

The feeding ecology of striped bass and the role of ontogeny

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Abstract

Amidst constantly changing biotic and abiotic conditions, a more thorough understanding of the ecological consequences of dynamic predator-prey interactions will likely enable increasingly sustainable fisheries management. This study assessed the diet of striped bass, a generalist marine predator in coastal Massachusetts that feed on a variety of prey species and impose top-down pressure on other important fishery species, such as the American lobster and Atlantic menhaden. We explored the role of ontogeny using both stomach content and stable isotope analyses. Empirical results from 158 striped bass collected in northern Massachusetts revealed that striped bass in this area may have shifted from feeding predominantly on Atlantic menhaden in the late 1990s and early 2000s to Atlantic mackerel in this study. Stable isotope data suggested that the diet of striped bass is significantly linked with ontogeny: larger fish feed more heavily on benthic prey, particularly in the latter half of their seasonal residency in Massachusetts. Our study suggests that large striped bass gain an energetic advantage, as indicated by a liver somatic index, by feeding on benthic prey, possibly due to decreased foraging costs. Collectively, this work illustrates the ability of predatory fish to capitalize on the variability of forage fish populations, but highlights the importance of invertebrate prey for large striped bass and proposes underlying mechanisms driving ontogenetic diet switches from piscivory to benthivory.

Keywords: striped bass (*Morone saxatilis*), ontogenetic diet switch, predator-prey interactions, stomach content analysis, stable isotope analysis

Introduction

Comprehensive knowledge of predator-prey interactions is an important underpinning of ecosystem approaches to fisheries management, which is increasingly receiving attention (*e.g.*, North Pacific Fishery Management Council 2019). Further, temporal variability in species distributions, abundances, and size-frequencies necessitates that we routinely monitor ecosystems and the consequences of changing predator-prey interactions (Hilborn *et al.*, 2017). For example, predators can have strong top-down effects on prey populations and alter ecosystems (Denno and Lewis, 2009). They exert control over the distribution of species (Connell, 1961), mediate trophic cascades (Carpenter *et al.*, 1985), and control the flow of nutrients within food webs (Trussell *et al.*, 2006; Hawlena and Schmitz, 2010). Conversely, the availability of prey can

fundamentally affect predators (Sherwood *et al.*, 2002). For instance, along the coast of Canada, declining capelin (*Mallotus villosus*) availability (an important prey species) may have contributed to reduced lipid storage and spawning potential in Atlantic cod (*Gadus morhua*) (Sherwood *et al.*, 2007). There is growing evidence, however, that the reliance of a predator population on forage fish abundance is largely context-dependent. Hilborn and colleagues (2017) argued that forage fish abundance rarely has a measurable impact on predator abundance in U.S. fisheries, in part because predators may exhibit significant behavioral plasticity and modify their feeding to account for the natural variability of prey populations.

An important step in investigating predator-prey interactions involves characterizing the suite of factors that can alter prey selection (Juanes *et al.*, 1994). Optimal Forag-

ing Theory (OFT) suggests that a predator will select prey items by balancing the costs of energy acquisition and consumption relative to the intake of energy. More specifically, OFT predicts that predators will select prey that maximize the difference between the energetic value of the prey and the energetic cost of pursuing, attacking, and handling the prey (Pyke *et al.*, 1977). However, other factors may prevent predators from consuming optimal prey, including the presence of competitors (intra- and inter-specific competition), avoidance of their own predators, and morphological limitations such as gape width (Hughes, 1990; Hambright, 1991; Einfalt and Wahl, 1997). For instance, Milinski (1982) found that sticklebacks consumed fewer optimal prey items in the presence of superior intra-specific competitors. Additionally, optimal prey may change as predators grow, as they may “switch” to consuming a completely new, often larger prey type (*i.e.*, an ontogenetic diet shift) to overcome the aerobic and anaerobic costs of prey consumption (Townsend and Winfield, 1985; Sherwood *et al.*, 2002). Fluctuations in the abundance of prey populations may, however, drive predators to consume less energy-dense but more abundant prey, leading to declines in predator condition (Sherwood *et al.*, 2007).

In the western Atlantic, significant historic and more recent fluctuations in the abundance of both striped bass (*Morone saxatilis*) and their prey emphasize that predator-prey interactions are dynamic (Hill *et al.*, 1989; Atlantic States Marine Fisheries Commission, 2014). The striped bass is a highly mobile and generalist predator that typically spawns in western Atlantic, mid-coast United States estuaries and brackish habitats and migrates north during the spring and summer where they feed heavily on economically valuable prey species like the American lobster (*Homarus americanus*) and Atlantic menhaden (*Brevoortia tyrannus*) (Bigelow *et al.*, 1953; Boreman *et al.*, 1987; Nelson *et al.*, 2003). However, striped bass also consumed large quantities of the Blueback herring (*Alosa aestivalis*) (Greene *et al.*, 2009), which has since declined in many coastal and riverine ecosystems (Atlantic States Marine Fisheries Commission, 2017). Striped bass may have shifted their diet in the late 1990s towards other *Clupeid* prey that were still prevalent like the Atlantic menhaden (Nelson *et al.*, 2003). Our ability to sustainably manage both striped bass and their prey populations amidst such dynamic ecosystems will require a holistic understanding of the causes and consequences of these interactions across space and time.

Our study explored the feeding ecology and potential role of ontogeny in striped bass during their spring and summer migration into Massachusetts (MA) where they

consume a variety of prey items from zooplankton and fish to large invertebrates, such as the American lobster and green crab (*Carcinus maenas*) (Chapoton and Sykes, 1961; Manooch, 1973; Nelson *et al.*, 2003). Striped bass spawn and spend the majority of the year in the western Atlantic, mid-coast United States, and the vast majority of studies on striped bass feeding ecology have been conducted in the southern half of their range, such as the Chesapeake Bay (Dovel, 1968; Gardinier and Hoff, 1982; Dunning *et al.*, 1997; Griffin and Margraf, 2003). By and large, these studies indicate that juveniles feed on zooplankton and small crustaceans, while adult striped bass are predominately piscivorous, but may also consume a small proportion of invertebrate prey (Manooch, 1973; Gardinier and Hoff, 1982; Griffin and Margraf, 2003; Overton *et al.*, 2009). In contrast to these studies, Nelson *et al.* (2003, 2006) conducted an extensive diet study on striped bass collected between 1997–2000, whereby half of the collected fish were from the North Shore region of coastal MA. Their results suggested that as striped bass grow, they rely more heavily on benthic decapod prey, while smaller adults feed more on forage fish. This apparent ontogenetic diet shift may have other consequences on striped bass since crustaceans, such as American lobsters, may generate proportionally less energy per gram wet weight as compared to forage fish such as Atlantic herring, *Clupea harengus* (Nelson *et al.*, 2006). Crustaceans also require more time for predatory fish to digest them (Langton and Center, 1982) and, as such, may represent a suboptimal prey choice. The mechanisms for this potential ontogenetic prey shift are unclear, along with the degree to which suboptimal prey consumption influences the condition and growth of striped bass (Sherwood *et al.*, 2002).

To assess the diet of striped bass in northern MA, we conducted stomach content and stable isotope analyses. Traditional stomach content analysis can result in precise identification of prey species but offers only a recent snapshot of what an individual has been consuming. An alternative approach, utilizing stable isotopic ratios in predator tissue, provides an approximate yet more holistic metric because it examines the assimilation of consumed prey into predator biomass. The stable isotope ratios of nitrogen ($\delta^{14}\text{N} / \delta^{15}\text{N}$) indicate trophic position due to the predictable enrichment of nitrogen for predators relative to their prey (Fry, 1988; Post, 2002). Conversely, the stable isotope ratios of carbon ($\delta^{13}\text{C} / \delta^{12}\text{C}$) do not fractionate as much between trophic levels, and thus indicate benthic versus pelagic feeding due to differences in the enrichment of carbon isotopes at the base of the food chain (Post, 2002). As such, our study used stomach content and stable isotope analyses to identify important prey taxa, evaluate the role of ontogeny, and explore whether diet

metrics correlate with predator condition. Thus, we used this approach to explore possible mechanisms underlying diet transitions in striped bass.

Materials and Methods

All methods were approved by Northeastern University's Institutional Animal Care and Use Committee. From 2012 to 2016, striped bass were collected via rod-and-reel from the North Shore region of MA between Nahant and Gloucester, centralized around Salem Sound (Fig. 1; $n = 158$, total length (TL) range = 41.3cm–111.8cm, mean = 77.4cm). Once caught, fish were euthanized via pithing, and TL and fork length of a fish were measured to the nearest tenth of a cm, and fish were placed on ice. A small white muscle plug was extracted from an area 1–3cm below the first dorsal fin for stable isotope analysis and was immediately placed in foil and frozen.

In the laboratory, stomach contents were extracted, and prey items were identified to the lowest taxon possible. The number of individuals by species and the weight (g) of each species were recorded. Prey specimens in good condition (*i.e.*, not digested) were saved and frozen for stable isotope analysis. Samples for stable isotope analysis were taken internally from prey as to reduce the likelihood of contamination. Multiple metrics were used to examine the importance of prey taxon for striped bass. First, empty stomachs were removed from further

stomach content analysis (these fish were included in stable isotope analyses, however). Percent weight (W) is a useful metric for comparing the relative energetic value of prey, especially when individuals from different taxa are of disparate sizes (Zale *et al.*, 2012). Percent weight was calculated as the fraction of the total weight of an individual taxon by the total weight of stomach contents for all fish with non-empty stomachs. To determine how often striped bass consumed particular prey, we calculated the frequency of occurrence (F) for each prey item: the fraction of stomachs with an individual taxon by the total number of non-empty stomachs. Both W and F metrics were determined for all striped bass and by size category, whereby fish with non-empty stomachs were separated based on those below and above the mean TL (mean TL was calculated based on non-empty stomachs). To examine the importance of forage fish versus benthic decapods, the following prey items were classified as benthic decapods: Jonah crabs (*Cancer borealis*), rock crabs, green crabs, unclassified crabs (*Cancriidae*), unclassified decapods (*Decapod*), Asian shore crabs (*Hemigrapsus sanguineus*), and American lobsters. While sand shrimp (*Crangon septemspinosa*) is of the Order Decapoda, we did not classify it as a benthic decapod given its propensity to swim off the substrate, and the different striped bass attack strategies used to consume Sand shrimp versus other, larger benthic decapods (note, only two Sand shrimp were found in striped bass stomachs in our study).

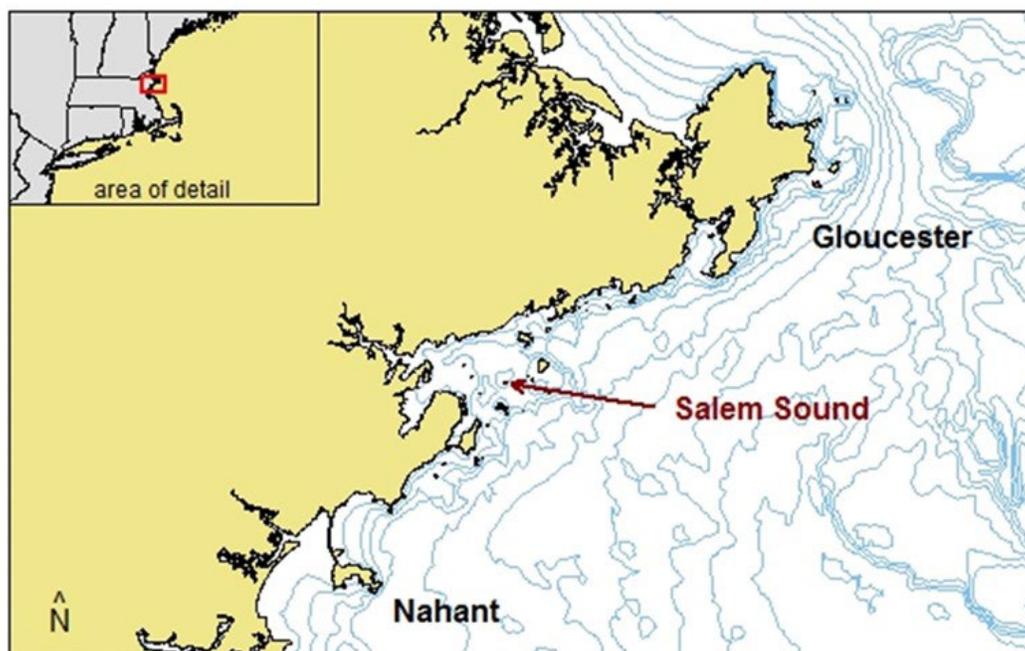


Fig. 1. Study area where striped bass were collected from 2012–2016 with inset map of Massachusetts.

To further explore the role of ontogeny in diet, stable isotope analysis was used as a longer-term approximation of predator diet because it measures prey that have been assimilated into muscle and other tissues (Post, 2002). Using sterile techniques, a small internal plug from each frozen sample was collected internally to avoid contamination. Each sample was then dried for 48 hours at 45°C and subsequently ground to a homogenous powder using a sterilized mortar and pestle. Samples were then weighed, placed in tin caps, and packed for shipment. All samples, including 10% duplicates (*i.e.*, separate sub-samples were taken from the same tissue to examine variation between replicate pairs), were sent to the Colorado Plateau Laboratories to be analyzed. Since lipid content can influence isotopic carbon signatures, prey and predator samples (Post *et al.*, 2007) were lipid-corrected by using methods of Skinner *et al.* (2016). As such, lipid percentages were generated based on a formula from Post *et al.* (2007), which was used as an input in another formula from Kiljunen *et al.* (2006) to correct $\delta^{13}\text{C}'$ values (hereby called $\delta^{13}\text{C}'$).

To estimate predator condition, two metrics were utilized. Liver somatic index (*LSI*) was calculated for each fish as: $LSI = \text{wet liver weight} / \text{wet body weight} * 100$ (Adams and McLean, 1985). An individual fish's *LSI* should be closely correlated with health since excess energy is stored as glycogen in the liver, typically after periods of high prey consumption (Hoque *et al.*, 1998). Thus, higher relative *LSI* values should indicate a healthier individual with greater energy stores. To explore the effects of diet on striped bass relative body size, the Relative Condition Factor (K_n) was used, which is standardized to account for allometric growth (Le Cren, 1951). Here, individual fish weight (w) was divided by the length specific mean weight (w') of striped bass in MA such that $K_n = w / w'$. Length specific mean weight was calculated according to the MA striped bass Monitoring Report for 2014: $\log_{10}(W_p) = -3.455 + 3.001 * \log_{10}(L_i)$, where W_p is weight in pounds (1 pound = 454 grams) and L_i is the total length in inches (1 inch = 2.54 cm) (Nelson, 2015).

Statistical Analysis

Linear regression models were used to explore the potential relationships between striped bass stable isotopic values for $\delta^{13}\text{C}'$ and $\delta^{15}\text{N}$ and striped bass TL and the day of year (day). We also examined the relationships between response variables, *LSI* and K_n , and potential predictors, striped bass TL and $\delta^{13}\text{C}'$, as a proxy for benthic feeding using linear regression models. As such, the four models were as follows; (1) $\delta^{13}\text{C}' = f(\text{striped bass TL} * \text{day})$; (2) $\delta^{15}\text{N} = f(\text{striped bass TL} * \text{day})$; (3) $LSI = f(\text{striped bass TL} * \delta^{13}\text{C}')$; (4) $K_n = f(\text{striped bass TL} * \delta^{13}\text{C}')$. All data

were modeled as normally-distributed errors (Gaussian GLM) in R (R Core Team, 2020) and models included an interactive term between covariate predictors. Assumptions of residual normality were assessed using normal quantiles plots, while homoscedasticity was inspected using residuals versus fitted values plots. Regression terms were deemed significant at $\alpha \leq 0.05$.

Results

Atlantic mackerel, *Scomber scombrus*, was the most important prey item by weight (42.8%), followed by American lobster (19.9%), unclassified fish prey (10.3%), and Menhaden (7.0%), while several other species were of much lower importance (Fig. 2). Frequency of occurrence of unclassified fish prey (33.3%), Atlantic mackerel (17.7%), American lobster (16.7%), and rock crabs, *Cancer irroratus*, (16.7%) were higher than other prey taxa consumed by striped bass (Table 1, Fig. 2a). When aggregated by size, small striped bass (*i.e.*, those below the 76.54cm mean TL for non-empty fish) and large striped bass had consumed a similar amount of fish prey, representing 79.5% and 61.2% of their diet by weight, and were found in 58.8% and 64.7% of non-empty stomachs, respectively (Fig. 2b). Conversely, large striped bass consumed more benthic decapods by weight (35.5%) and more frequently (51%) compared to small striped bass (13.2% and 35.3%, respectively). Examination of all striped bass (*i.e.*, those with prey in their stomachs and those with empty stomachs) revealed that the large and small fish had empty stomachs 39% and 32% of the time, respectively.

Stable isotope analysis revealed little variation between replicate pairs (mean of absolute differences between pairs) for striped bass muscle samples ($\delta^{13}\text{C}' = 0.19\text{‰}$, $\delta^{15}\text{N} = 0.20\text{‰}$, $n = 15$). Striped bass stable isotopic values were adjusted to account for trophic fractionation between predator and prey ($\delta^{13}\text{C}' = +0.8\text{‰}$, $\delta^{15}\text{N} = +3.4\text{‰}$, Fig. 3a) and then for plotting purposes and to visually compare striped bass to their prey, mean isotopic values for striped bass were plotted alongside prey values (Fig. 3b) (Zanden and Rasmussen, 2001). Both species of prey fish, Atlantic herring and Atlantic mackerel, had the highest $\delta^{15}\text{N}$ and lowest $\delta^{13}\text{C}'$ values among prey, indicating that they represent a higher trophic level and consume a more pelagic food source than crustacean prey. Meanwhile, the two crab species, green crab and rock crab, and the American lobster were of a lower trophic level and $\delta^{13}\text{C}'$ was highly enriched, indicating that these species represent benthic prey consumed by striped bass (Fig. 3a).

A model of stable carbon isotopes revealed a significant interaction between TL and day (degrees of freedom (DF)

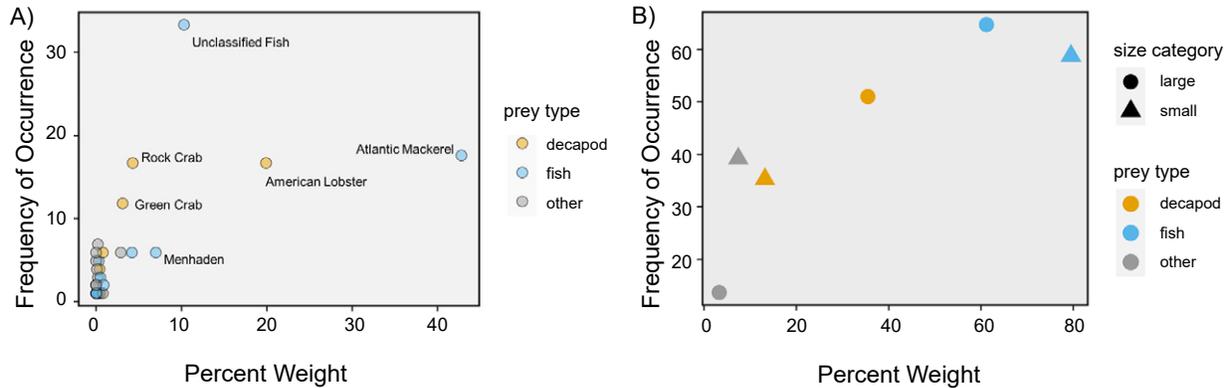


Fig. 2. Plots of prey taxon importance for striped bass collected along the north shore of Massachusetts from 2012–2016. **A)** Plot of stomach content data from all striped bass with the most important prey items by weight and frequency of occurrence are labeled. **B)** Stomach content data summarized by prey type for striped bass below (small = triangle points) and above (large = circle) points the mean total length (76.54cm). Points in both plots are coloured by prey type.

= 151, t -value = 2.456, p -value = 0.015; Fig. 4a). To aid in the visualization of this significant interaction, we conducted linear regression and quantified the slopes for the relationship between $\delta^{13}\text{C}'$ and day for striped bass whose length was ± 1 standard deviation from the mean, which revealed a positive slope for larger fish and negative slope for smaller fish (Fig. 4b). TL and day were not significantly related to $\delta^{15}\text{N}$ (DF = 151, TL: $t = -1.173$, $p = 0.243$; day: $t = -1.863$, $p = 0.064$; TL x day: $t = 1.569$, $p = 0.119$).

Examination of condition indices revealed significant interactions between stable carbon isotopic values, TL, and LSI (DF = 147, $t = 2.593$, $p = 0.011$; Fig. 5a). Again, we used linear regression to quantify the slopes for the

relationship between LSI and $\delta^{13}\text{C}'$ for striped bass whose length was ± 1 standard deviation from the mean to aid in result interpretation. This revealed a positive slope for larger fish and negative slope for smaller fish (Fig. 5b). Lastly, K_n was not significantly related to $\delta^{13}\text{C}'$ and TL (DF = 148, $\delta^{13}\text{C}'$: $t = -1.731$, $p = 0.09$; TL: $t = 1.798$, $p = 0.074$; TL x $\delta^{13}\text{C}'$: $t = 1.707$, $p = 0.09$).

Discussion

Our results indicated that striped bass in the North Shore region of MA maintain a diet high in Atlantic mackerel, which is in contrast to research two decades earlier that suggested striped bass diets were dominated by Atlantic

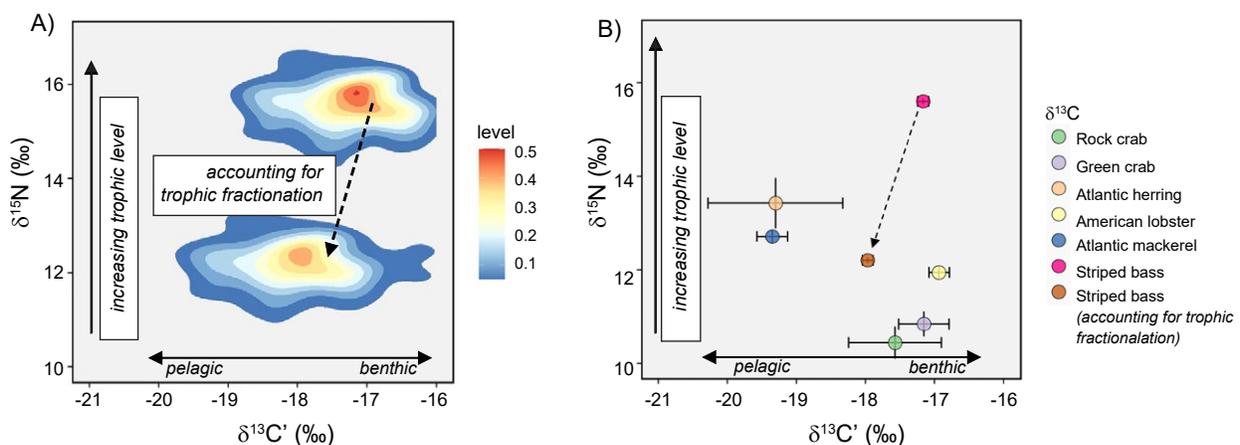


Fig. 3. Prey and striped bass stable isotopic values. Carbon stable isotopic values were lipid corrected and striped bass values are displayed with and without a correction for trophic fractionation. **A)** Mean stable isotopic values for important prey taxa and striped bass. **B)** Density plot for striped bass stable isotopic values showing the distribution of data.

Table 1. Summary of stomach contents by prey of Striped bass collected along the north shore of Massachusetts from 2012–2016. Note that the weight of one Atlantic herring (*Clupea harengus*) was lost, so the average weight of all other Atlantic herring was used as a proxy. In one other case, the weight of an unclassified fish (highly digested) was lost, so the weight of another unclassified fish of identical morphology (from a Striped bass caught on the same day), as recorded in a lab notebook, was used as a proxy.

taxon	total number of individuals	percent number	total weight (g)	percent weight	number of times in stomach	frequency of occurrence
<i>Ammodytes americanus</i>	8	0.7	16	0.3	5	4.9
<i>Amphipoda uncl</i>	86	7.9	2	0.0	5	4.9
<i>Brevoortia tyrannus</i>	6	0.6	331	7.0	6	5.9
<i>Cancer borealis</i>	6	0.6	25	0.5	1	1.0
<i>Cancer irroratus</i>	32	2.9	203	4.3	17	16.7
<i>Cancridae uncl</i>	6	0.6	40	0.8	6	5.9
<i>Carcinus maenas</i>	18	1.7	145	3.1	12	11.8
Cephalopoda	7	0.6	138	2.9	6	5.9
<i>Clupea harengus</i>	14	1.3	198	4.2	6	5.9
<i>Crangon septemspinosa</i>	2	0.2	1	0.0	2	2.0
Caprellidae	56	5.2	1	0.0	1	1.0
<i>Decapod uncl</i>	1	0.1	3	0.1	1	1.0
<i>Ensis directus</i>	1	0.1	0	0.0	1	1.0
<i>Etrumeus teres</i>	1	0.1	16	0.3	1	1.0
Euphausiidae	1	0.1	0	0.0	1	1.0
Gammaridae	488	44.9	10	0.2	7	6.9
<i>Gastropod</i>	11	1.0	12	0.2	3	2.9
<i>Hemigrapsus sanguineus</i>	8	0.7	17	0.4	4	3.9
<i>Homarus americanus</i>	28	2.6	937	19.9	17	16.7
<i>Idotea</i> sp.	12	1.1	2	0.0	2	2.0
<i>Idotea baltica</i>	12	1.1	2	0.0	6	5.9
<i>Melanogrammus aeglefinus</i>	1	0.1	3	0.1	1	1.0
<i>Mytilus edulis</i>	167	15.4	5	0.1	4	3.9
<i>Nereis virens</i>	7	0.6	38	0.8	1	1.0
<i>Osmerus mordax</i>	1	0.1	2	0.0	1	1.0
<i>Osteichthyes uncl</i>	65	6.0	486	10.3	34	33.3
<i>Pholis</i> sp.	6	0.6	22	0.5	3	2.9
<i>Scomber scombrus</i>	31	2.9	2 019	42.8	18	17.6
<i>Tautogolabrus adspersus</i>	2	0.2	41	0.9	2	2.0
Unclassified organism	2	0.2	0	0.0	2	2.0
TOTALS	1 086		4 716			

menhaden (Nelson *et al.*, 2003). The occurrence of Atlantic mackerel in striped bass diets increased over 10-fold, potentially indicating a major shift in local availability of forage fish. As opportunistic predators, striped bass appeared to have capitalized on the local variability of forage fish populations (Hilborn *et al.*, 2017). Additionally, Nelson *et al.* (2003) found that striped bass similar in size to those sampled in this study consumed predominantly Atlantic menhaden in the later summer months, which is when this forage fish typically migrates into nearshore waters along coastal MA. Anecdotal evidence suggests that Atlantic menhaden abundances in Salem Sound have been very low in recent years, whereas there was a considerable uptick in Atlantic mackerel spawning-stock-biomass and total biomass directly following the Nelson *et al.* (2003) diet study (42nd Northeast Regional Stock Assessment Workshop, 2006).

Stomach content analysis revealed that the American lobster may also be a critical prey item, and was the most important invertebrate taxa by weight, highlighting an interaction with another vital New England fishery. Catch of American lobster in MA was valued at over \$82 million in 2016, second only to Sea scallops (MA Division of Marine Fisheries Annual Report, 2016). Rock crabs were consumed at similar rates but are much smaller and thus likely represent a lesser energy source. This finding agrees with Nelson *et al.* (2003) in their study of adult striped bass throughout MA from 1997–2000, where crustaceans were found to represent ~45% of striped bass

diet by weight within the North Shore region. While fish in our study consumed a slightly smaller proportion of crustaceans, the overall consumption of juvenile American lobster remained high.

Analysis of stable isotopes offers a more holistic examination of diet ontogeny as we could sample all fish (including fish with empty stomachs) and because isotopic signatures integrate across longer periods (Post, 2002). As indicated by stable carbon isotopic signatures, striped bass consumed organisms from both benthic and pelagic environments during the beginning of the spring/summer migration into MA. As the summer progressed, large striped bass relied heavily on benthic prey. Given the time lag between prey consumption and assimilation into muscle tissue (Buchheister and Latour, 2010), it is plausible that large striped bass feed primarily on pelagic food sources before their immediate arrival into MA, followed by a switch to benthic prey in MA where there is higher availability of crustaceans such as American lobsters (Thunberg, 2007).

This ontogenetic diet switch is somewhat counterintuitive given that fish prey offers more energy per gram wet weight (Steimle and Terranova, 1985) and since crustaceans, like the American lobster, are partly composed of chitin (Boßelmann *et al.*, 2007), an organic material that is harder to digest than soft flesh. Analysis of striped bass *LSI* provides insight into possible explanations. Specifically, feeding on benthic organisms was slightly negatively

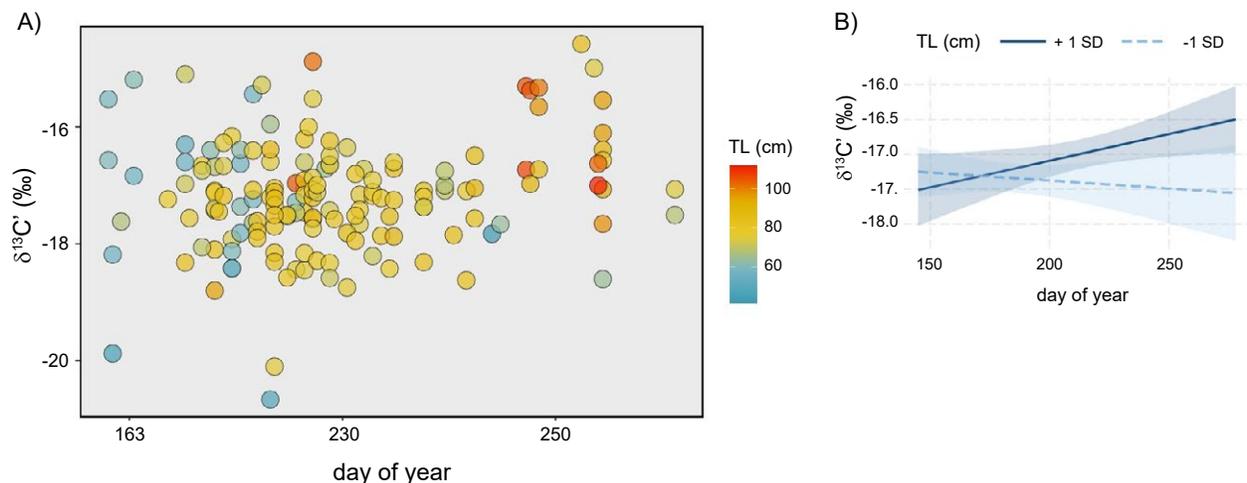


Fig. 4. Carbon isotopic values from the white muscle of striped bass collected along the north shore of Massachusetts from 2012–2016 ($n = 155$). Carbon isotopic values are compared to striped bass total length (TL) and the day of the year that each fish was caught. **A**) Points are coloured according to striped bass TL. **B**) Linear regression slopes for the relationship between carbon and day of year for striped bass whose length is +1 Standard Deviation (SD) from the mean (solid dark blue line) and -1 SD from the mean (dotted light blue line). Shaded regions represent 95% confidence intervals.

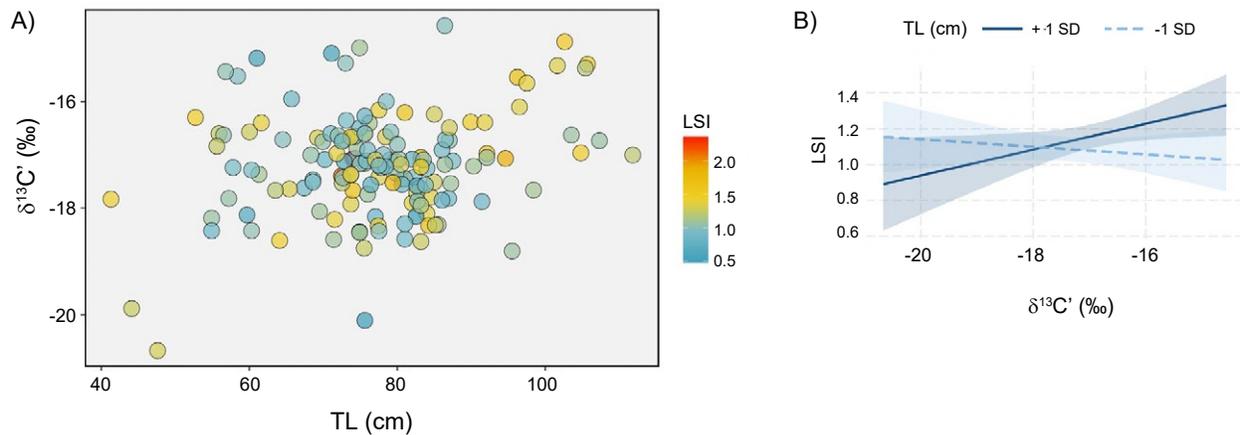


Fig. 5. Liver Somatic Index (LSI) compared to carbon isotopic values from the white muscle of striped bass collected along the north shore of Massachusetts from 2012–2016 ($n = 151$). Carbon isotopic values are compared to striped bass total length and LSI. **A)** Points are coloured according to LSI. **B)** Linear regression slopes for the relationship between $\delta^{13}C'$ and LSI for striped bass whose length is +1 Standard Deviation (SD) from the mean (solid dark blue line) and -1 SD from the mean (dotted light blue line). Shaded regions represent 95% confidence intervals.

correlated with the condition of small striped bass, as their livers weighed less relative to those of their pelagic-feeding counterparts. Conversely, benthic feeding seemed to significantly favour larger striped bass such that fish that fed on benthic prey items had larger livers, indicating that benthic feeding may allow these predators to build up better energy reserves. Given that striped bass experience decelerating growth by length, but their weight increases exponentially with age, large striped bass must propel a relatively heavier body through the water to capture prey. Chasing after fast-moving forage fish is thus potentially associated with high attack and pursuit costs for larger striped bass, while smaller, more streamlined individuals may be more capable of efficiently searching for and capturing forage fish. This finding is supported by work from a lake ecosystem, where pelagic Eurasian perch, *Perca fluviatilis*, were more streamlined than Eurasian perch feeding in the littoral zone (Quevedo *et al.*, 2009).

By consuming benthic decapod prey that are slower than forage fish and potentially easier to capture, large striped bass may be able to reduce the energetic costs associated with capturing prey; which aligns with OFT (Pyke *et al.*, 1977). This feeding strategy would allow striped bass to acquire increased energy reserves, as suggested by our LSI analysis. Similarly, work by Sherwood *et al.* (2002) suggested that the burst speed required to capture prey is an important component of foraging activity costs. In a lake ecosystem, the authors measured the lactate dehydrogenase levels in the white muscle of yellow perch, *Perca flavescens*, which is a proxy for anaerobic metabolism and burst swimming activity. Predatory Yellow perch

that exhibited ontogenetic variation in diet and shifted from consuming zooplankton to benthic invertebrates at first and later to large prey fish were able to reduce their anaerobic activity costs in a step-wise fashion with each diet switch. By resetting their activity costs after each ontogenetic prey switch, these fish were able to maintain growth and prevent a bioenergetic bottleneck. It is plausible that large striped bass switch to feeding more heavily on American lobsters and other large crustacean prey to reduce the metabolic costs of foraging. However, our findings do not rule out other explanations for this ontogenetic transition toward benthic invertebrates. For example, it is possible that smaller striped bass would benefit from consuming benthic invertebrates but are unable to due to morphological challenges (*e.g.*, limited gape size) or resource competition from larger individuals.

Collectively, our study illustrates the significance of ontogenetic diet transitions for predatory fish, whereby the apparent transition to benthic decapods by large striped bass highlights that diversity in prey availability is important for maintaining predator condition with growth. We provide explanations for the energetic basis for this diet ontogeny in striped bass that would be supported by OFT. Specifically, stomach content and stable isotope analyses suggest that diet is driven partly by ontogenetic processes, such that large striped bass may benefit energetically from the consumption of large crustaceans over forage fish prey. A proposed mechanism for this ontogenetic shift from piscivory to benthivory follows that smaller, more streamlined striped bass likely benefit from the consumption of energetically rich forage fish. Conversely,

large striped bass may suffer from increased attacking or searching costs associated with pelagic feeding and, as such, likely transition to benthic feeding, as suggested by enhancement in condition. Future experimental, comparative, and modeling studies should continue to unpack these mechanisms, providing additional insights into the complex relationships between predator and prey. Moreover, this study illustrates the variability of some predator-prey interactions over time but suggests that OFT can help to anticipate the consequences of fluctuating species abundances and size-frequency, spatial, and temporal distributions.

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