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MANAGEMENT BRIEF

Simulated Short-Term Impacts of the Atlantic Menhaden Reduction Fishery on Chesapeake Bay Water Quality

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Abstract
Atlantic menhaden *Brevoortia tyrannus* support an intense fishery in Chesapeake Bay, an estuary that is impaired by eutrophication and excess phytoplankton biomass. Since Atlantic menhaden are filter-feeding fish that consume plankton, including phytoplankton, fishery removals may negatively affect water quality and may therefore hinder bay restoration efforts. We performed a simulation to estimate the short-term (monthly and annual) water quality impacts caused by the reduction fishery harvesting its current total allowable catch of Atlantic menhaden in Chesapeake Bay (109,020 metric tons/year). A theoretical loss in net nitrogen removal (N_t) due to the fishery was estimated for each month, and the simulation was repeated for several scenarios to account for uncertainties associated with Atlantic menhaden feeding behavior. The largest potential impact of the fishery (i.e., absolute value of N_t) occurred in August for all scenarios, but depending on the value assumed for average feeding rate the fishery was estimated to have either a positive impact or a negative impact on water quality. The sum of N_t across months ranged from -5.78×10^5 to 1.85×10^7 kg of N/year, indicating that the harvested Atlantic menhaden could have contributed up to 0.38% or removed up to 12.19% of the estimated total nitrogen load for Chesapeake Bay. This large range probably captures all possible scenarios of Atlantic menhaden feeding intensity; however, the current understanding of their feeding rates as related to phytoplankton composition in Chesapeake Bay suggests that average feeding rates are relatively low and that the probable impact of the fishery on water quality is negligible.

Atlantic menhaden *Brevoortia tyrannus* are omnivorous filter feeders that are distributed along the Atlantic coast of North America. They are pelagic schooling fish, and juveniles and adults feed on phytoplankton, zooplankton, detritus, and amorphous matter (Peck 1893; Richards 1963; Jeffries 1975; Edgar and Hoff 1976; Lewis and Peters 1984, 1994). Atlantic menhaden are abundant in Chesapeake Bay during spring through late fall, and their ingestion of phytoplankton has the potential to improve water quality in the bay.

High levels of nutrient (and sediment) inputs from numerous sources (agriculture, wastewater, runoff, and air pollution) have rendered Chesapeake Bay a degraded ecosystem. Concurrent with population growth and development throughout the past century, an increasing trend in annual nitrogen input to the bay has stimulated an overabundance of phytoplankton (Harding 1994; Harding and Perry 1997). This excess primary production has resulted in reduced water quality and substantially altered benthic habitats (Hagy et al. 2004; Kemp et al. 2005). Therefore, water quality improvement in Chesapeake Bay requires a reduction in the amount of nitrogen input, an increase in the assimilation of nitrogen into the aquatic food web through the ingestion of phytoplankton, or both of these changes. Since Atlantic menhaden consume phytoplankton and are abundant in the bay, they represent a potential pathway for the assimilation of nitrogen and may play an important role in improving the water quality of the bay.

Despite the potential importance of their ecological role, Atlantic menhaden in Chesapeake Bay support an intense commercial reduction fishery, which processes them into fish meal, oil, and solubles. The processing plant is based in Reedville, Virginia, and the annual harvest for the reduction fishery has resulted in Reedville being ranked as the second- and third-largest U.S. fishing port in 2008 and 2009, respectively. This fishery operates in federal mid-Atlantic waters (>4.8 km [3 mi] offshore), the state waters (0–4.8 km offshore) of Virginia and North Carolina, and the Virginia portion of Chesapeake Bay (ASMFC 2006). There is no limit on the number of Atlantic menhaden that can be removed from the Atlantic Ocean; however, the annual reduction fishery harvest in Chesapeake Bay is currently capped at 109,020 metric tons—more than half of the average total harvest for 2005–2008 (155,000 metric tons; ASMFC 2010). Because Atlantic menhaden have the potential to improve water quality and because the fishery is able to remove a relatively

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large number of Atlantic menhaden from Chesapeake Bay each year, there is concern that the reduction fishery in the bay may be negatively affecting ecosystem health by diminishing this potential nitrogen assimilation pathway. Thus, a reduction in Atlantic menhaden harvest may be an effective management strategy for improving water quality in Chesapeake Bay.

The goal of this project was to evaluate the potential water quality impact of the Atlantic menhaden reduction fishery in Chesapeake Bay when the total allowable catch is harvested. The ingestion of phytoplankton and the associated net removal of nitrogen constitute the main pathway by which Atlantic menhaden could improve water quality; therefore, we estimated the potential loss in net nitrogen removal (from phytoplankton ingestion) that would be caused by an Atlantic menhaden harvest of 109,020 metric tons/year from the bay. There is an ontogenetic continuum in the minimum size of particles consumed by Atlantic menhaden (Durbin and Durbin 1975; Friedland et al. 1984; Lynch et al. 2010), and this continuum is largely governed by functional morphology (Friedland et al. 2006); thus, it was important to consider only those phytoplankton species that are large enough for consumption by harvest-susceptible Atlantic menhaden. Furthermore, estimating net nitrogen removal by Atlantic menhaden required the consideration of not only nitrogen ingestion (i.e., via phytoplankton ingestion) but also total nitrogen excretion, which in terms of water quality represents a negative feedback to the system. Using the best available estimates of Atlantic menhaden filtration and excretion, we performed a simulation of net nitrogen removal in relation to the temporal dynamics of the Atlantic menhaden fishery and the phytoplankton community in Chesapeake Bay.

METHODS

The Atlantic menhaden reduction fishery operates during May–December of each year (ASMFC 2006). To evaluate the impact of Atlantic menhaden harvests on water quality, we assumed that the fishery was operating at maximum capacity in Chesapeake Bay and we estimated the monthly loss in potential nitrogen assimilation (N_t) that would be caused by the fishery removals. To generate these estimates, monthly estimates of the amounts of nitrogen that would have been ingested (I_{Nt}) and excreted (E_{Nt}) by the theoretically harvested Atlantic menhaden were required and combined as follows:

$$N_t = I_{Nt} - E_{Nt}, \tag{1}$$

where N_t, I_{Nt}, and E_{Nt} are in units of kilograms of nitrogen (kg N) per month.

Estimates of I_{Nt} and E_{Nt} depend on several underlying processes. Many of these processes have not been thoroughly described, so we simulated N_t across a range of assumptions in an attempt to more fully characterize this uncertainty. Expanding equation (1) to incorporate these underlying processes results in the following relationship:

$$N_t = \overbrace{\left(n_t \times C_t \times F \times t_f \times \frac{16}{106} \times \frac{14}{12}\right)}^{I_{Nt}} - \overbrace{\left\{n_t \times [(E_{Nf} \times t_f) + (E_{Nx} \times t_x)]\right\}}^{E_{Nt}}, \tag{2}$$

where n_t represents the number of fish harvested per month, C_t is the average monthly phytoplankton carbon concentration available for consumption (kg of C/L), F is the rate of phytoplankton filtration by Atlantic menhaden (L·fish^{-1}·min^{-1}), t_f is the time (min) spent feeding per month, the term 16/106 is a molar relationship for N:C in phytoplankton (Redfield et al. 1966), and 14/12 is necessary for converting moles to mass (kg), which allows I_{Nt} to be expressed in terms of kilograms of nitrogen per month. To estimate E_{Nt}, we combined estimates of the rate of nitrogen excretion by Atlantic menhaden while feeding (E_{Nf}; kg N·fish^{-1}·min^{-1}) and the rate of excretion by the fish while not feeding (E_{Nx}; kg N·fish^{-1}·min^{-1}) and expanded those to the t_f and the time not spent feeding (t_x) during each month for the total monthly harvest (n_t). To evaluate the potential annual impact of the reduction fishery, the values of N_t were summed across months (ΣN_t).

We based our estimates of n_t on the average dynamics of the reduction fishery from 2006 to 2009. Detailed landings were reported for this fishery (NMFS 2007, 2008, 2009, 2010); the total harvest was presented in terms of biomass (mean = 154,182 metric tons) as well as number (mean = 507 × 10^6 fish). Using this relationship, we estimated the number of fish per metric ton (3,290). Total monthly landings throughout the fishing season (summarized in Table 1) were also reported (NMFS 2007, 2008, 2009, 2010). Under the assumption that the removals of Atlantic menhaden in Chesapeake Bay followed the average temporal dynamics in total landings, we applied the monthly proportions of the total harvest to the theoretical harvest of 109,020 metric tons and estimated the monthly numbers of fish removed from Chesapeake Bay (Table 1). It should be noted that since the harvest cap has been in place, the reduction fishery has never removed its entire Chesapeake Bay quota, and the accumulation of annual underages can be used to increase the quota in subsequent years up to a maximum of 122,740 metric tons (ASMFC 2010). Therefore, if landings ever exceed 109,020 metric tons in a given year, our simulation would underestimate water quality impacts by the reduction fishery in that year.

Instead of using bulk phytoplankton concentration to estimate C_t, we used the concentration of phytoplankton available for ingestion by the Atlantic menhaden harvested by the fishery. The reduction fishery in Chesapeake Bay harvests mainly age-1 to age-3 Atlantic menhaden (NMFS 2008). Several studies of Atlantic menhaden filtration and a study of Atlantic menhaden feeding morphology indicated that age-1 and older (age-1+) fish do not actively filter individual phytoplankton

TABLE 1. Minimum (Min), mean (Mean), and maximum (Max) total monthly landings by the Atlantic menhaden reduction fishery in Chesapeake Bay (2006–2009); theoretical estimates of the number of Atlantic menhaden removed by the reduction fishery each month (n_t) when harvesting the annual total allowable catch (109,020 metric tons); and estimates of the average monthly carbon concentration (C_t) for 16-μm and larger phytoplankton in the Virginia portion of Chesapeake Bay.

	Landings (10^3 metric tons)				
Month	Min	Mean	Max	n_t (10^7 fish)	C_t (10^{-6} kg/L)
May	0.58	4.31	8.70	0.95	1.42
Jun	19.00	22.34	29.50	5.08	1.46
Jul	28.53	29.18	30.20	6.73	1.25
Aug	32.50	35.63	40.40	8.17	1.19
Sep	20.90	25.21	29.50	5.79	0.93
Oct	25.80	28.05	29.70	6.48	1.00
Nov	4.55	6.84	9.60	1.55	6.35
Dec	0.79	4.92	12.70	1.12	7.77

smaller than roughly 13–16 μm from the water (Durbin and Durbin 1975; Friedland et al. 1984, 2006; Lynch et al. 2010). In fact, Durbin and Durbin (1975) determined that filtration efficiencies were less than 10% for adult Atlantic menhaden feeding on particles less than 30 μm in diameter. Therefore, we estimated average monthly C_t for phytoplankton 16-μm and larger in the Virginia portion of Chesapeake Bay (Table 1). These estimates were derived by using data from the U.S. Environmental Protection Agency Chesapeake Bay Program (CBP) online database (www.chesapeakebay.net/dataandtools.aspx?menuitem =14872) and from species-specific data for phytoplankton in the bay (J. Johnson, U.S. Environmental Protection Agency, CBP, personal communication). From the CBP database, we were able to obtain individual counts of phytoplankton by species (number/L), and J. Johnson (CBP) provided information on phytoplankton cell sizes and cellular carbon content (μg of C). By identifying 16-μm and larger species and multiplying the number per liter by the carbon content, we derived our monthly estimates of C_t (kg C/L). To account for variability in phytoplankton composition and biomass, we used average monthly C_t for data from 2000 to 2007.

The feeding rate F can be thought of as the liters of water that are cleared of phytoplankton per fish per minute. Since the response of F to phytoplankton concentration has not been described for age-1+ Atlantic menhaden, we used a single estimate of F for the entire simulation period. To date, two studies have reported values of F for age-1+ Atlantic menhaden feeding on phytoplankton (Durbin and Durbin 1975; Lynch et al. 2010). Durbin and Durbin (1975) performed experiments with individual species of phytoplankton, and Lynch et al. (2010) used raw Chesapeake Bay water to provide a natural assemblage of phytoplankton. In these studies, F ranged from 0.01 to 6.21 L·fish^{-1}·min^{-1}. Given the large range of F-values, we felt that it was not appropriate to perform only one simulation based on a single estimate; thus, we performed multiple simulations and used several estimates covering the potential range of F (0.01, 0.1, 0.5, 1.0, 2.0, and 6.0 L·fish^{-1}·min^{-1}).

Another parameter that is difficult to quantify for Atlantic menhaden is t_f. In a study of Atlantic menhaden predation in Narragansett Bay, Rhode Island, Durbin and Durbin (1998) assumed that Atlantic menhaden fed for 12 h/d. However, there are little data to support this assumption, so we chose to run the simulation under various scenarios of t_f (6, 12, and 24 h/d).

In addition to I_{Nt}, it was necessary to include estimates of nitrogen excretion by Atlantic menhaden on a per-fish, per-time basis during feeding (E_{Nf}) and nonfeeding (E_{Nx}) phases. These estimates were obtained from Lynch et al. (2010), who estimated total dissolved nitrogen excretion rates for age-1+ Atlantic menhaden while the fish fed on zooplankton (mean ± SE = 38.10 ± 3.30 μg N·fish^{-1}·min^{-1}) and while the fish were not feeding (27.41 ± 2.96 μg N·fish^{-1}·min^{-1}). Excretion rates are probably variable and may differ for Atlantic menhaden feeding on a natural assemblage of prey in the wild; however, reliable estimates of excretion in these conditions do not exist.

To put the estimated N_t in the context of total nitrogen load, we estimated average annual nitrogen input to Chesapeake Bay. We used existing data (1990–2001) and considered multiple sources of nitrogen, including riverine, atmospheric, and point sources. Riverine nitrogen inputs are measured at the fall lines of the nine Chesapeake Bay tributaries with stream gauges; these data are available from the U.S. Geological Survey's online database (va.water.usgs.gov/chesbay/RIMP/dataretrieval.html). The values were inflated by 20% to account for ungauged watershed area based on reported drainage areas for the nine U.S. Geological Survey gauges. Annual atmospheric deposition of nitrogen was estimated by using the method of Boynton et al. (1995), and data for point sources below the fall lines were obtained from the CBP online point source database (www.chesapeakebay.net/data_pointsource.aspx). Combining these sources allowed us to generate an average estimate of total annual nitrogen load to Chesapeake Bay.

Finally, it is fairly straightforward to adapt the model used for our simulation (equation 2) to an estimated population size to evaluate the ecological role of Atlantic menhaden. However, the amount of uncertainty surrounding population-level estimates drastically magnifies the total uncertainty around estimates of N_t. Although the most recent Atlantic menhaden stock assessment report provided annual estimates of coastwide population size by age (ASMFC 2010), estimating the impact on Chesapeake Bay water quality requires information on the proportion of the total Atlantic menhaden population that utilizes the bay on a monthly basis. This value significantly influences the estimates of N_t but cannot be reasonably determined given our current understanding of the spatiotemporal distribution of Atlantic menhaden. A rough population-level estimate of N_t can be generated by assuming that a fixed proportion of the coastwide population inhabits Chesapeake Bay during the simulation period. As an example, we assumed that 50% of the adult population is present in the bay and this population includes only age-1 and age-2 fish—the ages that typically constitute the largest proportion of catch in the bay (NMFS 2007, 2008, 2009, 2010). We calculated an average total population size of 11.0×10^9 Atlantic menhaden for 1990–2008 (a period of relatively consistent estimated abundance), and we used 5.5×10^9 as our assumed Chesapeake Bay population size. This number reflects an estimate of abundance at the beginning of the fishing year (ASMFC 2010). Because we assumed the abundance in Chesapeake Bay to be constant, it was considered to be an average for the simulation period and therefore was not directly affected by assumptions about immigration, emigration, natural mortality, or fishing mortality. Using this estimated Chesapeake Bay population size, we performed our simulation (equation 2) across the same ranges of F and t_f used for our evaluation of the fishery harvest cap. Note that for this example, (1) n_t represents the number of adult Atlantic menhaden in Chesapeake Bay each month rather than the number harvested and (2) ΣN_t is no longer a loss due to the fishery but instead is the amount of nitrogen that could be removed per year by the population of adult Atlantic menhaden in the bay.

RESULTS

Using a range of estimates for F and t_f, monthly estimates of N_t were generated throughout the representative fishing season (Figure 1). For the scenarios where F was assumed to be low (0.01–0.10 L·fish^{-1}·min^{-1}), N_t was negative throughout the year for all values of t_f. Also, estimates of N_t were mostly negative for the scenario in which F was 0.5 L·fish^{-1}·min^{-1} and t_f was 6 h/d. A negative value for N_t indicates that the harvested Atlantic menhaden represented a net source of nitrogen in terms of phytoplankton production. For this to occur, their diets would have to primarily consist of organisms other than phytoplankton, which would cause total nitrogen excretion to exceed the amount of nitrogen removed via phytoplankton ingestion. For these scenarios, the fishery may actually have a positive impact on water quality from a strictly eutrophication-centered perspective. For all other scenarios, N_t was mostly positive throughout the year, indicating that the reduction fishery generated a negative impact on water quality. When N_t was positive, the greatest impact of the fishery occurred in the month of August.

In addition to the monthly estimates, N_t was summed across months for each scenario to evaluate the potential annual impact of the reduction fishery. Since summing produces a single estimate for each scenario, we were able to perform the simulation iteratively (5,000 times) over small increments of F between 0.01 and 6.00 L·fish^{-1}·min^{-1}, resulting in nearly continuous estimates of ΣN_t across the range of F-values for each t_f (Figure 2). These continuous estimates facilitated an understanding of the transition points for assumed F-values beyond which ΣN_t became positive for each t_f. These transition points occurred at F-values of 0.6, 0.3, and 0.2 L·fish^{-1}·min^{-1} for t_f values equal to 6, 12, and 24 h/d, respectively (Figure 2, inset). For all combinations of F and t_f, estimates of ΣN_t ranged from -5.72×10^5 to 1.83×10^7 kg N/year.

Performing the simulation iteratively across the range of F-values highlighted the fine-scale impacts of assumed F on estimates of ΣN_t but did not precisely elucidate the impacts of assumed t_f. There is substantial uncertainty surrounding this parameter; therefore, we repeated the preceding sensitivity analysis across all possible values of t_f from 0 to 24 h/d by changing the assumed t_f by 1 min for each iteration (44,641 runs per F). For this analysis, the overall range of ΣN_t was -5.78×10^5 to 1.85×10^7 kg N/year, and the t_f transition points where ΣN_t became positive were 7.3, 3.4, 1.6, and 0.5 h/d for F-values equal to 0.5, 1.0, 2.0, and 6.0 L·fish^{-1}·min^{-1}, respectively; ΣN_t was never positive when F was equal to 0.01 or 0.10 L·fish^{-1}·min^{-1} (Figure 3).

Estimating the impact of the loss of nitrogen removal on Chesapeake Bay water quality requires an understanding of the total amount of nitrogen input to the bay each year. We estimated the average annual nitrogen input to be approximately 1.52×10^8 kg N. This is similar to a previously estimated average total nitrogen load ($\sim 1.61 \times 10^8$ kg N/year; Boynton et al. 1995). For the simulations across the continuous ranges of F and t_f, the amount of cumulative N_t reported was expressed as a percentage of this estimated total annual nitrogen load (Figures 2, 3). Depending on the assumed values for F and t_f, harvested Atlantic menhaden have the potential to remove 12.19% of the total nitrogen load or to contribute an additional 0.38% of the annual load, thus representing a source of nitrogen for phytoplankton.

Lastly, population-level estimates of net nitrogen removal (ΣN_t) by adult Atlantic menhaden were generated by using an assumed population size. For a moderate feeding rate (F = 0.5 L·fish^{-1}·min^{-1}), estimates of ΣN_t for this population ranged from -5.4×10^7 to 1.1×10^8 kg N/year, depending on the value assumed for t_f. This result suggests that the population may input an additional 35.3% of the total nitrogen load to Chesapeake Bay or may remove up to 73.7% of

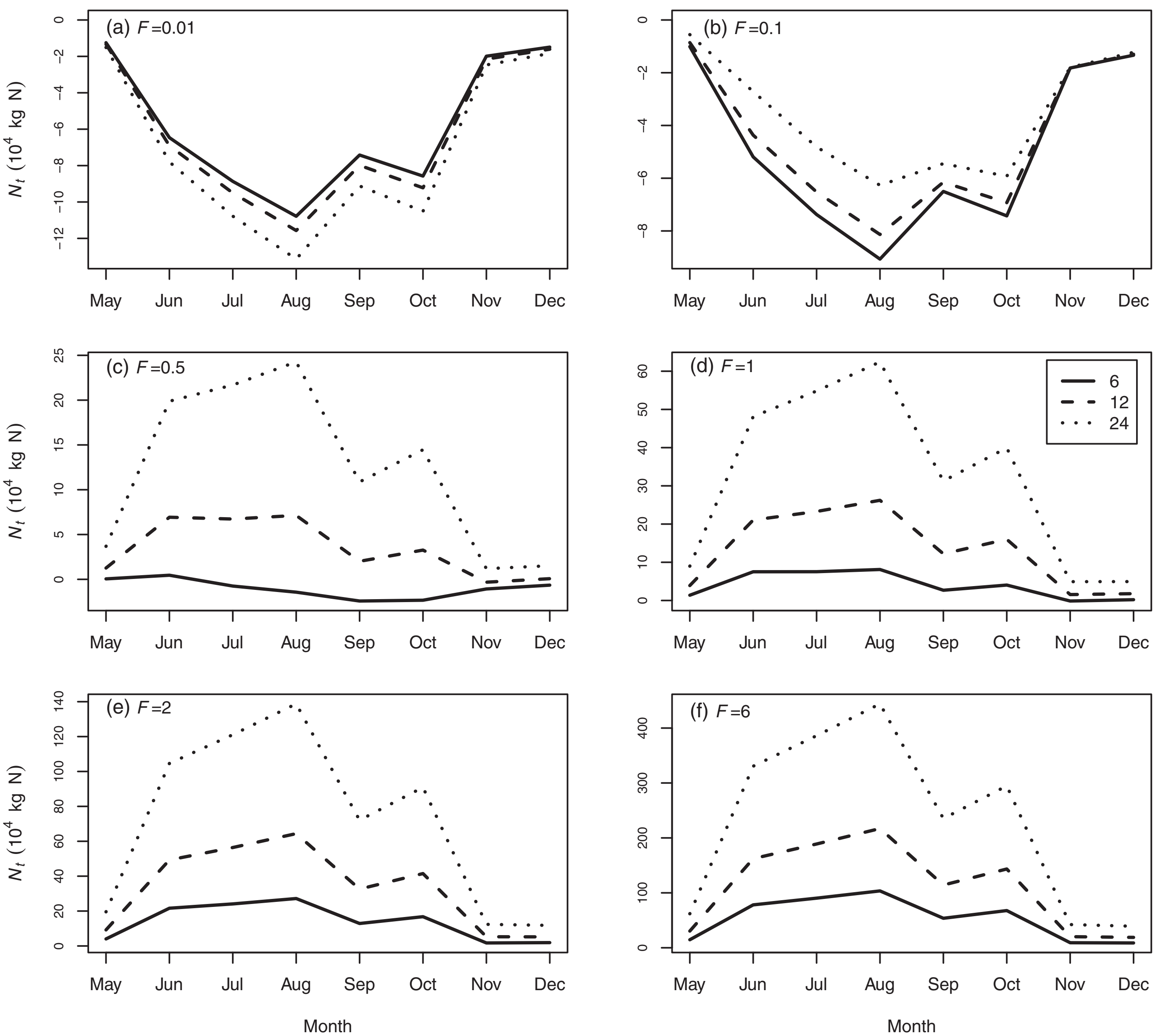

FIGURE 1. Simulated monthly loss of nitrogen removal (N_t) caused by the maximum harvest of Atlantic menhaden in the Chesapeake Bay reduction fishery. The simulation was run based on several estimates of average filtration rate (F; 0.01–6.00 L·fish^{-1}·min^{-1}) for Atlantic menhaden feeding on 16-μm and larger phytoplankton and based on three assumed values of time spent feeding (t_f = 6, 12, and 24 h/d).

the total nitrogen load. These are very rough estimates due to the substantial uncertainty surrounding several parameters (particularly n_t and F), but under this scenario the range of possible influence estimated for adult Atlantic menhaden in Chesapeake Bay is quite large and encompasses zero. By repeating the simulation over the full range of F-values (0.01–6.00 L·fish^{-1}·min^{-1}), we can account for uncertainty in the average F, but ΣN_t then ranges from -7.1×10^7 to 2.2×10^9 kg N/year, or −46.6% to 1,423.8% of the total annual nitrogen load.

DISCUSSION

The simulation of monthly nitrogen removal (via phytoplankton ingestion) by theoretically harvested Atlantic menhaden provides a range of estimates describing the potential impact of the Atlantic menhaden reduction fishery on Chesapeake Bay water quality. Several scenarios with variable assumptions about F and t_f are presented (Figure 1); although the magnitude of N_t changes substantially in response to changes in t_f, the general trends are quite similar for a given F.

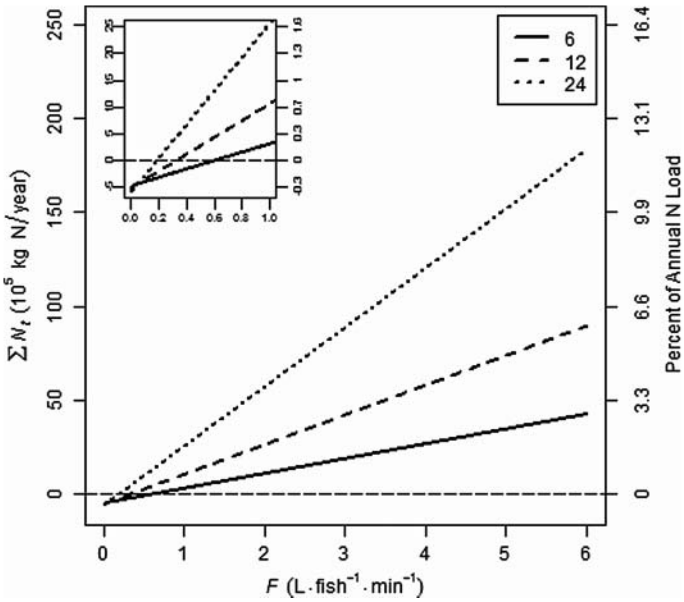

FIGURE 2. Simulated annual loss of nitrogen removal (ΣN_t) caused by the maximum harvest of Atlantic menhaden in the Chesapeake Bay reduction fishery. Estimates of ΣN_t are also expressed as a percentage of the annual nitrogen load to Chesapeake Bay. The simulation was run based on several estimates of average filtration rate (F) for Atlantic menhaden feeding on 16-μm and larger phytoplankton and based on three assumed values of time spent feeding ($t_f = 6$, 12, and 24 h/d). The inset panel highlights the results for F-values from 0 to 1 L·fish^{-1}·min^{-1}.

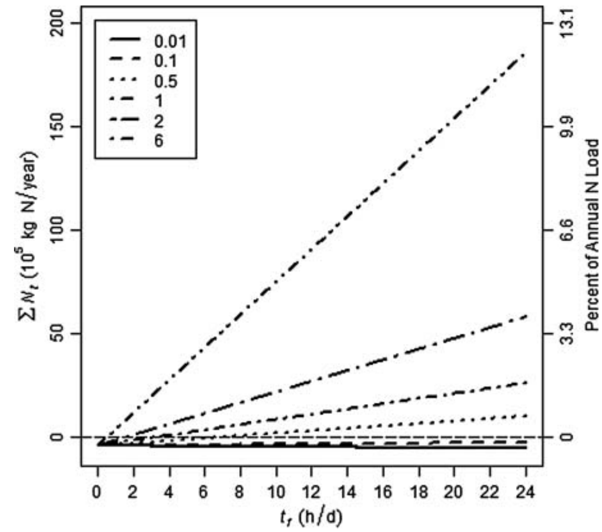

FIGURE 3. Simulated annual loss of nitrogen removal (ΣN_t) caused by the maximum harvest of Atlantic menhaden in the Chesapeake Bay reduction fishery. Estimates of ΣN_t are also expressed as a percentage of the annual nitrogen load to Chesapeake Bay. The simulation was run based on a range of assumed possible values of time spent feeding (t_f) and based on several estimates of average filtration rate (F; 0.01–6.00 L·fish^{-1}·min^{-1}) for Atlantic menhaden feeding on 16-μm and larger phytoplankton.

Changes in F, however, affected the temporal trend of estimated fishery impacts on water quality. The months that exhibited the smallest fishery impacts (i.e., when N_t was close to zero) were consistent throughout all scenarios and corresponded with the smallest monthly landings of Atlantic menhaden (Table 1). For all scenarios, the largest potential impact was typically in August, the month with the most fishery removals.

Overall, the variability in the simulation results makes it difficult to discern the actual monthly impacts of the fishery removals; however, the estimated temporal trends may still be informative in a management context. If the reduction fishery could be managed from an ecosystem-based perspective or perhaps simply in conjunction with water quality management, then our simulation results could be used to develop measures that aim to minimize potential fishery impacts. For instance, a time–area closure that reduces or eliminates Atlantic menhaden fishing in Chesapeake Bay during August (the month with the greatest potential impact) may be an effective management action. However, this measure would only benefit water quality if the harvested Atlantic menhaden were feeding on phytoplankton at a relatively high rate ($F = 1$–6 L·fish^{-1}·min^{-1}) throughout the fishing season. If this assumption holds, then a temporary closure in August could reduce the annual impact of the fishery (i.e., ΣN_t) by 24.2–25.9%, depending on F and t_f.

In addition to estimates of monthly water quality impacts of the Atlantic menhaden reduction fishery, the simulated cumulative annual impacts are informative for management because they put the total fishery impacts in context with the annual nitrogen load to Chesapeake Bay. However, due to uncertainty surrounding the values assumed for F and t_f, the estimated range is rather large and encompasses zero (-5.78×10^5 to 1.85×10^7 kg N/year), making it difficult to determine whether the impact of the fishery is measurable, negligible, or possibly beneficial to Chesapeake Bay water quality. An evaluation of the various scenarios used in the simulation may aid in determining a reasonable set of estimates. Since the assumed values of F and t_f essentially covered the entire possible range, it may be safe to assume that the most extreme estimates of ΣN_t are unrealistic. For instance, it is very unlikely that Atlantic menhaden feed on phytoplankton continuously at their maximum observed rate for 24 h/d throughout the entire fishing season (May–December). The maximum F used in our study was observed by Durbin and Durbin (1975) when Atlantic menhaden were feeding on an extremely large species of phytoplankton (the diatom *Ditylum brightwelli*; mean length = 79 μm). Large phytoplankters such as these probably do not comprise an appreciable proportion of the phytoplankton community in Chesapeake Bay (Marshall et al. 2005). When this extreme is excluded, the maximum F observed by Durbin and Durbin (1975) was 4.12 L·fish^{-1}·min^{-1}, measured for Atlantic menhaden feeding on a three-cell diatom chain (*Thalassiosira rotula*). In contrast to the relatively high F-values reported by Durbin and Durbin (1975), who measured rates for Atlantic menhaden feeding on single species, the values of F reported by Lynch et al. (2010) never exceeded 0.02 L·fish^{-1}·min^{-1}. These measurements represented F of bulk phytoplankton and were recorded when Atlantic menhaden were feeding on a natural assemblage of phytoplankters commonly found in Chesapeake Bay. Given the results of these earlier studies, it seems most likely that an average F for Atlantic menhaden feeding on 16-μm and larger phytoplankton throughout the year is more than 0.02 L·fish^{-1}·min^{-1} but less than 4.12 L·fish^{-1}·min^{-1}. This would limit the reasonable range of ΣN_t from -5.38×10^5 to 1.24×10^7 kg N/year, which represents from −0.35% to 8.15% of the estimated annual nitrogen load to Chesapeake Bay.

To obtain more precise estimates of N_t and ΣN_t, uncertainty in feeding behavior would clearly need to be addressed further. Friedland et al. (2006) described the ontogenetic continuum in the morphology of the Atlantic menhaden feeding apparatus. Those authors concluded that the minimum size threshold for particle retention by Atlantic menhaden increases with age in a nonlinear fashion; the minimum spacing was 7–8 μm for juveniles and 15–20 μm for adults. Experimental studies of Atlantic menhaden feeding (Durbin and Durbin 1975; Friedland et al. 1984; Lynch et al. 2010) corroborated the findings of Friedland et al. (2006) by showing that juveniles feed on smaller species of phytoplankton at much higher rates than do adults. This result suggests that adults are better suited for ingesting larger-sized particles, such as zooplankton. Also, if the natural plankton assemblages used in the feeding experiments of Lynch et al. (2010) are representative of typical Chesapeake Bay plankton, then phytoplankton probably constitute a small component of the diet for adult Atlantic menhaden in the bay. Thus, the findings of these studies indicate that the reduction fishery's impact is negligible or even beneficial to Chesapeake Bay water quality. Furthermore, Durbin and Durbin (1975) described a linear relationship between F and particle size, where F did not exceed 1 L·fish^{-1}·min^{-1} unless Atlantic menhaden were feeding on relatively large phytoplankton (chain length > 30 μm). Therefore, the ability to thoroughly address uncertainty surrounding average F requires an understanding of the size-structured biomass and distribution of plankton in Chesapeake Bay as related to the distribution of adult Atlantic menhaden. Currently, this relationship is not well understood—hence leading to our use of an average F throughout the simulation. In general, however, as was summarized by Kemp et al. (2005), phytoplankton composition in Chesapeake Bay (and other eutrophic environments) has exhibited a shift to dominance by smaller-sized species. Given this trend coupled with findings from studies of Atlantic menhaden filtration (Durbin and Durbin 1975; Friedland et al. 2006; Lynch et al. 2010), there is evidence to suggest that phytoplankton filtration by adult Atlantic menhaden in Chesapeake Bay is minimal, which would mean that the reduction fishery has little to no impact on water quality. However, if information on the distribution and composition of plankton as related to the distribution of Atlantic menhaden does become available, refined estimates could be obtained.

The purpose of this simulation was to evaluate the short-term water quality impacts imposed by the Atlantic menhaden reduction fishery under the current harvest cap, but fishery removals may also result in longer-term impacts on total population size. Therefore, we simulated population-level estimates to evaluate the ecological role of Atlantic menhaden as related to water quality. With consideration given to the assumptions and uncertainties associated with the population-level simulation, this analysis can be used to determine a target population size if the Atlantic menhaden management body seeks to address water quality concerns. However, caution must be exercised when interpreting our results. Given the population size used in the analysis, the range of N_t estimates increased considerably when compared with our evaluation of the harvest cap, and extreme N_t estimates outside the realm of possibility were observed. This suggests that while the impact of the fishery is probably negligible, there are conceivable scenarios wherein the baywide Atlantic menhaden population would influence water quality. However, refining these estimates requires a much better understanding of the distribution of Atlantic menhaden and their feeding behavior as related to the size-fractionated standing stock of phytoplankton. Also, juvenile Atlantic menhaden were not included in the simulation. Juveniles are likely to distribute differently in the estuary than adults, and they have been shown to filter smaller particles with higher efficiency (Friedland et al. 1984, 2006; Lynch et al. 2010). Therefore, analyses of the influence of juvenile Atlantic menhaden on water quality may require assumptions and data that differ from those used for adults.

While our study represents the first to directly estimate water quality impacts induced by the Atlantic menhaden reduction fishery, previous studies have estimated the population-level impacts of Atlantic menhaden on water quality (Rippetoe 1993; Durbin and Durbin 1998; Gottlieb 1998; Dalyander and Cerco 2010; Lynch et al. 2010). Many of these studies utilized comprehensive bioenergetics models to predict the impact of Atlantic menhaden (adults, juveniles, or both) on a range of variables, including primary productivity (Rippetoe 1993; Gottlieb 1998), nitrogen (Durbin and Durbin 1998; Lynch et al. 2010), and algal biomass (Dalyander and Cerco 2010). In general, these studies concluded that Atlantic menhaden either had a relatively small influence on water quality (Rippetoe 1993; Durbin and Durbin 1998; Dalyander and Cerco 2010) or (as with our study) that the estimated range of potential influence was large (Gottlieb 1998; Lynch et al. 2010). For Narragansett Bay Atlantic menhaden, Durbin and Durbin (1998) specified F-values that considered size structure of the phytoplankton community in the bay. However, the studies of Atlantic menhaden in Chesapeake Bay (Rippetoe 1993; Gottlieb 1998; Dalyander and Cerco 2010) did not account for this important characteristic and considered F to be constant irrespective of particle size. Our sensitivity analysis across values of F indicates that F substantially influences the perceived role of Atlantic menhaden in affecting water quality. This further emphasizes the importance of understanding Atlantic menhaden F in feeding on phytoplankton and the distribution of Atlantic menhaden in relation to phytoplankton composition and distribution.

Our simulation incorporated uncertainty surrounding the assumed values for F and t_f and resulted in wide-ranging estimates of N_t; however, there are other underlying sources of error that should be recognized. For example, monthly estimates of n_t reflected proportions of total Atlantic menhaden landings but may not have accurately represented trends in Chesapeake Bay landings. While we used hypothetical values for n_t to reflect maximum harvest, equation (2) could be used to generate historical, real-time, or predictive estimates of N_t given actual landings of Atlantic menhaden in Chesapeake Bay or landings associated with potential future management scenarios. Our assumed estimates of E_{Nt} may also introduce a potential source of error. We used two static estimates (E_{Nf} and E_{Nx}), but the amount of nitrogen excreted probably varies with diet and feeding intensity on a continuous basis. Unfortunately, these relationships have not been described. Furthermore, due to a lack of information, we ignored zooplankton ingestion by Atlantic menhaden; this likely represents a negative feedback in terms of water quality because zooplankton feed on phytoplankton and any ingestion of zooplankton by Atlantic menhaden could affect this other potential nitrogen assimilation pathway. The incorporation of zooplankton into the model, however, requires not only F for Atlantic menhaden feeding on zooplankton but also the filtration and excretion rates for zooplankton feeding on the phytoplankton community. Incorporating an understanding of these uncertainties as well as information regarding the phytoplankton species that constitute the diet of these fish may result in better estimates of the amount of nitrogen ingested. Finally, to evaluate the impact of the fishery on an ecosystem level, we used a single estimate of average annual total nitrogen input to Chesapeake Bay (1.52×10^8 kg N). This value does exhibit annual variation (SE $= 1.31 \times 10^7$ kg N), but this amount of variability did not substantially change the overall conclusions regarding fishery impacts on bay water quality.

This simulation study used the best available information to estimate the potential impact of the Atlantic menhaden reduction fishery on Chesapeake Bay water quality. Based on our current understanding of Atlantic menhaden feeding, the most likely scenario results in an estimate of ΣN_t that is close to zero and a negligible fishery impact on water quality. However, the wide range of estimates generated by the simulation incorporated uncertainty surrounding Atlantic menhaden feeding intensity. Thus, addressing this uncertainty in future analyses may improve our understanding of the impact of the Atlantic menhaden reduction fishery.

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