FEEDING ECOLOGY OF ATLANTIC MENHADEN (*BREVOORTIA TYRANNUS*) IN CHESAPEAKE BAY

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APPROVAL SHEET

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DEDICATION

To the memory of my grandmother, Catherine O'Hara Lynch (1926-2001), whose strength and wisdom are a continual source of motivation.

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PREFACE

Chapter 2 of this thesis will be submitted for publication in the Canadian Journal of Fisheries and Aquatic Sciences, and is formatted under the guidelines specified for that journal.

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CHAPTER 1: PROJECT OVERVIEW

INTRODUCTION

Atlantic menhaden (*Brevoortia tyrannus* Latrobe, 1802) are schooling pelagic fish distributed in nearshore and estuarine habitats along the western Atlantic Ocean from Nova Scotia to central Florida (Nicholson 1978, Murdy et al. 1997). Menhaden are estuarine-dependent, but each year large schools undertake extensive north-south seasonal migrations along the coast (Reintjes 1969, Nicholson 1978). The majority of the adult population is thought to aggregate off Cape Hatteras, NC in the winter months, and menhaden begin migrating northward with the onset of spring. By summer, they are stratified by age and size along the coast, with the larger older fish migrating the farthest north (Nicholson 1978, Quinlan et al. 1999).

Spawning occurs at all times of the year and throughout the migratory range, but peak spawning is considered to occur during winter, near Cape Hatteras (Higham and Nicholson 1964, Reintjes 1969, Arenholz 1991). Newly spawned larvae are advected into coastal bays and estuaries, potentially through a combination of vertical migration and ocean circulation (Hare et al. 1999, Rice et al. 1999). Larval menhaden remain in this habitat for six to eight months, where they metamorphose into juveniles and then return to sea (Reintjes 1969, Arenholz 1991). As larvae, menhaden feed selectively on zooplankton, but metamorphosis of the gill raker-alimentary tract complex allows juvenile and adult menhaden to feed by filtration on smaller particles, such as phytoplankton (June and Carlson 1971). Numerous field-based studies of the diets of juvenile and adult menhaden suggest that phytoplankton, zooplankton, detritus and amorphous matter are the primary dietary constituents (Peck 1893, Richards 1963, Jeffries 1975, Edgar and Hoff 1976, Lewis and Peters 1984, 1994). However, there is significant variability in the relative composition of the prey types between these studies. For example, Edgar and Hoff (1976) reported that adult Atlantic menhaden grazed primarily on the benthos, where the other studies characterized the diets as being primarily derived from planktonic particulates. This variability is likely related to differences between sampling environments, which may indicate that juvenile and adult menhaden advantageously feed on the particulate prey sources that are available. Oviatt et al. (1972) and Durbin and Durbin (1975) suggested that large schools of adult menhaden may be capable of significantly impacting phytoplankton and zooplankton concentrations in coastal waters. This impact is of potential ecological importance in estuaries like Chesapeake Bay, where nutrient loading stimulates phytoplankton production to levels far beyond that which can currently be removed by menhaden and other secondary consumers. This excess phytoplankton biomass causes biologically stressful zones of oxygen depletion throughout the bay in the spring and summer months (Malone et al. 1996, Kemp et al. 2005).

Atlantic menhaden fulfill another important ecological role in Chesapeake Bay and throughout their migratory range as a primary forage base for commercially and recreationally important piscivores, such as striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*) and weakfish (*Cynoscion regalis*) (Hartman and Brandt 1995). However, these top predators must compete for menhaden with a sizeable commercial fishery that harvests age-1 and greater (age-1+) menhaden for the processing of fish meal, fish oil and fish solubles. This coastal reduction fishery has undergone numerous area closures, and is currently restricted to the state waters of Virginia and North Carolina and the federal waters (>3 miles offshore) of all states between New Jersey and North Carolina. As of 2005, the menhaden reduction plant in Reedville, VA, with a total fleet of 11 vessels, is the only factory that continues to process Atlantic menhaden. An additional commercial fishery harvests menhaden for bait in almost all Atlantic coastal states, but this fishery only comprises approximately 17% of the total annual catch of menhaden. The average removal for 2000-2005 by the reduction fishery in Chesapeake Bay alone (104,400 t yr^{-1}) constituted approximately 58.5% of the total average annual catch (178,550 t yr^{-1}). While the coast-wide population of Atlantic menhaden has been declared healthy (fishing mortality is below the target value and the fecundity of the population is above the target value), concern has been raised for potential localized depletion in Chesapeake Bay (ASMFC 2006).

In addition to providing economic importance to the region, menhaden are considered a keystone species in the Chesapeake Bay ecosystem, because of their potential ability to regulate water quality and their role as a forage base. The possibility of localized depletion of this ecologically important species therefore, could have far-reaching impacts on Chesapeake Bay. The threat of cascading effects on the ecosystem resulting from a potentially depleted local population strongly supports a movement toward an ecosystem-based approach to marine resource management in the bay. In response to this pressing need, the Chesapeake Bay Program articulated the following three management goals in their Chesapeake 2000 agreement: (1) "*assess the effects of different population levels of filter feeders such as menhaden, oysters and clams on Bay* *water quality and habitat*", (2) "*develop ecosystem-based multi-species management plans for targeted species*", (3) "*revise and implement existing fisheries management plans to incorporate ecological, social and economic considerations, multi-species fisheries management and ecosystem approaches*" (CBP 2000). Achievement of these goals clearly depends on extensive knowledge of the role of Atlantic menhaden in the Chesapeake Bay ecosystem.

As filter feeding planktivores, menhaden remove plankton from the water column, resulting in a two-fold impact on water quality. The removal of particulates can improve water clarity, thereby increasing light penetration and subsequent enhancement of ecologically important submerged aquatic vegetation (Dennison et al. 1993, Kemp et al. 2005). Secondly, since excess nutrients can dramatically enhance phytoplankton biomass, the removal of phytoplankton by menhaden may mitigate the ever-growing problems associated with eutrophication. The assessment of the effects of various population levels of menhaden on water quality therefore, is dependent on estimates of menhaden filtration capacity, and the ability for menhaden to permanently remove nutrients from the system. Oviatt et al. (1972) suggested that schools of menhaden are capable of measurably decreasing phytoplankton concentrations and increasing ammonium concentrations in the vicinity of a school, but a clear understanding of population-level impacts is presently lacking.

When quantifying the removal of particulates by menhaden, the filtration and ingestion response of menhaden to various concentrations of prey is an important relationship to investigate. Termed functional response, Holling (1959*a*, 1959*b*, 1965) proposed three general relationships (type I, II or III) for describing the predatory response to prey density. The type I model represents a proportional relationship (linear response) between ingestion rates and prey density, and was described by Holling (1965) as being representative of filter feeders. The type II functional response curve is said to be typical of invertebrates that require time to capture and ingest food, causing ingestion rates to decelerate to an asymptote as prey concentrations increase. The type III response curve exhibits an initial lag of ingestion rates, followed by acceleration and then deceleration to an asymptote (sigmoid shape). Holling considered this indicative of a predator (vertebrate) feeding minimally below a certain threshold prey concentration, and then upon “learning” the value of the resource, ingestion rates increase to a saturation level. A variety of equations have been used to represent the processes described by Holling (Ivlev 1961, Parsons et al. 1967, Crowley 1973, Cushing 1978, Trexler et al. 1988, among others), though the original proposed forms of the models are often still applied.

Describing predation by menhaden in the context of functional response models can provide insight into the relationship between menhaden filtration and ingestion as governed by ambient prey concentrations. Also, since excess phytoplankton is directly linked to poor water quality in Chesapeake Bay, it is especially important to quantify the ingestion response to phytoplankton concentrations specifically. This combined with estimates of menhaden population size and estimates of phytoplankton biomass can be used to predict the amount of phytoplankton ingested by menhaden throughout Chesapeake Bay over time. Durbin et al. (1981) described a hyperbolic relationship between voluntary swimming speed and phytoplankton (chlorophyll *a*) concentration.

Since ingestion and filtration rates are likely related to swimming speed, a comparison of the two responses would be informative.

Estimating the impact that menhaden have on water quality depends not only on an evaluation of nutrient and particulate removal by menhaden, but also on quantifying the degree to which menhaden return nutrients (predominately nitrogen) to the ecosystem through excretion. By considering filtration and excretion rates, Durbin and Durbin (1998) estimated that 3-6% of the annual nitrogen export from Narragansett Bay, RI was due to menhaden assimilating nitrogen and migrating out of the system. To develop an estimate of nitrogen removal for menhaden in Chesapeake Bay, an understanding of filtration and ingestion rates are needed, as well as estimates of nitrogen excretion rates over various levels of feeding intensity. These estimates, in combination with a general understanding of the nutrient content of Chesapeake Bay phytoplankton, will facilitate the estimation of net removal of nitrogen by menhaden in Chesapeake Bay.

An assessment of the effects of different populations of menhaden on water quality (goal (1) CBP 2000) clearly depends on estimates of menhaden filtration and nitrogen excretion. Also, since the bulk of the commercial catch of menhaden in Chesapeake Bay is comprised of age-1 and age-2 fish (ASMFC 2006), it is important to estimate separate filtration and excretion rates for young-of-the-year (YOY) and age-1+ menhaden. Based solely on measurements of swimming rates and mean mouth area, Peck (1893) estimated that an average adult menhaden is capable of filtering 6.8 gal (25.74 l) of water per minute. From this, McHugh (1962) concluded that if the total annual adult menhaden population in Chesapeake Bay were present in the bay at the same time, then they could filter the volumetric equivalent of the entire Virginia portion of Chesapeake

Bay twice in a 24-hr period. According to McHugh (1967), this is likely an overestimate, and it is not based on any actual measurements of filtration rates. A number of other studies (Durbin and Durbin 1975, Durbin and Durbin 1981, Friedland et al. 1984) have attempted to quantify menhaden filtration and nutrient excretion rates, but none have measured the response by menhaden to a natural assemblage of Chesapeake Bay prey types.

To address this lack of crucial data, a series of laboratory experiments were performed to generate individual estimates of ingestion and excretion rates for YOY and age-1+ menhaden, using ambient water over various concentrations of a natural prey composition. The responses were modeled as a function of phytoplankton concentration, allowing the potential for extrapolating the individual estimates of nitrogen removal to various population-level estimates, thereby providing insight into the effects of Atlantic menhaden on Chesapeake Bay water quality.

OBJECTIVES AND HYPOTHESES

Development of the experimental design of the study was based on the following three main objectives and corresponding hypotheses:

1. *Ingestion of phytoplankton*: Describe the relationship between ingestion rates of phytoplankton by menhaden and phytoplankton concentration using Holling's (1959*a*, 1959*b*, 1965) proposed functional response models as candidates. **A type II functional response model was hypothesized as best representative of the response**, because type II models have been used for describing predation responses by several species of fishes (Ivlev 1961, Houde and Schekter 1980, Miller et al. 1992), and they are often assumed for fishes in bioenergetics and multispecies fisheries models. While a functional response curve has not previously been determined for menhaden, Durbin et al. (1981) described a hyperbolic relationship (resembling a type II functional response curve) between voluntary swimming speeds of menhaden and chl *a* concentration. A comparison of the ingestion rate and swimming speed responses would be informative, because swimming speeds are an important component of menhaden filtration and ingestion rates (Durbin and Durbin 1975).

2. *Excretion of nitrogen*: Determine the nitrogen excretion rate of menhaden over a range of feeding intensities and model that response as a function of phytoplankton concentration, using a suite of biologically reasonable candidate models. Durbin and Durbin (1981) defined a linear relationship between nitrogen concentrations and time for Narragansett Bay menhaden feeding on the diatom *Ditylum brightwelli*, allowing nitrogen excretion rates to be estimated by linear regression. The present study adopted that method, and calculated excretion rates of Chesapeake Bay menhaden in response to a natural assemblage of prey over a range of concentrations. **It was hypothesized that nitrogen excretion rates of menhaden will increase as feeding intensity increases, but will eventually saturate at some high prey concentration.**

3. *Net removal of nitrogen*: Estimate the potential impact of menhaden on water quality using the estimated rates of nitrogen removal through ingestion of phytoplankton and corresponding rates of nitrogen excretion to calculate rates of net removal of nitrogen for individual YOY and age-1+ menhaden. Cerco and Noel (2004) presented a range of phytoplankton-based carbon-to-chlorophyll ratios for Chesapeake Bay, which can be used with carbon-to-nitrogen Redfield composition (Redfield et al. 1966) to estimate nitrogen concentrations based on chlorophyll, allowing the conversion of chlorophyll *a* ingestion rates to nitrogen ingestion rates. By subtracting the nitrogen excretion rates from the corresponding nitrogen ingestion rates, rates of net

removal of nitrogen can then be estimated. **It was hypothesized that rates of net removal of nitrogen increase as phytoplankton concentration increases, and that YOY menhaden are capable of removing more phytoplankton-based nitrogen than age-1+ menhaden**, because of their capacity to filter smaller particles (Friedland 2006).

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CHAPTER 2: NET REMOVAL OF NITROGEN THROUGH INGESTION OF PHYTOPLANKTON BY ATLANTIC MENHADEN (*BREVOORTIA TYRANNUS*) IN CHESAPEAKE BAY

ABSTRACT

As filter-feeding planktivores, Atlantic menhaden (*Brevoortia tyrannus*) have the potential to positively impact water quality through the filtration and ingestion of phytoplankton and the assimilation of nutrients. To evaluate the impact of young-of-the-year (YOY) and age-1+ menhaden on Chesapeake Bay, a eutrophic estuary, age-specific rates of ingestion of phytoplankton (chlorophyll *a*) and excretion of nitrogen (N) were measured and modeled in response to phytoplankton concentration. Age-1+ menhaden exhibited virtually no ingestion of phytoplankton, while ingestion rates of YOY menhaden increased (0.028-3.851 μg chlorophyll *a* fish^{-1} min^{-1}) in response to increasing phytoplankton concentration. The YOY response was best described by the sigmoid-shaped type-III functional response model. Similarly, nitrogen excretion rates of age-1+ menhaden were relatively constant across phytoplankton concentrations, but for YOY menhaden, excretion rates increased (0.93-3.92 μg N fish^{-1} min^{-1}) as phytoplankton concentration increased. An asymptotic exponential model best described this response. By combining the YOY ingestion and excretion models, rates of net removal of nitrogen were modeled as a function of phytoplankton concentration, with values ranging from -1.73 to 131.58 μg N fish^{-1} min^{-1}.

INTRODUCTION

Describing the impact of filter feeders on the plankton community in aquatic ecosystems is fundamental to understanding nutrient cycling and trophic ecology, and therefore essential to effective ecosystem management. As human population growth accelerates in coastal regions, problems associated with excess nutrient loading and the subsequent stimulation of primary productivity increasingly threaten the health of estuaries. This is especially relevant in Chesapeake Bay, where continually increasing nutrient inputs have reduced water quality and substantially altered benthic habitats over the past century (Hagy et al. 2004, Kemp et al. 2005). With the dramatic disease and fishery-related decline in biomass of the eastern oyster (*Crassostrea virginica*), a historically abundant filter-feeder in Chesapeake Bay, management agencies have begun focusing attention on other secondary consumers, such as Atlantic menhaden (*Brevoortia tyrannus*) to assess their potential impact on water quality (CBP 2000).

Atlantic menhaden are considered a vital component of coastal and estuarine ecosystems along the east coast of North America. Described as a filter-feeding planktivore, menhaden travel in dense schools and feed by passing water over their highly specialized gill-rakers, which are capable of removing fine particulates from the water column (Peck 1893). Numerous studies have characterized the diets of juvenile and adult menhaden as primarily comprised of phytoplankton, zooplankton, detritus and amorphous matter (Peck 1893, Richards 1963, Jeffries 1975, Edgar and Hoff 1976, Lewis and Peters 1984, 1994). Furthermore, using estimates of filtration capacity, other studies have determined that menhaden schools may have a significant impact on the plankton community (McHugh 1967; Oviatt et al. 1972; Durbin and Durbin 1975).

In addition to potentially impacting water quality, menhaden fulfill another ecologically important role as a primary forage base for many commercially and recreationally important piscivores, such as striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*) and weakfish (*Cynoscion regalis*) (Hartman and Brandt 1995), making them a potentially important link in the transfer of primary production to higher trophic levels.

Menhaden are also of great commercial importance, in that they support a large reduction fishery that harvests age-1 and greater (age-1+) menhaden in the Virginia portion of Chesapeake Bay and in offshore waters for the processing of fish meal, fish oil and fish solubles. With the current trend toward an ecosystem-based approach to resource management it is imperative that there exist a clear understanding of the feeding ecology of ecologically and commercially important species, such as Atlantic menhaden.

While menhaden certainly have the potential to improve water quality and clarity through filtration, they also return nutrients (predominately nitrogen) to the water through excretion, which may be a negative feedback to the ecosystem. By considering filtration and excretion rates, Durbin and Durbin (1998) estimated that 3-6% of the annual nitrogen export from Narragansett Bay, RI (4.16×10^5 kg N) was due to menhaden assimilating nitrogen and migrating out of the system. Therefore, when quantifying the impact of menhaden on water quality, rates of both nitrogen ingestion and excretion must be considered.

In order to estimate the potential impact of Atlantic menhaden on Chesapeake Bay water quality, a series of laboratory experiments were performed, designed to measure particulate ingestion and nitrogen excretion rates of young-of-the-year (YOY) and age-1+ menhaden using a natural assemblage of prey over a range of concentrations. Ingestion rates of phytoplankton were then modeled in the context of Holling's (1959*a*, 1959*b*, 1965) description of a predator's functional response to prey concentration. Using estimates of nitrogen excretion and phytoplankton ingestion, net phytoplankton-based nitrogen removal rates were then calculated for the range of prey concentrations analyzed. Several previous studies (Durbin and Durbin 1975, Durbin and Durbin 1981, Friedland et al. 1984) have estimated menhaden filtration and nitrogen excretion rates, but none have measured and modeled the response to a natural assemblage of Chesapeake Bay prey types over a range of concentrations.

MATERIALS AND METHODS

Specimen collection

YOY Atlantic menhaden were captured by cast net in spring 2007 in the lower York River, a tributary to the lower Chesapeake Bay (Fig. 1), and were staged as YOY by fork length (FL = 35-150 mm, Reintjes 1969). Age-1+ menhaden were defined as greater than 150 mm FL, and were also captured in spring 2007 by a commercial pound-net fisherman located in Mobjack Bay, near the mouth of the York River (Fig. 1). All research specimens were held in a 1,514-liter circular tank on continuously flowing, unfiltered York River water thereby maintaining acclimation to natural conditions.

Experimental design

All experiments were conducted over a narrow time period in June 2007 in order to maintain a relatively consistent temperature (mean=24.99 °C, SD=1.38) and prey composition. A series of circular 341-liter tanks, equipped with sampling valves to minimize sampling-induced disturbances, and constant aeration to maintain suspension of prey, were available for each experiment. Normally, six tanks were filled with 200 l of 1-μm-filtered York River water 48 h prior to the onset of an experiment. Fish were moved into three of the tanks (15 fish per tank in the YOY experiments, and three fish per tank in the age-1+ experiments), and the three remaining tanks without fish present served as controls. The initial 48 h allowed the fish to acclimate to experimental conditions and evacuate existing material in the gut and intestine, which was intended to stimulate natural feeding behavior by the fish during the experiments (AFS (2004) considers 24 h to be the minimum amount of time required for a fish to recover from a disturbance). After 24 h of acclimation, 150 l of filtered seawater was drained and replaced in each tank, preventing ammonia concentrations from reaching levels toxic to the fish.

Immediately following the acclimation period, all feces that accumulated were removed by siphon, and a known volume of filtered water (150 l in high, and 100 l in low prey concentration experiments) was drained from each tank through the sampling valves. The water removed was then replaced by an identical volume of unfiltered York River water, and the experiment began immediately, lasting six hours (360 min). There was minimal variability in the concentration of phytoplankton in the ambient water across all experiments, so it was deemed ineffective to rely solely on ambient conditions to provide the range needed for modeling the functional response. To better control initial phytoplankton concentrations the added York River water was supplemented with a cultured phytoplankter (*Thalassiosira weissflogii* (size: 5-15 μm) – Reed Mariculture) native to Chesapeake Bay. The amount added was constant across all tanks within an experiment, but varied between experiments to achieve a range of total chlorophyll *a* (chl *a*) concentrations (3.9-203.2 μg l^{-1}).

The impact of menhaden on phytoplankton was estimated using measurements of chl *a* as a proxy for phytoplankton biomass. All reported chl *a* values represent total chl *a* and were not corrected for phaeophytin, because an initial examination of chl *a* filtration rates by menhaden indicated that menhaden did not distinguish between live and dead phytoplankton. Water samples were taken to determine initial (0 min) and final (360 min) concentrations of chl *a* within each tank, and were processed in triplicate by filtering 10 ml per sample through a 25 mm, 0.7 µm Whatman® glass-fiber filter. Chl *a* concentrations were then determined by fluorometry using the acetone extraction method described by Shoaf and Lium (1976) and the equations suggested by Jeffrey and Humphrey (1975). Also, a YSI 6600 sonde, equipped with a fluorometer was used for monitoring chl *a* concentrations hourly throughout each experiment.

In addition to the coarse estimates of phytoplankton biomass provided by fluorometry, a comprehensive analysis of the phytoplankton community was performed by directly counting the individual phytoplankters, and assigning them to a specific classification (autotrophic dinoflagellates, cryptophytes, cyanobacteria, diatoms, heterotrophic dinoflagellates) and size-range (<7, 7-15, 15-30, >30 µm). Samples were taken from each tank at the beginning of each experiment. The samples were fixed in glutaraldehyde, stained with Dapi, proflavind and calcoflour then counted using epifluorescent microscopy (Haas 1982). The initial percent composition of the phytoplankton community was then determined by classification and size-range for each experiment to compare the composition across the range of initial chl *a* concentrations.

Ingestion rates

Clearance and ingestion rates were calculated from the change in prey concentration throughout each experiment, and were expressed as volume of water cleared or amount of prey removed (ingested) per fish per minute. Harvey (1937) described a relationship between exponentially decreasing phytoplankton concentrations and feeding by the copepod *Calanus finmarchicus*, and used this relationship to estimate the "volume of water swept free" in a unit of time (clearance rate). Previous experimental studies have deemed this relationship appropriate for representing clearance rates of adult and YOY menhaden (Durbin and Durbin 1975, Friedland et al. 1984), prompting us to adopt this method and estimate particulate filtration rates as follows:

$$(1) \qquad F = \frac{V}{tN}(\Delta C_{adj})$$

where F is the clearance rate (l fish^{-1} min^{-1}), V is the volume of water in the tank (l), t is the duration of the experiment (min), N is the number of fish in the tank, and ΔC_{adj} is the change from initial to final of the log-transformed prey concentration, adjusted by the average change that occurred in tanks without fish, potentially a result of background grazing by zooplankton, and was calculated using:

$$(2) \qquad \Delta C_{adj} = (\log C_i - \log C_f)_{fish} - (\frac{1}{n}\sum_{j=1}^{n}[(\log C_i - \log C_f)_{nofish}]_j)$$

where C_i and C_f represent the initial and final prey concentrations (e.g., µg l^{-1} chl *a*) in each experimental tank, respectively. This model assumes that the fish fed continuously and at a constant rate throughout an experiment, thereby removing a constant proportion of the prey per unit of time.

The amount of food ingested was then estimated using the following relationship (Båmstedt et al. 2000):

$$(3) \qquad I = F * [\overline{C}]$$

where I is the ingestion rate (µg fish^{-1} min^{-1}, for chl *a*) and $[\overline{C}]$ is the average prey concentration (e.g., µg l^{-1} chl *a*) throughout the experiment, accounting for the assumed exponential decline, and was calculated from the equation:

$$(4) \qquad [\overline{C}] = \frac{C_i(1 - e^{-\Delta C_{adj}})}{\Delta C_{adj}}$$

Functional response

Menhaden ingestion rates were then modeled under the framework of the three models (type I, II and III) of a predator's functional response to prey concentration proposed by Holling (1959*a*, 1959*b*). The type I model represents a linear relationship between ingestion rates and prey concentration, and a form similar to that described by Holling was used (eq. 5). The type II model describes a decelerating response that saturates at an asymptote. Two versions of this model were used; the original disc equation (eq. 6) proposed by Holling (1959*a*, 1959*b*), which has been applied to fishes (Houde and Schekter 1980, Miller et al. 1992), and a modified version of the disc equation (eq. 7) proposed by Ivlev (1961), which was subsequently adapted to zooplankton grazing on phytoplankton by Parsons et al. (1967). This model allows for a prey density threshold below which no feeding occurs. The type III model is a sigmoid curve that represents an initial acceleration and then a deceleration of ingestion rates as prey concentrations increase. The version used is an adaptation of Holling's type III model as proposed by Trexler et al. (1988) (eq. 8). The models used are as follows:

(5) type I: $I = aC_i$

(6) type II *a*: $I = \dfrac{aC_i}{1 + aTC_i}$

(7) type II *b*: $I = I_m[1 - e^{d(C_0 - C_i)}]$

(8) type III: $I = P_1 e^{(-P_2 e^{(-P_3 C_i)})}$

In eq. 5 and 6 the estimated parameter *a* represents the instantaneous encounter or attack rate. In eq. 6 the parameter *T* is also estimated and represents the handling time (in minutes) required for ingestion of prey. In eq. 7 the parameters estimated were I_m (maximum rate of ingestion), *d* (a constant that governs the rate of change of *I* with respect to C_i) and C_0 (the prey density threshold below which no feeding occurs). Finally, eq. 8 is a Gompertz equation where the three parameters estimated (P_1, P_2, P_3) simply govern the shape of the curve.

The candidate models were fitted to the data and parameter estimates were derived using maximum likelihood estimation. An information-theoretic approach to model selection was then used for selecting the model that best described the functional response (Burnham and Anderson 2002). Akaike's information criterion, corrected for small sample size (AIC_c) was used as follows:

$$(9) \qquad AIC_c = -2\log(\ell(\hat{\theta})) + 2K + \frac{2K(K+1)}{n-K-1}$$

where $\ell(\theta)$ is the maximized likelihood, K is the number of estimable parameters and n is the sample size. The model with the lowest AIC_c represents that which fits best to the data out of the candidate models.

Nitrogen excretion rates

To quantify the degree to which nitrogen is returned to the ecosystem by menhaden, ammonium excretion rates (NH_4^+-ex) were estimated over a range of feeding intensities. Water samples were taken from each tank every two hours (0, 2, 4 and 6 h) during the experiments, and for two of the experiments (one YOY and one age-1+), water samples were taken at identical increments during the preliminary gastric evacuation/acclimation phase. These samples were taken after menhaden were in the experimental tanks for at least 24 h, and were used to determine baseline NH_4^+-ex for YOY and age-1+ menhaden when no feeding was occurring. All water samples were filtered through a 0.45 μm Puradisc® syringe filter, and were frozen for later analysis on a Lachat Autoanalyzer (Liao 2002). Each tank was treated as a single experimental unit, and all fish within a unit were assumed to excrete equal amounts of nitrogen at identical rates.

Durbin and Durbin (1981) described a linear increase in ammonium concentrations over time in tanks with feeding menhaden. Using this assumption, the NH_4^+-ex was estimated through linear regression. In addition to excretion by menhaden, there were likely background fluctuations of nitrogen concentrations within experimental tanks, potentially due to excretion by zooplankton. Therefore, excretion rates estimated for tanks with menhaden were corrected by subtracting the mean excretion rate from each experiment calculated in tanks with no fish present.

Ammonium was used as the primary source of nitrogen excretion, because Durbin and Durbin (1981) estimated nitrogen excretion rates for adult menhaden in Narragansett Bay, RI, and found that the majority (69.6%) of nitrogen excreted by menhaden was in the form of ammonium. Additional nitrogen was excreted as dissolved organic nitrogen (DON), and was found to be proportional to NH_4^+-ex across all experiments conducted. This allowed the development of a multiplication factor for estimating DON excretion rates from ammonium excretion rates (0.437). The current study used this multiplication factor to calculate total dissolved nitrogen excretion rates (TDN-ex) by totaling NH_4^+-ex and the estimated DON excretion rates.

Excretion rate models

TDN-ex was then modeled as a function of initial phytoplankton (chl *a*) concentration. Three candidate models were identified *a priori*, maximum likelihood was used for parameter estimation, and AIC_c was again used for selecting the best model of the three. The models used are as follows:

$$E_N = \beta_0 + \beta_1 C_i \tag{10}$$

$$E_N = E_{\max}(1 - e^{-r(C_i - c)}) \tag{11}$$

$$E_N = P_1 e^{(-P_2 e^{(-P_3 C_i)})} \tag{12}$$

where eq. 10 describes a linear response of TDN-ex to chl *a* concentration, E_N represents TDN-ex in μg N fish^{-1} min^{-1}, and β_0 and β_1 are parameters representing the intercept and slope of the line, respectively. Eq. 11 is an asymptotic exponential function with estimable parameters E_{max}, the maximum excretion rate, r, the rate of increase to the maximum rate and c, which allows for baseline nitrogen excretion when chl *a* concentration is zero. Eq. 12 is identical to eq. 8 and was selected after the type III functional response model was identified as the best representation of phytoplankton ingestion rates. This assumes that the response of excretion rates to prey concentration mimics that of the ingestion rates.

Net nitrogen removal

The TDN-ex and chl *a* ingestion rates were then used to calculate rates of net removal of nitrogen (R_N) through phytoplankton ingestion by menhaden across the initial chl *a* concentrations used in the experiments. Cerco and Noel (2004) presented a range of phytoplankton-based carbon-to-chlorophyll ratios (C:Chl) for Chesapeake Bay. Using the approximate lowest and highest monthly median C:Chl from their study (50 and 200 g C g^{-1} Chl, respectively) and the carbon-to-nitrogen (C:N) Redfield composition for phytoplankton (Redfield et al. 1966), low and high ingestion rates of nitrogen were developed from the chl *a* ingestion rates calculated by the present study. The corresponding TDN-ex were then subtracted from the nitrogen ingestion rates to calculate R_N. Also, the response of R_N to initial chl *a* concentration was modeled by subtracting the model selected as best representing TDN-ex from the functional response model that best described chl *a* ingestion rates.

Additional experiment

Initial analysis of clearance and ingestion rates across phytoplankton concentrations raised some concern regarding age-1+ menhaden feeding in the given experimental conditions. To alleviate this concern, a single additional experiment was performed with identical conditions; however, instead of unfiltered seawater, a concentrated mixture of zooplankton (predominately *Acartia tonsa*) was added as prey. The experiment duration was three hours instead of six, and was performed on YOY and age-1+ menhaden simultaneously (*n*=3 tanks per age group with three tanks without fish present to serve as controls). Water samples were taken from each tank at the beginning (t_0) and end (t_3) of the experiment by removing 10 l through the sampling valves. The sample was filtered through a 200 μm sieve, and the material retained was preserved in formalin for later counting. The concentration (number l^{-1}) of zooplankton in each tank was estimated and clearance and ingestion rates were calculated using equations (1-4), where C_i and C_f were expressed as number l^{-1} rather than μg l^{-1}. Also, additional water samples were taken from each tank at 0, 1.5 and 3 h for determining ammonium concentrations and calculating excretion rates in the manner previously described.

RESULTS

Ingestion rates

The assumption that menhaden fed continuously and at a constant rate during experiments was coarsely verified for YOY menhaden through visual inspection of chl *a* concentrations over time (Fig. 2a). Also, the observed decline in chl *a* concentrations in tanks without fish (Fig. 2a), potentially due to zooplankton grazing, emphasized the need for correcting the changes in prey concentration in the tanks with fish present by the changes that occurred in tanks with no fish present. This clear indication of ingestion of phytoplankton however was not observed for age-1+ menhaden (Fig. 2b). In these experiments changes in chl *a* concentrations were typically similar in tanks with fish to those in tanks without fish.

Mean chl *a* ingestion rates ranged from <0.5 μg fish^{-1} min^{-1} at low initial chl *a* concentrations (< 15 μg l^{-1}) to almost 4 μg fish^{-1} min^{-1} at relatively high initial concentrations (194 μg l^{-1}) for YOY menhaden, but never exceeded 1 μg fish^{-1} min^{-1} for age-1+ menhaden at any concentration (Table 1).

Functional response

All competing functional response models were fitted to the chl *a* ingestion rate data, and AIC_c values were calculated. For YOY menhaden the type III functional response model had the lowest AIC_c (-110.10), indicating that this model best represented the response of YOY ingestion rates to phytoplankton concentrations (Table 2). The corresponding type III parameter estimates are provided (Table 3). Also, when fitted to the data, this model clearly emphasized the sigmoidal nature of the response (Fig. 3a).

These modeling exercises were also performed on the data from the age-1+ experiments, but with the exception of a single data point (experimental tank) there was essentially no calculated ingestion of phytoplankton by these fish (Fig. 3b). Therefore, little confidence can be given to any statistical inferences obtained from these data.

Phytoplankton percent composition

The direct count and classification of phytoplankton was used to estimate initial percent composition of the phytoplankton community for each experiment. The total initial concentration of phytoplankton ranged from 118,019 to 555,901 cells ml^{-1}, but the initial percent composition was relatively constant across all experiments, irrespective of chl *a* concentration. Therefore, an average initial percent composition was calculated by size-range (Table 4) and by classification (Table 5) across all experiments within each age-group. Approximately 98% of all phytoplankton cells were cyanobacteria <7 µm in size.

Nitrogen excretion rates

The observed change in ammonium concentration during a typical feeding experiment verified the assumption of a linear increase in experimental tanks with feeding menhaden (Fig. 4a-b), providing confidence in the ammonium excretion rate estimates. Ammonium concentrations were higher in tanks with fish present at the beginning of each experiment, because while most of the water from the acclimation phase was exchanged with ambient water, some filtered water remained in the experimental tanks (typically 50 l) to allow the fish to continue swimming. In the tanks with fish present this water likely had much higher ammonium concentrations than those without fish. Mean NH_4^+-ex and TDN-ex were estimated across the range of initial chl *a* concentrations, and for the experiment where zooplankton was offered as the only prey (Table 6).

Excretion rate models

TDN-ex increased with chl *a* concentration for YOY menhaden, and AIC_c values indicated that the asymptotic exponential model best described the response of the three candidate models (Table 7). The nature of this response is emphasized through visual inspection of the model fit (Fig. 5a). The linear model was also strongly supported by AIC_c model selection (ΔAIC_c=2.06), so parameter estimates were provided for both competing models (Table 8). Nitrogen excretion rates of age-1+ menhaden were higher (18.88 to 28.25 μg N $fish^{-1}$ min^{-1}) than those of YOY menhaden (1.33 to 5.63 μg N $fish^{-1}$ min^{-1}) (Table 6); however, TDN-ex did not increase with chl *a* concentration for age-1+ menhaden (Fig. 5b), thus no attempt was made to model this response. Age-1+ menhaden did show elevated excretion rates (as did YOY menhaden) during the additional experiment where zooplankton was the only prey (Table 6), potentially resulting from a higher concentration of nitrogen in the prey (zooplankton versus ambient water).

Net nitrogen removal

The net removal rates of phytoplankton-based nitrogen were calculated for YOY menhaden only since there was essentially no measured ingestion of phytoplankton by age-1+ menhaden. Mean R_N was negative at low chl *a* concentrations, indicating a net input of nitrogen at low feeding intensities, and was as high as 131.57 µg N fish^{-1} min^{-1} at high chl *a* concentrations when C:Chl was high (Table 9). In addition to calculating R_N directly for each experiment, R_N was modeled as a function of chl *a* concentration using the models selected as best representative of ingestion and excretion by YOY menhaden as follows:

$$(13) \qquad R_N = \left[\left(\frac{C:Chl}{C:N}\right)\left(\frac{14}{12}\right)(typeIII)\right] - \left[0.74(AE) + 0.26(L)\right]$$

where in the first term the type III functional response model of ingestion rates of chl *a* (eq. 8), as selected by AIC_c, is converted to ingestion rates of nitrogen using estimates of C:Chl and C:N for phytoplankton. The molar conversion term (14/12) is also required, because C:Chl values were presented as g C g^{-1} chl (Cerco and Noel 2004), and C:N values were mol C mol^{-1} N (Redfield et al. 1966). The second term is the weighted model average of the two nitrogen excretion models selected as representative of TDN-ex, where *AE* refers to the asymptotic exponential model (eq. 11), *L* refers to the linear model (eq. 10) and 0.74 and 0.26 are the corresponding model weights (Table 7). The response of R_N to the range of chl *a* concentrations used in the experiments was then estimated for the two C:Chl ratios proposed (50 and 200) using eq. 13 and the corresponding parameter estimates (Tables 3 and 8). These model estimates were then overlaid with the calculated net nitrogen removal rates (Fig. 6).

DISCUSSION

Clearance and ingestion rates of total phytoplankton (chl *a*) were calculated over a range of initial phytoplankton concentrations for both YOY and age-1+ Atlantic menhaden. For YOY menhaden, the only comparative study of clearance rates of phytoplankton was conducted by Friedland et al. (1984) on fish collected from Chesapeake Bay and was based on experimental protocols originally established by Durbin and Durbin (1975). The present study differed methodologically from Friedland et al. (1984) in that assemblages of prey within ambient water were provided to YOY menhaden rather than various combinations of individually cultured phytoplankters, chl *a* was used as a measure of phytoplankton concentration rather than cell counts, and clearance rates were corrected for background changes in prey. These methodological differences preclude direct comparisons of clearance rates at specific prey concentrations.

Similarities between the findings of the present study and those of Friedland et al. (1984) emerge when compared qualitatively. For example, the lower clearance rates (0.01 – 0.06 l fish^{-1} min^{-1}) reported for small phytoplankton (<7 μm) by Freidland et al. (1984) were similar in magnitude to the highest clearance rates estimated in the present study (Table 1). This general agreement is likely due to the high percentage of small phytoplankton present in the ambient water provided in the experiments (Table 4). While the phytoplankton community in Chesapeake Bay continues to be dominated annually by diatoms, the smaller phytoplankters (dinoflagellates, cyanobacteria, etc.) often dominate in late spring and summer (Marshall et al. 2005). Thus the clearance and ingestion rates presented herein are likely reflective of the impact of menhaden predation on the overall phytoplankton community in late spring and summer in Chesapeake Bay, a time in which the bay serves as an important nursery for YOY menhaden (Luo et al. 2001). The rates reported by Friedland et al. (1984) however, better describe responses to individual species of phytoplankton.

For age-1+ menhaden, the only comparative study of clearance rates of phytoplankton was conducted by Durbin and Durbin (1975) on fish from Narragansett Bay, RI. Again, due to the aforementioned differences in experimental protocols only qualitative comparisons of the results are possible. In the present study, essentially no ingestion or clearance of phytoplankton was measured for age-1+ menhaden (Table 1), while Durbin and Durbin (1975) did report clearance rates for adult menhaden, but only for phytoplankton cells larger than 16.4 μm. The initial percent composition of phytoplankton by size range measured in the experimental tanks (Table 4) indicated that these larger phytoplankton cells and chains were available for consumption in the experiments, but in such a small percentage that potential ingestion by age-1+ menhaden likely had a negligible impact on the total concentration of phytoplankton. Durbin and Durbin (1998) suggested that the removal of zooplankton and large phytoplankton by schools of adult menhaden may actually enhance the growth of smaller phytoplankton by releasing grazing pressure from zooplankton. This determination is supported by the difference between clearance rates of phytoplankton and zooplankton estimated for age-1+ menhaden (Table 6).

In addition to the conclusions made by Durbin and Durbin (1998), the reported YOY and age-1+ clearance and ingestion rates support the findings from an analysis of the morphological development of the Atlantic menhaden gill raker feeding apparatus (Friedland et al. 2006). This study reported two lengths of menhaden at which allometric inflections of changes in branchiospinule spacing were found to occur (100 mm FL and 200 mm FL). Branchiospinule spacings form the sieve apertures governing particle size retention. The clearance and ingestion rates estimated for YOY and age-1+ menhaden (Table 1) are representative of two age-groups whose mean lengths (YOY: 73.6 mm ± 13.0 SD; age-1+: 188.7 mm ± 19.7 SD) were slightly shorter than the lengths corresponding to the allometric inflection points reported by Friedland et al. (2006). The estimate of branchiospinule spacing for juveniles (YOY) was approximately 16 μm, though YOY menhaden have been shown to efficiently filter particles smaller than 10 μm (Friedland et al. 1984), likely as a result of clumping of particles and crossflow filtration (Sanderson et al. 2001). The YOY clearance and ingestion rates support these earlier findings, because while YOY menhaden removed phytoplankton from the water in all experiments, their clearance rates were lower than previously reported rates, potentially due to the large percentage of phytoplankton smaller than 7 μm in the ambient water (Table 4). The branchiospinule spacing reported for adults was approximately 27 μm, explaining why clearance and ingestion rates of total phytoplankton were negligible for age-1+ fish.

Using the empirically-derived clearance rate calculations, ingestion rates were calculated and then modeled in terms of the functional response to prey concentration. The type III functional response model clearly emerged as the best of the four candidate models (Table 2), indicating that YOY menhaden exhibit a sigmoid response of ingestion rates to total phytoplankton concentrations in Chesapeake Bay (Fig. 3a). Holling (1965) revealed a general trend among the three types of responses as representative of three types of organisms (type I: filter feeders, type II: invertebrates, type III: vertebrates). Using this generalization, it would be predicted that menhaden (filter feeding vertebrates) exhibit either a type I or type III response. When considering the findings of Durbin et al. (1981) the type III response appears most likely. They measured swimming speeds of menhaden in response to phytoplankton (chl *a*) concentration, and described a hyperbolic response within relatively low chl *a* concentrations (< 11 μg l^{-1}). Increasing swimming speeds at low chl *a* concentrations may cause the observed initial acceleration of ingestion rates (Fig. 3a), characteristic of the type III functional response, because ingestion rates of nektonic filter feeders likely increase as swimming speed increases. In fact, Dunbrack and Giguere (1987) suggested that the findings of Durbin et al. (1981) support their hypothesis of a bioenergetic basis for the type III functional response. Also, in a study that estimated carrying capacity of YOY menhaden in Chesapeake Bay, Luo et al. (2001) assumed a type III functional response for menhaden on the basis of previously reported filtration rates. The conclusions of these previous studies (Durbin et al. 1981, Dunbrack and Giguere 1987, Luo et al. 2001) further supports the selection of the type III model as representative of the response of ingestion rates of YOY menhaden to chl *a* concentrations.

The biological significance of the type III functional response may be varied. Holling (1965) suggested that the sigmoid shape is representative of the predator “learning” the value of a certain prey type at low prey concentrations. Upon learning the value of the resource, the predator then increases consumption rates of prey, or switches to feeding on that prey type from another prey type, either of which may result in the sigmoid response. As previously stated, Dunbrack and Giguere (1987) suggest a bioenergetic basis for the type III response, indicating that feeding may be energetically inefficient for YOY menhaden at low phytoplankton concentrations, but as concentrations increase feeding becomes more energetically efficient. Another potential explanation may be that filtration efficiency is poor at very low phytoplankton concentrations, but then quickly increases as concentration increases. This phenomenon would incorporate the particle aggregation effects discussed by Friedland et al. (2006). A final possible explanation concerns regulation of the prey population, where the predator purposefully relaxes predation at low prey concentrations to allow enhancement of the prey population (Murdoch and Oaten 1975). This type of behavior however, may require high-level thought processes not believed achievable by menhaden.

Despite the biological meaning behind the type III functional response, the result is interesting, because there have been numerous cases where a type II response was assumed and characterized for fishes (Ivlev 1961, Houde and Schekter 1980, Miller et al. 1992). While this assumption may have been appropriate for these studies, the selection of a type III response for menhaden emphasizes the need for testing competing models before making an assumption.

Nitrogen excretion rates were calculated for YOY and age-1+ menhaden across a range of chl *a* concentrations, and were modeled for YOY menhaden (Fig. 5). Excretion rates for age-1+ menhaden were not modeled, because there was essentially no response to chl *a* concentration. Age-1+ menhaden did exhibit an elevated nitrogen excretion rate during the zooplankton-as-prey experiment (Table 6), potentially in response to increased feeding intensity, but all other age-1+ nitrogen excretion rates were more likely representative of baseline rates.

Durbin and Durbin (1981) determined that menhaden return to baseline nitrogen excretion rates after about one to two hours after cessation of feeding. Since the decline in chl *a* concentrations caused by YOY menhaden feeding typically slowed approximately one to two hours before the end of an experiment (Fig. 2a), it is assumed that the reported YOY excretion rates effectively represent those while feeding, but that the rates quickly returned to baseline (Table 6) shortly after termination of the six-hour experiment. The ingestion and excretion rates associated with this six-hour period therefore, may be reflective of a six-hour behavioral and physiological pattern. In the development of a bioenergetics model for Atlantic menhaden, Durbin and Durbin (1998) assumed that menhaden feed for approximately 12 h per day. If this is true, then perhaps menhaden perform the hypothesized six-hour behavioral cycle twice per day. Additional research is clearly needed to be certain.

Durbin and Durbin (1981) described a linear increase in the amount of nitrogen excreted in response to the amount of nitrogen consumed for adult menhaden captured in Narragansett Bay, RI, though the response of rates of nitrogen excretion to nitrogen consumed was not shown. Of the candidate models, the asymptotic exponential model best described the YOY excretion rate response (Table 7), indicating a saturation of TDN-ex at high chl *a* concentrations (Fig. 5a). This response may support the linear relationship described by Durbin and Durbin (1981), because while amount excreted may increase linearly, it is likely that the time associated with the physiological process of excretion causes the increasing rate of excretion to decelerate to a maximum excretion rate. It should be noted that strong support was also given to the linear model of YOY excretion rates (Table 7), so the best representation of the response may result from a weighted model average of the two.

The calculated chl *a* ingestion and nitrogen excretion rates, along with the associated models selected to represent the responses to phytoplankton concentration, were used to estimate net removal of phytoplankton-based nitrogen by YOY menhaden. These rates were estimated for two scenarios of phytoplankton-based C:Chl (50 and 200). It is likely the lower C:Chl is closest to the ratio experienced most often by YOY menhaden in Chesapeake Bay, because Cerco and Noel (2004) found that the most common values were between 25 and 50, and their plot of monthly median C:Chl indicated that the lower values are more common during the months when YOY menhaden are most abundant in the bay. Therefore, depending on the concentration of chl *a*, it is likely that during late spring through summer YOY menhaden generate a net flux of phytoplankton-based nitrogen ranging from -1.73 to 29.85 μg N fish^{-1} min^{-1} (Table 9). Eq. 13 is believed to successfully predict this response as a function of chl *a* concentration, while allowing flexibility in the C:Chl and C:N ratios used. Thus, the model is capable of incorporating some of the spatial and temporal variability present in the phytoplankton community in Chesapeake Bay.

Estimates of population-level impacts require good estimates of population size, and there is currently much uncertainty regarding total abundance of YOY menhaden in Chesapeake Bay. If resolved however, the nitrogen removal model can be applied to all individuals in the population from late spring through summer, allowing a relatively thorough assessment of the ecological role of YOY Atlantic menhaden in Chesapeake Bay, with respect to eutrophication and water quality.

Gottlieb (1998) presented a simulation model that assessed the ecological role of YOY menhaden in Chesapeake Bay under different fishery management scenarios. Using the lowest and highest estimates of YOY population size from that study (1.5 and 18.6 billion fish, respectively) and the likely range of nitrogen flux from the current study (-1.73 to 29.85 μg N fish^{-1} min^{-1}), population-level estimates of phytoplankton-based nitrogen flux due to YOY menhaden range from -2.60 to 555.15 kg N min^{-1}. When extrapolated to the 183-day management simulation presented by Gottlieb (1998), net nitrogen removed through ingestion of phytoplankton ranges from -6.84 x 10^{5} kg N to 1.46 x 10^{8} kg N. The values of nitrogen removal reported by Gottlieb (1998) ranged from 1.94 x 10^{5} to 25.0 x 10^{6} kg N, which were only achieved in the present study through a combination of the smaller estimated YOY population size (1.5 billion fish) and relatively low rates of nitrogen flux (1 to 7 μg N fish^{-1} min^{-1}).

Overall, the YOY and age-1+ findings support the results of several other studies of Atlantic menhaden ecology (Durbin and Durbin 1975, Freidland et al. 1984, Durbin and Durbin 1998, Gottlieb 1998, Friedland et al. 2006) while providing empirically-derived models of responses that have not been previously described. The conclusion that YOY menhaden seem to be capable of ingesting much more primary production, while maintaining lower nitrogen excretion rates than age-1+ fish is common across studies. Therefore, in terms of Chesapeake Bay water quality it is conceivable that age-1+ menhaden may exacerbate some of the problems associated with eutrophication through the potential enhancement of smaller phytoplankters, while to a certain extent, YOY menhaden may mitigate the effects.

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Table 1. Mean and standard error (SE) of clearance (*F*) and ingestion rates (*I*) of chl *a* for YOY and age-1+ menhaden over a range of initial mean phytoplankton (chl *a*) concentrations (each mean was calculated from n=3 experimental tanks).

Experiment type	Initial chl *a* conc. ($\mu g\ l^{-1}$)	*F* ± SE ($l\ fish^{-1}\ min^{-1}$)	*I* ± SE ($\mu g\ fish^{-1}\ min^{-1}$)
YOY	4.98	0.006 ± 0.001	0.028 ± 0.001
YOY	9.14	0.008 ± 0.002	0.075 ± 0.014
YOY	14.17	0.006 ± 0.001	0.082 ± 0.008
YOY	17.85	0.009 ± 0.001	0.142 ± 0.011
YOY	64.87	0.031 ± 0.003	1.341 ± 0.109
YOY	106.53	0.043 ± 0.005	2.651 ± 0.092
YOY	127.29	0.046 ± 0.002	3.451 ± 0.264
YOY	194.22	0.028 ± 0.002	3.851 ± 0.231
Age-1+	8.66	0.015 ± 0.005	0.119 ± 0.039
Age-1+	18.05	0.000 ± 0.000	0.005 ± 0.005
Age-1+	19.04	0.000 ± 0.000	0.000 ± 0.000
Age-1+	55.77	0.000 ± 0.000	0.000 ± 0.000
Age-1+	101.78	0.009 ± 0.009	0.826 ± 0.826

Table 2. YOY functional response model rankings.

Model	# parameters	n	-ln(ℓ)	AIC_c	ΔAIC_c	Model likelihood	W
Type I	2	42	-34.72	-65.13	44.97	0.00	0.00
Type II *a*	3	42	-36.13	-65.62	44.48	0.00	0.00
Type II *b*	4	42	-47.43	-85.79	24.31	0.00	0.00
Type III	4	42	-59.59	-110.10	0.00	1.00	1.00

Table 3. Parameter estimates ± asymptotic standard errors (SE) for the type III functional response model describing phytoplankton (chl *a*) ingestion rates by YOY Atlantic menhaden in response to initial prey concentration.

Parameter	Estimate ± SE
P1	4.18 ± 0.12
P2	4.59 ± 0.29
P3	0.02 ± 0.00

Table 4. Mean and standard error (SE) of initial percent composition of phytoplankton by size-range across all YOY and age-1+ feeding experiments.

Experiment type	Size range (μm)	Mean initial % composition ± SE
YOY	<7	97.78 ± 0.52
YOY	7-15	1.94 ± 0.45
YOY	15-30	0.23 ± 0.07
YOY	>30	0.04 ± 0.02
Age-1+	<7	98.61 ± 0.55
Age-1+	7-15	1.21 ± 0.48
Age-1+	15-30	0.15 ± 0.07
Age-1+	>30	0.02 ± 0.01

Table 5. Mean and standard error (SE) of initial percent composition of phytoplankton by classification across all YOY and age-1+ feeding experiments.

Experiment type	Classification	Mean initial % composition ± SE
YOY	Autotrophic dinoflagellate	0.03 ± 0.01
YOY	Heterotrophic dinoflagellate	0.00 ± 0.00
YOY	Cryptophyte	0.09 ± 0.01
YOY	Cyanobacteria	97.35 ± 0.52
YOY	Cyanobacteria chain	0.43 ± 0.22
YOY	Diatom	1.89 ± 0.43
YOY	Diatom chain	0.22 ± 0.06
Age-1+	Autotrophic dinoflagellate	0.01 ± 0.00
Age-1+	Heterotrophic dinoflagellate	0.00 ± 0.00
Age-1+	Cryptophyte	0.07 ± 0.02
Age-1+	Cyanobacteria	98.07 ± 0.68
Age-1+	Cyanobacteria chain	0.29 ± 0.29
Age-1+	Diatom	1.54 ± 0.59
Age-1+	Diatom chain	0.05 ± 0.04

Table 6. Mean and standard error (SE) of chl *a* clearance (*F*), ammonium excretion (NH_4^+-ex) and total dissolved nitrogen (TDN-ex) excretion rates for YOY and age-1+ menhaden over a range of initial mean phytoplankton (chl *a*) and zooplankton concentrations (each mean was calculated from n=3 experimental tanks).

Ambient water as prey				
Experiment Type	Initial chl *a* conc. (µg l^{-1})	*F* ± SE (l $fish^{-1}$ min^{-1})	NH_4^+-ex ± SE (µg N $fish^{-1}$ min^{-1})	TDN-ex ± SE (µg N $fish^{-1}$ min^{-1})
Age-1+: Baseline	NA*	NA*	19.07 ± 2.06	27.41 ± 2.96
Age-1+	19.04	0.00 ± 0.00	13.14 ± 2.74	18.88 ± 3.94
Age-1+	101.78	0.009 ± 0.009	19.66 ± 2.69	28.25 ± 3.87
YOY: Baseline	NA*	NA*	1.20 ± 0.09	1.73 ± 0.12
YOY	14.17	0.006 ± 0.001	0.93 ± 0.80	1.33 ± 1.15
YOY	64.87	0.031 ± 0.003	2.30 ± 0.10	3.30 ± 0.14
YOY	106.53	0.043 ± 0.005	3.32 ± 0.38	4.77 ± 0.55
YOY	127.29	0.046 ± 0.002	3.92 ± 0.21	5.63 ± 0.31
YOY	194.22	0.028 ± 0.002	2.83 ±0.49	4.06 ± 0.70
Zooplankton-only as prey				
Experiment Type	Initial zoop. conc. (no. l^{-1})	*F* ± SE (l $fish^{-1}$ min^{-1})	NH_4^+-ex ± SE (µg N $fish^{-1}$ min^{-1})	TDN-ex ± SE (µg N $fish^{-1}$ min^{-1})
Age-1+	7.83	0.331 ± 0.054	26.52 ± 2.30	38.10 ± 3.30
YOY	8.90	0.035 ± 0.018	6.39 ± 1.39	9.18 ± 1.99

*Not applicable.

Table 7. YOY nitrogen excretion rate model rankings.

Model	# parameters	*n*	-ln(ℓ)	AIC_c	ΔAIC_c	Model likelihood	*W*
Linear	3	18	13.64	34.99	2.06	0.36	0.26
Asymptotic exponential	4	18	10.93	32.93	0.00	1.00	0.74
Sigmoid	4	18	17.35	45.78	12.85	0.00	0.00

Table 8. Parameter estimates ± asymptotic standard errors (SE) for the two supported models of nitrogen excretion rates by YOY menhaden in response to chl *a* concentration.

Model	Parameter	Estimate ± SE
Asymptotic exponential	E_{max}	5.05 ± 0.67
Asymptotic exponential	r	0.02 ± 0.01
Asymptotic exponential	c	-16.78 ± 12.47
Linear	β_0	1.96 ± 0.49
Linear	β_1	0.02 ± 0.00

Table 9. Mean and standard error (SE) of net removal rates of phytoplankton-based nitrogen (R_N) by YOY menhaden over a range of initial mean phytoplankton (chl *a*) concentrations during late spring and early summer, using two separate carbon-to-chlorophyll ratios (C:Chl) (each mean was calculated from n=3 experimental tanks).

		R_N ± SE (μg N fish^{-1} min^{-1})	
Experiment Type	Initial chl *a* conc. (μg l^{-1})	C:Chl=50	C:Chl=200
YOY	0.00	-1.73 ± 0.12	-1.73 ± 0.12
YOY	14.17	-0.61 ± 1.13	1.56 ± 1.12
YOY	64.87	8.51 ± 0.82	43.94 ± 3.69
YOY	106.53	18.57 ± 0.35	88.59 ± 2.75
YOY	127.29	24.76 ± 2.62	115.91 ± 9.58
YOY	194.22	29.85 ± 1.42	131.58 ± 7.50

Fig. 1. Map of Chesapeake Bay, expanded from an inset map of the Mid-Atlantic United States. Black circles denote specimen collection sites from the York River (YR) and Mobjack Bay (MB).

Fig 2. Changes in phytoplankton (chl *a*) concentrations (±SD), as measured by a YSI 6600, throughout representative YOY (a) and age-1+ (b) menhaden feeding experiments. Solid circles represent tanks with fish present, and open circles represent tanks with fish absent.

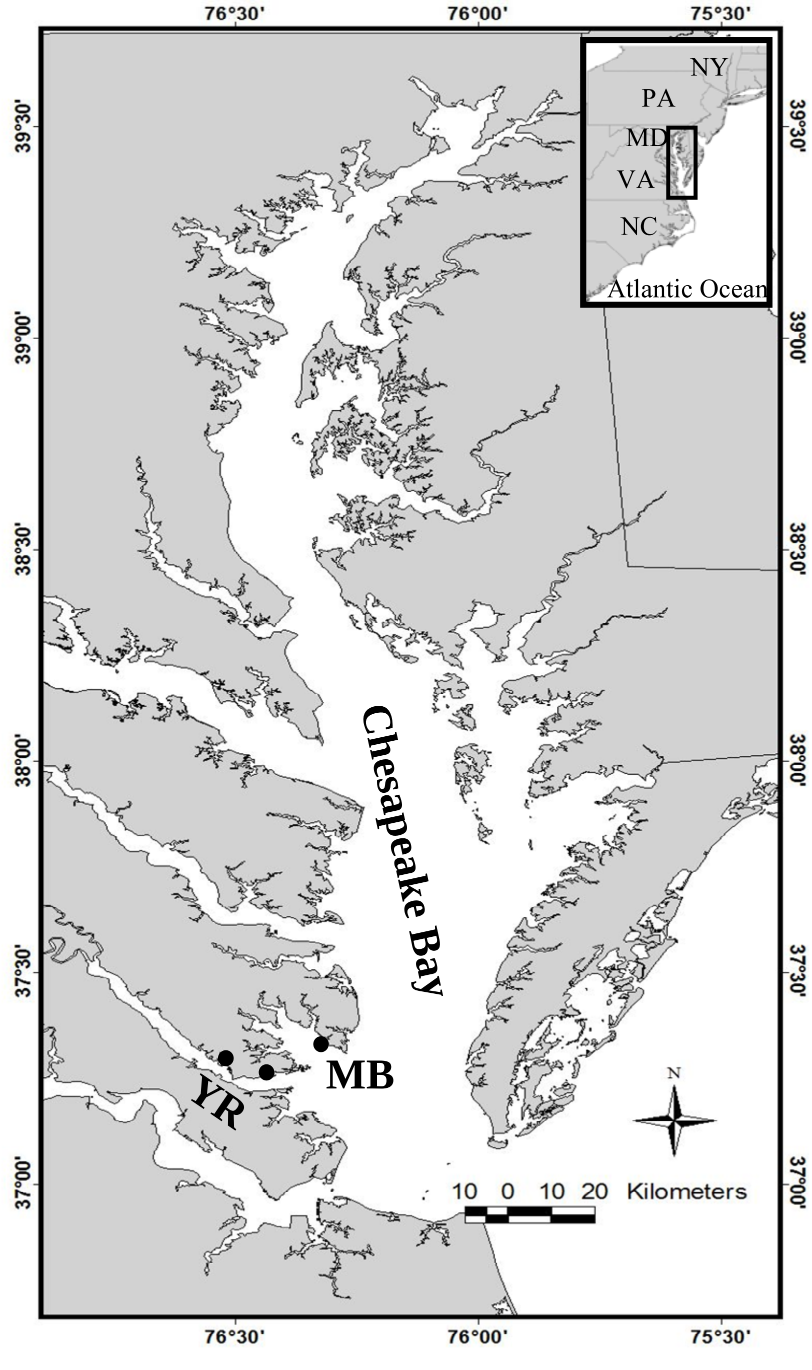
Fig. 3. Ingestion rates of total phytoplankton calculated for YOY (a) and age-1+ menhaden (b) over a range of initial phytoplankton (chl *a*) concentrations.
The solid line (a) represents the type III functional response model fitted to the YOY ingestion rate data.

Fig. 4. Changes in ammonium concentrations (±SD) over time within experimental tanks for representative YOY (a) and age-1+ (b) menhaden feeding experiments. Solid circles represent tanks with fish present, and open circles represent tanks with fish absent. The ranges of values of ammonium concentrations (y-axis) are different for the two representative experiments.

Fig 5. Total dissolved nitrogen excretion rates for YOY (a) and age-1+ menhaden (b) over a range of initial phytoplankton (chl *a*) concentrations. The solid line (a) represents the fit of the asymptotic exponential excretion rate model to the YOY data. The ranges of values of excretion rates (y-axis) are different between YOY and age-1+ experiments.

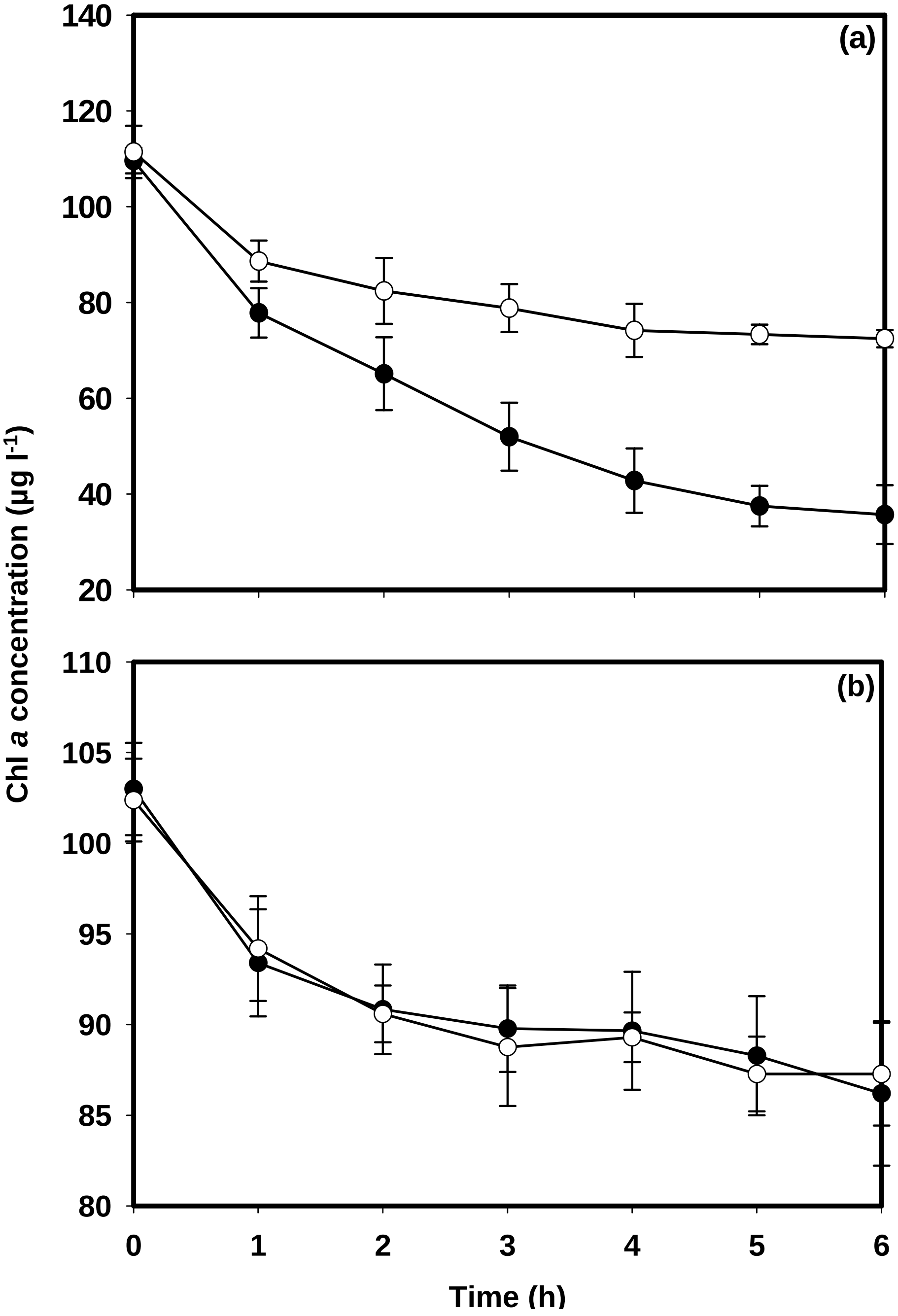
Fig 6. Rates of net removal of phytoplankton-based nitrogen for YOY menhaden over a range of chl *a* concentrations. All circles represent calculated rates. C:Chl=200 for open circles and 50 for filled circles. Lines represent the rates as predicted by the R_N model (eq. 13), where C:Chl=200 for the dashed line and 50 for the solid line.

Figure 1.



76°30'
76°00'
75°30'
39°30'
39°00'
38°30'
38°00'
37°30'
37°00'
NY
PA
MD
VA
NC
Atlantic Ocean
Chesapeake Bay
MB
YR
N
10 0 10 20 Kilometers

Figure 2.



140
120
100
80
60
40
20
(a)
110
105
100
95
90
85
80
(b)
0
1
2
3
4
5
6
Time (h)
Chl *a* concentration (µg l^{-1})

Figure 3.

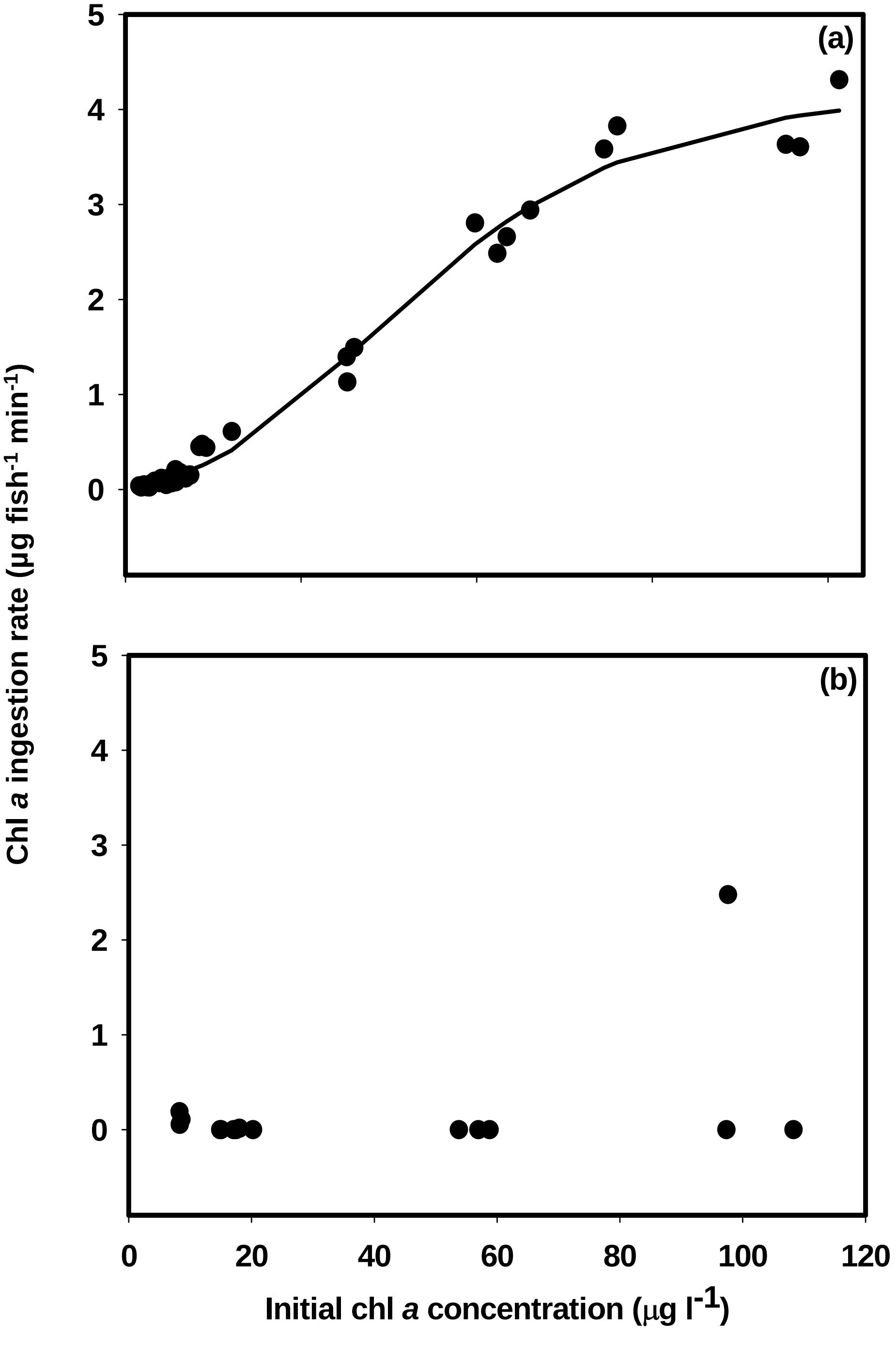
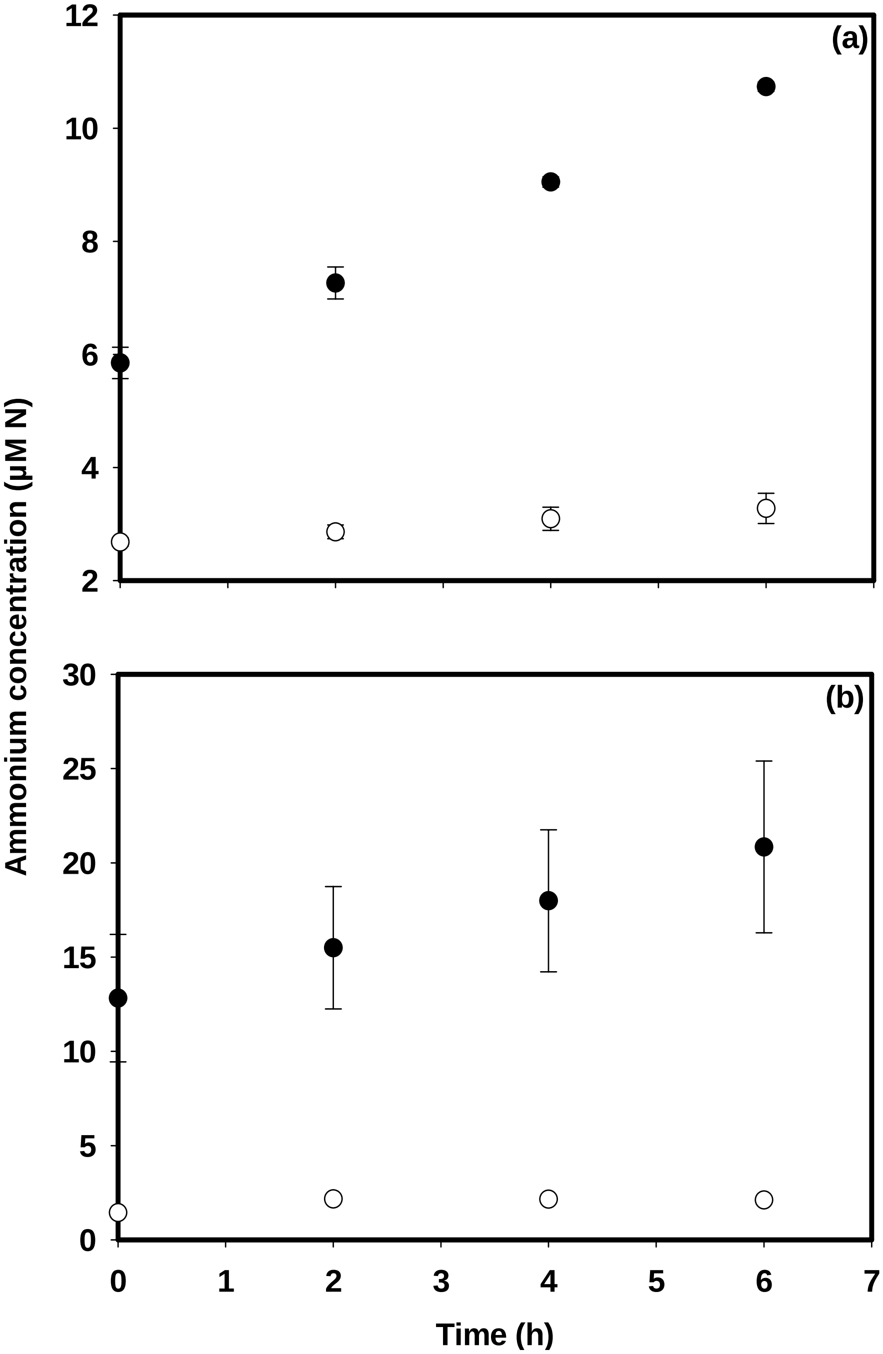

(a)
(b)
5
4
3
2
1
0
0
20
40
60
80
100
120
Chl *a* ingestion rate (µg fish^{-1} min^{-1})
Initial chl *a* concentration (µg l^{-1})

Figure 4.



(a)
(b)
Ammonium concentration (µM N)
Time (h)
12
10
8
6
4
2
30
25
20
15
10
5
0
0
1
2
3
4
5
6
7

Figure 5.

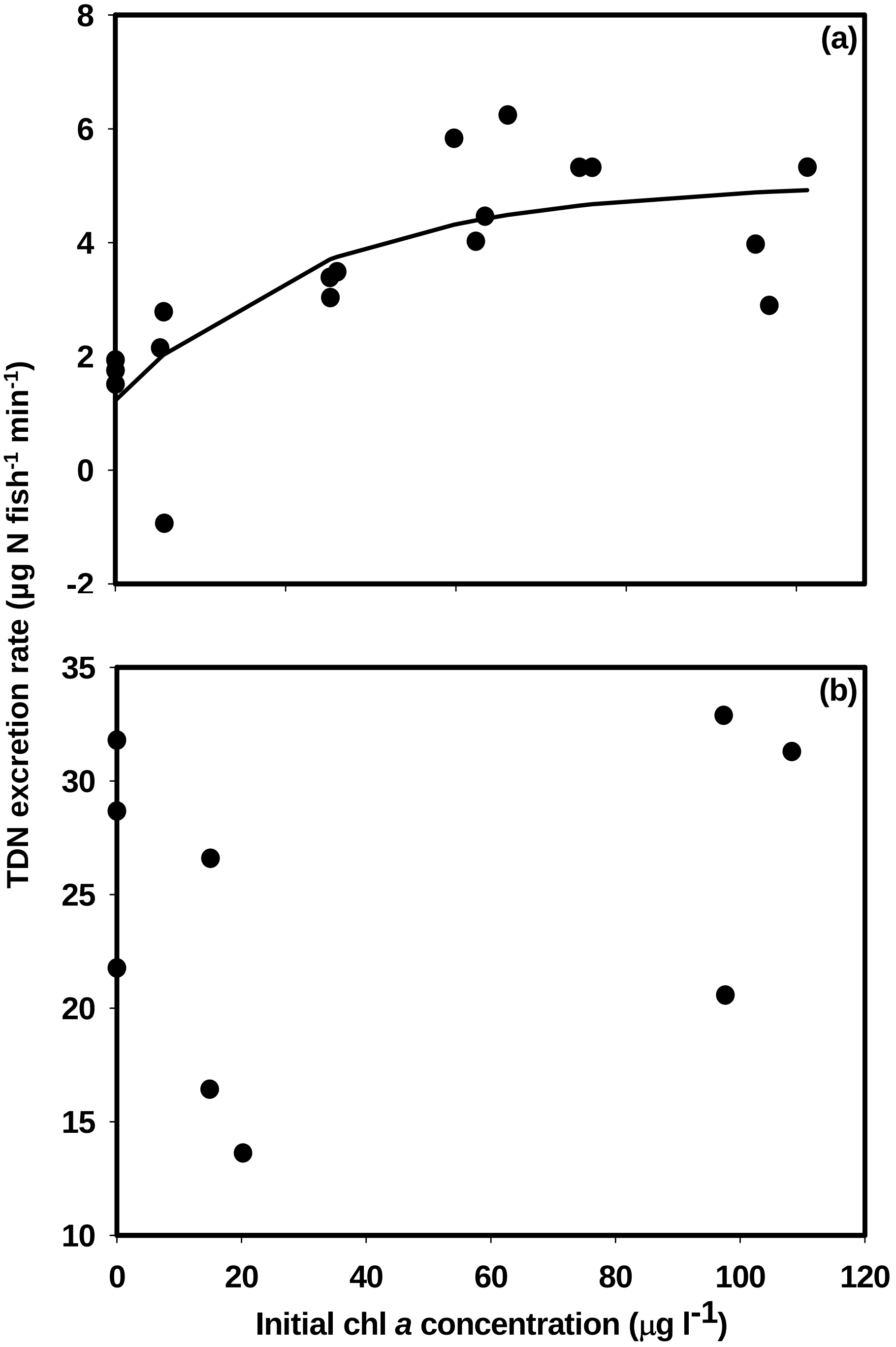
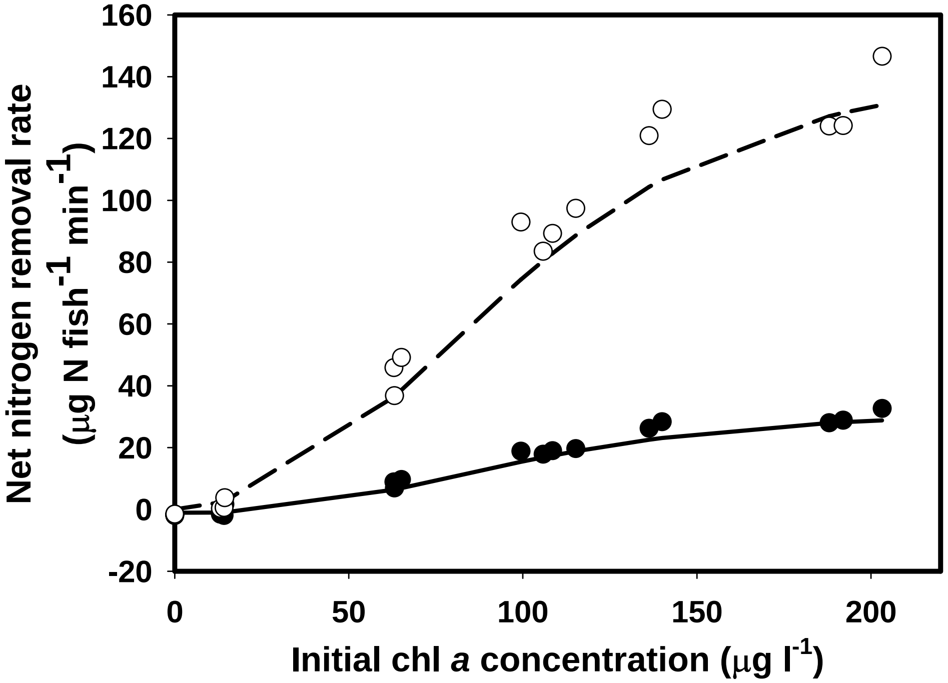

(a)
(b)
8
6
4
2
0
-2
35
30
25
20
15
10
0
20
40
60
80
100
120
TDN excretion rate (µg N fish^{-1} min^{-1})
Initial chl *a* concentration (µg l^{-1})

Figure 6.



Net nitrogen removal rate
(μg N fish-1 min-1)
160
140
120
100
80
60
40
20
0
-20
0
50
100
150
200
Initial chl *a* concentration (μg l-1)

CHAPTER 3: PROJECT SUMMARY

CONCLUSIONS

Aquatic filter feeders, such as Atlantic menhaden, have the potential to directly impact water quality through the ingestion and assimilation of primary production. This feeding strategy has led marine resource management to identify menhaden as a potentially important species in the restoration of impaired estuaries (CBP 2000). However, despite numerous studies (Peck 1893, Richards 1963, June and Carlson 1971, Oviatt et al. 1972, Jeffries 1975, Durbin and Durbin 1975, 1981 and 1998, Edgar and Hoff 1976, Lewis and Peters 1984, 1994, Friedland et al. 1984, Gottlieb 1998, among others), much ambiguity still exists with respect to the ecological role of Atlantic menhaden. In Chesapeake Bay, a crucial habitat for this estuarine-dependent species, estimates of population-level impacts on water quality may be considered a significant advancement toward an ecosystem-based approach to marine resource management. Yet, without a clear understanding of their ecological role on an individual basis, it is difficult to evaluate impacts by the entire population.

Through a series of experiments on YOY and age-1+ menhaden, an attempt was made to improve the understanding of the role of an individual menhaden. To ensure confidence in the empirically-derived results, the experimental design relied heavily on methods established in previous studies (Durbin and Durbin 1975, 1981, Friedland et al. 1984). By adapting these methods to address the objectives of this study, rates of ingestion and excretion were estimated for menhaden on an individual basis across a range of naturally-occurring phytoplankton concentrations with compositions typical of late spring through summer in Chesapeake Bay. Thus, given estimates of population size in numbers, these individual rates are readily applicable to entire populations.

The ontogenetic difference in ingestion rates of phytoplankton detected between YOY and age-1+ menhaden is an important observation that supports the findings of previous studies (Durbin and Durbin 1975, Friedland et al. 1984, Friedland et al. 2006). These studies (present study included) collectively showed that age-1+ menhaden are capable of ingesting only the largest size-fraction of phytoplankton in the ecosystem, while the minimum size threshold for YOY menhaden is much smaller. In public discussions regarding management of the menhaden fishery, filtration of phytoplankton and potential improvement of water quality are characteristics commonly mentioned in support of exercising caution with respect to the potential localized depletion of the Chesapeake Bay menhaden population. However, since the majority of the harvest continues to target age-1+ menhaden from late spring through fall in Chesapeake Bay (ASMFC 2006), and since the composition of the Chesapeake Bay phytoplankton community is typically dominated by smaller phytoplankters during this time (Marshall et al. 2005), it is unlikely that the removal of these fish in Chesapeake Bay directly results in a negative impact on water quality. Perhaps a stronger argument for restricting the fishery in an effort to prevent localized depletion in Chesapeake Bay should focus on the importance of the role of menhaden as a forage base for commercially, recreationally and ecologically important predators (Hartman and Brandt 1995); as well as the potential indirect impact on water quality through improving recruitment of YOY menhaden. YOY recruitment has been at historically low levels since the mid-1990's (ASMFC 2006), and it is conceivable that the observed recruitment failure is a result of a locally-depleted population of spawning adults.

The importance of high levels of YOY recruitment to Chesapeake Bay with respect to water quality is emphasized by the results presented. Ingestion rates of phytoplankton and excretion rates of nitrogen were estimated across a range of phytoplankton concentrations. While no trends were observed for age-1+ menhaden, ingestion and excretion rate responses to phytoplankton concentration were certainly documented for YOY menhaden (chapter 2: Figs. 2 and 4). In an effort to address objectives 1 and 2 (chapter 1), these responses were modeled using a biologically-reasonable suite of candidate models determined *a priori*, and an information-theoretic approach to model selection (Burnham and Anderson 2002).

The type III functional response model was identified as the best representation (of the candidate models) of the response of ingestion rates to phytoplankton concentration. This finding may support the hyperbolic relationship between swimming speeds of menhaden and phytoplankton concentration described by Durbin et al. (1981), since increased swimming speeds reported at low phytoplankton concentrations may actually drive the initial acceleration of ingestion rates (unique to type III) at those same low concentrations. Further exploration of this relationship would require additional experiments that measure phytoplankton ingestion rates and swimming speeds of menhaden concurrently.

Additionally, the response of nitrogen excretion rates to phytoplankton concentration was also characterized. In contrast to the availability of previously defined functional response models that were applied to menhaden ingestion rates, a suite of models describing the potential responses of nitrogen excretion rates have not been reported. Therefore, the models chosen were based on assumptions about the potential response. Of the candidate models, the asymptotic exponential function best described the response of nitrogen excretion rates to phytoplankton concentration. This is similar to the initial hypothesis of a response that increases to a saturation level, which was based on the assumption that the time associated with the physiological process of excretion causes the increasing rate of excretion to decelerate to a maximum rate at some high prey concentration (feeding intensity).

To address objective 3 (chapter 1), the empirically-derived models of ingestion and excretion were combined using estimates of nutrient compositions of phytoplankton (Redfield et al. 1966, Cerco and Noel 2004), allowing the estimation of net removal of nitrogen by YOY menhaden. Since a net removal of nitrogen through the ingestion of phytoplankton was documented for most of the phytoplankton concentrations analyzed (chapter 2: Table 9), it stands to reason that the presence of YOY menhaden may have a positive impact on water quality in Chesapeake Bay. By applying these individually-based models to estimates of YOY population size, while incorporating spatially and temporally explicit measurements of phytoplankton abundance throughout Chesapeake Bay, an assessment of the impact of YOY menhaden on Chesapeake Bay water quality can be obtained. This would directly address the first aforementioned goal of the Chesapeake 2000 agreement: "*assess the effects of different population levels of filter feeders such as menhaden, oysters and clams on Bay water quality and habitat*" (CBP 2000).

An earlier attempt to assess the ecological role of Atlantic menhaden in Chesapeake Bay was performed by Gottlieb (1998), who used STELLA modeling software to conduct a simulation of nitrogen removal by age-0 menhaden. This model was developed from an economic perspective with respect to fishery removals of age-0 (YOY) menhaden during a simulated 183-day fishing period. A comparison of the estimates of net nitrogen removal (chapter 2: Table 9) with the simulation presented by Gottlieb (1998) indicated similar findings when the lowest estimate of population size from the comparative study, and the lower estimates of net nitrogen removal are used. However, increasing either the estimates of population size or the estimates of net nitrogen removal causes disagreement between the two studies by at least an order of magnitude. This discrepancy emphasizes the importance of reliable estimates across time and space of YOY menhaden population size, chl *a* concentrations and C:Chl before using the derived model of net nitrogen removal to assess population-level impacts.

Overall, the documented findings improve upon our understanding of the ecological role of Atlantic menhaden in Chesapeake Bay, and support the results of several previous studies (Durbin and Durbin 1975, 1981, Friedland et al. 1984, 2006, Gottlieb 1998). While these may be meaningful contributions, it is also important to discuss some of the limitations of the study. Firstly, all experiments were conducted over a narrow temperature range and prey composition. Since the responses characterized were behavioral and physiological, it is likely that different environmental conditions (temperature, salinity, etc.) and different prey compositions would generate different responses. It is important to note however, that the temperature range and prey composition used in the study was intended to be representative of that which menhaden most frequently experience in Chesapeake Bay in late spring through summer. In addition, the density of menhaden in the experimental tanks was held constant across all experiments. It may be that feeding responses vary with respect to schooling density in nature, but the results presented are only reflective of a single density. Also, since menhaden serve as an important forage base for many predators, it is likely that schools of menhaden are frequently attacked in the wild. This disturbance almost certainly impacts all behavioral and physiological responses, yet the impact of this disturbance on ingestion and excretion rates is not captured in the findings of the present study since there were no natural predators of menhaden present in the experimental tanks.

It is recommended that future studies address some of these limitations in an effort to continue the advancement of our understanding of this important estuarine-dependent species. For example, a better description of the feeding response of menhaden to prey composition could be obtained through thorough analysis of the selectivity of prey ingested as governed by the type and size of prey available. An improvement of our understanding of the impact of season, location and schooling density on ingestion and excretion rates of menhaden could result from an analysis of the responses to a range of temperatures, salinities and school densities. Finally, describing the daily impact of menhaden on water quality would require an empirical estimation of the time spent feeding per day.

The inclusion of the suggested recommendations in concert with the findings presented may outline a path for best describing the impact of an individual Atlantic menhaden on water quality; which, given reliable estimates of menhaden population size and phytoplankton concentration and composition, can then be expressed on an ecosystem-wide basis.

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