

Quantifying Striped Bass (*Morone saxatilis*) Dependence on Saltmarsh-Derived Productivity Using Stable Isotope Analysis

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Abstract Each winter, populations of striped bass (*Morone saxatilis*) migrate north from the coastal mid-Atlantic region of the US to the coastal waters of New England. During this migration, striped bass spend significant time in estuaries and saltmarshes, presumably to forage. However, the extent to which saltmarsh productivity supports striped bass remains unresolved. We used a three-isotope Bayesian mixing model to determine the relative contribution of three primary producers [C4 saltmarsh cordgrass (*Spartina* spp.), phytoplankton, and benthic diatoms] to striped bass tissue. Phytoplankton (51 % contribution) and *Spartina*-derived sources (44 % contribution) are the primary sources of production to striped bass, while benthic diatoms made a relatively small contribution (5 %). Our results highlight the importance of saltmarshes to striped bass by showing that primary producers unique to saltmarsh ecosystems support a large proportion of striped bass production.

Keywords Saltmarsh · Food web · Estuaries · Stable isotopes · Striped bass · *Morone saxatilis*

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Introduction

Striped bass (*Morone saxatilis*) are an anadromous fish found throughout the Atlantic coast from Florida to Canada, with the majority of the population concentrated in the mid-Atlantic region near the Chesapeake Bay, USA (Berggren and Lieberman 1978; Kernehan et al. 1981). Juvenile striped bass remain in freshwater for approximately 2 years before transitioning into estuarine waters (Fay et al. 1983; Setzler-Hamilton et al. 1981). Around this time, many individuals join the migrating stock, which moves north in the spring and summer, and south again in the late fall and winter (Clark 1968; Merriman 1941; Westin and Rogers 1978), although some recent work has suggested that many females, which do not mature until age 4–6, do not migrate until after age 4 (Secor and Piccoli 2007). The vast majority of migratory fish are female (~90 %) indicating that most males either remain resident or make substantially shorter migrations than females (Bigelow and Schroeder 1953; Schaefer 1968).

Each year, some portion of the migratory population, typically from Delaware and Chesapeake Bays, moves north of Cape Cod to the northern most extent of the striped bass's range off the coast of New England and Canada (Kneebone et al. 2014; Mather et al. 2009). During this time, the large subadult (30–50 cm) and small adult (50–70 cm) striped bass spend a significant amount of time in New England estuaries and saltmarshes (Mather et al. 2009; Pautzke et al. 2010). They show high site fidelity, migrating to the same locations year after year (Kneebone et al. 2014; Mather et al. 2013b). While it is known that striped bass actively forage in coastal waters during this migration (Ferry and Mather 2012), the extent to which different coastal ecosystems and different sources of production support this foraging remains unresolved.

Some progress has been made in identifying temporal and spatial patterns in striped bass diet during their northern migration using gut content analysis. A synthesis of data from several estuaries within Massachusetts found that subadult and small adult striped bass consume a season-specific diet consisting primarily of Clupeids, such as Atlantic herring (*Clupea harengus*) and American shad (*Alosa sapidissima*) in the spring and Atlantic menhaden (*Brevoortia tyrannus*) in the fall (Ferry and Mather 2012). Invertebrates, mostly crustaceans, were present in the diet during all seasons throughout Massachusetts, but comprised the highest proportion of striped bass diet in the summer. American sand lance (*Ammodytes americanus*) comprised a considerable proportion of their diet in all seasons in Massachusetts' South Shore region (south of Boston, north of Cape Cod) and during spring and summer in northern Massachusetts, which includes the Plum Island Estuary, the site of our study. Atlantic silverside (*Menidia menidia*) comprised a considerable portion of striped bass diet in summer and fall in Massachusetts' South Shore and northern Massachusetts regions. Mummichog (*Fundulus heteroclitus*) was an important component of the diet for striped bass only in northern Massachusetts and only during summer and fall (Ferry and Mather 2012). These results are largely consistent with diets of large fish in northern Massachusetts, which have been shown to consume equal portions of fish and crustaceans during the summer (Nelson et al. 2003). These studies indicate that striped bass in Massachusetts rely on invertebrates for a higher proportion of their diets compared to striped bass in the mid-Atlantic region of the USA, which eat mostly fish (Overton et al. 2008, 2009). Despite this understanding of striped bass feeding ecology, there is very little knowledge about the sources of production for these prey items and the extent to which each of these prey items contributes to striped bass biomass. The Clupeids likely derive most of their energy from the water column, but the invertebrate, crustaceans, and mummichog are likely conduits for saltmarsh-derived productivity.

Methods utilizing multiple stable isotope ratios have enabled researchers to quantify the relative contributions of a number of different isotopic sources to an isotopic mixture, and have become vital tools in ecological research (Martínez del Río et al. 2009; Peterson and Fry 1987). However, previous studies using stable isotope analysis to study striped bass have focused only on larval bass, have not been used for source partitioning, and have focused on geographic regions outside of New England (Rast and Sutton 1985; Wainright et al. 1996). Deegan and Garritt (1997) used ^{13}C , ^{15}N , and ^{34}S to evaluate the use of saltmarsh-derived production by a number of nekton species in the Plum Island Sound estuary. They

found that several species show use of saltmarsh-derived production, including rainbow smelt, bluefish, Atlantic silverside, black-spotted stickleback, and green crab. However, their methods relied on a qualitative assessment of marsh dependence based on overlap of consumer isotope values to those of *Spartina*, and did not give precise estimates of the proportions that each primary producer contributes.

Here, we used a three-isotope mixing model to quantify the relative contributions of three sources, *Spartina* spp., benthic diatoms, and particulate organic matter (POM; a proxy for pelagic phytoplankton) to striped bass biomass. Stable isotope values represent a time-integrated signal of assimilated productivity, and thus isotope analysis complements the use of gut content analysis. The use of Bayesian inference in this model enables us to build probability distributions for each isotopic mixture (striped bass tissue), which captures several sources of natural variability and enables a robust prediction of uncertainty in the model solutions (Parnell et al. 2010).

The objective of this study was to quantify the contribution of saltmarsh-derived production to striped bass tissue. We hypothesized that striped bass migrate to New England marshes annually to forage and that saltmarsh-derived production will contribute significantly to the biomass of migrating striped bass in Plum Island Sound.

Methods

Site Description

The Plum Island Estuary (PIE) is a saltmarsh-dominated ecosystem in northeastern Massachusetts, bordered by the Merrimack River to the north and the Ipswich River to the south. C4 saltmarsh cordgrass, *Spartina* spp., is the dominant marsh flora, with *Spartina patens* occupying the high marsh and tall-form *Spartina alterniflora* occupying the creek banks (Deegan and Garritt 1997). The estuary experiences semidiurnal tides with a mean range of 2.7 m. Salinity ranges from 0 to 32 and varies in space and time depending on relative inputs from freshwater and tidal sources. Temperature ranges from $-1\text{ }^{\circ}\text{C}$ in the winter to $28\text{ }^{\circ}\text{C}$ in the summer (Zhao et al. 2010).

Stable Isotope Sampling and Preparation

All fish sampling was conducted under protocols approved by the Marine Biological Laboratory Animal Care and Use Committee protocols numbers 14–49 and 12–30. Striped bass were collected during the summer months (June–August) by hook and line in Plum Island Estuary (2012–2013). Fish were anesthetized to “handleable” by immersion in 35 mg/l solution of AQUI-S[®] for 2 min. Fish were weighed to the nearest gram

and measured to the nearest millimeter (total length). Tissue samples were taken from the flank muscle below the dorsal fin, above the lateral line using a 4 mm biopsy punch. Fish were then placed in an aerated seawater recovery tank for 5 min and released alive. Prior to stable isotope analysis, all samples were rinsed with de-ionized water (DI), dried (50 °C), and ground to a fine powder.

The three sources chosen, benthic diatoms, *Spartina* spp., and particulate organic matter (POM; a proxy for pelagic phytoplankton), represent the major primary production sources in the estuary and contribute significantly to the potential prey items of striped bass (Nelson et al. 2015; Ferry and Mather 2012). The food web sources used in this study were taken from the Plum Island Long-Term Ecological Research site stable isotope survey (Nelson et al. 2015; Deegan and Garritt 1997). Detailed information about the collection methods and data for the survey can be found at (<http://ecosystems.mbl.edu/PIE/data/HTL/HTL-PIE-YearlyIsotopeSurvey.html>). All the primary producer samples used for this study were collected annually in the fall (August–September) from 1999 to 2013 from the middle (N 42.76° W 70.83°) and lower (N 42.70° W 70.78°) regions of the estuary (Nelson et al. 2015).

Benthic diatoms were collected by placing five to seven 25 cm² sections of 210 µm mesh size Nitex screen on the sediment surface for 30 min at low tide during daylight hours. The diatoms migrate from the sediment through the mesh to the surface of the screen. The material on the surface of the screen was rinsed with de-ionized (DI) water onto a petri dish and was confirmed to be diatoms via microscopy. The sample is rinsed of carbonates using 10 % HCl, then filtered under suction in a 25 mm Gelman filter tower and flask onto a 25 mm 0.7 µm nominal pore size ashed glass microfiber filter, and dried at 50 °C (Tobias et al. 2003). Water column POM (a mix of live phytoplankton and dead organic matter) was collected via 50 µm plankton net on three replicate tows. The samples were stored frozen (−20 °C) until they were processed in the same way as the benthic diatom samples and dried at 50 °C. The Benthic diatom and POM samples remained on the filters for isotope analysis. The ashed glass filters do not contain carbon or nitrogen and do not affect the stable isotope values (Jones et al. 1999). Fifteen live leaves of *S. alterniflora* and *S. patens* were collected from various locations within the saltmarsh. Live leaves were cleaned, rinsed with DI, and dried after collection. Live *Spartina* and *Spartina* detritus have the same isotopic value, so this study does not distinguish between the two (Haines and Montague 1979).

Stable Isotope Sample Analysis

Stable isotope analysis was performed using a Europa ANCA-SL elemental analyzer attached to a continuous flow Europa 20-20 gas source stable isotope ratio mass spectrometer at the Marine Biological Laboratory in

Woods Hole, MA. For each sample, approximately 500 µg of tissue was wrapped in a tin capsule and analyzed for δ¹³C, δ¹⁵N, δ³⁴S, %C, %N, and %S. Isotope values are expressed in δ notation according to the following equation:

$$\delta X = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1000$$

where X represents ¹³C, ¹⁵N, or ³⁴S and R represents the ratio of heavy to light isotopes. Standards used for δ¹³C, δ¹⁵N, and δ³⁴S values were PeeDee Belemnite (PDB), ambient air (AIR), and Canyon Diablo Troilite (CDT) respectively. Duplicate values were obtained for ~20 % of samples for quality assurance purposes.

Stable Isotope Data Analysis

The relative contribution of each of three sources to striped bass muscle tissue was determined by a Bayesian mixing model performed by the SIAR package in R (R Development Core Team; Parnell et al. 2010) and solved with a Markov Chain Monte Carlo algorithm. One model was run to obtain total source contributions for the group of striped bass ($n=34$), while a separate model was run to obtain source contributions for each consumer separately. Sources included in the model were *Spartina* (C4 marsh cordgrass), particulate organic matter (POM; a proxy for phytoplankton), and benthic diatoms (Table 1). Striped bass isotope values were well constrained by these end members (Fig. 1). These primary producers comprise the vast majority of productivity in the lower and middle estuary. Other potential sources such as terrestrial or marsh C3 plants were excluded because there is no brackish habitat in the area where samples were collected, and the inclusion of such minor sources can introduce unnecessary uncertainty into the model. Corrections were made for elemental concentration in the sources and the trophic enrichment factor for each element, 0.6±0.3 for C, 3.0±0.75 for N, and 0.4±0.2 for S, relative to the trophic position of the consumers (Table 1).

Trophic level (TL) of the sampled fish was calculated by the following equation:

$$TL_{\text{consumer}} = \left(\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{source}} \right) / \Delta \delta^{15}N + 1$$

where δ¹⁵N_{source} represents the average δ¹⁵N value of all three sources, weighted by their relative contributions to the consumer's tissue (as determined by the output of the model), and Δ δ¹⁵N represents the trophic enrichment factor and is equal to 3.0 (Hussey et al. 2014; Minagawa and Wada 1984; Post 2002).

Results

The *Spartina* endmember had a mean δ¹⁵N value of 4.7±0.6, δ¹³C of −13.1±0.4, and δ³⁴S of 9.0±0.1. The water column

Table 1 Mean isotope values (\pm standard deviations) for the three organic matter sources used in the mixing model

Source	$\delta^{15}\text{N}$	% N	$\delta^{13}\text{C}$	% C	$\delta^{34}\text{S}$	% S
POM	3.4 ± 1.5	8.0 ± 1	-24.6 ± 1.5	51.0 ± 5	18.5 ± 1.5	0.8 ± 0.1
BD	3.1 ± 1.4	7.0 ± 1	-16.1 ± 2.1	48.0 ± 7	18.5 ± 1.5	0.6 ± 0.1
C4 Marsh	4.7 ± 0.6	1.5 ± 0.5	-13.1 ± 0.4	45.0 ± 4	9.0 ± 1.5	0.2 ± 0.1

end member POM had a mean $\delta^{15}\text{N}$ value of 3.4 ± 1.5 , $\delta^{13}\text{C}$ of -24.6 ± 1.5 , and $\delta^{34}\text{S}$ of 18.5 ± 1.5 . The benthic diatoms had a mean $\delta^{15}\text{N}$ value of 3.1 ± 1.4 , $\delta^{13}\text{C}$ of -16.1 ± 2.1 , and $\delta^{34}\text{S}$ of 18.5 ± 1.5 . The striped bass muscle tissue had a mean $\delta^{15}\text{N}$ value of 14.81 ± 1.5 , $\delta^{13}\text{C}$ of -17.9 ± 1.5 , and $\delta^{34}\text{S}$ of 11.58 ± 2.1 . Striped bass acquired the majority of their productivity from POM-derived sources (51 %) and *Spartina*-derived sources (44 %), while benthic diatoms made a relatively small contribution (5 %) (Fig. 2, Table 2). Source proportions for individual consumers ($n=34$) were distributed over a wide range (POM: 2–92 %; BD: 1–82 %; *Spartina*: 8–49 %) indicating considerable variability in individual striped bass feeding habits. The reduced major axis regression determined that

isotope values did not significantly correlate with fish weight or fish length indicating that isotopic composition does not vary as a function of size within the size range we examined (296–692 mm; 0.26–3.06 kg). Based on the lack of correlation with any body size metric, we pooled striped bass across size ranges and considered them as a single group. Mean trophic level of striped bass is 4.8 (SD = 0.46).

Discussion

Our results quantify and substantiate the importance of saltmarsh-derived productivity to migrating striped bass that has been suggested by previous studies (Boesch and Turner 1984; Ferry and Mather 2012). The heavy reliance on *Spartina* production by striped bass, an important coastal ocean fisheries species, demonstrates the importance of the coupling between saltmarsh ecosystems and the coastal ocean. This study provides evidence for spatially coupled food webs in coastal New England waters where striped bass act as apex predators in the saltmarsh during the summer and a vector for saltmarsh productivity as prey in the coastal ocean to apex consumers such as larger predatory fishes, sharks, and seals during their southern migration in the fall.

Although we demonstrate a strong contribution from saltmarsh-derived productivity to striped bass tissue, our results and previous diet studies suggest the diet of striped bass, in terms of specific prey items, is quite flexible (Pautzke et al. 2010). We observed no correlation with body size or weight and isotope value, indicating that striped bass diets likely remain flexible through the juvenile and small adult size classes. While saltmarshes are consistently productive ecosystems, there is a great deal of interannual variability in the production of prey items (Deegan 1990; Deegan and Garritt 1997; Nelson et al. 2015). Despite this variability in food resources, striped bass show strong site fidelity from year to year (Kneebone et al. 2014; Mather et al. 2013a). Thus, adaptive feeding strategies would be advantageous given the uncertainty of prey availability in any given year.

Given the flexibility in striped bass diet and the fact that our results are limited to a single estuary in a single season, we limited our interpretation of the results to fish that migrate and typically feed in estuaries. Striped bass in other regions that do not regularly access estuaries may have different feeding strategies or focus on more specific prey items in different habitats.

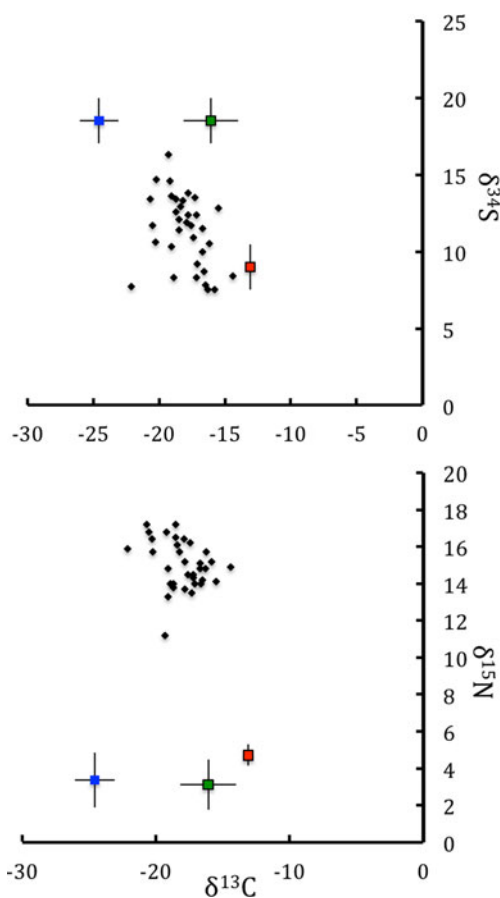


Fig. 1 Biplots of striped bass (black) and particulate organic matter ($\delta^{13}\text{C} = -24.6$) (blue square), benthic diatoms ($\delta^{13}\text{C} = -16.1$) (green square), and *Spartina* ($\delta^{13}\text{C} = -13.1$) (red square). $\delta^{13}\text{C}$ is plotted against $\delta^{34}\text{S}$ (top) and $\delta^{15}\text{N}$ (bottom)

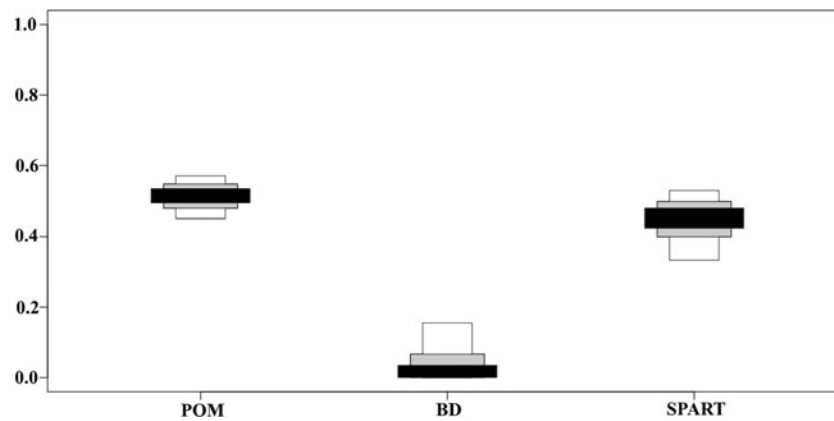


Fig. 2 Boxplots showing the relative proportions that each primary producer group contributes to total striped bass biomass in the marsh, as determined by the group Markov Chain Monte Carlo model. Bands represent the 50th (black), 75th (gray), and 95th (white) percent credible

intervals. *Spartina* (SPART) and phytoplankton (POM) contribute the vast majority of striped bass biomass, while benthic diatoms (BD) contribute negligibly

In addition, our sampling efforts occurred in the summer near the end of the growing season, just prior to when the fish would migrate back south. There is no information, to our knowledge, on striped bass stable isotope tissue turnover. However, information from similar species in the literature suggests that, as juvenile fish with more rapid growth rates, their tissue turnover is likely driven by growth and will be proportional to the amount of tissue they gained while in the estuary (Nelson et al. 2011; Vander Zanden et al. 2015). Therefore, our estimates may not precisely capture the full contribution of estuarine-derived production.

The striped bass in this study had a mean trophic level of 4.8 (SD=0.46), consistent with the available diet information and striped bass function as a mid-upper level consumer in the estuary (Ferry and Mather 2012). The lack of correlation with trophic level and body size suggests that, at least through the size range observed here, juvenile and subadult striped bass remain at a similar trophic level while using the estuary and do not undergo a strong ontogenetic shift in diet that results in an increased trophic level. For the same reasons noted above, this could be related to an adaptive feeding strategy to remain flexible in diet in the face of uncertain resource availability. Similar trophic patterns have been observed in bluefish (*Pomatomus saltatrix*), a generalist predator that typically uses estuaries to forage as subadults (Harding and Mann 2001; Lucena et al. 2000). Unlike striped bass, bluefish feed primarily in the water column,

opportunistically feeding on small clupeids (Harding and Mann 2001; Lucena et al. 2000).

In light of the results of this study, which demonstrate that striped bass caught in the marsh acquire a significant portion of their production from saltmarsh-derived sources, the issue of flexibility of resource use becomes critical given current rates of saltmarsh decline. Up to half of the world's total area of tidal marsh has been lost largely due to sea-level rise, loss of sediment supply, development (Millennium Ecosystem Assessment 2005), and eutrophication (Deegan et al. 2012). If striped bass are highly dependent on marsh-derived productivity, loss of marsh could indirectly translate into a decline in total biomass of striped bass. Thus, integrated, or ecosystem-based, management of striped bass and saltmarshes is advisable (Leslie and McLeod 2007). Our results suggest that healthy marshes likely contribute to the health of striped bass populations. We suggest that resource managers consider the role that saltmarshes serve in providing a unique and significant source of production to striped bass when making management decisions.

Table 2 Mean, mode, upper 95 %, and lower 95 % credible intervals of the contribution of the three primary production sources to striped bass biomass determine by the SIAR mixing model

Source	Mean	Mode	Lower 95 %	Upper 95 %
POM	0.51	0.51	0.45	0.57
BD	0.05	0.01	0.00	0.15
C4 Marsh	0.44	0.45	0.33	0.53

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References

Berggren, T., and J. Lieberman. 1978. Relative contribution of hudson, chesapeake, and roanoke striped bass, *morone-saxatilis*, stocks to atlantic coast fishery. *Fishery Bulletin* 76: 335–345.

- Bigelow, H.B., and W.C. Schroeder. 1953. *Fishes of the Gulf of Maine*: US Government Printing Office Washington.
- Boesch, D.F., and R.E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* 7: 460–468.
- Clark, J. 1968. Seasonal movements of striped bass contingents of Long Island Sound and the New York Bight. *Transactions of the American Fisheries Society* 97: 320–343.
- Deegan, L.A. 1990. Effects of estuarine environmental conditions on population dynamics of young-of-the-year gulf menhaden. *Marine Ecology Progress Series* 68: 195–205.
- Deegan, L.A., and R.H. Garritt. 1997. Evidence for spatial variability in estuarine food webs. *Marine Ecology Progress Series* 147: 31–47.
- Deegan, L.A., D.S. Johnson, R.S. Warren, B.J. Peterson, J.W. Fleeger, S. Fagherazzi, and W.M. Wollheim. 2012. Coastal eutrophication as a driver of salt marsh loss. *Nature* 490: 388–392.
- Fay, C.W., R.J. Neves, and G.B. Pardue. 1983. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic). Striped Bass: Virginia Polytechnic Inst. and State Univ., Blacksburg (USA). Dept. of Fisheries and Wildlife Sciences.
- Ferry, K.H., and M.E. Mather. 2012. Spatial and temporal diet patterns of subadult and small adult striped bass in Massachusetts estuaries: data, a synthesis, and trends across scales. *Marine and Coastal Fisheries* 4: 30–45.
- Haines, E., and C. Montague. 1979. Food sources of estuarine invertebrates analyzed using $^{13}\text{C}/^{12}\text{C}$ ratios. *Ecology* 60: 48–56.
- Harding, J.M., and R. Mann. 2001. Diet and habitat use by bluefish, *Pomatomus saltatrix*, in a Chesapeake Bay estuary. *Environmental Biology of Fishes* 60: 401–409.
- Hussey, N.E., M.A. MacNeil, B.C. McMeans, J.A. Olin, S.F. Dudley, G. Cliff, S.P. Wintner, S.T. Fennessy, and A.T. Fisk. 2014. Rescaling the trophic structure of marine food webs. *Ecology Letters* 17: 239–250.
- Jones, R.I., J. Grey, D. Sleep, and L. Arvola. 1999. Stable Isotope analysis of zooplankton carbon nutrition in humic lakes. *Oikos* 86: 97–104.
- Kernehan, R.J., M.R. Headrick, and R.E. Smith. 1981. Early life history of striped bass in the Chesapeake and Delaware Canal and vicinity. *Transactions of the American Fisheries Society* 110: 137–150.
- Kneebone, J., W.S. Hoffman, M.J. Dean, D.A. Fox, and M.P. Armstrong. 2014. Movement patterns and stock composition of adult Striped Bass tagged in Massachusetts coastal waters. *Transactions of the American Fisheries Society* 143: 1115–1129.
- Leslie, H.M., and K.L. McLeod. 2007. Confronting the challenges of implementing marine ecosystem-based management. *Frontiers in Ecology and the Environment* 5: 540–548.
- Lucena, F.M., T. Vaske, J.R. Ellis, and C.M. O'Brien. 2000. Seasonal variation in the diets of bluefish, *Pomatomus saltatrix* (Pomatomidae) and striped weakfish, *Cynoscion guatucupa* (Sciaenidae) in southern Brazil: implications of food partitioning. *Environmental Biology of Fishes* 57: 423–434.
- Martínez del Rio, C., N. Wolf, S.A. Carleton, and L.Z. Gannes. 2009. Isotopic ecology ten years after a call for more laboratory experiments. *Biological Reviews* 84: 91–111.
- Mather, M.E., J.T. Finn, K.H. Ferry, L.A. Deegan, and G.A. Nelson. 2009. Use of non-natal estuaries by migratory striped bass (*Morone saxatilis*) in summer.
- Mather, M., J. Finn, C. Kennedy, D. L.A., and J.M. Smith. 2013. What happens in an estuary doesn't stay there: patterns of biotic connectivity resulting from long term ecological research. *Oceanography* 26: 168–179.
- Mather, M.E., J.T. Finn, C.G. Kennedy, L.A. Deegan, and J.M. Smith. 2013. What happens in an estuary doesn't stay there: patterns of biotic connectivity resulting from long term ecological research.
- Merriman, D. 1941. *Studies on the striped bass (Roccus saxatilis) of the Atlantic coast*: US Government Printing Office.
- Millennium Ecosystem Assessment, 2005. *Ecosystems and Human Well-being*: Synthesis. Island Press, Washington, DC.
- Minagawa, M., and E. Wada. 1984. Stepwise enrichment of $\delta^{15}\text{N}$ along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica et Cosmochimica Acta* 48: 1135–1140.
- Nelson, G.A., B.C. Chase, and J. Stockwell. 2003. Food habits of striped bass (*Morone saxatilis*) in coastal waters of Massachusetts. *Journal of Northwest Atlantic Fishery Science* 32: 1.
- Nelson, J., J. Chanton, F. Coleman, and C. Koenig. 2011. Patterns of stable carbon isotope turnover in gag, *Mycteroperca microlepis*, an economically important marine piscivore determined with a non-lethal surgical biopsy procedure. *Environmental Biology of Fishes* 90: 243–252.
- Nelson, J.A., L.A. Deegan, and R.H. Garritt. 2015. Drivers of spatial and temporal variability in estuarine food webs. *Marine Ecology Progress Series* 533: 67–77.
- Overton, A.S., C.S. Manooch III, J.W. Smith, and K. Brennan. 2008. Interactions between adult migratory striped bass (*Morone saxatilis*) and their prey during winter off the Virginia and North Carolina Atlantic coast from 1994 through 2007. *Fishery Bulletin* 106: 174–182.
- Overton, A.S., F.J. Margraf, and E.B. May. 2009. Spatial and temporal patterns in the diet of striped bass in Chesapeake Bay. *Transactions of the American Fisheries Society* 138: 915–926.
- Pamell, A.C., R. Inger, S. Bearhop, and A.L. Jackson. 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS One* 5: e9672.
- Pautzke, S.M., M.E. Mather, J.T. Finn, L.A. Deegan, and R.M. Muth. 2010. Seasonal use of a New England estuary by foraging contingents of migratory striped bass. *Transactions of the American Fisheries Society* 139: 257–269.
- Peterson, B.J., and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annual review of ecology and systematics*: 293–320.
- Post, D.M. 2002. The long and short of food-chain length. *Trends in Ecology & Evolution* 17: 269–277.
- Rast, W., and J. Sutton. 1985. Use of stable carbon and nitrogen isotopes to trace the larval striped bass food chain in the Sacramento-San Joaquin Estuary. *California, April to September*: 88–164.
- Schaefer, R.H. 1968. *Sex composition of striped bass from the Long Island surf*: Department of Environmental Conservation.
- Secor, D.H., and P.M. Piccoli. 2007. Oceanic migration rates of Upper Chesapeake Bay striped bass (*Morone saxatilis*), determined by otolith microchemical analysis. *Fishery Bulletin* 105: 62–73.
- Setzler-Hamilton, E.M., W.R. Boynton, J.A. Mihursky, T.T. Polgar, and K.V. Wood. 1981. Spatial and temporal distribution of striped bass eggs, larvae, and juveniles in the Potomac estuary. *Transactions of the American Fisheries Society* 110: 121–136.
- Tobias, C., A. Giblin, J. McClelland, J. Tucker, and B. Peterson. 2003. Sediment DIN fluxes and preferential recycling of benthic microalgal nitrogen in a shallow macrotidal estuary. *Marine Ecology Progress Series* 257: 25–36.
- Vander Zanden, M.J., M.K. Clayton, E.K. Moody, C.T. Solomon, and B.C. Weidel. 2015. Stable isotope turnover and half-life in animal tissues: a literature synthesis. *PLoS One* 10: e0116182.
- Wainright, S.C., C.M. Fuller, R.H. Michener, and R.A. Richards. 1996. Spatial variation of trophic position and growth rate of juvenile striped bass (*Morone saxatilis*) in the Delaware River. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 685–692.
- Westin, D.T., and B.A. Rogers. 1978. *Synopsis of Biological Data on the Striped Bass, Morone saxatilis (Walbaum) 1972*: Graduate School of Oceanography, University of Rhode Island.
- Zhao, L., C. Chen, J. Vallino, C. Hopkinson, R.C. Beardsley, H. Lin, and J. Lerczak. 2010. Wetland-estuarine-shelf interactions in the Plum Island Sound and Merrimack River in the Massachusetts coast. *Journal of Geophysical Research: Oceans* 115: n/a-n/a.