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The Impacts of the Zebra Mussel (*Dreissena polymorpha*) on the Feeding Ecology of Early Life Stage Striped Bass (*Morone saxatilis*) and River Herring (*Alosa pseudoharengus* and *A. aestivalis*)

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HONORS THESIS

THE IMPACTS OF THE ZEBRA MUSSEL (*DREISSENA POLYMORPHA*) ON THE
FEEDING ECOLOGY OF EARLY LIFE STAGE STRIPED BASS (*MORONE
SAXATILIS*) AND RIVER HERRING (*ALOSA PSEUDOHARENGUS* AND *A.
AESTIVALIS*)

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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*) and river herring (*Alosa pseudoharengus* and *A. aestivalis*). 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 diet, species number doubled and the frequency of prevalent prey items increased up to four-fold during peak invasion years. Both then declined in 2008. Over time, striped bass fed increasingly on benthic prey rather than pelagic prey. Species number for river herring remained relatively constant over time, and they maintained a diet that consisted almost exclusively of pelagic prey. The frequency of some prevalent prey items in the river herring diet increased, others declined, and others exhibited no statistically significant change throughout the study period. After they arrived, zebra mussels became one of the main components of the striped bass diet, but they were never eaten by the river herring. Overall, the zebra mussel has changed many aspects of the striped bass diet, while river herring have attempted to maintain the same dietary structure that they had before the invasion began.

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INTRODUCTION

The zebra mussel (*Dreissena polymorpha*) is an invasive freshwater 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, NY, and have since become well established throughout the freshwater tidal length of the river (Strayer et al. 1996 and 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 spread, the substrate became dominated by their hard shells (Strayer 2009). Zebra mussels are highly efficient filter feeders; the population in the Hudson is able to filter the entire freshwater volume of the river in a day (Strayer et al. 1996). The mussels 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 in the Hudson (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 arrived, presently the ecosystem is showing 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 the river's natural predators, such as blue crabs, utilizing zebra mussels as a food source (Carlsson et al. 2011). This has led 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 secondary consumers, particularly early life stage fish species. The experiments and studies conducted on fish responses to zebra mussels have taken place on varying spatiotemporal scales and have yielded conflicting results. Some found that the presence of zebra mussels slowed larval and juvenile growth rates and decreased survival (Mayer et al. 2000; Pothoven et al. 2001; Bartsch et al. 2003; Raikow 2004; Strayer et al. 2004; Marvin and Strel'nikova 2011), while others found that there was no change in growth and survival (Richardson and Bartsch 1997; Mercer et al. 1999; Trometer and Busch 1999; Idrisi et al. 2001). Impacts on fish diets have also been varied with some finding significant changes in diet (Pothoven et al. 2001; Bartsch et al. 2003; Rennie et al. 2009; Marvin and Strel'nikova

2011), and others finding that diets exhibited no change (Mercer et al. 1999). Much of this research has been focused on mesocosm studies with in situ work taking place in various lakes.

Very few studies focusing on the impacts of the zebra mussel on fish have been conducted in riverine systems. River ecosystems are very different from lake ecosystems, particularly in the degree of water turbulence, which is generally higher in rivers, and chlorophyll biomass, which has been found to be lower in rivers (Pace et al. 1998). A study focusing on the effects of zebra mussels and turbulence on the survival of larval fish saw 90% mortality in mesocosms with both zebra mussels and turbulence, as compared to 17% mortality and 37% mortality in mesocosms with only zebra mussels or turbulence (Bartsch et al. 2003). This suggests that the additional stress of a zebra mussel invasion combined with the stress of naturally turbulent river waters could have catastrophic impacts on the abundance of riverine fish populations.

One study that has looked into how zebra mussels affect riverine fish was conducted on early lifestage fish in the Hudson River. The Hudson River estuary serves as an important nursery habitat for a variety of larval and juvenile fish species, and declines 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 river found that the 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. The fish could be less successful at obtaining food in these new foraging habitats, causing 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 the changes in the diet of two groups of pelagic fish in their early life stages, the striped bass (*Morone saxatilis*) and the river herring (*Alosa pseudoharengus* and *A. aestivalis*), from the Hudson River estuary over a twenty year time period that spans from before the zebra mussels arrived in the river until the present.

Striped bass were selected for this study because they are one of the few pelagic fish species that were able to maintain stable population sizes and apparent growth rates after the zebra mussel invasion (Strayer et al. 2004). Prior studies of larval and juvenile striped bass diets in the Hudson River show that bass rely heavily upon copepod consumption and supplement their diet with the cladocerans *Bosmina spp.* and *Leptodora sp.* (Bridgewater and Schmidt 1993; Limburg et al. 1997). There is also evidence that juvenile bass, like their adult counterparts, function as generalist predators (Howe and Juanes 2000). Though copepods were one of the least affected pelagic zooplankton groups in the Hudson River, *Bosmina* blooms were reported to have declined by over 50% (Pace et al. 1998, Strayer et al. 1999). The ability to forage as a generalist, combined with the resilience of one of their primary prey items, could allow the striped bass to better adjust to changes in available prey items.

Unlike the striped bass, the population sizes and apparent growth rates of both alewife (*A. pseudoharengus*) and blueback herring (*A. aestivalis*) were negatively and

significantly impacted by the zebra mussel invasion. Previous studies of larval and juvenile alewife and blueback herring diets have shown that they have very similar feeding habits with diets consisting primarily of calanoid and cyclopoid copepods as well as cladocerans such as *Bosmina spp.* and *Daphnia spp.* (Domermuth and Reed 1980; Crecco and Blake 1983; Limburg and Strayer 1987; MacNiell and Brandt 1990; Pothoven and Vanderploeg 2004; Pothoven and Madenjian 2008). Due to these similarities, and following common practice, alewife and blueback herring were grouped together for this study. They will be referred to as river herring for the duration of this paper. Historically, river herring rely more heavily on cladocerans in their diet than striped bass. *Bosmina spp.* can make up as much as 95% of the diet (Limburg et al. 1987). This dependence could have been a contributing factor to the river herring population declines seen by Strayer et al. (2004).

The objective of this study is to understand how the diets of striped bass and river herring have changed in response to the zebra mussel invasion in the Hudson River on an extended time scale as well as to link these potential changes in diet to the changes in population size and growth rate seen in Strayer et al.'s (2004) study. It is predicted that striped bass will be more successful at making foraging transitions than river herring because they have been more successful at surviving the zebra mussel invasion (Strayer et al. 2004). The diversity of prey will increase over time as the fish forage for unfamiliar prey items during the transition from pelagic to benthic feeding. 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, 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 the peak of the zebra mussel invasion and the present day. Fish were preserved in formalin and were identified to species by Normandeau Associates in Bedford, NH. The fish that were caught in 1988 were transported to the ichthyology collection at the New York State Museum in Albany, NY 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. Each fish needed to be large enough to dissect with 2 mm cutting surface spring dissecting scissors, and most were less than 50 mm long. Striped bass identity was confirmed 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). River herring were identified by the presence of a characteristic sharply sloping lower jaw as opposed to the shallow angle seen in the American shad (*A. sapidissima*) (R. Schmidt Bard College at Simon's Rock pers. comm. 2012). All of the fish selected came from the freshwater tidal length of the river between river kilometer 100 and river kilometer 248 to ensure that they were living in the presence of zebra mussels.

Dissection and Identification:

Once a fish was selected, it was prepared for dissection and then carefully dissected to mitigate specimen damage. Each fish was assigned a unique sample number, its standard length was measured, and it was weighed in a sealed container filled with water. Dissection occurred 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 and esophagus 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 and thirty river herring from each year for a total of 240 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 in each diet over time were determined by looking at changes in species number over time. 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 species number present in each year. The length-corrected least squares mean of species number was graphed for each year to show how prey diversity changed over time. A bar graph was generated to demonstrate the overall diversity of prey items present in each 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 in each diet, the prey items that were present in the most fish from each species were determined. In striped bass, changes in the four most prevalent prey items were observed, and in the river herring changes in the top five most prevalent prey items were observed. Before data analysis took place, it was arbitrarily decided to observe the four most prevalent prey items in each species' diet. Because there was only a one fish difference between the fourth and fifth most prevalent prey items in the river herring, it was decided to observe trends in five prey items instead of four. The total number of each prevalent prey item present in an individual fish and the length of the fish were then log transformed. ANCOVAs were conducted on the incidence of each predominant prey item. 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. For

each species, 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 each species was feeding pelagically or benthically for each year, an index was used. For each fish within a species, 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 from each species within a specific year was then averaged together to achieve an overall PHI for that year for that species. The changes in the yearly PHIs can then be compared to determine how the feeding habitats of each species 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:

Within the striped bass diet, copepods were the most numerous prey item found, which is best demonstrated by the non-log-transformed frequencies in Figure 1. A log-transformation reveals that the most frequently counted prey items in the diet were copepods, amphipods, zebra mussels and *Leptodora sp.* (Figure 2). Within the river herring diet, centric diatoms were the most numerous prey item (Figure 3). A log

transformation better shows that the most frequently counted prey items in the diet were centric diatoms, *Bosmina spp.*, copepods, and rotifers from the family Brachionidae (Figure 4). 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 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.

The species number analysis for prey diversity within striped bass and river herring diets showed that for striped bass species number changed significantly with year, while for river herring the species number did not change significantly over time. Between 1988 and 1999 species number in the striped bass diet doubled before declining by 42% in 2008 (Figure 5). An ANCOVA indicated that there was a significant year effect and length effect on species number within the striped bass diet (Table 1). The river herring ANCOVA showed that there was no significant year effect, but the effect of length was significant (Table 2). Species number in the river herring diet was always higher than that of the striped bass diet and did not change significantly after the zebra mussel invasion (Figure 5).

Prevalent Prey Items:

Within the striped bass diet, 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 3 a-d year p-value). Figure 6 shows that for each prey item the size-adjusted log-transformed frequency in the diet increased from 1988 to 1995 and then declined from 1999 to 2008. This trend is most pronounced in the copepods, which increased nearly four-fold in the diet between 1988 and 1995. Both zebra mussels and amphipods increased two-fold in the diet from 1988 to 1999, while *Leptodora sp.* increased one-fold during this same time period. 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. There was a significant length effect for each prevalent prey item except copepods (Table 3a). The length effect varied among years for only one prey species, *Leptodora* (Table 3d).

Copepods, *Bosmina spp.*, amphipods, *Leptodora sp.*, and ostracods in the subclass Podacopa were the most prevalent prey items in the river herring diet. The abundance of copepods, *Bosmina spp.*, and Podacopa varied from year to year, while no year effect was seen for amphipods and *Leptodora sp.* (Table 4 a-e year p-value). Figure 7 shows that copepod prey use increased three-fold from 1988 to 1999 and then returned to pre-invasion levels in 2008. The prevalence of *Bosmina spp.* and Podacopa declined three-fold and two-fold respectively from 1988 to 1995 and then recovered in 1999 and 2008. Use of *Leptodora sp.* and amphipods declined slightly, but not significantly, over time. There was a significant length effect as well as a significant length-by-year interaction effect for *Bosmina spp.*, *Leptodora sp.*, and Podacopa (Table 4 b, d, e). Amphipod prey

use exhibited only a significant length effect, and no length effect was seen in copepod prey use (Table 4 a and c).

Prey Habitat Index:

In the striped bass diet, the PHI in 1988 was nearly four, meaning that the 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 striped bass never fed entirely benthically, but the proportion of their diet that came from the benthos significantly increased (Figure 8). Figure 8 also shows that the river herring were feeding almost entirely pelagically in 1988, with a PHI value of nearly four. The PHI declined slightly in 1995, a peak mussel invasion year, but then recovered towards four in 1999 and remained there in 2008. River herring never fed benthically to the same degree that the striped bass did. ANOVAs for striped bass and river herring showed that the effect of year on PHI was significant (Tables 5 and 6). The benthic and pelagic scoring of each prey item can be found in Table 7 for striped bass and Table 8 for river herring.

DISCUSSION

The results from the striped bass diet study paint a conflicting picture. In accordance with what was hypothesized, prey diversity in the striped bass diet increased after the arrival of zebra mussels in the river. It was thought that this result would arise because the striped bass would be forced to search in new places for food, thus ingesting new prey items, due to previously documented declines in pelagic prey items in the river (Pace et al. 1998; Pace et al. 2010; Strayer et al. 2011). However, the analysis of prevalent prey items in the diet showed that the abundance of prevalent pelagic prey

items actually increased during peak invasion years. This could mean that although striped bass relied heavily on the pelagic food sources left in the river they added diversity to their diet by feeding on a variety of new benthic organisms in small quantities. In 2008, species number 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.

Contrary to what was hypothesized, both pelagic and benthic prevalent prey items increased in the diet during peak invasion years. Pelagic copepods, primarily calanoid, and *Leptodora sp.* increased in abundance in 1995 and 1999, relative to 1988, and then declined in 2008, supporting ecosystem recovery. Copepods were one of the groups that were the least affected by the zebra mussel invasion (Pace et al. 1998), which could explain the dramatic increase in the number of copepods that were present in the diet between 1988 and 1995. Since copepods were able to maintain pre-invasion population abundances and dynamics through 1995, they were likely one of the most readily available food sources for the striped bass. Unfortunately, there no data is available on *Leptodora* population trends in the Hudson during the zebra mussel invasion so it is unknown how this specific population responded, but most cladoceran populations in the river declined after the invasion (Pace et al. 1998). Amphipods, many of the genus *Gammarus*, and zebra mussels, both benthic invertebrates, were also prevalent in the diet and appeared more frequently during peak invasion years. The increase in these prey items supports the theory that striped bass would rely more heavily on benthic prey sources in order to make up for the loss of other pelagic food sources.

The most interesting addition to the bass diet after the zebra mussels arrived in the river was the zebra mussels themselves. Several factors lead to the conclusion that the bivalves present within the striped bass stomachs were zebra mussels. First, 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 (*M. americana*), American shad, and alewife from the Hudson River (K. Limburg SUNY ESF pers. comm. 2012). It would be logical to then conclude that the striped bass could also utilize the zebra mussels as a food source. Many of the mussels that were observed had byssal threads, meaning that they had already settled to the bottom of the river where the striped 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). Similar predatory behavior and population declines have been seen in other zebra mussel invasion areas, such as Lake Dardanelle in Arkansas (Magoulick and Lewis 2002). The ability of the striped bass to utilize zebra mussels as a food source, and have them contribute to such a large portion 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 the 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.

Unlike the striped bass, river herring prey diversity did not increase after the arrival of the zebra mussels. There were no significant changes in species number in river herring diets over time. This is surprising because evidence from river herring diet studies, zooplankton population studies, and fish population studies made it easy to conclude that river herring diets would be seriously impacted by the arrival of the zebra mussel (Limburg and Strayer 1987; Pace et al. 1998; Strayer et al. 2004). River herring consistently had a higher species number than the striped bass for each year. This is an interesting development because striped bass were thought to be more generalist predators than the river herring.

Changes in prevalent prey items and prey use within river herring diets were very different from striped bass diets. Instead of having all prey items respond in a similar fashion over time, river herring prevalent prey had a variety of responses to the zebra mussel invasion. Both *Bosmina spp.* and *Podacopa* followed the predicted trend of pelagic prey items and declined in abundance in the diet after the zebra mussel invasion. Early indications of ecosystem recovery were seen in both of these groups as abundance in the diet increased in both 1999 and 2008. However, abundance of *Bosmina spp.* and *Podacopa* never reached the same frequencies that were seen in the preinvasion year.

Over time, there were no significant changes in the prey use of *Leptodora sp.* and amphipods. As with the striped bass, the most prevalent amphipods in the river herring diet were *Gammarus spp.* but most of the amphipods found in stomachs were too damaged to identify to lower taxonomic levels. Copepods in river herring diets followed a similar abundance pattern as they did in striped bass diets. Abundance significantly increased in 1995 and 1999 and then declined in 2008. This is likely because copepod populations were resilient during the zebra mussel invasion. Their abundance in the diet likely declined in 2008 as other zooplankton species began to increase in abundance and were again available as prey items. There were no new additions of prevalent prey items after the zebra mussels arrived in the river. Although zebra mussels have been found in alewife stomachs before (Limburg SUNY ESF pers. comm. 2012), none of the river herring dissected in this study had zebra mussels in their stomachs. The river herring seemed to resist feeding in the benthos, which could explain the lack of zebra mussels.

River herring maintained an almost entirely pelagic feeding habitat over time. The herring exhibited their most benthic feeding in 1995, a peak zebra mussel invasion year, but even 1995 river herring fed heavily in the pelagic zone. The years 1999 and 2008 saw a recovery in PHI to essentially 100% pelagic feeding. The only benthic prey items found in the river herring diet were amphipods and nematodes, and nematodes occurred rarely. This combined with the crash and recovery in *Bosmina spp.* and Podacopa frequencies in the diet certainly contributed to the increase in benthic feeding in 1995 and the return to almost entirely pelagic feeding in 1999 and 2008.

Overall, striped bass appear to be much more capable of making changes to their feeding ecology when compared to river herring. Striped bass were able to increase their

degree of benthic feeding after the arrival of the zebra mussel as well as to begin utilizing the zebra mussels as a main food source. The river herring's apparent inability to feed in the benthos is likely a large contributing factor to their observed population declines after the zebra mussel invasion. If the trend of ecosystem recovery in the Hudson continues, river herring populations may be able to rebound with the return of their primary food sources.

This study provides an important look at how fish diets change in response to the zebra mussel invasion within a river ecosystem, an area that thus far is understudied. Much of the work done to understand the implications of the invasion on early life stage fish has taken place in mesocosm experiments or a laboratory setting. These experiments only focus on the immediate, short term, impacts of the invasion and do not provide a clear picture of change over time. A mesocosm study focusing on larval bluegill (*Lepomis macrochirus*) found that, in the presence of zebra mussels, larval growth rate was lowered by approximately 24% (Raikow 2004). In contrast, a mesocosm experiment looking at juvenile bluegill found the presence of zebra mussels did not impact the growth or survival of the fish (Richardson and Bartsch 1997). Marvin and Strel'nikova (2011) found that within a mesocosm in the presence of zebra mussels juvenile European perch (*Perca fluviatilis*) were forced to switch from feeding predominantly on *Bosmina* to feeding on chironomids. Mussel presence also slowed progression through developmental stages. An additional mesocosm experiment on larval fathead minnows (*Pimephales promelas*) showed that in the presence of both zebra mussels and turbulence fathead minnows had low survival rates. The fish also exhibited considerable diet plasticity throughout the experiment (Bartsch et al. 2003).

The longer term work involving the impacts of zebra mussels on fish populations and diets has taken place in the Great Lakes, where zebra mussels first became an issue as an invasive species in North America. In Lake Huron, Rennie et al. (2009) looked at changes in the isotopic signatures of lake whitefish (*Coregonus clupeaformis*) scales from 1947 through 2005 to see how fish diet changed over time. Their results showed that after the zebra mussel invasion, lake whitefish lived in shallower waters and exhibited a greater reliance on prey from the profundal zone. Overall, the energy content of their diet decreased by 13%. Lake whitefish in Lake Michigan showed declines in body condition, length at age, and weight at age after zebra mussels arrived in the lake in 1989 (Pothoven et al. 2001). Post-invasion the fish also added new prey items to their diet, including zebra mussels. In Lake Erie, a variety of fish, including alewife, white bass (*M. chrysops*), and white perch, were found to exhibit no significant changes in growth rate after the zebra mussels became established (Trometer and Busch 1999). Outside of the Great Lakes, bluegill and yellow perch (*P. flavescens*) growth rates did not change after zebra mussels arrived in Rice Lake, Ontario, while pumpkin seed growth rates actually increased (Mercer et al. 1999). None of these species changed the proportion of benthic to pelagic prey found in their diets. Two studies of young of the year yellow perch in Oneida Lake, New York, yielded conflicting results. One found that zebra mussels had no significant effects on the biomass, growth, and production of the perch (Idrisi et al. 2001), while the other showed that early juveniles and young of the year had increased growth rates post invasion (Mayer et al. 2000).

This study in conjunction with Strayer et al. (2004) provides the beginnings of a more comprehensive understanding of how fish in the Hudson River have responded to

the arrival and permanent establishment of zebra mussels. Similar to the Hudson River striped bass, other comprehensive diet studies have found that fish begin to utilize zebra mussels as a food source (Pothoven et al. 2001 and Rennie et al. 2009). Yellow perch, bluegill, and pumpkin seed have all been found to make no changes to their proportion of benthic to pelagic feeding (Mercer et al. 1999 and Mayer et al. 2000), just as Hudson River river herring did not change their PHI. It is clear that a fish's dietary response to zebra mussel invasions is very complex, is very dependent upon how the surrounding ecosystem responds, and can have a variety of impacts on fish growth and survival, from no effect to precipitous population declines. There is a clear need for more long term studies of changes in fish diets in zebra mussel infested areas, particularly in rivers, to better understand how different fish species respond on a system by system basis.

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FIGURES AND TABLES

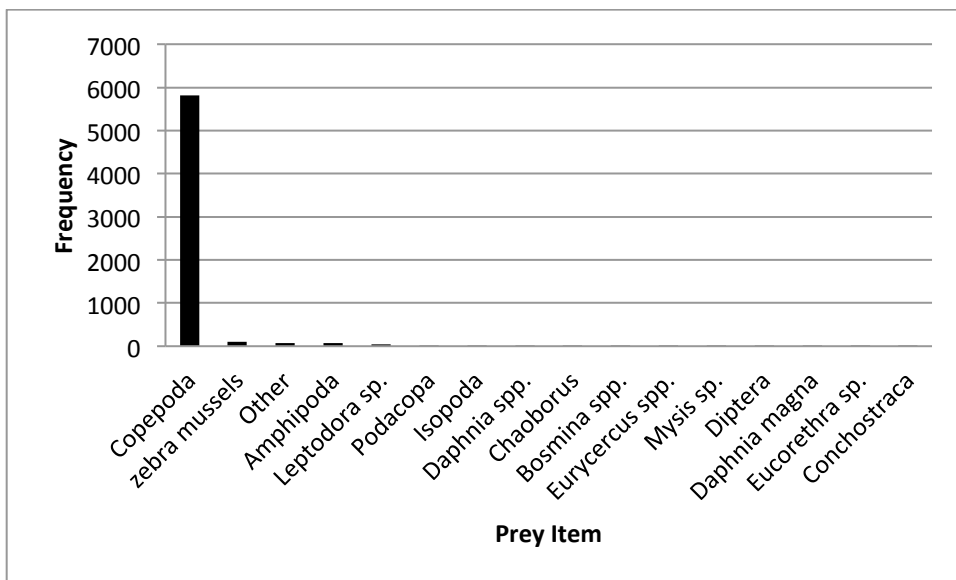


Figure 1. The frequency of prey items found in the striped bass diet across all four years (1988, 1995, 1999, and 2008) without log transformation illustrates the dominance of copepods in the diet.

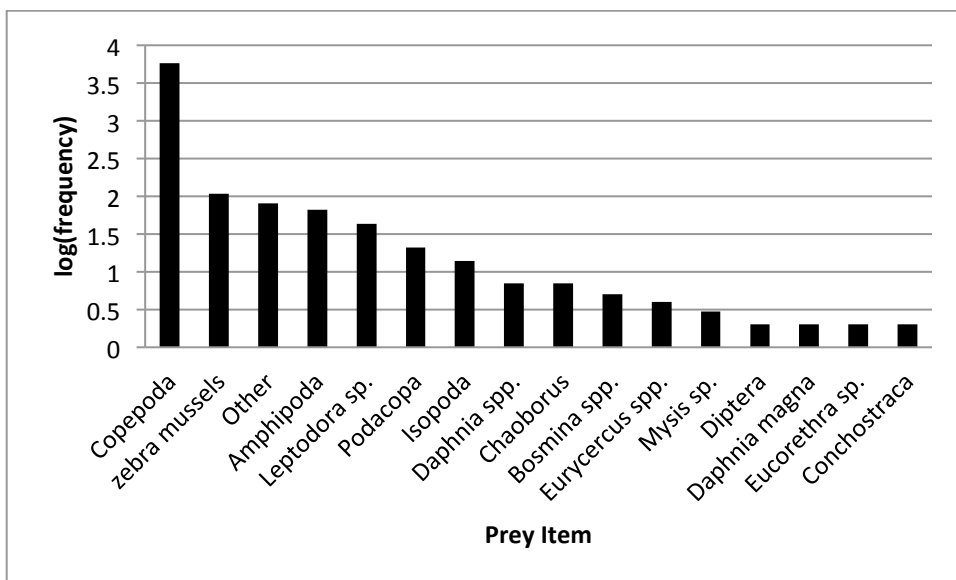


Figure 2. After a log transformation, the contribution of each prey item to the makeup of the striped bass diet across all years four becomes clearer.

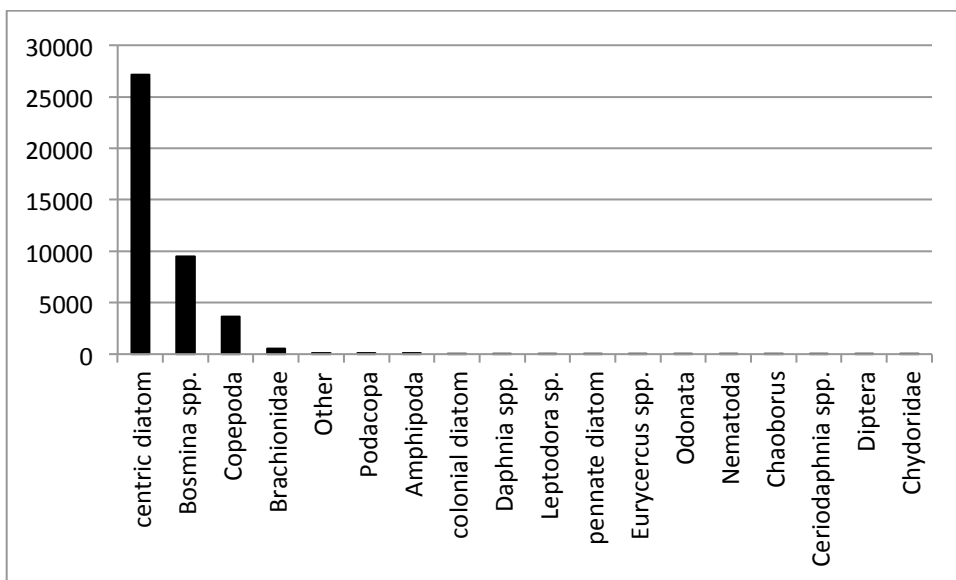


Figure 3. The frequency of prey items found in the river herring diet across all four years (1988, 1995, 1999, and 2008) without log transformation illustrates the dominance of centric diatoms in the diet.

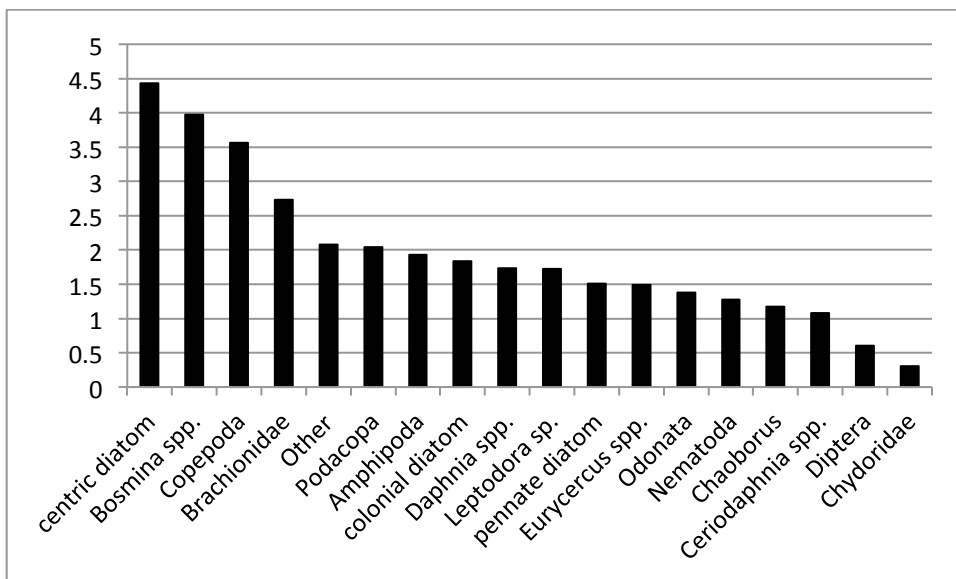


Figure 4. Log transformation makes the contribution of each prey item to the makeup of the river herring diet across all years four clearer.

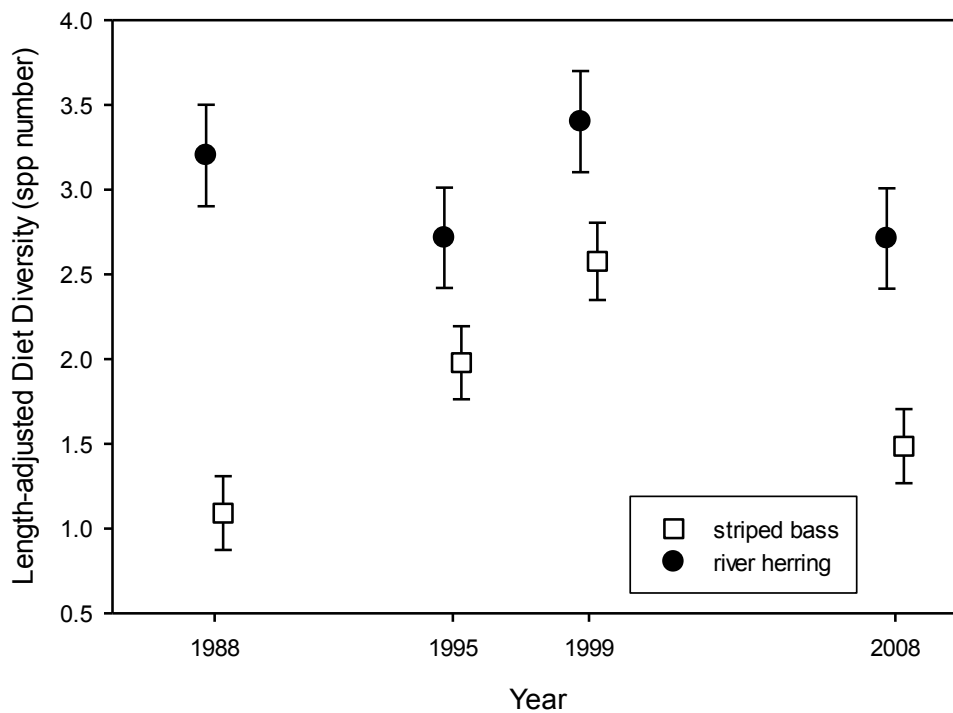


Figure 5. Changes in species number over time for striped bass and river herring over time.

Table 1. ANCOVA for changes in species number by year and length for striped bass.

Source	DF	Type III SS	Mean Square	F	Pr > F
Year	3	33.1	11.0	7.92	<.0001
Length	1	16.6	16.6	11.9	0.0008
Error	115	160	1.40		

Table 2. ANCOVA for changes in species number by year and length for river herring.

Source	DF	Type III SS	Mean Square	F	Pr > F
Year	3	10.9	3.65	1.39	0.250
Length	1	70.6	70.6	26.9	<.0001
Error	115	302	2.63		

Table 3. ANCOVA tables for each prevalent prey item in the striped bass diet: a) Copepoda b) Amphipoda c) *D. polymorpha* d) *Leptodora sp.*

a) Copepoda

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) Amphipoda

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) *D. polymorpha*

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		

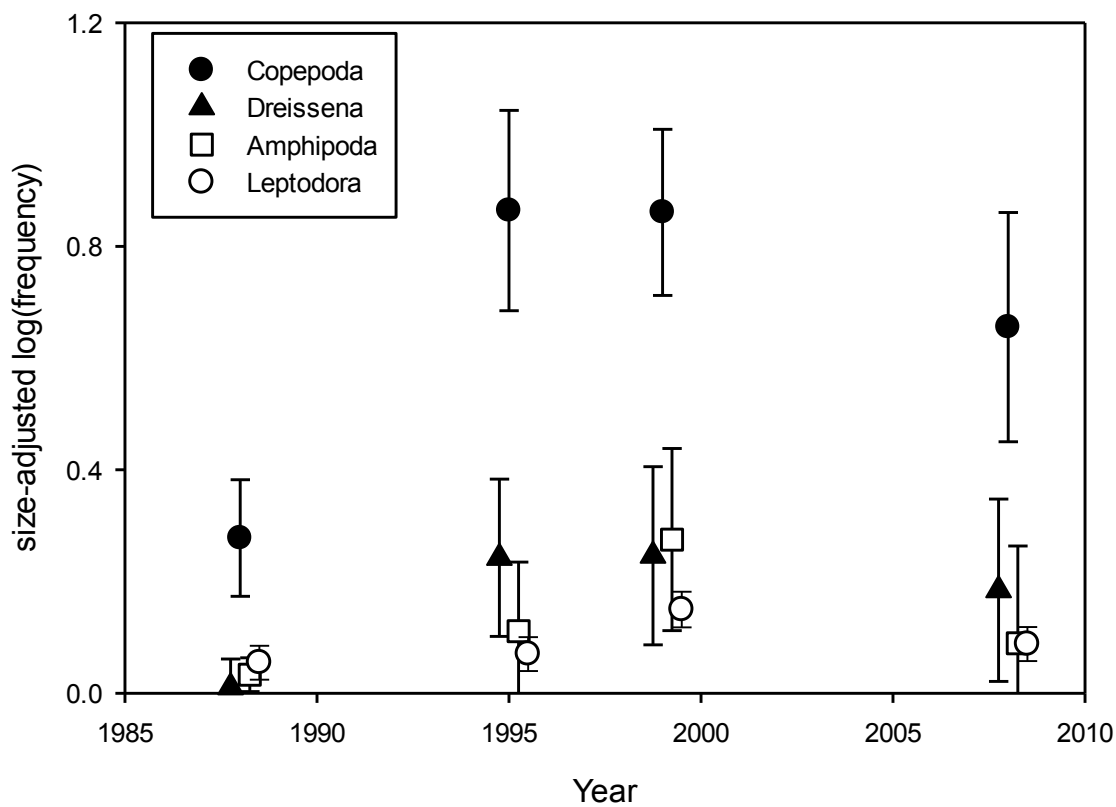


Figure 6. Changes in the size adjusted log transformed frequency of the most prevalent prey items (copepods, zebra mussels, amphipods, and *Leptodora sp.*) in the striped bass diet over time.

Table 4. ANCOVA tables for each prevalent prey item in the river herring diet: a) Copepoda b) *Bosmina* spp. c) Amphipoda d) *Leptodora* sp. e) Podacopa

a) Copepoda

Source	DF	Type III SS	Mean Square	F	Pr > F
Year	3	6.10	1.03	4.19	0.00074
Length	1	0.227	0.227	0.470	0.496
Error	119	61.9			

b) *Bosmina* spp.

Source	DF	Type III SS	Mean Square	F	Pr > F
Year	3	20.7	6.90	15.7	<.0001
Length	1	18.2	18.2	41.4	<.0001
Length by Year	3	21.5	7.18	16.3	<.0001
Error	112	49.3	0.440		

c) Amphipoda

Source	DF	Type III SS	Mean Square	F	Pr > F
Year	3	0.197	0.0657	1.45	0.231
Length	1	1.23	1.23	27.1	<.0001
Error	115	5.20	0.0452		

d) *Leptodora* sp.

Source	DF	Type III SS	Mean Square	F	Pr > F
Year	3	0.214	0.0715	2.36	0.0752
Length	1	0.327	0.327	10.8	0.0014
Length by Year	3	0.253	0.0843	2.78	0.0442
Error	112	3.39	0.0303		

e) Podacopa

Source	DF	Type III SS	Mean Square	F	Pr > F
Year	3	0.694	0.231	4.43	0.0056
Length	1	0.381	0.381	7.29	0.008
Length by Year	3	0.798	0.266	5.09	0.0024
Error	112	5.85	0.0522		

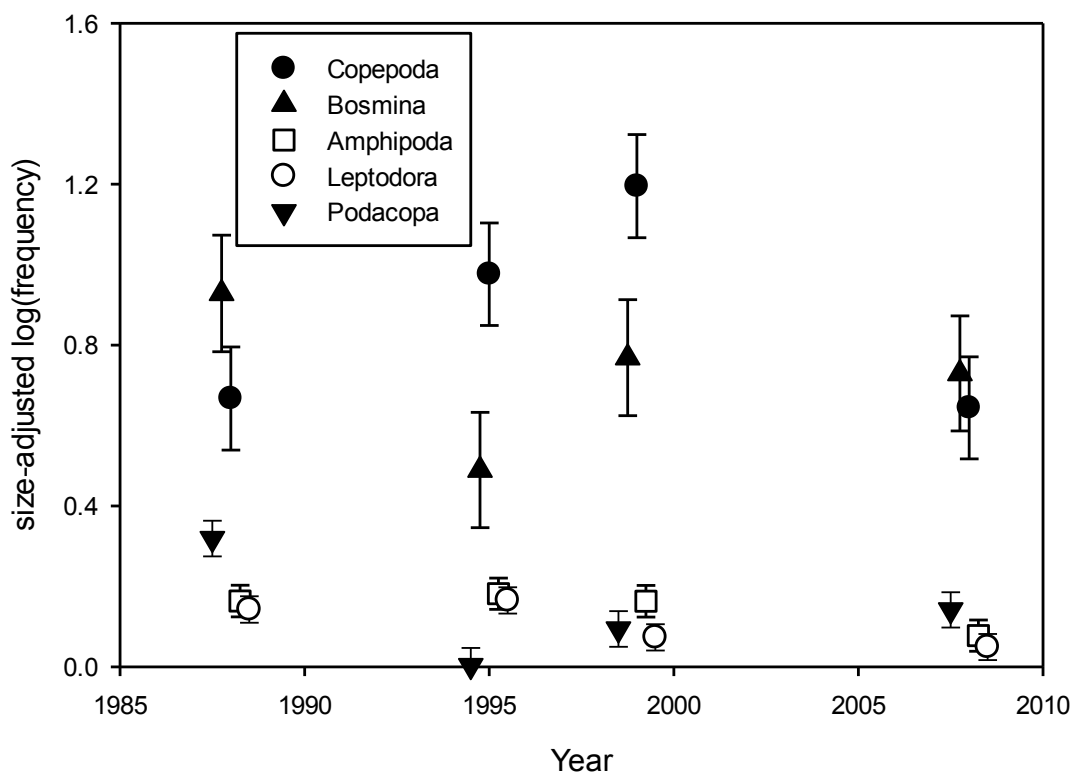


Figure 7. Changes in the size adjusted log transformed frequency of the most prevalent prey items (Copepoda, *Bosmina* spp., Amphipoda, *Leptodora* sp., and Podacopa) in the river herring diet over time.

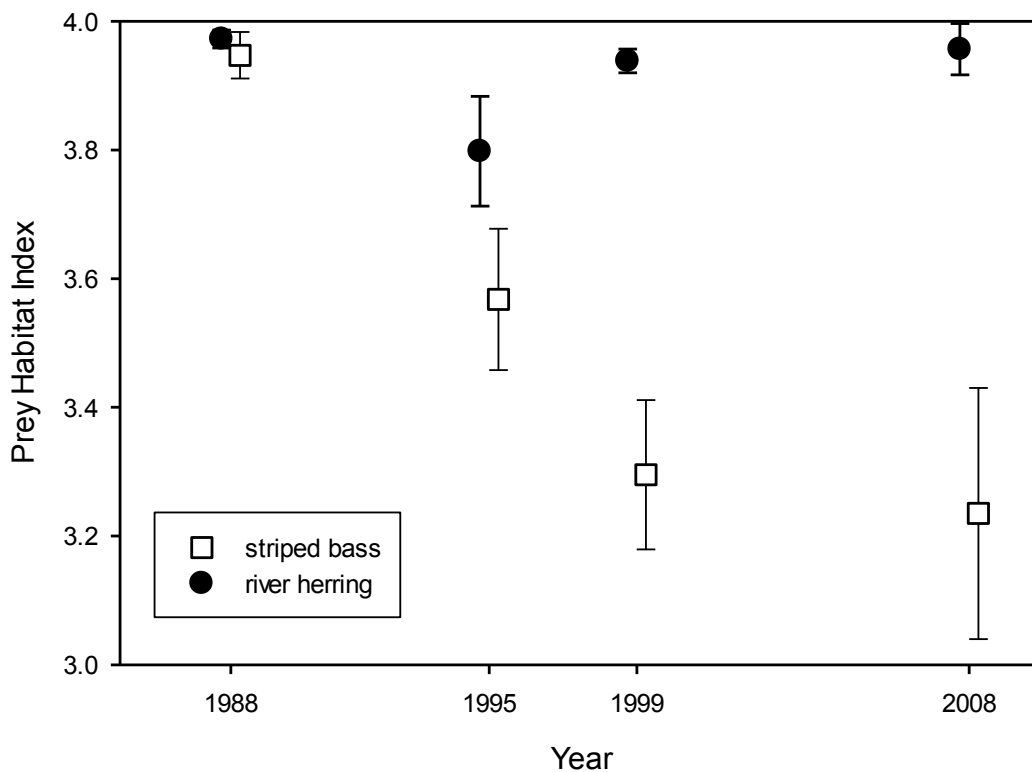


Figure 8. Changes in PHI over time for striped bass and river herring diets. PHI was measured on a scale from two to four where two represented feeding entirely on prey items from the benthos and four represented feeding entirely on prey items from the pelagic zone.

Table 5. ANOVA for changes in PHI for striped bass 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 6. ANOVA for changes in PHI for river herring by year.

Source	DF	Type III SS	Mean Square	F	Pr > F
Year	3	0.527	0.176	2.91	0.0381
Error	108	6.53	0.0605		

Table 7. 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
<i>Daphnia</i> spp.	pelagic	4
Copepoda - Cyclopoida	pelagic	4
Ostracoda - Podacopa	pelagic	4
Brachiopoda - Conchostraca	pelagic	4
Copepoda	pelagic	4
Chaoboridae - <i>Chaoborus</i>	pelagic	4
Amphipoda	benthic	2
Amphipoda - <i>Gammarus</i>	benthic	2
Amphipoda - <i>Pontoporeia affinis</i>	benthic	2
Amphipoda - <i>Hyaella</i>	benthic	2
<i>Leptodora</i> sp.	pelagic	4
Diptera	pelagic	4
Copepoda - Calanoida	pelagic	4
<i>Bosmina</i> spp.	pelagic	4
copepod nauplii	pelagic	4
<i>Daphnia magna</i>	pelagic	4
zebra mussel (<i>Dreissena polymorpha</i>)	benthic	2
Isopoda – <i>Lirceus</i>	benthic	2
Isopoda - <i>Caecidotea</i>	benthic	2
Mysid - <i>Mysis</i> sp.	benthic	2
Chaoboridae - <i>Eucoethra</i>	pelagic	4
<i>Eurycerus</i> spp.	pelagic	4
Isopoda	benthic	2

Table 8. List of every identifiable prey item in the river herring diet with their habitat type (benthic or pelagic) and value that was assigned to them for the PHI calculation.

Prey Item	Habitat	Value
<i>Daphnia spp.</i>	pelagic	4
Copepoda - Cyclopoida	pelagic	4
Ostracoda - Podacopa	pelagic	4
Copepoda	pelagic	4
Chaoboridae - <i>Chaoborus</i>	pelagic	4
Amphipoda	benthic	2
<i>Leptodora sp.</i>	pelagic	4
Diptera	pelagic	4
Copepoda - Calanoida	pelagic	4
<i>Bosmina spp.</i>	pelagic	4
Copepod nauplii	pelagic	4
centric diatom	pelagic	4
Nematoda	benthic	2
Amphipoda - <i>Gammarus</i>	benthic	2
<i>Eurycerus spp.</i>	pelagic	4
colonial diatom	pelagic	4
pennate diatom	pelagic	4
Rotifera - Brachionidae	pelagic	4
<i>Ceriodaphnia spp.</i>	pelagic	4
Odonata	pelagic	4
Chydoridae	pelagic	4