence odds one year post-Sandy compared to pre-Sandy and two years post-Sandy is unclear.

The ability to discern temporal trends in species and assemblage dynamics is hindered by a general lack of studies encompassing prolonged time scales (Magurran et al. 2010). This lack of long-term data becomes problematic when trying to discern the influence of anthropogenic impacts or episodic events, such as hurricanes, from natural annual variation in fish dynamics (Desmond et al. 2002, Houde et al. 2005, Magurran et al. 2010, Izzo et al. 2016). Although the time series analyzed in this study spanned one year pre-Sandy to two years post-Sandy, interannual variability in recruitment dynamics occurs without hurricane influences, making it difficult to discern long-term hurricane effects from interannual variation. A long-term monitoring program would have assisted in putting the observed “highs” and “lows” in perspective, as was done by Greenwood et al. (2006). The utility of long-term time series in attempting to understand the complex dynamics of the natural world has been stressed in the past (Callahan 1984, Franklin

1989, Cody 1996) and in more recent years (Hobbie et al. 2003, Magurran et al. 2010, Lindenmayer et al. 2012, Able 2016) and will continue to be important for understanding effects of episodic events, such as hurricanes, especially in the face of climate change which may drastically alter processes driving observed phenomena (Walther et al. 2002, Colbert et al. 2013, Walsh et al. 2016).

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References

Able KW (2015) Storms, fires, and ghosts. In: From lifesaving to marine research: Station 119. Down the Shore Publishing, West Creek, p 35–44

- Able KW (2016) Natural history: an approach whose time has come, passed, and needs to be resurrected. *ICES J Mar Sci* 73:2150–2155
- Able KW, Fahay MP (1998) The first year in the life of estuarine fishes in the Middle Atlantic Bight. Rutgers University Press, New Brunswick
- Able KW, Fahay MP (2010) Ecology of estuarine fishes: temperate waters of the western north Atlantic. Johns Hopkins University Press, Baltimore
- Able KW, Valenti JL, Grothues TM (2017) Fish larval supply to and within a lagoonal estuary: multiple sources for Barnegat Bay, New Jersey. *Environ Biol Fishes* 100:663–683
- Adams SM, Greeley MS, Law JM, Noga EJ, Zelikoff JT (2003) Application of multiple sublethal stress indicators to assess the health of fish in Pamlico Sound following extensive flooding. *Estuaries* 26:1365–1382
- Aretxabaleta AL, Butman B, Ganju NK (2014) Water level response in back-barrier bays unchanged following Hurricane Sandy. *Geophys Res Lett* 41:3163–3171
- Auguie B (2017) GridExtra: miscellaneous functions for ‘Grid’ graphics. cran.r-project.org/package=gridExtra
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- Beck MW, Heck Jr. KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51:633–641
- Beninger PG, Boldina I, Katsanevakis S (2012) Strengthening statistical usage in marine ecology. *J Exp Mar Biol Ecol* 426–427: 97–108
- Biggs CR, Lowerre-Barbieri SK, Erisman B (2018) Reproductive resilience of an estuarine fish in the eye of a hurricane. *Biol Lett* 14:1–5
- Bilinski J, Buchanan G, Frizzera D, Hazen R, Lippincott L, Procopio N, Ruppel B, Tucker T (2015) Damage assessment report on the effects of Hurricane Sandy on the state of New Jersey’s natural resources: final report. New Jersey Department of Environmental Protection Office of Science
- Bishop JM, Richmond BM, Zaremba NJ, Lunghino BD, Kane HH (2016) Hurricane Sandy washover deposits on southern Long Beach Island, New Jersey. U.S. Geological Survey Open-File Report 2016–1090
- Blake ES, Kimberlain TB, Berg RJ, Cangialosi JP, Beven II JL (2013) Tropical Cyclone

- Report: Hurricane Sandy (AL182012) 22 – 29 October 2012. National Hurricane Center
- Boesch DF, Diaz RJ, Virnstein RW (1976) Effects of Tropical Storm Agnes on soft-bottom macrobenthic communities of the James and York estuaries and the lower Chesapeake Bay. *Chesap Sci* 17:246–259
- Boldina I, Beninger PG (2016) Strengthening statistical usage in marine ecology: linear regression. *J Exp Mar Biol Ecol* 474: 81–91
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135
- Burkholder J, Eggleston D, Glasgow H, Brownie C, Reed R, Janowitz G, Posey M, Melia G, Kinder C, Corbett R, Toms D, Alphin T, Deamer N, Springer J (2004) Comparative impacts of two major hurricane seasons on the Neuse River and western Pamlico Sound ecosystems. *Proc Natl Acad Sci* 101:9291-9296
- Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociol Methods Res* 33:261–304
- Callahan JT (1984) Long-term ecological research. *Bioscience* 34:363–367
- Chizmadia PA, Kennish MJ, Ohori VL (1984) Physical description of Barnegat Bay. In: Kennish MJ, Lutz, RA (eds) Barber RT, Bowman M, Mooers CNK, Zeitzschel (series eds) *Lecture notes on coastal and estuarine studies: ecology of Barnegat Bay*, New Jersey. Springer Verlag, New York, p 1–28
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143
- Coastal Research Center (2012) Beach-dune performance assessment of New Jersey beach profile network (NJBPN) sites at Northern Ocean County, New Jersey after Hurricane Sandy related to FEMA disaster DR-NJ 4086. Coastal Research Center Report
- Cody ML (1996) Introduction to long-term community ecological studies. In: Cody ML, Smallwood JA (eds) *Long-term studies of vertebrate communities*. Academic Press, San Diego
- Colbert AJ, Soden BJ, Vecchi GA, Kirtman BP (2013) The impact of anthropogenic climate change on North Atlantic tropical cyclone tracks. *J Clim* 26:4088–4095
- Defne Z, Ganju NK (2015) Quantifying the residence time and flushing characteristics of a shallow, back-barrier estuary: application of hydrodynamic and particle tracking

- models. *Estuar Coasts* 38:1719–1734
- Desmond JS, Deutschman DH, Zedler JB (2002) Spatial and temporal variation in estuarine fish and invertebrate assemblages : analysis of an 11 -year data set. *Estuaries* 25:552–569
- Elliott, M, Quintino V (2007) The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Mar Pollut Bull* 54:640–645
- Federal Emergency Management Agency (2013) Hurricane Sandy in New Jersey and New York: building performance observations, recommendations, and technical guidance. Mitigation Assessment Team Report FEMA P-942
- Fenner DP (1991) Effects of Hurricane Gilbert on coral reefs, fishes and sponges at Cozumel, Mexico. *Bull Mar Sci* 48:719–730
- Festa PJ (1979) Analysis of the fish forage base in the Little Egg Harbor Estuary. New Jersey Department of Environmental Protection Report
- Forbes C, Rhome J, Mattocks C, Taylor A (2014) Predicting the storm surge threat of Hurricane Sandy with the National Weather Service SLOSH Model. *J Mar Sci Eng* 2:437–476
- Fox JW (2013) The intermediate disturbance hypothesis should be abandoned. *Trends Ecol Evol* 28:86–92
- Franklin JF (1989) Importance and justification of long-term studies in ecology. In: Likens G (ed) *Long-term studies in ecology: approaches and alternatives*. Springer, New York, p 3–19
- Garcia AM, Vieira JP, Winemiller KO (2001) Dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil) during cold and warm ENSO episodes. *J Fish Biol* 59:1218–1238
- Greenwood MFD, Stevens PW, Matheson RE (2006) Effects of the 2004 hurricanes on the fish assemblages in two proximate southwest Florida estuaries: change in the context of interannual variability. *Estuar Coasts* 29:985–996
- Griffiths SP (2001) Factors influencing fish composition in an Australian intermittently open estuary: is stability salinity-dependent?. *Estuar Coast Shelf Sci* 52:739–751
- Grossmann I, Morgan MG (2011) Tropical cyclones, climate change, and scientific uncertainty: what do we know, what does it mean, and what should be done? *Clim Change* 108:543–579
- Hall AR, Miller AD, Leggett HC, Roxburgh SH, Buckling A, Shea K (2012) Diversity–

- disturbance relationships: frequency and intensity interact. *Biol Lett* 8:768–771
- Hall TM, Sobel AH (2013) On the impact angle of Hurricane Sandy's New Jersey landfall. *Geophys Res Lett* 40:2312–2315
- Halverson JB, Rabenhorst T (2013) Hurricane Sandy: the science and impacts of a superstorm. *Weatherwise* 66:14–23
- Heupel MR, Simpfendorfer CA, Hueter RE (2003) Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle. *J Fish Biol* 63:1357–1363
- Hoagman WJ, Merriner JV (1977) The displacement and loss of larval fishes from the Rappahannock and James Rivers, Virginia, following a major tropical storm. In: Ruzecki EP, Schubel JR, Huggett RJ, Anderson AM, Wass ML, Marasco RJ, Lynch MP (eds) *The effects of Tropical Storm Agnes on the Chesapeake Bay estuarine system*. The Johns Hopkins University Press, Baltimore, p 591–593
- Hoagman WJ, Wilson WL (1977) The effects of Tropical Storm Agnes on fishes in the James, York, and Rappahannock Rivers of Virginia. In: Ruzecki EP, Schubel JR, Huggett RJ, Anderson AM, Wass ML, Marasco RJ, Lynch MP (eds) *The effects of Tropical Storm Agnes on the Chesapeake Bay estuarine system*. The Johns Hopkins University Press, Baltimore, p 464–473
- Hobbie JE, Carpenter SR, Grimm NB, Gosz JR, Seastedt TR (2003) The US Long Term Ecological Research Program. *Bioscience* 53:21–32
- Houde ED, Bichy J, Jung S (2005) Effects of Hurricane Isabel on fish populations and communities in Chesapeake Bay. In: Sellner KG (ed) *Hurricane Isabel in perspective*. Chesapeake Research Consortium Publication 05-160, Edgewater, p 193–199
- Izzo C, Doubleday ZA, Grammer GL, Gilmore KL, Alleway HK, Barnes TC, Disspain MCF, Giraldo AJ, Mazloumi N, Gillanders BM (2016) Fish as proxies of ecological and environmental change. *Rev Fish Biol Fish* 26:265–286
- Jackson G, Jones GK (1999) Spatial and temporal variation in nearshore fish and macroinvertebrate assemblages from a temperate Australian estuary over a decade. *Mar Ecol Prog Ser* 182:253–286
- James NC, Whitfield AK, Cowley PD (2008) Long-term stability of the fish assemblages in a warm-temperate South African estuary. *Estuar Coast Shelf Sci* 76:723–738
- Jivoff P, Able KW (2001) Characterization of the fish and selected decapods in Little Egg Harbor. *J Coast Res* 17:178–196

- Kaufman LS (1983) Effects of Hurricane Allen on reef fish assemblages near Discovery Bay, Jamaica. *Coral Reefs* 2:43–47
- Kennish MJ (2001) Physical description of the Barnegat Bay-Little Egg Harbor estuarine system. *J Coast Res SI* 32:13–27
- Kennish MJ, Lutz RA (1984) Ecology of Barnegat Bay. In: Barber RT, Bowman M, Mooers CNK, Zeitzschel (series eds) *Lecture notes on coastal and estuarine studies*. Springer Verlag, New York
- Kennish MJ, Paerl HW (2010) Coastal lagoons: critical habitats of environmental change. In: Kennish MJ, Paerl HW (eds) *Coastal lagoons: critical habitats of environmental change*. CRC Press, Boca Raton, p 1–16
- Knott DM, Martore RM (1991) The short-term effects of Hurricane Hugo on fishes and decapod crustaceans in the Ashley River and adjacent marsh creeks, South Carolina. *J Coast Res SI* 8:335–356
- Knutson TR, McBride JL, Chan J, Emanuel K, Holland G, Landsea C, Held I, Kossin JP, Srivastava AK, Sugi M (2010) Tropical cyclones and climate change. *Nat Geosci* 3:157–163
- Lenth R (2019) Emmeans: estimated marginal means, aka least-squares means. cran.r-project.org/package=emmeans
- Lindenmayer DB, Likens GE, Andersen A, Bowman D, Bull CM, Burns E, Dickman CR, Hoffmann AA, Keith DA, Liddell MJ, Lowe AJ, Metcalfe DJ, Phinn SR, Russell-Smith J, Thurgate N, Wardle GM (2012) Value of long-term ecological studies. *Austral Ecol* 37:745–757
- Magurran AE, Baillie SR, Buckland ST, Dick JM, Elston DA, Scott EM, Smith RI, Somerfield PJ, Watt AD (2010) Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends Ecol Evol* 25:574–582
- Mallin MA, Corbett CA (2006) How hurricane attributes determine the extent of environmental effects: multiple hurricanes and different coastal systems. *Estuar Coasts* 29:1046–1061
- Mann ME, Emanuel KA (2006) Atlantic hurricane trends linked to climate change. *Eos Trans AGU* 87:233–244
- Massie JA, Strickland BA, Santos RO, Hernandez J, Viadero N, Boucek RE, Willoughby H, Heithaus MR, Rehage JS (2019) Going downriver: patterns and cues in hurricane-driven movements of common snook in a subtropical coastal river. *Estuar Coasts*. DOI: <https://doi.org/10.1007/s12237-019-00617-y>

- McHugh JL (1976) Estuarine fisheries: are they doomed? In: Wiley M (ed) Estuarine processes: uses, stresses, and adaptation to the estuary. Academic Press, New York, p 15–27
- Meléndez-Vazquez F, Olmeda-Saldaña M, Cruz J, Arcila D, Betancur R (2019) Effects of Hurricane Maria in hamlet communities (Serranidae: *Hypoplectrus spp.*) in Puerto Rico. *Ecol Indic* 107:1–4
- Miles T, Seroka G, Glenn S (2017) Coastal ocean circulation during Hurricane Sandy. *J Geophys Res, C, Oceans* 122:7095–7114
- Miller AD, Roxburgh SH, Shea K (2011) How frequency and intensity shape diversity–disturbance relationships. *Proc Natl Acad Sci* 108:5643–5648
- Minchin PR (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69:89–107
- Miselis JL, Andrews BD, Nicholson RS, Defne Z, Ganju NK, Navoy A (2016) Evolution of Mid-Atlantic coastal and back-barrier estuary environments in response to a hurricane: implications for barrier-estuary connectivity. *Estuar Coasts* 39:916–934.
- Montane MM, Austin HM (2005) Effects of hurricanes on Atlantic croaker (*Micropogonias undulatus*) recruitment to Chesapeake Bay. In: Sellner KG (ed) Hurricane Isabel in perspective. Chesapeake Research Consortium Publication 05-160, Edgewater, p 185–192
- National Oceanic and Atmospheric Administration (2013) Hurricane/post-tropical cyclone Sandy, October 22 – 29, 2012. U.S. Department of Commerce, Silver Spring
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2019) Vegan: community ecology package. cran.r-project.org/package=vegan
- Olin JA, Cerrato RM, Nye JA, Sagarese SR, Sclafani M, Zacharias JP, Frisk MG (2019) Evidence for ecosystem changes within a temperate lagoon following a hurricane-induced barrier island breach. *Estuar Coasts* :1–15
- Olin M, Malinen T (2003) Comparison of gillnet and trawl in diurnal fish community sampling. *Hydrobiologia* 506–509:443–449
- Paerl HW, Christian RR, Bales JD, Peierls BL, Hall NS, Joyner AR, Riggs SR (2010) Assessing the response of the Pamlico Sound, North Carolina, USA to human and climatic disturbances: management implications. In: Kennish MJ, Paerl HW (eds) Coastal lagoons: critical habitats of environmental change. CRC Press, Boca Raton, p 17–42

- Paerl HW, Bales JD, Ausley LW, Buzzelli CP, Crowder LB, Eby LA, Fear JM, Go M, Peierls BL, Richardson TL, Ramus JS (2001) Ecosystem impacts of three sequential hurricanes (Dennis, Floyd, and Irene) on the United States' largest lagoonal estuary, Pamlico Sound, NC. *Proc Natl Acad Sci* 98:5655–5660
- Paerl HW, Valdes LM, Joyner AR, Peierls BL, Piehler MF, Riggs SR, Christian RR, Eby LA, Crowder LB, Ramus JS, Clesceri EJ, Buzzelli CP, Luetlich Jr. RA (2006) Ecological response to hurricane events in the Pamlico Sound system, North Carolina, and implications for assessment and management in a regime of increased frequency. *Estuar Coasts* 29:1033–1045
- Paperno R, Tremain DM, Adams DH, Sebastian AP, Sauer JT, Dutka-Gianelli J (2006) The disruption and recovery of fish communities in the Indian River Lagoon, Florida, following two hurricanes in 2004. *Estuar Coasts* 29:1004–1010
- Parrish CE, Dijkstra JA, O'Neil-Dunne JPM, McKenna L, Pe'eri S (2016) Post-Sandy benthic habitat mapping using new topobathymetric lidar technology and object-based image classification. *J Coast Res SI* 76:200–208
- Potter IC, Beckley LE, Whitfield AK, Lenanton RCJ (1990) Comparisons between the roles played by estuaries in the life cycles of fishes in temperate Western Australia and Southern Africa. *Environ Biol Fishes* 28:143–178
- Psuty NP, Ofiara DD (2002) Coastal storms: their importance to coastal systems and management. In: *Coastal hazard management: lessons and future directions from New Jersey*. Rutgers University Press, New Brunswick, p 106–132
- Ritchie Jr. DE (1977) Short-term response of fish to Tropical Storm Agnes in the mid-Chesapeake Bay. In: Ruzecki EP, Schubel JR, Huggett RJ, Anderson AM, Wass ML, Marasco RJ, Lynch MP (eds) *The effects of Tropical Storm Agnes on the Chesapeake Bay estuarine system*. The Johns Hopkins University Press, Baltimore, p 460–463
- Roman MR, Adolf JE, Bichy J, Boicourt WC, Harding Jr. LW, Houde ED, Jung S, Kimmel DG, Miller WD, Zhang X (2005) Chesapeake bay plankton and fish abundance enhanced by Hurricane Isabel. *Eos Trans AGU* 86:261–268
- RStudio Team (2018) RStudio: integrated development for R. <http://www.rstudio.com/>
- Sackett DK, Able KW, Grothues TM (2007) Dynamics of summer flounder, *Paralichthys dentatus*, seasonal migrations based on ultrasonic telemetry. *Estuar Coast Shelf Sci* 74:119–130
- Stevens MHH (2009) A primer of ecology with R. In: Gentleman R, Hornik K, Parmigiani G (series eds) *Use R!*. Springer Science & Business Media, New York

- Stevens PW, Blewett DA, Casey JP (2006) Short-term effects of a low dissolved oxygen event on estuarine fish assemblages following the passage of Hurricane Charley. *Estuar Coasts* 29:997–1003
- Sugihara T, Yearsley C, Durand JB, Psuty NP (1979) Comparison of natural and altered estuarine systems: analysis. Center for Coastal and Environmental Studies, New Brunswick
- Taghon GL, Ramey PA, Fuller CM, Petrecca RF, Grassle JP (2017) Benthic community structure and sediment properties in Barnegat Bay, New Jersey, before and after Hurricane Sandy. *Estuar Coasts* 40:160–172
- Tinoco AI (2017) Effects of Hurricane Sandy on Great South Bay, Long Island: assessing water quality, seagrass and associated nekton communities. MS thesis, Stony Brook University, Stony Brook, NY
- Tournois J, Darnaude AM, Ferraton F, Aliaume C, Mercier L, McKenzie DJ (2017) Lagoon nurseries make a major contribution to adult populations of a highly prized coastal fish. *Limnol Oceanogr* 62:1219–1233
- U.S. Geological Survey (2019) National Water Information System. waterdata.usgs.gov/nj/nwis/current/?type=tide;group_key=basin_cd
- Udyawer V, Chin A, Knip DM, Simpfendorfer CA, Heupel MR (2013) Variable response of coastal sharks to severe tropical storms: environmental cues and changes in space use. *Mar Ecol Prog Ser* 480:171–183
- Valenti JL, Grothues TM, Able KW (2017) Estuarine fish communities along a spatial urbanization gradient. *J Coast Res* SI 78:254–268
- Walsh KJE, McBride JL, Klotzbach PJ, Balachandran S, Camargo SJ, Holland G, Knutson TR, Kossin JP, Lee TC, Sobel A, Sugi M (2016) Tropical cyclones and climate change. *Wiley Interdiscip Rev Clim Chang* 7:65–89
- Walther G, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- Wasserman RJ, Strydom NA (2011) The importance of estuary head waters as nursery areas for young estuary- and marine-spawned fishes in temperate South Africa. *Estuar Coast Shelf Sci* 94:56–67
- Whitfield A, Elliott M (2011) Ecosystem and biotic classifications of estuaries and coasts. *Treatise Estuar Coast Sci* 1:99–124
- Wickham H (2016) *Ggplot2: elegant graphics for data analysis*. Springer Verlag, New

York

Wickham H, Pedersen TL (2019) Gtable: arrange ‘Grobs’ in tables. cran.r-project.org/package=gtable

Witting DA, Able KW, Fahay MP (1999) Larval fishes of a Middle Atlantic Bight estuary:

assemblage structure and temporal stability. *Can J Fish Aquat Sci* 56:222–230

Zuur AF, Ieno EN (2016) Beginner’s guide to zero-inflated models with R. Highland Statistics Ltd., Newburgh

Tables

Table 1. Effort (tows and sampling events) and environmental parameters for the years (2012 = pre-Sandy, 2013 = one year post-Sandy, 2014 = two years post-Sandy) and months sampled. Reported environmental parameters are the annual means and ranges, respectively, for April, June, August, and October. See Fig. 1 for sampling site locations

Month/year sampled	Tows (#)	Sampling Events (#)	Temperature (°C)	Salinity	Dissolved Oxygen (mg L ⁻¹)	pH	Water Depth (m)
April							
2012	136	45	15.2 11.4 – 21.6	25.85 19.55 – 30.60	7.47 4.31 – 10.19	7.78 6.10 – 8.22	1.7 0.6 – 5.5
2013	144	48	12.7 8.8 – 17.7	24.95 16.25 – 30.65	8.97 1.12 – 12.48	7.81 7.17 – 8.41	1.9 0.7 – 5.0
2014	144	48	14.8 10.8 – 19.4	22.61 12.09 – 30.13	8.10 4.14 – 10.86	7.71 6.87 – 8.20	1.8 0.8 – 5.2
June							
2012	142	47	23.1 17.4 – 30.0	24.41 14.86 – 30.49	6.13 0.30 – 14.89	7.70 6.66 – 8.39	1.8 0.6 – 6.2
2013	146	49	22.7 17.4 – 27.4	21.99 9.45 – 28.53	5.30 0.13 – 7.65	7.62 6.58 – 8.13	1.7 0.8 – 5.5
2014	143	48	25.3 17.8 – 28.8	23.61 13.24 – 29.85	6.28 0.34 – 8.99	7.61 6.78 – 8.17	1.7 0.6 – 5.4
August							
2012	147	49	25.2 22.7 – 29.3	25.72 15.38 – 31.48	5.49 0.06 – 11.18	7.68 6.67 – 8.35	1.9 0.6 – 5.5

Table 1 continued

Month/year sampled	Tows (#)	Sampling Events (#)	Temperature (°C)	Salinity	Dissolved Oxygen (mg L ⁻¹)	pH	Water Depth (m)
August							
2013	147	49	24.0 21.9 – 30.6	24.97 14.42 – 31.07	5.76 0.16 – 8.42	7.75 6.95 – 8.17	1.9 0.8 – 5.0
2014	142	48	24.7 21.6 – 30.6	22.15 11.88 – 28.98	5.49 0.02 – 8.70	7.64 6.75 – 8.18	1.7 0.8 – 4.7
October							
2012	147	49	15.9 14.6 – 20.6	25.65 18.24 – 31.36	7.31 0.13 – 10.25	7.84 7.17 – 8.15	1.8 0.9 – 5.5
2013	147	49	16.6 14.5 – 22.4	26.84 22.15 – 30.21	7.06 1.15 – 9.54	7.76 5.67 – 8.20	1.9 0.9 – 5.2
2014	146	49	18.6 16.6 – 20.9	25.55 16.67 – 30.48	6.93 3.29 – 8.84	7.76 7.13 – 8.09	1.9 0.9 – 5.7
Annual Totals and Means							
2012	572	190	19.9 11.4 – 30.0	25.41 14.86 – 31.48	6.58 0.06 – 14.89	7.75 6.10 – 8.39	1.8 0.6 – 6.2
2013	584	195	19.0 8.8 – 30.6	24.69 9.45 – 31.07	6.76 0.13 – 12.48	7.73 5.67 – 8.41	1.9 0.7 – 5.5
2014	575	193	20.8 10.8 – 30.6	23.49 11.88 – 30.48	6.70 0.02 – 10.86	7.68 6.75 – 8.20	1.8 0.6 – 5.7

Table 1 continued

Month/year sampled	Tows (#)	Sampling Events (#)	Temperature (°C)	Salinity	Dissolved Oxygen (mg L ⁻¹)	pH	Water Depth (m)
Seasonal Totals and Means							
April	424	141	14.2 8.8 – 21.6	24.44 12.09 – 30.65	8.19 1.12 – 12.48	7.77 6.10 – 8.41	1.8 0.6 – 5.5
June	431	144	23.7 17.4 – 30.0	23.32 9.45 – 30.49	5.90 0.13 – 14.89	7.64 6.58 – 8.39	1.7 0.6 – 6.2
August	436	146	24.7 21.6 – 30.6	24.29 11.88 – 31.48	5.58 0.02 – 11.18	7.69 6.67 – 8.35	1.8 0.6 – 5.5
October	440	147	17.1 14.5 – 22.4	26.01 16.67 – 31.36	7.10 0.13 – 10.25	7.79 5.67 – 8.20	1.9 0.9 – 5.7

Table 2. Total number of fish collected, observed species richness, and the mean \pm standard error of the mean for catch-per-unit-effort (CPUE), Shannon diversity, and standardized richness over the years (2012 = pre-Sandy, 2013 = one year post-Sandy, 2014 = two years post-Sandy) and months sampled

Month/year sampled	Fish (#)	Richness (#)	CPUE (# fish s ⁻¹)	Diversity	Standardized Richness (# species tow ⁻¹)
April					
2012	593	21	0.037 \pm 0.013	0.438 \pm 0.072	0.524 \pm 0.082
2013	97	21	0.006 \pm 0.002	0.598 \pm 0.124	0.319 \pm 0.071
2014	158	23	0.009 \pm 0.002	0.729 \pm 0.077	0.576 \pm 0.076
June					
2012	2,041	26	0.119 \pm 0.040	0.735 \pm 0.082	0.959 \pm 0.105
2013	536	25	0.030 \pm 0.005	0.748 \pm 0.087	0.966 \pm 0.105
2014	1,908	25	0.111 \pm 0.027	0.882 \pm 0.076	1.257 \pm 0.119
August					
2012	4,692	34	0.266 \pm 0.067	0.775 \pm 0.073	1.544 \pm 0.133
2013	2,945	33	0.167 \pm 0.028	0.392 \pm 0.067	0.939 \pm 0.099
2014	8,676	41	0.591 \pm 0.264	0.818 \pm 0.083	2.066 \pm 0.199
October					
2012	2,862	25	0.162 \pm 0.065	0.635 \pm 0.069	0.864 \pm 0.079
2013	1,896	20	0.108 \pm 0.060	0.349 \pm 0.072	0.537 \pm 0.072
2014	7,589	41	0.463 \pm 0.123	0.827 \pm 0.071	1.840 \pm 0.144

Table 2 continued

Month/year sampled	Fish (#)	Richness (#)	CPUE (# fish s ⁻¹)	Diversity	Standardized Richness (# species tow ⁻¹)
Annual Totals and Means					
2012	10,188	50	0.148 ± 0.027	0.664 ± 0.035	0.983 ± 0.058
2013	5,474	47	0.078 ± 0.017	0.514 ± 0.038	0.692 ± 0.048
2014	18,331	58	0.294 ± 0.074	0.819 ± 0.036	1.437 ± 0.082
Seasonal Totals and Means					
April	848	35	0.017 ± 0.005	0.592 ± 0.039	0.472 ± 0.045
June	4,485	34	0.086 ± 0.016	0.788 ± 0.045	1.061 ± 0.064
August	16,313	53	0.340 ± 0.091	0.664 ± 0.045	1.513 ± 0.093
October	12,347	49	0.244 ± 0.052	0.620 ± 0.042	1.081 ± 0.075

Table 3. Mean catch-per-unit-effort (number of fish 360s⁻¹) for all the species collected over the years (2012 = pre-Sandy, 2013 = one year post-Sandy, 2014 = two years post-Sandy) and months sampled. Superscripts on scientific names indicate the species is unique to a particular year (2 = 2012, 3 = 2013, 4 = 2014). Estuarine usage (T = transient, R = resident, SS = southern stray, ShS = shelf stray) based on Kennish & Lutz (1984) and Able & Fahay (2010). Species in the non-metric multidimensional scaling (NMDS) plot were coded by number for clarity (see Fig. 5); pairings are listed here

Scientific Name	Common Name	NMDS #	Estuarine Usage	April			June			August			October		
				2012	2013	2014	2012	2013	2014	2012	2013	2014	2012	2013	2014
<i>Alosa pseudoharengus</i> ²	Alewife	1	T	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Anchoa hepsetus</i>	Striped anchovy	2	T	0.000	0.000	0.000	0.000	0.000	0.000	1.265	0.123	0.563	0.000	0.020	0.082
<i>Anchoa mitchilli</i>	Bay anchovy	3	T	3.713	0.104	0.083	12.974	3.612	8.896	72.253	55.405	80.838	51.760	34.431	74.276
<i>Anguilla rostrata</i>	American eel	4	T	0.000	0.021	0.083	0.186	0.123	0.261	0.184	0.081	0.031	0.000	0.000	0.071
<i>Apeltes quadracus</i>	Fourspine stickleback	5	R	0.644	0.167	0.250	10.766	0.204	6.269	0.061	0.000	18.594	0.408	0.000	19.235
<i>Archosargus probatocephalus</i> ²	Sheepshead	6	SS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000
<i>Astroscopus guttatus</i> ³	Northern stargazer	7	ShS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000
<i>Bairdiella chrysoura</i>	Silver perch	8	T	0.022	0.000	0.000	0.000	0.000	0.000	9.503	0.367	4.969	2.265	0.429	3.531
<i>Brevoortia tyrannus</i>	Atlantic menhaden	9	T	2.844	0.083	0.000	7.697	1.020	3.792	0.123	0.367	0.625	0.618	0.286	0.143
<i>Caranx crysos</i> ⁴	Blue runner	10	SS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.042	0.000	0.000	0.000
<i>Caranx hippos</i>	Crevalle jack	11	SS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.083	0.000	0.021	0.000
<i>Centropristis striata</i>	Black seabass	12	T	0.067	0.000	0.104	0.213	0.102	0.166	0.327	0.061	0.385	0.020	0.000	0.204
<i>Chaetodon ocellatus</i> ⁴	Spotfin butterflyfish	13	SS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.031	0.000	0.000	0.020
<i>Chasmodes bosquianus</i>	Striped blenny	14	R	0.022	0.000	0.000	0.021	0.000	0.000	0.020	0.020	0.354	0.020	0.020	0.123

Table 3 continued

Scientific Name	Common Name	NMDS #	Estuarine Usage	April			June			August			October		
				2012	2013	2014	2012	2013	2014	2012	2013	2014	2012	2013	2014
<i>Chilomycterus schoepfi</i>	Striped burrfish	15	T	0.000	0.000	0.000	0.000	0.020	0.083	0.082	0.000	0.219	0.000	0.000	0.000
<i>Clupea harengus</i>	Atlantic herring	16	T	0.044	0.500	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Conger oceanicus</i> ²	Conger eel	17	T	0.022	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Cynoscion regalis</i>	Weakfish	18	T	0.000	0.000	0.000	0.000	0.000	0.000	0.408	0.102	0.188	0.020	0.000	0.082
<i>Dactylopterus volitans</i> ³	Flying gurnard	19	SS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000
<i>Dasyatis say</i>	Bluntnose stingray	20	SS	0.000	0.000	0.000	0.000	0.000	0.000	0.041	0.020	0.000	0.000	0.000	0.000
<i>Etropus microstomus</i>	Smallmouth flounder	21	T	0.000	0.021	0.063	0.000	0.000	0.103	0.000	0.000	0.021	0.020	0.000	0.041
<i>Eucinostomus argenteus</i> ²	Spotfin mojarra	22	SS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000
<i>Fundulus heteroclitus</i>	Mummichog	23	R	0.844	0.167	0.208	0.032	0.020	0.167	0.000	0.000	0.438	0.020	0.000	0.092
<i>Fundulus luciae</i> ³	Spotfin killifish	24	R	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Fundulus majalis</i> ⁴	Striped killifish	25	R	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Gadus morhua</i> ⁴	Atlantic Cod	26	T	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Gobiesox strumosus</i> ⁴	Skilletfish	27	SS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.063	0.000	0.000	0.082
<i>Gobiosoma bosc</i>	Naked goby	28	R	0.044	0.104	0.333	0.064	0.020	0.318	0.388	0.796	2.698	0.041	0.143	2.042
<i>Gobiosoma ginsburgi</i>	Seaboard goby	29	R	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.061	0.250	0.000	0.000	0.725
<i>Hippocampus erectus</i>	Lined seahorse	30	T	0.089	0.000	0.042	0.213	0.020	0.062	0.020	0.000	0.229	0.041	0.000	0.163
<i>Hypsoblennius hentz</i>	Feather blenny	31	R	0.022	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.208	0.000	0.000	0.123
<i>Ictalurus punctatus</i> ³	Channel catfish	32	R	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000

Table 3 continued

Scientific Name	Common Name	NMDS #	Estuarine Usage	April			June			August			October		
				2012	2013	2014	2012	2013	2014	2012	2013	2014	2012	2013	2014
<i>Lagodon rhomboides</i>	Pinfish	33	T	0.000	0.000	0.000	0.234	0.041	0.000	0.306	0.082	0.021	0.000	0.000	0.000
<i>Leiostomus xanthurus</i>	Spot	34	T	3.467	0.000	0.021	5.654	0.388	0.524	6.751	0.204	0.000	0.735	0.061	0.000
<i>Lepomis gibbosus</i> ⁴	Pumpkinseed	35	R	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.125	0.000	0.000	0.062
<i>Lepomis macrochirus</i> ⁴	Bluegill	36	R	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.021
<i>Leucoraja erinacea</i> ⁴	Little skate	37	ShS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020
<i>Lucania parva</i>	Rainwater killifish	38	R	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.265	0.000	0.051
<i>Lutjanus griseus</i> ⁴	Gray snapper	39	SS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.041
<i>Menidia beryllina</i>	Inland silverside	40	R	0.017	0.063	0.000	0.000	0.000	0.000	0.000	0.000	0.646	0.000	0.000	0.000
<i>Menidia menidia</i>	Atlantic silverside	41	T	0.222	0.021	0.229	0.213	0.388	4.651	0.449	0.633	84.896	0.102	2.653	49.133
<i>Menticirrhus saxatilis</i>	Northern kingfish	42	T	0.000	0.021	0.000	0.000	0.000	0.000	0.039	0.061	0.169	0.061	0.000	0.020
<i>Microgobius thalassinus</i>	Green goby	43	SS	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.041	0.042	0.020	0.020	0.000
<i>Micropogonias undulatus</i>	Atlantic croaker	44	T	0.111	0.063	0.000	0.075	0.102	0.000	0.102	0.020	0.000	0.287	0.041	3.898
<i>Morone americana</i>	White perch	45	R	0.000	0.083	0.000	0.000	0.000	0.042	0.041	0.000	0.000	0.000	0.000	0.166
<i>Morone saxatilis</i> ⁴	Striped bass	46	T	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Mugil cephalus</i> ²	Striped mullet	47	T	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000
<i>Mugil curema</i>	White mullet	48	T	0.000	0.000	0.000	0.000	0.000	0.000	0.082	0.000	0.083	0.000	0.000	0.000
<i>Mustelis canis</i>	Smooth dogfish	49	T	0.000	0.000	0.000	0.021	0.020	0.000	0.061	0.041	0.021	0.000	0.000	0.020
<i>Mycteroperca microlepis</i> ³	Gag	50	SS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000

Table 3 continued

Scientific Name	Common Name	NMDS #	Estuarine Usage	April			June			August			October		
				2012	2013	2014	2012	2013	2014	2012	2013	2014	2012	2013	2014
<i>Opsanus tau</i>	Oyster toadfish	51	R	0.000	0.104	0.021	0.149	0.143	0.323	0.224	0.286	1.386	0.163	0.000	0.469
<i>Paralichthys dentatus</i>	Summer flounder	52	T	0.044	0.063	0.104	0.319	0.388	1.037	0.306	0.123	0.919	0.347	0.061	0.245
<i>Peprilus triacanthus</i>	Butterfish	53	ShS	0.000	0.000	0.000	0.021	0.020	0.000	0.000	0.020	0.188	0.000	0.041	0.041
<i>Perca flavescens</i> ²	Yellow perch	54	R	0.000	0.000	0.000	0.027	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Pogonias cromis</i>	Black drum	55	T	0.049	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.021	0.000	0.000	0.020
<i>Pollachius virens</i>	Pollock	56	T	0.000	0.042	0.167	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Pomatomus saltatrix</i>	Bluefish	57	T	0.000	0.000	0.000	0.043	0.204	0.146	0.265	0.183	0.115	0.000	0.020	0.061
<i>Prionotus carolinus</i> ⁴	Northern searobin	58	T	0.000	0.000	0.042	0.000	0.000	0.020	0.000	0.000	0.021	0.000	0.000	0.020
<i>Pseudopleuronectes americanus</i>	Winter flounder	59	R	0.200	0.042	0.104	1.463	3.061	10.062	0.000	0.020	1.052	0.000	0.000	0.367
<i>Scophthalmus aquosus</i> ⁴	Windowpane	60	T	0.000	0.000	0.083	0.000	0.000	0.042	0.000	0.000	0.000	0.000	0.000	0.000
<i>Selene setapinnis</i>	Atlantic moonfish	61	SS	0.000	0.000	0.000	0.000	0.000	0.000	0.061	0.000	0.000	0.041	0.020	0.020
<i>Selene vomer</i>	Lookdown	62	SS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.063	0.000	0.041	0.000
<i>Sphoeroides maculatus</i>	Northern puffer	63	T	0.000	0.000	0.000	0.106	0.184	1.125	0.243	0.102	0.803	0.000	0.000	0.082
<i>Stenotomus chrysops</i>	Scup	64	T	0.000	0.000	0.000	0.000	0.000	0.042	0.041	0.020	0.000	0.000	0.000	0.000
<i>Strongylura marina</i> ⁴	Atlantic needlefish	65	T	0.000	0.000	0.000	0.000	0.000	0.041	0.000	0.000	0.000	0.000	0.000	0.000
<i>Symphurus plagiusa</i> ⁴	Blackcheek tonguefish	66	SS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.041
<i>Syngnathus fuscus</i>	Northern pipefish	67	T	0.533	0.167	0.667	2.192	0.735	1.738	1.755	0.612	10.542	0.857	0.327	10.133

Table 4. Post-hoc test results, for annual comparisons (2012 = pre-Sandy, 2013 = one year post-Sandy, 2014 = two years post-Sandy), of the species-specific Bernoulli Generalized Linear Mixed Models. Reported ratios and confidence intervals were back-transformed from the logit scale. Species were characterized by estuarine usage (T = transient, R = resident), dominant year class collected (0 [young-of-year], 1, or 1+ ages), and spawning duration for comparison. Characterizations are based on Kennish & Lutz (1984) and Able & Fahay (2010)

	Estuarine Usage	Dominant Year Classes Collected	Spawning Duration	2012 / 2013		2012 / 2014		2013 / 2014	
				Odds Ratio	p-value	Odds Ratio	p-value	Odds Ratio	p-value
<i>Anchoa mitchilli</i>	T	0, 1	Apr – Nov	1.286 0.698 – 2.371	0.599	1.406 0.762 – 2.595	0.393	1.093 0.597 – 2.003	0.936
<i>Apeltes quadracus</i>	R	0, 1	Apr – May	5.028 1.339 – 18.876	0.012	0.442 0.171 – 1.142	0.108	0.088 0.024 – 0.327	< 0.001
<i>Bairdiella chrysoura</i>	T	0, 1	Jun – Aug	10.391 3.492 – 30.923	< 0.001	1.357 0.591 – 3.116	0.666	0.131 0.045 – 0.382	< 0.001
<i>Brevoortia tyrannus</i>	T	0	Aug – Nov	1.591 0.636 – 3.983	0.462	1.888 0.731 – 4.881	0.259	1.187 0.438 – 3.219	0.915
<i>Gobiosoma bosc</i>	R	0, 1	May – Sep	0.444 0.147 – 1.339	0.196	0.079 0.027 – 0.227	< 0.001	0.178 0.075 – 0.420	< 0.001
<i>Leiostomus xanthurus</i>	T	0	Nov – Jan	8.622 3.572 – 20.811	< 0.001	34.794 8.927 – 135.609	< 0.001	4.035 0.985 – 16.525	0.053
<i>Menidia menidia</i>	T	0, 1	Apr – Jul	0.783 0.329 – 1.859	0.784	0.194 0.088 – 0.428	< 0.001	0.248 0.118 – 0.522	< 0.001
<i>Micropogonias undulatus</i>	T	0, 1	Aug – Nov	2.249 0.651 – 7.772	0.276	0.363 0.137 – 0.964	0.040	0.161 0.050 – 0.523	0.001

Table 4 continued

	Estuarine Usage	Dominant Year Classes Collected	Spawning Duration	2012 / 2013		2012 / 2014		2013 / 2014	
				Odds Ratio	p-value	Odds Ratio	p-value	Odds Ratio	p-value
<i>Opsanus tau</i>	R	0, 1, 1+	Jun – Aug	1.446 0.536 – 3.905	0.659	0.319 0.133 – 0.769	0.007	0.221 0.086 – 0.564	0.001
<i>Paralichthys dentatus</i>	T	0, 1, 1+	Sep – Mar	1.545 0.761 – 3.134	0.321	0.463 0.249 – 0.862	0.010	0.300 0.153 – 0.586	< 0.001
<i>Pseudopleuronectes americanus</i>	R	0, 1, 1+	Jan – Mar	0.518 0.212 – 1.266	0.196	0.186 0.078 – 0.447	< 0.001	0.360 0.167 – 0.777	0.005
<i>Syngnathus fuscus</i>	T	0, 1	Apr – Aug	2.157 1.015 – 4.583	0.044	0.297 0.148 – 0.596	< 0.001	0.138 0.064 – 0.298	< 0.001

Table S1. Post hoc test results of the catch per unit effort (CPUE) zero altered gamma generalized linear mixed model (GLMM). Reported ratios and confidence intervals from the Bernoulli and gamma GLMMs were back-transformed from the logit and log scales, respectively. 2012: pre-Sandy, 2013: 1 yr post-Sandy, 2014: 2 yr post-Sandy

Bernoulli GLMM		95% Confidence interval		
Comparison	Odds ratio	Lower limit	Upper limit	p
2012 / 2013	1.881	0.946	3.740	0.079
2012 / 2014	0.643	0.296	1.396	0.376
2013 / 2014	0.342	0.164	0.714	0.002
April / June	0.167	0.072	0.387	< 0.001
April / August	0.052	0.016	0.171	< 0.001
April / October	0.152	0.065	0.359	< 0.001
June / August	0.310	0.087	1.105	0.083
June / October	0.912	0.347	2.402	0.995
August / October	2.946	0.819	10.597	0.132
Gamma GLMM		95% Confidence interval		
Comparison	CPUE Ratio	Lower limit	Upper limit	p
April				
2012 / 2013	3.526	1.507	8.250	0.002
2012 / 2014	2.837	1.340	6.008	0.003
2013 / 2014	0.805	0.361	1.793	0.800
June				
2012 / 2013	3.250	1.725	6.121	< 0.001
2012 / 2014	0.864	0.446	1.675	0.864

Table S1 continued

Gamma GLMM		95% Confidence interval		
Comparison	CPUE Ratio	Lower limit	Upper limit	p
June				
2013 / 2014	0.266	0.145	0.487	< 0.001
August				
2012 / 2013	1.227	0.670	2.249	0.708
2012 / 2014	0.616	0.335	1.133	0.150
2013 / 2014	0.502	0.271	0.931	0.024
October				
2012 / 2013	1.572	0.804	3.073	0.253
2012 / 2014	0.302	0.160	0.570	< 0.001
2013 / 2014	0.192	0.099	0.372	< 0.001

Table S2. Post hoc test results for seasonal comparisons of the species-specific Bernoulli generalized linear mixed models. Reported ratios and confidence intervals were back-transformed from the logit scale. Silver perch *Bairdiella chrysoura* were not collected in June; therefore, those comparisons were omitted. See Table 4 for species characterizations

	April / June		April / August		April / October		June / August		June / October		August / October	
	Odds ratio	p	Odds ratio	p	Odds ratio	p	Odds ratio	p	Odds ratio	p	Odds ratio	p
<i>Anchoa mitchilli</i>	0.100 0.039 – 0.252	< 0.001	0.018 0.007 – 0.051	< 0.001	0.031 0.012 – 0.083	< 0.001	0.182 0.086 – 0.386	< 0.001	0.311 0.154 – 0.631	< 0.001	1.714 0.812 – 3.616	0.249
<i>Apeltes quadracus</i>	0.356 0.103 – 1.230	0.141	1.211 0.312 – 4.697	0.984	2.355 0.531 – 10.441	0.451	3.400 0.960 – 12.048	0.062	6.612 1.584 – 27.601	0.004	1.945 0.435 – 8.698	0.664
<i>Bairdiella chrysoura</i>			0.006 0.000 – 0.098	< 0.001	0.006 0.000 – 0.099	< 0.001					1.007 0.444 – 2.285	1.000
<i>Brevoortia tyrannus</i>	0.361 0.100 – 1.306	0.175	0.533 0.141 – 2.016	0.618	0.484 0.130 – 1.804	0.488	1.478 0.476 – 4.588	0.812	1.341 0.441 – 4.083	0.906	0.907 0.282 – 2.923	0.997
<i>Gobiosoma bosc</i>	1.776 0.450 – 7.013	0.706	0.202 0.065 – 0.624	0.002	0.375 0.120 – 1.178	0.123	0.114 0.032 – 0.407	< 0.001	0.211 0.059 – 0.761	0.010	1.859 0.720 – 4.797	0.335
<i>Leiostomus xanthurus</i>	0.143 0.040 – 0.512	0.001	0.185 0.052 – 0.662	0.004	0.634 0.162 – 2.486	0.827	1.297 0.502 – 3.350	0.896	4.442 1.430 – 13.800	0.004	3.425 1.104 – 10.625	0.027
<i>Menidia menidia</i>	0.184 0.056 – 0.602	0.001	0.253 0.076 – 0.839	0.017	0.153 0.047 – 0.495	< 0.001	1.374 0.562 – 3.361	0.798	0.830 0.357 – 1.932	0.942	0.604 0.251 – 1.452	0.452
<i>Micropogonias undulatus</i>	0.395 0.061 – 2.548	0.576	1.049 0.119 – 9.242	1.000	0.051 0.009 – 0.279	< 0.001	2.655 0.412 – 17.107	0.533	0.129 0.037 – 0.447	< 0.001	0.049 0.009 – 0.266	< 0.001
<i>Opsanus tau</i>	0.097 0.016 – 0.583	0.005	0.031 0.005 – 0.184	< 0.001	0.131 0.021 – 0.800	0.020	0.318 0.117 – 0.863	0.017	1.354 0.445 – 4.120	0.898	4.259 1.493 – 12.146	0.002

Table S2 continued

	April / June		April / August		April / October		June / August		June / October		August / October	
	Odds ratio	p	Odds ratio	p	Odds ratio	p	Odds ratio	p	Odds ratio	p	Odds ratio	p
<i>Paralichthys dentatus</i>	0.121 0.041 – 0.355	< 0.001	0.154 0.052 – 0.455	< 0.001	0.271 0.089 – 0.824	0.014	1.274 0.625 – 2.596	0.819	2.241 1.040 – 4.833	0.035	1.759 0.807 – 3.835	0.244
<i>Pseudopleuronec- tes americanus</i>	0.062 0.021 – 0.181	< 0.001	1.130 0.329 – 3.881	0.994	1.299 0.367 – 4.593	0.952	18.134 6.065 – 54.221	< 0.001	20.848 6.714 – 64.731	< 0.001	1.150 0.318 – 4.161	0.993
<i>Syngnathus fuscus</i>	0.756 0.300 – 1.904	0.865	0.380 0.153 – 0.945	0.032	0.509 0.205 – 1.265	0.226	0.503 0.208 – 1.217	0.188	0.673 0.278 – 1.632	0.660	1.338 0.569 – 3.148	0.818

Table S3. Post hoc test results of the diversity zero altered gamma generalized linear mixed model (GLMM). Reported ratios and confidence intervals from the Bernoulli and gamma GLMMs were back-transformed from the logit and log scales, respectively. 2012: pre-Sandy, 2013: 1 yr post-Sandy, 2014: 2 yr post-Sandy

Bernoulli GLMM		95% Confidence interval		
Comparison	Odds ratio	Lower limit	Upper limit	p
April				
2012 / 2013	1.114	0.249	4.978	0.985
2012 / 2014	0.420	0.099	1.783	0.337
2013 / 2014	0.377	0.077	1.847	0.321
June				
2012 / 2013	1.640	0.447	6.022	0.646
2012 / 2014	0.482	0.098	2.374	0.531
2013 / 2014	0.294	0.065	1.324	0.137
August				
2012 / 2013	10.317	1.596	66.719	0.010
2012 / 2014	1.956	0.241	15.876	0.733
2013 / 2014	0.190	0.044	0.819	0.021
October				
2012 / 2013	5.099	1.489	17.468	0.006
2012 / 2014	0.086	0.007	1.097	0.062
2013 / 2014	0.017	0.001	0.207	< 0.001

Table S3 continued

Gamma GLMM		95% Confidence interval		
Comparison	Diversity ratio	Lower limit	Upper limit	p
April				
2012 / 2013	0.685	0.412	1.141	0.192
2012 / 2014	0.750	0.495	1.137	0.237
2013 / 2014	1.094	0.679	1.764	0.898
June				
2012 / 2013	0.897	0.637	1.265	0.740
2012 / 2014	0.901	0.647	1.254	0.741
2013 / 2014	1.004	0.721	1.399	1.000
August				
2012 / 2013	1.489	1.073	2.066	0.012
2012 / 2014	0.909	0.676	1.223	0.730
2013 / 2014	0.610	0.440	0.847	0.001
October				
2012 / 2013	1.050	0.699	1.577	0.957
2012 / 2014	0.930	0.682	1.270	0.850
2013 / 2014	0.886	0.601	1.306	0.745

Table S4. Post hoc test results of the richness zero altered gamma generalized linear mixed model (GLMM). Reported ratios and confidence intervals from the Bernoulli and gamma GLMMs were back-transformed from the logit and log scales, respectively. 2012: pre-Sandy, 2013: 1 yr post-Sandy, 2014: 2 yr post-Sandy

Bernoulli GLMM		95% Confidence interval		
Comparison	Odds ratio	Lower limit	Upper limit	p
2012 / 2013	1.881	0.946	3.740	0.079
2012 / 2014	0.643	0.296	1.396	0.376
2013 / 2014	0.342	0.164	0.714	0.002
April / June	0.167	0.072	0.387	< 0.001
April / August	0.052	0.016	0.171	< 0.001
April / October	0.152	0.065	0.359	< 0.001
June / August	0.310	0.087	1.105	0.083
June / October	0.912	0.347	2.402	0.995
August / October	2.946	0.819	10.597	0.132
Gamma GLMM		95% Confidence interval		
Comparison	Richness ratio	Lower limit	Upper limit	p
April				
2012 / 2013	1.014	0.704	1.462	0.995
2012 / 2014	0.899	0.655	1.233	0.709
2013 / 2014	0.886	0.621	1.265	0.706
June				
2012 / 2013	1.020	0.779	1.335	0.984
2012 / 2014	0.753	0.573	0.988	0.039

Table S4 continued

Gamma GLMM		95% Confidence interval		
Comparison	CPUE Ratio	Lower limit	Upper limit	p
June				
2013 / 2014	0.738	0.565	0.964	0.021
August				
2012 / 2013	1.686	1.301	2.185	< 0.001
2012 / 2014	0.833	0.645	1.075	0.213
2013 / 2014	0.494	0.383	0.638	< 0.001
October				
2012 / 2013	1.387	1.052	1.827	0.015
2012 / 2014	0.516	0.398	0.668	< 0.001
2013 / 2014	0.372	0.284	0.487	< 0.001

Figures

Fig. 1. Locations of sampling sites and relevant landmarks within Barnegat Bay, New Jersey, U.S.A. Hurricane Sandy (diameter roughly 1850 km) made landfall in Brigantine on 29 October 2012. See Table 1 for additional sampling details

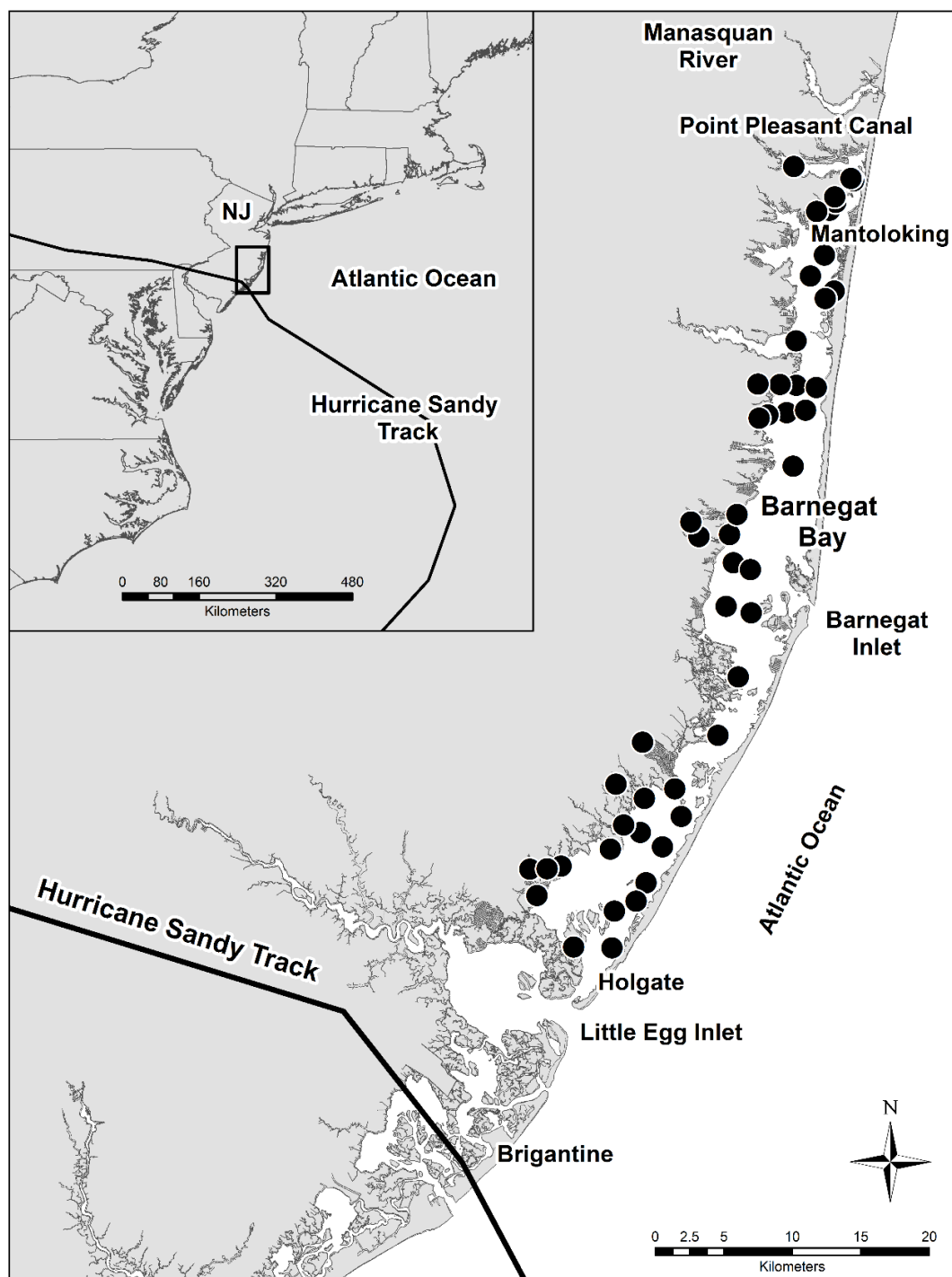


Fig. 2. Length frequency plots broken up by year (2012 = pre-Sandy, 2013 = one year post-Sandy, 2014 = two years post-Sandy) for select estuarine resident species. See Table 4 for additional species characteristics. Black vertical lines indicate yearly mean length for each species

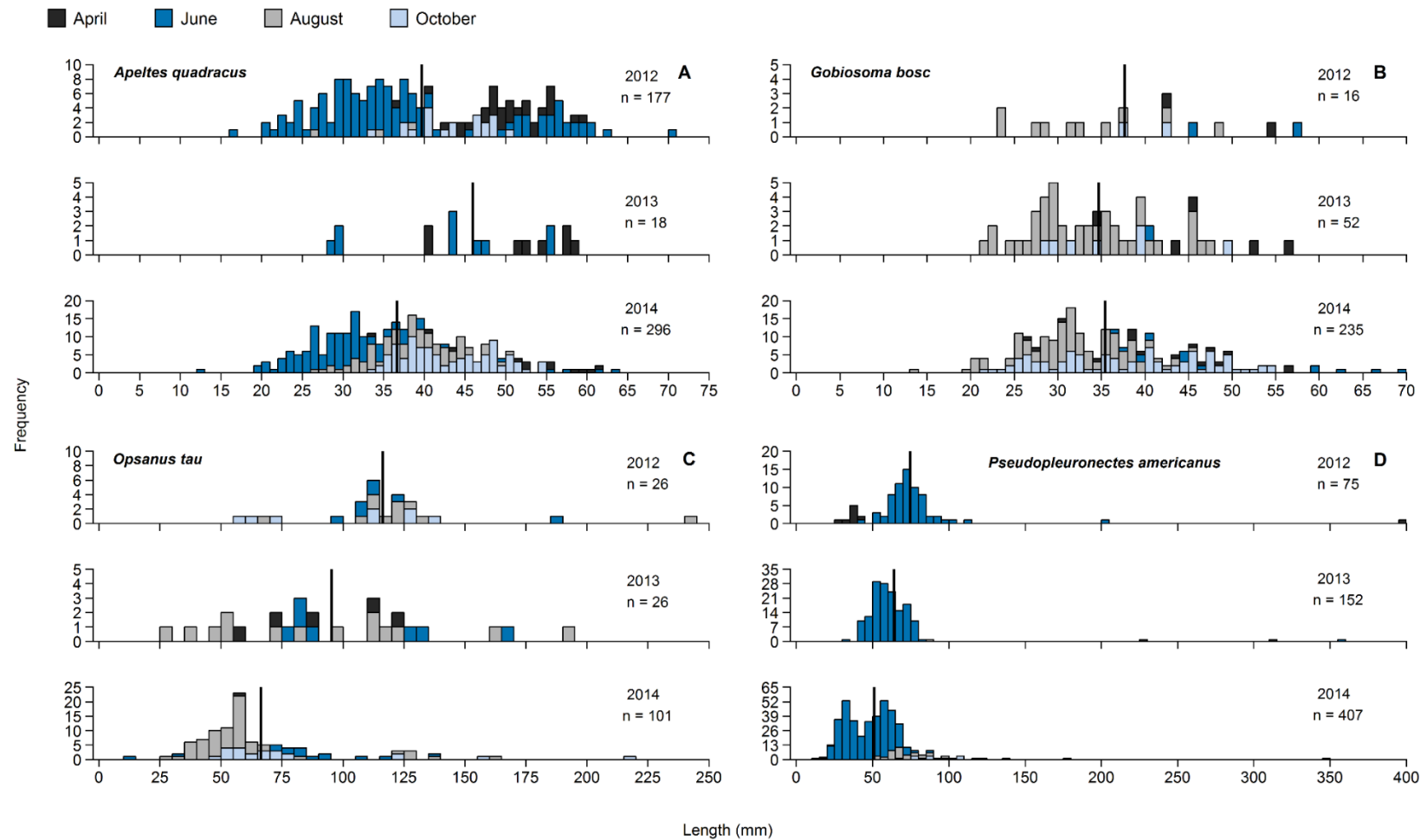


Fig. 3. Length frequency plots broken up by year (2012 = pre-Sandy, 2013 = one year post-Sandy, 2014 = two years post-Sandy) for select estuarine transient species. See Table 4 for additional species characteristics. Black vertical lines indicate yearly mean length for each species

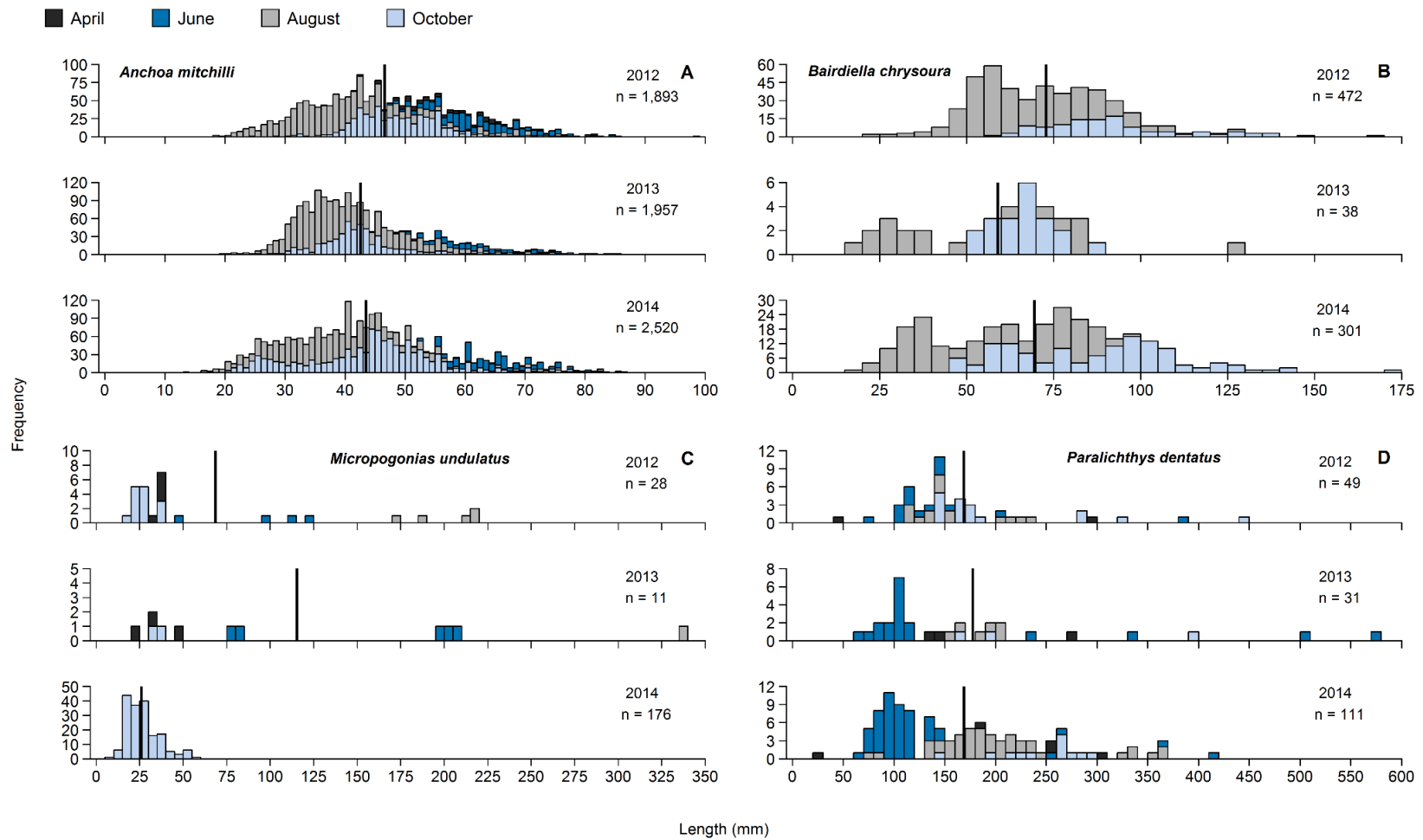


Fig. 4. Length frequency plots broken up by year (2012 = pre-Sandy, 2013 = one year post-Sandy, 2014 = two years post-Sandy) for select estuarine transient species. See Table 4 for additional species characteristics. Black vertical lines indicate yearly mean length for each species

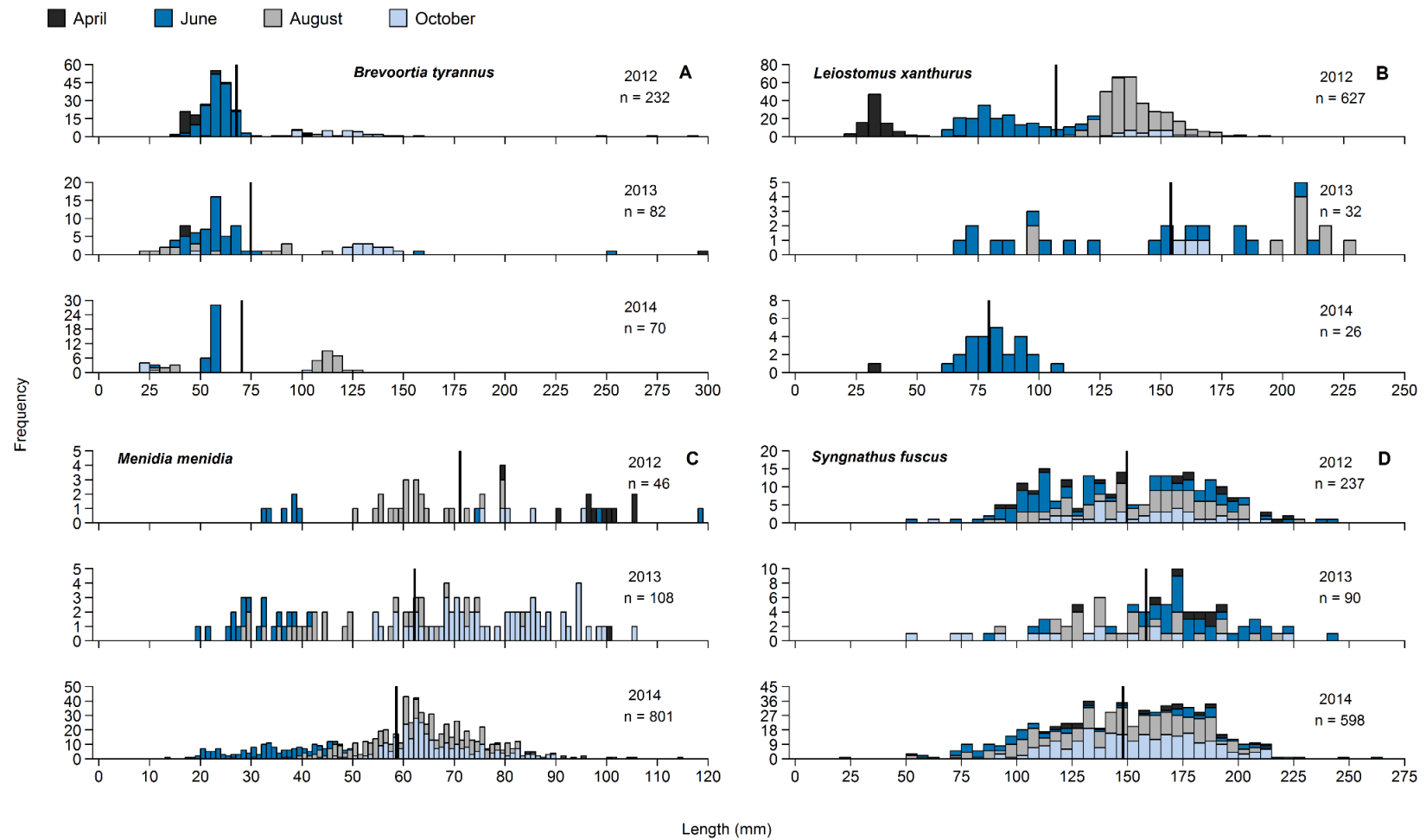
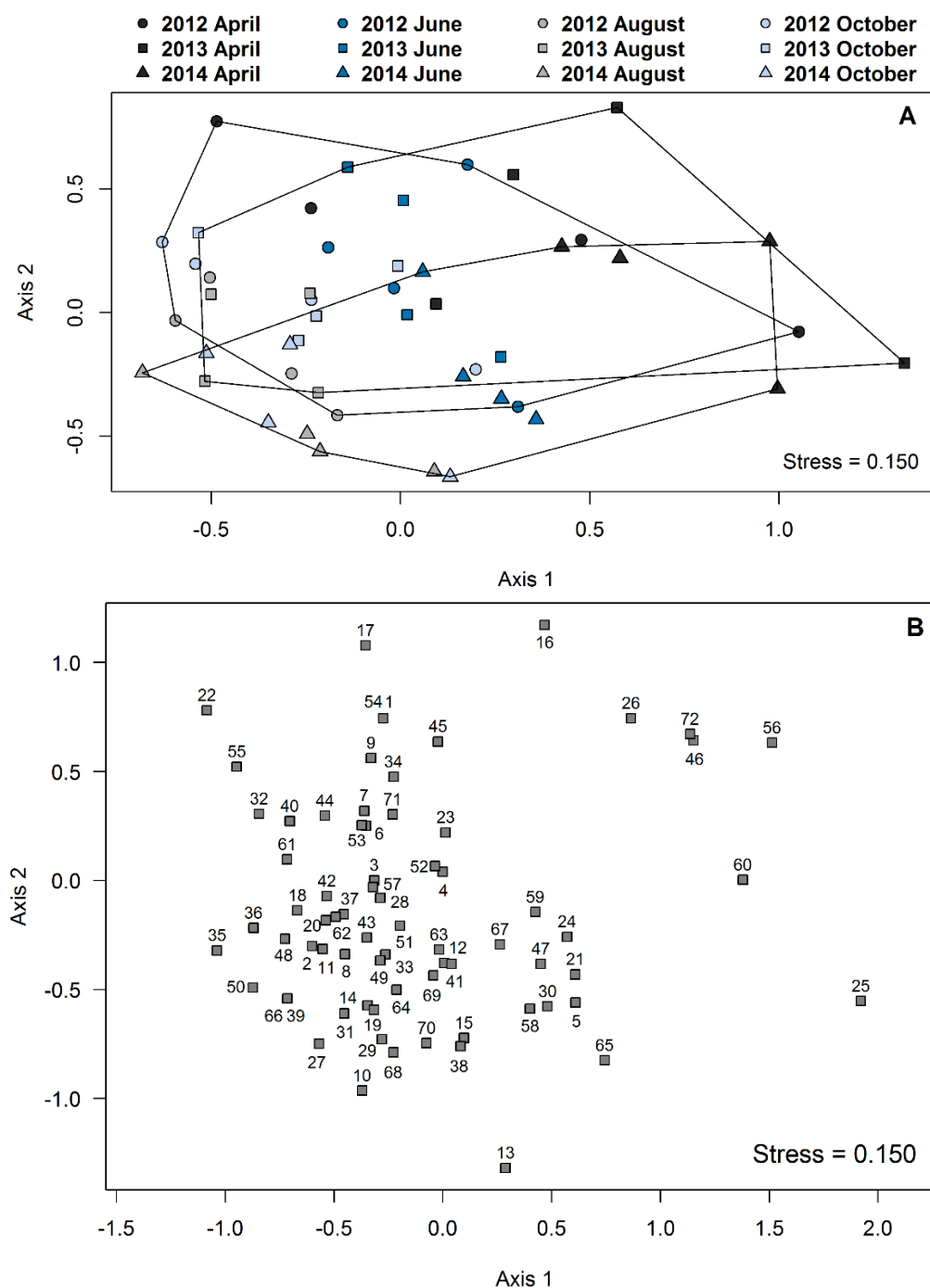


Fig. 5. (A) Non-metric multidimensional scaling (NMDS) sample plot. Assemblage similarity decreases by half per one unit change. Convex polygons enclose samples taken in the same year (2012 = pre-Sandy, 2013 = one year post-Sandy, 2014 = two years post-Sandy) (B) NMDS species plot which is in the same coenospace as the previous sample plot, but was separated for legibility. Species are coded by number for clarity (see Table 3 for pairings) and their locations are based on weighted averages. Only the first two axes of the NMDS are shown. Note the difference in scale between axes from the two plots



CHAPTER II

Subtidal Fish Habitat in a Temperate Lagoonal Estuary: The Importance of Habitat

Mosaics

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Abstract

Estuarine seascapes afford a mosaic of nursery habitats to a relatively diverse array of fishes. Research on fish usage of subtidal estuarine habitats has focused disproportionately on daytime sampling in submerged aquatic vegetation (SAV) and sand habitats. Here we compare the fish assemblages (species composition, abundance, diversity, richness, lengths) inhabiting all the dominant habitat types (upper creek, creek mouth, sand, SAV) within the subtidal habitat mosaic of a temperate lagoonal estuary in relation to seasonal, tidal, and diel cycles. Daytime otter trawling occurred at 45 sites within Barnegat Bay, New Jersey during 2012 – 2014. An additional day-night otter trawl survey was conducted at one sand and SAV site each during 2014 – 2016. Seventy-three species were observed and collections were dominated by juvenile and small adult fishes. Abundance, diversity, and richness peaked in the summer and fall months. Tidal shifts in species-specific abundances were observed in all habitats. Richness, overall, and

diversity in the sand habitat were higher at nighttime. Many fishes utilized all habitats, but others were partial to certain habitats and varied usage with ontogeny. Creek mouths and SAV supported fish assemblages with higher diversity and richness than sand habitats. Similar to SAV habitats, creek mouths were shallow, had higher salinities, and contained complex physical structure (macroalgae, marsh banks). This study reaffirmed that many interacting environmental characteristics shape fish assemblages and demonstrated the significance of marsh creeks, in addition to SAV, to the subtidal habitat mosaic of a Mid-Atlantic Bight estuary.

Introduction

A thorough understanding of fish species distribution patterns is important for elucidating complex processes and interactions relative to climate change effects (Underwood et al. 2000; Harley et al. 2006; Rijnsdorp et al. 2009; Izzo et al. 2016), resource management (Cody and Smallwood 1996; Fleischner 2005; Spellberg 2005), and conservation efforts (Wilson 1985; Noss 1998; Dayton 2003). The distributions of estuarine fishes are influenced by a variety of interconnected factors such as tidal (Rountree and Able 1992a; Kimball and Able 2012) and diel (Arendt et al. 2001; Clark et al. 2003) cycles and biotic (e.g. prey availability) (Manderson et al. 2000; Phelan et al. 2001) and abiotic (e.g. temperature, salinity, dissolved oxygen) (Tyler and Targett 2007; Schaffler et al. 2013) parameters, which vary temporally and spatially (Able and Fahay 2010).

The notion of spatial scale has received considerable attention in ecological studies (Wiens 1989; Cody and Smallwood 1996; Magurran et al. 2010). In estuarine systems,

spatial influences on fish distributions are frequently addressed in regards to habitat use (Heck et al. 1997; Able 1999). Numerous studies have compared fish assemblages inhabiting submerged aquatic vegetation (SAV) habitat with those in nearby unvegetated sand habitat. These studies often concluded fishes were more abundant and assemblages were more diverse within SAV habitat (Connolly 1994; Gray et al. 1996; Jenkins et al. 1997; Arrivillaga and Baltz 1999; Mattila et al. 1999; Castillo-Rivera et al. 2002; Lazzari 2002; Ribeiro et al. 2006), thus supporting the designation of SAV as nursery habitat (Beck et al. 2001; Litvin et al. 2018).

More recently there has been a shift away from identifying individual nursery habitats to embracing the more dynamic concept of “seascape nurseries”, which are mosaics of functionally interconnected habitats (Sheaves 2009; Nagelkerken et al. 2015). The seascape nursery approach recognizes fish habitat usage can vary during foraging, with ontogeny and tidal and diel cycles, and across temporal and spatial scales (Arendt et al. 2001; Nagelkerken 2007; Hammerschlag et al. 2010; Baker et al. 2013; Amorim et al. 2018), and acknowledges that multiple habitats serve different roles in sustaining fish populations (Sheaves 2009; Sheaves et al. 2015; Litvin et al. 2018). However, the potential for estuarine habitats other than SAV, such as oyster reefs, mud, and marsh creeks, to serve as important habitat within these mosaics remains largely understudied (Beck et al. 2001; Able and Fahay 2010; Boström et al. 2011; Hyndes et al. 2018). Given the ecological importance of estuaries to many fish species (Able 2005; Potter et al. 2015) and the diverse array of continual anthropogenic impacts on these coastal ecosystems (Kennish 1991; Halpern et al. 2008), understanding the patterns and complexities of fish habitat usage within estuarine habitat mosaics is vital to habitat

conservation efforts and sustaining healthy fish populations, particularly in highly productive lagoonal estuaries (Pérez-Ruzafa et al. 2019).

Lagoonal estuaries, shallow, elongated water bodies that are often partly separated from the ocean by a barrier (Whitfield and Elliott 2011), constitute approximately 13% of the world's coastline, with over 30% of the world's lagoonal coastline found in North America (Cromwell 1971). Lagoons contain regionally varying subtidal habitat mosaics, which may include SAV, sand, and marsh creek habitats, among others (Kennish and Paerl 2010a; Elliott and Whitfield 2011; Pérez-Ruzafa et al. 2019). Lagoons are highly susceptible to anthropogenic habitat degradation (Kennish et al. 2008; Kennish and Paerl 2010b; Pérez-Ruzafa et al. 2019) despite being essential to the growth and development of juvenile fishes (Yáñez Arancibia 1985; Pérez-Ruzafa and Marcos 2012; Tournois et al. 2017). Marsh creeks, which are often located on the landward side of lagoonal estuaries directly adjacent to urbanized areas (Phleger 1981), are particularly vulnerable to anthropogenic habitat degradation via processes such as shoreline armoring, dredging, and impervious surface creation that decrease water quality and destroy valuable fish habitat (Sugihara et al. 1979; Mallin and Lewitus 2004; Seilheimer et al. 2007; Kennish and Paerl 2010a; Bilkovic 2011). These creeks often support diverse fish assemblages (Rountree and Able 1992b; Desmond et al. 2000; Able et al. 2001; Garwood et al. 2019), yet their importance as fish habitat has rarely been assessed in relation to other habitats within estuarine habitat mosaics (Beck et al. 2001; Minello et al. 2003; Able and Fahay 2010).

In this study, we quantified seasonal, diel, and tidal fish usage of the dominant habitat types (marsh creek, sand, SAV) within the subtidal habitat mosaic of a temperate

lagoonal estuary in order to understand the importance and function of less frequently studied habitats (marsh creeks) in relation to SAV habitat (Beck et al. 2001; Boström et al. 2011; Hyndes et al. 2018). Structural characteristics of the fish assemblages (species composition, abundance, diversity, richness, lengths) within marsh creek, sand, and SAV habitats were used to assess each habitat's importance and function. We hypothesized that some fishes would primarily utilize a single habitat whereas others would utilize all the habitats surveyed, and that marsh creeks would serve as important habitat in addition to SAV within this temperate lagoonal estuary.

Methods

Study Area

The Atlantic and Gulf of Mexico coasts of the United States (U.S.) contain the longest stretch of coastal lagoons in the world (Nichols and Boon 1994). Barnegat Bay is a shallow (mean water depth < 2 meters), temperate lagoonal estuarine system (Chizmadia et al. 1984; Whitfield and Elliott 2011) that extends nearly 70 km along the U.S. Atlantic coast (Kennish 2001) (Fig. 1). Located in the Mid-Atlantic Bight (specifically within New Jersey), Barnegat Bay is connected directly to the Northwest Atlantic Ocean in the southern portion of the bay, via Little Egg Inlet, and in the central portion of the bay, via Barnegat Inlet. Additionally, the Point Pleasant Canal connects northern Barnegat Bay and the Manasquan River, which subsequently drains into the Atlantic Ocean (Fig. 1). Freshwater input to the system is dominated by tributaries (rivers, marsh creeks) located along the western shore of the bay (Chizmadia et al. 1984). Salinity is lowest near Toms River and northward, due to larger tributaries and greater

volume of freshwater input in the northern bay, and highest near the inlets (Little Egg and Barnegat) (Kennish 2001).

Barnegat Bay experiences four seasons annually (winter [December – February], spring [March – May], summer [June – August], fall [September – November]) and consequently exhibits a wide range of water temperatures (approximately -1°C in winter to 30°C in summer) (Kennish 2001). In addition to temperature, photoperiod varies by 40% seasonally (minimum: 9 hours in December, maximum: 15 hours in June). Due to its shallow nature, the majority of Barnegat Bay is well mixed, but two-layered flow is evident in the larger freshwater tributaries and deeper channels of the Intracoastal Waterway (Chizmadia et al. 1984). The modelled residence time of the estuary ranges from 0 – 50 days and is dependent on temporal (i.e. seasonal), spatial (i.e. location within the bay), tidal, meteorological, and offshore hydrodynamic factors (Defne and Ganju 2015). Barnegat Bay has semi-diurnal tides and a mean tidal range of 0.5 – 1.0 m. The largest tidal driven water volume exchange within the bay occurs at Little Egg Inlet (Kennish 2001).

The dominant subtidal habitats in Barnegat Bay include marsh creeks, with sandy mud bottoms, beds of SAV, and open water areas of the bay with sand or mud bottom (Chizmadia et al. 1984; Kennish 2001). The subtidal marsh creeks are located along the western shore of the bay, whereas the beds of SAV are most abundant along the eastern shore of the bay (Fig. 1). Undeveloped shorelines adjacent to marsh creeks are dominated by salt marsh flora (e.g. smooth cordgrass *Spartina alterniflora*, saltmeadow cordgrass *Spartina patens*) (Chizmadia et al. 1984; Kennish 2001). SAV beds consist predominantly of eelgrass *Zostera marina*, although widgeongrass *Ruppia maritima* is

also present in lower salinity SAV beds (Kennish 2001; Lathrop et al. 2001). Various species of drifting macroalgae (e.g. sea lettuce *Ulva lactuca*, Agardh's red weed *Agardhiella subulata*) are found in all habitats throughout the bay.

Field Survey Protocols

Daytime Survey

Daytime otter trawl sampling (4.9 m headrope, 19 mm mesh wings, and 6.3 mm mesh codend liner) for fishes consisted of three 120-second net tows at each of 45 sites during every sampling event (Fig. 1). This gear targeted small fishes (< 200 mm) (Able and Fahay 1998; Olin and Malinen 2003), which includes juveniles and species with small adult stages (Able and Fahay 2010). Sampling events occurred seasonally in April (spring), June (early summer), August (late summer), and October (fall) for three years (2012 – 2014) (Table 1). Sampling sites were distributed throughout the bay and encompassed the four dominant habitat types within the bay's subtidal habitat mosaic: the upper portion of marsh creeks (upper creek) (n = 10), marsh creek mouths (creek mouth) (n = 9), sand (n = 15), and SAV (n = 11) (Fig. 1). Sampling site habitat designations were based on prior studies (Sugihara et al. 1979; Jivoff and Able 2001) and reconnaissance sampling. All collected fishes were identified and counted, and the lengths (total or fork length or body width in mm, based on species) of the first 20 individuals of each species were recorded for each tow. Volume of any macroalgae collected in a tow was measured to the nearest liter. Temperature, salinity, dissolved oxygen, pH (bottom readings), water depth, and tidal stage (ebbing or flooding) were recorded at each site during every sampling event.

Day-Night Survey

In addition to the 2012 – 2014 daytime survey, a paired day-night otter trawl survey was performed over three years (2014 – 2016) in August, September (early fall), and October at one sand site and one SAV site (Fig. 1). The two sites were sampled during daytime (at least 1 hour after sunrise) and again during the subsequent nighttime period (at least 1 hour after sunset) following the sampling and data collection protocols described above.

Data Analysis

Assemblage Composition

Fishes were classified as estuarine residents, which reside in the estuary year round, estuarine transients, which make annual migrations in and out of the estuary, southern strays and shelf strays, which are occasional visitors to the estuary from warmer southern and continental shelf waters, respectively. In addition, species-specific mean lengths and length ranges for the fishes collected during the 2012 – 2014 and 2014 – 2016 surveys were determined to investigate the influence of life history stage on habitat usage. Length frequency plots were also constructed for select species. Only fish that could be identified to species were used for all analyses in this study.

Non-metric multidimensional scaling (NMDS) was used to visualize latent dissimilarities in fish assemblage composition between upper creek, creek mouth, sand, and SAV habitats using the 2012 – 2014 daytime survey data. The species-specific abundance data from the three trawl tows at each site were combined (tows are not

independent), standardized to species-specific catch-per-unit-effort (CPUE) (number of fish/s), and all values were root-root transformed. Using these CPUE values, dissimilarities were calculated on the Bray-Curtis index and projected as NMDS with the vegan package (version 2.5-4) (Oksanen et al. 2019) in RStudio (version 1.2.5001) (RStudio Team 2019). A convergent NMDS solution was reached using two dimensions (i.e. $k = 2$) (Clarke 1993) and the results were displayed as sample and species plots. Axes in the sample plot were centered, rotated so observation variance was maximized along the first axis, and scaled so a change of one unit indicated a halving of fish assemblage similarity between observations. The locations of the species labels in the species plot are weighted averages based on the CPUE data used in the NMDS.

NMDS was also used to visualize latent dissimilarities in diel fish assemblage composition between SAV and sand habitats using the 2014 – 2016 survey data. The species-specific abundance data from the three trawl tows at each site were combined and standardized to CPUE, resulting in nine daytime and nine nighttime sampling observations within each habitat. A convergent NMDS solution was reached using two dimensions and the results were displayed as sample and species plots as described above.

Canonical Correspondence Analysis (CCA) was used to examine correlations between fish assemblage composition and the measured environmental parameters from the 2012 – 2014 daytime survey (using Canoco software, version 4.5) (ter Braak and Smilauer 2012). The root-root transformed species-specific CPUE data and corresponding environmental data were used in the CCA analysis. CCA can only utilize sampling events that collected at least one individual resulting in 440 sampling

observations for this analysis. Results of the analysis were represented as a sample and environmental biplot and a separate corresponding species plot. Monte Carlo permutation tests were used to assess the significance of the first canonical axis and the significance of all canonical axes to guard against over-interpretation. Species loadings were calculated for the first two canonical axes. Only loadings greater than 0.320 or less than -0.320 were considered noteworthy and discussed (Comrey and Lee 2013).

Abundance

Fish abundances from the 2012 – 2014 daytime survey were compared across seasons, habitats, and tidal stages. The abundance data from the three trawl tows at each site were combined (regardless of species) and standardized to overall CPUE. There was a high frequency of zero-catch sampling events in the data set (90 of 530 events, 17%) prompting the use of a Bernoulli and gamma hurdle model, also known as a zero-altered gamma (ZAG) model, for the overall CPUE data. These models assume two processes influence the observed data distribution. The Bernoulli part of the model governs if fish will be present or absent (i.e. $CPUE > 0$ or $CPUE = 0$) and the gamma part of the model influences the CPUE magnitude, given that fish are present (i.e. $CPUE > 0$) (Zuur and Ieno 2016).

A ZAG model was fit to the 2012 – 2014 overall CPUE data and included season, habitat, and tidal stage as categorical covariates. For the Bernoulli portion of the model, the overall CPUE data were converted to presence or absence data and used as the response variable. For the gamma portion of the model, only sampling observations with non-zero overall CPUE values were used for the response variable. Interaction terms

were not included in the Bernoulli portion of the model, but the two-way interactions of habitat and month and habitat and tide were included in the gamma portion of the model based on model selection using Akaike information criterion (AIC) (Burnham and Anderson 2004). A site random effect was included in both portions of the model. The lme4 package (version 1.1-21) (Bates et al. 2015) in RStudio was used to run the overall CPUE ZAG Generalized Linear Mixed Model (GLMM) and all other GLMMs in this study. All subsequent analyses in this study were also performed in RStudio.

A general linear model was fit to the 2014 – 2016 day-night survey data to investigate the influence of diel cycling on fish abundances. Prior to analysis, the abundance data from the three trawl tows at each site were combined, standardized to overall CPUE, and log transformed. Season, habitat, and time of day (i.e. day or night) were categorical covariates and the interaction terms were not included in the model based on model selection using AIC. Tide was not included in this and all other day-night models since all but one sampling event occurred during flood tide.

The emmeans package (version 1.4.3.01) (Lenth 2019) was used post-hoc to compare variables of interest in the aforementioned abundance models. The reported ratios and confidence intervals from the GLMM were back-transformed from the logit and log scales, respectively; however, Z-tests were performed on the logit and log scales (Bolker et al. 2009). Reported ratios and confidence intervals from the general linear model were back-transformed from the log scale, but T-tests were performed on the log scale. Tukey's honest significant difference method was used to adjust for multiple comparisons.

Diversity

Using the 2012 – 2014 standardized species-specific CPUE data, Shannon diversity was calculated for each sampling event that did not have zero-catch, since diversity values are only defined when at least one individual is present (Stevens 2009). This resulted in 440 usable observations (90 of 530 events had zero-catch). There was a high frequency of zero diversity sampling events (i.e. events when one species was collected) in the data set (88 of 440 events, 20%) so a ZAG model was fit to the diversity data. Like the ZAG CPUE model previously described, the ZAG diversity model assumes two processes influence the observed data distribution. The Bernoulli part of the model governs if diversity will be present or absent (i.e. diversity > 0 or diversity $= 0$) and the gamma part of the model influences the diversity magnitude, given that diversity is present (i.e. diversity > 0).

A ZAG model was fit to the 2012 – 2014 diversity data and included season, habitat, and tidal stage as categorical covariates. For the Bernoulli portion of the model, the diversity data were converted to presence or absence and used as the response variable. For the gamma portion of the model, only sampling observations with non-zero diversity values were used for the response variable. Interaction terms were not included and a site random effect was included in both portions of the model based on model selection using AIC.

In order to investigate the influence of diel cycles on fish diversity, the 2014 – 2016 species-specific CPUE data were used to calculate Shannon diversity. A general linear model was fit to these data where season, habitat, and time of day were categorical covariates and the two-way interaction for habitat and time of day was included in the

model based on model selection using AIC. Post-hoc analyses for the diversity models followed the protocol previously described for the CPUE models.

Richness

Richness was determined for the 2012 – 2014 daytime data by totaling the number of unique species collected in the three trawl tows at each sampling site and standardized by dividing by the number of tows performed at that site during the sampling event (number species collected/tow). Given the high frequency of zero-catch sampling events in the data set (17%), a ZAG model was fit to the standardized richness data, as was done for CPUE and diversity. Interaction terms were not included and a site random effect was included in both portions of the model based on model selection using AIC.

Richness was also computed for the 2014 – 2016 day-night data and standardized using the same method as above. A general linear model was fit to these data where season, habitat, and time of day were categorical covariates and the interaction terms were not included in the model based on model selection using AIC. Post-hoc analyses for the richness models followed the protocol previously described for the CPUE and diversity models.

Results

Environmental Parameters

Daytime Survey

Daytime water temperatures ranged from 8.8 – 28.6 °C and were coldest in the spring, warmed in early and late summer, and began to cool again in fall (Fig 2).

Dissolved oxygen concentrations were lowest in the summer months and slightly higher in the spring and fall. Salinity, pH, and water depth were fairly consistent across seasons (Fig. 2).

Habitats on the eastern side of the bay (sand and SAV), closest to the inlets, often had higher salinities, dissolved oxygen, and pH than those on the western side of the bay (upper creek and creek mouth) (Fig. 1 & 2). Temperature was generally similar across habitats, with slightly warmer temperatures in the creek habitats. Hypoxic conditions (< 2 mg/L) occasionally occurred in all habitats except SAV with the majority of the hypoxic events (80%) occurring in upper creeks. Observed pH values ranged from 5.67 – 8.41 with the lowest pH values consistently recorded in upper creeks due to the influence of acidic Pine Barrens freshwater (Good and Good 1984). Upper creek and sand habitats had deeper water depths than creek mouth and SAV habitats (Fig. 2).

Temperature, dissolved oxygen, pH, and water depth were similar across tidal stages (Online Resource 1). In most habitats, salinity was slightly lower during ebb tides and higher during flood tides.

Macroalgae was observed in all seasons. The volume of macroalgae collected was smallest in the spring and increased in early summer, late summer, and fall (Table 1). Macroalgae was present in all habitats sampled. The largest volumes were collected in creek mouths. The smallest volumes of macroalgae were collected in sand upper creek habitats (Table 1). Macroalgae volume was similar during ebb and flood tides in all habitats (Online Resource 1).

Day-Night Survey

Water temperatures were warmest in August (24.8 ± 0.4 °C) and September (23.8 ± 0.3 °C) and cooled rapidly by October (18.4 ± 0.1 °C). Dissolved oxygen displayed the opposite trend of temperature, with values increasing in the fall (7.17 ± 0.22 mg/L) from lower concentrations in late summer (6.21 ± 0.27 mg/L) and early fall (6.26 ± 0.36 mg/L). Seasonal trends were not observed for salinity, pH, and water depth. Temperature, salinity, dissolved oxygen, pH, and water depth were similar between daytime and nighttime sampling events and across habitats (Table 2). Hypoxic conditions were not observed during the day-night survey.

Macroalgae was most abundant in August (0.292 ± 0.098 L/s) and September (0.238 ± 0.075 L/s) and less abundant in October (0.167 ± 0.070 L/s). Larger volumes of macroalgae were collected in the SAV habitat compared to the sand habitat, and the volume of observed macroalgae was similar during daytime and nighttime sampling events (Table 2).

Assemblage Composition

Daytime Survey

The fishes inhabiting Barnegat Bay represented varied modes of estuarine usage from estuarine transients ($n = 37$, e.g. bluefish *Pomatomus saltatrix*) and estuarine residents ($n = 22$, e.g. oyster toadfish *Opsanus tau*) to southern strays ($n = 14$, e.g. Atlantic moonfish *Selene setapinnis*) and shelf strays ($n = 3$, e.g. butterfish *Peprilus triacanthus*) (Table 3). The majority of fishes collected were young of the year juveniles

and species with small adult stages (e.g. bay anchovy *Anchoa mitchilli*), but larger individuals of certain species (e.g. summer flounder *Paralichthys dentatus*) were also collected (Table 3).

Fishes representing these life history stages were found in all habitats sampled. For some species, such as *A. mitchilli*, various life history stages often utilized the same habitats, as indicated by similar mean lengths and length ranges across habitat types (Fig. 3, Table 3). However, for other species, differences in habitat utilization by fish of varied life history stages were evident (Fig. 3). Larger silver perch *Bairdiella chrysoura* were found in sand habitat compared to all the other habitats. Similarly, spot *Leiostomus xanthurus* were larger in sand and creek mouth habitats than upper creeks or SAV, with the smallest individuals entirely absent from sand habitat. Additionally, the smallest and largest *P. dentatus* were most abundant in creek mouths and sand habitats and were less abundant in upper creeks or SAV habitats (Fig. 3, Table 3).

Fish assemblage composition shifted seasonally with some species only collected in a single month sampled and others collected across all months sampled (Table 4). For example, pollock *Pollachius virens*, a cool-water transient species, was only collected in April whereas fourspine stickleback *Apeltes quadracus*, an estuarine resident, was collected in all months sampled.

There was a large degree of overlap in fish assemblage composition between habitats (Fig. 4, Table 4). Only thirty six percent of the species collected were exclusively observed in a specific habitat; however, the majority of these species (88%) were rarely encountered (i.e. only one or two individuals were collected throughout the entire sampling duration), with the exception of inland silverside *Menidia beryllina*,

pumpkinseed *Lepomis macrochirus*, and black drum *Pogonias cromis*, of which 35, 9, and 4 individuals were collected solely in upper creek habitat, respectively (Table 4). The fish assemblages in upper creek and SAV were the most dissimilar in terms of species composition (Fig. 4).

In congruence with the NMDS analysis, the CCA indicated there was a large degree of overlap in fish assemblage composition among habitats (Fig. 5). Monte Carlo permutation tests indicated significance of the first canonical axis ($p = 0.004$) and all canonical axes ($p = 0.002$) in the CCA. Canonical axes only accounted for 3% of the total variation in the fish assemblage data. The first (39.4%) and second (27.3%) canonical axes accounted for over half of that 3% and therefore other axes are not discussed. The species-environmental correlations for the first two axes were high (0.615 and 0.613, respectively), but given the low percentage of the variance explained by the measured environmental parameters, factors not considered in this analysis must also be important in structuring these fish assemblages (McGarigal et al. 2000).

Of the measured environmental parameters, the water depth gradient was the most important in structuring the first axis, followed closely by the inversely correlated dissolved oxygen gradient (Fig. 5). Slight separation of samples from different habitats was evident along the first axis. SAV and creek mouth samples were grouped tighter near the high dissolved oxygen and shallow water depth portions of those gradients compared to sand and upper creek samples which were dispersed across the entire dissolved oxygen and water depth gradients. On the second axis, the temperature gradient accounted for the most variation.

Anchoa mitchilli, *A. quadracus*, Atlantic cod *Gadus morhua*, *L. xanthurus*, Atlantic silverside *Menidia menidia*, and northern pipefish *Syngnathus fuscus* loaded onto the first axis (Fig. 5, Online Resource 2). *Anchoa mitchilli*, *G. morhua*, and *L. xanthurus* were positively correlated with the first axis whereas the other three species were negatively correlated with the first axis and were closely associated with SAV habitat. *Anchoa mitchilli* negatively loaded- and spotted hake *Urophycis regia* and *P. virens* positively loaded- onto the second axis. As would be expected for cool-water transient species, *U. regia* and *P. virens* were associated with colder water temperatures (Fig. 5, Online Resource 2).

Species composition was fairly consistent across tidal stages, with many of the dominant species in the estuarine assemblage collected during both ebb and flood tides (Online Resource 3). Fishes that were collected during both tidal stages included estuarine residents, such as *A. quadracus* and *O. tau*, and transient species, such as *A. mitchilli* and *B. chrysoura*.

Day-Night Survey

The majority of fishes collected were juveniles and species with small adult stages (Table 5), and fishes representing these life history stages were collected both during the daytime and at nighttime. Large differences in mean length between fishes collected during daytime or nighttime were absent for the majority of species, including *Menidia menidia* (Table 5). However, *A. mitchilli* collected during the daytime in SAV were much smaller on average than those collected at nighttime in SAV and within sand habitat (Fig.

6, Table 5). Additionally, mean *B. chrysoura* length was smaller during the daytime than at nighttime in SAV habitat (Fig. 6, Table 5).

There was considerable overlap in fish assemblage composition between sand and SAV habitats (Fig. 7, Table 2). Additionally, daytime and nighttime fish assemblages were composed of many of the same species, but the extent of this similarity was habitat dependent. Fish assemblage composition in SAV was relatively similar, whereas in sand habitat a larger composition shift was evident between daytime and nighttime (Fig. 7, Table 2). Dusky anchovy *Anchoa lyolepis*, conger eel *Conger oceanicus*, and striped searobin *Prionotus evolans* were only observed during the day-night survey. Only one *A. lyolepis* and *P. evolans* each were collected (*A. lyolepis* during daytime and *P. evolans* during nighttime), whereas three *C. oceanicus* were collected all at nighttime.

Abundance

Daytime Survey

Over the sampling duration, a total of 33,048 fish were collected (Table 4). The odds of fish presence (Bernoulli portion of the CPUE ZAG GLMM) varied with season and habitat (Online Resource 4). Fish were less likely to be present in April compared to June (Odds Ratio [OR]: 0.134, 95% Confidence Interval [CI]: 0.054 – 0.331, $p < 0.001$), August (OR: 0.053, CI: 0.016 – 0.177, $p < 0.001$), and October (OR: 0.130, CI: 0.053 – 0.322, $p < 0.001$). No consistent trends were observed in fish presence odds for the June to August, June to October, and August to October comparisons (Online Resource 4).

The odds of fish presence ranged from lower to about equal in sand relative to SAV (OR: 0.380, CI: 0.143 – 1.009, $p = 0.053$) (Online Resource 4). Fish were less likely

to be present in upper creeks compared to creek mouths (OR: 0.303, CI: 0.092 – 0.992, $p = 0.048$) and more likely to be present in creek mouths than sand habitat (OR: 3.385, CI: 1.114 – 10.285, $p = 0.025$). Fish presence odds were roughly the same in upper creeks compared to sand habitat (OR: 1.025, CI: 0.420 – 2.499, $p = 1.000$) and creek mouths compared to SAV (OR: 1.285, CI: 0.376 – 4.394, $p = 0.953$). No consistent differences in fish presence odds were observed between upper creek and SAV habitats (OR: 0.389, CI: 0.135 – 1.118, $p = 0.099$). Tidal stage did not influence the odds of fish presence (OR: 1.357, CI: 0.801 – 2.301, $p = 0.257$) (Online Resource 4).

CPUE magnitude (gamma portion of the CPUE ZAG GLMM) varied with season (Online Resource 4). In all habitats, CPUE was smaller in April than in June, August, and October. June CPUE was also smaller than August and October CPUE in all habitats except upper creeks where no differences were observed. No trend was observed in the August and October CPUE comparison for any habitats (Online Resource 4). June was the only month where consistent differences in CPUE magnitude between habitats were observed. In June, upper creek CPUE was larger than sand CPUE (Ratio [R]: 3.828, CI: 1.315 – 11.147, $p = 0.007$) and sand CPUE was smaller than SAV CPUE (R: 0.359, CI: 0.130 – 0.992, $p = 0.047$). Tidal stage influenced CPUE magnitude in two of the four habitats sampled (Online Resource 4). CPUE was larger in upper creeks (R: 2.246, CI: 1.252 – 4.030, $p = 0.007$) and creek mouths (R: 1.778, CI: 1.028 – 3.073, $p = 0.039$) on ebb tides compared to flood tides. CPUE was fairly consistent across tidal stages in sand (R: 1.034, CI: 0.642 – 1.664, $p = 0.892$) and SAV (R: 0.980, CI: 0.550 – 1.745, $p = 0.945$) habitats.

Species-specific CPUE fluctuated seasonally (Table 4). *Anchoa mitchilli* was the most abundant species in all seasons sampled. Many species had the majority of their catch (i.e. greater than 50%) collected in either early or late summer. These species included winter flounder *Pseudopleuronectes americanus* (early), weakfish *Cynoscion regalis* (late), and *B. chrysoura* (late), among others. Fewer species had the majority of their catch collected in spring and fall (Table 4).

Anchoa mitchilli was the most abundant species collected in upper creek, creek mouth, and sand habitats, and *M. menidia* was the most abundant species collected in SAV habitat (Table 4). Various species were ubiquitous habitat users. These species included *A. mitchilli*, *B. chrysoura*, and *P. dentatus*, among others (Table 4). However, other species were more prevalent in one particular habitat. These species included *A. quadracus*, lined seahorse *Hippocampus erectus*, *M. menidia*, and *S. fuscus* (SAV), naked goby *Gobiosoma bosc* (creek mouth), and Atlantic menhaden *Brevoortia tyrannus*, *L. xanthurus*, and *M. beryllina* (upper creek) (Table 4).

Large differences in individual species CPUE between tidal stages were not observed, but smaller variations were evident for some fishes (Online Resource 3). *Gobiosoma bosc* were more abundant on ebb tides in upper creek, creek mouth, and sand habitats. *Paralichthys dentatus* were also more abundant on ebb tides in upper creek and sand habitats as were *P. americanus* in creek mouth and sand habitats (Online Resource 3). In SAV, *L. xanthurus* CPUE was larger on ebb tides than flood tides. *Brevoortia tyrannus* were more abundant in creek mouths on flooding than ebbing tides and more abundant in upper creeks on ebbing than flooding tides (Online Resource 3).

Day-Night Survey

Nearly 6,000 fish were collected during the day-night survey (Table 2). CPUE ranged from about equal to much larger in August relative to October (R: 3.038, CI: 0.905 – 10.196, $p = 0.077$) (Online Resource 5). There were no consistent differences in CPUE between August and September (R: 1.827, CI: 0.544 – 6.130, $p = 0.448$) and September and October (R: 1.663, CI: 0.496 – 5.582, $p = 0.561$). CPUE was smaller at the sand site compared to the SAV site (R: 0.231, CI: 0.102 – 0.525, $p = 0.001$) and did not exhibit a clear trend between daytime and nighttime (R: 1.287, CI: 0.567 – 2.920, $p = 0.534$) (Online Resource 5).

Menidia menidia was the most abundant species collected at the SAV site during daytime or nighttime (Table 2). At the sand site, *M. menidia* was the most abundant species during the day and *M. menidia* and *S. fuscus* were the most abundant species at night. Similar to daytime sampling, *A. quadracus*, *M. menidia*, and *S. fuscus* were more prevalent in SAV than sand habitat. Seventy four percent of species had the majority of their catch collected during nighttime, including *B. chrysoura*, black seabass *Centropristis striata*, and *P. americanus*. In contrast, *A. mitchilli* and *M. menidia* were among the species that were more prevalent during the day, particularly in sand habitat (Table 2).

Diversity

Daytime Survey

Mean Shannon diversity ranged from 0.425 to 0.977 across the months and habitats sampled (Table 1). The odds of observing diversity in April were lower than in

August (R: 0.382, CI: 0.148 – 0.985, $p = 0.045$), but were not consistently different for the other monthly comparisons (Online Resource 6). Diversity ranged from more likely to be observed to roughly equal odds of occurrence in creek mouths compared to sand habitats (R: 2.532, CI: 0.998 – 6.421, $p = 0.051$). No consistent trends were observed in diversity presence odds for the remaining habitat comparisons. Tidal stage did not influence the odds of observing diversity (R: 0.921, CI: 0.561 – 1.510, $p = 0.744$) (Online Resource 6).

Diversity was larger in June relative to August (R: 1.276, CI: 1.017 – 1.600, $p = 0.030$), but there were no clear differences in diversity magnitude between April and June, April and August, April and October, June and October, and August and October (Online Resource 6). Creek mouth diversity was larger than sand diversity (R: 1.382, CI: 1.029 – 1.857, $p = 0.025$), sand diversity was smaller than SAV diversity (R: 0.699, CI: 0.524 – 0.931, $p = 0.007$), and creek mouth diversity was roughly equal to SAV diversity (R: 0.966, CI: 0.711 – 1.312, $p = 0.991$). No consistent trends were observed for the upper creek to creek mouth, upper creek to sand, and upper creek to SAV diversity comparisons. Further, there was no consistent difference in diversity between tidal stages (R: 1.054, CI: 0.917 – 1.210, $p = 0.460$) (Online Resource 6).

Day-Night Survey

Diversity did not differ between August, September, and October (Online Resource 5). At night, sand diversity was larger than SAV diversity (Difference [D]: 0.704, CI: 0.321 – 1.087, $p = 0.001$). There was no consistent difference between habitat diversity during the day (D: -0.168, CI: -0.551 – 0.215, $p = 0.378$). Within sand habitat,

diversity was much smaller during daytime compared to nighttime (D: -1.135, CI: -1.518 – -0.752, $p < 0.001$), but there was no clear difference between daytime and nighttime diversity within SAV habitat (D: -0.263, CI: -0.646 – 0.120, $p = 0.171$) (Online Resource 5).

Richness

Daytime Survey

Seventy species were collected throughout daytime sampling with the largest richness values occurring summer through fall (Table 1 & 4). Due to the nature of presence and absence data, the odds of observing richness (Online Resource 7) are identical to the odds of fish presence (Online Resource 4), which were previously described in the “Abundance: Daytime Survey” section and therefore are not repeated here.

The magnitude of observed richness varied with season and habitat (Online Resource 7). Richness was smaller in April than in June (R: 0.644, CI: 0.512 – 0.810, $p < 0.001$), August (R: 0.480, CI: 0.383 – 0.602, $p < 0.001$), and October (R: 0.625, CI: 0.498 – 0.785, $p < 0.001$). June richness was also smaller than August richness (R: 0.746, CI: 0.612 – 0.908, $p = 0.001$), and August richness was larger than October richness (R: 1.303, CI: 1.072 – 1.583, $p = 0.003$). No trend was observed in the June and October richness comparison (R: 0.971, CI: 0.797 – 1.184, $p = 0.982$) (Online Resource 7).

Richness was larger in creek mouths than in sand habitat (R: 1.508, CI: 1.122 – 2.029, $p = 0.002$) and smaller in sand habitat relative to SAV (R: 0.686, CI: 0.517 – 0.912, $p = 0.004$). Creek mouth richness was roughly equal to SAV richness (R: 1.035,

CI: 0.756 – 1.419, $p = 0.992$). No consistent trends were observed for the upper creek to creek mouth, upper creek to sand, and upper creek to SAV comparisons. Richness did not differ between tidal stages (R: 1.027, CI: 0.911 – 1.158, $p = 0.662$) (Online Resource 7).

Day-Night Survey

Thirty one species were collected throughout the sampling duration (Table 2). Richness was larger in August than October (D: 0.903, CI: 0.182 – 1.623, $p = 0.012$) and ranged from roughly equal to larger in September compared to October (D: 0.667, CI: -0.054 – 1.387, $p = 0.074$) (Online Resource 5). There were no consistent differences in richness between August and September (D: 0.236, CI: -0.484 – 0.957, $p = 0.702$) or the sand and SAV sites (D: -0.083, CI: -0.571 – 0.404, $p = 0.730$). However, daytime richness was smaller than nighttime richness (D: -1.083, CI: -1.571 – -0.596, $p < 0.001$) (Online Resource 5).

Discussion

Upper marsh creeks, marsh creek mouths, sand, and SAV were all important fish habitats within the subtidal habitat mosaic of a temperate lagoonal estuary. The analyzed structural characteristics (composition, abundance, diversity, richness, lengths) indicated these habitats supported abundant and diverse fish assemblages composed of fishes from many life history stages and with varied modes of estuarine usage. Collected fishes included shelf and southern strays, estuarine residents, and transient species from cold and warm waters, signifying the importance of the habitat mosaic within this Mid-

Atlantic Bight estuary to the broader coastal estuarine seascape as both year round and seasonal fish habitat.

Temporal Variation

The observed seasonal shifts in fish composition, abundance, diversity, and richness in this study are typical of estuaries and have been previously documented in the lower portion of this estuary (Szedlmayer and Able 1996; Jivoff and Able 2001), other estuaries along the U.S. east and Gulf coasts (Ross et al. 1987; Heck et al. 1989; Able et al. 1996), and estuaries located on other continents (Claridge et al. 1986; Hoeksema and Potter 2006; Plavan et al. 2010). Along the U.S. east coast, these shifts are driven by seasonal migrations and spawning patterns, which directly influence the occurrence of juveniles within- (Able and Fahay 2010; Furey and Sulikowski 2011) and supply of larval fishes to- estuaries (Able and Fahay 1998; Love et al. 2009; Able et al. 2017). These seasonal shifts driven by migrations and spawning occur on an annual basis, and although species abundances tend to vary from year to year, estuarine species composition often remains relatively constant (Jackson and Jones 1999; Witting et al. 1999; James et al. 2008), even following episodic disturbance events, as was observed for the fish assemblage in this study system following Hurricane Sandy (Valenti et al. 2020).

Although the Barnegat Bay fish assemblage was relatively stable in the years following the storm (Valenti et al. 2020), when Hurricane Sandy made landfall just south of the bay in late October 2012 (National Oceanic and Atmospheric Administration 2013), natural and anthropogenic debris washed into estuarine and coastal waters potentially impacting the bay's subtidal habitat mosaic (Bilinski et al. 2015). However,

habitat designations were consistent throughout the duration of this study indicating that Hurricane Sandy did not significantly modify or destroy the defining structural elements of the assessed habitats.

Habitat and Tidal Influence

Marsh creeks, sand, and SAV were critical components of the bay's subtidal habitat mosaic. The fish assemblages in these habitats shared many species in common; however, the odds of fish presence, diversity, and richness, the magnitudes of these metrics, and species-specific abundances varied between habitats, emphasizing the importance, but also the uniqueness of each habitat to the subtidal habitat mosaic. In particular, creek mouths often had higher odds of presence and larger magnitudes for diversity and richness when compared to sand habitats, and similar results were obtained when SAV was compared to sand habitat. These results support the general consensus that fishes are often more abundant and assemblages more diverse within SAV compared to sand (Connolly 1994; Gray et al. 1996; Jenkins et al. 1997; Arrivillaga and Baltz 1999; Mattila et al. 1999; Castillo-Rivera et al. 2002; Ribeiro et al. 2006) and confirmed the hypothesis that marsh creeks, especially creek mouths, serve as important habitat in addition to SAV within the habitat mosaic of this temperate lagoonal estuary.

Although few other studies have explicitly compared subtidal marsh creek fish assemblages to those in other habitats, especially across expansive spatial and temporal scales, those available still provide for valuable comparison. Weinstein and Brooks (1983) evaluated nighttime fish community composition and structure in a tidal marsh creek (two sites: upstream and downstream) and an adjacent seagrass bed (two sites: Z.

marina and *R. maritima*) within the Chesapeake Bay (Virginia). They determined richness and diversity were higher in the sea grass bed, fishes were more abundant in the marsh creek, and both habitats supported habitat specialist and ubiquitous fish species. Within lower Barnegat Bay and adjacent Great Bay, Szedlmayer and Able (1996) found eelgrass habitat had higher richness than lower salinity marsh creek and sand habitats, but CPUE was similar across habitat types.

These studies support the notion that marsh creeks are important habitat for estuarine fishes, but they differ from the current study in that SAV habitat was more diverse and supported higher richness than marsh creek habitat. In addition to the Weinstein and Brooks (1983) study being conducted at nighttime, a potential reason for these differing results is the number of sites (habitat replicates) sampled. Weinstein and Brooks (1983) evaluated two seagrass sites and two marsh creek sites, and Szedlmayer and Able (1996) sampled two eelgrass, two upper creek, and three sand sites. The relatively small sample sizes in these studies may lend localized, site-specific conclusions that may not always be applicable at larger spatial scales (Wiens 1989; Bell et al. 1992). Further, it is important to emphasize that the creek sites in Szedlmayer and Able (1996) were lower salinity, upper creeks, as was one of the creek sites in Weinstein and Brooks (1983). These creek sites are analogous to the upper creek habitat in this study, and therefore a direct comparison of creek mouth habitats, which exhibited abundance, diversity, and richness values similar to those in SAV habitat in this study, was not possible.

The high diversity and richness observed at creek mouths likely resulted from a variety of interacting environmental factors. Similar to SAV sites, creek mouths tended to

be shallow, fairly well oxygenated, and had higher salinities and complex physical structure (macroalgae, marsh banks), distinguishing them from upper creek (deeper, lower salinity, lower dissolved oxygen) and sand (deeper, unstructured/less complex structure) habitats. Water depth (Baltz et al. 1993; Akin et al. 2003; Rypel et al. 2007), salinity (Loneragan et al. 1987; Barletta et al. 2005), and dissolved oxygen (Fraser 1997; McKinsey and Chapman 1998) are known to influence fish assemblage structural characteristics, as was evident in this study where water depth and dissolved oxygen gradients accounted for the majority of inter-habitat variation in fish assemblages. In addition, the rugose nature of marsh creek banks and the abundance of macroalgae in creek mouths may provide refuge from predators in a way similar to seagrasses (Gillanders 2006). The predation refuge afforded by seagrass beds is often cited as a driver of the high fish diversity and richness observed there (Orth et al. 1984; Main 1987; Heck et al. 1997; Heck and Orth 2006), and although large volumes of macroalgae can negatively impact estuarine fish and crab abundances and diversity (Deegan et al. 2002), it has also been demonstrated to support high abundances of fishes and crabs and provide shelter from predators (Kulczycki et al. 1981; Wilson et al. 1990; Sogard and Able 1991; Heck et al. 2003; Adams et al. 2004).

Further, salt marshes are known to be highly productive ecosystems (Costanza et al. 1997; Wilson 2002; Costanza et al. 2014) that serve as habitat for a variety of fishes and other fauna (Rountree and Able 2007). These fishes convert marsh production to biomass, which is transferred to nearby estuarine waters through predator – prey interactions (Stevens et al. 2006); this process was described by Kneib (1997) as the “trophic relay”. A clear example of the trophic relay occurs when fishes make foraging-

based migrations up marsh creeks during flooding tides in order to access the marsh surface and subsequently migrate back down the creeks as water levels start to ebb (Kleypas and Dean 1983; Hettler 1989; Rountree and Able 1992a; Potthoff and Allen 2003). In this study, tidal related changes in subtidal fish assemblage abundance (overall and species-specific) were observed in upper creek and creek mouth habitats and likely coincided with fish movements up and down marsh creeks. Tides are known to modify intertidal fish assemblage structure (Kneib and Wagner 1994; Hampel et al. 2003; Kimball and Able 2012) and are a main factor in the transfer of energy from the marsh to the estuary (Rozas 1995). The high productivity of the marsh ecosystem, availability of prey items and predation refuge, and direct access to the marsh surface via tidal cycles may have all played a role in supporting the diverse fish assemblages observed in marsh creek mouths.

Species-specific Trends

The fishes documented in this study closely reflect fish collections from previous studies performed at the southern end of Barnegat Bay and in adjacent Great Bay and often exhibited similar habitat-specific use patterns (Sogard and Able 1991; Rountree and Able 1992b; Able et al. 1996; Szedlmayer and Able 1996; Jivoff and Able 2001). Many species collected were ubiquitous habitat users and several did not have the majority of their catch occur in one particular habitat, such as *A. mitchilli*, *B. chrysoura*, and *P. dentatus*. This is a commonality of many estuarine fishes along the U.S. east coast (Able and Fahay 2010).

Contrary to those with ubiquitous habitat usage, certain fishes did exhibit habitat-specific utilization patterns. The majority of *G. bosc* were collected in creek mouths with many also collected in upper creeks and far fewer observed in sand or SAV habitats. This trend coincided with that of Jivoff and Able (2001). Sogard and Able (1991) observed the opposite trend, with more *G. bosc* in SAV than creeks, but the creeks they sampled were unvegetated in contrast to the large abundances of macroalgae in creeks in this study which may explain the discrepancy in habitat use patterns. In other estuaries where they are present, oyster reefs are common habitat of *G. bosc* (Dahlberg and Conyers 1973; Breitburg 1989; Harding and Mann 2000; Lehnert and Allen 2002; Harding et al. 2020), but in estuaries such as Barnegat Bay where oyster reefs are not abundant, marshes may provide the best alternate structure (Hendon et al. 2000; Peterson et al. 2000).

Brevoortia tyrannus, *L. xanthurus*, and *M. beryllina* were most abundant in the lower salinity, upper creek habitat. *Brevoortia tyrannus* were documented in higher abundances in upper creeks on ebbing tides, possibly as they moved out of areas with receding water levels, and in higher abundances in creek mouths on flooding tides, likely as they entered the creeks. Larval and juvenile *B. tyrannus* utilize freshwater and lower salinity habitats and eventually move into higher salinity areas as they continue to grow (Lewis et al. 1972; Able et al. 2007). Previous studies have documented this habitat use pattern in New Jersey (Rountree and Able 1992b; Szedlmayer and Able 1996; Jivoff and Able 2001) and elsewhere (Friedland et al. 1996; Love et al. 2006; Houde et al. 2016). *Leiostomus xanthurus* often utilize lower salinity portions of estuaries (Massman 1954), though they can be found in higher salinity areas as well (Szedlmayer and Able 1996; Jivoff and Able 2001), as was observed in this study. As such, the upper and mouth

portions of marsh creeks are important habitat for *L. xanthurus* (Weinstein and Brooks 1983; Weinstein et al. 1984; Ross 2003; Able et al. 2007) and provide tidal access to the marsh surface for foraging (Currin et al. 1984; O'Neil and Weinstein 1988; Hettler 1989; Feller et al. 1990). *Menidia beryllina* were only collected in upper creek habitat. They tend to inhabit lower salinity, upper reaches of estuaries (Gosline 1948; Weinstein et al. 1980; Bengtson 1984), including marsh pools (Talbot and Able 1984; Coorey et al. 1985), which are in close proximity to submerged vegetation (Franks 1970) upon which they likely attach their eggs (Able and Fahay 2010). Earlier studies have noted higher abundances of *M. beryllina* in creeks compared to other habitats with subtidal habitat mosaics (Able et al. 1996; Jivoff and Able 2001).

Various estuarine species were consistently more abundant in SAV than other subtidal estuarine habitats. The vast majority of *A. quadracus* were collected in SAV where they commonly build nests (Reisman 1963; Rowland 1974; Courtenay and Keenleyside 1983). This habitat use pattern is consistent throughout the range of *A. quadracus* (Maine to Virginia) (Weinstein and Brooks 1983; Heck et al. 1989; Sogard and Able 1991; Raposa and Oviatt 2000; Lazzari et al. 2003). In this study, *H. erectus* were most abundant in SAV, though they were collected in all other habitats as well. Support for this habitat association from past studies is mixed. Some indicated *H. erectus* may have an inclination for SAV (Weinstein and Brooks 1983) and algae habitats (Sogard and Able 1991; Able and Fahay 1998), but others reported this species also occurred in unvegetated substrates (Rountree and Able 1992b; Able et al. 1996; Fraser 1997; Teixeira and Musick 2001). *Menidia menidia*, a pelagic species, have been collected in nearly all estuarine habitats (Richards and Castagna 1970; Hettler 1989;

Szedlmayer and Able 1996; Jivoff and Able 2001). Similar to *M. beryllina*, they rely upon vegetation, largely *S. alterniflora* and algae mats, as a substrate to attach their eggs (Middaugh 1981; Middaugh et al. 1981; Conover and Kynard 1984; Balouskus and Targett 2012). Here, *M. menidia* were most abundant in SAV which contrasts Sogard and Able (1991) where the majority were observed in marsh creeks. *Syngnathus fuscus* was another SAV habitat specialist, with the second largest abundances observed in macroalgae rich creek mouths. This association with vegetated habitats has also been documented in Maine (Lazzari and Stone 2006), Massachusetts (Heck et al. 1989), New York (Briggs and O'Connor 1971; Raposa and Oviatt 2000), Virginia (Weinstein and Brooks 1983), and previously in New Jersey (Tatham et al. 1984; Sogard and Able 1991; Jivoff and Able 2001).

In addition to habitat-specific usage patterns, some species exhibited different trends in habitat use with ontogeny – a common occurrence among marine and estuarine fishes (Gillanders et al. 2003; Dando 2011; Kimirei et al. 2013; Amorim et al. 2018). Larger *B. chrysoura* and *L. xanthurus* were found in sand habitat compared to SAV habitats. Beds of SAV often contain many juvenile and small adult fishes while unvegetated habitats are dominated by larger individuals (Bell and Pollard 1989; Connolly 1994; Gray et al. 1996), likely due to the lack of predation refuge provided for their prey (Orth et al. 1984; Heck et al. 1997). For *P. dentatus*, the smallest and largest individuals were most abundant in creek mouth and sand habitats indicating that these habitats may offer some benefit (e.g. predation refuge, food) to individuals of this species. Previous studies have demonstrated marsh creeks serve as important young of year habitat for *P. dentatus* (Wyanski 1990; Packer et al. 1999), and that juvenile and

adult *P. dentatus* undergo tidal driven foraging migrations in and out of marsh creeks (Rountree and Able 1992a; Szedlmayer and Able 1993).

Diel Patterns

Comparison of the habitat related results from the daytime and day-night surveys yielded mixed conclusions. In the day-night study, CPUE was smaller in sand than SAV habitat, which coincided with the finding of the larger daytime study, though only for the month of June. However, richness did not differ between the two habitats in the day-night study which was in contrast to the daytime study where richness was larger in SAV than sand habitat. Further, in the daytime study, diversity was larger in SAV compared to sand whereas in the day-night study diversity only differed at night and was larger at the sand site. The findings of these two studies highlight the importance of site selection and spatial and temporal scales in the results of scientific studies (Wiens 1989; Bell et al. 1992; Hyndes et al. 2018).

Daytime and nighttime fish assemblages shared many of the same species, but composition shifts were evident, particularly in sand habitat where predatory fishes (e.g. *C. striata*, *B. chrysoura*, *P. dentatus*, *P. americanus*) emerged or became more abundant at night. Various other studies have noted diel shifts in fish assemblage composition (Rountree and Able 1993; Gray et al. 1998; Hoeksema and Potter 2006; Hagan and Able 2008) and the increase in abundance of predatory fishes at nighttime (Robblee and Zieman 1984; Becker and Suthers 2014). In addition, although day-night differences in length were not observed for the majority of species, *B. chrysoura* were notably larger on average at night in SAV due to bigger individuals (> 90 mm) collected solely at

nighttime. In Florida, *B. chrysoura* are known to be nocturnally active (Livingston 1976; Sogard et al. 1989) and larger predatory fishes commonly make foraging migrations into shallower areas at night (Robblee and Zieman 1984; Rountree and Able 1997; Gray et al. 1998; Becker and Suthers 2014).

Even though overall CPUE did not differ between daytime and nighttime, which is contrary to usual findings (Orth and Heck 1980; Unsworth et al. 2007; Johnson et al. 2008; Castillo-Rivera et al. 2010; but see Sogard et al. [1987]), common prey species, such as *M. menidia*, were less abundant at night in the sand habitat. In a study involving artificial seagrass plots in a cove adjacent to Barnegat Bay, Sogard and Able (1994) also documented fewer *M. menidia* at nighttime. Becker and Suthers (2014) found that bait fish schooling was common during the day, but this behavior did not persist at night and fishes became more dispersed. This may explain the decreased bait fish abundance observed here; however, the possibility that these fishes also relocated to other habitats not sampled at night (e.g. marsh creeks, see Rountree and Able [1993]) cannot be dismissed (Becker et al. 2011).

The increase in species diversity (Mattila et al. 1999; Morrison et al. 2002) and richness (Robblee and Zieman 1984; Methven et al. 2001; Hoeksema and Potter 2006; Unsworth et al. 2007) at night documented here has also been observed in other nearshore marine and estuarine habitats. Diel variations in species composition, abundance, diversity, richness, and lengths are often driven by the availability of prey items and changing predation pressures (Robertson 1980; Sogard and Able 1994; Hindell et al. 2000). However, the observed increases in select species CPUE and lengths, diversity, and richness at night could also be a function of gear avoidance. Fish can more

easily visualize and avoid the sampling gear during the day, but due to decreased visibility, can do so less effectively at night resulting in increased abundances and diversity documented during nighttime sampling (Rountree and Able 1993; Guest et al. 2003).

Summary and Conclusions

The influence of season, time of day, and tidal stage on fish assemblages inhabiting subtidal marsh creeks, sand, and SAV habitats within a temperate lagoonal estuary (Barnegat Bay, New Jersey) were quantified using structural characteristics (species composition, abundance, diversity, richness, length) in order to understand the importance and function of subtidal marsh creeks relative to SAV within the habitat mosaic. All habitats sampled were frequented by juvenile and adult resident, transient, southern stray, and shelf stray species in all seasons indicating the importance of the habitat mosaic in this estuary to the broader Mid-Atlantic Bight seascape (Able and Fahay 1998; Able and Fahay 2010). Many fishes were ubiquitous habitat users, but some were habitat specialists, demonstrating the value and unique nature of each of the four habitats sampled to the estuarine habitat mosaic (Nagelkerken et al. 2015). This study also highlighted the considerations of site selection, as not all sites representing the same habitat will afford equal value, and spatial and temporal scales when drawing broad conclusions regarding habitat importance (Wiens 1989; Bell et al. 1992; Boström et al. 2011; Hyndes et al. 2018; Schrandt et al. 2018).

The creek mouths sampled in this study contained large volumes of macroalgae and supported particularly diverse fish assemblages rivaling that of SAV, though species

composition in these two habitats was certainly not identical and the two habitats are by no means redundant or interchangeable (Sogard and Able 1991; Jenkins et al. 2015).

Further study comparing subtidal marsh creek fish assemblages, especially those in creek mouths, in relation to other structural and non-structural habitats are warranted given the current lack of research available on this subject (Heck et al. 2003; Gillanders 2006; Boström et al. 2011; Hyndes et al. 2018) and the growing realization that the presence of structure in general may be as or more important than the actual type of structure itself (e.g. seagrass versus oyster reefs) in supporting fish assemblages (Jenkins and Wheatley 1998; Heck et al. 2003).

Specifically, valuable studies would: (i) investigate the potential for subtidal creek mouths to serve as nursery habitat as defined by Beck et al. (2001), (ii) document exactly how fishes are utilizing this habitat (e.g. shelter, foraging, etc.) to truly ascertain the value of creek mouths as habitat (Sheaves et al. 2015), (iii) explore the ability for subtidal creek mouths to support abundant and diverse fish assemblages when macroalgae is not present given its ephemeral nature (Sogard and Able 1991; Wilson et al. 2014) and assumed importance in serving as structure to the fish assemblage observed there, (iv) take place in other estuarine systems with environmentally (e.g. salinity, depth) similar and dissimilar creeks to explore the trends observed here across geographic and environmental gradients (Bradley et al. 2019), and (v) include the influence of complete seasonal, diel, and tidal cycles, unlike the coarser scales used to assess these variables here, given the clear effect these variables have on fish assemblage structure (Rountree and Able 1993; Kneib and Wagner 1994; Able and Fahay 2010).

Fully understanding the function of marsh creeks within estuarine seascapes is important given the continued urbanization (anthropogenic land development) of coastal areas. The *S. alterniflora* dominated shorelines of many temperate marsh creeks are developed and armored (e.g. bulkheaded), and in some cases transformed into lagoons for housing development. The main stems of these urbanized creeks are often dredged with subsequent impacts to creek structure and water quality (Sugihara et al. 1979, and here where 80% of hypoxic conditions occurred in upper creeks), and this in turn can alter the fish communities residing there (Bilkovic 2011; Lowe and Peterson 2014). The urbanization of marsh creeks and impacts to other intertidal and subtidal habitats pose a threat to estuarine nursery seascapes worldwide, especially those within lagoonal estuaries which are highly susceptible to anthropogenic habitat degradation (Kennish et al. 2008; Kennish and Paerl 2010b; Pérez-Ruzafa et al. 2019).

Lagoonal estuaries are essential to the growth and development of juvenile fishes (Yáñez Arancibia 1985), including many of recreational and commercial importance (Tournois et al. 2017; Pérez-Ruzafa et al. 2019; Andolina et al. 2020). In this study, these species included *B. tyrannus*, *C. striata*, *C. regalis*, *L. xanthurus*, *P. dentatus*, *P. saltatrix*, and tautog *Tautoga onitis*, among many others. Fisheries-relevant species were collected in all habitats sampled, and many of those species were most abundant in habitats other than SAV (e.g. *B. tyrannus*, *L. xanthurus*), indicating that marsh creeks (Rountree and Able 1992b; Rountree and Able 1992a; Szedlmayer and Able 1993) and sand habitats (Gray et al. 1996; Gray et al. 1998) are also important in sustaining fisheries along with SAV, for which the relationship is well documented (Gillanders 2006; Hyndes et al. 2018). A more complete understanding of the role of estuarine habitat mosaics in

supporting abundant and diverse faunal assemblages, especially those in lagoonal estuaries, is critical to managing and conserving already shifting fisheries resources due to climate change (Anthony et al. 2009; Chapman 2012; Pérez-Ruzafa and Marcos 2012).

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References

- Able, K.W. 1999. Measures of juvenile fish habitat quality: Examples from a national estuarine research reserve. In *Fish habitat: Essential fish habitat and rehabilitation*, ed. L. Benaka, 134–147. Bethesda: American Fisheries Society.
- Able, K.W. 2005. A re-examination of fish estuarine dependence: Evidence for connectivity between estuarine and ocean habitats. *Estuarine, Coastal and Shelf Science* 64: 5–17.
- 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. *Reviews in Fisheries Science* 15: 1–61.
- Able, K.W., and M.P. Fahay. 1998. *The first year in the life of estuarine fishes in the Middle Atlantic Bight*. New Brunswick: Rutgers University Press.
- Able, K.W., and M.P. Fahay. 2010. *Ecology of estuarine fishes: Temperate waters of the western North Atlantic*. Baltimore: Johns Hopkins University Press.
- Able, K.W., D.M. Nemerson, R. Bush, and P. Light. 2001. Spatial variation in Delaware Bay (U.S.A.) marsh creek fish assemblages. *Estuaries* 24: 441–452.
- Able, K.W., J.L. Valenti, and T.M. Grothues. 2017. Fish larval supply to and within a lagoonal estuary: Multiple sources for Barnegat Bay, New Jersey. *Environmental Biology of Fishes* 100: 663–683.
- Able, K.W., D.A. Witting, R.S. McBride, R.A. Rountree, and K.J. Smith. 1996. Fishes of polyhaline estuarine shores in Great Bay-Little Egg Harbor, New Jersey: A case study of seasonal and habitat influences. In *Estuarine Shores: Evolution, Environments and Human Alterations*, ed. K.F. Nordstrom and C.T. Roman, 335–353. New York: Wiley.
- Adams, A.J., J.V. Locascio, and B.D. Robbins. 2004. Microhabitat use by a post-settlement stage estuarine fish: Evidence from relative abundance and predation among habitats. *Journal of Experimental Marine Biology and Ecology* 299: 17–33.

- Akin, S., K.O. Winemiller, and F.P. Gelwick. 2003. Seasonal and spatial variations in fish and macrocrustacean assemblage structure in Mad Island Marsh estuary, Texas. *Estuarine, Coastal and Shelf Science* 57: 269–282.
- Amorim, E., S. Ramos, M. Elliott, and A.A. Bordalo. 2018. Dynamic habitat use of an estuarine nursery seascape: Ontogenetic shifts in habitat suitability of the European flounder (*Platichthys flesus*). *Journal of Experimental Marine Biology and Ecology* 506: 49–60.
- Andolina, C., P. Franzoi, A.L. Jackson, A. Mazzola, and S. Vizzini. 2020. Vegetated habitats trophically support early development stages of a marine migrant fish in a coastal lagoon. *Estuaries and Coasts* 43: 424–437.
- Anthony, A., J. Atwood, P. August, C. Byron, S. Cobb, C. Foster, C. Fry, et al. 2009. Coastal lagoons and climate change: Ecological and social ramifications in U.S. Atlantic and Gulf Coast ecosystems. *Ecology and Society* 14: 1–29.
- Arendt, M.D., J.A. Lucy, and D.A. Evans. 2001. Diel and seasonal activity patterns of adult tautog, *Tautoga onitis*, in lower Chesapeake Bay, inferred from ultrasonic telemetry. *Environmental Biology of Fishes* 62: 379–391.
- Arrivillaga, A., and D.M. Baltz. 1999. Comparison of fishes and macroinvertebrates on seagrass and bare-sand sites on Guatemala's Atlantic coast. *Bulletin of Marine Science* 65: 301–319.
- Baillie, C.J., J.M. Fear, and F.J. Fodrie. 2015. Ecotone effects on seagrass and saltmarsh habitat use by juvenile nekton in a temperate estuary. *Estuaries and Coasts* 38: 1414–1430.
- Baker, R., B. Fry, L.P. Rozas, and T.J. Minello. 2013. Hydrodynamic regulation of salt marsh contributions to aquatic food webs. *Marine Ecology Progress Series* 490: 37–52.
- Balouskus, R.G., and T.E. Targett. 2012. Egg deposition by Atlantic silverside, *Menidia menidia*: Substrate utilization and comparison of natural and altered shoreline type. *Estuaries and Coasts* 35: 1100–1109.
- Baltz, D.M., C. Rakocinski, and J.W. Fleeger. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environmental Biology of Fishes* 36: 109–126.

- Barletta, M., A. Barletta-Bergan, U. Saint-Paul, and G. Hubold. 2005. The role of salinity in structuring the fish assemblages in a tropical estuary. *Journal of Fish Biology* 66: 45–72.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.
- Beck, M.W., K.L. Heck., K.W. Able, D.L. Childers, D.B. Eggleston, B.M. Gillanders, B. Halpern, et al. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* 51: 633–641.
- Becker, A., P.D. Cowley, A.K. Whitfield, J. Järnegren, and T.F. Næsje. 2011. Diel fish movements in the littoral zone of a temporarily closed South African estuary. *Journal of Experimental Marine Biology and Ecology* 406: 63–70.
- 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. *Estuarine, Coastal and Shelf Science* 144: 82–88.
- Bell, J.D., D.J. Ferrell, S.E. McNeill, and D.G. Worthington. 1992. Variation in assemblages of fish associated with deep and shallow margins of the seagrass *Posidonia australis*. *Marine Biology* 114: 667–676.
- Bell, J.D., and D.A. Pollard. 1989. Ecology of fish assemblages and fisheries associated with seagrasses. In *Biology of seagrasses: A treatise on the biology of seagrasses with special reference to the Australasian region*, ed. A.W.D. Larkum, A.J. McComb, and S.A. Shepherd, 565–609. Amsterdam: Elsevier.
- Bengtson, D.A. 1984. Resource partitioning by *Menidia menidia* and *Menidia beryllina* (Osteichthyes: Atherinidae). *Marine Ecology Progress Series* 18: 21–30.
- Bilinski, J., G. Buchanan, D. Frizzera, R. Hazen, L. Lippincott, N. Procopio, B. Ruppel, and T. Tucker. 2015. Damage assessment report on the effects of Hurricane Sandy on the state of New Jersey's natural resources: Final report. Trenton: New Jersey Department of Environmental Protection.
- Bilkovic, D.M. 2011. Response of tidal creek fish communities to dredging and coastal development pressures in a shallow-water estuary. *Estuaries and Coasts* 34: 129–147.

- Bolker, B.M., M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H.H. Stevens, and J.S.S. White. 2009. Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24: 127–135.
- Boström, C., S.J. Pittman, C. Simenstad, and R.T. Kneib. 2011. Seascape ecology of coastal biogenic habitats: Advances, gaps, and challenges. *Marine Ecology Progress Series* 427: 191–217.
- ter Braak, C.J.F., and P. Smilauer. 2012. *Canoco reference manual and user's guide: Software for ordination (version 5.0)*. New York: Microcomputer Power.
- Bradley, M., R. Baker, I. Nagelkerken, and M. Sheaves. 2019. Context is more important than habitat type in determining use by juvenile fish. *Landscape Ecology* 34: 427–442.
- Breitburg, D.L. 1989. Demersal schooling prior to settlement by larvae of the naked goby. *Environmental Biology of Fishes* 26: 97–103.
- Briggs, P.T., and J.S. O'Connor. 1971. Comparison of shore-zone fishes over naturally vegetated and sand-filled bottoms in Great South Bay. *New York Fish and Game Journal* 18: 15–41.
- Burnham, K.P., and D.R. Anderson. 2004. Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research* 33: 261–304.
- Castillo-Rivera, M., R. Zárate-Hernández, S. Ortiz-Burgos, and J. Zavala-Hurtado. 2010. Diel and seasonal variability in the fish community structure of a mud-bottom estuarine habitat in the Gulf of Mexico. *Marine Ecology* 31: 633–642.
- Castillo-Rivera, M., J.A. Zavala-Hurtado, and R. Zarate. 2002. Exploration of spatial and temporal patterns of fish diversity and composition in a tropical estuarine system of Mexico. *Reviews in Fish Biology and Fisheries* 12: 167–177.
- Chapman, P.M. 2012. Management of coastal lagoons under climate change. *Estuarine, Coastal and Shelf Science* 110: 32–35.
- Chizmadia, P.A., M.J. Kennish, and V.L. Otori. 1984. Physical description of Barnegat Bay. In *Ecology of Barnegat Bay, New Jersey*, ed. M.J. Kennish and R.A. Lutz, 1–28. New York: Springer-Verlag.

- Claridge, P.N., I.C. Potter, and M.W. Hardisty. 1986. Seasonal changes in movements, abundance, size composition and diversity of the fish fauna of the Severn Estuary. *Journal of the Marine Biological Association of the United Kingdom* 66: 229–258.
- Clark, K.L., G.M. Ruiz, and A.H. Hines. 2003. Diel variation in predator abundance, predation risk and prey distribution in shallow-water estuarine habitats. *Journal of Experimental Marine Biology and Ecology* 287: 37–55.
- Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–143.
- Cody, M.L., and J.A. Smallwood, ed.. 1996. *Long-term studies of vertebrate communities*. San Diego: Academic Press.
- Comrey, A.L., and H.B. Lee. 2013. *A first course in factor analysis*. New York: Psychology Press.
- Connolly, R.M. 1994. A comparison of fish assemblages from seagrass and unvegetated areas of a southern Australian estuary. *Australian Journal of Marine and Freshwater Research* 45: 1033–1044.
- Conover, D.O., and B.E. Kynard. 1984. Field and laboratory observations of spawning periodicity and behavior of a northern population of the Atlantic silverside, *Menidia menidia* (Pisces: Atherinidae). *Environmental Biology of Fishes* 11: 161–171.
- Coorey, D.N., K.W. Able, and J.K. Shisler. 1985. Life history and food habits of the inland silversides, *Menidia beryllina*, in a New Jersey salt marsh. *Bulletin of the New Jersey Academy of Science* 30: 29–38.
- Costanza, R., R. D’Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, et al. 1997. The value of the world’s ecosystem services and natural capital. *Nature* 387: 253–260.
- Costanza, R., R. de Groot, P. Sutton, S. van der Ploeg, S.J. Anderson, I. Kubiszewski, S. Farber, and R.K. Turner. 2014. Changes in the global value of ecosystem services. *Global Environmental Change* 26: 152–158.
- Courtenay, S.C., and M.H.A. Keenleyside. 1983. Nest site selection by the fourspine stickleback, *Apeltes quadracus* (Mitchill). *Canadian Journal of Zoology* 61: 1443–

1447.

- Cromwell, J.E. 1971. Barrier coast distribution: A world-wide survey. In *Abstracts, 2nd National Coastal Shallow Water Research Conference*, 50. California: University of Southern California University Press.
- Curran, B.M., J.P. Reed, and J.M. Miller. 1984. Growth, production, food consumption, and mortality of juvenile spot and croaker: A comparison of tidal and nontidal nursery areas. *Estuaries* 7: 451–459.
- Dahlberg, M.D., and J.C. Conyers. 1973. An ecological study of *Gobiosoma bosci* and *G. ginsburgi* (Pisces, Gobiidae) on the Georgia coast. *Fishery Bulletin* 71: 279–287.
- Dando, P. R. 2011. Site fidelity, homing and spawning migrations of flounder *Platichthys flesus* in the Tamar estuary, South West England. *Marine Ecology Progress Series* 430: 183–196.
- Dayton, P.K. 2003. The importance of the natural sciences to conservation. *The American Naturalist* 162: 1–13.
- Deegan, L.A., A. Wright, S.G. Ayvazian, J.T. Finn, H. Golden, R.R. Merson, and J. Harrison. 2002. Nitrogen loading alters seagrass ecosystem structure and support of higher trophic levels. *Aquatic Conservation: Marine and Freshwater Ecosystems* 12: 193–212.
- Defne, Z., and N.K. Ganju. 2015. Quantifying the residence time and flushing characteristics of a shallow, back-barrier estuary: Application of hydrodynamic and particle tracking models. *Estuaries and Coasts* 38: 1719–1734.
- Desmond, J.S., J.B. Zedler, and G.D. Williams. 2000. Fish use of tidal creek habitats in two southern California salt marshes. *Ecological Engineering* 14: 233–252.
- Elliott, M., and A.K. Whitfield. 2011. Challenging paradigms in estuarine ecology and management. *Estuarine, Coastal and Shelf Science* 94: 306–314.
- Feller, R.J., B.C. Coull, and B.T. Hentsch. 1990. Meiobenthic copepods: Tracers of where juvenile *Leiostomus xanthurus* (Pisces) feed? *Canadian Journal of Fisheries & Aquatic Sciences* 47: 1913–1919.
- Fleischner, T.L. 2005. Natural history and the deep roots of resource management.

Natural Resources Journal 45: 1–13.

- Franks, J.S. 1970. An investigation of the fish population within the inland waters of Horn Island, Mississippi, a barrier island in the Northern Gulf of Mexico. *Gulf Research Reports* 3: 3–104.
- Fraser, T.H. 1997. Abundance, seasonality, community indices, trends and relationships with physicochemical factors of trawled fish in upper Charlotte Harbor, Florida. *Bulletin of Marine Science* 60: 739–763.
- Friedland, K.D., D.W. Ahrenholz, and J.F. Guthrie. 1996. Formation and seasonal evolution of Atlantic menhaden juvenile nurseries in coastal estuaries. *Estuaries* 19: 105–114.
- Furey, N.B., and J.A. Sulikowski. 2011. The fish assemblage structure of the Saco River Estuary. *Northeastern Naturalist* 18: 37–44.
- Garwood, J.A., D.M. Allen, M.E. Kimball, and K.M. Boswell. 2019. Site fidelity and habitat use by young-of-the-year transient fishes in salt marsh intertidal creeks. *Estuaries and Coasts* 42: 1387–1396.
- Gillanders, B.M. 2006. Seagrasses, fish, and fisheries. In *Seagrasses: Biology, ecology, and conservation*, ed. A.W.D. Larkum, R.J. Orth, and C.M. Duarte, 503–536. Dordrecht: Springer.
- Gillanders, B.M., K.W. Able, J.A. Brown, D.B. Eggleston, and P.F. Sheridan. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: An important component of nurseries. *Marine Ecology Progress Series* 247: 281–295.
- Gittman, R.K., C.H. Peterson, C.A. Currin, F.J. Fodrie, M.F. Piehler, and J.F. Bruno. 2016. Living shorelines can enhance the nursery role of threatened estuarine habitats. *Ecological Applications* 26: 249–263.
- Good, R.E., and N.F. Good. 1984. The Pinelands National Reserve: An ecosystem approach to management. *BioScience* 34: 169–173.
- Gosline, W.A. 1948. Speciation in the fishes of the genus *Menidia*. *Evolution* 2: 306–313.
- Gray, C.A., R.C. Chick, and D.J. McElligott. 1998. Diel changes in assemblages of fishes

- associated with shallow seagrass and bare sand. *Estuarine, Coastal and Shelf Science* 46: 849–859.
- Gray, C.A., D.J. McElligott, and R.C. Chick. 1996. Intra- and inter-estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. *Marine and Freshwater Research* 47: 723–735.
- Grothues, T.M., and K.W. Able. 2020. Shoreline infrastructure degradation and increasing littoral naturalization accommodates juvenile fish and crab assemblages in heavily urbanized upper New York Harbor. *Restoration Ecology*. doi:10.1111/rec.13163.
- Guest, M.A., R.M. Connolly, and N.R. Loneragan. 2003. Seine nets and beam trawls compared by day and night for sampling fish and crustaceans in shallow seagrass habitat. *Fisheries Research* 64: 185–196.
- Hagan, S.M., and K.W. Able. 2008. Diel variation in the pelagic fish assemblage in a temperate estuary. *Estuaries and Coasts* 31: 33–42.
- Halpern, B.S., S. Walbridge, K.A. Selkoe, C.V. Kappel, F. Micheli, C. D'Agrosa, J.F. Bruno, et al. 2008. A global map of human impact on marine ecosystems. *Science* 319: 948–952.
- Hammerschlag, N., M.R. Heithaus, and J.E. Serafy. 2010. Influence of predation risk and food supply on nocturnal fish foraging distributions along a mangrove-seagrass ecotone. *Marine Ecology Progress Series* 414: 223–235.
- Hampel, H., A. Cattrijsse, and M. Vincx. 2003. Tidal, diel and semi-lunar changes in the faunal assemblage of an intertidal salt marsh creek. *Estuarine, Coastal and Shelf Science* 56: 795–805.
- Harding, J.M., D.M. Allen, E.R. Haffey, and K.M. Hoffman. 2020. Site fidelity of oyster reef blennies and gobies in saltmarsh tidal creeks. *Estuaries and Coasts* 43: 409–423.
- Harding, J.M., and R.L. Mann. 2000. Estimates of naked goby (*Gobiosoma bosc*), striped blenny (*Chasmodes bosquianus*) and Eastern oyster (*Crassostrea virginica*) larval production around a restored Chesapeake Bay oyster reef. *Bulletin of Marine Science* 66: 29–45.

- Harley, C.D.G., A.R. Hughes, K.M. Hultgren, B.G. Miner, C.J.B. Sorte, C.S. Thornber, L.F. Rodriguez, L. Tomanek, and S.L. Williams. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters* 9: 228–241.
- Heck, K.L., K.W. Able, M.P. Fahay, and C.T. Roman. 1989. Fishes and decapod crustaceans of Cape Cod eelgrass meadows: Species composition, seasonal abundance patterns and comparison with unvegetated substrates. *Estuaries* 12: 59–65.
- Heck, K.L., G. Hays, and R.J. Orth. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series* 253: 123–136.
- Heck, K.L., D.A. Nadeau, and R. Thomas. 1997. The nursery role of seagrass beds. *Gulf of Mexico Science* 15: 50–54.
- Heck, K.L., and R.J. Orth. 2006. Predation in seagrass beds. In *Seagrasses: Biology, ecology, and conservation*, ed. A.W.D. Larkum, R.J. Orth, and C.M. Duarte, 537–550. Dordrecht: Springer.
- Hendon, J.R., M.S. Peterson, and B.H. Comyns. 2000. Spatio-temporal distribution of larval *Gobiosoma bosc* in waters adjacent to natural and altered marsh-edge habitats of Mississippi coastal waters. *Bulletin of Marine Science* 66: 143–156.
- Hettler, W.F. 1989. Nekton use of regularly-flooded saltmarsh habitat in North Carolina, USA. *Marine Ecology Progress Series* 56: 111–118.
- Hindell, J.S., G.P. Jenkins, and M.J. Keough. 2000. Variability in abundances of fishes associated with seagrass habitats in relation to diets of predatory fishes. *Marine Biology* 136: 725–737.
- Hoeksema, S.D., and I.C. Potter. 2006. Diel, seasonal, regional and annual variations in the characteristics of the ichthyofauna of the upper reaches of a large Australian microtidal estuary. *Estuarine, Coastal and Shelf Science* 67: 503–520.
- Holland, A.F., D.M. Sanger, C.P. Gawle, S.B. Lerberg, M.S. Santiago, G.H.M. Riekerk, L.E. Zimmerman, and G.I. Scott. 2004. Linkages between tidal creek ecosystems and the landscape and demographic attributes of their watersheds. *Journal of Experimental Marine Biology and Ecology* 298: 151–178.
- Houde, E.D., E.R. Annis, L.W. Harding, M.E. Mallonee, and M.J. Wilberg. 2016. Factors

- affecting the abundance of age-0 Atlantic menhaden (*Brevoortia tyrannus*) in Chesapeake Bay. *ICES Journal of Marine Science* 73: 2238–2251.
- Hyndes, G.A., P. Francour, P. Guidetti, K.L. Heck, and G. Jenkins. 2018. The roles of seagrasses in structuring associated fish assemblages and fisheries. In *Seagrasses of Australia: Structure, ecology and conservation*, ed. A.W.D. Larkum, G.A. Kendrick, and P.J. Ralph, 589–627. Cham: Springer International Publishing.
- Izzo, C., Z.A. Doubleday, G.L. Grammer, K.L. Gilmore, H.K. Alleway, T.C. Barnes, M.C.F. Disspain, A.J. Giraldo, N. Mazloumi, and B.M. Gillanders. 2016. Fish as proxies of ecological and environmental change. *Reviews in Fish Biology and Fisheries* 26: 265–286.
- Jackson, G., and G.K. Jones. 1999. Spatial and temporal variation in nearshore fish and macroinvertebrate assemblages from a temperate Australian estuary over a decade. *Marine Ecology Progress Series* 182: 253–268.
- James, N.C., A.K. Whitfield, and P.D. Cowley. 2008. Long-term stability of the fish assemblages in a warm-temperate South African estuary. *Estuarine, Coastal and Shelf Science* 76: 723–738.
- Jenkins, G.P., T. Kenner, A. Brown, and R. Coleman. 2015. Fish assemblages in locations with alternative structured habitats in an eelgrass, *Zostera*, dominated bay: Biodiversity value and potential for refuge. *Estuarine, Coastal and Shelf Science* 161: 25–37.
- Jenkins, G.P., H.M.A. May, M.J. Wheatley, and M.G. Holloway. 1997. Comparison of fish assemblages associated with seagrass and adjacent unvegetated habitats of Port Phillip Bay and Corner Inlet, Victoria, Australia, with emphasis on commercial species. *Estuarine, Coastal and Shelf Science* 44: 569–588.
- Jenkins, G.P., and M.J. Wheatley. 1998. The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: Comparison of shallow seagrass, reef-algal and unvegetated sand habitats, with emphasis on their importance to recruitment. *Journal of Experimental Marine Biology and Ecology* 221: 147–172.
- Jivoff, P., and K.W. Able. 2001. Characterization of the fish and selected decapods in Little Egg Harbor. *Journal of Coastal Research*: 178–196.

- Johnson, D.D., D. Rotherham, and C.A. Gray. 2008. Sampling estuarine fish and invertebrates using demersal otter trawls: Effects of net height, tow duration and diel period. *Fisheries Research* 93: 315–323.
- Kennish, M.J. 1991. *Ecology of estuaries: Anthropogenic effects*. Boca Raton: CRC Press.
- Kennish, M.J. 2001. Physical description of the Barnegat Bay-Little Egg Harbor estuarine system. *Journal of Coastal Research* 32: 13–27.
- Kennish, M.J., R.J. Livingston, D. Raffaelli, and K. Reise. 2008. Environmental future of estuaries. In *Aquatic ecosystems: Trends and global prospects*, ed. N. Polunin, 188–208. Cambridge: Cambridge University Press.
- Kennish, M.J., and H.W. Paerl. 2010a. Coastal lagoons: Critical habitats of environmental change. In *Coastal lagoons: Critical habitats of environmental change*, ed. M.J. Kennish and H.W. Paerl, 1–16. Boca Raton: CRC Press.
- Kennish, M.J., and H.W. Paerl, ed. 2010b. *Coastal lagoons: Critical habitats of environmental change*. Boca Raton: CRC Press.
- Kimball, M.E., and K.W. Able. 2012. Tidal migrations of intertidal salt marsh creek nekton examined with underwater video. *Northeastern Naturalist* 19: 475–486.
- Kimirei, I.A., I. Nagelkerken, M. Trommelen, P. Blankers, N. van Hoytema, D. Hoeijmakers, C.M. Huijbers, Y.D. Mgaya, and A.L. Rypel. 2013. What drives ontogenetic niche shifts of fishes in coral reef ecosystems? *Ecosystems* 16: 783–796.
- Kleypas, J., and J.M. Dean. 1983. Migration and feeding of the predatory fish, *Bairdiella chrysura* Lacépède, in an intertidal creek. *Journal of Experimental Marine Biology and Ecology* 72: 199–209.
- Kneib, R.T. 1997. The role of tidal marshes in the ecology of estuarine nekton. In *Oceanography and marine biology: An annual review*, ed. A.D. Ansell, R.N. Gibson, and M. Barnes, 35:163–220. London: UCL Press.
- Kneib, R.T. 2003. Bioenergetic and landscape considerations for scaling expectations of nekton production from intertidal marshes. *Marine Ecology Progress Series* 264: 279–296.

- Kneib, R.T., and S.L. Wagner. 1994. Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Marine Ecology Progress Series* 106: 227–238.
- Kulczycki, G.R., R.W. Virnstein, and W.G. Nelson. 1981. The relationship between fish abundance and algal biomass in a seagrass-drift algae community. *Estuarine, Coastal and Shelf Science* 12: 341–347.
- Lathrop, R.G., R.M. Styles, S.P. Seitzinger, and J.A. Bogner. 2001. Use of GIS mapping and modeling approaches to examine the spatial distribution of seagrasses in Barnegat Bay, New Jersey. *Estuaries* 24: 904–916.
- Lazzari, M.A. 2002. Epibenthic fishes and decapod crustaceans in northern estuaries: A comparison of vegetated and unvegetated habitats in Maine. *Estuaries* 25: 1210–1218.
- Lazzari, M.A., S. Sherman, and J.K. Kanwit. 2003. Nursery use of shallow habitats by epibenthic fishes in Maine nearshore waters. *Estuarine, Coastal and Shelf Science* 56: 73–84.
- Lazzari, M.A., and B.Z. Stone. 2006. Use of submerged aquatic vegetation as habitat by young-of-the-year epibenthic fishes in shallow Maine nearshore waters. *Estuarine, Coastal and Shelf Science* 69: 591–606.
- Lehnert, R.L., and D.M. Allen. 2002. Nekton use of subtidal oyster shell habitat in a southeastern U.S. estuary. *Estuaries* 25: 1015–1024.
- Lenth, R. 2019. emmeans: Estimated marginal means, aka least-squares means. R package version 1.4.3.01.
- Lewis, R.M., P.H. Wilkens, and H.R. Gordy. 1972. A description of young Atlantic menhaden, *Brevoortia tyrannus*, in the White Oak River estuary, North Carolina. *Fishery Bulletin* 70: 115–118.
- Litvin, S.Y., M.P. Weinstein, M. Sheaves, and I. Nagelkerken. 2018. What makes nearshore habitats nurseries for nekton? An emerging view of the nursery role hypothesis. *Estuaries and Coasts* 41: 1539–1550.
- Livingston, R.J. 1976. Diurnal and seasonal fluctuations of organisms in a north Florida estuary. *Estuarine and Coastal Marine Science* 4: 373–400.

- Loneragan, N.R., I.C. Potter, R.C.J. Lenanton, and N. Caputi. 1987. Influence of environmental variables on the fish fauna of the deeper waters of a large Australian estuary. *Marine Biology* 94: 631–641.
- Love, J.W., A.K. Johnson, and E.B. May. 2006. Spatial and temporal differences of Atlantic menhaden (*Brevoortia tyrannus*) recruitment across major drainages (1966–2004) of the Chesapeake Bay watershed. *Estuaries and Coasts* 29: 794–801.
- Love, J.W., D.F. Luers, and B.D. Williams. 2009. Spatio-temporal patterns of larval fish ingress to Chincoteague Bay, Maryland, USA during winter and spring 2004 to 2007. *Marine Ecology Progress Series* 377: 203–212.
- Lowe, M.R., and M.S. Peterson. 2014. Effects of coastal urbanization on salt-marsh faunal assemblages in the northern Gulf of Mexico. *Marine and Coastal Fisheries* 6: 89–107.
- Magurran, A.E., S.R. Baillie, S.T. Buckland, J.M. Dick, D.A. Elston, E.M. Scott, R.I. Smith, P.J. Somerfield, and A.D. Watt. 2010. Long-term datasets in biodiversity research and monitoring: Assessing change in ecological communities through time. *Trends in Ecology and Evolution* 25: 574–582.
- Main, K.L. 1987. Predator avoidance in seagrass meadows: Prey behavior, microhabitat selection, and cryptic coloration. *Ecology* 68: 170–180.
- Mallin, M.A., and A.J. Lewitus. 2004. The importance of tidal creek ecosystems. *Journal of Experimental Marine Biology and Ecology* 298: 145–149.
- Manderson, J.P., B.A. Phelan, A.W. Stoner, and J. Hilbert. 2000. Predator-prey relations between age-1+ summer flounder (*Paralichthys dentatus*, Linnaeus) and age-0 winter flounder (*Pseudopleuronectes americanus*, Walbaum): Predator diets, prey selection, and effects of sediments and macrophytes. *Journal of Experimental Marine Biology and Ecology* 251: 17–39.
- Massman, W.H. 1954. Marine fishes in fresh and brackish waters of Virginia rivers. *Ecology* 35: 75–78.
- Mattila, J., G. Chaplin, M.R. Eilers, K.L. Heck, J.P. O’Neal, and J.F. Valentine. 1999. Spatial and diurnal distribution of invertebrate and fish fauna of a *Zostera marina* bed and nearby unvegetated sediments in Damariscotta River, Maine (USA). *Journal of Sea Research* 41: 321–332.

- McGarigal, K., S. Cushman, and S. Stafford. 2000. *Multivariate statistics for wildlife and ecology research*. New York: Springer-Verlag.
- McKinsey, D.M., and L.J. Chapman. 1998. Dissolved oxygen and fish distribution in a Florida spring. *Environmental Biology of Fishes* 53: 211–223.
- Methven, D.A., R.L. Haedrich, and G.A. Rose. 2001. The fish assemblage of a Newfoundland estuary: Diel, monthly and annual variation. *Estuarine Coastal and Shelf Science* 52: 669–687.
- Meyer, D.L., and M.H. Posey. 2019. Salt marsh habitat size and location do matter: The influence of salt marsh size and landscape setting on nekton and estuarine finfish community structure. *Estuaries and Coasts* 42: 1353–1373.
- Middaugh, D.P. 1981. Reproductive ecology and spawning periodicity of the Atlantic silverside, *Menidia menidia* (Pisces: Atherinidae). *Copeia* 1981: 766–776.
- Middaugh, D.P., G.I. Scott, and J.M. Dean. 1981. Reproductive behavior of the Atlantic silverside, *Menidia menidia* (Pisces, Atherinidae). *Environmental Biology of Fishes* 6: 269–276.
- Minello, T.J., K.W. Able, M.P. Weinstein, and C.G. Hays. 2003. Salt marshes as nurseries for nekton: Testing hypothesis on density, growth and survival through meta-analysis. *Marine Ecology Progress Series* 246: 39–59.
- Minello, T.J., and L.P. Rozas. 2002. Nekton in Gulf Coast wetlands: Fine-scale distributions, landscape patterns, and restoration implications. *Ecological Applications* 12: 441–455.
- Morrison, M.A., M.P. Francis, B.W. Hartill, and D.M. Parkinson. 2002. Diurnal and tidal variation in the abundance of the fish fauna of a temperate tidal mudflat. *Estuarine Coastal and Shelf Science* 54: 793–807.
- Nagelkerken, I., M. Sheaves, R. Baker, and R.M. Connolly. 2015. The seascape nursery: A novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries* 16: 362–371.
- Nagelkerken, I. 2007. Are non-estuarine mangroves connected to coral reefs through fish migration? *Bulletin of Marine Science* 80: 595–607.

- National Oceanic and Atmospheric Administration. 2013. Hurricane/post-tropical cyclone Sandy, October 22 – 29, 2012. Silver Spring: United States Department of Commerce.
- Nichols, M.M., and J.D. Boon. 1994. Sediment transport processes in coastal lagoons. In *Coastal lagoon processes*, ed. B. Kjerfve, 60: 157–219. Amsterdam: Elsevier.
- Noss, R.F. 1998. Does conservation biology need natural history? *Wild Earth* 8: 10–14.
- O’Neil, S.P., and M.P. Weinstein. 1988. Feeding habitats of spot, *Leiostomus xanthurus*, in polyhaline versus meso-oligohaline tidal creeks and shoals. *Fishery Bulletin* 85: 785–796.
- Oksanen, J., F.G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P.R. Minchin, et al. 2019. vegan: Community ecology package. R package version 2.5-4.
- Olin, M., and T. Malinen. 2003. Comparison of gillnet and trawl in diurnal fish community sampling. *Hydrobiologia* 506–509: 443–449.
- Orth, R.J., and K.L. Heck. 1980. Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay: Fishes. *Estuaries* 3: 278–288.
- Orth, R.J., K.L. Heck, and J. van Montfrans. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7: 339–350.
- Packer, D.B., S.J. Griesbach, P.L. Berrien, C.A. Zetlin, D.L. Johnson, and W.W. Morse. 1999. Summer flounder, *Paralichthys dentatus*, life history and habitat characteristics. Highlands: National Marine Fisheries Service.
- Partyka, M.L., and M.S. Peterson. 2008. Habitat quality and salt-marsh species assemblages along an anthropogenic estuarine landscape. *Journal of Coastal Research* 24: 1570–1581.
- Pérez-Ruzafa, A., and C. Marcos. 2012. Fisheries in coastal lagoons: An assumed but poorly researched aspect of the ecology and functioning of coastal lagoons. *Estuarine, Coastal and Shelf Science* 110: 15–31.
- Pérez-Ruzafa, A., I.M. Pérez-Ruzafa, A. Newton, and C. Marcos. 2019. Coastal lagoons:

- Environmental variability, ecosystem complexity, and goods and services uniformity. In *Coasts and estuaries: The future*, ed. E. Wolanski, J.W. Day, M. Elliott, and R. Ramachandran, 253–276. Amsterdam: Elsevier.
- Peterson, M.S., B.H. Comyns, J.R. Hendon, P.J. Bond, and G.A. Duff. 2000. Habitat use by early life-history stages of fishes and crustaceans along a changing estuarine landscape: differences between natural and altered shoreline sites. *Wetlands Ecology and Management* 8: 209–219.
- Phelan, B.A., J.P. Manderson, A.W. Stoner, and A.J. Bejda. 2001. Size-related shifts in the habitat associations of young-of-the-year winter flounder (*Pseudopleuronectes americanus*): Field observations and laboratory experiments with sediments and prey. *Journal of Experimental Marine Biology and Ecology* 257: 297–315.
- Phleger, F.B. 1981. A review of some general features of coastal lagoons. In *Unesco technical papers in marine science: Coastal lagoon research, present and future*, 33: 7–13. Beaufort: United Nations Educational, Scientific and Cultural Organization.
- Pittman, S.J., C.A. McAlpine, and K.M. Pittman. 2004. Linking fish and prawns to their environment: A hierarchical landscape approach. *Marine Ecology Progress Series* 283: 233–254.
- Plavan, A.A., C. Passadore, and L. Gimenez. 2010. Fish assemblage in a temperate estuary on the Uruguayan coast: Seasonal variation and environmental influence. *Brazilian Journal of Oceanography* 58: 299–314.
- Potter, I.C., J.R. Tweedley, M. Elliott, and A.K. Whitfield. 2015. The ways in which fish use estuaries: A refinement and expansion of the guild approach. *Fish and Fisheries* 16: 230–239.
- Potthoff, M.T., and D.M. Allen. 2003. Site fidelity, home range, and tidal migrations of juvenile pinfish, *Lagodon rhomboides*, in salt marsh creeks. *Environmental Biology of Fishes* 67: 231–240.
- Raposa, K.B., and C.A. Oviatt. 2000. The influence of contiguous shoreline type, distance from shore, and vegetation biomass on nekton community structure in eelgrass beds. *Estuaries* 23: 46–55.
- Reisman, H.M. 1963. Reproductive behavior of *Apeltes quadracus*, including some

- comparisons with other gasterosteid fishes. *Copeia* 1: 191–192.
- Ribeiro, J., L. Bentes, R. Coelho, J.M.S. Gonçalves, P.G. Lino, P. Monteiro, and K. Erzini. 2006. Seasonal, tidal and diurnal changes in fish assemblages in the Ria Formosa lagoon (Portugal). *Estuarine, Coastal and Shelf Science* 67: 461–474.
- Richards, C.E., and M. Castagna. 1970. Marine fishes of Virginia's eastern shore (inlet and marsh, seaside waters). *Chesapeake Science* 11: 235–248.
- Rijnsdorp, A.D., M.A. Peck, G.H. Engelhard, C. Möllmann, and J.K. Pinnegar. 2009. Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science* 66: 1570–1583.
- Robblee, M.B., and J.C. Zieman. 1984. Diel variation in the fish fauna of a tropical seagrass feeding ground. *Bulletin of Marine Science* 34: 335–345.
- Robertson, A.I. 1980. The structure and organization of an eelgrass fish fauna. *Oecologia* 47: 76–82.
- Ross, S.T., R.H. McMichael, and D.L. Ruple. 1987. Seasonal and diel variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf zone. *Estuarine, Coastal and Shelf Science* 25: 391–412.
- Ross, S.W. 2003. The relative value of different estuarine nursery areas in North Carolina for transient juvenile marine fishes. *Fishery Bulletin* 101: 384–404.
- Rountree, R.A., and K.W. Able. 1992a. Foraging habits, growth, and temporal patterns of salt-marsh creek habitat use by young-of-year summer flounder in New Jersey. *Transactions of the American Fisheries Society* 121: 765–776.
- Rountree, R.A., and K.W. Able. 1992b. Fauna of polyhaline subtidal marsh creeks in southern New Jersey: Composition, abundance and biomass. *Estuaries* 15: 171–185.
- Rountree, R.A., and K.W. Able. 1993. Diel variation in decapod crustacean and fish assemblages in New Jersey polyhaline marsh creeks. *Estuarine, Coastal and Shelf Science* 37: 181–201.
- Rountree, R.A., and K.W. Able. 1997. Nocturnal fish use of New Jersey marsh creek and adjacent bay shoal habitats. *Estuarine, Coastal and Shelf Science* 44: 703–711.

- Rountree, R.A., and K.W. Able. 2007. Spatial and temporal habitat use patterns for salt marsh nekton: Implications for ecological functions. *Aquatic Ecology* 41: 25–45.
- Rowland, W.J. 1974. Reproductive behavior of the fourspine stickleback, *Apeltes quadracus*. *Copeia* 1974: 183–194.
- Rozas, L.P. 1995. Hydroperiod and its influence on nekton use of the salt marsh: A pulsing ecosystem. *Estuaries* 18: 579–590.
- RStudio Team. 2019. RStudio: Integrated development for R. RStudio, Inc., Boston, MA.
- Rypel, A.L., C.A. Layman, and D.A. Arrington. 2007. Water depth modifies relative predation risk for a motile fish taxon in Bahamian tidal creeks. *Estuaries and Coasts* 30: 518–525.
- Schaffler, J.J., J. van Montfrans, C.M. Jones, and R.J. Orth. 2013. Fish species distribution in seagrass habitats of Chesapeake Bay are structured by abiotic and biotic factors. *Marine and Coastal Fisheries* 5: 114–124.
- Schrandt, M.N., T.S. Switzer, C.J. Stafford, K.E. Flaherty-Walia, R. Paperno, and R.E. Matheson. 2018. Similar habitats, different communities: Fish and large invertebrate assemblages in eastern Gulf of Mexico polyhaline seagrasses relate more to estuary morphology than latitude. *Estuarine, Coastal and Shelf Science* 213: 217–229.
- Seilheimer, T.S., A. Wei, P. Chow-Fraser, and N. Eyles. 2007. Impact of urbanization on the water quality, fish habitat, and fish community of a Lake Ontario marsh, Frenchman's Bay. *Urban Ecosystems* 10: 299–319.
- Sheaves, M. 2009. Consequences of ecological connectivity: The coastal ecosystem mosaic. *Marine Ecology Progress Series* 391: 107–115.
- Sheaves, M., R. Baker, I. Nagelkerken, and R.M. Connolly. 2015. True value of estuarine and coastal nurseries for fish: Incorporating complexity and dynamics. *Estuaries and Coasts* 38: 401–414.
- Sogard, S.M., and K.W. Able. 1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. *Estuarine, Coastal and Shelf Science* 33: 501–519.
- Sogard, S.M., and K.W. Able. 1994. Diel variation in immigration of fishes and decapod

- crustaceans to artificial seagrass habitat. *Estuaries* 17: 622–630.
- Sogard, S.M., G.V.N. Powell, and J.G. Holmquist. 1987. Epibenthic fish communities on Florida Bay banks: Relations with physical parameters and seagrass cover. *Marine Ecology Progress Series* 40: 25–39.
- Sogard, S.M., G.V.N. Powell, and J.G. Holmquist. 1989. Utilization by fishes of shallow, seagrass-covered banks in Florida Bay: 2. Diel and tidal patterns. *Environmental Biology of Fishes* 24: 81–92.
- Spellberg, I.F. 2005. *Monitoring ecological change*. New York: Cambridge University Press.
- Stevens, M.H.H. 2009. *A primer of ecology with R*. New York: Springer Science & Business Media.
- Stevens, P.W., C.L. Montague, and K.J. Sulak. 2006. Fate of fish production in a seasonally flooded saltmarsh. *Marine Ecology Progress Series* 327: 267–277.
- Sugihara, T., C. Yearsley, J.B. Durand, and N.P. Psuty. 1979. Comparison of natural and altered estuarine systems: Analysis. New Brunswick: Center for Coastal and Environmental Studies.
- Szedlmayer, S.T., and K.W. Able. 1993. Ultrasonic telemetry of age-0 summer flounder, *Paralichthys dentatus*, movements in a southern New Jersey estuary. *Copeia* 3: 728–736.
- Szedlmayer, S.T., and K.W. Able. 1996. Patterns of seasonal availability and habitat use by fishes and decapod crustaceans in a southern New Jersey estuary. *Estuaries* 19: 697–709.
- Talbot, C.W., and K.W. Able. 1984. Composition and distribution of larval fishes in New Jersey high marshes. *Estuaries* 7: 434–443.
- Tatham, T.R., D.J. Danila, and D.L. Thomas. 1984. Fishes of Barnegat Bay. In *Ecology of Barnegat Bay, New Jersey*, ed. M.J. Kennish and R.A. Lutz, 241–280. New York: Springer-Verlag.
- Teixeira, R.L., and J.A. Musick. 2001. Reproduction and food habits of the lined seahorse, *Hippocampus erectus* (Teleostei: Syngnathidae) of Chesapeake Bay,

- Virginia. *Revista Brasileira de Biologia* 61: 79–90.
- Thistle, M.E., D.C. Schneider, R.S. Gregory, and N.J. Wells. 2010. Fractal measures of habitat structure: Maximum densities of juvenile cod occur at intermediate eelgrass complexity. *Marine Ecology Progress Series* 405: 39–56.
- Tournois, J., A.M. Darnaude, F. Ferraton, C. Aliaume, L. Mercier, and D.J. McKenzie. 2017. Lagoon nurseries make a major contribution to adult populations of a highly prized coastal fish. *Limnology and Oceanography* 62: 1219–1233.
- Tyler, R.M., and T.E. Targett. 2007. Juvenile weakfish *Cynoscion regalis* distribution in relation to diel-cycling dissolved oxygen in an estuarine tributary. *Marine Ecology Progress Series* 333: 257–269.
- Underwood, A.J., M.G. Chapman, and S.D. Connell. 2000. Observations in ecology: You can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology* 250: 97–115.
- Unsworth, R.K.F., E. Wylie, D.J. Smith, and J.J. Bell. 2007. Diel trophic structuring of seagrass bed fish assemblages in the Wakatobi Marine National Park, Indonesia. *Estuarine, Coastal and Shelf Science* 72: 81–88.
- Valenti, J.L., T.M. Grothues, and K.W. Able. 2020. Juvenile fish assemblage recruitment dynamics in a mid-Atlantic estuary: Before and after Hurricane Sandy. *Marine Ecology Progress Series* 641: 177–193.
- Weinstein, M.P., and H.A. Brooks. 1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: Community composition and structure. *Marine Ecology Progress Series* 12: 15–27.
- Weinstein, M.P., L. Scott, S.P. O'Neil, R.C. Siegfried, and S.T. Szedlmayer. 1984. Population dynamics of spot, *Leiostomus xanthurus*, in polyhaline tidal creeks of the York River estuary, Virginia. *Estuaries* 7: 444–450.
- Weinstein, M.P., S.L. Weiss, and M.F. Walters. 1980. Multiple determinants of community structure in shallow marsh habitats, Cape Fear River estuary, North Carolina, USA. *Marine Biology* 58: 227–243.
- Whitfield, A., and M. Elliott. 2011. Ecosystem and biotic classifications of estuaries and coasts. In *Treatise on estuarine and coastal science*, ed. E. Wolanski and D.S.

- McLusky, 1: 99–124. Waltham: Academic Press.
- Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385–397.
- Wilson, E.O. 1985. The biological diversity crisis: A challenge to science. *Issues in Science and Technology* 2: 20–29.
- Wilson, J. 2002. Productivity, fisheries and aquaculture in temperate estuaries. *Estuarine, Coastal and Shelf Science* 55: 953–967.
- Wilson, K.A., K.W. Able, and K.L. Heck. 1990. Predation rates on juvenile blue crabs in estuarine nursery habitats: Evidence for the importance of macroalgae (*Ulva lactuca*). *Marine Ecology Progress Series* 58: 243–251.
- Wilson, S.K., C.J. Fulton, M. Depczynski, T.H. Holmes, M.M. Noble, B. Radford, and P. Tinkler. 2014. Seasonal changes in habitat structure underpin shifts in macroalgae-associated tropical fish communities. *Marine Biology* 161: 2597–2607.
- Witting, D.A., K.W. Able, and M.P. Fahay. 1999. Larval fishes of a Middle Atlantic Bight estuary: Assemblage structure and temporal stability. *Canadian Journal of Fisheries & Aquatic Sciences* 56: 222–230.
- Wyanski, D.M. 1990. Patterns of habitat utilization in 0-age summer flounder (*Paralichthys dentatus*). Gloucester Point: The College of William and Mary.
- Yáñez Arancibia, A., ed. 1985. *Fish community ecology in estuaries and coastal lagoons*. Mexico: Universidad Nacional Autónoma de México.
- Zuur, A.F., and E.N. Ieno. 2016. *Beginner's guide to zero-inflated models with R*. Newburgh: Highland Statistics Ltd.

Tables

Table 1. Number of sampling events (N), catch-per-unit-effort (CPUE), Shannon diversity, standardized richness, and algae volume observed during the daytime, seasonal survey within upper creek, creek mouth, sand, and submerged aquatic vegetation (SAV) habitats. CPUE, diversity, richness, and algae values are reported as the mean \pm standard error of the mean followed by the percent of sampling events (% occurrence) where each parameter was greater than zero

	N	CPUE (fish/s)	CPUE % Occurrence	Shannon Diversity	Diversity % Occurrence	Richness (species/tow)	Richness % Occurrence	Algae Volume (L/s)	Algae % Occurrence
April									
Upper Creek	27	0.030 \pm 0.017	59	0.579 \pm 0.113	44	0.491 \pm 0.109	59	0.020 \pm 0.009	89
Creek Mouth	26	0.019 \pm 0.008	77	0.584 \pm 0.121	50	0.615 \pm 0.102	77	0.112 \pm 0.027	100
Sand	43	0.004 \pm 0.001	37	0.548 \pm 0.095	28	0.248 \pm 0.056	37	0.011 \pm 0.003	93
SAV	33	0.014 \pm 0.004	64	0.576 \pm 0.106	46	0.515 \pm 0.096	64	0.065 \pm 0.023	100
June									
Upper Creek	29	0.130 \pm 0.048	83	0.758 \pm 0.075	76	0.934 \pm 0.120	83	0.015 \pm 0.004	90
Creek Mouth	26	0.083 \pm 0.027	96	0.977 \pm 0.109	92	1.423 \pm 0.145	96	0.516 \pm 0.142	96
Sand	44	0.040 \pm 0.014	86	0.524 \pm 0.078	57	0.705 \pm 0.081	86	0.011 \pm 0.002	93
SAV	33	0.136 \pm 0.048	94	0.886 \pm 0.094	82	1.354 \pm 0.154	94	0.063 \pm 0.018	100
August									
Upper Creek	30	0.236 \pm 0.078	87	0.464 \pm 0.090	73	1.011 \pm 0.132	87	0.009 \pm 0.007	73
Creek Mouth	27	0.363 \pm 0.123	100	0.810 \pm 0.103	89	1.827 \pm 0.229	100	0.315 \pm 0.078	93
Sand	44	0.312 \pm 0.063	96	0.454 \pm 0.075	77	1.326 \pm 0.143	96	0.040 \pm 0.017	68
SAV	33	0.539 \pm 0.375	100	0.856 \pm 0.093	88	1.904 \pm 0.241	100	0.161 \pm 0.038	85
October									
Upper Creek	30	0.177 \pm 0.060	83	0.732 \pm 0.112	70	1.111 \pm 0.150	83	0.008 \pm 0.003	73
Creek Mouth	27	0.225 \pm 0.088	89	0.727 \pm 0.095	78	1.321 \pm 0.189	89	0.368 \pm 0.100	100
Sand	45	0.204 \pm 0.074	91	0.425 \pm 0.075	60	0.800 \pm 0.094	91	0.025 \pm 0.006	84
SAV	33	0.442 \pm 0.185	94	0.644 \pm 0.085	73	1.217 \pm 0.192	94	0.103 \pm 0.032	100

Table 2. Number of sampling events and fish collected and the environmental parameters, mean catch-per-unit-effort (CPUE), Shannon diversity, and richness (\pm standard error of the mean) for the day-night survey. See Table 3 for common names and estuarine usage for each species. Dusky anchovy *Anchoa lyolepis*, conger eel *Conger oceanicus*, and striped searobin *Prionotus evolans* (all estuarine transients) were only collected during the day-night survey

	Sand		Submerged Aquatic Vegetation	
	Day	Night	Day	Night
Sampling Events	9	9	9	9
Temperature (°C)	22.1 \pm 1.0	22.2 \pm 1.0	22.3 \pm 1.1	22.6 \pm 1.2
Salinity	30.99 \pm 0.37	30.81 \pm 0.41	30.38 \pm 0.53	30.55 \pm 0.48
Dissolved Oxygen (mg/L)	6.33 \pm 0.40	6.45 \pm 0.25	6.70 \pm 0.47	6.71 \pm 0.33
pH	7.91 \pm 0.06	7.89 \pm 0.06	7.89 \pm 0.04	7.94 \pm 0.04
Water Depth (m)	1.2 \pm 0.1	1.0 \pm 0.1	1.2 \pm 0.1	1.1 \pm 0.1
Algae Volume (L/s)	0.089 \pm 0.028	0.163 \pm 0.056	0.291 \pm 0.098	0.385 \pm 0.135
Total Fish Collected	736	213	2845	2083
Overall CPUE (fish/s)	0.227 \pm 0.080	0.066 \pm 0.015	0.878 \pm 0.451	0.673 \pm 0.215
Species CPUE (fish/360s)				
<i>Anchoa hepsetus</i>	0.222 \pm 0.222	0.000 \pm 0.000	0.000 \pm 0.000	0.000 \pm 0.000
<i>Anchoa lyolepis</i>	0.000 \pm 0.000	0.000 \pm 0.000	0.111 \pm 0.111	0.000 \pm 0.000
<i>Anchoa mitchilli</i>	13.667 \pm 5.986	2.778 \pm 1.553	3.111 \pm 2.988	6.500 \pm 2.092
<i>Anguilla rostrata</i>	0.000 \pm 0.000	0.000 \pm 0.000	0.000 \pm 0.000	0.111 \pm 0.111
<i>Apeltes quadracus</i>	0.000 \pm 0.000	0.111 \pm 0.111	3.111 \pm 1.662	5.167 \pm 2.836
<i>Bairdiella chrysoura</i>	0.222 \pm 0.222	3.444 \pm 2.015	3.222 \pm 1.211	7.500 \pm 1.708
<i>Brevoortia tyrannus</i>	0.000 \pm 0.000	0.000 \pm 0.000	0.000 \pm 0.000	0.111 \pm 0.111
<i>Centropomus striata</i>	0.333 \pm 0.167	2.222 \pm 0.641	0.111 \pm 0.111	0.222 \pm 0.147
<i>Chilomycterus schoepfi</i>	0.000 \pm 0.000	0.111 \pm 0.111	0.000 \pm 0.000	0.111 \pm 0.111
<i>Conger oceanicus</i>	0.000 \pm 0.000	0.111 \pm 0.111	0.000 \pm 0.000	0.222 \pm 0.222
<i>Etropus microstomus</i>	0.889 \pm 0.772	2.000 \pm 0.577	0.000 \pm 0.000	0.000 \pm 0.000
<i>Fundulus heteroclitus</i>	0.000 \pm 0.000	0.000 \pm 0.000	0.111 \pm 0.111	0.000 \pm 0.000
<i>Gobiosoma strumosus</i>	0.000 \pm 0.000	0.111 \pm 0.111	0.000 \pm 0.000	0.000 \pm 0.000
<i>Gobiosoma bosc</i>	0.000 \pm 0.000	0.333 \pm 0.333	0.111 \pm 0.111	0.556 \pm 0.377
<i>Hippocampus erectus</i>	0.444 \pm 0.176	0.333 \pm 0.167	0.556 \pm 0.294	0.444 \pm 0.338
<i>Lagodon rhomboides</i>	0.000 \pm 0.000	0.000 \pm 0.000	0.000 \pm 0.000	0.111 \pm 0.111
<i>Menidia menidia</i>	63.069 \pm 29.671	3.556 \pm 1.345	264.889 \pm 155.706	151.389 \pm 71.28
<i>Menticirrhus saxatilis</i>	0.444 \pm 0.338	0.889 \pm 0.351	0.000 \pm 0.000	0.000 \pm 0.000

Table 2 continued

	Sand		Submerged Aquatic Vegetation	
	Day	Night	Bay	Night
Species CPUE (fish/360s)				
<i>Opsanus tau</i>	0.000 ± 0.000	0.222 ± 0.147	1.556 ± 1.203	2.000 ± 0.601
<i>Paralichthys dentatus</i>	0.000 ± 0.000	0.222 ± 0.147	0.000 ± 0.000	0.000 ± 0.000
<i>Pogonias cromis</i>	0.000 ± 0.000	0.111 ± 0.111	0.000 ± 0.000	0.000 ± 0.000
<i>Pomatomus saltatrix</i>	0.111 ± 0.111	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
<i>Prionotus carolinus</i>	0.111 ± 0.111	0.111 ± 0.111	0.000 ± 0.000	0.000 ± 0.000
<i>Prionotus evolans</i>	0.000 ± 0.000	0.111 ± 0.111	0.000 ± 0.000	0.000 ± 0.000
<i>Pseudopleuronectes americanus</i>	0.111 ± 0.111	1.444 ± 0.503	0.667 ± 0.553	3.444 ± 2.180
<i>Sphoeroides maculatus</i>	0.111 ± 0.111	0.778 ± 0.364	1.222 ± 0.596	1.278 ± 0.741
<i>Symphurus plagiatus</i>	0.000 ± 0.000	0.111 ± 0.111	0.000 ± 0.000	0.000 ± 0.000
<i>Syngnathus fuscus</i>	1.889 ± 0.455	3.556 ± 1.192	37.222 ± 13.763	62.722 ± 17.565
<i>Tautoga onitis</i>	0.000 ± 0.000	0.444 ± 0.294	0.111 ± 0.111	0.222 ± 0.147
<i>Tautogolabrus adspersus</i>	0.000 ± 0.000	0.111 ± 0.111	0.000 ± 0.000	0.000 ± 0.000
<i>Trinectes maculatus</i>	0.111 ± 0.111	0.444 ± 0.242	0.000 ± 0.000	0.000 ± 0.000
Diversity	0.652 ± 0.167	1.787 ± 0.084	0.820 ± 0.147	1.083 ± 0.106
Species Observed	14	24	14	17
Standardized Richness (species/tow)	1.407 ± 0.206	2.778 ± 0.329	1.778 ± 0.184	2.574 ± 0.316

Table 3. Habitat-specific mean length \pm standard error of the mean (mm; length range in parentheses) for species collected during the daytime survey. Asterisks denote species measured as fork length (*) or body width (**); all others were measured as total length. Species were classified by estuarine usage (T = transient, R = resident, SoS = Southern Stray, ShS = Shelf Stray) following Tatham et al. (1984) and Able and Fahay (2010)

Scientific Name	Common Name	Estuarine Usage	Upper Creek	Creek Mouth	Sand	Submerged Aquatic Vegetation
<i>Alosa pseudoharengus</i> *	Alewife	T	51.0			
<i>Anchoa hepsetus</i> *	Striped anchovy	T		74.5 \pm 6.1 (44 – 107)	62.4 \pm 2.0 (44 – 109)	55.0 \pm 5.0 (50 – 60)
<i>Anchoa mitchilli</i> *	Bay anchovy	T	43.0 \pm 0.4 (18 – 98)	43.5 \pm 0.3 (13 – 85)	45.8 \pm 0.2 (16 – 86)	41.7 \pm 0.4 (16 – 75)
<i>Anguilla rostrata</i>	American eel	T	333.2 \pm 67.9 (56 – 825)	111.4 \pm 19.6 (61 – 416)	753.5 \pm 16.5 (737 – 770)	162.0 \pm 51.9 (53 – 550)
<i>Apeltes quadracus</i>	Fourspine stickleback	R	38.0 \pm 9.5 (27 – 57)	29.1 \pm 0.6 (22 – 49)	52.5 \pm 2.5 (50 – 55)	39.2 \pm 0.5 (12 – 70)
<i>Archosargus probatocephalus</i> *	Sheepshead	SoS		73.0		
<i>Astrosopus guttatus</i>	Northern stargazer	ShS			13.0	
<i>Bairdiella chrysoura</i>	Silver perch	T	68.4 \pm 4.7 (20 – 126)	75.0 \pm 1.5 (17 – 170)	88.0 \pm 2.1 (32 – 139)	61.9 \pm 0.9 (25 – 120)
<i>Brevoortia tyrannus</i> *	Atlantic menhaden	T	71.8 \pm 1.8 (20 – 290)	67.1 \pm 13.8 (20 – 300)	66.5 \pm 29.2 (20 – 270)	71.5 \pm 2.5 (69 – 74)
<i>Caranx crysos</i> *	Blue runner	SoS			145.0 \pm 3.0 (142 – 148)	
<i>Caranx hippos</i> *	Creville jack	SoS	86.0			
<i>Centropristis striata</i>	Black seabass	T	141.0	117.5 \pm 10.9 (42 – 182)	83.2 \pm 12.4 (31 – 195)	107.2 \pm 10.0 (23 – 185)
<i>Chaetodon ocellatus</i>	Spotfin butterflyfish	SoS				35.0 \pm 13.0 (22 – 48)
<i>Chasmodes bosquianus</i>	Striped blenny	R	47.0 \pm 5.8 (30 – 55)	51.4 \pm 3.0 (30 – 73)	51.5 \pm 7.5 (44 – 59)	68.0 \pm 4.8 (56 – 78)
<i>Chilomycterus schoepfi</i>	Striped burrfish	T		261.0 \pm 23.0 (238 – 284)	152.1 \pm 27.1 (23 – 215)	142.4 \pm 18.6 (85 – 225)
<i>Clupea harengus</i> *	Atlantic herring	T		43.9 \pm 1.2 (34 – 60)	83.0	
<i>Cynoscion regalis</i>	Weakfish	T	103.0 \pm 14.4 (69 – 162)	75.5 \pm 4.7 (69 – 89)	126.0 \pm 15.0 (41 – 308)	
<i>Dactylopterus volitans</i>	Flying gurnard	SoS				66.0
<i>Dasyatis say</i> **	Bluntnose stingray	SoS				211.0
<i>Etropus microstomus</i>	Smallmouth flounder	T/R		70.5 \pm 8.5 (62 – 79)	90.5 \pm 8.4 (73 – 124)	69.0 \pm 4.8 (60 – 82)
<i>Eucinostomus argenteus</i> *	Spotfin mojarra	SoS	64.0			
<i>Fundulus heteroclitus</i>	Mummichog	R	52.3 \pm 1.5 (28 – 76)	42.5 \pm 16.5 (26 – 59)		51.4 \pm 2.6 (33 – 67)
<i>Fundulus luciae</i>	Spotfin killifish	R				35.0
<i>Fundulus majalis</i>	Striped killifish	R				62.0

Table 3 continued

Scientific Name	Common Name	Estuarine Usage	Upper Creek	Creek Mouth	Sand	Submerged Aquatic Vegetation
<i>Gadus morhua</i>	Atlantic cod	T	53.0			
<i>Gobiesox strumosus</i>	Skilletfish	SoS	60.0	49.0 ± 7.0 (42 – 56)		
<i>Gobiosoma bosc</i>	Naked goby	R	36.7 ± 0.8 (24 – 56)	31.9 ± 0.7 (13 – 66)	36.8 ± 1.8 (25 – 49)	39.4 ± 3.3 (20 – 69)
<i>Gobiosoma ginsburgi</i>	Seaboard goby	T/R	28.3 ± 2.1 (24 – 34)		28.9 ± 1.4 (22 – 39)	34.8 ± 1.0 (26 – 48)
<i>Hippocampus erectus</i>	Lined seahorse	T		132.0 ± 3.0 (129 – 135)	74.0 ± 15.5 (21 – 108)	101.3 ± 4.7 (38 – 163)
<i>Hypsoblennius hentz</i>	Feather blenny	R		76.0 ± 7.0 (69 – 83)	57.0	70.0 ± 15.0 (55 – 85)
<i>Ictalurus punctatus</i> *	Channel catfish	R	214.0			
<i>Lagodon rhomboides</i> *	Pinfish	T	127.0 ± 6.0 (121 – 133)	105.7 ± 9.5 (89 – 122)	172.0	66.3 ± 8.6 (35 – 137)
<i>Leiostomus xanthurus</i> *	Spot	T	88.4 ± 2.0 (25 – 187)	121.1 ± 3.8 (23 – 213)	140.1 ± 1.7 (77 – 229)	99.4 ± 7.7 (21 – 184)
<i>Lepomis gibbosus</i> *	Pumpkinseed	R	124.4 ± 9.5 (75 – 165)			
<i>Lepomis macrochirus</i> *	Bluegill	R	139.0			
<i>Leucoraja erinacea</i> **	Little skate	ShS			260.0	
<i>Lucania parva</i>	Rainwater killifish	R		30.0		30.7 ± 1.0 (22 – 35)
<i>Lutjanus griseus</i>	Gray snapper	SoS		64.0		
<i>Menidia beryllina</i> *	Inland silverside	R	29.4 ± 1.8 (22 – 58)			
<i>Menidia menidia</i> *	Atlantic silverside	T/R	66.8 ± 1.4 (40 – 105)	54.7 ± 3.7 (13 – 114)	60.4 ± 2.2 (20 – 105)	59.1 ± 0.6 (18 – 118)
<i>Menticirrhus saxatilis</i>	Northern kingfish	T	43.0	98.7 ± 36.8 (30 – 270)	93.5 ± 18.5 (57 – 143)	
<i>Microgobius thalassinus</i>	Green goby	SoS	43.0 ± 3.0 (40 – 46)	22.0 ± 4.0 (18 – 26)		42.0
<i>Micropogonias undulatus</i>	Atlantic croaker	T	33.4 ± 1.8 (18 – 112)	29.1 ± 2.6 (11 – 120)	50.2 ± 10.2 (5 – 336)	
<i>Morone americana</i> *	White perch	R	154.4 ± 20.9 (80 – 279)	182.0 ± 18.0 (164 – 200)	240.0	
<i>Mugil cephalus</i> *	Striped mullet	T				185.0
<i>Mugil curema</i> *	White mullet	T	132.5 ± 2.1 (124 – 138)	139.0		197.0
<i>Mustelus canis</i>	Smooth dogfish	T		414.3 ± 69.3 (343 – 553)	441.0 ± 94.0 (347 – 535)	499.0 ± 5.2 (490 – 508)
<i>Mycteroperca microlepis</i>	Gag	SoS		141.0		
<i>Opsanus tau</i>	Oyster toadfish	R	104.6 ± 14.8 (39 – 160)	77.2 ± 4.6 (27 – 216)	90.6 ± 15.2 (39 – 241)	82.0 ± 8.6 (35 – 192)
<i>Paralichthys dentatus</i>	Summer flounder	T	184.3 ± 11.7 (76 – 295)	153.7 ± 11.8 (25 – 390)	174.5 ± 12.1 (45 – 501)	161.0 ± 11.7 (81 – 324)
<i>Peprilus triacanthus</i> *	Butterfish	ShS	34.8 ± 3.7 (21 – 51)		66.0 ± 13.0 (18 – 111)	

Table 3 continued

Scientific Name	Common Name	Estuarine Usage	Upper Creek	Creek Mouth	Sand	Submerged Aquatic Vegetation
<i>Perca flavescens</i> *	Yellow perch	R	181.0			
<i>Pogonias cromis</i>	Black drum	T	266.8 ± 24.7 (232 – 338)			
<i>Pollachius virens</i> *	Pollock	T		55.7 ± 4.5 (47 – 62)	55.7 ± 4.4 (49 – 64)	43.5 ± 1.7 (40 – 48)
<i>Pomatomus saltatrix</i> *	Bluefish	T	136.3 ± 9.6 (66 – 207)	128.0 ± 22.3 (50 – 199)	125.1 ± 18.4 (57 – 290)	127.7 ± 12.2 (78 – 159)
<i>Prionotus carolinus</i>	Northern searobin	T	41.0		118.0 ± 27.0 (91 – 145)	71.0 ± 24.0 (47 – 95)
<i>Pseudopleuronectes americanus</i>	Winter flounder	T/R	59.4 ± 1.4 (22 – 115)	49.6 ± 2.8 (18 – 201)	60.7 ± 5.4 (21 – 395)	56.4 ± 1.4 (14 – 310)
<i>Scophthalmus aquosus</i>	Windowpane	T		57.0	115.3 ± 15.7 (84 – 132)	66.0 ± 5.0 (61 – 71)
<i>Selene setapinnis</i> *	Atlantic moonfish	SoS	54.5 ± 0.5 (54 – 55)	51.0 ± 1.0 (50 – 52)	63.0	
<i>Selene vomer</i> *	Lookdown	SoS		50.0		
<i>Sphoeroides maculatus</i>	Northern puffer	T	21.2 ± 1.5 (16 – 24)	96.9 ± 12.3 (26 – 163)	80.2 ± 20.0 (7 – 262)	70.9 ± 6.5 (13 – 276)
<i>Stenotomus chrysops</i> *	Scup	T			134.0 ± 33.5 (100 – 201)	140.5 ± 25.5 (115 – 166)
<i>Strongylura marina</i> *	Atlantic needlefish	T				90.0 ± 5.0 (85 – 95)
<i>Symphurus plagiusa</i>	Blackcheek tonguefish	SoS	65.0	71.0		
<i>Syngnathus fuscus</i>	Northern pipefish	T	158.3 ± 18.2 (111 – 191)	141.1 ± 2.8 (52 – 248)	138.4 ± 5.5 (75 – 262)	152.3 ± 1.3 (24 – 244)
<i>Synodus foetens</i> *	Inshore lizardfish	T				138.0
<i>Tautoga onitis</i>	Tautog	T/R		99.2 ± 8.2 (55 – 140)	88.7 ± 25.1 (33 – 192)	76.8 ± 8.6 (25 – 169)
<i>Tautoglabrus adspersus</i>	Cunner	T/R		81.0 ± 55.0 (26 – 136)	40.7 ± 1.8 (30 – 66)	50.4 ± 5.5 (27 – 79)
<i>Trinectes maculatus</i>	Hogchoker	R	67.4 ± 4.7 (42 – 135)	115.0 ± 35.5 (55 – 178)	116.2 ± 14.4 (70 – 155)	
<i>Urophycis regia</i>	Spotted hake	T		128.3 ± 3.0 (124 – 137)	119.6 ± 8.3 (71 – 209)	102.1 ± 5.9 (71 – 196)

Table 4. Seasonal species-specific mean catch-per-unit-effort (number of fish/360s), total number of fish collected, and number of species observed in upper creek (CKU), creek mouth (CKM), sand, and submerged aquatic vegetation (SAV) habitats during the daytime survey. See Table 3 for full scientific names, common names, and estuarine usage for each species

	April				June				August				October			
	CKU	CKM	SAND	SAV	CKU	CKM	SAND	SAV	CKU	CKM	SAND	SAV	CKU	CKM	SAND	SAV
<i>A. pseudoharengus</i>	0.000	0.000	0.000	0.000	0.034	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>A. hepsetus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.067	0.481	1.295	0.061	0.000	0.037	0.067	0.000
<i>A. mitchilli</i>	2.003	3.808	0.256	0.030	9.510	18.269	9.409	1.273	66.067	108.912	100.291	16.485	54.712	65.778	67.933	39.439
<i>A. rostrata</i>	0.074	0.077	0.023	0.000	0.320	0.577	0.000	0.061	0.100	0.074	0.045	0.227	0.033	0.037	0.000	0.045
<i>A. quadracus</i>	0.037	0.038	0.023	1.394	0.078	1.962	0.000	23.141	0.000	0.278	0.000	26.909	0.000	0.000	0.022	29.136
<i>A. probatocephalus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.037	0.000	0.000
<i>A. guttatus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000
<i>B. chrysoura</i>	0.000	0.038	0.000	0.000	0.000	0.000	0.000	0.000	0.300	6.968	1.977	12.515	0.867	7.333	0.378	1.273
<i>B. tyrannus</i>	0.667	0.115	0.070	0.000	19.991	0.462	0.000	0.061	1.667	0.000	0.091	0.000	1.510	0.148	0.044	0.000
<i>C. crysos</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.045	0.000	0.000	0.000	0.000	0.000
<i>C. hippos</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.034	0.000	0.000	0.000
<i>C. striata</i>	0.000	0.038	0.000	0.152	0.034	0.192	0.000	0.303	0.000	0.241	0.409	0.273	0.000	0.148	0.089	0.061
<i>C. ocellatus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.045	0.000	0.000	0.000	0.030
<i>C. bosquianus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.133	0.370	0.023	0.061	0.000	0.185	0.022	0.061
<i>C. schoepfi</i>	0.000	0.000	0.000	0.000	0.000	0.077	0.045	0.000	0.000	0.000	0.114	0.288	0.000	0.000	0.000	0.000
<i>C. harengus</i>	0.000	0.962	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>C. regalis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.100	0.148	0.591	0.000	0.133	0.000	0.022	0.000
<i>D. volitans</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	0.000	0.000
<i>D. say</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	0.000	0.000
<i>E. microstomus</i>	0.000	0.000	0.023	0.061	0.000	0.000	0.090	0.030	0.000	0.000	0.023	0.000	0.000	0.074	0.000	0.030
<i>E. argenteus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.033	0.000	0.000	0.000
<i>F. heteroclitus</i>	2.037	0.000	0.000	0.000	0.328	0.038	0.000	0.000	0.167	0.037	0.000	0.455	0.000	0.000	0.000	0.167

Table 4 continued

	April				June				August				October			
	CKU	CKM	SAND	SAV	CKU	CKM	SAND	SAV	CKU	CKM	SAND	SAV	CKU	CKM	SAND	SAV
<i>F. luciae</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>F. majalis</i>	0.000	0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>G. morhua</i>	0.037	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>G. strumosus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.037	0.000	0.000	0.033	0.037	0.000	0.000
<i>G. bosc</i>	0.593	0.077	0.000	0.000	0.078	0.385	0.000	0.061	1.400	4.463	0.182	0.364	0.970	1.370	0.178	0.000
<i>G. ginsburgi</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.100	0.000	0.227	0.091	0.033	0.000	0.089	0.864
<i>H. erectus</i>	0.000	0.000	0.047	0.121	0.000	0.000	0.023	0.394	0.000	0.074	0.000	0.303	0.000	0.000	0.044	0.182
<i>H. hentz</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.023	0.061	0.000	0.074	0.000	0.000
<i>I. punctatus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>L. rhomboides</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.394	0.067	0.111	0.023	0.091	0.000	0.000	0.000	0.000
<i>L. xanthurus</i>	4.148	0.115	0.000	1.242	9.306	0.769	0.250	0.061	2.167	1.511	3.341	1.485	0.800	0.222	0.178	0.030
<i>L. gibbosus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.200	0.000	0.000	0.000	0.102	0.000	0.000	0.000
<i>L. macrochirus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.034	0.000	0.000	0.000
<i>L. erinacea</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.022	0.000
<i>L. parva</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.037	0.000	0.439
<i>L. griseus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.037	0.000	0.000
<i>M. beryllina</i>	0.139	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>M. menidia</i>	0.333	0.154	0.209	0.000	0.000	0.942	0.567	5.569	9.633	0.704	1.182	114.182	0.500	0.407	2.378	72.045
<i>Men. saxatilis</i>	0.000	0.038	0.000	0.000	0.000	0.000	0.000	0.000	0.033	0.148	0.091	0.000	0.000	0.037	0.000	0.000
<i>M. thalassinus</i>	0.037	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.033	0.074	0.000	0.030	0.033	0.000	0.000	0.030
<i>M. undulatus</i>	0.222	0.000	0.000	0.000	0.086	0.115	0.023	0.000	0.000	0.000	0.136	0.000	2.202	1.963	0.956	0.000
<i>M. americana</i>	0.037	0.077	0.023	0.000	0.069	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.271	0.000	0.000	0.000
<i>M. cephalus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030
<i>M. curema</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.200	0.037	0.000	0.030	0.000	0.000	0.000	0.000

Table 4 continued

	April					June					August			October		
	CKU	CKM	SAND	SAV		CKU	CKM	SAND	SAV		CKU	CKM	SAND	SAV		CKU
Total Fish Collected	289	178	60	168	1385	763	628	1622	2545	3488	4950	4902	1906	2191	3296	4677
Species Observed	19	17	18	13	19	21	17	21	27	28	34	33	26	28	22	22

Table 5. Mean length \pm standard error of the mean (mm; length range in parentheses) for species collected during the day-night survey. An asterisk denotes species measured as fork length; all others were measured as total length. See Table 2 for common names

	Sand		Submerged Aquatic Vegetation	
	Day	Night	Day	Night
<i>Anchoa hepsetus</i> *	70.0 \pm 2.0 (68 – 72)			
<i>Anchoa lyolepis</i> *			40.0	
<i>Anchoa mitchilli</i> *	48.3 \pm 0.5 (34 – 65)	54.4 \pm 1.5 (44 – 76)	22.4 \pm 0.5 (20 – 31)	45.9 \pm 0.9 (34 – 70)
<i>Anguilla rostrata</i>				271.0
<i>Apeltes quadracus</i>		41.0	37.8 \pm 0.9 (30 – 51)	37.4 \pm 1.2 (26 – 52)
<i>Bairdiella chrysoura</i>	43.5 \pm 2.5 (41 – 46)	76.3 \pm 4.2 (49 – 176)	57.7 \pm 3.3 (27 – 87)	74.5 \pm 3.2 (33 – 130)
<i>Brevoortia tyrannus</i> *				84.0
<i>Centropristis striata</i>	95.0 \pm 32.9 (43 – 156)	66.2 \pm 6.8 (42 – 160)	65.0	119.5 \pm 55.5 (64 – 175)
<i>Chilomycterus schoepfi</i>		100.0		98.0
<i>Conger oceanicus</i>		309.0		219.5 \pm 32.5 (187 – 252)
<i>Etropus microstomus</i>	64.1 \pm 3.3 (54 – 83)	56.6 \pm 2.5 (33 – 80)		
<i>Fundulus heteroclitus</i>			101.0	
<i>Gobiesox strumosus</i>		52.0		
<i>Gobiosoma bosc</i>		31.7 \pm 4.4 (23 – 37)	34.0	42.4 \pm 2.7 (35 – 51)
<i>Hippocampus erectus</i>	111.5 \pm 8.1 (97 – 132)	107.7 \pm 11.4 (90 – 129)	117.6 \pm 3.4 (110 – 130)	115.3 \pm 11.4 (88 – 137)
<i>Lagodon rhomboides</i> *				130.0
<i>Menidia menidia</i> *	66.6 \pm 0.8 (40 – 90)	66.2 \pm 2.3 (38 – 107)	64.8 \pm 0.7 (36 – 91)	65.6 \pm 0.7 (36 – 115)
<i>Menticirrhus saxatilis</i>	164.3 \pm 20.5 (108 – 201)	128.4 \pm 13.2 (76 – 191)		
<i>Opsanus tau</i>		56.5 \pm 1.5 (55 – 58)	53.6 \pm 1.7 (45 – 65)	77.0 \pm 8.8 (38 – 141)
<i>Paralichthys dentatus</i>		252.5 \pm 22.5 (230 – 275)		
<i>Pogonias cromis</i>		110.0		
<i>Pomatomus saltatrix</i> *	101.0			

Table 5 continued

	Sand		Submerged Aquatic Vegetation	
	Day	Night	Day	Night
<i>Prionotus carolinus</i>	65.0	79.0		
<i>Prionotus evolans</i>		94.0		
<i>Pseudopleuronectes americanus</i>	68.0	84.2 ± 3.4 (63 – 106)	76.8 ± 4.1 (63 – 91)	76.9 ± 1.6 (58 – 92)
<i>Sphoeroides maculatus</i>	130.0	114.1 ± 9.2 (72 – 142)	126.5 ± 7.2 (87 – 178)	129.1 ± 4.0 (100 – 151)
<i>Symphurus plagiusa</i>		78.0		
<i>Syngnathus fuscus</i>	125.3 ± 5.0 (85 – 165)	135.3 ± 5.4 (42 – 189)	140.9 ± 2.0 (71 – 210)	148.0 ± 1.6 (53 – 219)
<i>Tautoga onitis</i>		76.8 ± 6.3 (66 – 95)	109.0	120.0 ± 2.0 (118 – 122)
<i>Tautogolabrus adspersus</i>		34.0		
<i>Trinectes maculatus</i>	175.0	166.5 ± 5.3 (152 – 176)		

Online Resource 1. Number of sampling events, environmental parameters, mean catch-per-unit-effort (CPUE), Shannon diversity, richness, and the percent of sampling events (% occurrence) where each parameter was greater than zero across tidal stages for the daytime survey

	Upper Creek		Creek Mouth		Sand		Submerged Aquatic Vegetation	
	Ebb	Flood	Ebb	Flood	Ebb	Flood	Ebb	Flood
Sampling Events	52	64	57	49	97	79	42	90
Temperature (°C)	20.1 ± 0.7	20.2 ± 0.6	19.9 ± 0.6	20.3 ± 0.7	19.9 ± 0.5	19.2 ± 0.5	18.8 ± 0.7	19.7 ± 0.5
Salinity	21.13 ± 0.61	23.47 ± 0.50	23.83 ± 0.56	24.27 ± 0.48	24.30 ± 0.47	25.91 ± 0.47	23.97 ± 0.84	26.40 ± 0.41
Dissolved Oxygen (mg/L)	4.68 ± 0.39	5.12 ± 0.30	6.81 ± 0.23	6.84 ± 0.24	7.00 ± 0.16	7.28 ± 0.18	7.68 ± 0.24	7.37 ± 0.15
pH	7.35 ± 0.05	7.42 ± 0.04	7.71 ± 0.02	7.69 ± 0.05	7.79 ± 0.02	7.79 ± 0.03	7.90 ± 0.03	7.92 ± 0.02
Water Depth (m)	2.0 ± 0.1	2.0 ± 0.1	1.6 ± 0.1	1.5 ± 0.1	2.3 ± 0.1	2.1 ± 0.1	1.2 ± 0.1	1.1 ± 0.0
Algae Volume (L/s)	0.016 ± 0.006	0.010 ± 0.003	0.370 ± 0.081	0.279 ± 0.049	0.021 ± 0.007	0.024 ± 0.006	0.087 ± 0.025	0.103 ± 0.018
Algae % Occurrence	79	83	98	96	85	85	98	96
Overall CPUE (fish/s)	0.196 ± 0.054	0.105 ± 0.028	0.186 ± 0.062	0.162 ± 0.051	0.148 ± 0.034	0.132 ± 0.042	0.260 ± 0.132	0.293 ± 0.143
CPUE % Occurrence	77	80	88	94	85	70	86	89
Diversity	0.609 ± 0.081	0.656 ± 0.063	0.828 ± 0.074	0.739 ± 0.081	0.485 ± 0.054	0.462 ± 0.060	0.750 ± 0.086	0.760 ± 0.058
Diversity % Occurrence	64	69	77	78	59	52	69	73

Online Resource 1 continued

	Upper Creek		Creek Mouth		Sand		Submerged Aquatic Vegetation	
	Ebb	Flood	Ebb	Flood	Ebb	Flood	Ebb	Flood
Standardized Richness (species/tow)	0.966 ± 0.118	0.840 ± 0.077	1.333 ± 0.140	1.265 ± 0.129	0.825 ± 0.080	0.709 ± 0.080	1.155 ± 0.170	1.291 ± 0.121
Richness % Occurrence	77	80	88	94	85	70	86	89

Online Resource 2. Canonical correspondence analysis (CCA) species loadings for the first two canonical axes in the daytime survey CCA. Loadings in **bold** were those considered noteworthy for discussion. See Figure 5 for CCA plots

Scientific Name	Common Name	Axis 1	Axis 2
<i>Alosa pseudoharengus</i>	Alewife	0.076	0.035
<i>Anchoa hepsetus</i>	Striped anchovy	0.075	-0.273
<i>Anchoa mitchilli</i>	Bay anchovy	0.390	-0.361
<i>Anguilla rostrata</i>	American eel	0.045	0.080
<i>Apeltes quadracus</i>	Fourspine stickleback	-0.343	0.068
<i>Archosargus probatocephalus</i>	Sheepshead	-0.035	-0.007
<i>Astroscopus guttatus</i>	Northern stargazer	0.043	-0.022
<i>Bairdiella chrysoura</i>	Silver perch	-0.164	-0.186
<i>Brevoortia tyrannus</i>	Atlantic menhaden	0.319	0.149
<i>Caranx crysos</i>	Blue runner	0.036	-0.060
<i>Caranx hippos</i>	Crevalle jack	-0.003	0.015
<i>Centropristis striata</i>	Black seabass	-0.182	-0.212
<i>Chaetodon ocellatus</i>	Spotfin butterflyfish	-0.087	0.002
<i>Chasmodes bosquianus</i>	Striped blenny	-0.018	0.039
<i>Chilomycterus schoepfi</i>	Striped burrfish	-0.127	-0.159
<i>Clupea harengus</i>	Atlantic herring	-0.088	0.203
<i>Cynoscion regalis</i>	Weakfish	0.137	-0.140
<i>Dactylopterus volitans</i>	Flying gurnard	0.001	-0.150
<i>Dasyatis say</i>	Bluntnose stingray	0.001	-0.150
<i>Etropus microstomus</i>	Smallmouth flounder	-0.111	0.006
<i>Eucinostomus argenteus</i>	Spotfin mojarra	0.073	0.012
<i>Fundulus heteroclitus</i>	Mummichog	-0.028	0.192
<i>Fundulus luciae</i>	Spotfin killifish	-0.063	-0.023
<i>Fundulus majalis</i>	Striped killifish	-0.087	0.101
<i>Gadus morhua</i>	Atlantic cod	0.337	0.117
<i>Gobiesox strumosus</i>	Skilletfish	0.000	0.038
<i>Gobiosoma bosc</i>	Naked goby	0.068	0.135
<i>Gobiosoma ginsburgi</i>	Seaboard goby	-0.113	-0.076
<i>Hippocampus erectus</i>	Lined seahorse	-0.302	0.013
<i>Hypsoblennius hentz</i>	Feather blenny	-0.023	-0.028
<i>Ictalurus punctatus</i>	Channel catfish	0.088	0.026
<i>Lagodon rhomboides</i>	Pinfish	-0.107	-0.100
<i>Leiostomus xanthurus</i>	Spot	0.323	-0.071
<i>Lepomis gibbosus</i>	Pumpkinseed	0.174	0.194
<i>Lepomis macrochirus</i>	Bluegill	0.106	0.152
<i>Leucoraja erinacea</i>	Little skate	0.005	-0.043

Online Resource 2 continued

Scientific Name	Common Name	Axis 1	Axis 2
<i>Lucania parva</i>	Rainwater killifish	-0.126	0.018
<i>Lutjanus griseus</i>	Gray snapper	-0.030	0.031
<i>Menidia beryllina</i>	Inland silverside	0.041	0.113
<i>Menidia menidia</i>	Atlantic silverside	-0.343	-0.023
<i>Menticirrhus saxatilis</i>	Northern kingfish	0.034	-0.073
<i>Microgobius thalassinus</i>	Green goby	0.025	0.115
<i>Micropogonias undulatus</i>	Atlantic croaker	0.147	0.031
<i>Morone americana</i>	White perch	0.088	0.220
<i>Mugil cephalus</i>	Striped mullet	-0.001	0.080
<i>Mugil curema</i>	White mullet	0.079	-0.009
<i>Mustelus canis</i>	Smooth dogfish	0.021	-0.153
<i>Mycteroperca microlepis</i>	Gag	-0.004	-0.024
<i>Opsanus tau</i>	Oyster toadfish	-0.105	-0.117
<i>Paralichthys dentatus</i>	Summer flounder	0.128	-0.143
<i>Peprilus triacanthus</i>	Butterfish	0.072	-0.131
<i>Perca flavescens</i>	Yellow perch	0.131	0.064
<i>Pogonias cromis</i>	Black drum	0.083	0.086
<i>Pollachius virens</i>	Pollock	-0.207	0.386
<i>Pomatomus saltatrix</i>	Bluefish	0.213	-0.092
<i>Prionotus carolinus</i>	Northern searobin	-0.078	0.052
<i>Pseudopleuronectes americanus</i>	Winter flounder	-0.152	-0.031
<i>Scophthalmus aquosus</i>	Windowpane	-0.088	0.231
<i>Selene setapinnis</i>	Atlantic moonfish	0.062	-0.024
<i>Selene vomer</i>	Lookdown	-0.017	-0.031
<i>Sphoeroides maculatus</i>	Northern puffer	-0.155	-0.254
<i>Stenotomus chrysops</i>	Scup	0.001	-0.146
<i>Strongylura marina</i>	Atlantic needlefish	-0.072	-0.005
<i>Symphurus plagiusa</i>	Blackcheek tonguefish	0.002	0.053
<i>Syngnathus fuscus</i>	Northern pipefish	-0.578	-0.035
<i>Synodus foetens</i>	Inshore lizardfish	-0.010	-0.041
<i>Tautoga onitis</i>	Tautog	-0.162	-0.119
<i>Tautoglabrus adspersus</i>	Cunner	-0.142	-0.097
<i>Trinectes maculatus</i>	Hogchoker	0.135	0.089
<i>Urophycis regia</i>	Spotted hake	-0.214	0.449

Online Resource 3. Species-specific mean catch-per-unit-effort (number of fish/360s), total number of fish collected, and number of species observed in all habitats across tidal stages during the daytime survey. See Table 3 for common names and estuarine usage for each species

[illegible]

Online Resource 3 continued

	Upper Creek		Creek Mouth		Sand		Submerged Aquatic Vegetation	
	Ebb	Flood	Ebb	Flood	Ebb	Flood	Ebb	Flood
<i>Fundulus heteroclitus</i>	0.500 ± 0.245	0.680 ± 0.594	0.035 ± 0.025	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.131 ± 0.109	0.167 ± 0.167
<i>Fundulus luciae</i>	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.011 ± 0.011
<i>Fundulus majalis</i>	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.011 ± 0.011
<i>Gadus morhua</i>	0.019 ± 0.019	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
<i>Gobiosox strumosus</i>	0.019 ± 0.019	0.000 ± 0.000	0.035 ± 0.025	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
<i>Gobiosoma bosc</i>	1.463 ± 0.423	0.207 ± 0.096	2.289 ± 1.129	0.796 ± 0.322	0.155 ± 0.068	0.013 ± 0.013	0.048 ± 0.033	0.133 ± 0.064
<i>Gobiosoma ginsburgi</i>	0.077 ± 0.060	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.113 ± 0.104	0.038 ± 0.022	0.202 ± 0.119	0.256 ± 0.256
<i>Hippocampus erectus</i>	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.041 ± 0.041	0.031 ± 0.018	0.025 ± 0.018	0.167 ± 0.083	0.289 ± 0.116
<i>Hypsoblennius hentz</i>	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.041 ± 0.041	0.010 ± 0.010	0.000 ± 0.000	0.024 ± 0.024	0.011 ± 0.011
<i>Ictalurus punctatus</i>	0.019 ± 0.019	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
<i>Lagodon rhomboides</i>	0.000 ± 0.000	0.031 ± 0.031	0.018 ± 0.018	0.041 ± 0.029	0.010 ± 0.010	0.000 ± 0.000	0.024 ± 0.024	0.167 ± 0.085
<i>Leiostomus xanthurus</i>	5.096 ± 3.054	3.217 ± 1.261	0.523 ± 0.405	0.816 ± 0.431	1.021 ± 0.633	0.848 ± 0.404	2.167 ± 1.457	0.022 ± 0.022
<i>Lepomis gibbosus</i>	0.174 ± 0.128	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
<i>Lepomis macrochirus</i>	0.020 ± 0.020	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
<i>Leucoraja erinacea</i>	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.013 ± 0.013	0.000 ± 0.000	0.000 ± 0.000
<i>Lucania parva</i>	0.000 ± 0.000	0.000 ± 0.000	0.018 ± 0.018	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.345 ± 0.311	0.011 ± 0.011
<i>Lutjanus griseus</i>	0.000 ± 0.000	0.000 ± 0.000	0.018 ± 0.018	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
<i>Menidia beryllina</i>	0.668 ± 0.598	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
<i>Menidia menidia</i>	5.577 ± 5.538	0.359 ± 0.247	0.404 ± 0.249	0.724 ± 0.348	1.350 ± 0.976	0.785 ± 0.487	19.512 ± 13.836	61.22 ± 37.858
<i>Menticirrhus saxatilis</i>	0.000 ± 0.000	0.016 ± 0.016	0.070 ± 0.043	0.041 ± 0.029	0.000 ± 0.000	0.051 ± 0.040	0.000 ± 0.000	0.000 ± 0.000
<i>Microgobius thalassinus</i>	0.038 ± 0.027	0.016 ± 0.016	0.000 ± 0.000	0.041 ± 0.041	0.000 ± 0.000	0.000 ± 0.000	0.048 ± 0.033	0.000 ± 0.000
<i>Micropogonias undulatus</i>	0.462 ± 0.314	0.790 ± 0.347	0.702 ± 0.632	0.327 ± 0.166	0.330 ± 0.180	0.228 ± 0.095	0.000 ± 0.000	0.000 ± 0.000
<i>Morone americana</i>	0.176 ± 0.157	0.063 ± 0.044	0.035 ± 0.025	0.000 ± 0.000	0.000 ± 0.000	0.013 ± 0.013	0.000 ± 0.000	0.000 ± 0.000

Online Resource 3 continued

	Upper Creek		Creek Mouth		Sand		Submerged Aquatic Vegetation	
	Ebb	Flood	Ebb	Flood	Ebb	Flood	Ebb	Flood
<i>Mugil cephalus</i>	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.024 ± 0.024	0.000 ± 0.000
<i>Mugil curema</i>	0.077 ± 0.077	0.031 ± 0.031	0.000 ± 0.000	0.020 ± 0.020	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.011 ± 0.011
<i>Mustelus canis</i>	0.000 ± 0.000	0.000 ± 0.000	0.018 ± 0.018	0.041 ± 0.029	0.000 ± 0.000	0.025 ± 0.018	0.024 ± 0.024	0.022 ± 0.022
<i>Mycteroperca microlepis</i>	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.020 ± 0.020	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
<i>Opsanus tau</i>	0.115 ± 0.059	0.031 ± 0.022	0.527 ± 0.146	0.684 ± 0.267	0.113 ± 0.057	0.025 ± 0.018	0.119 ± 0.078	0.294 ± 0.129
<i>Paralichthys dentatus</i>	0.346 ± 0.095	0.141 ± 0.049	0.423 ± 0.152	0.367 ± 0.119	0.596 ± 0.135	0.190 ± 0.051	0.286 ± 0.098	0.156 ± 0.063
<i>Peprilus triacanthus</i>	0.000 ± 0.000	0.125 ± 0.125	0.000 ± 0.000	0.000 ± 0.000	0.031 ± 0.018	0.063 ± 0.038	0.000 ± 0.000	0.000 ± 0.000
<i>Perca flavescens</i>	0.025 ± 0.025	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
<i>Pogonias cromis</i>	0.038 ± 0.027	0.034 ± 0.034	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
<i>Pollachius virens</i>	0.000 ± 0.000	0.000 ± 0.000	0.053 ± 0.053	0.000 ± 0.000	0.031 ± 0.023	0.000 ± 0.000	0.024 ± 0.024	0.033 ± 0.025
<i>Pomatomus saltatrix</i>	0.250 ± 0.095	0.141 ± 0.058	0.088 ± 0.038	0.061 ± 0.035	0.113 ± 0.055	0.038 ± 0.022	0.000 ± 0.000	0.072 ± 0.029
<i>Prionotus carolinus</i>	0.000 ± 0.000	0.016 ± 0.016	0.000 ± 0.000	0.000 ± 0.000	0.020 ± 0.014	0.000 ± 0.000	0.000 ± 0.000	0.022 ± 0.016
<i>Pseudopleuronectes americanus</i>	0.327 ± 0.236	2.559 ± 2.203	1.491 ± 0.916	0.224 ± 0.106	0.964 ± 0.449	0.177 ± 0.074	3.857 ± 2.413	2.578 ± 0.703
<i>Scophthalmus aquosus</i>	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.020 ± 0.020	0.031 ± 0.023	0.000 ± 0.000	0.000 ± 0.000	0.022 ± 0.016
<i>Selene setapinnis</i>	0.019 ± 0.019	0.016 ± 0.016	0.018 ± 0.018	0.020 ± 0.020	0.000 ± 0.000	0.013 ± 0.013	0.000 ± 0.000	0.000 ± 0.000
<i>Selene vomer</i>	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.020 ± 0.020	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
<i>Sphoeroides maculatus</i>	0.000 ± 0.000	0.078 ± 0.056	0.227 ± 0.083	0.041 ± 0.041	0.113 ± 0.044	0.076 ± 0.030	0.476 ± 0.338	0.572 ± 0.217
<i>Stenotomus chrysops</i>	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.031 ± 0.023	0.000 ± 0.000	0.000 ± 0.000	0.022 ± 0.016
<i>Strongylura marina</i>	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.022 ± 0.022
<i>Symphurus plagiusa</i>	0.000 ± 0.000	0.016 ± 0.016	0.018 ± 0.018	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
<i>Syngnathus fuscus</i>	0.000 ± 0.000	0.063 ± 0.038	2.184 ± 0.621	1.092 ± 0.306	0.268 ± 0.111	0.291 ± 0.102	11.06 ± 7.108	8.294 ± 3.002
<i>Synodus foetens</i>	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.024 ± 0.024	0.000 ± 0.000
<i>Tautoga onitis</i>	0.000 ± 0.000	0.000 ± 0.000	0.140 ± 0.064	0.122 ± 0.063	0.041 ± 0.032	0.025 ± 0.018	0.119 ± 0.078	0.194 ± 0.078

Online Resource 3 continued

	Upper Creek		Creek Mouth		Sand		Submerged Aquatic Vegetation	
	Ebb	Flood	Ebb	Flood	Ebb	Flood	Ebb	Flood
<i>Tautoglabrus adspersus</i>	0.000 ± 0.000	0.000 ± 0.000	0.018 ± 0.018	0.020 ± 0.020	0.186 ± 0.186	0.013 ± 0.013	0.095 ± 0.067	0.089 ± 0.044
<i>Trinectes maculatus</i>	0.116 ± 0.053	0.260 ± 0.185	0.018 ± 0.018	0.041 ± 0.041	0.031 ± 0.018	0.025 ± 0.018	0.000 ± 0.000	0.000 ± 0.000
<i>Urophycis regia</i>	0.000 ± 0.000	0.000 ± 0.000	0.070 ± 0.034	0.000 ± 0.000	0.072 ± 0.037	0.089 ± 0.063	0.024 ± 0.024	0.189 ± 0.110
Total Fish Collected	3668	2457	3781	2839	5183	3751	3366	8003
Species Observed	32	30	38	32	35	35	30	40

Online Resource 4. Post-hoc test results of the catch-per-unit-effort (CPUE) zero altered gamma model for the daytime, seasonal survey within upper creek, creek mouth, sand, and submerged aquatic vegetation (SAV) habitats. Reported ratios and confidence intervals from the Bernoulli and gamma models were back-transformed from the logit and log scales, respectively

Bernoulli Comparison	Odds Ratio	95% Confidence Interval	p-value
April / June	0.134	0.054 – 0.331	< 0.001
April / August	0.053	0.016 – 0.177	< 0.001
April / October	0.130	0.053 – 0.322	< 0.001
June / August	0.396	0.107 – 1.464	0.263
June / October	0.974	0.344 – 2.761	1.000
August / October	2.464	0.666 – 9.108	0.287
Upper Creek / Creek Mouth	0.303	0.092 – 0.992	0.048
Upper Creek / Sand	1.025	0.420 – 2.499	1.000
Upper Creek / SAV	0.389	0.135 – 1.118	0.099
Creek Mouth / Sand	3.385	1.114 – 10.285	0.025
Creek Mouth / SAV	1.285	0.376 – 4.394	0.953
Sand / SAV	0.380	0.143 – 1.009	0.053
Ebb / Flood	1.357	0.801 – 2.301	0.257
Gamma Comparison	CPUE Ratio	95% Confidence Interval	p-value
Upper Creek			
April / June	0.227	0.081 – 0.637	0.001
April / August	0.170	0.060 – 0.480	< 0.001
April / October	0.223	0.077 – 0.645	0.002
June / August	0.749	0.284 – 1.977	0.870
June / October	0.985	0.364 – 2.670	1.000
August / October	1.316	0.507 – 3.413	0.881
Creek Mouth			
April / June	0.225	0.084 – 0.605	0.001
April / August	0.056	0.021 – 0.148	< 0.001
April / October	0.075	0.026 – 0.216	< 0.001
June / August	0.248	0.099 – 0.621	0.001
June / October	0.332	0.123 – 0.900	0.023
August / October	1.340	0.507 – 3.543	0.867

Online Resource 4 continued

Gamma Comparison	CPUE Ratio	95% Confidence Interval	p-value
Sand			
April / June	0.274	0.103 – 0.729	0.004
April / August	0.030	0.011 – 0.078	< 0.001
April / October	0.056	0.021 – 0.150	< 0.001
June / August	0.108	0.050 – 0.232	< 0.001
June / October	0.204	0.094 – 0.442	< 0.001
August / October	1.896	0.897 – 4.009	0.125
SAV			
April / June	0.263	0.103 – 0.668	0.001
April / August	0.100	0.039 – 0.259	< 0.001
April / October	0.083	0.031 – 0.224	< 0.001
June / August	0.382	0.166 – 0.877	0.016
June / October	0.315	0.134 – 0.741	0.003
August / October	0.825	0.355 – 1.919	0.936
April			
Upper Creek / Creek Mouth	1.654	0.454 – 6.033	0.750
Upper Creek / Sand	3.165	0.864 – 11.598	0.103
Upper Creek / SAV	1.187	0.333 – 4.230	0.986
Creek Mouth / Sand	1.913	0.538 – 6.800	0.554
Creek Mouth / SAV	0.717	0.208 – 2.474	0.901
Sand / SAV	0.375	0.109 – 1.287	0.172
June			
Upper Creek / Creek Mouth	1.642	0.510 – 5.285	0.695
Upper Creek / Sand	3.828	1.315 – 11.147	0.007
Upper Creek / SAV	1.374	0.443 – 4.263	0.889
Creek Mouth / Sand	2.331	0.810 – 6.710	0.168
Creek Mouth / SAV	0.837	0.273 – 2.566	0.977
Sand / SAV	0.359	0.130 – 0.992	0.047
August			
Upper Creek / Creek Mouth	0.544	0.176 – 1.683	0.509
Upper Creek / Sand	0.551	0.198 – 1.535	0.441
Upper Creek / SAV	0.701	0.234 – 2.095	0.838
Creek Mouth / Sand	1.013	0.368 – 2.787	1.000

Online Resource 4 continued

Gamma Comparison	CPUE Ratio	95% Confidence Interval	p-value
August			
Creek Mouth / SAV	1.289	0.433 – 3.835	0.933
Sand / SAV	1.272	0.477 – 3.393	0.923
October			
Upper Creek / Creek Mouth	0.554	0.168 – 1.829	0.582
Upper Creek / Sand	0.794	0.277 – 2.279	0.943
Upper Creek / SAV	0.439	0.144 – 1.345	0.233
Creek Mouth / Sand	1.434	0.487 – 4.220	0.827
Creek Mouth / SAV	0.793	0.253 – 2.490	0.954
Sand / SAV	0.553	0.204 – 1.501	0.423
Ebb			
Upper Creek / Creek Mouth	1.069	0.400 – 2.859	0.998
Upper Creek / Sand	2.237	0.913 – 5.478	0.096
Upper Creek / SAV	1.275	0.454 – 3.578	0.931
Creek Mouth / Sand	2.092	0.882 – 4.963	0.124
Creek Mouth / SAV	1.192	0.437 – 3.253	0.970
Sand / SAV	0.570	0.227 – 1.428	0.394
Flood			
Upper Creek / Creek Mouth	0.846	0.317 – 2.255	0.972
Upper Creek / Sand	1.029	0.410 – 2.583	1.000
Upper Creek / SAV	0.556	0.226 – 1.369	0.337
Creek Mouth / Sand	1.217	0.481 – 3.076	0.949
Creek Mouth / SAV	0.657	0.264 – 1.637	0.639
Sand / SAV	0.540	0.232 – 1.257	0.239
Upper Creek			
Ebb / Flood	2.246	1.252 – 4.030	0.007
Creek Mouth			
Ebb / Flood	1.778	1.028 – 3.073	0.039
Sand			
Ebb / Flood	1.034	0.642 – 1.664	0.892

Online Resource 4 continued

Gamma Comparison	CPUE Ratio	95% Confidence Interval	p-value
SAV			
Ebb / Flood	0.980	0.550 – 1.745	0.945

Online Resource 5. Post-hoc test results of the catch-per-unit-effort (CPUE), Shannon diversity, and richness models for the day-night survey within sand and submerged aquatic vegetation (SAV) habitats. Reported ratios and confidence intervals from the CPUE model were back-transformed from the log scale

Comparison		95% Confidence Interval	p-value
CPUE			
	CPUE Ratio		
August / September	1.827	0.544 – 6.130	0.448
August / October	3.038	0.905 – 10.196	0.077
September / October	1.663	0.496 – 5.582	0.561
Sand / SAV	0.231	0.102 – 0.525	0.001
Day / Night	1.287	0.567 – 2.920	0.534
Diversity			
	Diversity Difference		
August – September	-0.100	-0.501 – 0.301	0.813
August – October	0.031	-0.370 – 0.432	0.980
September – October	0.131	-0.270 – 0.531	0.703
Day			
Sand – SAV	-0.168	-0.551 – 0.215	0.378
Night			
Sand – SAV	0.704	0.321 – 1.087	0.001
Sand			
Day – Night	-1.135	-1.518 – -0.752	< 0.001
SAV			
Day – Night	-0.263	-0.646 – 0.120	0.171
Richness			
	Richness Difference		
August – September	0.236	-0.484 – 0.957	0.702
August – October	0.903	0.182 – 1.623	0.012
September – October	0.667	-0.054 – 1.387	0.074
Sand – SAV	-0.083	-0.571 – 0.404	0.730
Day – Night	-1.083	-1.571 – -0.596	< 0.001

Online Resource 6. Post-hoc test results of the Shannon diversity zero altered gamma model for the daytime, seasonal survey within upper creek, creek mouth, sand, and submerged aquatic vegetation (SAV) habitats. Reported ratios and confidence intervals from the Bernoulli and gamma models were back-transformed from the logit and log scales, respectively

Bernoulli Comparison	Odds Ratio	95% Confidence Interval	p-value
April / June	0.453	0.177 – 1.159	0.133
April / August	0.382	0.148 – 0.985	0.045
April / October	0.666	0.274 – 1.622	0.644
June / August	0.843	0.340 – 2.095	0.963
June / October	1.471	0.627 – 3.450	0.650
August / October	1.745	0.739 – 4.120	0.343
Upper Creek / Creek Mouth	0.909	0.307 – 2.695	0.996
Upper Creek / Sand	2.301	0.909 – 5.827	0.097
Upper Creek / SAV	1.228	0.450 – 3.352	0.953
Creek Mouth / Sand	2.532	0.998 – 6.421	0.051
Creek Mouth / SAV	1.351	0.493 – 3.701	0.869
Sand / SAV	0.534	0.230 – 1.241	0.223
Ebb / Flood	0.921	0.561 – 1.510	0.744
Gamma Comparison	Diversity Ratio	95% Confidence Interval	p-value
April / June	0.870	0.659 – 1.148	0.569
April / August	1.109	0.844 – 1.459	0.765
April / October	1.020	0.771 – 1.348	0.998
June / August	1.276	1.017 – 1.600	0.030
June / October	1.173	0.929 – 1.480	0.295
August / October	0.919	0.733 – 1.153	0.775
Upper Creek / Creek Mouth	0.808	0.586 – 1.116	0.325
Upper Creek / Sand	1.118	0.826 – 1.512	0.780
Upper Creek / SAV	0.781	0.572 – 1.066	0.173
Creek Mouth / Sand	1.382	1.029 – 1.857	0.025
Creek Mouth / SAV	0.966	0.711 – 1.312	0.991
Sand / SAV	0.699	0.524 – 0.931	0.007
Ebb / Flood	1.054	0.917 – 1.210	0.460

Online Resource 7. Post-hoc test results of the richness zero altered gamma model for the daytime, seasonal survey within upper creek, creek mouth, sand, and submerged aquatic vegetation (SAV) habitats. Reported ratios and confidence intervals from the Bernoulli and gamma models were back-transformed from the logit and log scales, respectively

Bernoulli Comparison	Odds Ratio	95% Confidence Interval	p-value
April / June	0.134	0.054 – 0.331	< 0.001
April / August	0.053	0.016 – 0.177	< 0.001
April / October	0.130	0.053 – 0.322	< 0.001
June / August	0.396	0.107 – 1.464	0.263
June / October	0.974	0.344 – 2.761	1.000
August / October	2.464	0.666 – 9.108	0.287
Upper Creek / Creek Mouth	0.303	0.092 – 0.992	0.048
Upper Creek / Sand	1.025	0.420 – 2.499	1.000
Upper Creek / SAV	0.389	0.135 – 1.118	0.099
Creek Mouth / Sand	3.385	1.114 – 10.285	0.025
Creek Mouth / SAV	1.285	0.376 – 4.394	0.953
Sand / SAV	0.380	0.143 – 1.009	0.053
Ebb / Flood	1.357	0.801 – 2.301	0.257
Gamma Comparison	Richness Ratio	95% Confidence Interval	p-value
April / June	0.644	0.512 – 0.810	< 0.001
April / August	0.480	0.383 – 0.602	< 0.001
April / October	0.625	0.498 – 0.785	< 0.001
June / August	0.746	0.612 – 0.908	0.001
June / October	0.971	0.797 – 1.184	0.982
August / October	1.303	1.072 – 1.583	0.003
Upper Creek / Creek Mouth	0.770	0.555 – 1.070	0.173
Upper Creek / Sand	1.162	0.862 – 1.566	0.570
Upper Creek / SAV	0.797	0.582 – 1.092	0.251
Creek Mouth / Sand	1.508	1.122 – 2.029	0.002
Creek Mouth / SAV	1.035	0.756 – 1.419	0.992
Sand / SAV	0.686	0.517 – 0.912	0.004
Ebb / Flood	1.027	0.911 – 1.158	0.662

Figures

Fig. 1. Locations of sampling sites and relevant landmarks within Barnegat Bay, New Jersey, U.S.A. All sites were included in the daytime survey. The two sampling sites in the southern bay encompassed by circles were those used in the day-night survey. See Tables 1 and 2 for additional details of the daytime and day-night survey efforts, respectively

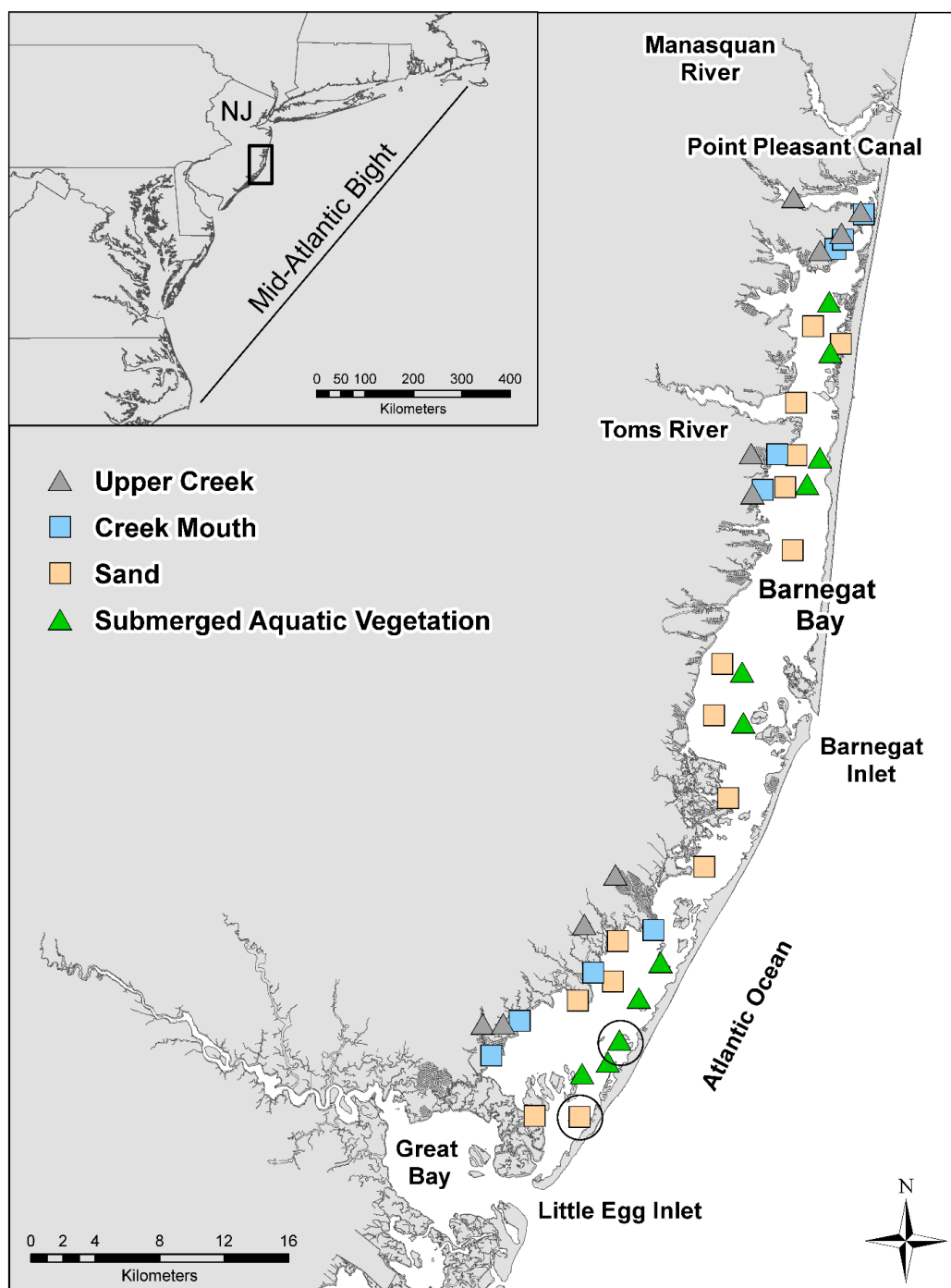


Fig. 2. Box and whisker plot showing the seasonality of temperature (Temp.), salinity, dissolved oxygen (D.O.), pH, and depth across all habitats from the daytime survey. The horizontal line within each box represents the median, the lower and upper horizontal edges of each box correspond to the first (Q1) and third (Q3) quartiles, respectively, and the lower and upper whiskers end at $Q1 - (1.5 \times (Q3 - Q1))$ and $Q3 + (1.5 \times (Q3 - Q1))$, respectively. Points beyond the whiskers are considered outliers and are plotted separately

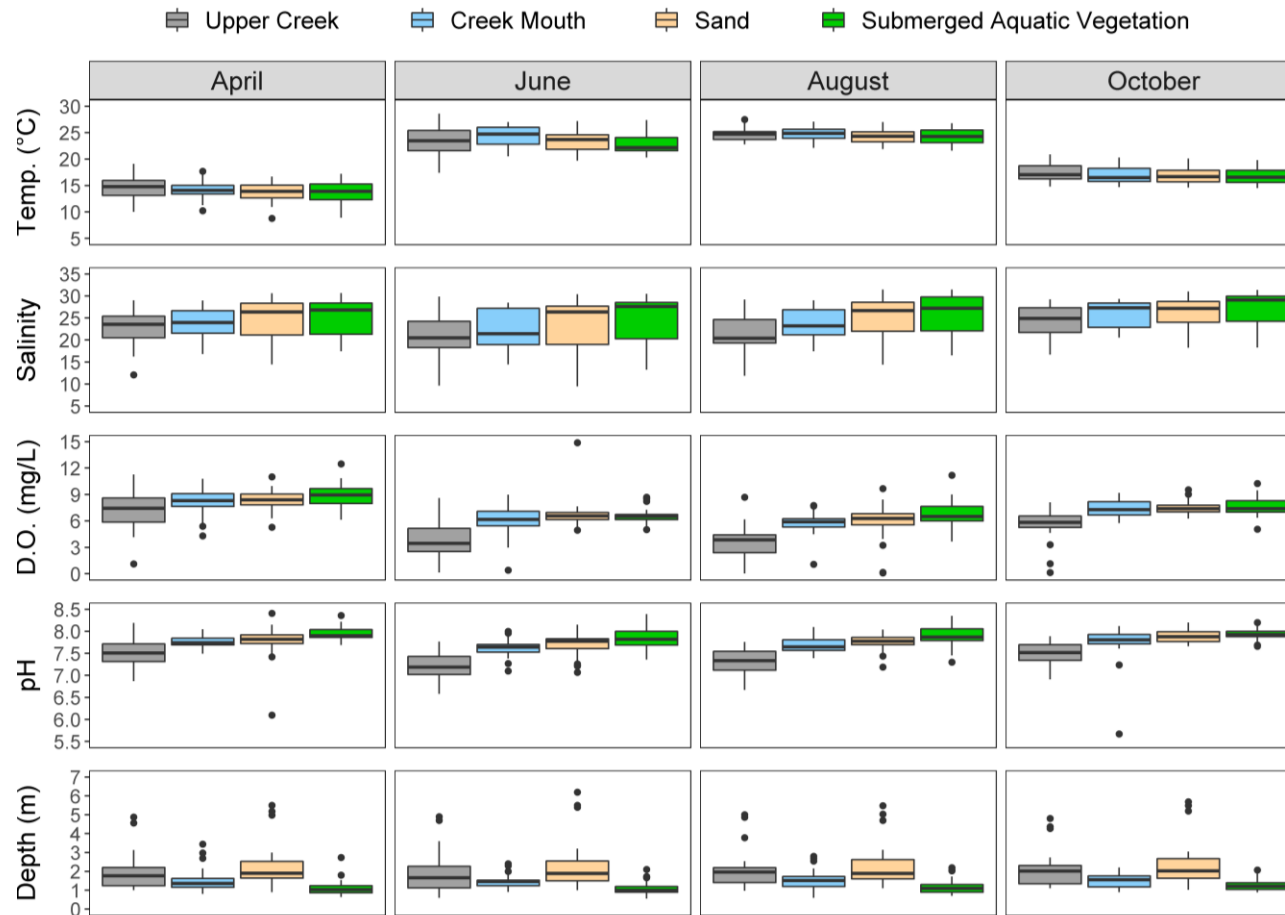


Fig. 3. Length frequency plots from the daytime survey: (a) bay anchovy *Anchoa mitchilli*, (b) silver perch *Bairdiella chrysoura*, (c) spot *Leiostomus xanthurus*, and (d) summer flounder *Paralichthys dentatus*. Note the difference in scale between plots

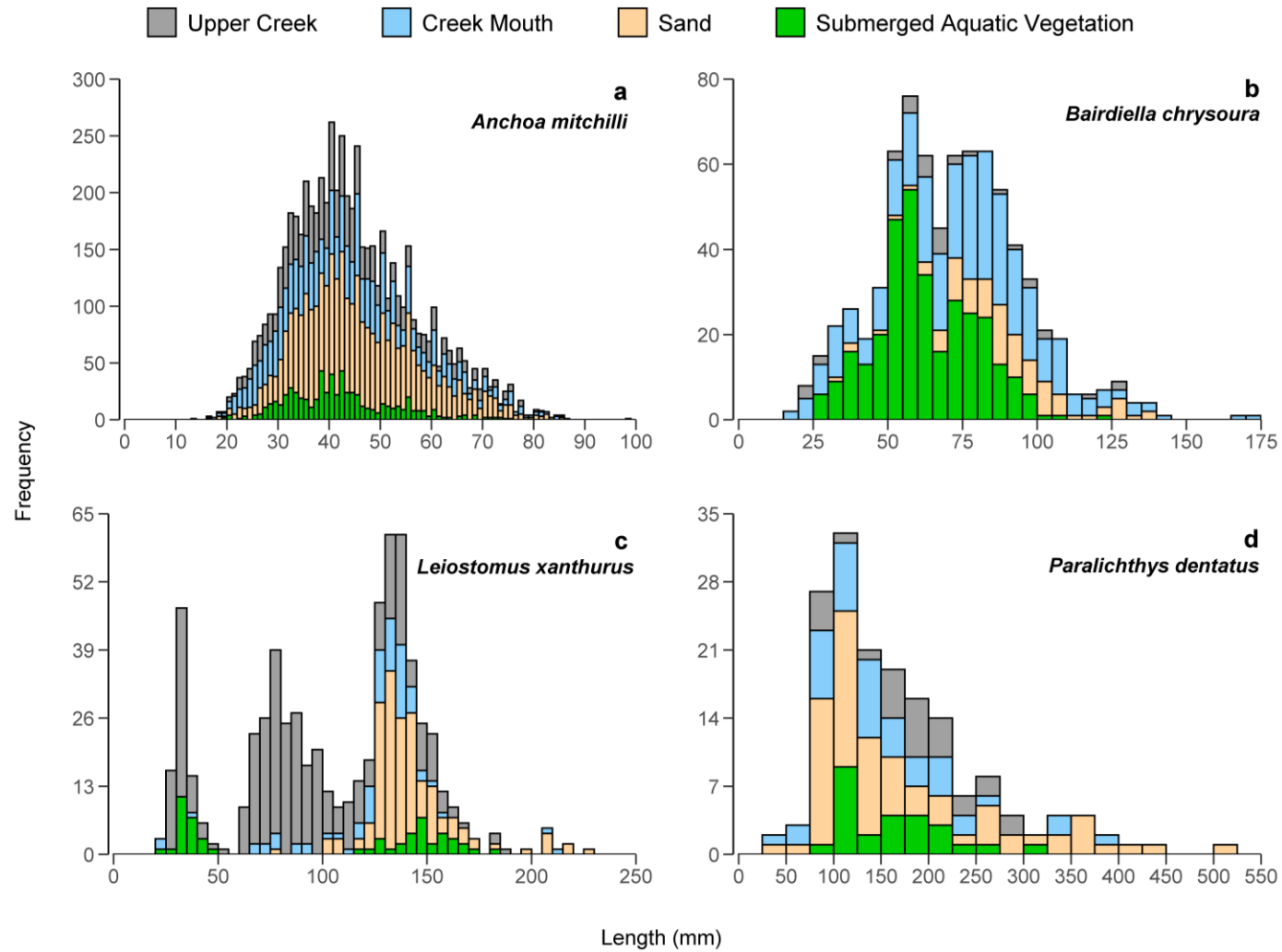


Fig. 4. Non-metric multidimensional scaling (NMDS) sample (a) and species (b) plots for the daytime survey. In the sample plot, convex polygons enclose samples taken within the same habitat, and fish assemblage similarity decreases by half per one unit change along the axes. The NMDS species plot is in the same dimensions as the corresponding sample plot, but was separated for legibility. Fish scientific names were abbreviated as the first three letters of the genus and first three letters of the species for clarity (see Table 3 for full scientific names). Note the difference in scale between axes in the sample and species plots

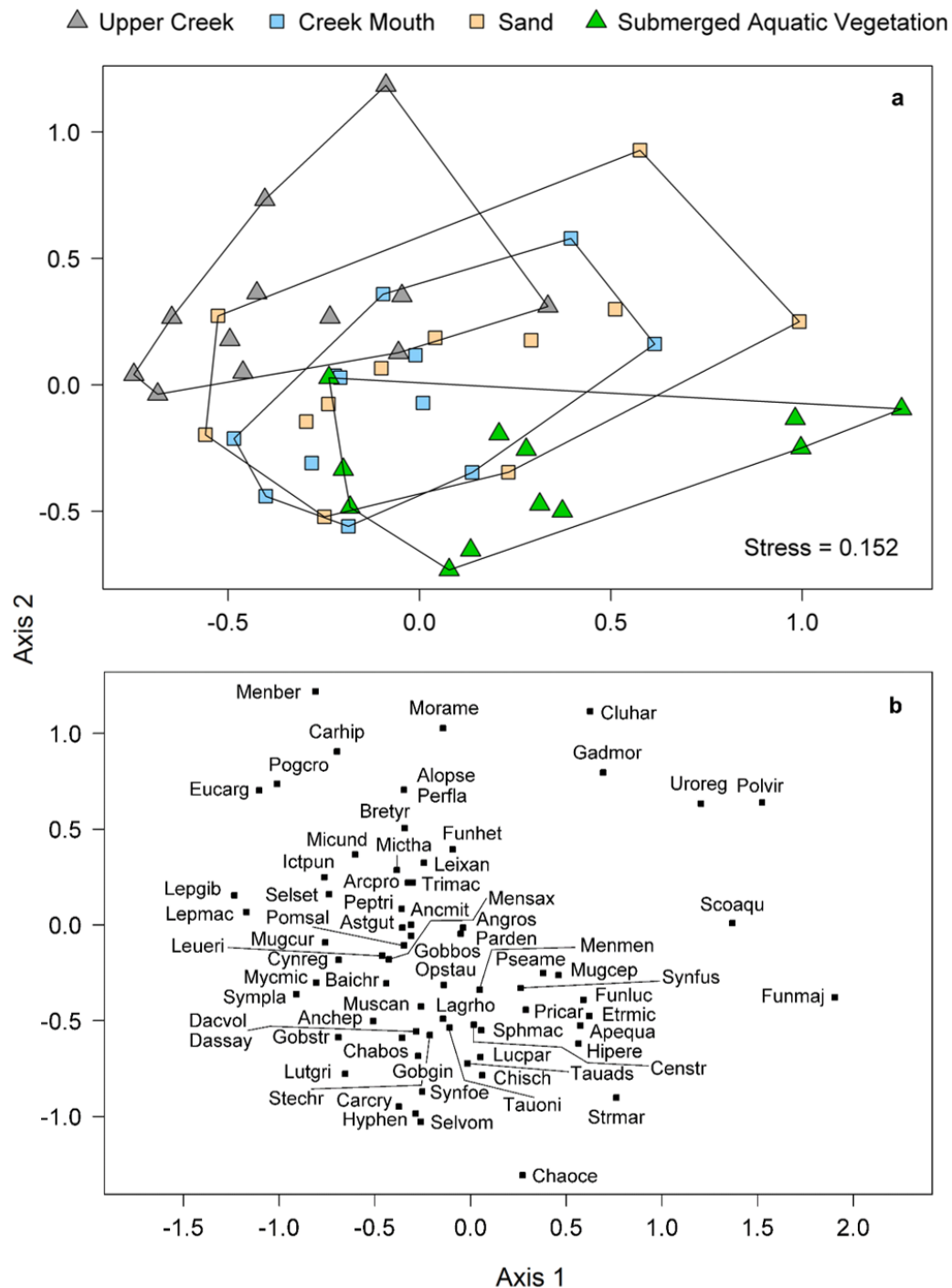


Fig. 5. (a) Canonical correspondence analysis (CCA) biplot of samples and environmental parameters (D.O. = dissolved oxygen, depth = water depth) from the daytime survey. The arrows in the biplot point in the direction of an increase in value for the respective environmental parameter. Sampling observations are located in ordination space based on the associated environmental parameters and are also positioned at the centroid of all the species collected during that observation (b) CCA species plot, which is in the same coenospace as the previous biplot, but was separated for legibility. Fish scientific names were abbreviated as the first three letters of the genus and first three letters of the species for clarity (see Table 3 for full scientific names). Species locations indicate the preferred environmental characteristics of each species (based on the samples collected) and therefore the abundance of a species declines with distance from the species' location in ordination space (McGarigal et al. 2000). See Online Resource 2 for species loadings. Only the first two axes of the biplot and species plots are shown. Note the difference in scale between axes in plots a and b

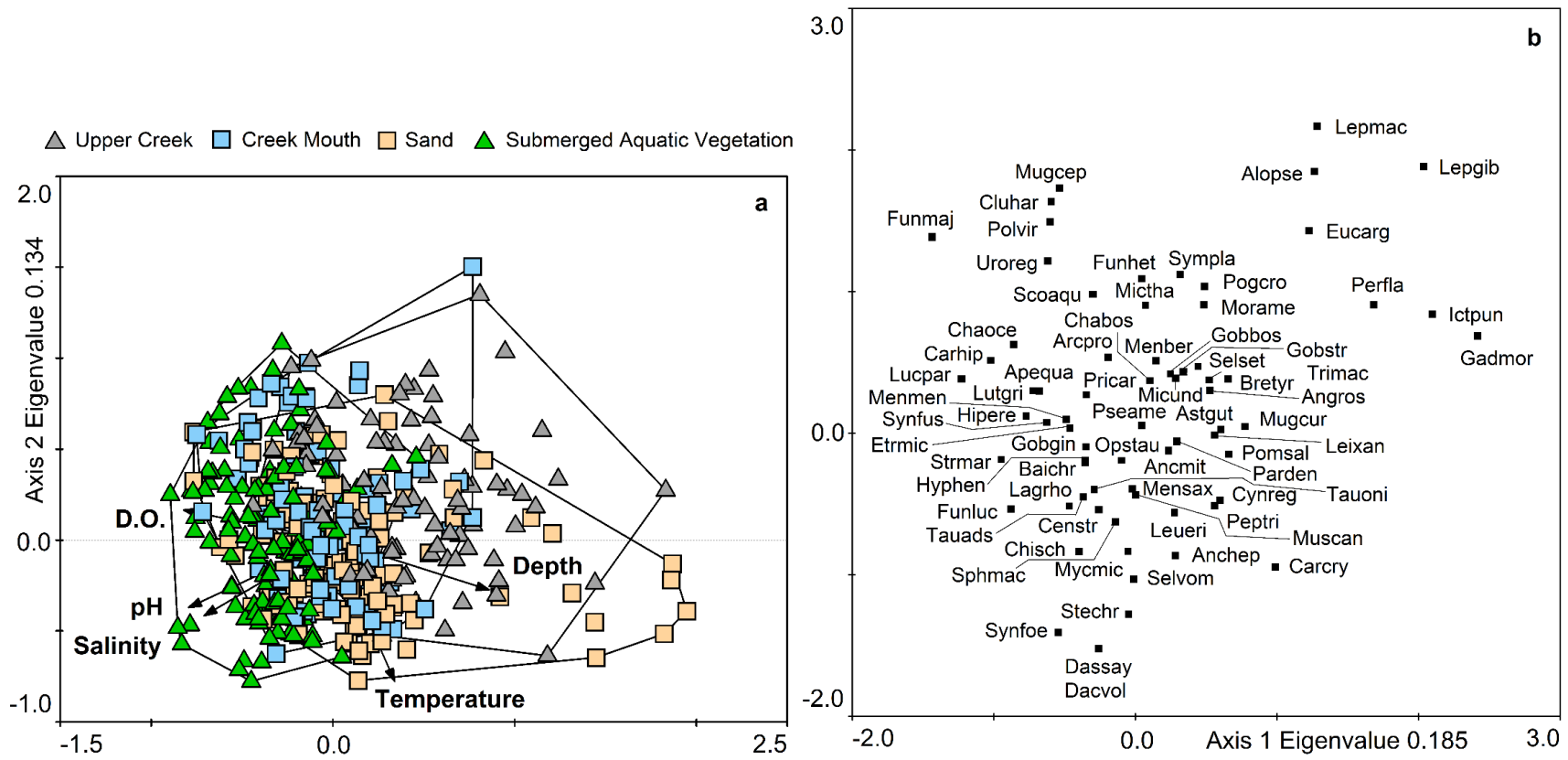


Fig. 6. Length frequency plots for select species from the day-night survey: (a) bay anchovy *Anchoa mitchilli* and (b) silver perch *Bairdiella chrysoura*. Note the difference in scale between plots

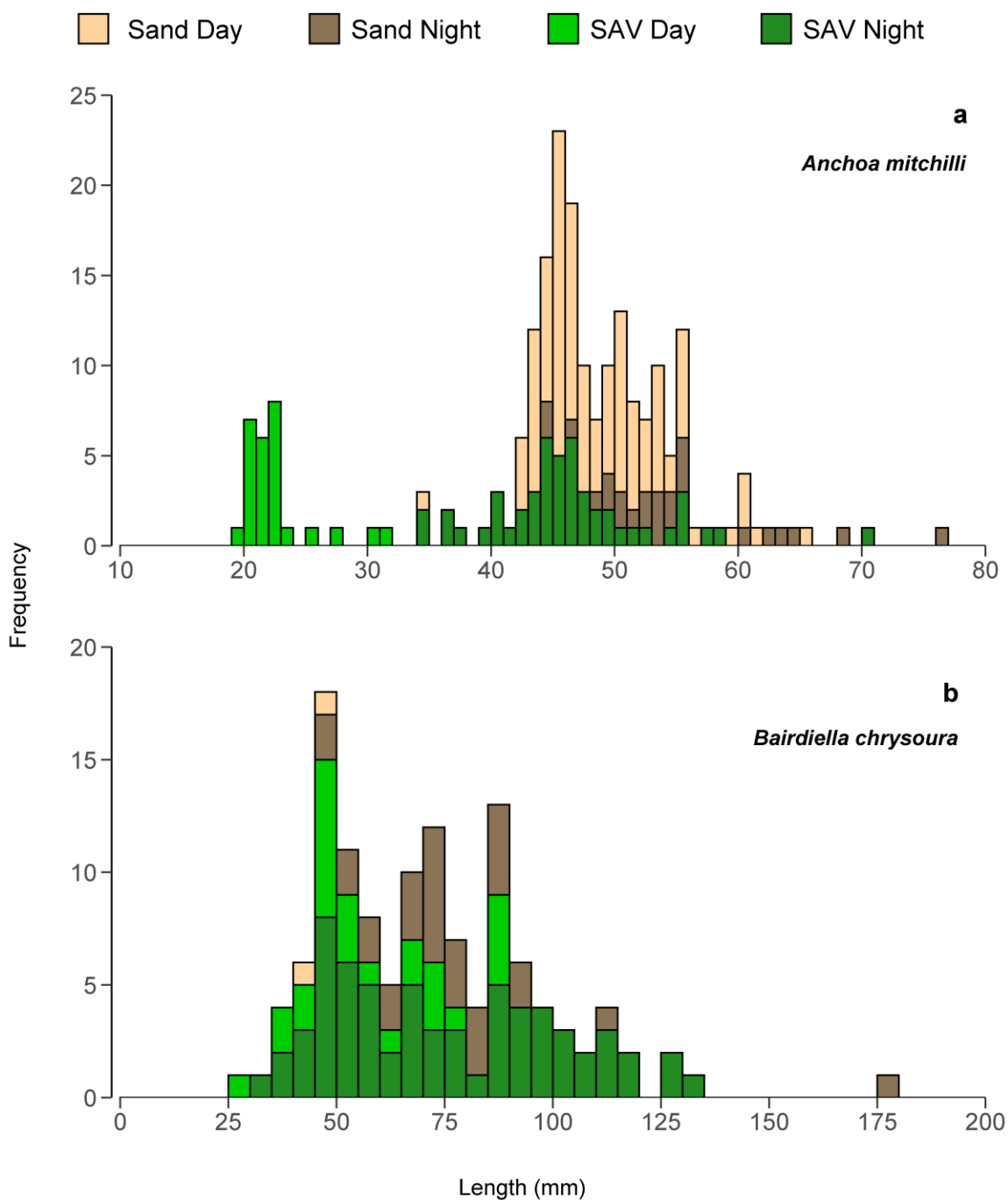
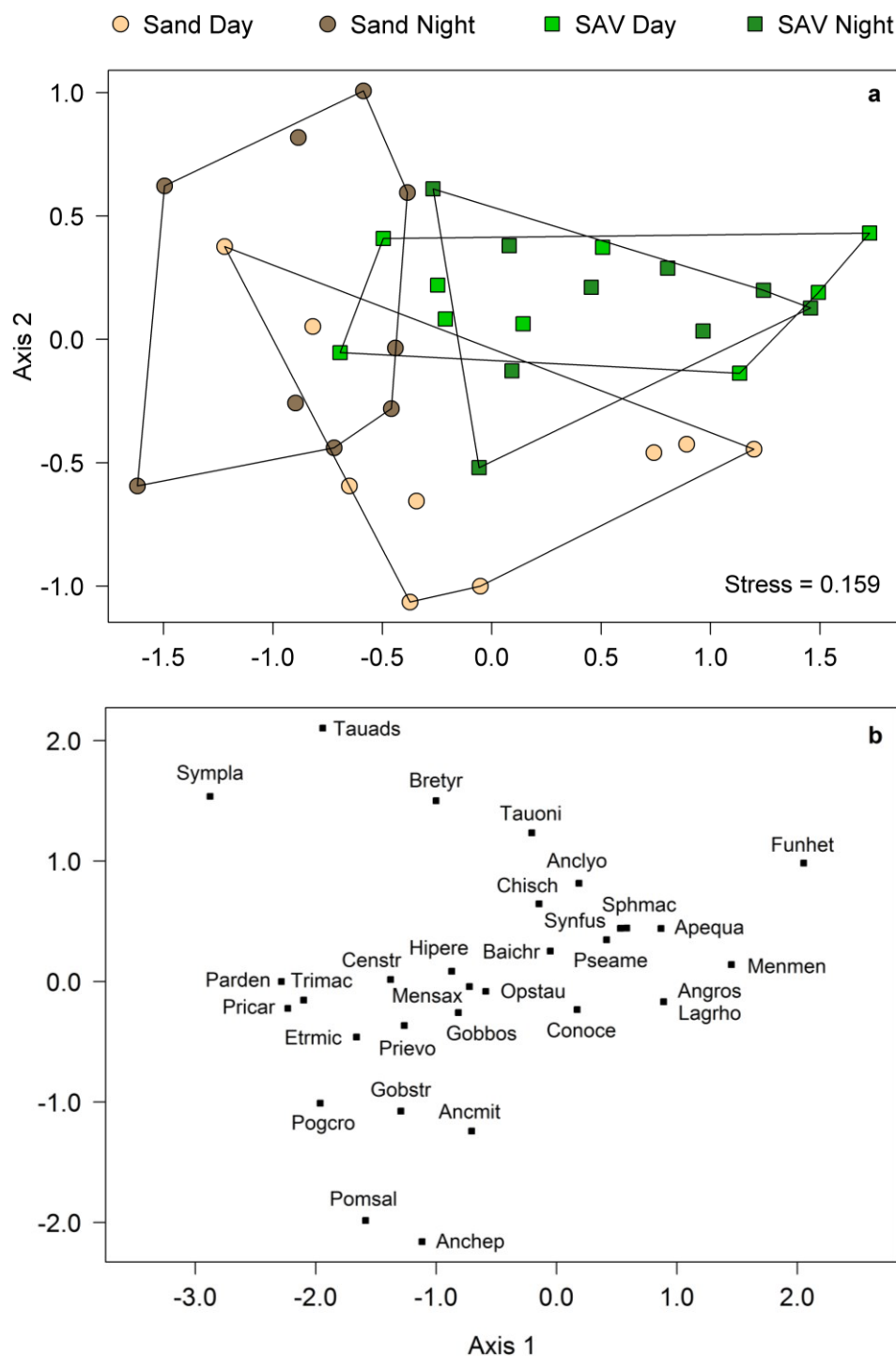


Fig. 7. Non-metric multidimensional scaling (NMDS) sample (a) and species (b) plots for the day-night survey in sand and submerged aquatic vegetation (SAV) habitats. In the sample plot, convex polygons enclose samples taken during the same time of day and within the same habitat, and fish assemblage similarity decreases by half per one unit change along the axes. The NMDS species plot is in the same dimensions as the sample plot, but was separated for legibility. Fish scientific names were abbreviated as the first three letters of the genus and first three letters of the species for clarity (see Table 2 for full scientific names). Note the difference in scale between axes in the sample and species plots



CHAPTER III

Estuarine Fish Communities along a Spatial Urbanization Gradient

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Abstract

The human population surrounding Barnegat Bay, New Jersey has increased dramatically in recent decades. Consequently, urbanization (anthropogenic development) of the watershed has occurred resulting in shoreline hardening and habitat destruction. A resulting gradient of urbanization increases from the southern to the northern portion of the bay's watershed. The objective of this study was to investigate cumulative impacts of urbanization in Barnegat Bay by assessing species composition, abundance, and diversity of fish communities in relation to the large-scale urbanization gradient in the watershed. Otter trawl surveys occurred in April, June, August, and October of three years (2012 – 2014) at 40 sampling sites stratified along the urbanization gradient. The sampling sites included four different representative subtidal subhabitats: open bay (soft bottom),

submerged aquatic vegetation (SAV) beds, upper marsh creek, and marsh creek mouth. Analyses did not reveal strong differences in fish communities among strata that could be solely attributed to the urbanization gradient. Fish species composition was similar among strata whereas species abundances and diversity differed among strata. Many of the observed differences in abundance and diversity were attributed to ecological variables unassociated with the urbanization gradient. Further study on potential urbanization effects should include investigations at the species level and smaller scales.

Introduction

Humans rely on the marine ecosystem for many resources and services such as food, climate regulation, and recreation (Costanza *et al.*, 1997), but have altered this ecosystem directly through resource overexploitation, habitat alteration, and nutrient loading (Reid *et al.*, 2005). In the United States (U.S.), more than 50% of the population resides within coastal counties (Crossett *et al.*, 2004), which endangers the continued provision of ecosystem services (Agardy *et al.*, 2005) and makes coastal ecosystems particularly vulnerable to human perturbations (Hinrichsen, 1998). The east coast of the U.S. is an area highly impacted by humans (Gittman *et al.*, 2015; Halpern *et al.*, 2008). New Jersey in particular is the most densely populated state in the U.S. (1,202 persons per square mile) with a majority of the population living along the coastline (Crossett *et al.*, 2004). Within New Jersey, the Barnegat Bay watershed has become increasingly urbanized (developed). From 2000 to 2010, the population in the watershed increased by 11.7% (59,992 people) (Kauffman and Cruz-Ortiz, 2012). However, the urbanization (anthropogenic development) in the watershed is not evenly distributed. The northern

portion of the watershed is highly urbanized in comparison to the southern portion, creating a gradient of urbanization within the watershed. The continued human population growth in the Barnegat Bay watershed and resultant construction of impervious surfaces increased the volume of non-point source pollution entering the estuary which subsequently caused water quality degradation through eutrophication (Kennish, 2001c; Kennish and Fertig, 2012). In addition to water quality degradation, essential marsh habitat has been destroyed by marsh infilling, dredging, bulkheading, and lagoon construction (Kennish, 2001c).

The response of fish communities to urbanization is varied. Several studies have documented impacts of urbanization on species composition, abundance, and diversity within fish communities (Able, Manderson, and Studholme, 1998; Bilkovic and Roggero, 2008; Davis, Levin, and Walther, 2002; Hendon, Peterson, and Comyns, 2000; Partyka and Peterson, 2008; Peterson *et al.*, 2000). For instance, Balouskus and Targett (2016) demonstrated fish were more abundant along natural marsh shorelines compared to altered rip-rap shorelines. In addition, urbanization may impact fishes physiologically or bioenergetically (Luther *et al.*, 2004; Wedge, Anderson, and DeVries, 2015). In the lower Hudson River estuary, juvenile tautog (*Tautoga onitis*) and winter flounder (*Pseudopleuronectes americanus*) had decreased growth rates under piers when compared to open-water and pile field subhabitats (Able, Manderson, and Studholme, 1999). Furthermore, over longer time periods, Hall-Scharf, Switzer, and Stallings (2016) found diet shifts in spotted seatrout (*Cynoscion nebulosus*) could be attributed to the loss of seagrass habitat due to urbanization.

Urbanization generally results in undesirable changes to ecosystems such as habitat destruction, increased runoff, and eutrophication, among others (Kennish, 2001c; Walsh *et al.*, 2005; Wedge, Anderson, and DeVries, 2015). Individually, many of these changes are small in scale, but can become large-scale as they accumulate within a system. Peterson and Lowe (2009) give the example of bulkheads. One bulkhead destroys marsh habitat, but as more bulkheads accumulate they become a large-scale issue, resulting in fragmented habitat throughout the system. The objective of this study was to investigate potential cumulative impacts of urbanization in Barnegat Bay by assessing species composition, abundance, and diversity of fish communities in relation to the large-scale gradient of urbanization in the watershed. In this study, urbanization was intentionally used as a broad term in order to encompass all components of anthropogenic development (*e.g.* roads, residences, bulkheads, *etc.*) that are found in the study system.

Like many estuaries, Barnegat Bay serves as a nursery habitat for a diversity of economically and ecologically important fishes (Able, Wilson, and Barnshaw, 1990; Kennish, 2001c). Since the quality of these nursery habitats and the fauna that utilize them can be impacted by urbanization in a variety of ways (Peterson and Lowe, 2009), and the impacts of urbanization on fish communities within Barnegat Bay have not been previously addressed, study of these interactions is warranted. Previous surveys of the fishes in Barnegat Bay have been conducted (Able and Fahay, 1996; Danila, Milstein, and Associates, 1979; Jivoff and Able, 2001; Marcellus, 1972; Tatham, Danila, and Thomas, 1984; Tatham *et al.*, 1977; Voughlitois, 1983; Voughlitois *et al.*, 1987), but none surveyed the fish communities throughout the bay and therefore a complete estuarine inventory of the fishes and an assessment of their response to the large-scale urbanization

gradient do not exist. In addition, a number of recent studies across numerous systems (Balouskus and Targett 2016; Gittman *et al.* 2016; Munsch, Cordell, and Toft, 2015) point to shoreline modification as having an immediate, but spatially narrow effect on shoreline fishes, effectively changing the assemblage along modified shorelines to be characteristic of deeper-water (estuarine) assemblages. In those studies, shoreline alterations are effectively treated as point-source stressors. In contrast, there has been little work investigating whether estuarine assemblages respond to the accumulation of these features that are not in their immediate environment, in effect investigating them as accumulated non-point-source stressors. This is especially compelling because the offshore estuarine habitat can account for a considerably greater volume and surface area than the nearshore habitat, even after accounting for flooded marsh within the latter.

Methods

Study Area

Barnegat Bay is a shallow (average water depth < 2 meters) (Chant, 2001), lagoon type estuary that extends along the coast of New Jersey for approximately 70 km (Kennish, 2001a). This estuary is connected directly to the Atlantic Ocean at Little Egg Inlet, Barnegat Inlet, and indirectly through the Point Pleasant Canal which joins the bay and the Manasquan River estuary (Figure 1). Freshwater inflow originates from tributaries along the bay's western shore. The northern bay has the largest tributaries and greatest freshwater influence. Salinity is highest near Little Egg and Barnegat Inlets and lowest (<15 ppt) near Toms River. Water temperature ranges from -1.4°C in winter to nearly 30°C in summer. The highest temperatures are commonly recorded in Oyster

Creek which is influenced by thermal discharges from the Oyster Creek Nuclear Generating Station (Kennish, 2001a). Barnegat Bay is well mixed; however, two layer flow may be evident in deeper waters (Chizmadia, Kennish, and Ohori, 1984). The flushing time varies both seasonally and spatially, and is reported to range from 0 – 50 days depending on the initial particle location and the quantity and magnitude of forces acting on the particle (*i.e.* tidal forcing, hydrodynamic forcing, stream flow, and meteorological forcing) (Chant, 2001; Defne and Ganju, 2015).

The dominant structural habitat types in Barnegat Bay include marsh creeks and beds of submerged aquatic vegetation (SAV) (Lathrop *et al.*, 2001). These beds, which are most abundant in the eastern portion of the bay, consist of eelgrass (*Zostera marina*), widgeon grass (*Ruppia maritima*), and macroalgae, which is seasonally dominated by sea lettuce (*Ulva lactuca*) (Lathrop *et al.*, 2001). Other habitat types include open bay (soft bottom) habitats with no well-defined structural components.

Sampling Location and Techniques

The extent of urbanization along Barnegat Bay was quantified from New Jersey Department of Environmental Protection (NJDEP) land use data. Five strata were classified based on the “% Urban” land variable (Table 1). Urbanization increased from stratum I to stratum V (Figure 1).

Each stratum included two replicate sampling sites in each of four different subhabitats: open bay, SAV beds, upper marsh creek, and marsh creek mouth. Sampling sites representative of each habitat were selected based on prior studies (*e.g.* Beach Haven West study [Sugihara *et al.*, 1979]) and reconnaissance sampling. The latter

ensured habitat designations were correct and the sampling sites were accessible by boat. Daytime sampling at each site consisted of three 120-second otter trawl tows (4.9 m headrope, 19 mm mesh wings, 6.3 mm mesh codend liner). Sampling was repeated seasonally (April, June, August, and October) over three years (2012 – 2014) resulting in 12 sampling events at each of the 40 sites. From each tow, all fishes were identified and counted. Every time a site was sampled the water depth was recorded in addition to temperature, salinity, dissolved oxygen, and pH which were recorded with a hand-held Yellow Springs Instrument (YSI) meter (Professional Series, Professional Plus, Model: Pro 10102030).

Community Analyses

The data from the three replicate trawl tows at each site per sampling event were combined and standardized to species-specific mean catch-per-unit-efforts (CPUE's) (*i.e.* mean number of species X collected per second of tow). The species-specific mean CPUE's for all 12 sampling events at a given site were then averaged in order to obtain site-specific mean CPUE's for each species. This allowed for an examination of the differences in fish communities among strata.

Two multivariate ordination techniques were used to examine the fish communities. Samples were ordered by Principal Component Analysis (PCA) to examine latent trends in the fish communities. Samples were also ordered using Canonical Correspondence Analysis (CCA) to examine correlations between fish communities and environmental parameters (temperature, salinity, pH, dissolved oxygen, water depth) (McGarigal, Cushman, and Stafford, 2000). Sample symbols in the PCA and CCA plots

were identified (post-hoc) by the stratum in which they were located. For all analyses, only fish that could be identified to the species level were included (*i.e.* less than 2% of the data were excluded). For the PCA, mean CPUE data were $\log(y + 1)$ transformed and the species scores were post transformed (divided by standard deviation). Within the plots, scaling focused on inter-sample distances and the data were centered by species. For the CCA, mean CPUE data were also $\log(y + 1)$ transformed and within the plots scaling focused on inter-sample distances (scaling type = biplot). The significance of the first canonical axis and the significance of all canonical axes together were tested using Monte Carlo permutation tests under the full model (unrestricted permutations = 499). For a more detailed description of the scaling and other methods used in these analyses see ter Braak and Šmilauer (2012). Ordination was performed in Canoco for Windows version 4.5. RStudio for Windows (version 0.99.442) was used to calculate species loadings for the first two principal components of the PCA and first two canonical axes of the CCA. Species loadings greater than 0.710 or less than -0.710 were considered excellent, greater than 0.630 or less than -0.630 were considered very good, greater than 0.550 or less than -0.550 were considered good, greater than 0.450 or less than -0.450 were considered fair, and greater than 0.320 or less than -0.320 were considered poor. Loadings less than 0.320 and also greater than -0.320 were not considered. Loading values that met the above criteria accounted for greater than 50%, 40%, 30%, 20%, and 10% of the variance within the component or axis, respectively (Comrey, 1973).

Species-specific mean CPUE values per stratum were calculated by averaging the site-specific mean CPUE values for each species for all eight sampling sites within a stratum. The stratum-specific mean CPUE values for each species were used to determine

species richness, Shannon-Wiener diversity, and Simpson's diversity for each stratum, and Jaccard dissimilarity indices between all strata. Both binary and quantitative Jaccard dissimilarity indices were computed to investigate dissimilarity in species composition and species abundance, respectively. Species accumulation curves were computed for each stratum. The vegan package (version 2.4-1) (Oksanen *et al.*, 2016) within RStudio for Windows (version 0.99.442) was used to calculate Shannon-Wiener diversity, Simpson's diversity, Jaccard dissimilarity indices, and the species accumulation curves.

Results

Collections included 29,511 fish representing 69 species from 1,434 trawl tows (Table 2). Bay anchovy (*Anchoa mitchilli*), Atlantic silverside (*Menidia menidia*), and fourspine stickleback (*Apeltes quadracus*) were the three most abundant species sampled, representing 53%, 19%, and 7% of the total fish collected, respectively.

Environmental Parameters

Mean temperature was similar (varied by less than one °C) among all strata (Table 3). Stratum III had the highest recorded temperature value due to thermal discharge from the Oyster Creek Nuclear Generating Station. Mean salinity varied by greater than seven ppt among certain strata and was greatest in strata I and III as a result of proximity to Little Egg Inlet and Barnegat Inlet, respectively. Mean salinity was lowest in the northern portion of the bay (strata IV and V). Mean dissolved oxygen was similar for strata I, II, IV, and V (range: 6.63 – 6.85 mg/L) with stratum III having a slightly higher mean value (7.11 mg/L). Hypoxic conditions (less than 2 mg/L) were

recorded in strata II, IV, and V. Mean pH varied by less than 0.2 among strata with the lowest pH value recorded in stratum I likely due to influence of acidic Pine Barren waters. Mean water depth varied by up to 0.5 meters among strata. Water depth ranges were similar with the exception of stratum V whose maximum recorded water depth was nearly three meters greater than all other strata (Table 3).

Ordinations

The first (eigenvalue = 0.690) and second (eigenvalue = 0.277) principal components accounted for a majority of the variance in the fish community data (96.7%) and therefore subsequent components are not discussed. Atlantic silverside, fourspine stickleback, northern pipefish (*Syngnathus fuscus*), lined seahorse (*Hippocampus erectus*), Atlantic needlefish (*Strongylura marina*), rainwater killifish (*Lucania parva*), spotfin butterflyfish (*Chaetodon ocellatus*), and pinfish (*Lagodon rhomboides*) each accounted for greater than 50% of the variation within the first principal component (*i.e.* loading scores greater than 0.710) (Figure 2a, Table 4). Winter flounder accounted for greater than 20% of the variance within the first component and tautog, pollock (*Pollachius virens*), northern puffer (*Sphoeroides maculatus*), and seaboard goby (*Gobiosoma ginsburgi*) each accounted for greater than 10% of the variance. On the first component, bay anchovy was inversely correlated to the previously named species and accounted for greater than 10% of the variation. Bay anchovy accounted for the majority of the variation (> 50%) on the second principal component whereas mummichog (*Fundulus heteroclitus*), bluefish (*Pomatomus saltatrix*), little skate (*Raja erinacea*), and

weakfish (*Cynoscion regalis*) each only accounted for greater than 10% of the variance within the second component (Figure 2a, Table 4).

In order to compare fish communities along the urbanization gradient in Barnegat Bay, sampling sites were plotted in ordination space (based on their site-specific mean CPUE for each species) and color coded by the stratum in which they were located. The high degree of overlap between sampling sites suggested fish communities were similar among strata (Figure 2b). A different convex polygon encloses the sampling sites from each stratum to further illustrate the overlap of sites from different strata in ordination space. The notable differences in convex polygons are attributed to one site from stratum I, two sites from stratum II, and two sites from stratum III which had larger mean CPUE values for Atlantic silverside, among other species, when compared to the rest of the sampling sites (Figure 2b).

Canonical axes accounted for 29.4% of the variance in the fish community data. The first (eigenvalue = 0.487) and second (eigenvalue = 0.106) canonical axes captured a majority of that variance (88.2%) and therefore subsequent axes are not discussed. The first and second canonical axes accounted for 72.4% and 15.8% of the variance in the species-environmental relationship, respectively (Table 5a). Species environment correlations were 0.804 and 0.615 for the first and second canonical axes, respectively. The first canonical axis ($p = 0.0020$) and all canonical axes ($p = 0.0020$) were determined to be significant based on Monte Carlo permutations tests.

Sixteen species significantly loaded on the first canonical axis (Table 4). Of those species, 13 were negatively correlated and three were positively correlated with the first canonical axis. Of those that were negatively correlated, Atlantic silverside (#37)

explained the most variation (> 40%) followed by northern puffer (#60), spotfin butterflyfish (#12), and northern pipefish (#64), each of which accounted for greater than 30% of the variance within the first axis (Figure 3a, Table 4). Lined seahorse (> 20%) (#27), fourspine stickleback (> 20%) (#5), tautog (> 10%) (#66), rainwater killifish (> 10%) (#34), Atlantic needlefish (> 10%) (#62), pinfish (> 10%) (#30), seaboard goby (> 10%) (#26), winter flounder (> 10%) (#55), and striped burrfish (*Chilomycterus schoepfi*) (> 10%) (#14) explained less of the variation. Bay anchovy (#3), spot (*Leiostomus xanthurus*) (#31), and Atlantic menhaden (*Brevoortia tyrannus*) (#9) were positively correlated with the first canonical axis and each explained greater than 10% of the variation. Atlantic menhaden (#9), inland silverside (*Menidia beryllina*) (#36), and bluntnose stingray (*Dasyatis say*) (#19) accounted for the most variation on the second canonical axis (> 20%). Pinfish (#30), lookdown (*Selene vomer*) (#59), mangrove snapper (*Lutjanus griseus*) (#35), spot (#31), conger eel (*Conger oceanicus*) (#16), skilletfish (*Gobiesox strumosus*) (#24), and crevalle jack (*Caranx hippos*) (#10) each explained greater than 10% of the variation on the second canonical axis. Bay anchovy (#3) was inversely correlated to the previously named species and accounted for greater than 10% of the variation on the second canonical axis (Figure 3a, Table 4).

Dissolved oxygen, pH, and salinity were negatively correlated with the first canonical axis while water depth and temperature were positively correlated (Figure 3b, Table 5b). The dissolved oxygen gradient explained the majority of the variation on the first canonical axis followed by the inversely correlated water depth gradient. The temperature gradient explained the majority of the variation on the second canonical axis, again followed by the inversely correlated water depth gradient. Correlations between

most environmental parameters were weak; however, of importance are dissolved oxygen and temperature which were inversely correlated, and dissolved oxygen and salinity, pH and salinity, and pH and dissolved oxygen which were positively correlated (Table 5b).

The location of each species in relation to the environmental gradients (arrows) (Figure 3a and b) indicates the optimal conditions for each species (McGarigal, Cushman, and Stafford, 2000). The species spread along the first canonical axis mainly portrayed the distribution of realized dissolved oxygen optima and the second canonical axis mainly portrayed that for temperature. The pattern on the second canonical axis is evident as one based on regional (subtropical southern vs. temperate northern) affiliation. Southern strays such as mangrove snapper (#35), lookdown (#59), and bluntnose stingray (#19) were at opposite ends of the temperature gradient from little skate (#56), winter flounder (#55), and cunner (*Tautoglabrus adspersus*) (#67) which occurred in cooler waters (Figure 3a and b). The location of each sample point indicates the environmental conditions at each sampling site (based on placement around the arrows) in addition to the species' realized niches (based on proximity to species symbols). Sampling sites from different strata overlapped in ordination space, indicating the range in environmental parameters and fish communities were similar among strata (Figure 3b). Notable differences between strata were attributed to one site in stratum V which was deeper than other sampling sites and one site in stratum III which had a higher mean temperature than all other sampling sites (Figure 3b). The latter site is directly influenced by the thermal discharge from the Oyster Creek Nuclear Generating Station.

Species Composition

Although not identical, species composition was similar among strata. Of the 69 species collected, only five were unique to (*i.e.* only collected in) stratum I, seven were unique to stratum II, five were unique to stratum III, and three were unique to stratum V (Table 6). Of those 20 species that were unique to particular strata only three had mean CPUE \pm standard error of the mean (SEM) ranges that did not include zero. Two of these three species were found in stratum II (blackcheek tonguefish [*Symphurus plagiusa*] and pumpkinseed [*Lepomis gibbosus*]) and one was found in stratum III (spotfin butterflyfish). The other 49 species were collected in two or more strata. Jaccard dissimilarities indicated no strata were greater than 50% dissimilar in terms of species composition (Table 7a). Out of all strata, strata I and IV were least dissimilar (*i.e.* most similar) (28.8%) and strata II and III were most dissimilar (49.2%). Strata I, II, and V were least dissimilar to stratum IV whereas strata III and IV were least dissimilar to stratum I. Stratum I was most dissimilar to stratum V and stratum II was most dissimilar to stratum III. Strata III and IV were most dissimilar to stratum II and stratum V was most dissimilar to strata I and III (Table 7a).

Species Abundance

Mean stratum CPUE was largest in stratum III and smallest in stratum II (Table 2), but was not significantly different among strata based on a one way analysis of variance (ANOVA) ($\alpha = 0.05$, $p > 0.8$). However, thirty nine species had mean CPUE's that differed among strata (*i.e.* species X mean CPUE \pm SEM for stratum Y did not overlap with that of stratum Z) (Table 6). American butterfish (*Peprilus triacanthus*) and bluntnose stingray had larger mean CPUE's in stratum I and stratum III, respectively,

when compared to strata II, IV, and V. American eel (*Anguilla rostrata*) and bay anchovy were more abundant in stratum V and strata IV and V, respectively, than in strata I and III and stratum III, respectively (Table 6). Striped blenny (*Chasmodes bosquianus*), summer flounder (*Paralichthys dentatus*), and winter flounder had smaller mean CPUE's in strata I, II, III, and IV, stratum I, and strata I, II, and IV, respectively, than in stratum V. Atlantic silverside, fourspine stickleback, and northern pipefish were not as abundant in strata IV and V, strata I, II, IV and V, and strata I, II, and III, respectively, compared to strata II and III, stratum III, and strata I, II, and III, respectively (Table 6).

The three most abundant species collected (*i.e.* largest mean CPUE) differed for each stratum. Bay anchovy was the most abundant species collected in all strata with the exception of stratum III in which the most abundant species collected was Atlantic silverside. Atlantic silverside was the second most abundant species collected in strata I and II, whereas in stratum III it was fourspine stickleback, stratum IV it was Atlantic menhaden, and stratum V it was winter flounder. For strata I and V, the third most abundant species collected was spot. This varied for strata II and IV and stratum III where silver perch (*Bairdiella chrysoura*) and bay anchovy were the third most abundant species collected, respectively (Table 6).

Jaccard dissimilarities indicated certain strata were greater than 50% dissimilar in terms of species abundance (Table 7b). Out of all strata, strata IV and V were least dissimilar (*i.e.* most similar) (27.7%) and strata III and V were most dissimilar (84.2%). Strata I and III were least dissimilar to stratum II and stratum II was least dissimilar to stratum I. Strata IV and V were least dissimilar to each other. Strata I, II, IV, and V were most dissimilar to stratum III and stratum III was most dissimilar to stratum V (Table 7b).

Species Diversity

Rarefaction curves indicated enough individuals were sampled to adequately characterize species diversity within each stratum (Figure 4). Species richness (*i.e.* the number of species collected) varied among strata (Table 2). The highest species richness was observed in stratum I and the lowest in stratum V. Shannon-Wiener diversity and Simpson's diversity indices ranked stratum III as the most diverse followed by stratum I, stratum II, stratum IV, and lastly, stratum V which ranked as the least diverse (Table 2).

Discussion

There are a few considerations when interpreting the results from this study. First, trawls of the size used in this study selectively target smaller fishes (< 100 mm) (Olin and Malinen, 2003). Within Barnegat Bay this size range is biased towards juvenile fishes, but does include the adult stage of some resident species. Given that juvenile occurrence within estuaries tends to follow an annual cycle (Able and Fahay, 2010) and the importance of estuaries as nursery habitat (Peterson and Lowe, 2009), an examination of urbanization effects on smaller fishes was perhaps the most appropriate in terms of sensitivity and ecological relevance. Second, cumulative impacts of urbanization may not have been captured in the sampling design due to disturbance by Superstorm Sandy, a combined hurricane remnant and Nor'easter which made landfall in this area in October 2012. Temporary alterations of the region's hydrodynamics (Kunz *et al.*, 2013) may have influenced the supply and distribution of larval and juvenile fishes within the bay. It is

unlikely, although possible, that the subsequent return to usual hydrodynamic conditions reestablished fish communities identical to fish communities pre-Superstorm Sandy.

Composition

Species composition was similar, though not identical, among strata as supported by the Jaccard dissimilarity index, PCA, and CCA. The Jaccard dissimilarity index demonstrated strata were only moderately dissimilar to each other and did not consistently indicate that northern strata were more dissimilar to southern strata and vice versa. Furthermore, it cannot be stated with certainty that 17 of the 20 species that were unique to certain strata, and likely increased dissimilarity among strata, were present in one stratum and not another since their respective mean CPUE \pm SEM ranges included zero.

Sampling sites from different strata overlapped in ordination space for both PCA and CCA, demonstrating that latent variation in the fish communities was not attributable to the large-scale urbanization gradient. The species that accounted for a majority of the variation on the first principal component and first canonical axis (*e.g.* Atlantic silverside, northern pipefish, lined seahorse, *etc.*) were highly comparable. The species that accounted for a majority of the variation on the second principal component (*e.g.* bay anchovy, mummichog, bluefish, *etc.*) and second canonical axis (*e.g.* bay anchovy, Atlantic menhaden, inland silverside, *etc.*) were different. This information in combination with a high species-environment correlation on the first canonical axis, a lower species-environment correlation on the second canonical axis, roughly equal variance explained by the first principal component and first canonical axis, and less

variance explained by the second canonical axis versus the second principal component indicated the measured environmental parameters in the CCA accounted for most of the latent variation in the fish communities (McGarigal, Cushman, and Stafford, 2000). However, there were other variables unaccounted for (*e.g.* possibly predator-prey interactions, quantitative habitat characteristics, distance from inlets, *etc.*) which were needed to better explain the variation on the second principal component (McGarigal, Cushman, and Stafford, 2000).

Although the measured environmental parameters accounted for most of the latent variation in the fish communities, salinity did not explain a majority of this variation on the first or second canonical axes even though there is a north-south salinity gradient in Barnegat Bay (Kennish, 2001a). On the first and second canonical axes, salinity ranked fourth and fifth out of five environmental parameters in the amount of variation explained, respectively. Therefore, it is unlikely that the salinity gradient in the bay confounded attempts to detect cumulative impacts of urbanization on fish communities. This is not to say that salinity has no affect in structuring fish communities. It is well known many individual species have an optimal salinity range (Able and Fahay, 2010), but within this study, the salinity gradient in the bay did not strongly influence fish communities as a whole.

Recall that dissolved oxygen and temperature accounted for the most variation on the first and second canonical axes, respectively. Both of these parameters were relatively constant along the north-south gradient in Barnegat Bay (*i.e.* did not differ with the urbanization gradient). Instead, the observed gradients in dissolved oxygen and temperature were possibly related to different subhabitats. For instance, SAV beds are

located along the eastern side of Barnegat Bay (Lathrop *et al.*, 2001) and therefore directly influenced by oxygen rich ocean waters as compared to upper marsh creeks, which occasionally have low dissolved oxygen concentrations (Sugihara *et al.*, 1979). It is plausible that the observed variation in fish communities was related to subhabitat given fish use a variety of estuarine subhabitats (Kanouse, La Peyre, and Nyman, 2006) and some species utilize a particular subhabitat more frequently than other available subhabitats (Able and Fahay, 2010; Arrivillaga and Baltz, 1999; Sogard and Able, 1991).

The Oyster Creek Nuclear Generating Station, in stratum III, takes in water from the bay to cool the power plant condensers and subsequently releases the heated water back into the bay. Mortality of fishes due to the thermal discharge, impingement of fishes on intake screens, and entrainment of fishes in the cooling system have been documented (Danila, Milstein, and Associates, 1979; Tatham *et al.*, 1977). Although these impacts are well known, no distinct differences between stratum III and other strata in terms of species composition could be attributed to the Oyster Creek Nuclear Generating Station.

Abundance

Mean CPUE did not differ among strata; however, thirty nine species had mean CPUE's that differed among strata. For many of those species, differences in mean CPUE could be attributed to ecological variables unassociated with the large-scale urbanization gradient. For example, American butterfish and bluntnose stingray had larger mean CPUE's in strata closest to inlets. This is reasonable since juvenile American butterfish (Able and Fahay, 2010) and bluntnose stingray (Wiley and Simpfendorfer, 2007) are marine species that occur primarily in the ocean. American eel had a larger mean CPUE

in stratum V than in those strata closest to inlets possibly due to their catadromous nature (Able and Fahay, 2010). Lastly, Atlantic silverside and northern pipefish had larger mean CPUE's in the southern portion of the bay. These species were commonly collected in SAV beds with 89% and 83% of their catches occurring in this habitat, respectively. Smaller mean CPUE's in the northern bay could be attributed to less dense SAV beds (Lathrop *et al.*, 2001) and a shift in dominant vegetation from eelgrass to widgeon grass (Lathrop and Haag, 2011).

Conversely, some differences in mean species CPUE among strata were not as easily related to ecological variables. Bay anchovy, summer flounder, striped blenny, and winter flounder had larger mean CPUE's in northern Barnegat Bay; however, the salinity tolerance and habitat usage of these species is known to be broad (Able and Fahay, 2010). Larger mean CPUE's in the northern bay may have been associated with other ecological variables not quantified such as predator-prey interactions. For instance, bay anchovy and winter flounder are known dietary components of summer flounder in the Barnegat Bay region (Festa, 1979). Larger mean CPUE's in the northern bay may have also been associated with undocumented habitat characteristics (*e.g.* bottom substrate, *etc.*) which could have been related to the large-scale urbanization gradient.

The Jaccard dissimilarity index did not consistently indicate that northern strata were more dissimilar to southern strata and vice versa. Stratum III was highly dissimilar to all other strata in terms of species abundances. Fourspine stickleback among other species had larger mean CPUE's in stratum III when compared to other strata. The drivers of this trend were not readily apparent, but could have been related to the unique hydrodynamics in the stratum. Barnegat Inlet efficiently flushes the area enclosed in

stratum III and as such particle residence time is low (Defne and Ganju, 2015); however, small coves directly inside the inlet could favor larval deposition (Chant *et al.*, 2000). In addition, the SAV beds directly inside the inlet could entrain larvae the same way particles are trapped (Ward, Kemp, and Boynton, 1984). Both of these mechanisms could have influenced the abundances of fishes in stratum III.

Diversity

Species richness, Shannon-Wiener diversity, and Simpson's diversity indicated that the northern, more urbanized portion of the bay (strata IV and V) had decreased diversity compared to the southern portion of the bay (strata I – III). It is possible the decreased diversity was in some way associated with the urbanization gradient as studies have found decreased diversity in relation to urbanization elsewhere, albeit at smaller scales (Balouskus and Targett, 2016; Bilkovic and Roggero, 2008). It is also possible the observed differences were unassociated with the large-scale urbanization gradient. For example, the decreased diversity in the northern bay could have been associated with stratum proximity to Barnegat and Little Egg inlets, through which estuarine-dependent larval and juvenile fish access the estuary. Stratum III was nearest an inlet, followed by strata I, II, IV, and V, which was the rank order of diversity determined by Shannon-Wiener and Simpson's indices. Although stratum V is indirectly connected to the Atlantic Ocean through the Point Pleasant Canal and Manasquan River Estuary, it is the least diverse of all strata. A recent study by Able, Valenti, and Grothues (in review) found larval fish composition was similar at Little Egg Inlet, Barnegat Inlet, and the Point Pleasant Canal; however, larval abundance for many species was larger at the inlet sites.

The observed differences in abundance were possibly due to the small tidal exchange at the Point Pleasant Canal relative to Little Egg Inlet and Barnegat Inlet (Kennish, 2001b). The decreased larval supply through the Point Pleasant Canal in addition to the distance from the two major inlets may account for the lower diversity in the northern bay, independent of the urbanization gradient.

Conclusion

Differences in fish communities among strata that could be solely attributed to the large-scale urbanization gradient in the Barnegat Bay watershed were not readily apparent. Fish species composition was similar among strata whereas species abundances and diversity differed among strata. Most of the observed, but relatively minor, differences in abundance and diversity were attributed to ecological variables unassociated with the large-scale urbanization gradient, although it is difficult to irrefutably support or deny the role of the urbanization gradient in the observed trends.

The absence of an obvious response by fish communities to the large-scale urbanization gradient might have been due to a lack of cumulative impacts. Small urbanization related changes (*e.g.* bulkheads) may not have accumulated to the point in which they caused shifts in fish community structure (*i.e.* species composition, abundance, and diversity). Alternatively, fish communities naturally fluctuate on different spatial and temporal scales due to migrations, variation in larval supply, and residence in a variable estuarine environment (Maes *et al.*, 2004). Therefore, any cumulative impacts present may not be evident because of the annual turnover of the fish fauna. Each year brings a new set of recruits (Able and Fahay, 2010) that emigrate from the estuary in the

fall and may not return in subsequent years. Furthermore, fish communities respond similarly to this natural variation and anthropogenic variation (*i.e.* shifts in fish community structure), making it difficult to separate impacts of the two; this is defined as the Estuarine Quality Paradox (Elliott and Quintino, 2007). In order to resolve this paradox, Elliott and Quintino (2007) suggest functional characteristics (*e.g.* trophic relationships, primary and secondary production, community metabolism) in addition to structural characteristics be used to determine anthropogenic impacts in estuarine systems.

Although fish communities in Barnegat Bay did not exhibit differences readily relatable to the urbanization gradient, impacts at the species level and smaller scales are still possible, as documented for estuarine fishes affected by the Macondo Oil Spill (Able *et al.*, 2015; Fodrie *et al.*, 2014; Whitehead *et al.*, 2012). As such, this study should be treated as one component of assessing the response of fishes to urbanization in Barnegat Bay. The objective of this study was to investigate potential cumulative impacts of urbanization by assessing species composition, abundance, and diversity of fish communities in relation to the large-scale gradient of urbanization in the watershed. In this study, urbanization was intentionally used as a broad term in order to encompass all components of anthropogenic development and no effort was made to discern impacts of a particular component. Further study is necessary and will include investigations at the species level and smaller scales, where urbanization impacts were demonstrated to be most readily detectable (Bilkovic and Roggero, 2008). For example, investigation of fish community structure in urbanized marsh creeks versus natural marsh creeks will determine potential impacts of bulkheaded shorelines.

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References

- Able, K.W. and Fahay, M.P., 1996. Natural history patterns for estuarine fishes during the first year: a progress report. *Proceedings of the Barnegat Bay Ecosystem Workshop* (Toms River, New Jersey), pp. 185-191.
- Able, K.W. and Fahay, M.P., 2010. *Ecology of Estuarine Fishes: Temperature Waters of the Western North Atlantic*. Baltimore, Maryland: Johns Hopkins University Press, 566p.
- Able, K.W.; López-Duarte, P.C.; Fodrie, F.J.; Jensen, O.P.; Martin, C.W.; Roberts, B.J.; Valenti, J.; O'Connor, K., and Halbert, S.C., 2015. Fish assemblages in Louisiana salt marshes : Effects of the Macondo oil spill. *Estuaries and Coasts*, 38(5), 1385-1398.
- Able, K.W.; Manderson, J.P., and Studholme, A.L., 1998. The distribution of shallow water juvenile fishes in an urban estuary: The effects of manmade structures in the lower Hudson River. *Estuaries*, 21(48), 731-744.
- Able, K.W.; Manderson, J.P., and Studholme, A.L., 1999. Habitat quality for shallow water fishes in an urban estuary: The effects of man-made structures on growth. *Marine Ecology Progress Series*, 187, 227-235.

- Able, K.W.; Valenti, J.L., and Grothues, T.M., in review. Fish larval supply to and within a lagoonal estuary: Multiple sources for Barnegat Bay, New Jersey. *Environmental Biology of Fishes*.
- Able, K.W.; Wilson, K.A., and Barshaw, D.E., 1990. *Assessing the Effects of Development Pressure on Barnegat Bay: Impacts of Marinas on Juvenile Fishes and Crabs*. Tuckerton, New Jersey: Rutgers University, Institute of Marine and Coastal Sciences, Rutgers University Marine Field Station, 31p.
- Agardy, T.; Alder, J.; Dayton, P.; Curran, S.; Kitchingman, A.; Wilson, M.; Catenazzi, A.; Restrepo, J.; Birkeland, C.; Blaber, S.; Saifullah, S.; Branch, G.; Boersma, D.; Nixon, S.; Dugan, P.; Davidson, N., and Vörösmarty, C., 2005. Coastal systems. In: Baker, J.; Moreno Casasola, P.; Lugo, A.; Sua'ez Rodríguez, A.; Dan, L., and Tang, L. (eds.), *Millenium Ecosystem Assessment: Ecosystems and Human Well-being: Current Status and Trends*. Washington, D.C.: Island Press, pp. 513-550.
- Arrivillaga, A. and Baltz, D.M., 1999. Comparison of fishes and macroinvertebrates on seagrass and bare-sand sites on Guatemala's Atlantic coast. *Bulletin of Marine Science*, 65(2), 301-319.
- Balouskus, R.G. and Targett, T.E., 2016. Fish and blue crab density along a riprap-sill-hardened shoreline: Comparisons with *Spartina* marsh and riprap. *Transactions of the American Fisheries Society*, 145(4), 766-773.
- Bilkovic, D.M. and Roggero, M.M., 2008. Effects of coastal development on nearshore estuarine nekton communities. *Marine Ecology Progress Series*, 358, 27-39.
- Chant, R.J., 2001. Tidal and subtidal motion in a shallow bar-built multiple inlet/bay system. In: Kennish, M.J. (ed.), *Barnegat Bay-Little Egg Harbor, New Jersey: Estuary and Watershed Assessment*. *Journal of Coastal Research*, Special Issue No. 32, pp. 102-114.
- Chant, R.J.; Curran, M.C.; Able, K.W., and Glenn, S.M., 2000. Delivery of winter flounder (*Pseudopleuronectes americanus*) larvae to settlement habitats in coves near tidal inlets. *Estuarine, Coastal and Shelf Science*, 51(5), 529-541.
- Chizmadia, P.A.; Kennish M.J., and Otori, V.L., 1984. Physical description of Barnegat Bay. In: Kennish, M.J. and Lutz, R.A. (eds.), *Ecology of Barnegat Bay, New Jersey*. New York, New York: Springer-Verlag, pp. 1-28.
- Comrey, A.L. and Lee, H.B., 2013. *A First Course in Factor Analysis*. New York, New York: Psychology Press, 429p.
- Costanza, R.; D'Arge, R.; de Groot, R.; Farber, S.; Grasso, M.; Hannon, B.; Limburg, K.; Naeem, S.; O'Neill, R.V.; Paruelo, J.; Raskin, R.G.; Sutton, P., and van den Belt, M.,

1997. The value of the world's ecosystem services and natural capital. *Nature*, 387, 253-260.
- Crossett, K.M.; Culliton, T.J.; Wiley, P.C., and Goodspeed, T.R., 2004. *Population Trends Along the Coastal United States: 1980-2008*. Silver Spring, Maryland: National Oceanic and Atmospheric Administration, 54p.
- Danila, D.J.; Milstein, C.B., and Associates, 1979. *Ecological Studies for the Oyster Creek Generating Station: Progress Report for the Period September 1977-August 1978: Finfish, Shellfish, and Plankton*. Ithaca, New York: Ichthyological Associates, Inc., 391p.
- Davis, J.L.D.; Levin, L.A., and Walther, S.M., 2002. Artificial armored shorelines: Sites for open-coast species in a southern California bay. *Marine Biology*, 140(6), 1249-1262.
- Defne, Z. and Ganju, N.K., 2015. Quantifying the residence time and flushing characteristics of a shallow, back-barrier estuary: Application of hydrodynamic and particle tracking models. *Estuaries and Coasts*, 38(5), 1719-1734.
- Elliott, M. and Quintino, V., 2007. The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Marine Pollution Bulletin*, 54(6), 640-645.
- Festa, P.J., 1979. *Analysis of the Fish Forage Base in the Little Egg Harbor Estuary*. Galloway, New Jersey: New Jersey Department of Environmental Protection, Division of Fish, Game and Shellfisheries, Bureau of Fisheries, Nacote Creek Research Station, *Report 24M*, 342p.
- Fodrie, F.J.; Able, K.W.; Galvez, F.; Heck Jr., K.L.; Jensen, O.P.; Lopez-Duarte, P.C.; Martin, C.W.; Turner, R.E., and Whitehead, A., 2014. Integrating organismal and population responses of estuarine fishes in Macondo spill research. *BioScience*, 64(9), 778-788.
- Gittman, R.K.; Fodrie, F.J.; Popowich, A.M.; Keller, D.A.; Bruno, J.F.; Currin, C.A.; Peterson, C.H., and Piehler, M.F., 2015. Engineering away our natural defenses: An analysis of shoreline hardening in the US. *Frontiers in Ecology and the Environment*, 13(6), 301-307.
- Gittman, R.K.; Peterson, C.H.; Currin, C.A.; Joel Fodrie, F.; Piehler, M.F., and Bruno, J.F., 2016. Living shorelines can enhance the nursery role of threatened estuarine habitats. *Ecological Applications*, 26(1), 249-263.
- Hall-Scharf, B.J.; Switzer, T.S., and Stallings, C.D., 2016. Ontogenetic and long-term diet shifts of a generalist juvenile predatory fish in an urban estuary undergoing dramatic changes in habitat availability. *Transactions of the American Fisheries*

Society, 145(3), 502-520.

- Halpern, B.S.; Walbridge, S.; Selkoe, K.A.; Kappel, C.V.; Micheli, F.; D'Agrosa, C.; Bruno, J.F.; Casey, K.S.; Ebert, C.; Fox, H.E.; Fujita, R.; Heinemann, D.; Lenihan, H.S.; Madin, E.M.P.; Perry, M.T.; Selig, E.R.; Spalding, M.; Steneck, R., and Watson, R., 2008. A global map of human impact on marine ecosystems. *Science*, 319(5865), 948-952.
- Hendon, J.R.; Peterson, M.S., and Comyns, B.H., 2000. Spatio-temporal distribution of larval *Gobiosoma bosc* in waters adjacent to natural and altered marsh-edge habitats of Mississippi coastal waters. *Bulletin of Marine Science*, 66(1), 143-156.
- Hinrichsen, D., 1998. *Coastal Waters of the World: Trends, Threats, and Strategies*. Washington, D.C.: Island Press, 102p.
- Jivoff, P. and Able, K.W., 2001. Characterization of the fish and selected decapods in Little Egg Harbor. In: Kennish, M.J. (ed.), *Barnegat Bay-Little Egg Harbor, New Jersey: Estuary and Watershed Assessment. Journal of Coastal Research*, Special Issue No. 32, pp. 178-196.
- Kanouse, S.; La Peyre, M.K., and Nyman, J.A., 2006. Nekton use of *Ruppia maritima* and non-vegetated bottom habitat types within brackish marsh ponds. *Marine Ecology Progress Series*, 327, 61-69.
- Kauffman, G.J. and Cruz-Ortiz, C., 2012. *Economic Value of the Barnegat Bay Watershed*. Newark, Delaware: University of Delaware, Institute for Public Administration, IPA Water Resources Agency, 66p.
- Kennish, M.J., 2001a. Characterization of the Barnegat Bay-Little Egg Harbor estuary and watershed. In: Kennish, M.J. (ed.), *Barnegat Bay-Little Egg Harbor, New Jersey: Estuary and Watershed Assessment. Journal of Coastal Research*, Special Issue No. 32, pp. 3-12.
- Kennish, M.J., 2001b. Physical Description of the Barnegat Bay-Little Egg Harbor Estuarine System. In: Kennish, M.J. (ed.), *Barnegat Bay-Little Egg Harbor, New Jersey: Estuary and Watershed Assessment. Journal of Coastal Research*, Special Issue No. 32, pp. 13-27.
- Kennish, M.J., 2001c. State of the estuary and watershed: An overview. In: Kennish, M.J. (ed.), *Barnegat Bay-Little Egg Harbor, New Jersey: Estuary and Watershed Assessment. Journal of Coastal Research*, Special Issue No. 32, pp. 243-273.
- Kennish, M.J. and Fertig, B., 2012. Application and assessment of a nutrient pollution indicator using eelgrass (*Zostera marina* L.) in Barnegat Bay-Little Egg Harbor estuary, New Jersey. *Aquatic Botany*, 96(1), 23-30.

- Kunz, M.; Mühr, B.; Kunz-Plapp, T.; Daniell, J.E.; Khazai, B.; Wenzel, F.; Vannieuwenhuyse, M.; Comes, T.; Elmer, F.; Schröter, K., and Fohringer, J., 2013. Investigation of Superstorm Sandy 2012 in a multi-disciplinary approach. *Natural Hazards and Earth System Sciences*, 13(10), 2579-2598.
- Lathrop, R.G. and Haag, S.M., 2011. *Assessment of Seagrass Status in the Barnegat Bay-Little Egg Harbor Estuary System: 2003 and 2009*. New Brunswick, New Jersey: Rutgers University, 18p.
- Lathrop, R.G.; Styles, R.M.; Seitzinger, S.P., and Bognar, J.A., 2001. Use of GIS mapping and modeling approaches to examine the spatial distribution of seagrasses in Barnegat Bay, New Jersey. *Estuaries*, 24(6), 904-916.
- Luther, G.W.; Ma, S.; Trouwborst, R.; Glazer, B.; Blickley, M.; Scarborough, R.W., and Mensinger, M.G., 2004. The roles of anoxia, H₂S, and storm events in fish kills of dead-end canals of Delaware inland bays. *Estuaries*, 27(3), 551-560.
- Maes, J.; Van Damme, S.; Meire, P., and Ollevier, F., 2004. Statistical modeling of seasonal and environmental influences on the population dynamics of an estuarine fish community. *Marine Biology*, 145(5), 1033-1042.
- Marcellus, K.L., 1972. Fishes of Barnegat Bay, New Jersey, with Particular Reference to Seasonal Influences and Possible Effects of Thermal Discharges. New Brunswick, New Jersey: Rutgers University, Ph.D. dissertation, 190p.
- McGarigal, K.; Cushman, S., and Stafford, S., 2000. *Multivariate Statistics for Wildlife and Ecology Research*. New York: Springer-Verlag, 283p.
- Munsch, S.H.; Cordell, J.R., and Toft, J.D., 2015. Effects of shoreline engineering on shallow subtidal fish and crab communities in an urban estuary: A comparison of armored shorelines and nourished beaches. *Ecological Engineering*, 81, 312-320.
- Oksanen, J.; Guillaume Blanchet, F.; Friendly, M.; Kindt, R.; Legendre, P.; McGlinn, D.; Minchin, P.R.; O'Hara, R.B.; Simpson, G.L.; Solymos, P.; Stevens, M.H.H.; Szoecs, E., and Wagner, H., 2016. *Package 'vegan': Community Ecology Package*. <https://cran.r-project.org/web/packages/vegan/vegan.pdf>.
- Olin, M. and Malinen, T., 2003. Comparison of gillnet and trawl in diurnal fish community sampling. *Hydrobiologia*, 506(1), 443-449.
- Partyka, M.L. and Peterson, M.S., 2008. Habitat quality and salt-marsh species assemblages along an anthropogenic estuarine landscape. *Journal of Coastal Research*, 24(6), 1570-1581.
- Peterson, M.S.; Comyns, B.H.; Hendon, J.R.; Bond, P.J., and Duff, G.A., 2000. Habitat

- use by early life-history stages of fishes and crustaceans along a changing estuarine landscape: Differences between natural and altered shoreline sites. *Wetlands Ecology and Management*, 8(2), 209-219.
- Peterson, M.S. and Lowe, M.R., 2009. Implications of cumulative impacts to estuarine and marine habitat quality for fish and invertebrate resources. *Reviews in Fisheries Science*, 17(4), 505-523.
- Reid, W.V.; Mooney, H.A.; Cropper, A.; Capistrano, D.; Carpenter, S.R.; Chopra, K.; Dasgupta, P.; Dietz, T.; Duraiappah, A.K.; Hassan, R.; Kasperson, R.; Leemans, R.; May, R.M.; McMichael, T. (A.J.); Pingali, P.; Samper, C.; Scholes, R.; Watson, R.T.; Zakri, A.H.; Shidong, Z.; Ash, N.J.; Bennett, E.; Kumar, P.; Lee, M.J.; Raudsepp-Hearne, C.; Simons, H.; Thonell, J., and Zurek, M.B., 2005. *Ecosystems and Human Well-being: Synthesis*. Washington, D.C.: Millenium Ecosystem Assessment, 155p.
- Sogard, S.M. and Able, K.W., 1991. A comparison of eelgrass, sea lettuce, macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. *Estuarine, Coastal and Shelf Science*, 33(5), 501-519.
- Sugihara, T.; Yearsley, C.; Durand, J.B., and Psuty, N.P., 1979. *Comparison of Natural and Altered Estuarine Systems: Analysis*. New Brunswick, New Jersey: Rutgers University, Center for Coastal and Environmental Studies, 256p.
- Tatham, T.R.; Danila, D.J., and Thomas, D.L., 1984. Fishes of Barnegat Bay. In: Kennish, M.J. and Lutz, R.A. (eds.), *Ecology of Barnegat Bay, New Jersey*. New York, New York: Springer-Verlag, pp. 241-290.
- Tatham, T.R.; Danila, D.J.; Thomas, D.L., and Associates, 1977. *Ecological Studies for the Oyster Creek Generating Station: Volume One Fin- and Shellfish*. Forked River, New Jersey: Ichthyological Associates, Inc., 354p.
- ter Braak, C.J.F. and Šmilauer, P., 2012. *Canoco Reference Manual and User's Guide: Software for Ordination (version 5.0)*. Ithaca, New York: Microcomputer Power, 496p.
- Voglitois, J.J., 1983. The Ichthyofauna of Barnegat Bay, New Jersey: Relationships Between Long-Term Temperature Fluctuations and the Population Dynamics and Life History of Estuarine Fishes During a Five Year Period, 1976-1980. New Brunswick, New Jersey: Rutgers University, Master's thesis, 303p.
- Voglitois, J.J.; Able, K.W.; Kurtz, R.J., and Tighe, K.A., 1987. Life history and population dynamics of the bay anchovy in New Jersey. *Transactions of the American Fisheries Society*, 116(2), 141-154.
- Walsh, C.J.; Roy, A.H.; Feminella, J.W.; Cottingham, P.D.; Groffman, P.M., and Morgan

- II, R.P., 2005. The urban stream syndrome: Current knowledge and the search for a cure. *Journal of the North American Benthological Society*, 24(3), 706-723.
- Ward, L.G.; Kemp, W.M., and Boynton, W.R., 1984. The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Marine Geology*, 59(1-4), 85-103.
- Wedge, M.; Anderson, C.J., and DeVries, D., 2015. Evaluating the effects of urban land use on the condition of resident salt marsh fish. *Estuaries and Coasts*, 38(6), 2355-2365.
- Whitehead, A.; Dubansky, B.; Bodinier, C.; Garcia, T.I.; Miles, S.; Pilley, C.; Raghunathan, V.; Roach, J.L.; Walker, N.; Walter, R.B.; Rice, C.D., and Galvez, F., 2012. Genomic and physiological footprint of the Deepwater Horizon oil spill on resident marsh fishes. *Proceedings of the National Academy of Sciences*, 109(50), 20298-20302.
- Wiley, T.R. and Simpfendorfer, C.A., 2007. The ecology of elasmobranchs occurring in the Everglades National Park, Florida: Implications for conservation and management. *Bulletin of Marine Science*, 80(1), 171-189.

Tables

Table 1. Land use characteristics (based on 2009 New Jersey Department of Environmental Protection data) and human population estimates of each stratum (see Figure 1) in the Barnegat Bay watershed. The human population estimates are based on estimates of human population per township, or part of a township, using data from the Ocean County Planning Department (January 2011) and the 2010 U.S. Census Bureau. The percent of urban land increased from stratum I to stratum V.

Stratum	Estimated Human Population	% Agriculture	% Barren Land	% Forest	% Urban	% Water	% Wetlands
I	6,017	0.1	0.4	2.3	10.6	64.2	22.4
II	6,257	0.2	0.5	3.0	12.6	51.4	32.4
III	7,387	0.1	0.8	7.1	13.5	62.3	16.3
IV	22,855	0.1	0.8	5.8	21.1	57.3	14.9
V	38,800	0.0	0.6	4.1	30.0	50.9	14.4

Table 2. The total number of net tows and fish collected over the three year sampling duration, mean number of fish collected \pm standard error of the mean (SEM), and three different diversity indices for each stratum. The mean number of fish collected did not differ among strata, but species richness, Shannon-Wiener diversity, and Simpson's diversity varied among strata.

Stratum	# Tows	# Fish	Mean # Fish per 360s (3 Trawl Tows) \pm SEM	Species Richness	Shannon-Wiener Diversity	Simpson's Diversity
I	287	5,516	0.835 ± 0.477	50	1.69	0.664
II	288	4,629	0.706 ± 0.467	42	1.26	0.554
III	285	8,651	1.62 ± 0.838	47	1.72	0.721
IV	286	5,765	0.871 ± 0.672	39	1.12	0.399
V	288	4,950	0.747 ± 0.582	36	1.05	0.388
Overall	1,434	29,511	0.955 ± 0.168	69	1.74	0.695

Table 3. Stratum-specific means \pm SEM and ranges for temperature, salinity, dissolved oxygen, pH, and water depth measured during this study. There was a pronounced difference in mean salinity among strata.

Stratum	Temperature ($^{\circ}\text{C}$)	Salinity (ppt)	Dissolved Oxygen (mg/L)	pH	Water Depth (m)
I	19.6 ± 0.2	28.11 ± 0.53	6.74 ± 0.27	7.68 ± 0.07	1.7 ± 0.2
	8.8 - 26.7	20.01 - 31.48	2.40 - 12.48	5.67 - 8.10	0.9 - 3.2
II	20.2 ± 0.1	25.11 ± 1.49	6.63 ± 0.37	7.64 ± 0.12	1.5 ± 0.2
	10.0 - 28.6	9.66 - 30.44	1.15 - 9.54	6.58 - 8.39	0.9 - 3.4
III	20.5 ± 0.7	26.87 ± 0.44	7.11 ± 0.15	7.83 ± 0.02	2.0 ± 0.3
	10.9 - 30.6	22.04 - 31.36	3.66 - 11.18	7.30 - 8.20	0.6 - 3.1
IV	20.1 ± 0.1	21.18 ± 0.35	6.73 ± 0.34	7.79 ± 0.07	1.5 ± 0.2
	12.9 - 27.5	9.45 - 25.96	0.20 - 9.47	6.89 - 8.35	0.6 - 3.1
V	19.6 ± 0.3	20.42 ± 0.54	6.85 ± 0.22	7.72 ± 0.05	1.9 ± 0.5
	10.8 - 28.2	13.24 - 28.91	0.16 - 11.27	7.07 - 8.41	0.7 - 6.2

Table 4. Principal Component Analysis (PCA) species loadings for principal components (PC) one and two and Canonical Correspondence Analysis (CCA) species loadings for canonical axes one and two. Loadings considered to be significant were underlined (see “Ordinations” under “Methods” section). See Figure 3a for usage of the “Fig. 3a Species Number” column.

Common Name	Scientific Name	PC1 Loadings	PC2 Loadings	Axis 1 Loadings	Axis 2 Loadings	Fig. 3a Species Number
Alewife	<i>Alosa pseudoharengus</i>	0.042	-0.095	-0.174	0.109	1
American butterfish	<i>Peprilus triacanthus</i>	-0.080	0.128	0.075	-0.172	49
American eel	<i>Anguilla rostrata</i>	0.171	0.238	0.017	0.141	4
Atlantic croaker	<i>Micropogonias undulatus</i>	-0.152	0.177	0.254	0.107	40
Atlantic herring	<i>Clupea harengus</i>	-0.035	-0.038	-0.036	-0.002	15
Atlantic menhaden	<i>Brevoortia tyrannus</i>	-0.111	0.162	<u>0.330</u>	<u>0.510</u>	9
Atlantic moonfish	<i>Selene setapinnis</i>	-0.069	0.006	0.117	0.243	58
Atlantic needlefish	<i>Strongylura marina</i>	<u>0.910</u>	0.234	<u>-0.422</u>	0.083	62
Atlantic silverside	<i>Menidia menidia</i>	<u>0.983</u>	0.159	<u>-0.687</u>	0.139	37
Bay anchovy	<i>Anchoa mitchilli</i>	<u>-0.406</u>	<u>0.914</u>	<u>0.401</u>	<u>-0.367</u>	3
Black drum	<i>Pogonias cromis</i>	0.009	-0.138	-0.061	0.116	51
Black sea bass	<i>Centropristis striata</i>	0.221	0.163	-0.125	-0.132	11*
Blackcheek tonguefish	<i>Symphurus plagiusa</i>	-0.003	-0.069	-0.075	-0.005	63
Bluefish	<i>Pomatomus saltatrix</i>	-0.080	<u>0.399</u>	0.219	-0.018	53
Bluegill	<i>Lepomis macrochirus</i>	-0.019	-0.157	0.239	0.286	33
Bluntnose stingray	<i>Dasyatis say</i>	-0.034	-0.247	0.144	<u>0.464</u>	19
Broad-striped anchovy	<i>Anchoa hepsetus</i>	-0.161	0.186	0.161	-0.149	2
Channel catfish	<i>Ictalurus punctatus</i>	-0.019	-0.157	0.239	0.286	29
Conger eel	<i>Conger oceanicus</i>	-0.019	-0.112	0.118	<u>0.335</u>	16
Creville jack	<i>Caranx hippos</i>	-0.028	-0.124	0.138	<u>0.319</u>	10
Cunner	<i>Tautoglabrus adspersus</i>	0.153	0.208	-0.090	-0.111	67

Table 4 continued.

Common Name	Scientific Name	PC1 Loadings	PC2 Loadings	Axis 1 Loadings	Axis 2 Loadings	Fig. 3a Species Number
Feather blenny	<i>Hypsoblennius hertz</i>	-0.034	-0.229	0.067	0.305	28
Flathead grey mullet	<i>Mugil cephalus</i>	-0.019	-0.145	-0.010	-0.218	43
Flying gurnard	<i>Dactylopterus volitans</i>	-0.022	-0.130	0.045	0.008	18
Fourspine stickleback	<i>Apeltes quadracus</i>	<u>0.951</u>	0.208	<u>-0.531</u>	0.098	5
Gag grouper	<i>Mycteroperca microlepis</i>	-0.031	-0.037	-0.042	0.005	46
Green goby	<i>Microgobius thalassinus</i>	-0.119	0.157	0.074	-0.062	39*
Hogchoker	<i>Trinectes maculatus</i>	-0.090	-0.083	0.249	0.108	68
Inland silverside	<i>Menidia beryllina</i>	-0.043	-0.035	0.272	<u>0.488</u>	36
Inshore lizardfish	<i>Synodus foetens</i>	-0.022	-0.130	0.045	0.008	65
Lined seahorse	<i>Hippocampus erectus</i>	<u>0.921</u>	0.163	<u>-0.534</u>	0.107	27
Little skate	<i>Raja erinacea</i>	-0.082	<u>0.352</u>	0.049	-0.105	56
Lookdown	<i>Selene vomer</i>	-0.032	-0.168	0.120	<u>0.445</u>	59
Mangrove snapper	<i>Lutjanus griseus</i>	-0.016	-0.175	0.080	<u>0.441</u>	35
Mummichog	<i>Fundulus heteroclitus</i>	0.176	<u>0.420</u>	0.000	0.139	22
Naked goby	<i>Gobiosoma bosc</i>	-0.137	0.091	0.201	0.119	25
Northern kingfish	<i>Menticirrhus saxatilis</i>	-0.058	-0.192	0.130	0.258	38
Northern pipefish	<i>Syngnathus fuscus</i>	<u>0.944</u>	0.206	<u>-0.584</u>	0.086	64
Northern puffer	<i>Sphoeroides maculatus</i>	<u>0.388</u>	-0.108	<u>-0.614</u>	0.142	60
Northern searobin	<i>Prionotus carolinus</i>	-0.133	0.210	0.172	-0.094	54*
Northern stargazer	<i>Astroscopus guttatus</i>	-0.031	-0.057	0.068	-0.038	7
Oyster toadfish	<i>Opsanus tau</i>	0.281	0.040	-0.166	0.174	47
Pinfish	<i>Lagodon rhomboides</i>	<u>0.738</u>	-0.006	<u>-0.417</u>	<u>0.447</u>	30
Pollock	<i>Pollachius virens</i>	<u>0.396</u>	0.004	-0.169	-0.056	52
Pumpkinseed	<i>Lepomis gibbosus</i>	-0.019	-0.157	0.239	0.286	32
Rainwater killifish	<i>Lucania parva</i>	<u>0.906</u>	0.225	<u>-0.428</u>	0.074	34

Table 4 continued.

Common Name	Scientific Name	PC1 Loadings	PC2 Loadings	Axis 1 Loadings	Axis 2 Loadings	Fig. 3a Species Number
Scup	<i>Stenotomus chrysops</i>	-0.115	0.216	0.086	-0.141	61
Seaboard goby	<i>Gobiosoma ginsburgi</i>	<u>0.369</u>	0.057	<u>-0.401</u>	0.053	26
Sheepshead	<i>Archosargus probatocephalus</i>	-0.046	-0.002	0.070	-0.117	6
Silver perch	<i>Bairdiella chrysoura</i>	0.307	0.219	-0.316	-0.067	8
Skilletfish	<i>Gobiesox strumosus</i>	-0.060	-0.093	0.166	<u>0.332</u>	24
Smallmouth flounder	<i>Etropus microstomus</i>	0.083	0.239	0.037	-0.056	20
Smooth dogfish	<i>Mustelus canis</i>	-0.077	-0.041	0.098	0.000	45
Spot	<i>Leiostomus xanthurus</i>	-0.113	-0.080	<u>0.382</u>	<u>0.429</u>	31
Spotfin butterflyfish	<i>Chaetodon ocellatus</i>	<u>0.904</u>	0.163	<u>-0.587</u>	0.110	12
Spotfin killifish	<i>Fundulus luciae</i>	0.112	-0.062	-0.304	0.057	23
Spotfin mojarra	<i>Eucinostomus argenteus</i>	-0.024	-0.122	0.023	-0.229	21
Spotted hake	<i>Urophycis regia</i>	-0.087	0.075	-0.007	-0.063	69*
Striped bass	<i>Morone saxatilis</i>	-0.025	-0.087	0.013	-0.043	42
Striped blenny	<i>Chasmodes bosquianus</i>	-0.157	0.218	0.113	-0.030	13
Striped burrfish	<i>Chilomycterus schoepfi</i>	0.281	0.202	<u>-0.337</u>	-0.176	14
Summer flounder	<i>Paralichthys dentatus</i>	-0.156	0.290	0.298	-0.153	48
Tautog	<i>Tautoga onitis</i>	<u>0.415</u>	-0.033	<u>-0.435</u>	0.090	66
Weakfish	<i>Cynoscion regalis</i>	-0.182	<u>0.344</u>	0.309	0.096	17
White mullet	<i>Mugil curema</i>	-0.034	-0.086	0.057	0.056	44
White perch	<i>Morone americana</i>	-0.069	-0.099	0.316	0.259	41
Windowpane flounder	<i>Scophthalmus aquosus</i>	0.026	-0.097	-0.093	0.004	57*
Winter flounder	<i>Pseudopleuronectes americanus</i>	<u>0.457</u>	-0.071	<u>-0.352</u>	-0.295	55
Yellow perch	<i>Perca flavescens</i>	-0.019	-0.157	0.239	0.286	50

Table 5. (a) Summary of results from the Canonical Correspondence Analysis (CCA) (b) CCA correlation matrix describing correlations between the measured environmental parameters and the first and second canonical axes, in addition to correlations between environmental parameters.

	Axis 1	Axis 2	Temperature	Salinity	Dissolved Oxygen	pH	Depth
a. CCA Results							
Eigenvalues	0.487	0.106	-	-	-	-	-
Species-environment correlations	0.804	0.615	-	-	-	-	-
Percentage variance of:			-	-	-	-	-
species data	21.2	4.6	-	-	-	-	-
species-environment relation	72.4	15.8	-	-	-	-	-
Sum of all eigenvalues	2.292		-	-	-	-	-
Sum of all canonical eigenvalues	0.673		-	-	-	-	-
b. CCA Correlation Matrix							
Temperature	0.1892	0.4659	1.0000	-	-	-	-
Salinity	-0.4551	0.1607	-0.2696	1.0000	-	-	-
Dissolved Oxygen	-0.7118	-0.1975	-0.3691	0.5018	1.0000	-	-
pH	-0.4693	-0.2545	-0.3011	0.4069	0.8175	1.0000	-
Depth	0.5187	-0.3078	-0.2996	-0.2173	-0.2721	-0.1015	1.0000

Table 6. Species-specific mean number of fish collected \pm SEM for each stratum. An asterisk after a common name indicates that species mean CPUE \pm SEM range differed between at least two strata (i.e. species X mean CPUE for stratum Y did not overlap with that of stratum Z).

Common Name	Mean Number of Fish per 360s (3 Trawl Tows) \pm SEM				
	I	II	III	IV	V
Alewife	0 \pm 0	0.0104 \pm 0.0104	0 \pm 0	0 \pm 0	0 \pm 0
American butterflyfish*	0.0313 \pm 0.0219	0 \pm 0	0.0208 \pm 0.0208	0 \pm 0	0 \pm 0
American eel*	0.0208 \pm 0.0208	0.0784 \pm 0.0673	0.0521 \pm 0.0415	0.0703 \pm 0.0484	0.187 \pm 0.072
Atlantic croaker*	0.376 \pm 0.237	0.125 \pm 0.067	0.521 \pm 0.452	0.728 \pm 0.397	0.0729 \pm 0.0509
Atlantic herring	0.240 \pm 0.240	0 \pm 0	0 \pm 0	0.0227 \pm 0.0227	0 \pm 0
Atlantic menhaden	3.65 \pm 3.37	0.346 \pm 0.247	1.15 \pm 1.12	3.21 \pm 2.86	0.302 \pm 0.140
Atlantic moonfish	0.0104 \pm 0.0104	0 \pm 0	0.0208 \pm 0.0208	0.0104 \pm 0.0104	0 \pm 0
Atlantic needlefish	0 \pm 0	0 \pm 0	0.0207 \pm 0.0207	0 \pm 0	0 \pm 0
Atlantic silverside*	7.91 \pm 5.74	12.1 \pm 8.8	49.5 \pm 39.3	1.11 \pm 0.58	1.47 \pm 1.09
Bay anchovy*	31.7 \pm 12.1	30.1 \pm 11.1	15.2 \pm 9.25	46.4 \pm 16	40.1 \pm 13
Black drum	0.0104 \pm 0.0104	0.0227 \pm 0.0227	0 \pm 0	0 \pm 0	0.0104 \pm 0.0104
Black sea bass*	0.167 \pm 0.047	0.0885 \pm 0.0389	0.364 \pm 0.127	0.0322 \pm 0.0157	0.0625 \pm 0.0208
Blackcheek tonguefish*	0 \pm 0	0.0208 \pm 0.0136	0 \pm 0	0 \pm 0	0 \pm 0
Bluefish*	0.0729 \pm 0.0332	0.0625 \pm 0.0305	0.0781 \pm 0.0405	0.115 \pm 0.063	0.135 \pm 0.035
Bluegill	0 \pm 0	0.0106 \pm 0.0106	0 \pm 0	0 \pm 0	0 \pm 0
Bluntnose stingray*	0.0104 \pm 0.0104	0 \pm 0	0.0208 \pm 0.0136	0 \pm 0	0 \pm 0
Broad-striped anchovy*	0.0625 \pm 0.0305	0.0521 \pm 0.0270	0.542 \pm 0.227	0.198 \pm 0.109	0.0208 \pm 0.0136
Channel catfish	0 \pm 0	0.0104 \pm 0.0104	0 \pm 0	0 \pm 0	0 \pm 0
Conger eel	0 \pm 0	0 \pm 0	0.0104 \pm 0.0104	0 \pm 0	0 \pm 0
Crevalle jack	0 \pm 0	0 \pm 0	0.0417 \pm 0.0417	0 \pm 0	0.0107 \pm 0.0107
Cunner*	0.0313 \pm 0.0219	0 \pm 0	0.271 \pm 0.181	0 \pm 0	0 \pm 0

Table 6 continued.

Common Name	Mean Number of Fish per 360s (3 Trawl Tows) \pm SEM				
	I	II	III	IV	V
Feather blenny*	0.0104 \pm 0.0104	0 \pm 0	0.135 \pm 0.070	0.0227 \pm 0.0227	0.0208 \pm 0.0136
Flathead grey mullet	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0.0104 \pm 0.0104
Flying gurnard	0.0104 \pm 0.0104	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
Fourspine stickleback*	0.240 \pm 0.216	0.102 \pm 0.044	26.6 \pm 21.6	0.750 \pm 0.638	0.240 \pm 0.127
Gag grouper	0.0104 \pm 0.0104	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
Green goby*	0.0208 \pm 0.0208	0 \pm 0	0 \pm 0	0.0208 \pm 0.0208	0.0313 \pm 0.0152
Hogchoker	0.153 \pm 0.119	0.0210 \pm 0.0138	0.0313 \pm 0.0152	0.0208 \pm 0.0136	0.0940 \pm 0.0714
Inland silverside	0.323 \pm 0.323	0.0078 \pm 0.0078	0 \pm 0	0.0313 \pm 0.0313	0 \pm 0
Inshore lizardfish	0.0104 \pm 0.0104	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
Lined seahorse*	0.0833 \pm 0.0417	0 \pm 0	0.260 \pm 0.173	0.0104 \pm 0.0104	0 \pm 0
Little skate	0.0104 \pm 0.0104	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
Lookdown*	0.0104 \pm 0.0104	0 \pm 0	0.0417 \pm 0.0315	0 \pm 0	0 \pm 0
Mangrove snapper	0 \pm 0	0 \pm 0	0.0104 \pm 0.0104	0 \pm 0	0 \pm 0
Mummichog	0.0313 \pm 0.0219	0.0729 \pm 0.0729	0.214 \pm 0.202	0.630 \pm 0.630	0.0104 \pm 0.0104
Naked goby*	0.458 \pm 0.272	0.352 \pm 0.124	0.542 \pm 0.448	0.358 \pm 0.156	1.36 \pm 0.70
Northern kingfish*	0.0417 \pm 0.0315	0 \pm 0	0.0729 \pm 0.0484	0.0673 \pm 0.0563	0 \pm 0
Northern pipefish*	2.48 \pm 1.29	1.41 \pm 0.55	8.63 \pm 7.18	1.05 \pm 0.76	0.323 \pm 0.151
Northern puffer*	0.229 \pm 0.172	0.146 \pm 0.075	0.567 \pm 0.224	0.181 \pm 0.054	0.125 \pm 0.042
Northern searobin	0.0104 \pm 0.0104	0.0100 \pm 0.0100	0.0104 \pm 0.0104	0.0104 \pm 0.0104	0 \pm 0
Northern stargazer	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0.0104 \pm 0.0104
Oyster toadfish*	0.214 \pm 0.129	0.240 \pm 0.084	0.620 \pm 0.325	0.0744 \pm 0.0333	0.260 \pm 0.116
Pinfish*	0.0313 \pm 0.0219	0.0208 \pm 0.0208	0.229 \pm 0.083	0.0104 \pm 0.0104	0.0417 \pm 0.0223
Pollock*	0.0104 \pm 0.0104	0 \pm 0	0.0417 \pm 0.0273	0.0445 \pm 0.0342	0 \pm 0
Pumpkinseed*	0 \pm 0	0.0943 \pm 0.0106	0 \pm 0	0 \pm 0	0 \pm 0

Table 6 continued.

Common Name	Mean Number of Fish per 360s (3 Trawl Tows) \pm SEM				
	I	II	III	IV	V
Rainwater killifish	0 \pm 0	0.0104 \pm 0.0104	0.151 \pm 0.151	0 \pm 0	0.0104 \pm 0.0104
Scup	0.0104 \pm 0.0104	0.0104 \pm 0.0104	0.0104 \pm 0.0104	0 \pm 0	0 \pm 0
Seaboard goby*	0.0313 \pm 0.0219	0.0104 \pm 0.0104	0.443 \pm 0.238	0 \pm 0	0.0313 \pm 0.0313
Sheepshead	0 \pm 0	0.0104 \pm 0.0104	0 \pm 0	0 \pm 0	0 \pm 0
Silver perch*	3.61 \pm 1.92	1.43 \pm 1.19	2.21 \pm 1.15	1.85 \pm 0.89	0.844 \pm 0.295
Skilletfish*	0 \pm 0	0 \pm 0	0.0417 \pm 0.0315	0.0104 \pm 0.0104	0.0104 \pm 0.0104
Smallmouth flounder*	0.0521 \pm 0.0415	0.0309 \pm 0.0218	0.0208 \pm 0.0136	0.0104 \pm 0.0104	0 \pm 0
Smooth dogfish*	0.0521 \pm 0.0313	0.0208 \pm 0.0208	0.0104 \pm 0.0104	0 \pm 0	0 \pm 0
Spot*	4.15 \pm 2.55	0.262 \pm 0.138	0.615 \pm 0.298	1.60 \pm 0.49	1.59 \pm 0.67
Spotfin butterflyfish*	0 \pm 0	0 \pm 0	0.026 \pm 0.018	0 \pm 0	0 \pm 0
Spotfin killifish	0.0104 \pm 0.0104	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
Spotfin mojarra	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0.0104 \pm 0.0104
Spotted hake*	0.146 \pm 0.080	0.0521 \pm 0.0219	0.0417 \pm 0.0273	0.0312 \pm 0.0152	0 \pm 0
Striped bass	0 \pm 0	0 \pm 0	0.0104 \pm 0.0104	0 \pm 0	0 \pm 0
Striped blenny*	0 \pm 0	0 \pm 0	0.0313 \pm 0.0219	0.0417 \pm 0.0273	0.167 \pm 0.061
Striped burrfish*	0.0313 \pm 0.0219	0.0517 \pm 0.0218	0.0781 \pm 0.0338	0.0208 \pm 0.0136	0 \pm 0
Summer flounder*	0.250 \pm 0.059	0.279 \pm 0.103	0.344 \pm 0.100	0.416 \pm 0.145	0.438 \pm 0.112
Tautog*	0.104 \pm 0.052	0.0833 \pm 0.0445	0.339 \pm 0.102	0.0104 \pm 0.0104	0.0104 \pm 0.0104
Weakfish*	0.0417 \pm 0.0315	0.0104 \pm 0.0104	0.0208 \pm 0.0136	0.0729 \pm 0.0484	0.0417 \pm 0.0315
White mullet	0.0417 \pm 0.0417	0.0208 \pm 0.0208	0 \pm 0	0.0104 \pm 0.0104	0.0104 \pm 0.0104
White perch*	0.0313 \pm 0.0219	0.0952 \pm 0.0839	0 \pm 0	0.0313 \pm 0.0219	0.0104 \pm 0.0104
Windowpane flounder	0.0104 \pm 0.0104	0.0104 \pm 0.0104	0 \pm 0	0.0104 \pm 0.0104	0.0104 \pm 0.0104
Winter flounder*	0.396 \pm 0.160	0.786 \pm 0.220	1.47 \pm 1.07	0.85 \pm 0.45	3.49 \pm 1.64
Yellow perch	0 \pm 0	0.0134 \pm 0.0134	0 \pm 0	0 \pm 0	0 \pm 0

Table 7. (a) Results of the binary Jaccard dissimilarity index. The binary index only used species presence/absence data and so was used as a metric of dissimilarity in species composition among strata (b) Results of the quantitative Jaccard dissimilarity index. The quantitative index incorporated species abundance data and so was used as a metric of dissimilarity in species abundance among strata.

Stratum	I	II	III	IV	V
a. Binary Percent Dissimilarities					
I	0	-	-	-	-
II	41.4	0	-	-	-
III	35.6	49.2	0	-	-
IV	28.8	41.2	37.7	0	-
V	49.1	44.0	49.1	37.0	0
b. Quantitative Percent Dissimilarities					
I	0	-	-	-	-
II	30.3	0	-	-	-
III	76.1	73.7	0	-	-
IV	42.5	49.3	83.0	0	-
V	45.7	44.9	84.2	27.7	0

Figures

Source: Adapted from Valenti, Grothues, and Able (2017). Reproduced with permission from the Coastal Education and Research Foundation.

Figure 1. Sampling sites (black circles), strata (I – V), and locations of importance within Barnegat Bay. Urbanization increased from stratum I to stratum V. See Table 1 for detailed land use characteristics of each stratum.

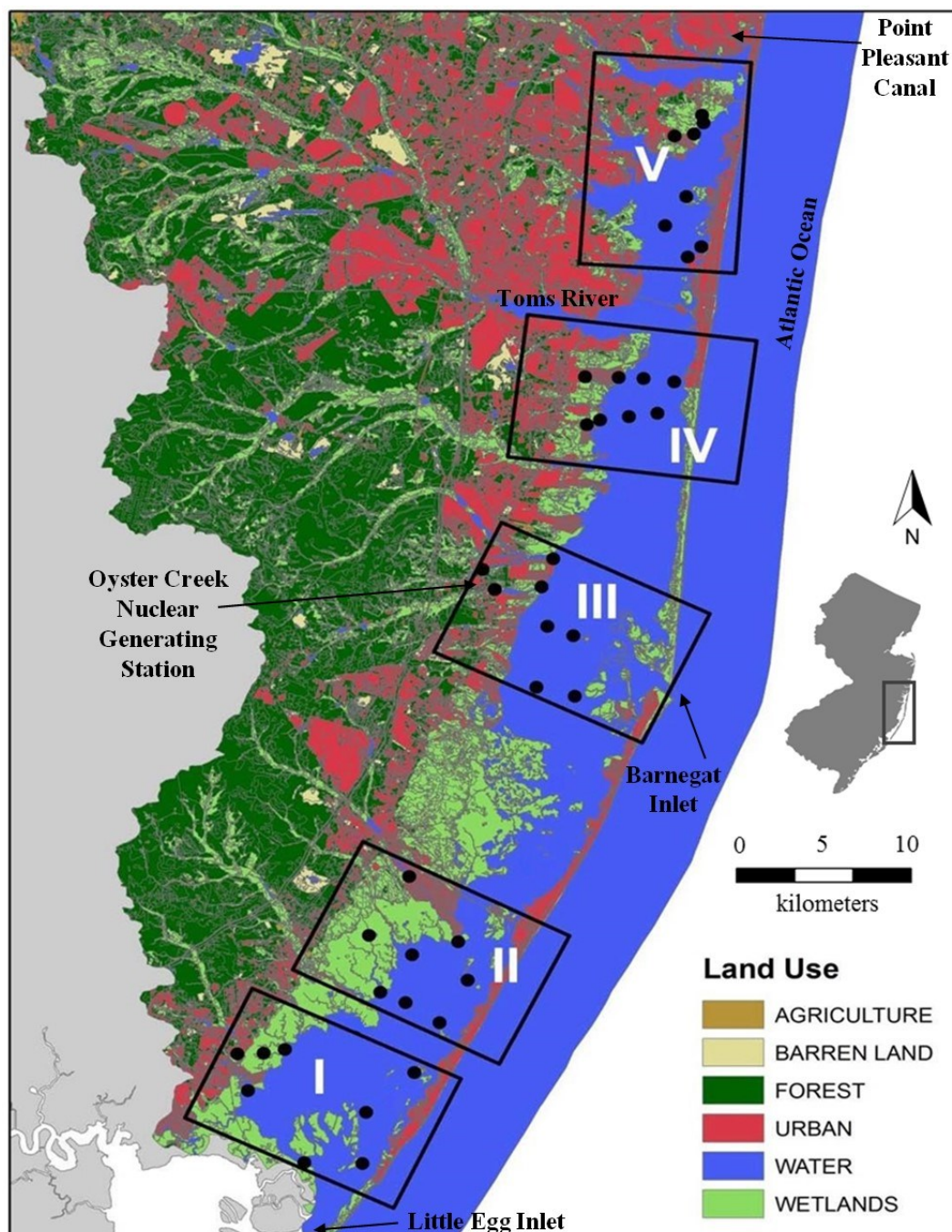


Figure 2. (a) Principal Component Analysis (PCA) scatterplot of species distributed along the first two principal components. Arrows point in the direction of an increase in abundance of the respective species. Some species labels were removed for clarity purposes and are enclosed in a box within the respective quadrant from which they were removed. Those species labels removed from the lower left quadrant were too numerous to list on the figure and as such are listed here: sheephead, northern stargazer, crevalle jack, Atlantic herring, conger eel, flying gurnard, spotfin mojarra, skilletfish, channel catfish, pumpkinseed, bluegill, mangrove snapper, inland silverside, striped bass, flathead grey mullet, white mullet, gag grouper, yellow perch, lookdown, blackcheek tonguefish, and inshore lizardfish. This plot is in the same coenospace as the subsequent sample plot, but was separated for legibility. (b) PCA scatterplot of samples coded by the stratum in which they were collected. A different convex polygon encloses the sampling sites from each stratum. Samples from different strata overlapped indicating similarity in species composition among strata. Note the difference in scale of the principal components from the preceding species plot.

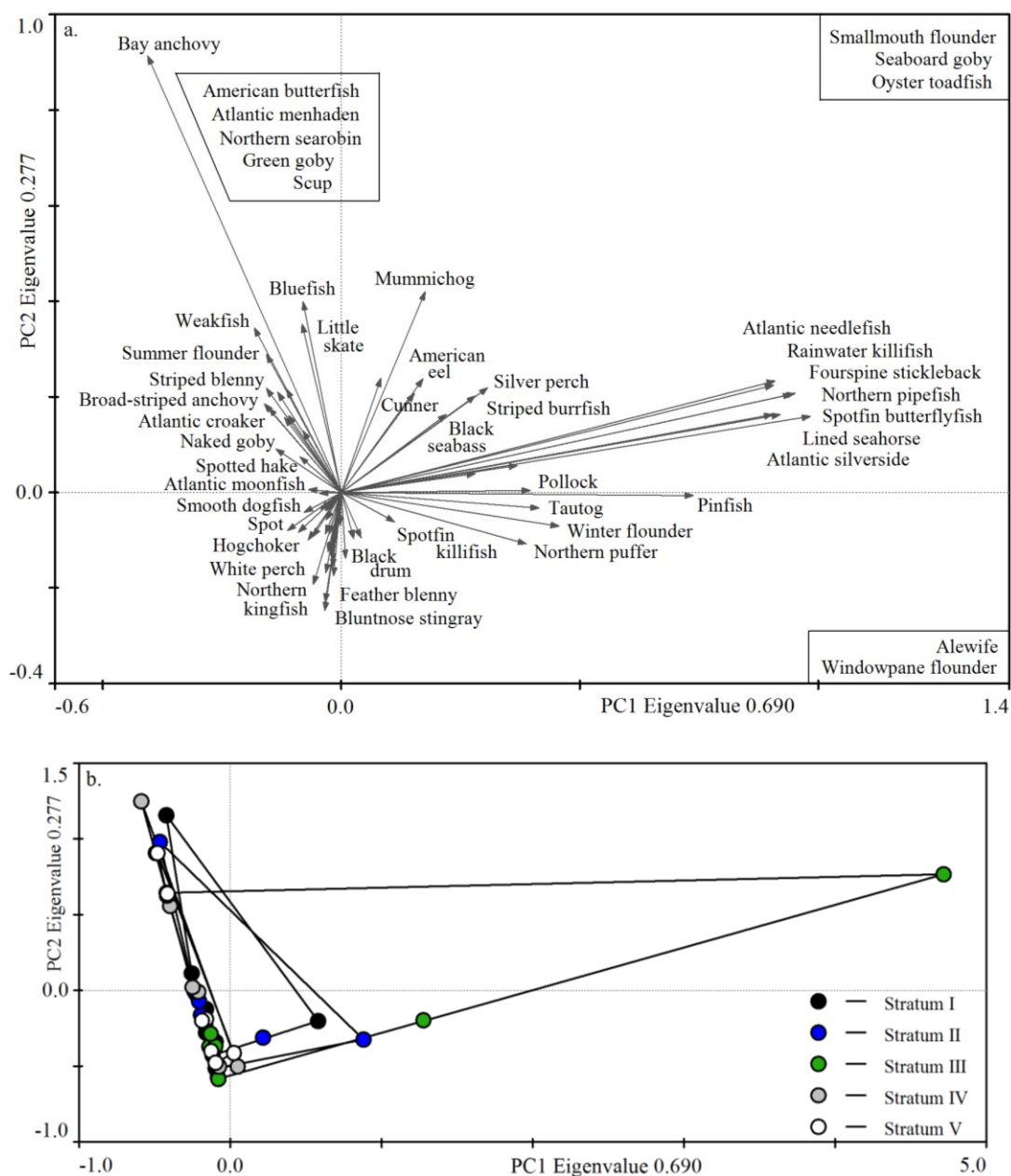


Figure 3. (a) Canonical Correspondence Analysis (CCA) scatter plot of species distributed along the first two canonical axes. Species were coded by number for legibility. Species-number pairings are available in the “Fig. 3a Species Number” column of Table 4. In the “Fig. 3a Species Number” column, a number with an asterisk afterwards indicates it is not present on the species plot due to space restrictions. Those species symbols which were not labeled are indicated by a light gray fill color in the plot. This plot is in the same coenospace as the subsequent biplot, but is separated for legibility. (b) CCA biplot (samples and environmental parameters) showing samples coded by the stratum in which they were collected. Arrows point in the direction of an increase in the magnitude of the respective environmental parameter. Note the difference in scale of the canonical axes from the preceding species plot.

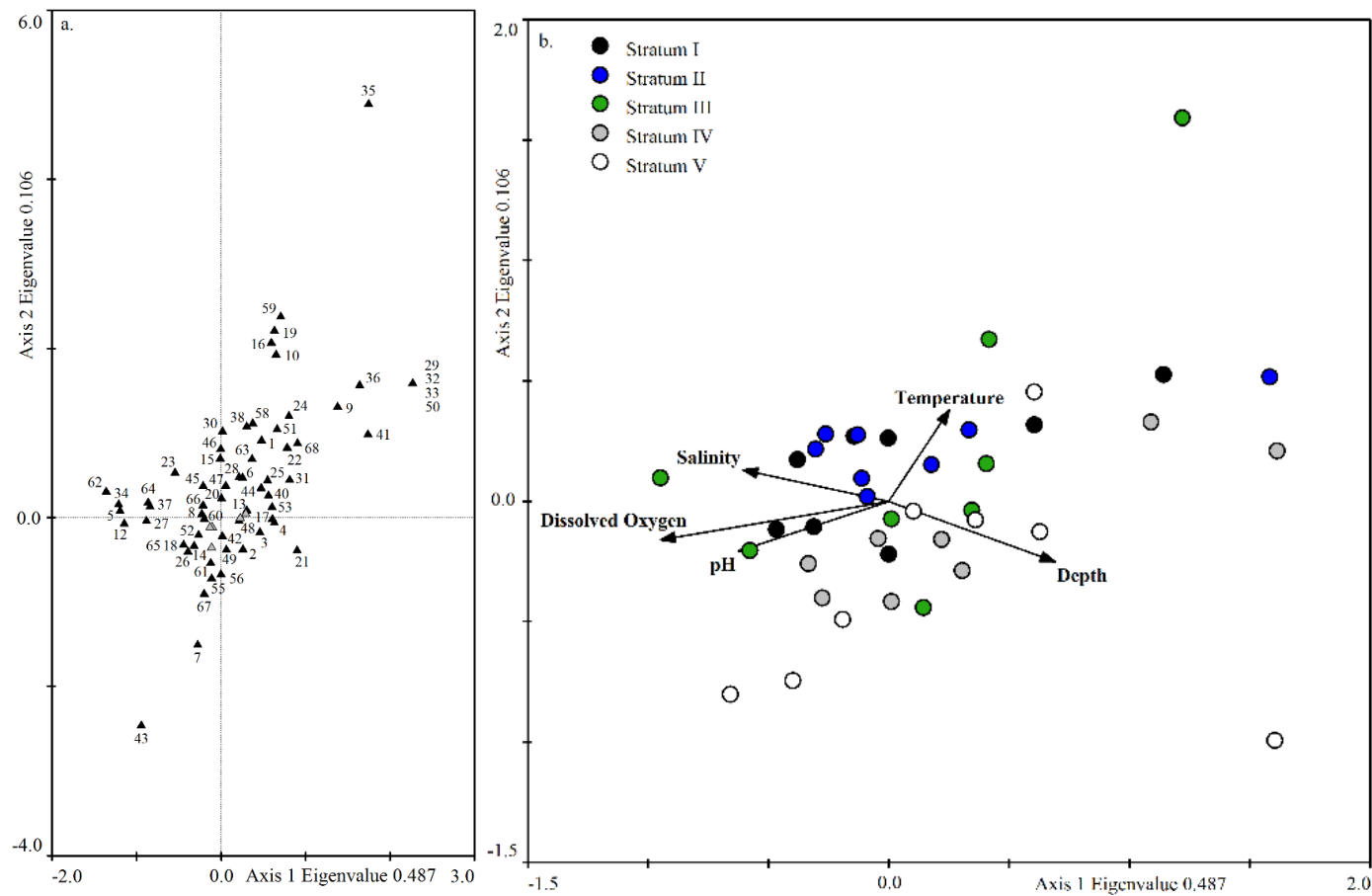


Figure 4. Rarefaction curves for each stratum displaying the mean number of species collected as a function of the number of individuals collected. Gray polygons indicate the 95% confidence interval for the mean rarefaction curve.

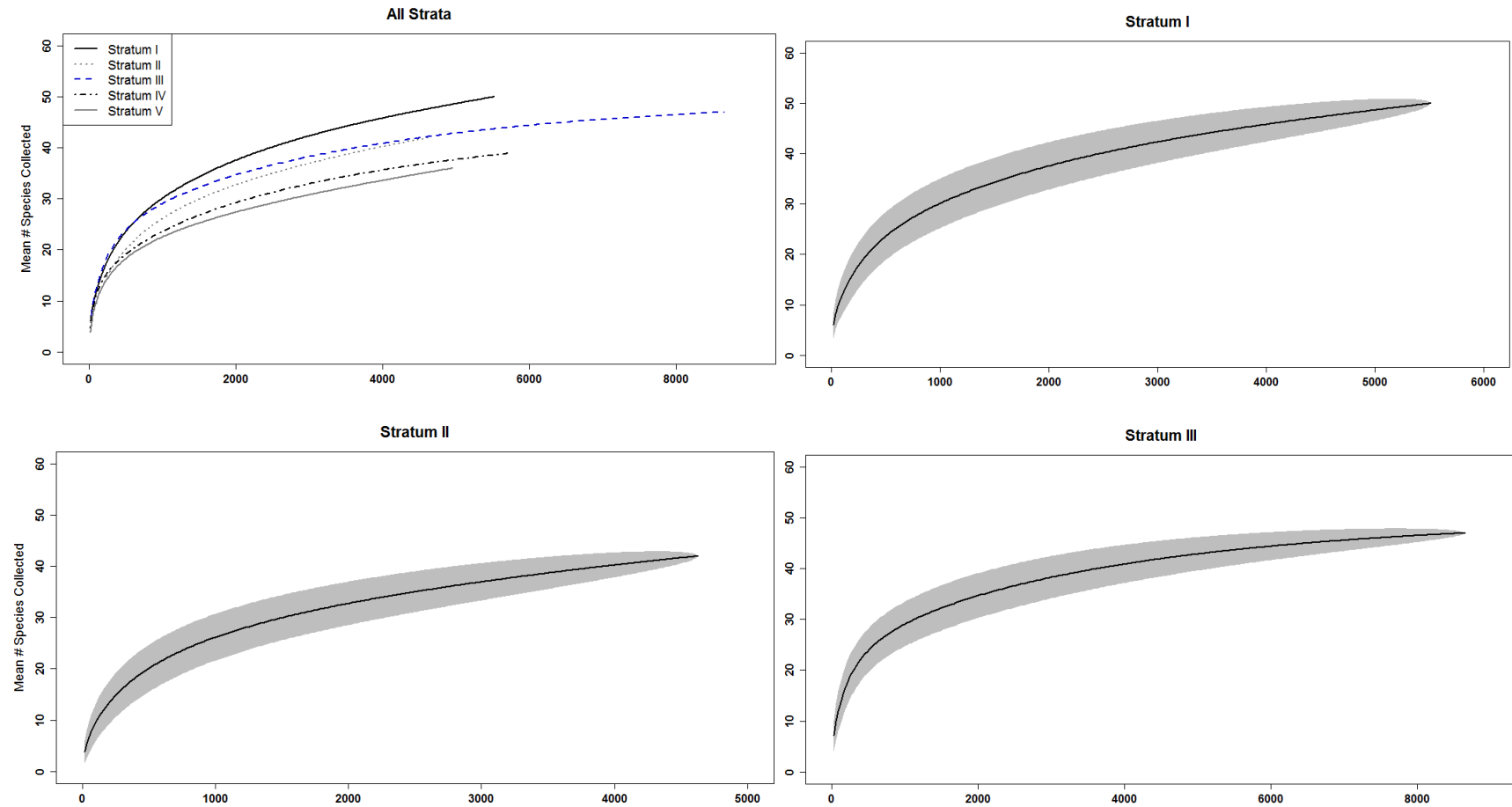
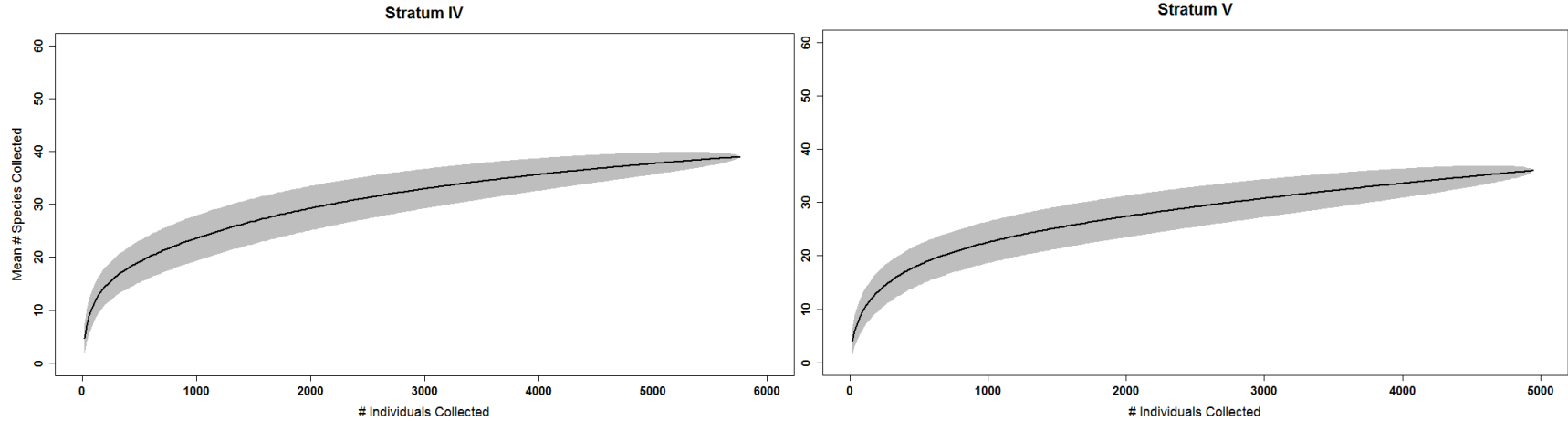


Figure 4 continued.



CHAPTER IV

The Influence of Shoreline Armoring: Structural Differences in Subtidal Fish Assemblages from Salt Marsh Creeks and Lagoon Housing Complexes

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Abstract

Coastal land development has resulted in the armoring of estuarine shorelines, consequently destroying valuable wetland habitat and severing connectivity between terrestrial and aquatic environments. The impact of shoreline armoring on intertidal and shallow-subtidal estuarine fish assemblages has been well documented, but few studies have considered the potential impact on fishes within deeper, subtidal waters further from the shore. Here we compare structural characteristics (composition, abundance, diversity, richness, length distributions) of subtidal fish assemblages inhabiting deeper waters (> 1 m) in reference marsh creeks, with vegetated shorelines (natural creeks), and lagoon housing complexes, with bulkheaded shoreline, (armored creeks) in a temperate lagoonal estuary (Barnegat Bay, New Jersey). Otter trawls were used to survey the fish assemblages in two habitats (upper creek and creek mouth) within each of four creeks (two sets of paired natural and armored creeks) for three years (2012 – 2014) in April,

June, August, and October of each year. Shoreline armoring did not appear to influence creek mouth fish assemblages, but differences were evident in upper creek fish assemblages indicating that the influence of shoreline armoring can extend to fishes in deeper waters. Within upper creek habitat, diversity and richness were consistently higher in natural creeks. Species composition overlapped among creek types, but the majority of estuarine residents, including mummichog *Fundulus heteroclitus* and naked goby *Gobiosoma bosc*, were only collected or were more abundant in natural upper creeks. Differences in upper creek fish assemblages were attributed to the decreased connectivity to the marsh and the deeper water depths observed in armored creeks. Conversely, the presence of nearby marsh habitat and relatively shallow water in armored creek mouths likely precluded differences between natural and armored creek mouth fish assemblages. It is clear that shallow waters and connectivity between terrestrial and aquatic estuarine environments are imperative for sustaining intact fish assemblages.

Introduction

Coastal areas are susceptible to storm floodwaters, sea level rise, and shoreline erosion (Nicholls and Small 2002). Shoreline armoring, the placement of hard, vertical structure, such as bulkheads, sea walls, and riprap revetment, along the natural shoreline, is frequently implemented as a defense mechanism against these threats (Charlier et al. 2005; Dugan et al. 2011; Gittman et al. 2015). Within the continental United States (U.S.), roughly 14% of coastal shoreline has been armored, and sheltered shoreline (e.g. shoreline within estuaries) has been armored more frequently than open shoreline (i.e. shoreline exposed to the ocean) (Gittman et al. 2015).

The armoring of sheltered shorelines alters or destroys the highly productive salt marsh ecosystems that dominate the coastal regions of many temperate estuaries (Costanza et al. 1997; Wilson 2002; Lotze et al. 2006; Costanza et al. 2014; Newton et al. 2020). Over 50% of tidal salt marshes within the U.S. have been lost to urbanization (anthropogenic land development) (Kennish 2001a; Kennish 2016). This is concerning given that salt marshes are essential components of estuarine habitat mosaics (Minello et al. 2003; Sheaves 2009; Sheaves et al. 2015) and serve as nursery areas for a variety of fishes and other fauna (Rountree and Able 2007; Peterson and Lowe 2009; Nagelkerken et al. 2015). In particular, the shallow waters of salt marsh creeks support diverse fish assemblages (Weinstein and Brooks 1983; Rountree and Able 1992a; Desmond et al. 2000; Able et al. 2001; Garwood et al. 2019) and serve as a conduit for the transfer of marsh production to estuarine waters (Weinstein et al. 1980; Kneib 1997; Micheli and Peterson 1999; Stevens et al. 2006), yet are highly susceptible to shoreline armoring.

The past and continued urbanization of coastal areas make marsh creeks especially vulnerable to shoreline armoring (Bilkovic 2011; Kennish 2016). During the urbanization process, shallow marsh creeks with gradually sloping banks dominated by native marsh grasses are often transformed into lagoon housing complexes with deepened channels and armored shorelines, altering creek water quality and destroying valuable fish habitat (Sugihara et al. 1979; Mallin and Lewitus 2004). These changes can drastically influence the structure (composition, abundance, diversity) of the fish assemblage residing within an urbanized creek (Bilkovic 2011; Lowe and Peterson 2014; Balouskus and Targett 2016; Rudershausen et al. 2016; Rudershausen et al. 2018).

Various studies have investigated the impacts of shoreline armoring on intertidal and shallow-subtidal (< 1 m) fish assemblages within salt marsh habitat (Peterson et al. 2000; Holland et al. 2004; Bilkovic and Roggero 2008; Lowe and Peterson 2014; Balouskus and Targett 2016; Rudershausen et al. 2016; Balouskus and Targett 2018; Crum et al. 2018; Rudershausen et al. 2018); however, fewer studies have considered the potential impact on fishes within deeper-subtidal creek habitat further from the shore (but see Bilkovic [2011]). Although deeper-water fish assemblages may be less dependent overall on the shoreline than their shallow-water counterparts, many of these fishes still utilize shallow water habitats for reproduction and rely upon the shallow-water faunal assemblages as prey items (Weinstein et al. 1980; Kneib 1997; Stevens et al. 2006). For example, Atlantic silverside *Menidia menidia*, a pelagic prey species, use native marsh grasses along the U.S. east coast as a substrate to attach their eggs (Middaugh et al. 1981; Balouskus and Targett 2012). Further, various predatory fishes make foraging-based migrations up marsh creeks on flood tides into shallow waters and onto the inundated marsh surface in order to access the diversity of prey items available there (Kleypas and Dean 1983; Hettler 1989; Rountree and Able 1992b; Potthoff and Allen 2003).

The objective of this study was to determine the response of deep-subtidal marsh creek fish assemblages (i.e. those within the central portion of marsh creeks > 1 m deep) to shoreline armoring by comparing the assemblages residing within reference salt marsh creeks and lagoon housing complexes. Structural characteristics (species composition, abundance, diversity, richness, lengths) of the fish assemblages inhabiting marsh creeks and lagoon complexes with varying degrees of natural (e.g. native marsh grass) and armored (e.g. bulkheaded) shoreline within Barnegat Bay (New Jersey, U.S.) were

assessed. Barnegat Bay has lost over 25% of its salt marshes in the previous century due to urbanization, and between 36 – 45% of the bay's shoreline is estimated to be armored with bulkhead (Kennish 2001b; Lathrop and Bognar 2001). Extensive lagoon complexes and bayside development are prevalent in the northern portion of Barnegat Bay (Kennish 2001b; Kennish 2001c; Valenti et al. 2017), and although many of the marsh creeks have armored shorelines, the potential impact of this armoring on the fish assemblages inhabiting the creeks has not been studied.

Methods

Area of Study

Barnegat Bay is a shallow (mean water depth < 2 m), lagoonal estuary (Whitfield and Elliott 2011) that is approximately 70 km long and between 2 – 6 km wide (Chizmadia et al. 1984; Kennish 2001b). Two inlets (Barnegat and Little Egg) connect the bay to the Atlantic Ocean and a third indirect connection to the ocean is established through the Point Pleasant Canal and Manasquan River. Salinity is lower in the northern portion of the bay than in the central and southern bay due to the larger tributaries (e.g. the Toms River) and the greater volume of freshwater input in the northern bay (Chizmadia et al. 1984; Kennish 2001b). Barnegat Bay exhibits seasonally varying water temperatures ranging from approximately -1 to 30°C and has a mean tidal range of 0.5 – 1.0 m (Kennish 2001b). The water column is generally well mixed due to the shallowness of the bay, but two-layered flow is evident in deeper waters, including those of the Intracoastal Waterway (Chizmadia et al. 1984; Kennish 2001b). The modelled bay residence time ranges from 0 – 50 days and depends heavily on the initial particle

location and the quantity and magnitude of forces (e.g. tidal, offshore coastal, riverine, metrological) modelled as acting on the particle (Defne and Ganju 2015).

Marsh creeks are abundant along the western shore of the bay (Kennish 2001b). Unarmored creek shorelines are dominated by marsh grasses such as smooth cordgrass *Spartina alterniflora* and saltmeadow cordgrass *Spartina patens* (Chizmadia et al. 1984; Kennish 2001b). Urbanized land, characterized by impervious cover and altered vegetation and drainage, has increased along with the human population within the Barnegat Bay watershed in recent decades (Lathrop and Bognar 2001; Kauffman and Cruz-Ortiz 2012; Valenti et al. 2017) and is most dense in the northern portion of the watershed (Kennish 2001b; Kennish 2001c; Valenti et al. 2017).

Shoreline Classification

Two reference marsh creeks and two lagoon housing complexes in northern Barnegat Bay were selected for study. For simplicity, the reference marsh creeks will be referred to as “natural” creeks (natural intertidal vegetation dominates the shoreline), and the lagoon housing complexes will be referred to as “armored” creeks (armoring dominates the shoreline). Creeks were broken up into two groups, with one natural creek and one armored creek in each group, based on their location within the bay (Fig. 1). The approximate percentage of natural and armored shoreline within each creek was determined using high resolution aerial imagery in ArcGIS software (New Jersey Office of Information Technology 2013) (Fig. 2 & 3, Table 1). For all creeks, shoreline classification was performed at the 1:1000 scale, with closer examinations performed

when necessary. Mosquito ditches joined to the creeks were not included in shoreline classifications.

Survey of Fish Assemblages

Within each creek, two sites were sampled: the upper creek and the creek mouth (Fig. 1, 2, & 3). Daytime otter trawl sampling consisted of three 120-second net tows (net dimensions: 4.9 m headrope, 19 mm mesh wings, and 6.3 mm mesh codend liner) at each of the 8 sites. Otter trawls target small fishes (< 200 mm) (Olin and Malinen 2003); in Barnegat Bay this includes juveniles and species with small adult stages (Able and Fahay 1998; Able and Fahay 2010). Sampling was repeated at each site in April, June, August, and October for three years (2012 – 2014), resulting in 12 sampling events at each site (Table 2). For each tow, fishes were identified and counted, and the lengths (total or fork length in mm, based on species) of the first 20 individuals of each species were recorded. Water depth and bottom water readings for temperature, salinity, dissolved oxygen, and pH were recorded at each site during every sampling event. Sites were sampled evenly across ebb and flood tides to negate the potential influence of tidal stage on fish assemblage structure (Hampel et al. 2003; Kimball and Able 2012).

Data Analyses

Species Composition

Only fish that could be identified to species were used for this and all other analyses in this study. Fishes were classified as estuarine residents, estuarine transients, and southern strays based on their usage of the estuary (Tatham et al. 1984; Able and

Fahay 2010). Non-metric multidimensional scaling (NMDS) was used to visualize latent dissimilarities in fish assemblage composition between natural and armored creeks. The species-specific abundance data from the three trawl tows at each site were combined, standardized to species-specific catch-per-unit-effort (CPUE) (number of fish/s), and root-root transformed. Bray-Curtis dissimilarities were projected as NMDS with the *vegan* package (version 2.5-6) (Oksanen et al. 2019) in RStudio (version 1.2.5001) (RStudio Team 2019). Separate NMDS analyses were performed for upper creek and creek mouth habitats. For both habitats, convergent NMDS solutions were reached using two dimensions (i.e. $k = 2$) (Clarke 1993) and the results were displayed as separate sample and species plots. The axes in the plots were centered and rotated so the sample variance was maximized along the first axis. The axes were also scaled so a change of one unit indicated a 50% reduction in fish assemblage similarity between samples. In the species plots, the locations of the species labels represent weighted averages based on the CPUE data.

Canonical Correspondence Analysis (CCA) was used to examine the relationship between the fish assemblages observed and the environmental parameters recorded (temperature, salinity, dissolved oxygen, pH, water depth, and the percentage of armored shoreline in a creek). Separate analyses were completed for upper creek and creek mouth habitats. Results of both analyses were represented as biplots (samples and environmental parameters) and separate species plots. In order to guard against over-interpretation, Monte Carlo permutation tests were used to assess the significance of the first canonical axis and the significance of all canonical axes in both analyses. Species loadings were also calculated for the first two canonical axes of both analyses; loadings greater than

0.320 or less than -0.320 were considered worth discussing (Comrey and Lee 2013).

CCA was performed using Canoco (version 4.5) (ter Braak and Smilauer 2012). All other analyses in this study were completed in RStudio.

Abundance and Length

The abundance data from the three trawl tows at each site were combined, standardized to overall CPUE, and root-root transformed. Separate general linear models were fit to the upper creek and creek mouth CPUE data sets. Creek type (i.e. natural or armored) and group (i.e. Group 1 or Group 2) were categorical covariates in both models and the interaction term was only included in the upper creek model based on model selection using Akaike information criterion (AIC) (Burnham and Anderson 2004). The emmeans package (version 1.4.6) (Lenth 2020) was used to compare differences in CPUE between creek type and groups post-hoc ($H_0: \mu_1 - \mu_2 = 0$). The modelled values were back-transformed from the root-root scale prior to post-hoc testing and calculation of the reported differences and confidence intervals.

Due to the non-normality of the species-specific CPUE data, exact Fisher-Pitman permutation tests (also known as randomization tests) were used to compare differences in mean CPUE between natural and armored creeks for fishes that comprised $\geq 1\%$ of the total catch in upper creek or creek mouth habitats ($H_0: \mu_1 - \mu_2 = 0$). Permutation tests rearrange the categorical labels (in this case “natural” or “armored”) associated with the experimental data values. Each possible rearrangement results in a new permutation, and a test statistic is computed for each of these new permutations. In the “exact” case used here, the test statistics for all possible permutations were determined. The proportion of

permutations that produced a test statistic greater than or equal to the experimental test statistic is the p-value (Anderson 2001; Berry et al. 2002; Tebbs and Bower 2003; Edgington 2011). The permutation tests in this study were implemented with the coin package (version 1.3-1) (Hothorn et al. 2006; Hothorn et al. 2008).

Species-specific mean lengths and length ranges were determined for all fishes. Due to the non-normality of the species-specific length data, exact Fisher-Pitman permutation tests were also used to compare differences in mean length between natural and armored creeks for fishes that comprised $\geq 1\%$ of the total catch in upper creek or creek mouth habitats ($H_0: \mu_1 - \mu_2 = 0$). Additionally, length frequency distribution plots were constructed for select species.

Diversity and Richness

The species-specific CPUE data were used to calculate Shannon diversity for all sampling events where at least one fish was collected (Shannon diversity is only defined when at least one individual is present) (Stevens 2009). Additionally, the number of species collected in the three trawl tows at each site were determined and standardized to richness by dividing by the number of tows performed (number species/tow). Separate general linear models were fit to the upper creek and creek mouth diversity and richness datasets. Creek type and group were categorical covariates in all four models and the interaction term was not included in any of the models based on model selection using AIC. Post-hoc analyses (using the emmeans package) were used to compare differences in diversity and richness between creek type and groups ($H_0: \mu_1 - \mu_2 = 0$).

Results

Environmental Parameters

The length of shoreline in armored creeks was much greater than that of the natural creeks (Table 1). The Group 1 and Group 2 natural creeks had 30 and 0% armored shoreline, respectively, compared to the 90 and 92% armored shoreline in the Group 1 and Group 2 armored creeks.

Upper Creek

Upper creeks ranged from 20 – 47 m wide at the locations of the sampling sites (Table 1). Temperature, dissolved oxygen, and pH were similar between natural and armored creeks within the same group (Table 2). The same trend was observed for salinity with one exception: salinity was slightly higher in the Group 1 natural creek than the Group 1 armored creek. Water depths at trawl locations (center channel) were over 1 m deeper on average in armored upper creeks than natural upper creeks, regardless of group (Table 2). The sloping shore profiles in natural creeks would make water depths even shallower on average than represented by this measurement in the channel.

Creek Mouth

Creek mouth widths ranged from 143 – 456 m at the locations of the sampling sites (Table 1). Temperature, salinity, dissolved oxygen, and pH were similar between natural and armored creeks within the same group (Table 2). Water depth was slightly deeper in the Group 1 armored creek mouth compared to that of the respective natural creek. The

opposite was observed for Group 2, where the natural creek mouth had slightly deeper water depths on average (Table 2).

Species Composition

Upper Creek

Estuarine residents (n = 11, e.g. naked goby *Gobiosoma bosc*), estuarine transients (n = 16, e.g. bay anchovy *Anchoa mitchilli*), and southern strays (n = 4, e.g. green goby *Microgobius thalassinus*) were all collected within upper creek habitats (Table 3). Seven of the eleven resident species (64%) were only collected in natural creeks, including mummichog *Fundulus heteroclitus*, oyster toadfish *Opsanus tau*, and striped blenny *Chasmodes bosquianus*. On the contrary, ten of the sixteen transient species (63%), such as Atlantic menhaden *Brevoortia tyrannus*, spot *Leiostomus xanthurus*, and Atlantic croaker *Micropogonias undulatus*, were found in both natural and armored creeks. Of the four southern stray species, two were collected solely in natural creeks (Creville jack *Caranx hippos* and *M. thalassinus*) and two were collected solely in armored creeks (spotfin mojarra *Eucinostomus argenteus* and skilletfish *Gobiesox strumosus*) (Table 3).

The NMDS analysis indicated there was some overlap in overall species composition between natural and armored creeks, though slight separation of natural and armored creek assemblages was evident along the second axis (Fig. 4a). Monte Carlo permutation tests indicated significance of the first ($p = 0.022$) and all canonical axes ($p = 0.002$) in the CCA, which also demonstrated some overlap in species composition (Fig. 5a). All canonical axes accounted for 17% of the total variation in the creek assemblage

data; however, only the first and second axes are discussed since they accounted for more than sixty percent of the total variation. The species-environmental correlations for the first (0.830) and second (0.762) canonical axes were strong, yet other environmental parameters not considered may be important in structuring these creek assemblages given the relatively small percentage of variance explained by all canonical axes in the analysis (McGarigal et al. 2000).

The percentage of armored shoreline explained the most sample variation along the first canonical axis, followed by the temperature and water depth gradients, respectively (Fig. 5a). The salinity gradient accounted for the most variation along the second canonical axis, and was not strongly associated with creek type (Fig. 5a).

Fundulus heteroclitus, *G. bosc*, *L. xanthurus*, *M. thalassinus*, *O. tau*, winter flounder *Pseudopleuronectes americanus*, and northern puffer *Sphoeroides maculatus* loaded most heavily onto the first canonical axis (Fig. 5b, Table 4). *Leiostomus xanthurus*, *P. americanus*, and *S. maculatus* positively loaded onto this axis and therefore were associated with the higher percentage of armored shoreline and deeper water depth portions of those gradients. The other four species negatively loaded onto the axis and were associated with the lower percentage of armored shoreline and shallower water depth portions of those respective gradients. Fourspine stickleback *Apeltes quadracus*, *F. heteroclitus*, inland silverside *Menidia beryllina*, and white perch *Morone americana* positively loaded (associated with lower salinity), and *O. tau*, summer flounder *Paralichthys dentatus*, and bluefish *Pomatomus saltatrix* negatively loaded (associated with higher salinity) onto the second canonical axis (Fig. 5b, Table 4).

Creek Mouth

Estuarine residents ($n = 8$, e.g. *G. bosc*), estuarine transients ($n = 24$, e.g. silver perch *Bairdiella chrysoura*), and southern strays ($n = 2$, e.g. Atlantic moonfish *Selene setapinnis*) were all collected within creek mouth habitats (Table 5). Six of the eight resident species (75%) and 14 of the 24 transient species (58%) were collected in both natural and armored creeks. The southern strays (*G. strumosus* and *S. setapinnis*) were collected solely in armored creeks (Table 5).

The large degree of sample overlap within the NMDS analysis indicated species composition was similar between natural and armored creeks (Fig. 4c). The CCA portrayed similar results, with samples from natural and armored creeks broadly overlapping in ordination space (Fig. 6a). However, Monte Carlo permutation tests indicated the first ($p = 0.222$) and all canonical axes ($p = 0.076$) in the CCA were not significant and thus are not discussed further.

Abundance and Length

Upper Creek

Of the 7249 fishes collected in this study, 3158 (44%) were collected in upper creek habitats. Overall CPUE was larger in the Group 1 natural creek than the Group 1 armored creek and did not differ between Group 2 creeks (Fig. 7, Table 6). Group 1 natural creek CPUE was larger than Group 2 natural creek CPUE. Armored creek CPUE did not differ between groups. (Fig. 7, Table 6).

Anchoa mitchilli was the most abundant species collected in natural and armored upper creeks (Table 3). The second and third most abundant species collected in natural

and armored upper creeks were *B. tyrannus* and *G. bosc* and *L. xanthurus* and *P. americanus*, respectively. CPUE for five of the nine species that composed $\geq 1\%$ of the total upper creek catch varied between natural and armored creeks. Those species were *Anchoa mitchilli*, *B. chrysoura*, *P. dentatus* (estuarine transients), *F. heteroclitus*, and *G. bosc* (estuarine residents), and all were more abundant in natural creeks than armored creeks (Table 3). Additionally, *B. chrysoura* and *F. heteroclitus* were only collected in natural creeks. *Brevoortia tyrannus*, *P. americanus*, *L. xanthurus*, and Atlantic croaker *Micropogonias undulatus* (all estuarine transients, though some *P. americanus* may reside year round in the estuary) CPUE did not differ between natural and armored creeks (Table 3).

Mean lengths of *A. mitchilli* and *P. dentatus* differed between natural and armored upper creeks (Fig. 8, Table 3). *Anchoa mitchilli* collected in natural creeks were slightly larger on average than those collected in armored creeks as individuals > 50 mm were collected more frequently in natural creeks. *Paralichthys dentatus* from natural creeks were smaller on average than those in armored creeks due to individuals < 246 mm being solely collected in natural creeks (Fig. 8, Table 3). Mean lengths for *B. tyrannus*, *P. americanus*, *L. xanthurus*, *G. bosc*, and *M. undulatus* were similar between natural and armored creeks, but the size range of fishes observed differed for some of these species. The smallest *B. tyrannus* and *P. americanus* were only collected in natural and armored creeks, respectively, and *Micropogonias undulatus* > 45 mm were not collected in armored creeks (Table 3).

Creek Mouth

Fifty-six percent of fishes ($n = 4091$) were collected in creek mouth habitat. Overall CPUE did not differ between natural and armored creeks or between groups (Fig. 7, Table 6). *Anchoa mitchilli* was the most abundant species collected regardless of creek type (Table 5). The second and third most abundant species collected in natural and armored creek mouths were *O. tau* and *M. menidia* and *B. chrysoura* and *G. bosc*, respectively. CPUE did not vary between natural and armored creeks for any of the eight species that composed $\geq 1\%$ of the total creek mouth catch (Table 5).

Mean lengths of *A. mitchilli* and *L. xanthurus* differed between natural and armored creek mouths (Fig. 9, Table 5). *Anchoa mitchilli* collected in natural creeks were slightly smaller on average than those collected in armored creeks due to fewer fish > 50 mm being collected in natural creeks. *Leiostomus xanthurus* were larger on average in natural creeks since individuals < 108 mm were only collected in armored creeks (Fig. 9, Table 5). Although mean lengths for *B. chrysoura*, *M. undulatus*, *M. menidia*, *P. dentatus*, and northern pipefish *Syngnathus fuscus* were similar in natural and armored creeks, the observed length ranges differed. Broader length ranges were observed in armored creeks for both *B. chrysoura* and *P. dentatus*. The largest *M. undulatus* and *S. fuscus* were only collected in armored creeks, whereas the largest *M. menidia* were only collected in natural creeks (Table 5).

Diversity and Richness

Upper Creek

Shannon diversity and richness were larger in natural creeks than armored creeks and did not differ between groups (Fig. 7, Table 6). Twenty-eight species were collected

in upper creek habitat. Twenty-five of the 28 species were collected in natural creeks and 16 of the 28 were collected in armored creeks. Twelve species, including *F. heteroclitus* and *M. menidia*, were unique to natural creeks and three species (black seabass *Centropristis striata*, *E. argenteus*, and *G. strumosus*) were unique to armored creeks (Table 3). Six of the twelve species unique to natural creeks were collected during more than one sampling event. Of the species unique to armored creeks, only one individual of each was collected.

Creek Mouth

Diversity and richness did not differ between natural and armored creek mouths or between groups (Fig. 7, Table 6). Of the 31 species collected at creek mouths, 22 were collected in natural creeks and 27 were collected in armored creeks. Four species were solely collected in natural creeks and nine were solely collected in armored creeks (Table 5). However, only one species each of those collected solely in natural or armored creeks was observed during more than one sampling event.

Discussion

The creation of lagoon complexes appeared to influence the structure of deep-subtidal fish assemblages within upper creeks, but not creek mouths. Though natural and armored upper creek fish assemblages were composed of many of the same fish species, certain resident fishes were only collected in the natural upper creeks. Further, overall abundance in Group 1 and diversity and richness (regardless of the group) were greater in natural upper creeks. These differences were likely driven by a combination of the deeper

waters and lack of connectivity with the marsh in armored upper creeks since various estuarine fishes rely on shallow waters and access to the marsh surface for reproduction, foraging, and predation refuge (Weinstein 1979; Weinstein et al. 1980; Middaugh et al. 1981; McIvor and Odum 1988; Hettler 1989; Minello et al. 2003; Potthoff and Allen 2003; Stevens et al. 2006; Peterson and Lowe 2009; Banikas and Thompson 2012; Allen et al. 2017). Conversely, the fact that creek mouth sampling sites were further from the shoreline in general, and that armored creek mouth fish assemblages inhabited relatively shallow water and were within close proximity to marsh habitat, likely accounted for the lack of differences in composition, abundance (overall and species-specific), diversity, and richness when compared to natural creek mouth assemblages.

To our knowledge only one other study has examined the influence of shoreline armoring on the structure of deep-water marsh creek fish assemblages. Bilkovic (2011) assessed the impact of dredging and associated modifications, such as shoreline armoring, on deeper-water fish assemblages in Virginia tidal creeks. Contrary to the findings here, shoreline armoring did not strongly influence the fish assemblages in dredged and undredged creeks, likely due to the similar water depths and percentages of armored shoreline in the creeks examined. Studies by Kornis et al. (2017) and Munsch et al. (2015a) also investigated the influence of shoreline armoring on fishes inhabiting deeper waters further from shore. Although these studies did not take place solely within marsh creek habitat, the observed fish assemblages were notably different between the natural and armored shorelines surveyed. Further, Maxted et al. (1997) determined dead end canals in Delaware and Maryland coastal bays, similar to the lagoon complexes studied here, had degraded benthic macroinvertebrate assemblages, lower dissolved

oxygen levels, higher sediment contaminant concentrations, and greater abundances of a pollution-tolerant polychaete worm compared to non-canal sites. Together, these studies support the notion that fish and invertebrate assemblages inhabiting deeper subtidal habitat are indeed influenced by shoreline armoring.

Contrary to deep-water assemblages, the influence of shoreline armoring on intertidal and shallow-subtidal fish assemblage structure has been regularly documented. Lowe and Peterson (2014) determined intact natural creeks and urbanized creeks in coastal Mississippi had dissimilar fish assemblages and that resident and transient species were differentially affected by shoreline armoring, as was observed in this study. Similarly, Bilkovic and Roggero (2008) documented diverse fish assemblages along natural or moderately altered shorelines compared to the few species observed along armored shorelines in heavily developed areas. Various other studies on intertidal and shallow-subtidal fish assemblages have also detected changes in species composition and reduced abundances and diversity along armored shorelines (Peterson et al. 2000; Balouskus and Targett 2016; Rudershausen et al. 2016; Torre and Targett 2016; Balouskus and Targett 2018; Rudershausen et al. 2018).

In this study, species-specific differences in abundance between natural and armored upper creeks were observed for estuarine resident and transient species, but residents appeared to be disproportionately influenced by shoreline armoring. A majority of estuarine residents, including *F. heteroclitus*, *G. bosc*, *M. menidia*, and *C. bosquianus*, were more abundant or only collected in natural upper creeks. This is not surprising given the reliance of these and other resident species on shallow salt marsh habitat and the lack of connectivity to this habitat in armored upper creeks. For example, *F. heteroclitus* occur

in shallow habitats and are particularly abundant in salt marshes where they deposit their eggs at the base of marsh grasses or in empty ribbed mussel *Geukensia demissa* shells (Able and Castagna 1975; Talbot and Able 1984; Yozzo and Smith 1998; Able and Hagan 2003; MacKenzie and Dionne 2008). Other studies have also documented decreased *F. heteroclitus* abundances (Rudershausen et al. 2016; Balouskus and Targett 2018; Rudershausen et al. 2018), biomass (Kornis et al. 2018), and productivity (Crum et al. 2018) along armored shorelines. In addition to the reliance of *F. heteroclitus* on the salt marsh for reproduction, the observed differences in abundance are likely also driven by the increased predation risk and decreased prey availability for *F. heteroclitus* in creeks with deeper waters and steeper banks (McIvor and Odum 1988; Banikas and Thompson 2012), such as those with armored shorelines.

Similar to *F. heteroclitus*, many other resident species are highly dependent on unaltered marsh creeks as habitat. Although there are likely resident and transient contingents (Able and Fahay 2010), all *M. menidia* rely on salt marsh grasses as a substrate to attach their eggs (Middaugh et al. 1981; Middaugh 1981) and have been shown to deposit eggs in greater densities along *Spartina* shorelines than armored shorelines (Balouskus and Targett 2012). *Gobiosoma bosc* and *C. bosquianus* also occupy shallow marsh habitats, including marsh creeks (Rountree and Able 1992a; Jivoff and Able 2001; Harding et al. 2020), thus explaining their greater abundance in natural upper creeks. In a study by Hendon et al. (2000), abundances of larval *G. bosc* were higher along natural shoreline compared to altered shoreline, demonstrating the importance of salt marsh habitat to various life stages of this species. Further, given the

high site fidelity exhibited by *G. bosc* and *C. bosquianus*, their absence or decreased abundances may be an indication of habitat degradation (Harding et al. 2020).

Proportionally fewer estuarine transients exhibited strong associations to natural upper creeks over armored upper creeks, perhaps in part due to their lesser dependence on marsh habitat or their ability to move greater distances than many resident fauna with smaller home ranges (Lotrich 1975; Able and Fahay 2010; Harding et al. 2020). However, certain transient species that forage within marsh creeks and along the marsh edge, including *A. mitchilli*, *B. chrysoura*, and *P. dentatus*, were more abundant in natural upper creeks than armored upper creeks (Kleypas and Dean 1983; Hettler 1989; Rountree and Able 1992b). The affinity for natural upper marsh creeks exhibited by estuarine residents and transients, specifically many common prey items (*A. mitchilli*, *F. heteroclitus*, *M. menidia*) and predatory species (*B. chrysoura*, *P. dentatus*), suggests that shoreline armoring could have unintended impacts on various components of the estuarine food web (Seitz et al. 2006; Munsch et al. 2017).

The mean lengths of a few transient species (*A. mitchilli*, *P. dentatus*, and *L. xanthurus*) differed between natural and armored creeks. Wedge et al. (2015) determined Gulf killifish *Fundulus grandis* and sailfin molly *Poecilia latipinna* were larger (longer and heavier) and in overall better condition (based on lengths, weights, liver somatic index, and caloric density) in natural creeks compared to urban creeks and attributed these differences to altered habitat and prey availability in the urban creeks (Weinstein et al. 2009). However, in this study, those species that exhibited differences in mean length were not always larger in natural creeks. For example in upper creek habitat, *A. mitchilli* were larger in natural creeks due to fewer large individuals in armored creeks, but *P.*

dentatus were smaller in natural creeks relative to armored creeks since smaller fishes were not present in armored creeks. Munsch et al. (2016) and Kornis et al. (2018) also observed smaller fishes in shallower waters and natural creeks, respectively. The shorter mean lengths observed for *P. dentatus* in natural upper creeks may be due to the shallow water refuge and expansive marsh nursery this habitat provides that armored upper creeks do not (Minello et al. 2003; Peterson and Lowe 2009), and may not necessarily equate to poorer fish condition in natural creeks. Since additional condition data were not collected in this study, and various explanations exist for the observed trends in mean length within upper creek and creek mouth habitats, it was difficult to definitively attribute differences in length directly to shoreline armoring.

It is evident that shoreline armoring can influence the structure of both shallow- and deep-water fish assemblages, yet shoreline armoring and other types of coastal land development can also result in functional changes to fish assemblages (Munsch et al. 2017; Dugan et al. 2018). Watershed urbanization and shoreline armoring impact fish reproduction (Limburg and Schmidt 1990; Hendon et al. 2000; Balouskus and Targett 2012), productivity (Crum et al. 2018), body condition (Krebs et al. 2014a; Lowe and Peterson 2015; Wedge and Anderson 2017), and foraging (Seitz et al. 2006; Lowe and Peterson 2015; Munsch et al. 2015b; Torre and Targett 2017). Further, these impacts are not exclusive to salt marsh estuarine environments or fishes. Impacts of urbanization have also been documented in mangrove habitat (Krebs et al. 2014a; Krebs et al. 2014b), fresh water lakes and streams (Beauchamp et al. 1994; Jennings et al. 1999; Wang et al. 2000; Wang et al. 2001; Scheuerell and Schindler 2004), and for various species of invertebrates (Maxted et al. 1997; Lerberg et al. 2000; Bilkovic et al. 2006; Seitz et al.

2006; Wang et al. 2012; Lowe and Peterson 2014), birds (DeLuca et al. 2004; Dugan and Hubbard 2006; Dugan et al. 2008), and the diamondback terrapin *Malaclemys terrapin* (Isdell et al. 2015).

Various studies have reported the occurrence of urbanization thresholds (e.g. the percentage of developed land), past which faunal assemblages are notably different (Limburg and Schmidt 1990; Wang et al. 1997; DeLuca et al. 2004; Holland et al. 2004; Bilkovic et al. 2006; Bilkovic and Roggero 2008). Although not directly determined in this study, a shoreline armoring threshold for the creeks in this system is suspected to lie above 30% armored shoreline given the Group 1 natural creek shoreline was 30% armored and supported an upper creek fish assemblage more similar to the Group 2 natural creek (with no armored shoreline) than the Group 1 or Group 2 armored creeks, which were 90 and 92% armored, respectively. However, thresholds can vary based on the urbanization metric used and the spatial scale observed. For example, in the James River, Virginia, marked changes in fish assemblages were observed when $\geq 68\%$ developed land was present within a 100 m buffer of a sampled site, but a much lower urbanization threshold, $\geq 23\%$ developed land, was detected for larger scale buffers of 200 and 1000 m (Bilkovic and Roggero 2008).

Similar to the large scale threshold observed in the aforementioned study, Holland et al. (2004) determined that structural alterations to South Carolina tidal creek faunal assemblages, and also functional changes in the corresponding food webs, were evident when watershed impervious land coverage reached 20 – 30%. However, even lower thresholds of 10 – 20% urban land or armored shoreline within a watershed have been observed to influence stream integrity (Booth and Jackson 1997), freshwater fish

assemblages (Limburg and Schmidt 1990; Wang et al. 1997), macrobenthic assemblages (Bilkovic et al. 2006), and marsh bird communities (DeLuca et al. 2004). Relationships between habitat coverage/complexity and the associated fauna have also been documented in seagrass (Pittman et al. 2004; Thistle et al. 2010; Boström et al. 2011) and intertidal marsh habitats (Minello and Rozas 2002; Kneib 2003). These studies highlight the importance of preserving natural land cover and shorelines, especially salt marshes within estuarine systems, as a way to negate cumulative impacts resulting from the continued urbanization of coastal areas (Peterson and Lowe 2009).

Even small patches of marsh and access to shallow waters can help to sustain abundant and diverse faunal assemblages (Minello and Rozas 2002; Partyka and Peterson 2008; Bilkovic et al. 2016; Rudershausen et al. 2016; Meyer and Posey 2019), including within highly urbanized estuaries (Grothues and Able 2020). These small, or even fragmented, stretches of marsh create connectivity between marsh patches and other estuarine habitats (Partyka and Peterson 2008; Baillie et al. 2015). Salt marshes located near armored shorelines may also subsidize these urbanized areas, offsetting the impacts of shoreline armoring on the local nekton assemblage (Seitz et al. 2006; Bilkovic 2011). Marsh shoreline subsidizing was hypothesized, at least in part, to explain the fish assemblage similarity at natural and armored creek mouths in this study, in addition to the shallow water depths and further proximity of the sampling site from shore (relative to upper creeks) observed in both creek types. Yet, the location and size of salt marsh patches within a seascape are essential components of their effectiveness in sustaining an unaltered state, as different patch locations promote varying levels of connectivity between habitats and different size salt marshes support variable nekton population

densities (Minello and Rozas 2002; Kneib 2003; Partyka and Peterson 2008; Meyer and Posey 2019). At the very least, stretches of unaltered shoreline should be incorporated into future costal development plans with careful consideration given to the location and size of the proposed natural extents.

Implications

A more comprehensive and sustainable alternative for preserving natural shoreline and preventing the cumulative impacts associated with habitat fragmentation, while also protecting coastal property, is the use of living shorelines (Bilkovic and Roggero 2008). Living shorelines rely on the natural resources that dominate a specific geographic area (e.g. salt marsh, oyster reefs, etc.) to create all or the majority of a shoreline stabilization structure, simultaneously protecting coastal property and permitting continued connectivity between terrestrial and aquatic environments (Bilkovic et al. 2016; Bilkovic et al. 2017). Coastal wetlands are innately capable of stabilizing shorelines (Gedan et al. 2011; Shepard et al. 2011) and the benefits of living shorelines to both nekton and humans are apparent. Living shorelines supported higher nekton abundances and diversity when compared to completely armored shorelines (e.g. bulkheads) (Balouskus and Targett 2016; Gittman et al. 2016a; Gittman et al. 2016b). Further, these natural stabilization structures have proved to be better coastal defenses against hurricanes than engineered bulkheads, and even cost less to maintain (Gittman et al. 2014; Smith et al. 2017; Smith et al. 2018).

Though living shorelines may not be suitable to achieve the goals of every costal protection project (Gedan et al. 2011), they should be used preferentially where possible

given the documented benefits to coastal ecosystems and property owners (Gittman et al. 2016a). Although progress has been made in recent years, further outreach to coastal property owners is needed to clearly convey the potential benefits of living shorelines over armored shorelines such as bulkheads, which are often thought to be superior coastal protection structures (Smith et al. 2017). Additional studies to assess the long-term resilience and impacts of living shorelines are also warranted (Bilkovic et al. 2016; Smith et al. 2020). In Barnegat Bay, living shorelines would greatly reduce the ecological impacts that have occurred and those that are expected to occur following the continued urbanization of the watershed (Conway and Lathrop 2005). Living shorelines should continue to be promoted as an alternative to armored shorelines in current and future coastal property protection projects in New Jersey (Rella et al. 2018), especially given the resiliency of intact coastal habitats to sea-level rise (Arkema et al. 2013).

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References

- Able, K.W., and M. Castagna. 1975. Aspects of undescribed reproductive behavior in *Fundulus heteroclitus* (Pisces: Cyprinodontae) from Virginia. *Chesapeake Science* 16: 282–284.
- Able, K.W., and M.P. Fahay. 1998. *The first year in the life of estuarine fishes in the middle Atlantic Bight*. New Brunswick: Rutgers University Press.
- Able, K.W., and M.P. Fahay. 2010. *Ecology of estuarine fishes: Temperate waters of the western North Atlantic*. Baltimore: Johns Hopkins University Press.
- Able, K.W., and S.M. Hagan. 2003. Impact of common reed *Phragmites australis* on essential fish habitat: Influence on reproduction, embryological development, and larval abundance of mummichog (*Fundulus heteroclitus*). *Estuaries* 26: 40–50.
- Able, K.W., D.M. Nemerson, R. Bush, and P. Light. 2001. Spatial variation in Delaware Bay (U.S.A.) marsh creek fish assemblages. *Estuaries* 24: 441–452.
- Allen, D.M., V. Ogburn-Matthews, and P.D. Kenny. 2017. Nekton use of flooded salt marsh and an assessment of intertidal creek pools as low-tide refuges. *Estuaries and Coasts* 40: 1450–1463.
- Anderson, M.J. 2001. Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 626–639.
- Arkema, K.K., G. Guannel, G. Verutes, S.A. Wood, A. Guerri, M. Ruckelshaus, P. Kareiva, M. Lacayo, and J.M. Silver. 2013. Coastal habitats shield people and property from sea-level rise and storms. *Nature Climate Change* 3: 913–918.
- Baillie, C.J., J.M. Fear, and F.J. Fodrie. 2015. Ecotone effects on seagrass and saltmarsh habitat use by juvenile nekton in a temperate estuary. *Estuaries and Coasts* 38: 1414–1430.

- Balouskus, R.G., and T.E. Targett. 2012. Egg deposition by Atlantic silverside, *Menidia menidia*: Substrate utilization and comparison of natural and altered shoreline type. *Estuaries and Coasts* 35: 1100–1109.
- Balouskus, R.G., and T.E. Targett. 2016. Fish and blue crab density along a riprap-sill-hardened shoreline: Comparisons with *Spartina* marsh and riprap. *Transactions of the American Fisheries Society* 145: 766–773.
- Balouskus, R.G., and T.E. Targett. 2018. Impact of armored shorelines on shore-zone fish density in a mid-Atlantic, USA, estuary: Modulation by hypoxia and temperature. *Estuaries and Coasts* 41: 144–158.
- Banikas, E.M., and J.S. Thompson. 2012. Predation risk experienced by mummichog, *Fundulus heteroclitus*, in intertidal and subtidal salt marsh habitats. *Estuaries and Coasts* 35: 1346–1352.
- Beauchamp, D.A., E.R. Byron, and W.A. Wurtsbaugh. 1994. Summer habitat use by littoral-zone fishes in Lake Tahoe and the effects of shoreline structures. *North American Journal of Fisheries Management* 14: 385–394.
- Berry, K.J., P.W. Mielke, and H.W. Mielke. 2002. The Fisher-Pitman Permutation Test: An attractive alternative to the F test. *Psychological Reports* 90: 495–502.
- Bilkovic, D.M. 2011. Response of tidal creek fish communities to dredging and coastal development pressures in a shallow-water estuary. *Estuaries and Coasts* 34: 129–147.
- Bilkovic, D.M., M. Mitchell, P. Mason, and K. Duhring. 2016. The role of living shorelines as estuarine habitat conservation strategies. *Coastal Management* 44: 161–174.
- Bilkovic, D.M., M.M. Mitchell, J.D. Toft, and M.K. La Peyre. 2017. A primer to living shorelines. In *Living shorelines: The science and management of nature-based coastal protection*, ed. D. M. Bilkovic, M.M. Mitchell, M.K. La Peyre, and J.D. Toft, 3–10. Boca Raton: CRC Press.
- Bilkovic, D.M., M. Roggero, C.H. Hershner, and K.H. Havens. 2006. Influence of land use on macrobenthic communities in nearshore estuarine habitats. *Estuaries and Coasts* 29: 1185–1195.

- Bilkovic, D.M., and M.M. Roggero. 2008. Effects of coastal development on nearshore estuarine nekton communities. *Marine Ecology Progress Series* 358: 27–39.
- Booth, D.B., and C.R. Jackson. 1997. Urbanization of aquatic systems: Degradation thresholds, stormwater detection, and the limits of mitigation. *Journal of the American Water Resources Association* 33: 1077–1090.
- Boström, C., S.J. Pittman, C. Simenstad, and R.T. Kneib. 2011. Seascape ecology of coastal biogenic habitats: Advances, gaps, and challenges. *Marine Ecology Progress Series* 427: 191–217.
- ter Braak, C.J.F., and P. Smilauer. 2012. *Canoco reference manual and user's guide: Software for ordination (version 5.0)*. New York: Microcomputer Power.
- Burnham, K.P., and D.R. Anderson. 2004. Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research* 33: 261–304.
- Charlier, R.H., M.C.P. Chaineux, and S. Morcos. 2005. Panorama of the history of coastal protection. *Journal of Coastal Research* 21: 79–111.
- Chizmadia, P.A., M.J. Kennish, and V.L. Otori. 1984. Physical description of Barnegat Bay. In *Ecology of Barnegat Bay, New Jersey*, ed. M.J. Kennish and R.A. Lutz, 1–28. New York: Springer-Verlag.
- Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–143.
- Comrey, A.L., and H.B. Lee. 2013. *A first course in factor analysis*. New York: Psychology Press.
- Conway, T.M., and R.G. Lathrop. 2005. Alternative land use regulations and environmental impacts: Assessing future land use in an urbanizing watershed. *Landscape and Urban Planning* 71: 1–15.
- Costanza, R., R. D'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, et al. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260.
- Costanza, R., R. de Groot, P. Sutton, S. van der Ploeg, S.J. Anderson, I. Kubiszewski, S. Farber, and R.K. Turner. 2014. Changes in the global value of ecosystem services.

Global Environmental Change 26: 152–158.

- Crum, K.P., R.G. Balouskus, and T.E. Targett. 2018. Growth and movements of mummichogs (*Fundulus heteroclitus*) along armored and vegetated estuarine shorelines. *Estuaries and Coasts* 41: 131–143.
- Defne, Z., and N.K. Ganju. 2015. Quantifying the residence time and flushing characteristics of a shallow, back-barrier estuary: Application of hydrodynamic and particle tracking models. *Estuaries and Coasts* 38: 1719–1734.
- DeLuca, W.V., C.E. Studds, L.L. Rockwood, and P.P. Marra. 2004. Influence of land use on the integrity of marsh bird communities of Chesapeake Bay, USA. *Wetlands* 24: 837–847.
- Desmond, J.S., J.B. Zedler, and G.D. Williams. 2000. Fish use of tidal creek habitats in two southern California salt marshes. *Ecological Engineering* 14: 233–252.
- Dugan, J.E., L. Airolidi, M.G. Chapman, S.J. Walker, and T. Schlacher. 2011. Estuarine and coastal structures: Environmental effects, a focus on shore and nearshore structures. In *Treatise on estuarine and coastal science*, ed. E. Wolanski and D.S. McLusky, 8: 17–41. Waltham: Academic Press.
- Dugan, J.E., K.A. Emery, M. Alber, C.R. Alexander, J.E. Byers, A.M. Gehman, N. McLenaghan, and S.E. Sojka. 2018. Generalizing ecological effects of shoreline armoring across soft sediment environments. *Estuaries and Coasts* 41: 180–196.
- Dugan, J.E., and D.M. Hubbard. 2006. Ecological responses to coastal armoring on exposed sandy beaches. *Shore & Beach* 74: 10–16.
- Dugan, J.E., D.M. Hubbard, I.F. Rodil, D.L. Revell, and S. Schroeter. 2008. Ecological effects of coastal armoring on sandy beaches. *Marine Ecology* 29: 160–170.
- Edgington, E.S. 2011. Randomization tests. In *International encyclopedia of statistical science*, ed. M. Lovric. Berlin: Springer.
- Garwood, J.A., D.M. Allen, M.E. Kimball, and K.M. Boswell. 2019. Site fidelity and habitat use by young-of-the-year transient fishes in salt marsh intertidal creeks. *Estuaries and Coasts* 42: 1387–1396.
- Gedan, K.B., M.L. Kirwan, E. Wolanski, E.B. Barbier, and B.R. Silliman. 2011. The

present and future role of coastal wetland vegetation in protecting shorelines: Answering recent challenges to the paradigm. *Climatic Change* 106: 7–29.

- Gittman, R.K., F.J. Fodrie, A.M. Popowich, D.A. Keller, J.F. Bruno, C.A. Currin, C.H. Peterson, and M.F. Piehler. 2015. Engineering away our natural defenses: An analysis of shoreline hardening in the US. *Frontiers in Ecology and the Environment* 13: 301–307.
- Gittman, R.K., C.H. Peterson, C.A. Currin, F.J. Fodrie, M.F. Piehler, and J.F. Bruno. 2016a. Living shorelines can enhance the nursery role of threatened estuarine habitats. *Ecological Applications* 26: 249–263.
- Gittman, R.K., A.M. Popowich, J.F. Bruno, and C.H. Peterson. 2014. Marshes with and without sills protect estuarine shorelines from erosion better than bulkheads during a Category 1 hurricane. *Ocean and Coastal Management* 102: 94–102.
- Gittman, R.K., S.B. Scyphers, C.S. Smith, I.P. Neylan, and J.H. Grabowski. 2016b. Ecological consequences of shoreline hardening: A meta-analysis. *BioScience* 66: 763–773.
- Grothues, T.M., and K.W. Able. 2020. Shoreline infrastructure degradation and increasing littoral naturalization accommodates juvenile fish and crab assemblages in heavily urbanized upper New York Harbor. *Restoration Ecology*. doi:10.1111/rec.13163
- Hampel, H., A. Cattrijsse, and M. Vincx. 2003. Tidal, diel and semi-lunar changes in the faunal assemblage of an intertidal salt marsh creek. *Estuarine, Coastal and Shelf Science* 56: 795–805.
- Harding, J.M., D.M. Allen, E.R. Haffey, and K.M. Hoffman. 2020. Site fidelity of oyster reef blennies and gobies in saltmarsh tidal creeks. *Estuaries and Coasts* 43: 409–423.
- Hendon, J.R., M.S. Peterson, and B.H. Comyns. 2000. Spatio-temporal distribution of larval *Gobiosoma bosc* in waters adjacent to natural and altered marsh-edge habitats of Mississippi coastal waters. *Bulletin of Marine Science* 66: 143–156.
- Hettler, W.F. 1989. Nekton use of regularly-flooded saltmarsh habitat in North Carolina, USA. *Marine Ecology Progress Series* 56: 111–118.

- Holland, A.F., D.M. Sanger, C.P. Gawle, S.B. Lerberg, M.S. Santiago, G.H.M. Riekerk, L.E. Zimmerman, and G.I. Scott. 2004. Linkages between tidal creek ecosystems and the landscape and demographic attributes of their watersheds. *Journal of Experimental Marine Biology and Ecology* 298: 151–178.
- Hothorn, T., K. Hornik, M.A. van de Wiel, and A. Zeileis. 2006. A lego system for conditional inference. *The American Statistician* 60: 257–263.
- Hothorn, T., K. Hornik, M.A. van de Wiel, and A. Zeileis. 2008. Implementing a class of permutation tests: The coin package. *Journal of Statistical Software* 28: 1–23.
- Isdell, R.E., R.M. Chambers, D.M. Bilkovic, and M. Leu. 2015. Effects of terrestrial-aquatic connectivity on an estuarine turtle. *Diversity and Distributions* 21: 643–653.
- Jennings, M.J., M.A. Bozek, G.R. Hatzenbeler, E.E. Emmons, and M.D. Staggs. 1999. Cumulative effects of incremental shoreline habitat modification on fish assemblages in north temperate lakes. *North American Journal of Fisheries Management* 19: 18–27.
- Jivoff, P., and K.W. Able. 2001. Characterization of the fish and selected decapods in Little Egg Harbor. *Journal of Coastal Research* 32: 178–196.
- Kauffman, G.J., and C. Cruz-Ortiz. 2012. Economic value of the Barnegat Bay watershed. Newark: University of Delaware.
- Kennish, M.J. 2001a. Coastal salt marsh systems in the U.S.: A review of anthropogenic impacts. *Journal of Coastal Research* 17: 731–748.
- Kennish, M.J. 2001b. Physical description of the Barnegat Bay-Little Egg Harbor estuarine system. *Journal of Coastal Research* 32: 13–27.
- Kennish, M.J. 2001c. Characterization of the Barnegat Bay-Little Egg Harbor Estuary and watershed. *Journal of Coastal Research* 32: 3–12.
- Kennish, M.J. 2016. Anthropogenic impacts. In *Encyclopedia of estuaries*, ed. M.J. Kennish, 29–35. Dordrecht: Springer Netherlands.
- Kimball, M.E., and K.W. Able. 2012. Tidal migrations of intertidal salt marsh creek nekton examined with underwater video. *Northeastern Naturalist* 19: 475–486.

- Kleypas, J., and J.M. Dean. 1983. Migration and feeding of the predatory fish, *Bairdiella chrysura* Lacépède, in an intertidal creek. *Journal of Experimental Marine Biology and Ecology* 72: 199–209.
- Kneib, R.T. 1997. The role of tidal marshes in the ecology of estuarine nekton. *Oceanography and marine biology: An annual review* 35: 163–220.
- Kneib, R.T. 2003. Bioenergetic and landscape considerations for scaling expectations of nekton production from intertidal marshes. *Marine Ecology Progress Series* 264: 279–296.
- Kornis, M.S., D.M. Bilkovic, L.A. Davias, S. Giordano, and D.L. Breitburg. 2018. Shoreline hardening affects nekton biomass, size structure, and taxonomic diversity in nearshore waters, with responses mediated by functional species groups. *Estuaries and Coasts* 41: 159–179.
- Kornis, M.S., D. Breitburg, R. Balouskus, D.M. Bilkovic, L.A. Davias, S. Giordano, K. Heggie, et al. 2017. Linking the abundance of estuarine fish and crustaceans in nearshore waters to shoreline hardening and land cover. *Estuaries and Coasts* 40: 1464–1486.
- Krebs, J.M., S.S. Bell, and C.C. McIvor. 2014a. Assessing the link between coastal urbanization and the quality of nekton habitat in mangrove tidal tributaries. *Estuaries and Coasts* 37: 832–846.
- Krebs, J.M., C.C. McIvor, and S.S. Bell. 2014b. Nekton community structure varies in response to coastal urbanization near mangrove tidal tributaries. *Estuaries and Coasts* 37: 815–831.
- Lathrop, R.G., and J.A. Bognar. 2001. Habitat loss and alteration in the Barnegat Bay region. *Journal of Coastal Research* 32: 212–228.
- Lenth, R. 2020. emmeans: Estimated marginal means, aka least-squares means. R package version 1.4.6. <https://CRAN.R-project.org/package=emmeans>.
- Lerberg, S.B., A.F. Holland, and D.M. Sanger. 2000. Responses of tidal creek macrobenthic communities to the effects of watershed development. *Estuaries* 23: 838–853.
- Limburg, K.E., and R.E Schmidt. 1990. Patterns of fish spawning in Hudson River

- tributaries: Response to an urban gradient? *Ecology* 71: 1238–1245.
- Lotrich, V.A. 1975. Summer home range and movements of *Fundulus heteroclitus* (Pisces: Cyprinodontidae) in a tidal creek. *Ecology* 56: 191–198.
- Lotze, H.K., H.S. Lenihan, B.J. Bourque, R.H. Bradbury, G. Cooke, M.C. Kay, S.M. Kidwell, M.X. Kirby, C.H. Peterson, and J.B.C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312: 1806–1809.
- Lowe, M.R., and M.S. Peterson. 2014. Effects of coastal urbanization on salt-marsh faunal assemblages in the northern Gulf of Mexico. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 6: 89–107.
- Lowe, M.R., and M.S. Peterson. 2015. Body condition and foraging patterns of nekton from salt marsh habitats arrayed along a gradient of urbanization. *Estuaries and Coasts* 38: 800–812.
- MacKenzie, R.A., and M. Dionne. 2008. Habitat heterogeneity: Importance of salt marsh pools and high marsh surfaces to fish production in two Gulf of Maine salt marshes. *Marine Ecology Progress Series* 368: 217–230.
- Mallin, M.A., and A.J. Lewitus. 2004. The importance of tidal creek ecosystems. *Journal of Experimental Marine Biology and Ecology* 298: 145–149.
- Maxted, J.R., S.B. Weisberg, J.C. Chaillou, R.A. Eskin, and F.W. Kutz. 1997. The ecological condition of dead-end canals of the Delaware and Maryland coastal bays. *Estuaries* 20: 319–327.
- McGarigal, K., S. Cushman, and S. Stafford. 2000. *Multivariate statistics for wildlife and ecology research*. New York: Springer-Verlag.
- McIvor, C.C., and W.E. Odum. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. *Ecology* 69: 1341–1351.
- Meyer, D.L., and M.H. Posey. 2019. Salt marsh habitat size and location do matter: The influence of salt marsh size and landscape setting on nekton and estuarine finfish community structure. *Estuaries and Coasts* 42: 1353–1373.
- Micheli, F., and C.H. Peterson. 1999. Estuarine vegetated habitats as corridors for

- predator movements. *Conservation Biology* 13: 869–881.
- Middaugh, D.P. 1981. Reproductive ecology and spawning periodicity of the Atlantic silverside, *Menidia menidia* (Pisces: Atherinidae). *Copeia* 1981: 766–776.
- Middaugh, D.P., G.I. Scott, and J.M. Dean. 1981. Reproductive behavior of the Atlantic silverside, *Menidia menidia* (Pisces, Atherinidae). *Environmental Biology of Fishes* 6: 269–276.
- Minello, T.J., K.W. Able, M.P. Weinstein, and C.G. Hays. 2003. Salt marshes as nurseries for nekton: Testing hypothesis on density, growth and survival through meta-analysis. *Marine Ecology Progress Series* 246: 39–59.
- Minello, T.J., and L.P. Rozas. 2002. Nekton in Gulf Coast wetlands: Fine-scale distributions, landscape patterns, and restoration implications. *Ecological Applications* 12: 441–455.
- Munsch, S.H., J.R. Cordell, and J.D. Toft. 2015a. Effects of shoreline engineering on shallow subtidal fish and crab communities in an urban estuary: A comparison of armored shorelines and nourished beaches. *Ecological Engineering* 81: 312–320.
- Munsch, S.H., J.R. Cordell, and J.D. Toft. 2015b. Effects of seawall armoring on juvenile Pacific salmon diets in an urban estuarine embayment. *Marine Ecology Progress Series* 535: 213–229.
- Munsch, S.H., J.R. Cordell, and J.D. Toft. 2016. Fine-scale habitat use and behavior of a nearshore fish community: Nursery functions, predation avoidance, and spatiotemporal habitat partitioning. *Marine Ecology Progress Series* 557: 1–15.
- Munsch, S.H., J.R. Cordell, and J.D. Toft. 2017. Effects of shoreline armouring and overwater structures on coastal and estuarine fish: Opportunities for habitat improvement. *Journal of Applied Ecology* 54: 1373–1384.
- Nagelkerken, I., M. Sheaves, R. Baker, and R.M. Connolly. 2015. The seascape nursery: A novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries* 16: 362–371.
- New Jersey Office of Information Technology. 2013. New Jersey 2012 - 2013 high resolution orthophotography, NAD83 NJ state plane feet, MrSID tiles. Trenton: Office of Geographic Information Systems.

- Newton, A., J. Icely, S. Cristina, G. Perillo, R.E. Turner, D. Ahsan, S. Cragg, et al. 2020. Anthropogenic, direct pressures on coastal wetlands. *Frontiers in Ecology and Evolution*. doi:10.3389/fevo.2020.00144
- Nicholls, R.J., and C. Small. 2002. Improved estimates of coastal population and exposure to hazards released. *Eos, Transactions American Geophysical Union* 83: 301–305.
- Oksanen, J., F.G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P.R. Minchin, et al. 2019. vegan: Community ecology package. R package version 2.5-6. <https://CRAN.R-project.org/package=vegan>.
- Olin, M., and T. Malinen. 2003. Comparison of gillnet and trawl in diurnal fish community sampling. *Hydrobiologia* 506–509: 443–449.
- Partyka, M.L., and M.S. Peterson. 2008. Habitat quality and salt-marsh species assemblages along an anthropogenic estuarine landscape. *Journal of Coastal Research* 24: 1570–1581.
- Peterson, M.S., B.H. Comyns, J.R. Hendon, P.J. Bond, and G.A. Duff. 2000. Habitat use by early life-history stages of fishes and crustaceans along a changing estuarine landscape: Differences between natural and altered shoreline sites. *Wetlands Ecology and Management* 8: 209–219.
- Peterson, M.S., and M.R. Lowe. 2009. Implications of cumulative impacts to estuarine and marine habitat quality for fish and invertebrate resources. *Reviews in Fisheries Science* 17: 505–523.
- Pittman, S.J., C.A. McAlpine, and K.M. Pittman. 2004. Linking fish and prawns to their environment: A hierarchical landscape approach. *Marine Ecology Progress Series* 283: 233–254.
- Potthoff, M.T., and D.M. Allen. 2003. Site fidelity, home range, and tidal migrations of juvenile pinfish, *Lagodon rhomboides*, in salt marsh creeks. *Environmental Biology of Fishes* 67: 231–240.
- Rella, A., J. Miller, and E. Hauser. 2018. An overview of the living shorelines initiative in New York and New Jersey. In *Living shorelines: The science and management of nature-based coastal protection*, ed. D.M. Bilkovic, M.M. Mitchell, M.K. La Peyre,

- and J.D. Toft, 65–86. Boca Raton: CRC Press.
- Rountree, R.A., and K.W. Able. 1992a. Fauna of polyhaline subtidal marsh creeks in southern New Jersey: Composition, abundance and biomass. *Estuaries* 15: 171–185.
- Rountree, R.A., and K.W. Able. 1992b. Foraging habits, growth, and temporal patterns of salt-marsh creek habitat use by young-of-year summer flounder in New Jersey. *Transactions of the American Fisheries Society* 121: 765–776.
- Rountree, R.A., and K.W. Able. 2007. Spatial and temporal habitat use patterns for salt marsh nekton: Implications for ecological functions. *Aquatic Ecology* 41: 25–45.
- RStudio Team. 2019. RStudio: Integrated development for R. Boston: RStudio, Inc. <http://www.rstudio.com/>.
- Rudershausen, P.J., J.A. Buckel, M.A. Dueker, S.J. Poland, and E. Hain. 2016. Comparison of fish and invertebrate assemblages among variably altered tidal creeks in a coastal landscape. *Marine Ecology Progress Series* 544: 15–35.
- Rudershausen, P.J., J.H. Merrell, and J.A. Buckel. 2018. Fragmentation of habitat affects communities and movement of nekton in salt marsh tidal creeks. *Marine Ecology Progress Series* 586: 57–72.
- Scheuerell, M.D., and D.E. Schindler. 2004. Changes in the spatial distribution of fishes in lakes along a residential development gradient. *Ecosystems* 7: 98–106.
- Seitz, R.D., R.N. Lipcius, N.H. Olmstead, M.S. Seebo, and D.M. Lambert. 2006. Influence of shallow-water habitats and shoreline development on abundance, biomass, and diversity of benthic prey and predators in Chesapeake Bay. *Marine Ecology Progress Series* 326: 11–27.
- Sheaves, M. 2009. Consequences of ecological connectivity: The coastal ecosystem mosaic. *Marine Ecology Progress Series* 391: 107–115.
- Sheaves, M., R. Baker, I. Nagelkerken, and R.M. Connolly. 2015. True value of estuarine and coastal nurseries for fish: Incorporating complexity and dynamics. *Estuaries and Coasts* 38: 401–414.
- Shepard, C.C., C.M. Crain, and M.W. Beck. 2011. The protective role of coastal marshes: A systematic review and meta-analysis. *PLoS ONE* 6: e27374.

- Smith, C.S., R.K. Gittman, I.P. Neylan, S.B. Scyphers, J.P. Morton, F. Joel Fodrie, J.H. Grabowski, and C.H. Peterson. 2017. Hurricane damage along natural and hardened estuarine shorelines: Using homeowner experiences to promote nature-based coastal protection. *Marine Policy* 81: 350–358.
- Smith, C.S., B. Puckett, R.K. Gittman, and C.H. Peterson. 2018. Living shorelines enhanced the resilience of saltmarshes to Hurricane Matthew (2016). *Ecological Applications* 28: 871–877.
- Smith, C.S., M.E. Rudd, R.K. Gittman, E.C. Melvin, V.S. Patterson, J.J. Renzi, E.H. Wellman, and B.R. Silliman. 2020. Coming to terms with living shorelines: A scoping review of novel restoration strategies for shoreline protection. *Frontiers in Marine Science*. doi:10.3389/fmars.2020.00434
- Stevens, M.H.H. 2009. *A primer of ecology with R*. New York: Springer Science & Business Media.
- Stevens, P.W., C.L. Montague, and K.J. Sulak. 2006. Fate of fish production in a seasonally flooded saltmarsh. *Marine Ecology Progress Series* 327: 267–277.
- Sugihara, T., C. Yearsley, J.B. Durand, and N.P. Psuty. 1979. Comparison of natural and altered estuarine systems: Analysis. New Brunswick: Center for Coastal and Environmental Studies.
- Talbot, C.W., and K.W. Able. 1984. Composition and distribution of larval fishes in New Jersey high marshes. *Estuaries* 7: 434–443.
- Tatham, T.R., D.J. Danila, and D.L. Thomas. 1984. Fishes of Barnegat Bay. In *Ecology of Barnegat Bay, New Jersey*, ed. M.J. Kennish and R.A. Lutz, 241–280. New York: Springer-Verlag.
- Tebbs, J.M., and K.M. Bower. 2003. Some comments on the robustness of student t procedures. *Journal of Engineering Education* 92: 91–94.
- Thistle, M.E., D.C. Schneider, R.S. Gregory, and N.J. Wells. 2010. Fractal measures of habitat structure: Maximum densities of juvenile cod occur at intermediate eelgrass complexity. *Marine Ecology Progress Series* 405: 39–56.
- Torre, M.P., and T.E. Targett. 2016. Nekton assemblages along riprap-altered shorelines

- in Delaware Bay, USA: Comparisons with adjacent beach. *Marine Ecology Progress Series* 548: 209–218.
- Torre, M.P., and T.E. Targett. 2017. Feeding by bluefish and weakfish along riprap-hardened shorelines: Comparisons with adjacent sandy beach in Delaware Bay, USA. *Transactions of the American Fisheries Society* 146: 341–348.
- Valenti, J.L., T.M. Grothues, and K.W. Able. 2017. Estuarine fish communities along a spatial urbanization gradient. *Journal of Coastal Research* 78: 254–268.
- Wang, B., D. Liu, S. Liu, Y. Zhang, D. Lu, and L. Wang. 2012. Impacts of urbanization on stream habitats and macroinvertebrate communities in the tributaries of Qiangtang River, China. *Hydrobiologia* 680: 39–51.
- Wang, L., J. Lyons, P. Kanehi, R. Bannerman, and E. Emmons. 2000. Watershed urbanization and changes in fish communities in southeastern Wisconsin streams. *Journal of the American Water Resources Association* 36: 1173–1189.
- Wang, L., J. Lyons, and P. Kanehl. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. *Environmental Management* 28: 255–266.
- Wang, L., J. Lyons, P. Kanehl, and R. Gatti. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. *Fisheries* 22: 6–12.
- Wedge, M., and C.J. Anderson. 2017. Urban land use affects resident fish communities and associated salt marsh habitat in Alabama and west Florida, USA. *Wetlands* 37: 715–727.
- Wedge, M., C.J. Anderson, and D. DeVries. 2015. Evaluating the effects of urban land use on the condition of resident salt marsh fish. *Estuaries and Coasts* 38: 2355–2365.
- Weinstein, M.P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. *Fishery Bulletin* 77: 339–357.
- Weinstein, M.P., and H.A. Brooks. 1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: Community composition and structure. *Marine Ecology Progress Series* 12: 15–27.
- Weinstein, M.P., S.Y. Litvin, and V.G. Guida. 2009. Essential fish habitat and wetland

restoration success: A tier III approach to the biochemical condition of common mummichog *Fundulus heteroclitus* in common reed *Phragmites australis*- and smooth cordgrass *Spartina alterniflora*-dominated salt marshes. *Estuaries and Coasts* 32: 1011–1022.

Weinstein, M.P., S.L. Weiss, and M.F. Walters. 1980. Multiple determinants of community structure in shallow marsh habitats, Cape Fear River Estuary, North Carolina, USA. *Marine Biology* 58: 227–243.

Whitfield, A., and M. Elliott. 2011. Ecosystem and biotic classifications of estuaries and coasts. In *Treatise on estuarine and coastal science*, ed. E. Wolanski and D.S. McLusky, 1: 99–124. Waltham: Academic Press.

Wilson, J.G. 2002. Productivity, fisheries and aquaculture in temperate estuaries. *Estuarine, Coastal and Shelf Science* 55: 953–967.

Yozzo, D.J., and D.E. Smith. 1998. Composition and abundance of resident marsh-surface nekton: Comparison between tidal freshwater and salt marshes in Virginia, USA. *Hydrobiologia* 362: 9–19.

Tables

Table 1. Shoreline characteristics of the natural and armored creeks sampled. Widths represent the shortest distance from bank to bank through the sampling site, with the exception of the natural creek mouth in Group 1 where sampling occurred just outside the creek mouth due to insufficient water depth for trawling in the mouth proper. See Fig. 1 for the locations of each creek within Barnegat Bay and Fig. 2 and 3 for aerial images with shoreline classifications

	Group 1		Group 2	
	Natural	Armored	Natural	Armored
Total Shoreline (m)	2233	23982	2333	13946
Natural Shoreline (%)	70	10	100	8
Armored Shoreline (%)	30	90	0	92
Upper Width (m)	20	38	47	30
Mouth Width (m)	143	357	456	266

Table 2. Number of sampling events and environmental parameters (mean \pm standard error) at each sampling site

	Upper Creek				Creek Mouth			
	Group 1		Group 2		Group 1		Group 2	
	Natural	Armored	Natural	Armored	Natural	Armored	Natural	Armored
Sampling Events	12	12	12	12	11	12	12	12
Temperature ($^{\circ}\text{C}$)	20.6 ± 1.4	20.6 ± 1.3	20.6 ± 1.7	19.9 ± 1.4	20.1 ± 1.7	20.2 ± 1.5	20.0 ± 1.5	19.9 ± 1.5
Salinity	21.58 ± 0.64	19.33 ± 0.51	21.58 ± 0.98	21.91 ± 0.85	21.60 ± 0.76	20.53 ± 0.54	21.28 ± 1.08	21.81 ± 0.93
Dissolved Oxygen (mg/L)	5.07 ± 0.48	4.85 ± 0.60	6.21 ± 0.67	5.80 ± 0.77	7.02 ± 0.35	6.84 ± 0.38	6.51 ± 0.63	6.51 ± 0.52
pH	7.56 ± 0.08	7.42 ± 0.07	7.58 ± 0.05	7.53 ± 0.08	7.85 ± 0.06	7.79 ± 0.06	7.67 ± 0.07	7.63 ± 0.06
Water Depth (m)	1.2 ± 0.1	2.3 ± 0.1	1.2 ± 0.0	2.3 ± 0.1	1.2 ± 0.1	1.6 ± 0.0	1.6 ± 0.0	1.3 ± 0.0

Table 3. Species-specific mean catch-per-unit-effort (CPUE) (\pm standard error) and mean length (\pm standard error; range in parentheses) for all fishes collected in natural and armored upper creeks. Differences in mean CPUE and mean length were only tested for species that composed $\geq 1\%$ of the total catch. Superscripts denote species collected solely in natural creeks (*) and armored creeks (**) and those measured as fork length (\dagger) (all others were measured as total length). Species were classified by estuarine usage (T = transient, R = resident, SS = Southern Stray) following Tatham et al. (1984) and Able and Fahay (2010)

	Estuarine Usage	% of Total	CPUE (fish/s)			Length (mm)		
			Natural	Armored	p	Natural	Armored	p
<i>Anchoa mitchilli</i> [†]	T	73	0.422 \pm 0.067	0.217 \pm 0.059	0.026	42.8 \pm 0.6 (18 – 98)	36.8 \pm 0.7 (20 – 80)	< 0.001
<i>Brevoortia tyrannus</i> [†]	T	11	0.162 \pm 0.049	0.075 \pm 0.029	0.139	58.0 \pm 1.4 (20 – 112)	57.7 \pm 2.6 (39 – 111)	0.928
<i>Pseudopleuronectes americanus</i>	T/R	5	0.032 \pm 0.018	0.082 \pm 0.039	0.239	62.4 \pm 8.2 (39 – 86)	56.6 \pm 1.1 (22 – 89)	0.210
<i>Leiostomus xanthurus</i> [†]	T	4	0.118 \pm 0.033	0.109 \pm 0.037	0.857	114.3 \pm 3.8 (32 – 155)	119.6 \pm 3.3 (25 – 160)	0.295
<i>Fundulus heteroclitus</i> *	R	2	0.081 \pm 0.034	0.000 \pm 0.000	0.050	52.6 \pm 1.5 (36 – 74)		-
<i>Gobiosoma bosc</i>	R	2	0.140 \pm 0.033	0.036 \pm 0.021	0.011	36.6 \pm 1.1 (25 – 56)	41.0 \pm 1.8 (29 – 49)	0.076
<i>Bairdiella chrysoura</i> *	T	1	0.093 \pm 0.028	0.000 \pm 0.000	0.004	61.9 \pm 6.6 (20 – 125)		-
<i>Micropogonias undulatus</i>	T	1	0.041 \pm 0.023	0.054 \pm 0.022	0.685	33.8 \pm 5.3 (18 – 112)	32.1 \pm 2.3 (24 – 45)	0.904
<i>Paralichthys dentatus</i>	T	1	0.114 \pm 0.026	0.031 \pm 0.017	0.016	181.8 \pm 10.7 (98 – 267)	274.8 \pm 10.6 (246 – 295)	0.001
<i>Anguilla rostrata</i>	T	<1	0.032 \pm 0.018	0.019 \pm 0.013		543.0 \pm 45.4 (420 – 680)	395.0 \pm 124.0 (271 – 519)	
<i>Apeltes quadracus</i> *	R	<1	0.010 \pm 0.010	0.000 \pm 0.000		57.0		
<i>Caranx hippos</i> * [†]	SS	<1	0.010 \pm 0.010	0.000 \pm 0.000		86.0		
<i>Centropristis striata</i> **	T	<1	0.000 \pm 0.000	0.010 \pm 0.010			141.0	
<i>Chasmodes bosquianus</i> *	R	<1	0.023 \pm 0.016	0.000 \pm 0.000		47.0 \pm 5.8 (30 – 55)		
<i>Cynoscion regalis</i>	T	<1	0.013 \pm 0.013	0.010 \pm 0.010		75.3 \pm 4.9 (69 – 85)	162.0	
<i>Eucinostomus argenteus</i> ** [†]	SS	<1	0.000 \pm 0.000	0.010 \pm 0.010			64.0	
<i>Gobiosoma strumosus</i> **	SS	<1	0.000 \pm 0.000	0.010 \pm 0.010			60.0	
<i>Gobiosoma ginsburgi</i> *	T/R	<1	0.013 \pm 0.013	0.000 \pm 0.000		28.7 \pm 2.9 (24 – 34)		

Table 3 continued

	Estuarine Usage	% of Total	CPUE (fish/s)			Length (mm)		
			Natural	Armored	p	Natural	Armored	p
<i>Menidia beryllina</i> *†	R	<1	0.013 ± 0.013	0.000 ± 0.000		52.0 ± 2.5 (49 – 57)		
<i>Menidia menidia</i> *†	T/R	<1	0.032 ± 0.018	0.000 ± 0.000		93.6 ± 7.8 (63 – 105)		
<i>Microgobius thalassinus</i> *	SS	<1	0.029 ± 0.016	0.000 ± 0.000		43.0 ± 3.0 (40 – 46)		
<i>Morone americana</i> †	R	<1	0.010 ± 0.010	0.011 ± 0.011		226.0	221.5 ± 8.5 (213 – 230)	
<i>Opsanus tau</i> *	R	<1	0.042 ± 0.020	0.000 ± 0.000		105.5 ± 18.9 (39 – 160)		
<i>Pogonias cromis</i> *	T	<1	0.010 ± 0.010	0.000 ± 0.000		232.0		
<i>Pomatomus saltatrix</i> †	T	<1	0.056 ± 0.023	0.029 ± 0.016		140.5 ± 12.5 (78 – 207)	146.3 ± 33.5 (83 – 197)	
<i>Prionotus carolinus</i> *	T	<1	0.010 ± 0.010	0.000 ± 0.000		41.0		
<i>Sphoeroides maculatus</i>	T	<1	0.013 ± 0.013	0.011 ± 0.011		19.3 ± 1.8 (16 – 22)	24.0 ± 0.0 (24 – 24)	
<i>Trinectes maculatus</i>	R	<1	0.061 ± 0.022	0.010 ± 0.010		70.0 ± 8.4 (45 – 110)	135.0	

Table 4. Canonical correspondence analysis (CCA) species loadings for the first two canonical axes of the upper creek CCA and creek mouth CCA. Loadings in **bold** were those considered noteworthy for discussion (see “Data Analyses: Species Composition” section). All abbreviated names, which were used in the NMDS and CCA plots (see Fig. 4, 5, and 6), are listed in conjunction with full scientific and common names

Scientific Name	Common Name	NMDS and CCA	Upper Creek		Creek Mouth	
			Axis 1	Axis 2	Axis 1	Axis 2
<i>Anchoa hepsetus</i>	Striped anchovy	Anchep			-0.288	-0.057
<i>Anchoa mitchilli</i>	Bay anchovy	Ancmit	-0.081	-0.128	-0.592	-0.246
<i>Anguilla rostrata</i>	American eel	Angros	0.154	0.061	0.198	0.536
<i>Apeltes quadracus</i>	Fourspine stickleback	Apequa	-0.275	0.708	0.133	0.326
<i>Bairdiella chrysoura</i>	Silver perch	Baichr	-0.292	-0.286	-0.419	-0.115
<i>Brevoortia tyrannus</i>	Atlantic menhaden	Bretyr	0.142	-0.167	-0.274	0.049
<i>Caranx hippos</i>	Crevalle jack	Carhip	-0.195	-0.182		
<i>Centropristis striata</i>	Black seabass	Censtr	0.277	0.076	-0.020	-0.141
<i>Chasmodes bosquianus</i>	Striped blenny	Chabos	-0.151	0.002	-0.088	0.254
<i>Chilomycterus schoepfi</i>	Striped burrfish	Chisch			-0.110	-0.101
<i>Clupea harengus</i>	Atlantic herring	Cluhar			0.255	-0.296
<i>Cynoscion regalis</i>	Weakfish	Cynreg	0.049	-0.151	-0.131	-0.018
<i>Eucinostomus argenteus</i>	Spotfin mojarra	Eucarg	0.070	-0.095		
<i>Fundulus heteroclitus</i>	Mummichog	Funhet	-0.330	0.471		
<i>Gobiosox strumosus</i>	Skilletfish	Gobstr	0.007	0.059	-0.010	0.095
<i>Gobiosoma bosc</i>	Naked goby	Gobbos	-0.561	0.101	-0.184	0.161
<i>Gobiosoma ginsburgi</i>	Seaboard goby	Gobgin	-0.084	-0.135		
<i>Hypsoblennius hentz</i>	Feather blenny	Hyphen			-0.033	-0.203
<i>Lagodon rhomboides</i>	Pinfish	Lagrho			-0.176	0.248

Table 4 continued

Scientific Name	Common Name	NMDS and CCA	Upper Creek		Creek Mouth	
			Axis 1	Axis 2	Axis 1	Axis 2
<i>Leiostomus xanthurus</i>	Spot	Leixan	0.335	-0.074	-0.426	-0.144
<i>Menidia beryllina</i>	Inland silverside	Menber	-0.275	0.708		
<i>Menidia menidia</i>	Atlantic silverside	Menmen	-0.307	0.170	0.482	-0.149
<i>Menticirrhus saxatilis</i>	Northern kingfish	Mensax			0.007	-0.483
<i>Microgobius thalassinus</i>	Green goby	Mictha	-0.367	0.056		
<i>Micropogonias undulatus</i>	Atlantic croaker	Micund	0.008	0.131	-0.251	-0.155
<i>Morone americana</i>	White perch	Morame	-0.033	0.609		
<i>Mugil curema</i>	White mullet	Mugcur			-0.225	-0.019
<i>Opsanus tau</i>	Oyster toadfish	Opstau	-0.332	-0.400	-0.020	0.366
<i>Paralichthys dentatus</i>	Summer flounder	Parden	-0.290	-0.369	-0.114	-0.174
<i>Pogonias cromis</i>	Black drum	Pogcro	-0.169	-0.232		
<i>Pollachius virens</i>	Pollock	Polvir			0.538	0.172
<i>Pomatomus saltatrix</i>	Bluefish	Pomsal	-0.067	-0.349	-0.245	0.160
<i>Prionotus carolinus</i>	Northern searobin	Pricar	-0.057	-0.002		
<i>Pseudopleuronectes americanus</i>	Winter flounder	Pseame	0.636	0.190	0.103	-0.049
<i>Scophthalmus aquosus</i>	Windowpane	Scoaqu			0.394	-0.322
<i>Selene setapinnis</i>	Atlantic moonfish	Selset			-0.147	-0.097
<i>Sphoeroides maculatus</i>	Northern puffer	Sphmac	0.398	0.006	-0.149	-0.356
<i>Syngnathus fuscus</i>	Northern pipefish	Synfus			0.277	-0.050
<i>Tautoga onitis</i>	Tautog	Tauoni			-0.125	0.058
<i>Trinectes maculatus</i>	Hogchoker	Trimac	-0.206	-0.314		
<i>Urophycis regia</i>	Spotted hake	Uroreg			0.234	0.010

Table 5. Species-specific mean catch-per-unit-effort (CPUE) (\pm standard error) and mean length (\pm standard error; range in parentheses) for all fishes collected in natural and armored creek mouths. Differences in mean CPUE and mean length were only tested for species that composed $\geq 1\%$ of the total catch. Superscripts denote species collected solely in natural (*) and armored (**) creeks and those measured as fork length (\dagger) (all others were measured as total length). Species were classified by estuarine usage (T = transient, R = resident, SS = Southern Stray) following Tatham et al. (1984) and Able and Fahay (2010)

	Estuarine Usage	% of Total	CPUE (fish/s)			Length (mm)		
			Natural	Armored	p	Natural	Armored	p
<i>Anchoa mitchilli</i> [†]	T	88	0.292 \pm 0.070	0.407 \pm 0.076	0.274	36.1 \pm 0.6 (16 – 81)	44.1 \pm 0.6 (21 – 84)	< 0.001
<i>Gobiosoma bosc</i>	R	2	0.054 \pm 0.026	0.094 \pm 0.034	0.376	32.3 \pm 1.4 (22 – 45)	30.3 \pm 0.9 (19 – 54)	0.255
<i>Leiostomus xanthurus</i> [†]	T	2	0.032 \pm 0.024	0.077 \pm 0.032	0.277	129.5 \pm 1.7 (108 – 157)	114.9 \pm 5.2 (24 – 153)	0.029
<i>Bairdiella chrysoura</i>	T	1	0.036 \pm 0.025	0.103 \pm 0.031	0.099	69.9 \pm 2.4 (52 – 98)	69.2 \pm 6.2 (20 – 165)	0.920
<i>Menidia menidia</i> [†]	T/R	1	0.077 \pm 0.029	0.031 \pm 0.017	0.164	44.4 \pm 6.5 (13 – 114)	55.0 \pm 14.3 (23 – 87)	0.546
<i>Micropogonias undulatus</i>	T	1	0.014 \pm 0.014	0.054 \pm 0.028	0.288	21.8 \pm 3.8 (15 – 31)	32.2 \pm 3.7 (11 – 120)	0.258
<i>Paralichthys dentatus</i>	T	1	0.038 \pm 0.022	0.090 \pm 0.027	0.149	130.3 \pm 15.2 (80 – 234)	161.7 \pm 21.5 (25 – 338)	0.316
<i>Syngnathus fuscus</i>	T	1	0.040 \pm 0.019	0.088 \pm 0.027	0.167	140.5 \pm 31.4 (74 – 200)	137.0 \pm 11.7 (76 – 248)	0.907
<i>Anchoa hepsetus</i> ^{**†}	T	<1	0.000 \pm 0.000	0.037 \pm 0.021			82.7 \pm 7.2 (53 – 107)	
<i>Anguilla rostrata</i>	T	<1	0.044 \pm 0.020	0.019 \pm 0.013		113.5 \pm 28.6 (62 – 244)	68.5 \pm 2.5 (66 – 71)	
<i>Apeltes quadracus</i>	R	<1	0.049 \pm 0.023	0.022 \pm 0.015		29.0 \pm 1.1 (23 – 34)	26.0 \pm 1.1 (23 – 28)	
<i>Brevoortia tyrannus</i> [†]	T	<1	0.027 \pm 0.020	0.059 \pm 0.021		51.9 \pm 3.6 (20 – 58)	59.3 \pm 12.1 (22 – 106)	
<i>Centropristis striata</i>	T	<1	0.020 \pm 0.014	0.019 \pm 0.013		85.0 \pm 12.0 (73 – 97)	154.5 \pm 7.5 (147 – 162)	
<i>Chasmodes bosquianus</i>	R	<1	0.032 \pm 0.018	0.015 \pm 0.015		55.5 \pm 9.6 (32 – 73)	50.9 \pm 1.8 (45 – 58)	
<i>Chilomycterus schoepfi</i> ^{**}	T	<1	0.000 \pm 0.000	0.010 \pm 0.010			284	
<i>Clupea harengus</i> ^{*†}	T	<1	0.012 \pm 0.012	0.000 \pm 0.000		53.5 \pm 0.5 (53 – 54)		
<i>Cynoscion regalis</i> ^{**}	T	<1	0.000 \pm 0.000	0.014 \pm 0.014			75.5 \pm 4.7 (69 – 89)	
<i>Gobiesox strumosus</i> ^{**}	SS	<1	0.000 \pm 0.000	0.010 \pm 0.010			42	

Table 5 continued

	Estuarine Usage	% of Total	CPUE (fish/s)			Length (mm)		
			Natural	Armored	p	Natural	Armored	p
<i>Hypsoblennius hentz</i> *	R	<1	0.012 ± 0.012	0.000 ± 0.000		76.0 ± 7.0 (69 – 83)		
<i>Lagodon rhomboides</i> †	T	<1	0.010 ± 0.010	0.010 ± 0.010		106	89	
<i>Menticirrhus saxatilis</i> *	T	<1	0.042 ± 0.019	0.000 ± 0.000		109.6 ± 43.0 (30 – 270)		
<i>Mugil curema</i> **†	T	<1	0.000 ± 0.000	0.010 ± 0.010			139	
<i>Opsanus tau</i>	R	<1	0.087 ± 0.026	0.044 ± 0.021		72.4 ± 7.1 (30 – 115)	68.7 ± 12.3 (35 – 138)	
<i>Pollachius virens</i> *†	T	<1	0.013 ± 0.013	0.000 ± 0.000		55.7 ± 4.5 (47 – 62)		
<i>Pomatomus saltatrix</i> †	T	<1	0.020 ± 0.014	0.038 ± 0.018		151.0 ± 23.0 (128 – 174)	85.0 ± 29.1 (50 – 172)	
<i>Pseudopleuronectes americanus</i>	T/R	<1	0.017 ± 0.017	0.036 ± 0.020		52.9 ± 2.1 (41 – 65)	47.9 ± 6.3 (25 – 73)	
<i>Scophthalmus aquosus</i> **	T	<1	0.000 ± 0.000	0.010 ± 0.010			57	
<i>Selene setapinnis</i> **†	SS	<1	0.000 ± 0.000	0.010 ± 0.010			52	
<i>Sphoeroides maculatus</i>	T	<1	0.033 ± 0.018	0.021 ± 0.015		64.0 ± 22.0 (26 – 125)	112.0 ± 42.8 (27 – 163)	
<i>Tautoga onitis</i> **	T/R	<1	0.000 ± 0.000	0.010 ± 0.010			116	
<i>Urophycis regia</i> **	T	<1	0.000 ± 0.000	0.010 ± 0.010			127	

Table 6. Post-hoc test results of the catch-per-unit-effort (CPUE), Shannon diversity, and richness models for upper creek and creek mouth habitats. All differences and confidence intervals are reported on the response scale

Comparison		95% Confidence Interval	p-value
Upper Creek CPUE		CPUE Difference	
Group 1			
Natural – Armored	0.227	0.014 – 0.440	0.037
Group 2			
Natural – Armored	0.018	-0.031 – 0.067	0.466
Natural			
Group 1 – Group 2	0.229	0.016 – 0.441	0.035
Armored			
Group 1 – Group 2	0.020	-0.031 – 0.071	0.437
Creek Mouth CPUE		CPUE Difference	
Natural – Armored	-0.033	-0.112 – 0.046	0.404
Group 1 – Group 2	0.053	-0.031 – 0.136	0.212
Upper Creek Diversity		Diversity Difference	
Natural – Armored	0.363	0.082 – 0.645	0.013
Group 1 – Group 2	-0.066	-0.348 – 0.215	0.638
Creek Mouth Diversity		Diversity Difference	
Natural – Armored	0.066	-0.277 – 0.409	0.698
Group 1 – Group 2	0.012	-0.332 – 0.355	0.946
Upper Creek Richness		Richness Difference	
Natural – Armored	0.823	0.442 – 1.204	< 0.001
Group 1 – Group 2	0.295	-0.086 – 0.676	0.126
Creek Mouth Richness		Richness Difference	
Natural – Armored	-0.283	-0.790 – 0.225	0.268
Group 1 – Group 2	0.301	-0.207 – 0.808	0.239

Figures

Fig. 1. Sampling sites in northern Barnegat Bay, New Jersey. See Tables 1 and 2 for site characteristics and sampling effort and Fig. 2 and 3 for aerial imagery of each creek

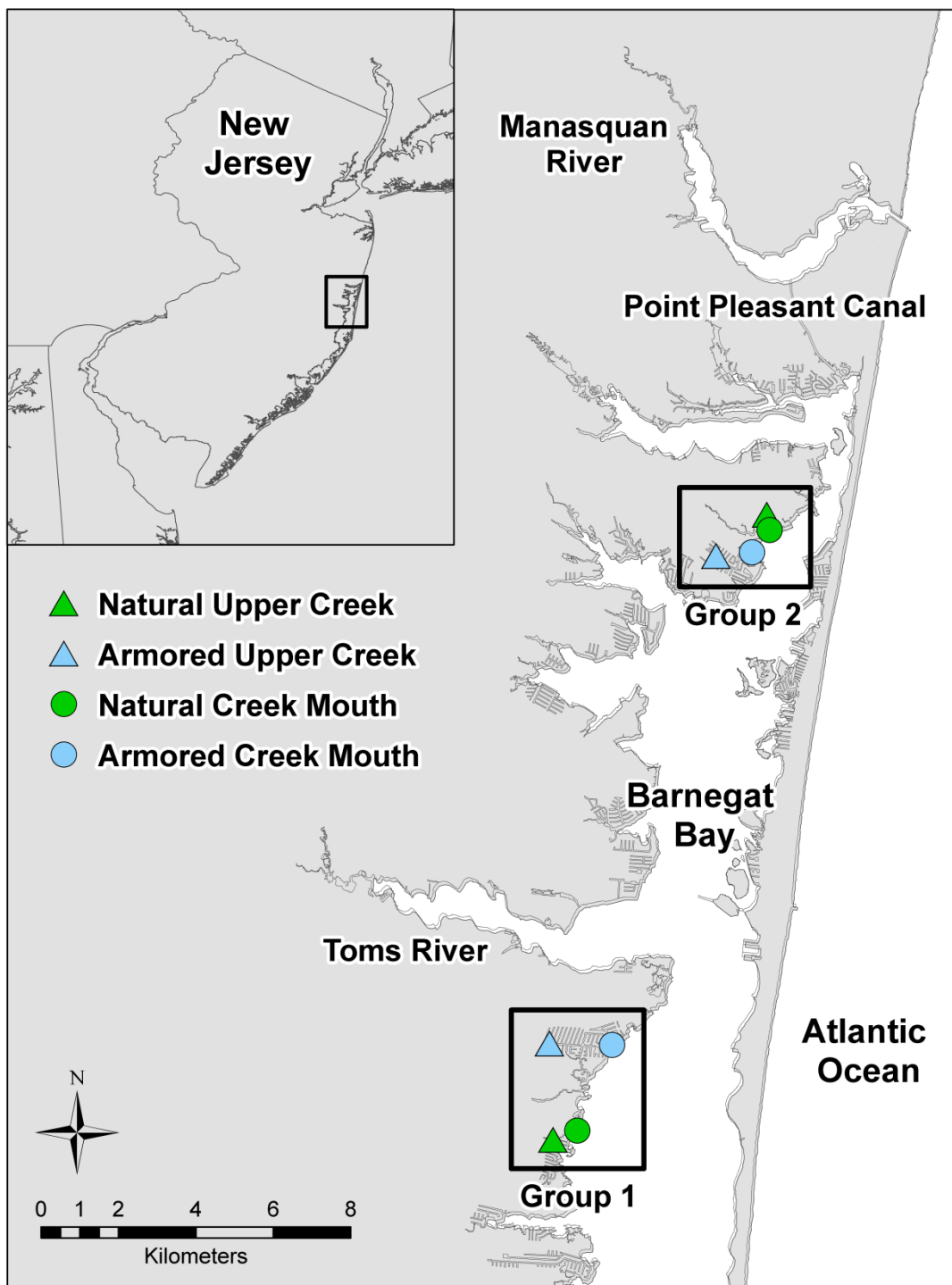


Fig. 2. Aerial imagery of Group 1 creeks. Natural shoreline is outlined in green and armored shoreline is outlined in blue. White circles indicate the sampling sites. The scale is indicated on each map. The natural stretch of shoreline near the armored upper creek site is a bank surrounded by forested land, not salt marsh. See Fig. 1 for locations of each study creek within the bay



Fig. 3. Aerial imagery of Group 2 creeks. Natural shoreline is outlined in green and armored shoreline is outlined in blue. White circles indicate the sampling sites. The scale is indicated on each map. See Fig. 1 for locations of each study creek within the bay

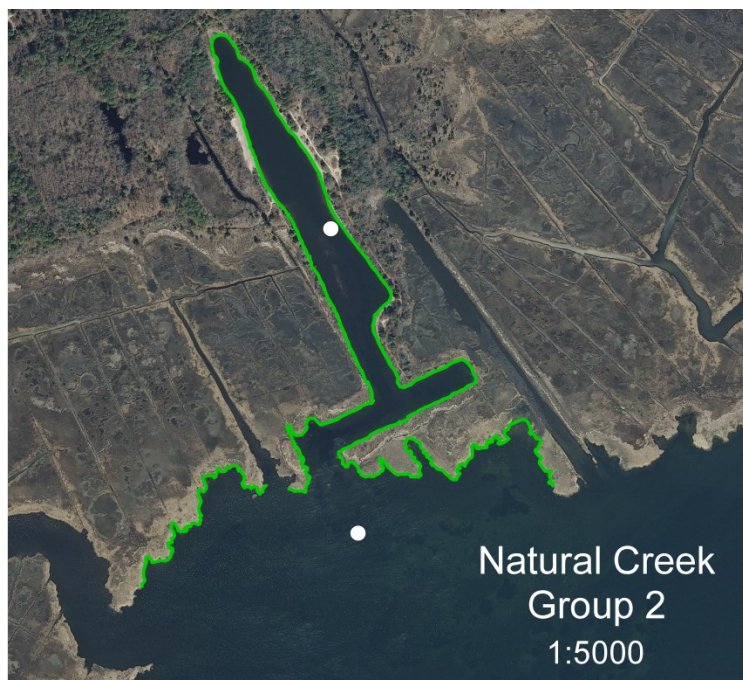


Fig. 4. Non-metric multidimensional scaling sample and species plots for upper creek (a & b) and creek mouth (c & d) habitats. Convex polygons enclose samples taken within natural and armored creeks. The species plots are in the same dimensions as the corresponding sample plots, but were separated for legibility. Species names were abbreviated as the first three letters of the genus and first three letters of the species for clarity (see Table 4 for full scientific and common names). Fish assemblage similarity decreases by half per one unit change along the axes. Note the difference in scale between plot axes

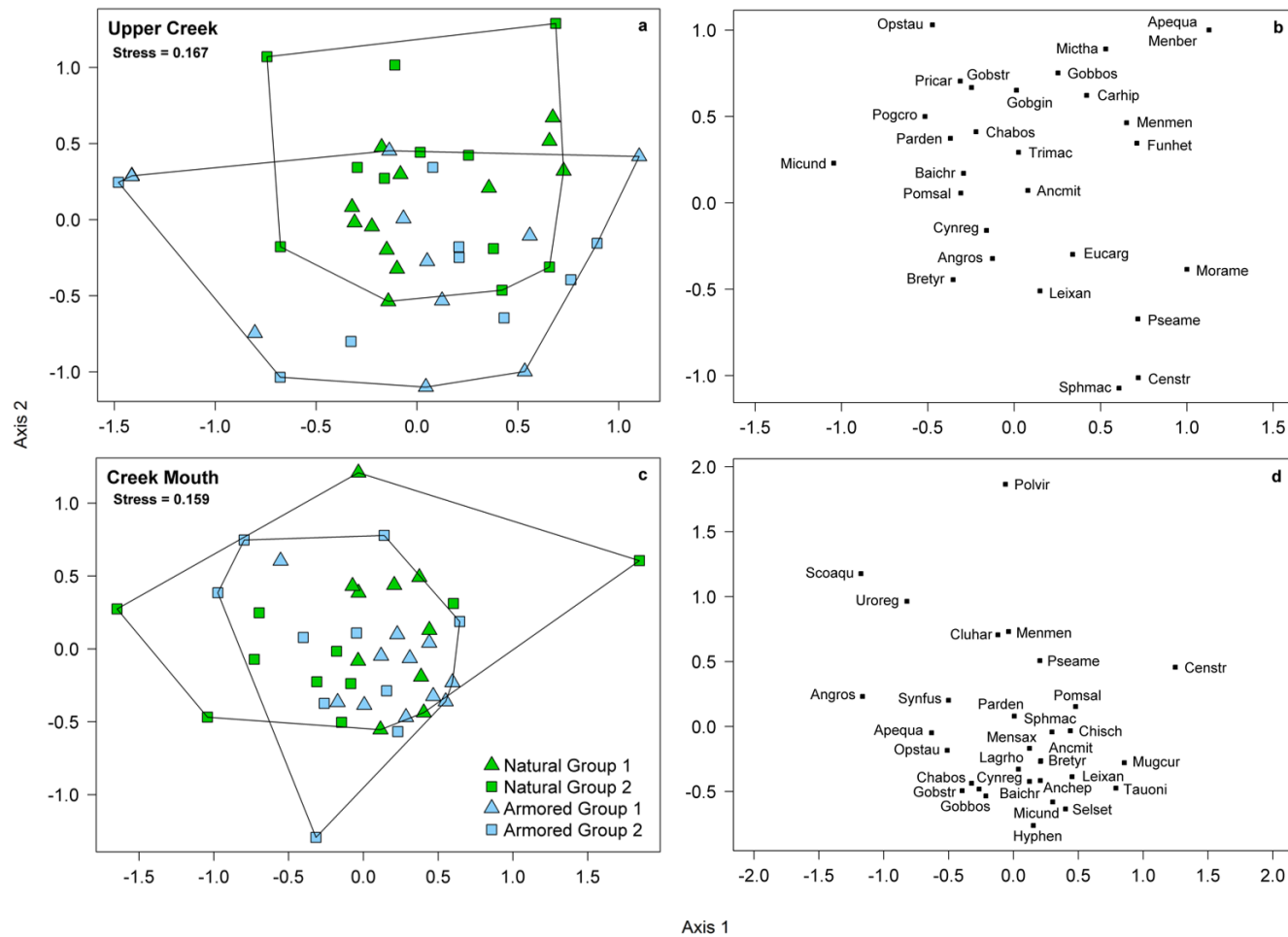


Fig. 5. (a) Upper creek canonical correspondence analysis (CCA) biplot of samples and environmental parameters (D.O. = dissolved oxygen). The arrows in the biplot represent the measured environmental gradients and point in the direction of an increase in the respective environmental parameter. Sampling observations are located in ordination space based on the associated environmental parameters and are also positioned at the centroid of all the species collected during that observation (b) Upper creek CCA species plot, which is in the same coenospace as the previous biplot, but was separated for legibility. Fish scientific names were abbreviated as the first three letters of the genus and first three letters of the species for clarity (see Table 4 for full scientific and common names). Species locations indicate the preferred environmental characteristics of each species (based on the samples collected) and therefore the abundance of a species declines with distance from the species' location in ordination space (McGarigal et al. 2000). Only the first two axes of the biplot and species plots are shown

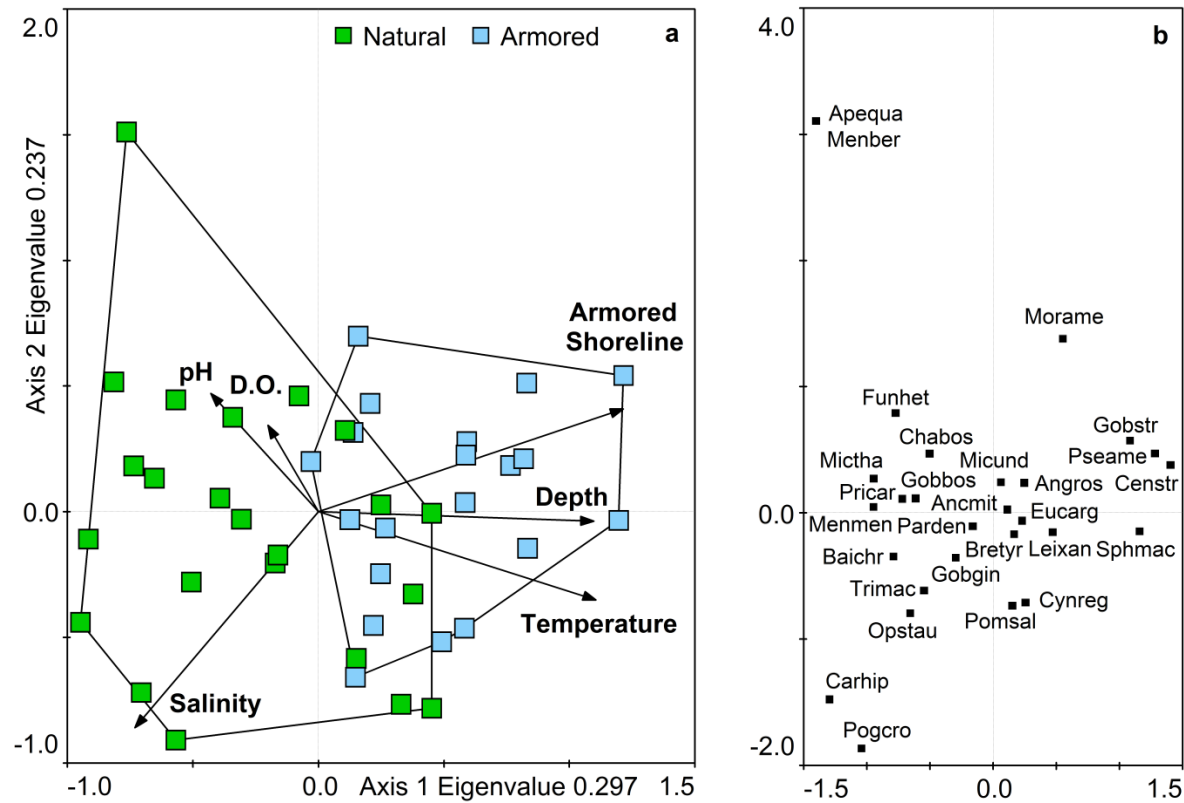


Fig. 6. (a) Creek mouth canonical correspondence analysis (CCA) biplot of samples and environmental parameters (D.O. = dissolved oxygen) (b) Creek mouth CCA species plot, which is in the same dimensions as the previous biplot, but was separated for legibility. Fish scientific names were abbreviated as the first three letters of the genus and first three letters of the species for clarity (see Table 4 for full scientific and common names). Only the first two axes of the biplot and species plots are shown. See the Fig. 5 caption for a brief description of CCA plot interpretation

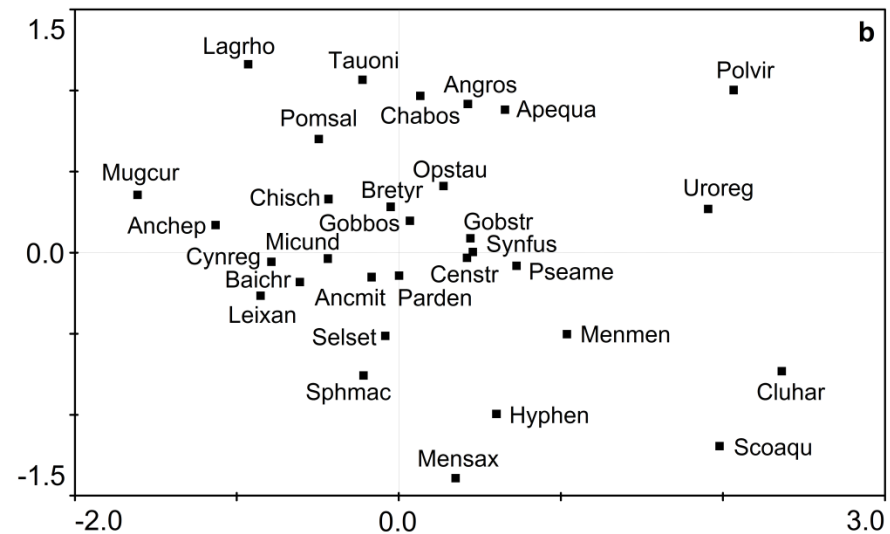
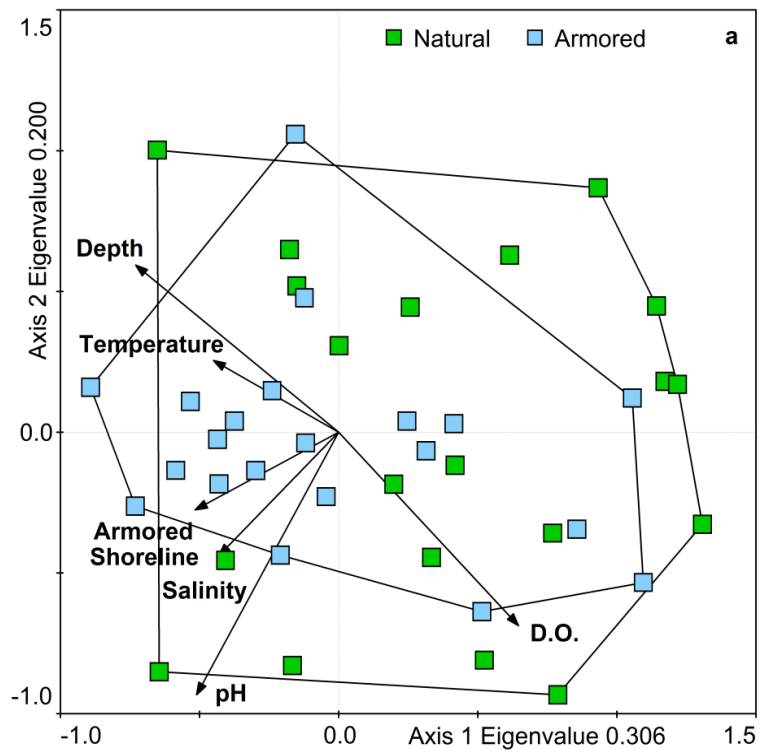


Fig. 7. Mean catch-per-unit-effort (CPUE), Shannon diversity, and richness in natural and armored upper creek and creek mouth habitats. Error bars represent standard errors

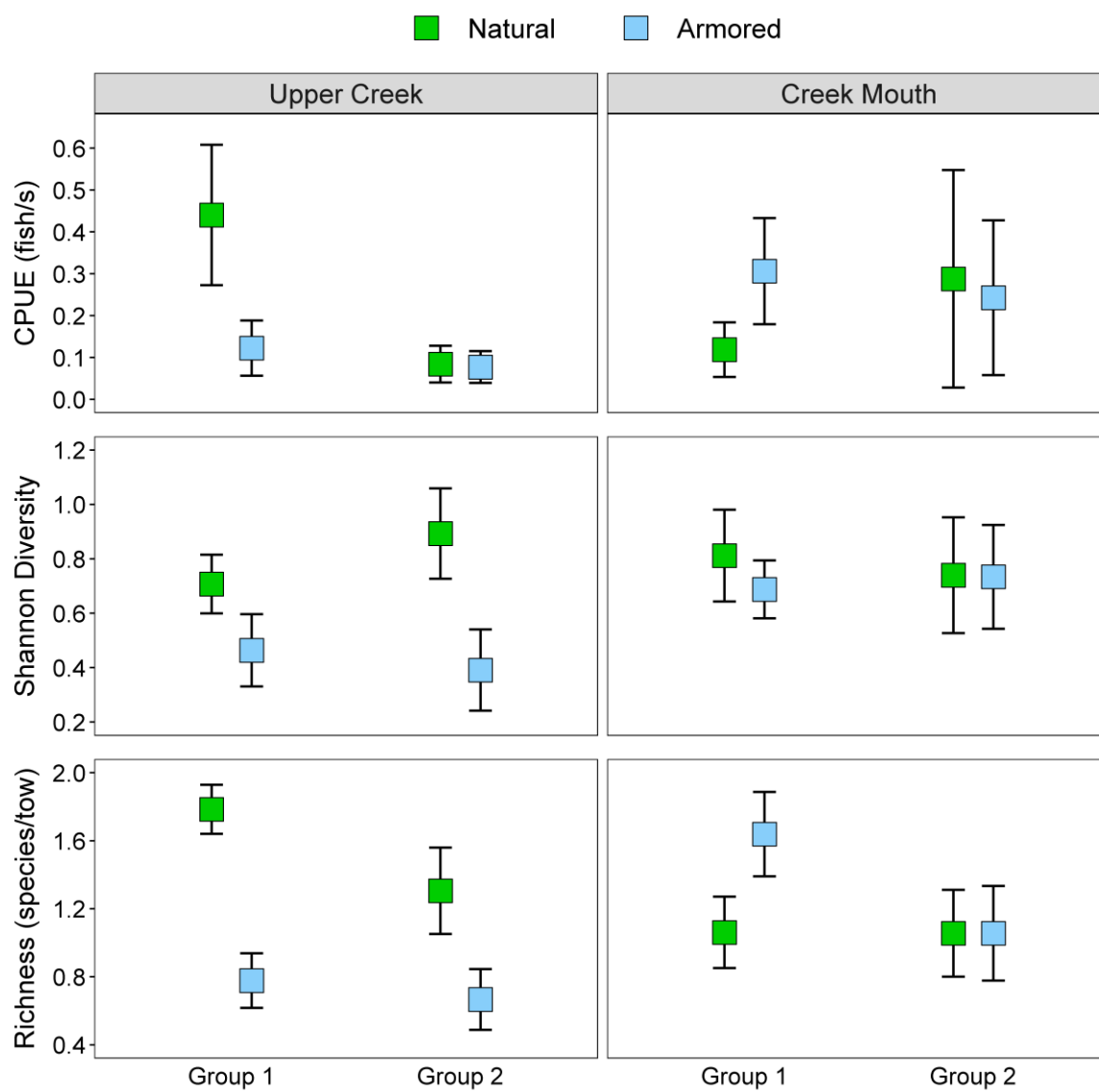


Fig. 8. Length frequency plots for select species collected in upper creek habitat: (a) bay anchovy *Anchoa mitchilli* (b) summer flounder *Paralichthys dentatus*. Note the difference in scale between plots

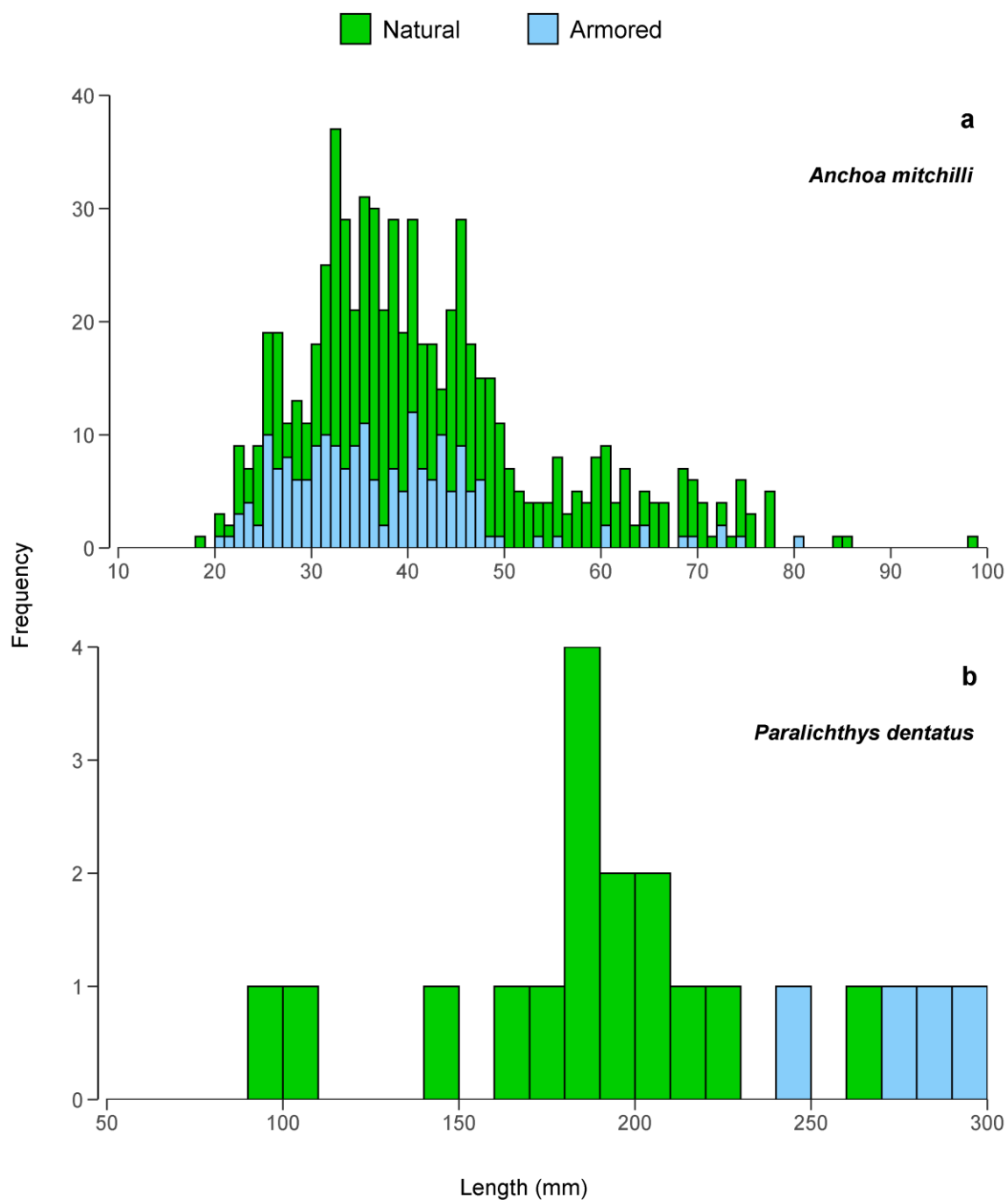
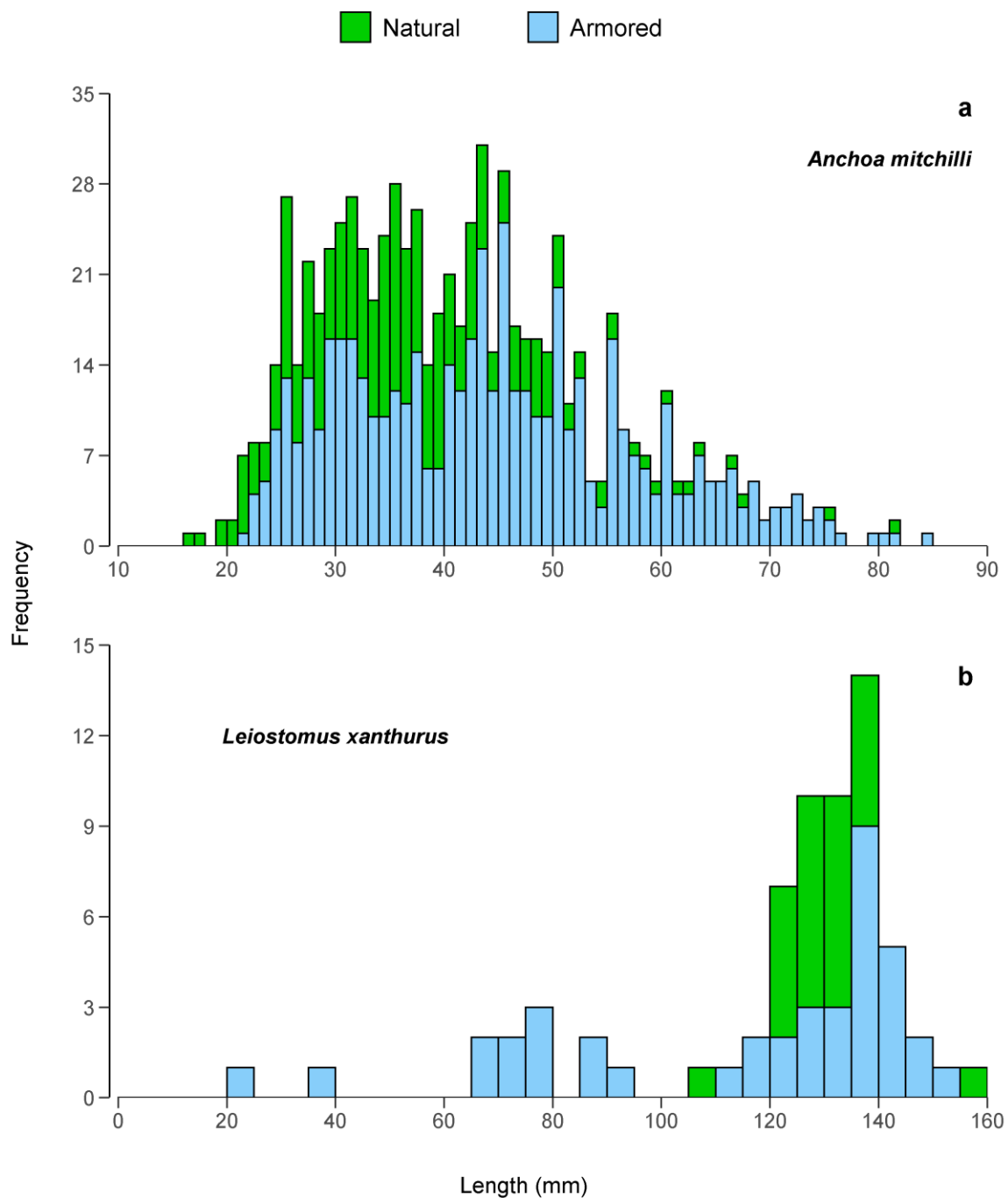


Fig. 9. Length frequency plots for select species collected in creek mouth habitat: (a) bay anchovy *Anchoa mitchilli* (b) spot *Leiostomus xanthurus*. Note the difference in scale between plots



CONCLUSION

Understanding urbanization impacts on coastal ecosystems is critical given the exponential growth of the human population and our continued urbanization of coastal areas (Dugan et al. 2011; Niemelä et al. 2011). Studying coastal urbanization impacts on fishes is particularly important given their role as a food source, significance to the global economy, and reliance on these areas as nursery habitat (Yáñez Arancibia 1985; National Marine Fisheries Service 2018). Lagoonal estuaries, such as Barnegat Bay, are essential nursery areas for juvenile fishes, including many recreationally and commercially important species (Tournois et al. 2017; Pérez-Ruzafa et al. 2019; Andolina et al. 2020).

This dissertation was the first assessment of the influence of urbanization on the fishes in Barnegat Bay, New Jersey. The results of this research demonstrated the habitat mosaic within Barnegat Bay supported a diversity of juvenile and adult fishes, and although the fish assemblage was relatively stable following the large, natural disturbance of Hurricane Sandy (Valenti et al. 2020), anthropogenic urbanization in the Barnegat Bay watershed has caused localized changes in fish assemblages which fortunately do not seem to have accumulated to large-scale assemblage impacts (Valenti et al. 2017). In a broader sense, this research (i) addressed less commonly studied ecological topics such as: the long-term response of fishes to hurricane passage, fish usage of entire estuarine habitat mosaics, evaluation of urbanization impacts on a large spatial scale, and the response of deep-water creek fish assemblages to shoreline armoring, (ii) performed an inventory of the fishes inhabiting the entire bay (previously undocumented), which can be used as a baseline for future studies, and (iii) provided information useful for fisheries and coastal management to the New Jersey Department of Environmental Protection.

However, given this was the first assessment of urbanization impacts on fishes within the bay, further study is certainly warranted. Specifically, the functional response of fishes, which was not addressed in this dissertation, is a key component to fully understanding the influence of urbanization on the fish assemblages in the Barnegat Bay (Elliott and Quintino 2007). In addition, this research highlighted the significance of spatial scale when assessing the influence of anthropogenic stressors on estuarine fishes and thus should be an important consideration for future studies. Further, the research presented here focused analyses on entire fish assemblages and to some extent certain species. Thus, studies directed at the species and individual scales are still needed for a comprehensive assessment of urbanization impacts across ecological scales.

It is clear from this and other research that coastal ecosystems can be altered directly and indirectly by human development. Management plans that balance the preservation of coastal habitats with the needs of stakeholders will be essential to effectively conserving coastal areas and the associated fauna, especially in this era of climate change and sea level rise.

References

- Andolina, C., P. Franzoi, A.L. Jackson, A. Mazzola, and S. Vizzini. 2020. Vegetated habitats tropically support early development stages of a marine migrant fish in a coastal lagoon. *Estuaries and Coasts* 43: 424–437.
- Dugan, J.E., L. Airolidi, M.G. Chapman, S.J. Walker, and T. Schlacher. 2011. Estuarine and coastal structures: Environmental effects, a focus on shore and nearshore structures. In *Treatise on estuarine and coastal science*, ed. E. Wolanski and D.S. McLusky, 8: 17–41. Waltham: Academic Press.
- Elliott, M., and V. Quintino. 2007. The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Marine Pollution Bulletin* 54: 640–645.
- National Marine Fisheries Service. 2018. Fisheries economics of the United States, 2016.

- U.S. Department of Commerce, National Oceanic and Atmospheric Administration
Technical Memo: NMFS-F/SPO-187.
- Niemelä, J., J. Breuste, T. Elmqvist, G. Guntenspergen, P. James, and N. McIntyre. 2011.
Urban ecology: Patterns, processes and applications. New York: Oxford University
Press.
- Pérez-Ruzafa, A., I.M. Pérez-Ruzafa, A. Newton, and C. Marcos. 2019. Coastal lagoons:
Environmental variability, ecosystem complexity, and goods and services
uniformity. In *Coasts and estuaries: The future*, ed. E. Wolanski, J.W. Day, M.
Elliott, and R. Ramachandran, 253–276. Amsterdam: Elsevier.
- Tournois, J., A.M. Darnaude, F. Ferraton, C. Aliaume, L. Mercier, and D.J. McKenzie.
2017. Lagoon nurseries make a major contribution to adult populations of a highly
prized coastal fish. *Limnology and Oceanography* 62: 1219–1233.
- Valenti, J.L., T.M. Grothues, and K.W. Able. 2017. Estuarine fish communities along a
spatial urbanization gradient. In: *A comprehensive assessment of Barnegat Bay–
Little Egg Harbor, New Jersey*, ed. G.A. Buchanan, T.J. Belton, and B. Paudel,
Journal of Coastal Research Special Issue No. 78: 254–268.
- Valenti, J.L., T.M. Grothues, and K.W. Able. 2020. Juvenile fish assemblage recruitment
dynamics in a mid-Atlantic estuary: Before and after Hurricane Sandy. *Marine
Ecology Progress Series* 641: 177–193.
- Yáñez Arancibia, A., ed. 1985. *Fish community ecology in estuaries and coastal lagoons*.
Mexico: Universidad Nacional Autónoma de México.