The effects of increased snail (*Nassarius obsoletus*) density on the diet of the salt marsh mummichog (*Fundulus heteroclitus*)

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Abstract. Human activities have dramatically altered the global nitrogen cycle approximately doubling the rate of nitrogen input into the biosphere. Linda Deegan and her team are in the midst of conducting a long-term fertilization experiment at the Plum Island Sound estuary in order to understand how ecosystem function changes when excess nutrients (70-100 uM NO₃⁻ and 5-7 uM PO₄³⁻) are added. They have found that excess nutrients (eutrophication) increased benthic microalgal biomass, snail (*Nassarius obsoletus*) density and biomass, and decreased mummichog (*Fundulus heteroclitus*) biomass. Relative to the reference creek, snail density and biomass in the fertilized creek quadrupled, whereas mummichog biomass decreased by one third. This suggests that increased snail densities might affect the mummichogs’ ability to access protein. This mechanism might explain the crash in mummichog biomass seen after 5.5 years of fertilization, but has not previously been quantified. In the lab, we conducted feeding trials with three snail density treatments of no snails (0), low snails (9), and high snails (36). After each feeding trial, I used gut content analysis and a mixing model using C:N ratios obtained from the CHN analyzer to quantify the percent protein and plant material in the gut contents of the mummichogs. For the field component, I collected mummichogs and took small plugs of lateral muscle tissue for stable isotope analysis. We used stable nitrogen isotope (Δ15N) values in order to examine if increased snail density altered the trophic position of mummichogs.

We found that the highest snail density treatment (36) did not affect the ability for mummichogs to obtain protein and that increased snail densities in the field were not correlated with mummichog trophic position. We also found that sediment particle size (% clay and silt vs. % sand) might have made a difference in the ability for mummichogs to access protein. These results suggest that increased snail densities do not affect the ability for mummichogs to obtain protein; thus this mechanism is not connected to the crash in the mummichog population seen at Plum Island. It is important to identify the mechanism contributing to this crash in the mummichog population because mummichog export production contributes significantly to valuable fisheries species and could potentially decrease fishery yields.

Key words: eutrophication, Plum Island Sound estuary, food web, diet, benthic invertebrates, feeding trials, *Fundulus heteroclitus*, *Nassarius obsoletus*.

Introduction

Nitrogen is a fundamental component of living organisms and a key element in many terrestrial and marine ecosystems, as nitrogen is often a limiting nutrient (Vitousek et al. 1997,
Gruber and Galloway 2008). However, human activities have dramatically altered the global nitrogen cycle approximately doubling the rate of nitrogen input into terrestrial and marine ecosystems (Vitousek et al. 1997). Humans have converted forests to agricultural fields, golf courses, and lawns effectively increasing the amount of fertilizer use, which is a major source of nitrogen entering estuaries. In addition, humans have also increased the amount of land used for urban, commercial, and residential land use, which releases large quantities of reactive nitrogen from wastewater into estuaries (Foley et al. 2005). Consequently, changes in land use have increased the mobility and load of reactive nitrogen from the land to aquatic ecosystems (Deegan et al. 2012). This can lead to harmful algal blooms, hypoxia, and change the composition and functioning of estuarine ecosystems, which could synergistically work to accelerate the loss of biological diversity (Vitousek et al. 1997). It is essential to understand the long-term effects of nutrients on ecosystems in order to encourage land use practices that minimize the harmful effects of nitrogen loading on ecosystems.

**Plum Island Fertilization Experiment:** It is important to understand how ecosystem function changes when excess nutrients are added. For nine years (2004-2012), Linda Deegan and her team (2012) have enriched marsh waters to nutrient levels that are considered moderately to highly eutrophic (70-100 uM NO$_3^-$ and 5-7 uM PO$_4^{3-}$) by adding nutrients directly to the flooding tide in two formerly non-enriched creeks. This mimics the way anthropogenic nutrients are typically delivered to marsh ecosystems (Deegan et al. 2007). Two additional creeks serve as references without nutrient enrichment with background nutrient levels (< 4.5 μM NO$_3^-$ and < 1.2 μM PO$_4^{3-}$) (Deegan et al. 2007, Lockfield 2011).

**Changes in Primary Producers:** Recent experiments have shown a shift in primary producers in Sweeney creek and Clubhead creek after nutrient additions (Table 1). *S. alterniflora* and *S. patens* growth was shown to increase and benthic microalgal biomass was shown to be 60% higher than initial baseline and reference creeks (Deegan et al. 2007). Nutrient enrichment was shown to support more benthic microalgal biomass as seen with an increase in chl a concentrations (mg/m$^2$) (Johnson and Short 2012) (Fig. 1).

**Changes in Animal Composition:** Recently, studies have shown that increasing nitrogen inputs may alter animal species composition. Johnson and Short have shown that nutrient enrichment may increase mudsnails (*Nassarius obsoletus*) because of an increase in benthic microalgal biomass. Although mudsnails require both plant and animal tissue for growth, they
primarily feed on benthic microalgae (Johnson and Short 2012). After six years of nutrient enrichment, Pascal and colleagues (2012) have shown that *N. obsoletus* consumed 2.5 times more benthic microalgal production compared to reference creeks. In the enriched creek, Johnson and Short (2012) have discovered that adults are 14% larger, mean *N. obsoletus* densities are 3.9 times higher, and the mean shell-free biomass of *N. obsoletus* is 4.0 times higher compared to the reference creek (Fig. 2). Nelson and colleagues have found changes in fish biomass with nutrient enrichment. Initially eutrophication was shown to increase mummichog production because of bottom-up stimulation of nutrients. However, after approximately 5.5 years of fertilization the system seemed to have reached a tipping point in which fish biomass precipitously decreased. After nine years of fertilization, mummichog biomass was shown to decrease by one third relative to the reference creek (Nelson et al. 2012, unpublished data, unreferenced) (Fig. 3). Relative to the reference creek, snail density and biomass in the fertilized creek quadrupled, whereas mummichog biomass decreased by one third (Fig. 2 and 3). This phenomenon may be explained by the increased direct or indirect competition for food between the long-lived snail and the short-lived mummichog (Johnson and Short 2012).

**Plum Island Sound Food Web:** In a typical ecological food web both bottom-up and top-down forces control ecosystem structure and function (Lockfield 2011, Valiela et al. 2004). Bottom-up effects occur when nutrients limit primary production, which then limits the growth of organisms at successively higher trophic levels (Lockfield 2011). At the Plum Island Sound estuary, nutrient addition has been shown to stimulate benthic algal primary production, which in turn propagates to higher trophic levels so that benthic invertebrate and mummichog production increases (Lockfield 2011, Valiela et al. 2004). Top-down effects occur when predators limit organisms at lower trophic levels by consuming primary producers or indirectly through trophic cascades when predators consume herbivores (Lockfield 2011, Valiela et al. 2004). At Plum Island, mummichogs are top predators in salt marshes and consume a mixed diet of benthic invertebrates, benthic algae, and bulk detritus (Lockfield 2011, Weisberg and Lotrich 1986, Johnson and Short 2012). However, mummichogs would prefer to consume benthic invertebrates because proteinaceous material supports higher growth rates (Weisberg and Lotrich 1986). Juvenile mummichogs also eat a larger proportion of protein than adults because increased growth rates promote higher survival rates (Gutjahr-Gobell 1998, Deegan et al. 2007).

Mummichogs have been suggested to indirectly increase benthic algae through a trophic
cascade. In late summer, mummichogs are capable of consuming 3–10 times the benthic invertebrate production (Deegan et al. 2007). In the absence of predators, benthic invertebrates are capable of grazing more than 60% of the microalgal community per day (Carman et al. 1997, Deegan et al. 2007). Although benthic grazers can exert strong top-down control on the benthic algal community, mummichogs decrease the benthic invertebrate population and thus release the benthic algae from grazing pressure (Kneib 1997, Sarda et al. 1998, Deegan et al. 2007). This suggests that mummichogs are at the top of a trophic cascade that enables benthic algae to proliferate (Deegan et al. 2007).

However at Plum Island, nutrient enrichment has also increased the abundance of mudsnails, which may interfere with the typical ecological food web proposed above. The increase in benthic algal production promotes the growth of mudsnails as they primarily feed on benthic microalgae (Johnson and Short 2012). Several factors may allow mudsnails to more effectively access the benthic algal food resource decreasing energy flow to mummichogs (James Nelson, MBL, pers. comm.). For instance, mudsnails remain inactive in the same creek during the winter and can live to at lease five years (Scheltema 1964). In contrast, mummichogs return to these creeks every growing season, resulting in 54% annual mortality of adults and 99.5% annual mortality of young-of-the-year (Valiela et al. 1977, Meredith and Lotrich 1979). In addition, mudsnails have few predators because of their tough shells, while mummichogs have many predators such as blue crabs, wading birds, and large predatory fish (James Nelson, MBL, pers. comm., Kneib 1982, Valiela et al. 1977).

Because of these factors, snails may be able to access more energy through direct or indirect competition between mummichogs, potentially contributing to the decline in mummichog populations. Thus, snails may be responsible for a trophic bottleneck in the Plum Island estuary (Jimmy Nelson, MBL, pers. comm.). This phenomenon in which snail density increases four times and mummichog biomass decreases by one third in the fertilized creek suggests that there may be some mechanism in which snails affect the mummichogs’ ability to access benthic invertebrates, which may be linked to the crash in the mummichog population seen at Plum Island.

In this short study, our goal was to identify this mechanism by examining how increased snail densities would affect the ability for mummichogs to obtain protein. We hypothesized that snails would either increase or decrease the ability for mummichogs to access protein. We
examined mummichog gut contents and stable isotopic composition because these tools reflect how much protein mummichogs consume and assimilate. To test this hypothesis in the lab, we conducted feeding trials in tanks with snail densities mimicking those observed in Plum Island. I examined mummichog gut contents and used a mixing model from CHN analysis to determine the percent protein and plant material in the gut contents. In the field, we examined the relative difference in stable nitrogen isotope values between mummichogs and snails in order to examine if increased snail densities altered the trophic position of mummichogs. This study might allow us to connect the ability of mummichogs to obtain protein to the crash in the mummichog population seen at the Plum Island Sound estuary.

**Study Locations**

**Plum Island Estuary:** Plum Island is a salt marsh dominated system in northeastern Massachusetts, which is currently unaffected by eutrophication. Approximately 39.8 km$^2$ out of the total estuary (59.8 km$^2$) is dominated by *Spartina alterniflora* in vegetated wetlands (Deegan et al. 2012). Deegan and colleagues (2007) have chosen four experimental marsh creek systems (Sweeney, West, Clubhead, and Nelson) with similar geomorphology along the Rowley River (Fig. 4). Sweeney Creek has been fertilized with 70-100 uM of and 5-7 uM of PO$_4^{3-}$ for nine years, while Clubhead has been fertilized with the same concentration of nutrients for four years. West and Nelson creeks have not been fertilized, as they are reference creeks. Marsh vegetation follows the typical trend of salt marsh plant communities in which tall *Spartina alterniflora* is found in the low marsh along creek banks while *Spartina patens*, short *Spartina alterniflora* and *Distichlis spicata* (salt grass) are found in the high marsh (Deegan et al. 2007).

**Waquoit Bay:** Waquoit Bay is a shallow coastal lagoon (1.8 – 3m) around 600 ha located on the southern shore of Cape Cod. The bay becomes stratified because fresh water enters by ground water transport and streams. We conducted our study in three of nine interconnected sub-watersheds sites within the Waquoit Bay estuarine system (Jehu Pond, Hamblin Pond, and Sage Lot Pond) (Fig. 5). These sites are shallow sub-embayments with fringing salt marshes (Deegan et al. 2002). They are subject to different nitrogen loads because of differences in land use history within each sub watershed. Sage Lot and Hamblin Ponds experience 7 uM NO$_3^-$ and Jehu Pond experiences 13 uM NO$_3^-$ (Bowen et al. 2006). Jehu Pond, Hamblin Pond, and Sage Lot Pond have similar physical characteristics as salinity ranges seasonally between 20 ‰ and 32 ‰.
and temperature ranges between 9°C and 30°C (Deegan et al. 2002).

**Tank Experiments**

*Sample Collections*: To determine if increased snail densities affect mummichog diet, we established three treatment groups: no snails (0), low snails (9), and high snails (36) for a total of nine experiments. To determine if different sediment types affect the ability of mummichogs to access protein, we collected the top two mm of sediment from three experimental creeks from Plum Island estuary: West creek (reference), Clubhead (4-year fertilized creek), and Sweeney Creek (9-year fertilized creek) and three ponds from Waquoit Bay: Sage Lot Pond, Hamblin Pond, and Jehu Pond. We collected snails from the field and we collected mummichogs with minnow traps baited with bagels.

*Feeding Trials*: We added about two cm of sediment to each tank. Once the sediment settled we added the different snail densities (0, 9, and 36) to each tank and allowed the snails to feed for 48 hours. We determined the snail densities by scaling down from snail densities observed in Plum Island (Johnson and Short 2012). I then added six mummichogs to each tank that had been starved for at least 48 hours in order to keep a constant feeding pressure and allowed them to feed for 48 hours (James Nelson, MBL, pers. comm.) After the 48 hour feeding trial, I froze the mummichogs, and thawed them.

*Gut Content Analysis*: I dissected a total of 162 mummichogs from the tank experiments, removed the gut contents, and examined them under a dissecting microscope in order to qualitatively assess the percentage of their diet consisting of protein and plant material.

*CHN analysis*: I dried a composite sample of six gut contents from each tank in an oven set at 60°C, ground the gut contents to a powder, and ran the samples for carbon and nitrogen on the CHN analyzer.

*Mixing model*: From the CHN analysis, we used the average C:N ratio of the gut contents from each of the treatments (0, 9, and 36) (6.55). We used the average C:N ratio of benthic algae (18) and the C:N ratio of protein (3.5) in order to calculate the percent protein and percent plant material the mummichogs consumed (Atkinson et al. 1983, James Nelson, MBL, pers. comm.)

\[
6.55 = 18A + 3.5(1-A)
\]
Field Component

Sample Collections: We collected snails (*N. obsoletus*) in both Sweeney and West creeks and from the three ponds in Waquoit Bay. I collected frozen mummichogs, which were kept in a freezer in Plum Island. They were previously caught in August with flume nets. I collected mummichogs with minnow traps baited with bagels in each of the three sites in Waquoit Bay.

Stable Isotope Analysis: I filleted the mummichogs, took plugs of muscle tissue, and dried the muscle tissue at 60°C (James Nelson, MBL, pers. comm.). I used composite samples of snails (5) and used composite samples of mummichogs (3-8) for stable isotope analysis. Stable isotope analyses for C and N was then performed at the Stable Isotope Laboratory, MBL using a dual-inlet Finnigan MAT Delta S isotope ratio mass spectrometer with a Heraeus elemental analyzer preparation system. Atmospheric N₂ gas was used as the standard (Logan et al. 2005). Stable isotope ratios are expressed as parts per thousand differences and are calculated from the standard in the following equation (Peterson and Fry 1987). The stable nitrogen isotope (delta 15N) value is a trophic tracer, which allowed me to determine the trophic position of the mummichogs in each sub watershed by taking the relative difference between the delta 15N value of the mummichogs and the snails.

\[ \text{Delta 15N} = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 10^3 \]

where \( R \) is the ratio of heavy and light isotopes in a sample, 15N/14N.

Snail Densities: Methods are in Katherine-Anne Glover’s manuscript (SES 2012).

Sediment particle size: In order to determine if there is a difference between sediment particle size from the creeks in Plum Island and the creeks in Waquoit Bay, we retrieved sieved subsamples of wet sediment from each site and sorted them into three fractions of clay + silt (< 63 um) sand (63 um to 2 mm) and gravel (> 2 mm). To determine the percent composition of each sediment size class, we dried and weighed each particle size fraction (Carmichael and Valiela 2005).

Results

The gut content analysis was not a good proxy for the actual protein in the gut contents of the mummichogs shown with an \( R^2 \) of 0.20. The gut content analysis also showed that I
overestimated the amount of protein. In many instances, I eyeballed the fish gut contents at 100% protein when the gut contents actually contained between 70 and 90% protein (Fig. 6).

The highest snail density treatment (36) did not affect the ability for mummichogs to obtain protein, as there was no difference in percent protein in the gut contents across all three treatments. At a snail density of zero, the percent protein in the gut contents was 83%. At a snail density of nine, the percent protein in the gut contents was 82% and at a snail density of 36, the percent protein in the gut contents was 84% (Fig. 7).

We also found that mummichog trophic position was not correlated with increased snail densities. At a snail density of 580 snails/m² the relative difference in del 15N was 1.8, while at a snail density of 1, the relative difference in del 15N was slightly higher at 2.3. The largest difference in del 15N (3.2) occurred at a snail density of 266 snails/m² (Fig. 8).

We also found that sediment particle size (% clay and silt vs. % sand) might have made a difference in the ability for mummichogs to access benthic invertebrates from the sediment. The highest percentage of protein in the gut contents of mummichogs occurred at a sediment particle size composition of 22% clay and silt and 78% sand with 87-89 % protein in the gut contents across the three different snail densities. The lowest percentage of protein in the gut contents occurred at a sediment particle size composition of 79% clay and silt and 21% sand with 75-80 % protein in the gut contents across the three different snail densities. There was no relationship in the percent protein in gut contents based on the different snail densities (Fig. 9).

Discussion

At Plum Island, eutrophication initially increased mummichog biomass because of bottom-up stimulation of nutrients. However, after 5.5 years of eutrophication, the system reached a tipping point in which mummichog biomass eventually decreased to levels below the reference creek. In addition, after the same period of eutrophication, snail density and biomass increased by four times relative to the reference creek. The ability for mummichogs to obtain protein is crucial for mummichog growth and survival (Weisberg and Lotrich 1986, Gutjahr-Gobell 1998, Deegan et al. 2007). Thus, a possible mechanism for the decrease in mummichog biomass may be due to increased snail densities because snails may affect the ability for mummichogs to obtain protein. Thus, we quantified whether increased snail densities affected the ability for mummichogs to obtain protein.
Although we increased snail densities by four times relative to ambient snail densities in the tank experiments, this did not affect the ability for mummichogs to obtain protein. We expected to see a difference in the percent protein in the gut contents of mummichogs at the highest snail densities. In the field, we expected the trophic position of the mummichogs to be either higher or lower at the highest snail densities. This is because changes in the availability of benthic invertebrates could 1) increase the amount of protein in the gut contents and shift the mummichog trophic position up because mummichogs would have more access to benthic invertebrates. On the other hand, changes in the availability of benthic invertebrates could 2) decrease the amount of protein in the gut contents and shift the mummichog trophic position down because the snails could interfere with the ability for mummichogs to access benthic invertebrates. However, we found no difference in the percent protein in the gut contents of mummichogs across three different snail density treatments in the lab and we found no difference in mummichog trophic position with increased snail densities in the field (Fig. 7 and 8). In essence, both tank and field experiments support the conclusion that increased snail densities do not affect the ability for mummichogs to obtain protein. However, Fox and colleagues (2009) observed that in a highly eutrophic estuary, *N. obsoletus* densities were 67 times higher (600 ind. m$^{-2}$) compared to an oligotrophic estuary (9 ind. m$^{-2}$) in Waquoit Bay (Cape Cod, Massachusetts, USA), which conflicts with our results. In Waquoit Bay, this may be explained by the fact that the sites we chose were not highly eutrophic as the highest nitrate concentration was 13 uM NO$_3^-$ (Bowen et al. 2006).

In the short term, snails do not affect the ability for mummichogs to obtain protein. Thus, there must be another driver or mechanism contributing to the crash in the mummichog population seen at Plum Island. The mechanism may still be the ability for mummichogs to obtain protein, but could be instead driven by sediment particle size. We found that a sediment composition of 22% clay and silt and 78% sand, allowed mummichogs to access more protein (Fig. 9). This could be because this particular sediment composition makes it more conducive for benthic invertebrates to live in or because it allows mummichogs to access benthic invertebrates more successfully. It is also possible that the mechanism is not related to the ability for mummichogs to obtain protein. Instead, the snails could be interfering with benthic invertebrate reproduction thereby decreasing benthic invertebrate and mummichog populations over time. Ultimately, we can only conclude that the ability for mummichogs to obtain benthic invertebrates
via increased snail density did not contribute to the decline in the mummichog population at Plum Island.

It is important to identify the mechanism contributing to this crash in the mummichog population because mummichogs are some of the most ecologically important fish in estuarine ecosystems. Mummichogs provide a significant source of organic matter (nitrogen) to the open ocean, as mummichogs become prey for higher trophic-level organisms such as striped bass, bluefish, white perch, and blue crabs (McMahon et al. 2005). For instance, mummichogs may provide an important trophic subsidy to striped bass (James Nelson, MBL, pers. comm.). Mummichog export production is an important link between highly productive salt marsh ecosystems and open ocean ecosystems as mummichogs affect valuable fisheries species and yields (McMahon et al. 2005). Many humans also depend on these economically important predatory fish for their livelihoods.

Humans have the ability to drastically alter species composition and food webs in marine ecosystems. In the past, multiple human influences have altered the abundance and composition of organisms at every trophic level in the food web. Humans have rapidly transformed ecosystems by both bottom-up (nutrient loading), and top-down (exploitation) effects. Nutrient loading can cause shifts in primary producer communities, which has unpredictable consequences (Lotze and Milewski 2004). Fishing down marine food webs (exploitation) often times leads to the decline and extinction of top-level predators, which can alter species composition at lower trophic levels (Pauly et al. 1998). Both of these effects indicate common signs of degradation in marine ecosystems (Lotze and Milewski 2004). It is our responsibility to understand how we are altering food webs in order to ameliorate some of these effects on marine ecosystems. We have seen examples in the past in which simple protection and restoration measures have led to the recovery of some species. These examples may provide future guidance for a more sustainable relationship between humans and the marine environment (Lotze and Milewski 2004).

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(Callinectes sapidus) on the population-size structure of the common mummichog, Fundulus heteroclitus. Estuarine Coastal and Shelf Science 14:159-165.


**Figures and Tables**

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Deegan et al. 2007
Figure 1. Average chl a concentration (mg/m$^2$) as a measure of benthic microalgal biomass in the reference and nutrient-enriched creek (Johnson and Short 2011).

Figure 2. Average *N. obsoletus* biomass (g/m$^2$) in the reference and nutrient-enriched creeks (Johnson and Short 2011).
Figure 3. The ratio of *Fundulus heteroclitus* (mummichog) biomass production (enriched/reference) versus years of nutrient enrichment (Nelson et al. 2012, unpublished data, unreferenced).
Figure 4. An aerial photo of the Plum Island estuary in the Rowley River region. The areas outlined in white are experimental marshes. We collected sediment at SW (Sweeney Creek), CL (Clubhead Creek), and WE (West Creek) and snails at SW and WE (Deegan et al. 2007).
Figure 5. The seven sub watersheds in Waquoit Bay. We chose Hamblin (7 uM NO$_3^-$), Sage Lot (7 uM NO$_3^-$), and Jehu (13 uM NO$_3^-$) for our field sites (Deegan et al. 2002, Bowen et al. 2006).
Figure 6. The percent protein in mummichog gut contents based on gut content analysis (qualitative) versus percent protein using a mixing model with C:N ratios (quantitative).
Figure 7. Snail density treatments of zero, ambient, and high (4x) versus the percent protein in the gut contents of mummichogs using C:N ratios from a mixing model.
**Figure 8.** Snail density/m$^2$ versus the difference in del 15N of snails and mummichogs as a way to measure the relative trophic position of mummichogs.

**Figure 9.** The percent clay and silt versus the percent protein in the gut contents of mummichogs with densities of no snails, low snails, and high snails (4x).