WILLIAM & MARY
CHARTERED 1693

W&M ScholarWorks

VIMS Articles

7-2005

Viable gut passage of cyanobacteria through the filter-feeding fish Atlantic menhaden, Brevoortia tyrannus

KD Friedland

DW Ahrenholz

LW Haas
Virginia Institute of Marine Science

Follow this and additional works at: https://scholarworks.wm.edu/vimsarticles

Part of the Marine Biology Commons

Recommended Citation

SHORT COMMUNICATION

Viable gut passage of cyanobacteria through the filter-feeding fish Atlantic menhaden, *Brevoortia tyrannus*

KEVIN D. FRIEDLAND[1]*, DEAN W. AHRENHOLZ[2] AND LEONARD W. HAAS[3]

[1]UMASS/NOAA COOPERATIVE MARINE EDUCATION AND RESEARCH PROGRAM, BLAISDELL HOUSE, UNIVERSITY OF MASSACHUSETTS, AMHERST, MA 01003, USA; [2]NATIONAL MARINE FISHERIES SERVICE, BEAUFORT LABORATORY, BEAUFORT, NC 28516, USA AND [3]VIRGINIA INSTITUTE OF MARINE SCIENCE, GLOUCESTER POINT, VA 23062, USA

*CORRESPONDING AUTHOR: kevin.friedland@noaa.gov

We examined the contents of the alimentary tract of juvenile Atlantic menhaden, an obligate filter-feeding fish, with epifluoresence microscopy. All plankton taxa and detrital material observed in plankton samples from the sampling area could also be found in the esophagus of the fish. The corresponding plankton taxa were absent from the pre-feces sampled in the hindgut with the exception of cyanobacteria, which were found intact and fluorescing as they do in nature. The survival of cyanobacteria during gut passage and their presence in menhaden feces may enhance both nutrient availability and the delivery of these cells to the benthos. Additionally, diatoms frustules were found in the pre-feces, which may affect the sequestration of biogenic silica. These results may have bearing on the formation of cyanobacteria blooms, nutrient flow in estuaries and the delivery of material to the sediment.

INTRODUCTION

Atlantic menhaden, *Brevoortia tyrannus*, is an obligate filter feeding fish distributed along the East Coast of the United States. As juveniles, menhaden live in the mesohaline and oligohaline zones of estuaries where their distribution is often positively correlated with phytoplankton abundance (Friedland *et al.*, 1989; Friedland *et al.*, 1996). The plankton filtering capability of juveniles can be inferred from clearing rate data for 14-cm fork length fish, which represents the upper limit of the juvenile size spectra. These fish can filter uniformly sized particles in a range of 7–9 μm in diameter at filtration efficiencies of approximately 10% (Friedland *et al.*, 1984). Of greater relevance to fish in the wild, particle retention at size is enhanced when a background of other particles is present, typical of a water column with detritus and other plankton particles (Friedland *et al.*, 1984). This effect causes menhaden to retain cells smaller than their effective filtering capability. There is an ontogenetic shift in filtering capability as the fish increase in age and size. The effective pore size of the gill rakers of menhaden juveniles typical of spring and summer nursery residents (7.5-cm fork length) is 60% of the pore size of 14-cm fish, suggesting that juveniles can retain picoplankton including bacteria and cyanobacteria (Friedland, unpublished data). Menhaden adults (26-cm fork length) start to show significant filtration efficiencies on particles >20 μm and filter zooplankton at higher efficiency than juveniles (Durbin and Durbin, 1975).

The role of menhaden in coastal and estuarine ecosystems has long been an area of intense interest. McHugh (McHugh, 1967) concluded that the annual harvest of menhaden from the Chesapeake Bay could filter the water of the entire Bay twice in the span of

24 h, suggesting that menhaden filter ecologically significant volumes of water and may have the capacity to affect 'top down' control on some plankton components. A more direct ecological effect was observed by Oviatt *et al.* (Oviatt *et al.*, 1972) who showed that menhaden schools locally decreased phytoplankton and increased ammonia concentrations. Durbin and Durbin (Durbin and Durbin, 1998) constructed a bioenergetics model for migrating adult menhaden grazing in Narragansett Bay that illustrated their role in both creating spatial heterogeneity in plankton prey and in the transformation and transport of nutrients accounting for upward of 6% of the total nitrogen exported annually from the Bay system.

The ecological role of menhaden is more complex and intriguing in estuaries typically used as nurseries by juveniles. These systems may receive juvenile recruitments numbering in the tens of billions of fish, which has stimulated interest in the capability of these systems to sustain the growth of such large numbers of fish (Luo *et al.*, 2001), the role of menhaden as a mechanism of nutrient removal (Gottlieb, 1998) and the interaction with other fish such as striped bass which prey on menhaden (Uphoff, 2003). The fish tend to concentrate in the shoal portions of estuaries (Friedland *et al.*, 1996), which means they are feeding on plankton influenced by nutrients from both freshwater input and benthic regeneration. Additionally, their proximity to the benthos could contribute to benthos-related processes.

We collected plankton water samples and juvenile menhaden from the Neuse River in North Carolina, USA over six collection dates during 1983. The phytoplankton were enumerated from water samples collected by simple bottle grabs at the surface at each location a fish trawl was made. An inventory of major seston categories present in the water column was made by staining preserved phytoplankton with proflavin hemisulfate and examining them with epifluorescent microscopy (Haas, 1982). The fish were collected live in a surface trawl (Friedland *et al.*, 1989) and kept on ice until return to the laboratory, usually within one hour. At least five fish were dissected each collection day and the contents of the alimentary canal were sampled at several locations (June and Carlson, 1971). The two locations we report on are the esophagus immediately behind the epibranchial organs (Friedland, 1985) and the hindgut or the region immediately before the anal vent. Contents in the latter location can be expected to be identical to material excreted by the fish, i.e. pre-feces. The material in the gut tract was eluted with 0.2 μm filtered seawater and stained with the same proflavin hemisulfate stain used for the water column plankton samples and examined with epifluorescent microscopy.

The phytoplankton cells found in the esophagus were generally intact and were readily observed as they autofluoresced red or orange amongst the dull green background of detrital material. It was also possible to identify bacteria cells, which were often associated with clumps of detritus. We found that all of the major taxonomic groups of plankton observed in the water samples were also represented in the material concentrated in the esophagus (Table I). This confirmed that the fish were ingesting most plankton taxa available in the water column. The hindgut samples were dominated by detrital material, with two exceptions. We saw empty diatom frustules and many intact, autofluorescing coccoid cyanobacteria cells, likely the genus *Synechococcus*. The cyanobacteria, which were on the order of 1–2 μm in diameter, had the same physical appearance and autofluoresced the same color as cells observed in both the water samples and in the esophagus material. The constituents of the esophagus were different than observed in the hindgut (sign test, $p = .004$).

Cyanobacteria, appearing in a number of different forms, are considered symptomatic of eutrophication in estuaries (Paerl *et al.*, 2003). Many cyanobacteria are filamentous and may not be ingested by menhaden, but the coccoid cyanobacteria, genus *Synechococcus*, is a major component of the estuarine phytoplankton community in regions utilized by menhaden (Ray *et al.*, 1989; Davis *et al.*, 1997). Though difficult to quantify, some fraction of the standing crop of these coccoid forms must be ingested by menhaden in Chesapeake Bay and its tidal subestuaries.

We can identify several potential problems with the interpretation of these data. First, the absence of other phytoplankton taxa in the prefecal material might represent a false negative. Gut passage times for menhaden

Table I: Plankton taxa identified in two locations of the alimentary canal of Atlantic menhaden

Plankton or particles	Identified in esophagus	Identified in hind gut
Crytophyceae	Present	Absent
Dinophyceae	Present	Absent
Haptophyceae	Present	Absent
Chrysophyceae	Present	Absent
Xanthophyceae	Present	Absent
Euglenophyceae	Present	Absent
Prasinophyceae	Present	Absent
Chlorophyceae	Present	Absent
Bacillariophyceae	Present	Absent[a]
Cyanophyceae	Present	Present
Detritus	Present	Present

[a]Empty diatom frustules were observed

are on the order of hours, so we can't categorically dismiss the possibility of a false negative since we didn't sample the water that would have been precursor to the pre-feces we sampled. However, for a false negative to occur, juvenile menhaden in North Carolina would have had to have filtered over long periods and in multiple locations, monocultures of cyanobacteria. We believe this is highly unlikely. Second, the presence of cyanobacteria in the pre-feces might have been a false positive. This could only occur through contamination of the pre-feces samples. We cannot identify a source of contamination that would introduce only these cells into the pre-feces. Finally, were the cyanobacteria we observed viable cells possessing a mucoid layer needed to resist digestion? The presence of a mucoid outer layer is typical of many but not all coccoid cyanobacteria (Perkins *et al.*, 1981). Coccoid cyanobacteria are typically grazed by eucaryotic microflagellates and commonly observed in their food vacuoles (Perkins *et al.*, 1981; Haas, 1982; Ray *et al.*, 1989). In one instance, the first stages of digestion for coccoid cyanobacteria ingested by a heterotrophic flagellate, based on the disappearance of autofluorescence in recently ingested cells, was observed to be about 3 min (Sieracki *et al.*, 1987). If the cyanobacteria were digested by menhaden, we should not have seen autofluorescencing cells in the pre-feces. The complete absorption of cells by heterotrophs may take many hours (Öpik and Flynn, 1989), but the appearance of intact cells in the menhaden hindgut, after traversing the alimentary canal of the fish, further supports the contention that the cells were undigested.

The role of fish gut passage in enhancing cyanobacteria productivity has recently been reported for a number of species residing in eutrophic lakes. Lewin *et al.* (Lewin *et al.*, 2003) showed that some cyanobacteria have mucilaginous coverings that provide protection during fish gut passage. In addition to surviving gut passage through lake roach, *Rutilus rutilus*, it was shown experimentally that one of the dominant cyanobacteria species ingested by roach, *Microcystis* spp., has enhanced phosphorus uptake while in the alimentary canal of the fish. Kolmakov and Gladyshev (Kolmakov and Gladyshev, 2003) reported that *Microcystis aeruginosa* had significantly increased growth and potential photosynthesis after gut passage through a carp species *Carassius auratus*. However, the growth of other forms like the single-celled *Synechocystis salina* were not increased. It would be of interest to know whether menhaden have an important role in enhancing the development of cyanobacteria blooms in coastal ecosystems through some mechanism related to gut passage. Even if gut passage did not enhance the nutritive state of the cyanobacteria, if they remain in the water column after being voided by the fish, the observation

that competing phytoplankton were removed through menhaden feeding and digestion, should favor cyanobacteria by the reducing competition for water column nutrients.

Alternatively, menhaden, and in particular menhaden juveniles, may be accelerating the deposition of cyanobacteria and detritus to the benthos in estuaries. It appears that large zooplankton and fish feces make a much larger contribution to the sedimentary flux of material to the benthos than initially thought (Turner, 2002). The delivery of both live cells and other organic material to the benthos has been viewed as a rate process related to cell size and nutritional condition and the activity of various planktivores. Nanophytoplankton (i.e. <20 μm) are less likely to sink appreciably on their own and the fecal pellets of small zooplankton appear to contribute less to sedimentary flux than initially thought due to the recycling of their feces that occurs in the water column. Instead, large zooplankton and fish produce fecal pellets more likely to stay intact and sink fast enough to be deposited. Considering that the distribution of juvenile menhaden is concentrated in specific regions of the estuary (Friedland *et al.*, 1996), and the relatively shoal nature of these areas, this flux may be intense.

The presence of diatom frustules in menhaden pre-feces may be an indication of sequestration of silicon that contributes to the seasonal shift in estuarine plankton communities. The spring bloom of diatoms and zooplankton typical of temperate estuaries provides a size spectrum of food that facilitates rapid growth of fish and shellfish (Officer and Ryther, 1980). The shift to communities dominated by flagellates and cyanobacteria is considered indicative of nitrogen and phosphorous loading, but also may be related to transient declines in water column silicon (Turner and Rabalais, 1994; Rocha *et al.*, 2002). This introduces another potential interaction between menhaden and the plankton community; menhaden feeding and defecation may accelerate the removal of silica from the water column of estuaries and thus contribute to the conditions that favor the community shift to flagellates and cyanobacteria.

REFERENCES

Davis, L. N., Phillips, K. A. and Marshall, H. G. (1997) Seasonal abundance of autotrophic Picoplankton in the Pagan River, a nutrient enriched subestuary of the James River, Virginia. *Va. J. Sci.*, **48**, 211–218.

Durbin, E. and Durbin, A. (1975) Grazing rates of the Atlantic menhaden *Brevoortia tyrannus* as a function of particle size and concentration. *Mar. Biol.*, **33**, 265–277.

Durbin, A. G. and Durbin, E. G. (1998) Effects of menhaden predation on plankton populations in Narragansett Bay, Rhode Island. *Estuaries*, **21**, 449–465.

Friedland, K. D. (1985) Functional morphology of the branchial basket structures associated with feeding in the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae). *Copeia*, **10**, 1018–1027.

Friedland, K. D., Ahrenholz, D. W. and Guthrie, J. F. (1989) Influence of plankton on distribution patterns of the filter-feeder *Brevoortia tyrannus* (Pisces: Clupeidae). *Mar. Ecol. Prog. Ser.*, **54**, 1–11.

Friedland, K. D., Ahrenholz, D. W. and Guthrie, J. F. (1996) Formation and seasonal evolution of Atlantic menhaden juvenile nurseries in coastal estuaries. *Estuaries*, **19**, 105–114.

Friedland, K. D., Haas, L. W. and Merriner, J. V. (1984) Filtering rates of the juvenile Atlantic menhaden *Brevoortia tyrannus* (Pisces: Clupeidae), with consideration of the effects of detritus and swimming speed. *Mar. Biol.*, **84**, 109–117.

Gottlieb, S. J. (1998) Nutrient removal by age-0 Atlantic menhaden (*Brevoortia tyrannus*) in Chesapeake Bay and implications for seasonal management of the fishery. *Ecol. Model.*, **112**, 111–130.

Haas, L. W. (1982) Improved epifluorescence microscopy for observing planktonic micro-organisms. *Ann. Inst. Oceanogr., Paris*, **58**, 261–266.

June, F. C. and Carlson, F. T. (1971) Food of young Atlantic Menhaden, *Brevoortia tyrannus*, in relation to metamorphosis. *Fish. Bull.*, **68**, 493–512.

Kolmakov, V. I. and Gladyshev, M. I. (2003) Growth and potential photosynthesis of cyanobacteria are stimulated by viable gut passage in crucian carp. *Aquat. Ecol.*, **37**, 237–242.

Lewin, W. C., Kamjunke, N. and Mehner, T. (2003) Phosphorus uptake by *Microcystis* during passage through fish guts. *Limnol. Oceanogr.*, **48**, 2392–2396.

Luo, J. G., Hartman, K. J., Brandt, S. B. *et al.* (2001) A spatially-explicit approach for estimating carrying capacity: an application for the Atlantic menhaden (*Brevoortia tyrannus*) in Chesapeake Bay. *Estuaries*, **24**, 545–556.

McHugh, J. L. (1967) Estuarine nekton. In G. H. Lauff (ed.), *Estuaries*. American Association For the Advancement of Science, Washington, DC, pp. 581–620

Officer, C. B. and Ryther, J. H. (1980) The possible importance of silicon in marine eutrophication. *Mar. Ecol. Prog. Ser.*, **3**, 83–91.

Öpik, H. and Flynn, K. J. (1989) The digestive process of the dinoflagellate, *Oxyrrhis marina* Dujardin, feeding on the chlorophyte, *Dunaliella primolecta* butcher: a combined study of ultrastructure and free amino acids. *New Phytol.*, **113**, 143–151.

Oviatt, C. A., Gall, A. L. and Nixon, S. W. (1972) Environmental effects of Atlantic menhaden on surrounding waters. *Chesap. Sci.*, **13**, 321–323.

Paerl, H. W., Dyble, J., Moisander, P. H. *et al.* (2003) Microbial indicators of aquatic ecosystem change: current applications to eutrophication studies. *FEMS Microbiol. Ecol.*, **46**, 233–246.

Perkins, F. O., Haas, L. W., Phillips, D. E. *et al.* (1981) Ultrastructure of a marine *Synechococcus* possessing spinae. *Can. J. Microbiol.*, **27**, 318–329.

Ray, R. T., Haas, L. W. and Sieracki, M. E. (1989) Autotrophic picoplankton dynamics in a Chesapeake Bay sub-estuary. *Mar. Ecol. Prog. Ser.*, **52**, 273–285.

Rocha, C., Galvao, H. and Barbosa, A. (2002) Role of transient silicon limitation in the development of cyanobacteria blooms in the Guadiana estuary, south-western Iberia. *Mar. Ecol. Prog. Ser.*, **228**, 35–45.

Sieracki, M. E., Haas, L. W., Caron, D. A. *et al.* (1987) Effect of fixation on particle retention by microflagellates: underestimation of grazing rates. *Mar. Ecol. Prog. Ser.*, **38**, 251–258.

Turner, J. T. (2002) Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. *Aquat. Microb. Ecol.*, **27**, 57–102.

Turner, R. E. and Rabalais, N. N. (1994) Coastal eutrophication near the Mississippi River Delta. *Nature*, **368**, 619–621.

Uphoff, J. H. (2003) Predator-prey analysis of striped bass and Atlantic menhaden in upper Chesapeake Bay. *Fish. Manage. Ecol.*, **10**, 313–322.