THE IMPACTS OF THE ZEBRA MUSSEL (*DREISSENA POLYMORPHA*) ON THE FEEDING ECOLOGY OF EARLY LIFE STAGE STRIPED BASS (*MORONE SAXATILIS*)

A Final Report of the Tibor T. Polgar Fellowship Program

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ABSTRACT

Despite numerous studies of the ecological effects of the zebra mussel (*Dreissena polymorpha*) invasion in the Hudson River Estuary, the impacts on larval and juvenile fishes have been poorly characterized. In this study, changes in early life stage fish diets upon invasion of the zebra mussel were analyzed, focusing on the striped bass (*Morone saxatilis*). Changes in prey diversity, frequency of prevalent prey items, and a prey habitat index from 1988 (before the mussels arrived), to 2008 were quantified. Sample years bracketed a period of increasing mussel impacts, followed by a period of apparent ecosystem recovery. For the striped bass, prey diversity increased during peak invasion years and then declined in 2008. A similar trend was seen with the frequency of prevalent prey. After they arrived, zebra mussels became one of the main components of the diet. Over time, bass fed increasingly on benthic prey rather than pelagic prey. Overall, the zebra mussel has changed many aspects of the striped bass diet, some in surprising ways, and although some of those aspects are returning to their pre-invasion condition, others are remaining the same as they were during peak invasion years.

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INTRODUCTION

Invasive species have a remarkable ability to alter the environment into which they are introduced. The zebra mussel (*Dreissena polymorpha*) is an invasive bivalve from Eurasia that has thrived outside of its native range. Zebra mussels first arrived in the Great Lakes region of the United States in the mid 1980s. The mussels have since spread rapidly throughout the freshwater systems of the eastern half of the country. By 1991, zebra mussels had reached the northernmost point of the Hudson River Estuary, the Federal Lock and Dam at Troy, and have since become well established throughout the freshwater tidal length of the river (Strayer and Malcom 2006).

After arriving in the Hudson, zebra mussels began to change both the abiotic and biotic components of the ecosystem. The benthic substrate of the freshwater tidal Hudson was once dominated by mud and sand, but as the mussels have spread the substrate is now dominated by the mussels' hard shells (Strayer 2009). Zebra mussels are highly efficient filter feeders that feed on a variety of freshwater organisms depending upon their size. Small mussels feed primarily on phytoplankton, while larger mussels can consume both phytoplankton and small zooplankton (Pace et al. 2010). By 1992, zebra mussels had caused an 80-90% decline in phytoplankton biomass (Pace et al. 1998). Declines in phytoplankton led to increases in water clarity and nutrient levels, including nitrogen and phosphorous (Strayer 2009). All microzooplankton groups in the freshwater tidal portion of the Hudson River declined after the zebra mussel invasion, and an overall 70% decline in zooplankton biomass was seen by 1995 (Pace et al. 1998). These declines in primary consumers were likely caused by both bottom-up food web effects from the phytoplankton decline as well as the direct consumption of zooplankton by larger zebra mussels (Pace et al. 1998; Strayer et al. 2011).

Despite the huge changes that have occurred in the Hudson River Estuary since the zebra mussels' arrival, the ecosystem has shown signs of recovery. In recent years, the Hudson has seen declines in zebra mussel population density, filtration rate, body size, and annual survivorship in the river (Strayer et al. 2011). It is thought that these declines could be driven by natural predators, such as blue crabs, in the river utilizing zebra mussels as a food source (Carlsson et al. 2011), leading to a recovery in primary consumer abundance (Pace et al. 2010).

Many of the impacts of the zebra mussel are poorly understood due to the difficulties associated with studies covering large spatial scales and because many of the variables are difficult to measure and analyze (Strayer 2009). One of these poorly understood areas is the impact that zebra mussels have had on the secondary consumers of the Hudson, particularly early life stage fish species. The Hudson River estuary serves as an important nursery habitat for a variety of larval and juvenile fish species, and a decline in phytoplankton could continue to translate up the food web to the fish that live in the river. An extensive study of both pelagic and littoral larval and juvenile fish in the Hudson River Estuary found that pelagic species have declined in population size and exhibited slower growth rates since the arrival of the zebra mussel, while littoral species were relatively unaffected (Strayer et al. 2004). Early life stage pelagic fish are dependent upon their food source of pelagic primary consumers to grow and thrive. Presumably, the decline in pelagic food sources caused these fish to begin foraging in the benthos, where the populations of primary consumers were less affected. Being less successful at obtaining food in these new foraging habitats could cause declines in populations and growth rates. Although it is assumed that the declines in early life stage fish were caused by the declines in their pelagic food source, no studies have been done to observe how the diet and feeding ecology of these fish has changed. This study focuses on changes in the diet of the early life stages of one Hudson River Estuary pelagic fish species, the striped bass (*Morone saxatilis*), over a twenty year time period that spans from before the zebra mussels arrived in the river until the present.

The ability of striped bass populations to maintain stable population abundances, distributions, and apparent growth rates, may indicate that they were able to successfully change their diets in response to changes made by zebra mussels. Striped bass are known to be generalist predators and may have been better able to adapt to changes in prey availability when compared to the other pelagic fish species in the study by Strayer et al. 2004.

It is predicted that as striped bass forage for unfamiliar prey items during the transition from pelagic to benthic feeding the diversity of their prey will increase over time. The most abundant prey items should also change over time due to the presumed pelagic to benthic feeding shift. In the most recent study year, results could be similar to those found before the zebra mussel invasion due to the observed recovery of zooplankton in the Hudson River.

METHODS

Year and Fish Selection:

All of the fish used in this study were provided by Hudson River Utilities annual survey of fish populations in the Hudson River, and methods for the survey can be found in the annual Year Class Report for the Hudson River Estuary Monitoring Program (ASA Analysis and Communication 2001). Fish were caught in the river during a 20 year period spanning across the zebra mussel invasion. 1988 was selected as the initial year of the study to show what fish diets were like before the zebra mussels arrived in the river. The years 1995, 1999, and 2008 were selected to represent years during peak zebra mussel invasion and the present day. Fish were preserved in formalin and were identified to species by Normandeau Associates in Bedford, New Hampshire. The fish that were caught in 1988 were transported to the ichthyology collection at the New York State Museum in Albany, New York where they were transferred from formalin to 70% ethanol and their species identifications were confirmed. The fish from all other years remained in the storage facilities of Normandeau Associates. Fish from 1995, 1999, and 2008 were obtained from Normandeau's facilities in Bedford. The fish from 1988 were obtained from the New York State Museum in Albany.

Fish were selected for dissection based on a variety of factors including their size, the condition of their preservation, confirmation of their species identification, and where they were caught in the river. Fish were excluded if they were dried out due to evaporation of the formalin they were preserved in, or if their bodies had been otherwise damaged. Fish needed to be large enough to dissect with 2 mm cutting surface spring dissecting scissors, and most fish were less than 50 mm long. Once a fish was selected to be dissected, it was confirmed that it was a striped bass by counting the number of anal fin rays it possessed. A striped bass should possess 13-14 anal fin rays as opposed to the white perch, which has 12 anal fin rays (Waldman et al. 1999). Using this external character to distinguish between striped bass and white perch was found to be 96% accurate when the fish were 8.0 mm and larger (Waldman et al. 1999). All of the bass selected came from the freshwater tidal length of the river between river kilometer 100 and river kilometer 248.

Dissection and Identification:

Once a striped bass was selected, it was prepared for dissection and then carefully dissected to mitigate specimen damage. Each bass was assigned a unique sample number, its standard length was measured, and it was weighed in a sealed container filled with water. The fish was dissected under a dissecting scope using 2 mm or 4 mm spring dissecting scissors. The fish was first cut from the vent up towards the lateral line and then across to the operculum. A second cut was then made through the pectoral girdle and the operculum angled up towards the eye. Finally, a cut was made through the operculum connecting the first and second cuts. This allowed the esophagus, stomach, and intestines to be easily removed from the body cavity with forceps. Once removed from the body cavity, the intestines and any part of the gill basket that may have been extracted with the stomach were snipped off with the dissecting scissors. Any fat bodies that were still attached to the stomach were removed with forceps.

After the stomach was removed and cleared of any fat, the gut contents were removed. To do this, a cut was made from the esophagus to the end of the stomach. The stomach was then spread open and its contents were removed with a pipette. The contents of the stomach were preserved in 70% ethanol in microcentrifuge tubes marked with the fish's sample number. This procedure was followed for thirty striped bass from each year for a total of 120 fish. Stomach contents were identified on a Sedgewick-Rafter gridded counting slide under a compound light microscope. Each prey item was counted and identified to the lowest taxonomic level possible using Peckarsky et al.'s Freshwater Macroinvertebrates of Northeastern North America (1990) and the University of New Hampshire's Image-Based Key to the Zooplankton of the Northeast (USA) (Haney et al. 2010). Some prey items that could be identified to taxon were noted for presence but not counted individually because it was likely that they were ingested in conjunction with another prey item (i.e. copepod eggs and spermatophores).

Data analysis:

Changes in prey diversity over time were determined using the Shannon-Wiener Diversity Index:

$$\mathrm{H} = \left(-\sum_{i=1}^{n} p_i \log p_i\right)/\mathrm{S}$$

where p_i is the number of individuals for species number i divided by the total number of individuals, and S is the species richness of the sample (Shannon 1948). The length of each fish was log transformed and an analysis of covariance (ANCOVA) was conducted [using SAS version 9.3] for the two main effects of length and year as well as the interaction effect of length-by-year. If the interaction effect of length by year was found to be not significant, it was dropped and only the two main effects were run. A least-squares-means estimation was used to correct for the effect of variation in fish size on the diversity of prey present in each year. The length-corrected least squares mean of diversity was graphed for each year to show how prey diversity changed over time. A bar graph was generated to demonstrate the overall diversity present in the striped bass diet throughout the entire study. The abundance of each prey item was log transformed to enhance the presence of prey items present in low abundance and diminish the presence of prey items present in high abundance so that prey diversity could be better visualized.

To determine the changes in predominant prey items, the four prey items that were present in the highest numbers in the fish diet were determined. The decision to look at the four most abundant prey items was arbitrary. The total number of each prey item present in an individual fish and the length of the fish were then log transformed. An ANCOVA was conducted on the incidence of each one of the predominant prey items. The two main effects of length and year were tested as well as the interaction effect of length by year. If length by year was not significant, it was dropped and only the two main effects were run. A least squares means estimation was run in SAS to correct for the effect of fish size. The logarithm of frequency of prey items for each year was then plotted with the error for the least squares means.

To determine the degree to which the fish for each year were feeding pelagically or benthically, a weighted average was used. For each fish, the total number of each prey item was multiplied by two if the prey item lived in the benthos or by four if the prey item lived in the pelagic zone. These values were then totaled and divided by the total number of prey items found within that fish. The resulting value was termed the fish's prey habitat index (PHI). This method is a modified version of the trophic level equation used by Pauly and Palomeres (2000) and Stergiou and Karpouzi (2002). Each fish's PHI within a specific year was then averaged together to achieve an overall PHI for that year. The changes in the yearly PHIs can then be compared to determine how the feeding habitats of the fish have changed over time. PHIs closer to four indicate that the fish are feeding mostly pelagically, while PHIs closer to two indicate that the fish are feeding mostly benthically. The PHIs obtained for each year were plotted with standard errors.

RESULTS

Prey Diversity:

Copepods were the most dominant prey item, which is best demonstrated by the non-log-transformed frequencies in Figure 1. A log-transformation reveals that the most prevalent prey items in the diet were copepods, amphipods, zebra mussels and *Leptodora sp.* (Figure 2). Items classified as "Other" included items that could not be attributed to a specific organism such as eggs, dismembered arthropod legs, and small worms that could not be identified to a taxon. These items occurred rarely and often only within a single fish. Although some amphipods, isopods, and copepods could be identified to more specific levels of classification, many of the finer details of the organisms were damaged or lost due to ingestion by the bass and the preservation process. In order to better demonstrate the portion of the diet contributed by each of these groups, organisms that could be identified to higher taxonomic levels were combined with the less specific group.

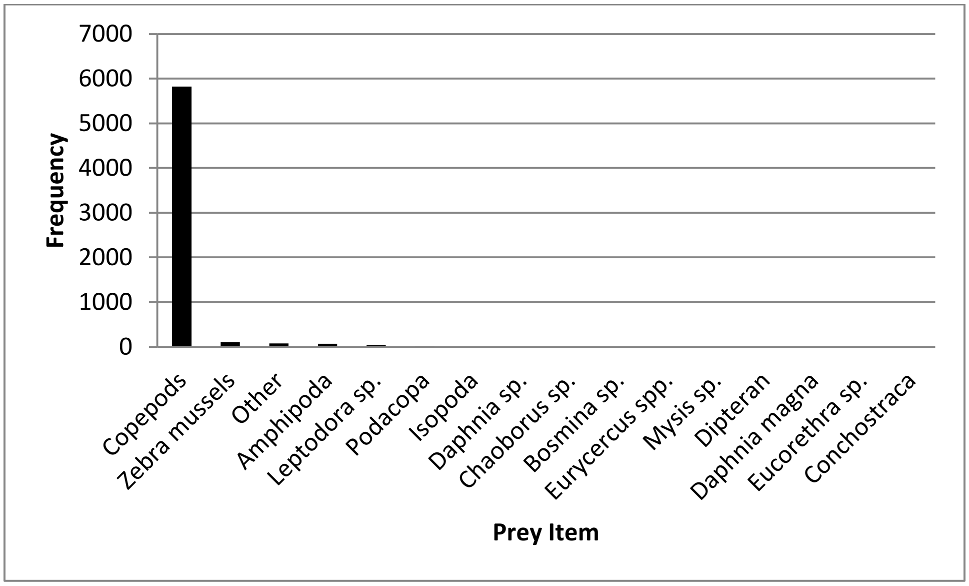

Figure 1. The frequency of prey items found in the striped bass diet across all four years (1988, 1995, 1999, and 2008) without log transformation illustrates the dominance of copepods in the diet.

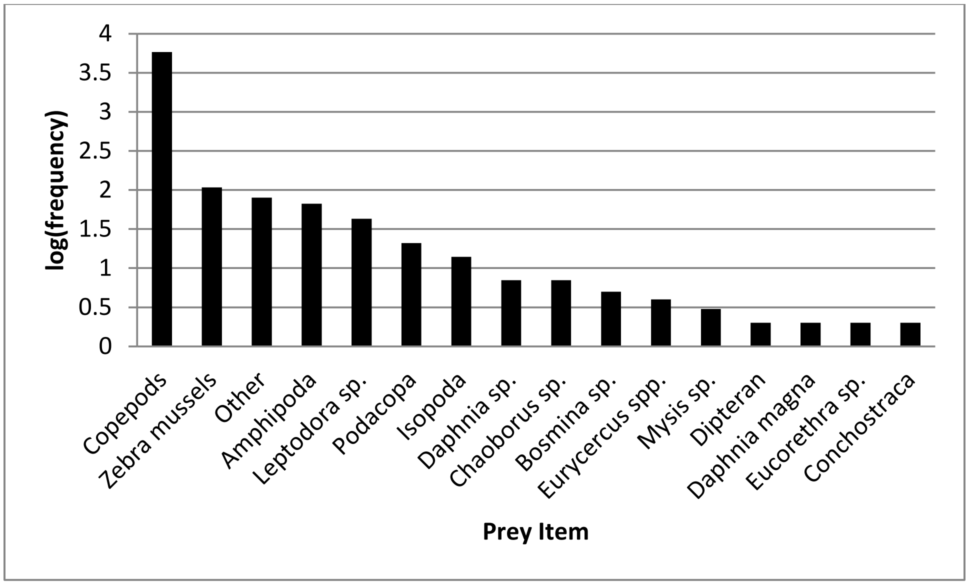

Figure 2. After a log transformation, the contribution of each prey item to the makeup of the striped bass diet across all years four becomes clearer.

The Shannon-Wiener diversity index showed that diversity was higher during the years of peak mussel invasion, 1995 and 1999, and then declined in 2008. In the first ANCOVA that was run, the effect of length by year was found to be not significant with a p-value of 0.3038. The reduced model showed that the year effect had a p-value of less than .0001 and the length effect had a p-value of 0.0690 (Table 1). Diversity in the diet significantly increased between 1988 and 1995, remained the same in 1999, and then declined significantly in 2008 to levels lower than in 1988 (Figure 3). These changes in diversity appear to have been strongly driven by changes in species number rather than changes species evenness.

Table 1. ANCOVA for changes in the Shannon-Wiener diversity index by year and length.

Source	DF	Type III SS	Mean Square	F	Pr > F
Year	3	0.758	0.253	7.84	<.0001
Length	1	0.109	0.109	3.37	0.0690
Error	115	3.71	0.0322		

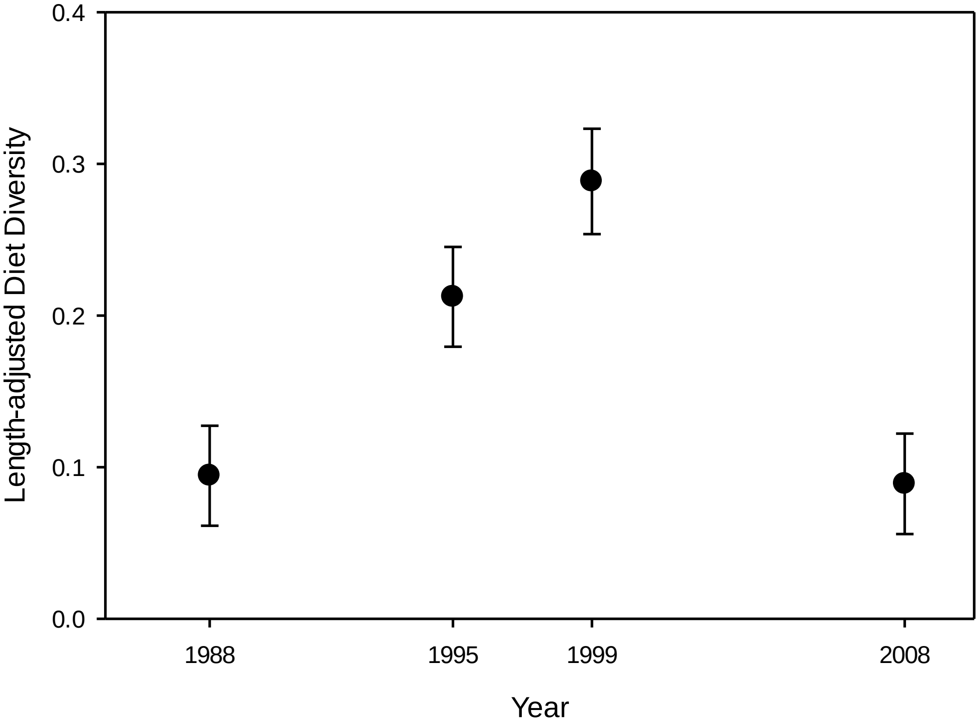

Figure 3. The changes in the Shannon-Wiener diversity index over time show that there was a significant increase in prey diversity between 1988 and 1995. A significant decrease in prey diversity between 1999 and 2008 was also seen.

Prevalent Prey Items:

An analysis of the prey diversity showed that the most prevalent prey items were copepods, amphipods, zebra mussels, and *Leptodora sp*. The abundance of each prey item varied from year to year (Table 2 a-d). Figure 4 shows that for each prey item the size adjusted log transformed frequency in the diet increases from 1988 to 1995 and then declines from 1999 to 2008. This trend is most pronounced in the copepods. Zebra mussels were not present in the diet in 1988, but appeared in striped bass stomachs in 1995 and remained present in the diet through 2008. Generally, as fish length increased the number of prey items within each fish also increased (Figure 5). This length effect was significant for each prey item except copepods (Table 2a). The length effect varied among years for only one prey species, *Leptodora* (Table 2d). In larger fish, the number of prey items seems to decrease with length. This could be due to the low sample size of larger fish or because the fish are able to eat larger prey items and thus consume fewer individuals. *Leptodora sp.* was the only prey item in which there was a significant interaction effect of length by year.

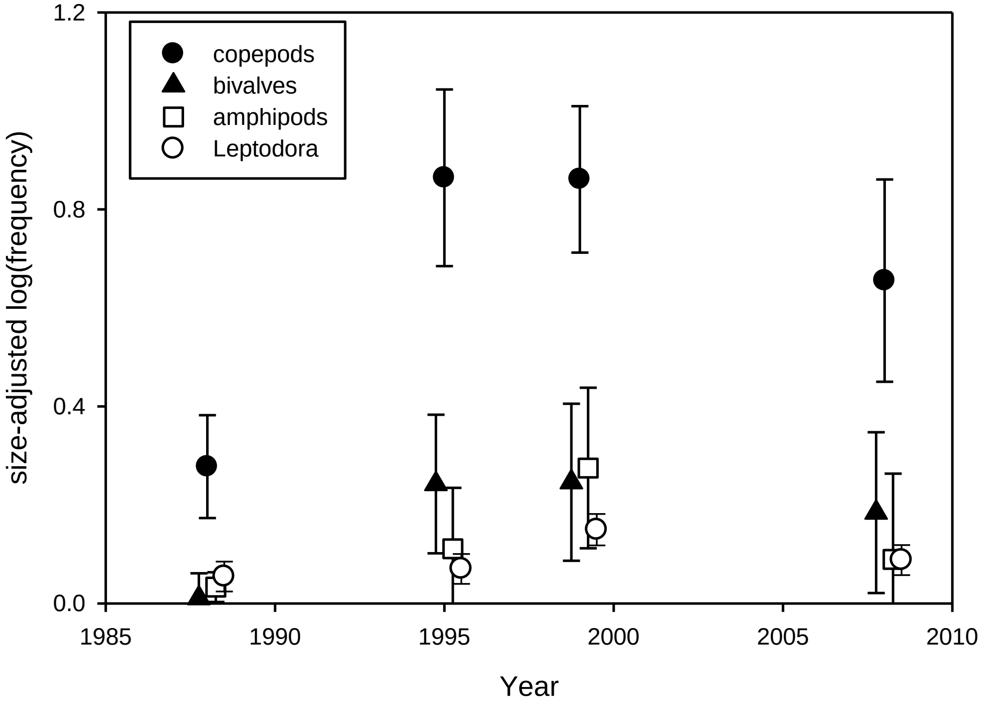

Figure 4. Changes in the size adjusted log transformed frequency of the most prevalent prey items (copepods, zebra mussels, amphipods, and *Leptodora sp.*) in the diet over time.

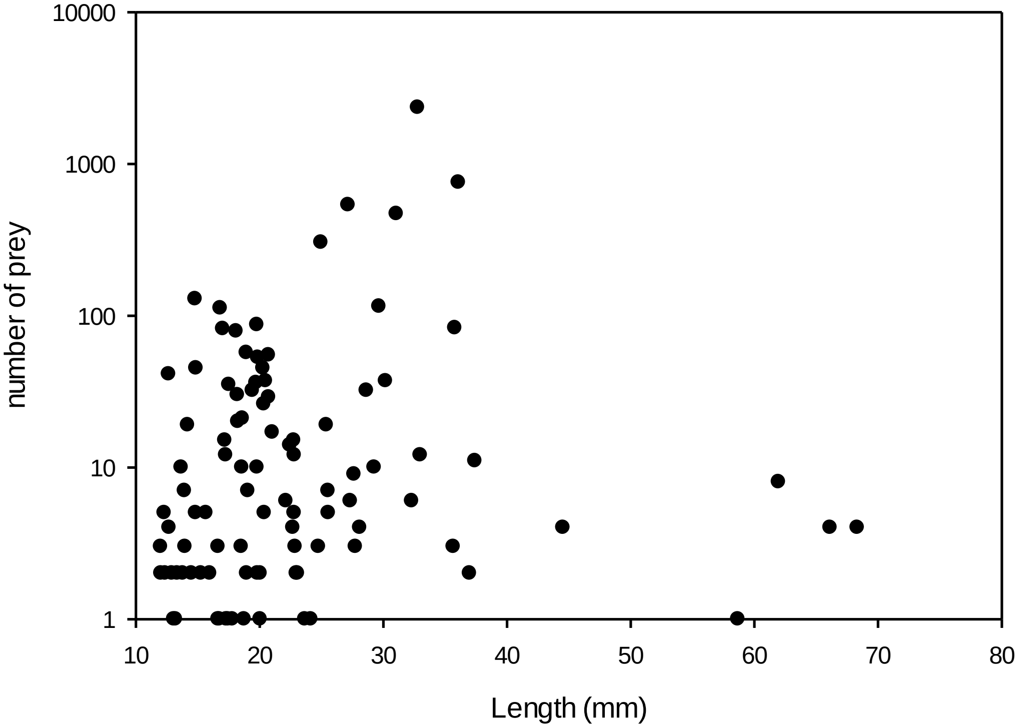

Figure 5. The number of prey items in a fish generally increased until the fish was around 40 mm in length and then decreased.

Table 2. ANCOVA tables for each prevalent prey item: a) copepods b) amphipods c) zebra mussels e) *Leptodora sp*.

a) Copepods

Source	DF	Type III SS	Mean Square	F	Pr > F
Year	3	6.62	2.21	3.78	0.0125
Length	1	0.236	0.236	0.4	0.526
Error	115	67.2	0.584		

b) Amphipods

Source	DF	Type III SS	Mean Square	F	Pr > F
Year	3	0.846	0.282	9.62	<.0001
Length	1	0.425	0.425	14.5	0.0002
Error	115	3.37	0.0293		

c) Zebra Mussels

Source	DF	Type III SS	Mean Square	F	Pr > F
Year	3	1.07	0.356	6.01	0.0008
Length	1	0.276	0.276	4.66	0.0330
Error	115	6.82	0.0593		

d) *Leptodora sp.*

Source	DF	Type III SS	Mean Square	F	Pr > F
Year	3	0.345	0.115	4.65	0.0042
Length	1	0.0711	0.0711	2.87	0.0928
Length by Year	3	0.369	0.123	4.97	0.0028
Error	112	2.77	0.0247		

Prey Habitat Index:

The PHI was used to determine the degree to which bass were feeding pelagically or benthically. The PHI in 1988 was nearly four, meaning that striped bass were feeding almost entirely pelagically. In subsequent years, the PHI steadily declined towards two, but never fell below three. This indicates that the fish never fed entirely benthically, but the proportion of their diet that came from the benthos significantly increased as indicated in Figure 6. An ANOVA showed that the effect of year on PHI was significant (Table 3). The benthic and pelagic scoring of each prey item can be found in Table 4.

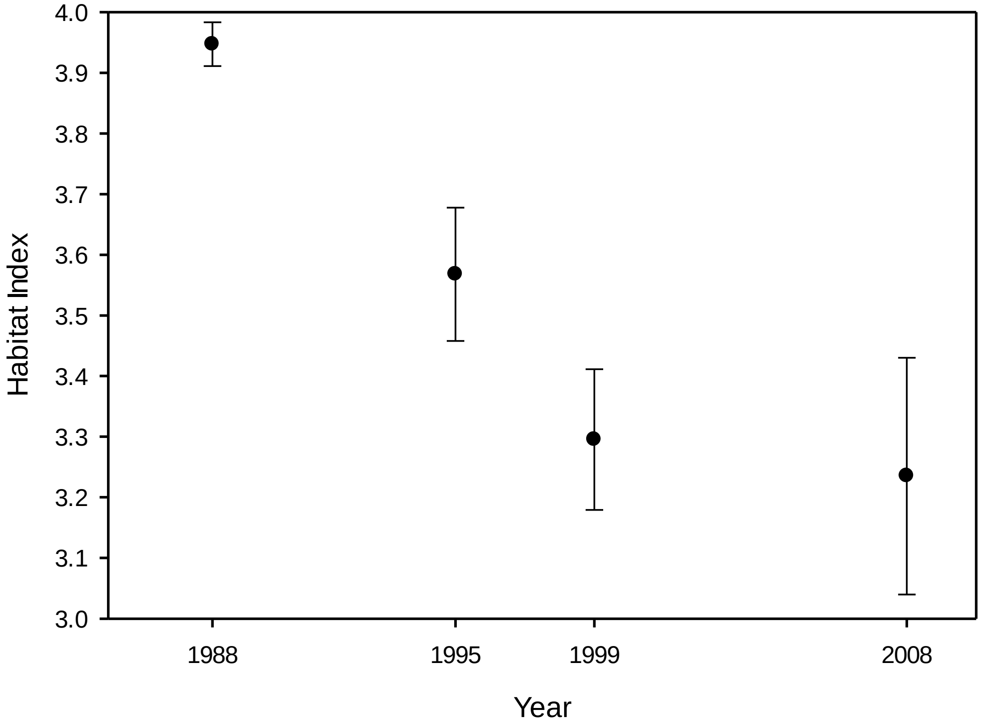

Figure 6. The PHI over time shows a steady decline in value from 4 (pelagic feeding) towards 2 (benthic feeding) as striped bass diets adjusted to zebra mussel induced ecosystem changes. PHI was measured on a scale from two to four where two represented feeding entirely on prey items from the benthos and four represented feeding entirely on prey items from the pelagic zone.

Table 3. ANOVA for changes in PHI by year.

Source	DF	Type III SS	Mean Square	F	Pr > F
year	3	6.58	2.19	5.59	0.0014
error	93	36.4	0.392		

Table 4. List of every identifiable prey item in the striped bass diet with their habitat type (benthic or pelagic) and value that was assigned to them for the PHI calculation.

Prey Item	Habitat	Value
Daphnia sp.	pelagic	4
Copepod - Cyclopoida	pelagic	4
Crustacea - Podacopa	pelagic	4
Crustacea - Conchostraca	pelagic	4
Copepod	pelagic	4
Chaoboridae - *Chaoborus*	pelagic	4
Amphipoda	benthic	2
Amphipoda - *Gammarus*	benthic	2
Amphipoda - *Pontoporeia affinis*	benthic	2
Amphipoda - *Hyalella*	benthic	2
Leptodora kindtii	pelagic	4
Dipteran	pelagic	4
Copepod - Calanoida	pelagic	4
Bosmina sp.	pelagic	4
Copepod nauplii	pelagic	4
Daphnia magna	pelagic	4
Zebra Mussel	benthic	2
Isopoda - *Lirceus*	benthic	2
Isopoda - *Caecidotea*	benthic	2
Mysid - *Mysis sp.*	benthic	2
Chaoboridae - *Eucorethra*	pelagic	4
Eurycercus spp.	pelagic	4
Isopoda	benthic	2

DISCUSSION

In the years following the zebra mussel invasion, prey diversity significantly increased, the abundance of prevalent prey items significantly increased, and prey habitat index declined indicating a transition from pelagic feeding to benthic feeding in early life stage striped bass. Prey diversity then declined in 2008 to a level similar to what was seen in 1988. In 2008, the abundance of each prevalent prey item also declined. No recovery was seen in the 2008 prey habitat index, indicating that although there were some signs of diet recovery, striped bass were still feeding more benthically than pelagically. The changes in prey diversity and PHI during peak invasion years were consistent with how the diet was expected to change, while changes in the abundance of prevalent prey items as well as the lack of PHI recovery in later years were not expected.

In accordance with the hypothesis, prey diversity in the diet increased after the arrival of zebra mussels in the river. This was most likely because the documented decline in pelagic prey items in the river (Pace et al. 1998; Pace et al. 2010; Strayer et al. 2011) forced striped bass to search in new places for food and resulted in the ingestion of new prey items. In 2008, the Shannon-Wiener diversity index returned to a value similar to what was seen in 1988, consistent with the ecosystem recovery reported by Pace et al. (2010). Overall, the results for diversity changes in the striped bass diet corresponded with the predicted response for a generalist predator.

Abundance of prevalent pelagic prey items actually increased during peak zebra mussel invasion years, rather than decreasing as was hypothesized. Pelagic copepods were the most abundant of all of the most prevalent prey items and were primarily from the order Calanoida. The dramatic increase in the number of copepods that were present in the diet between 1988 and 1995 could be explained by Pace et al.’s (1998) study of zooplankton in the Hudson River. Copepods were one of the groups that were least affected by the zebra mussel invasion and they maintained pre-invasion population abundances and dynamics through 1995. This could mean that striped bass consumed more copepods during peak invasion years because they were one of the only food sources left in the pelagic zone. Most amphipods were too damaged to classify more specifically, but of those that were, many were *Gammarus sp*. As benthic invertebrates, the increased presence of amphipods in the striped bass diets during peak invasion years supports the hypothesis that the bass would be feeding more heavily on benthic prey items.

There were no obvious changes in the patterns of prey use after the arrival of zebra mussels, contrary to what was expected. Copepods, amphipods, and *Leptodora sp.* were all present in the diet of the 1988 striped bass. The most interesting addition to the bass diet after the zebra mussels arrived in the river was the zebra mussels themselves. It has not yet been definitively confirmed that the bivalves present in the striped bass stomachs are zebra mussels; however, there are several factors that indicate that this is a safe assumption. The mussels did not appear in the striped bass diet in the 1988 fish, but were present frequently and abundantly in fish from 1995, 1999, and 2008. In addition, zebra mussels have been found in the stomachs of larval white perch (*Morone americana*), American shad (*Alosa sapidissima*), and alewife (*Alosa pseudoharengus*) from the Hudson River (K. Limburg SUNY ESF pers. comm. 2012). It would be logical to then conclude that striped bass could also utilize zebra mussels as a food source. A positive identification has been precluded thus far due to the absence of the characteristic zebra stripes on the mussel, possibly due to discoloration during the preservation process or because the mussels themselves were not mature enough to possess their stripes. Many of the mussels that were observed had byssal threads, meaning that they had already settled to the bottom of the river where the bass then consumed them. Some of the natural predators in the Hudson River Estuary, particularly blue crabs and larval white perch, have begun to utilize zebra mussels as a food source, which may explain a decline in zebra mussel size and population density in recent years (Carlsson et al. 2011; Strayer et al. 2011; K. Limburg SUNY ESF pers. comm. 2012). The ability of striped bass to utilize zebra mussels as a food source, and have them contribute to such a large proportion of the diet, may explain why the bass were able to maintain their population sizes and growth rates despite the drastic changes that were occurring in the Hudson River.

As expected, the striped bass were feeding pelagically in 1988, before the zebra mussels arrived in the Hudson River, and then began to feed increasingly in benthic habitats after zebra mussels had spread throughout the length of the river. Although the amount of benthic organisms present in the diet did increase in 1995, 1999, and 2008, causing the PHI to decline from four towards two, the PHI never fell below three, meaning that for all years the striped bass were never feeding more benthically than pelagically. In 2008, the PHI remained similar to that seen in 1999 instead of increasing to indicate a return towards pelagic feeding as was expected based on the evidence for ecosystem recovery.

This study is part of a larger proof-of-concept study which includes studying the changes in diet in early life stage alewife, blueback herring (*Alosa aestivalis*), and American shad. In the future it will be expanded to include many more years as well as an increase in the sample size in order to more accurately discern changes in prey diversity, prevalent prey items, and PHI.

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