

# Sieving Functional Morphology of the Gill Raker Feeding Apparatus of Atlantic Menhaden

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**ABSTRACT** Menhaden occupy an important position in estuarine food webs, thus the rate processes associated with their feeding are critical to the ecosystem management of fishery and ecological resources. Atlantic menhaden feed on a wide range of plankton, the size and food quality of which change ontogenetically. We analyzed the functional morphology of the menhaden feeding apparatus in a size series of menhaden representative of juveniles and the adult migratory stock. The physical dimensions of gill arches and rakers increased isometrically with fish length; however, branchiospinule spacing, the dimension that forms the sieve apertures of the branchial basket, scaled allometrically with fish length. Juvenile menhaden from North Carolina have branchiospinule spacings that averaged 12  $\mu\text{m}$ , with three arch subsections of average spacing < 10  $\mu\text{m}$ . Spacings did not increase with juvenile growth until the first allometric inflection point at approximately 100 mm fork length (FL). Spacing data for juveniles from other locations suggests spacing increases with latitude. Spacings increase with fish length in adults until a second inflection at 200 mm FL, after which spacing averages 37  $\mu\text{m}$ . These data suggest menhaden juveniles filter smaller plankton with higher filtration efficiency than previously considered and that regional recruitment may affect adult distribution through foraging preferences. *J. Exp. Zool.* 305A:974-985, 2006. © 2006 Wiley-Liss, Inc. †This article is a U.S. Government work and, as such, is in the public domain in the United States of America.

**How to cite this article:** Friedland KD, Ahrenholz DW, Smith JW, Manning M, Ryan J. 2006. Sieving functional morphology of the gill raker feeding apparatus of Atlantic menhaden. *J. Exp. Zool.* 305A:974-985.

The role of Atlantic menhaden, *Brevoortia tyrannus*, in estuarine and coastal ecosystems is distinguished by their population numbers and their ability to filter extremely small plankton. Since they are so abundant, it is assumed their filter feeding has a significant impact on estuarine food webs (McHugh, '67). Since Atlantic menhaden are fished intensively, their abundance can be assessed using virtual population analysis (Vaughan and Merriner, '91). The assessments provide age-disaggregated population sizes that can be spatially allocated between juvenile nurseries and adult forage areas. The observed relationship between juvenile menhaden abundance and phytoplankton gradients, which reflects gradient search by the fish (Friedland et al., '89, '96), suggests a predictive capability in assessing juvenile ecosystem impacts (Gottlieb, '98; Brandt and Mason, 2003). The adults

display similar behaviors only at larger spatial scales (Kemmerer et al., '74; Kemmerer, '80). Thus, we can estimate the distribution of various age menhaden among ecosystem components with a reasonable degree of precision. However, what is not clear is the fraction of the plankton community removed from the water column by the filter feeding of variously sized menhaden.

Menhaden diet has been qualitatively described with traditional stomach content analysis and quantitatively described by clearing rate

Grant sponsor: NOAA Chesapeake Bay Program Office.

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Received 6 July 2006; Revised 8 September 2006; Accepted 8 September 2006

Published online 13 October 2006 in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/jez.a.348.

experiments that estimate filtration efficiency. The first qualitative examinations of menhaden stomach contents showed that adult menhaden are omnivorous feeders utilizing phytoplankton (especially diatoms and dinoflagellates), zooplankton, amorphous matter, and material specifically identified as detritus (Peck, 1893). Peck hypothesized that menhaden diet composition reflected the plankton in the surface waters they occupied. Subsequent stomach content work has done little to quantitatively test this hypothesis owing to the difficulty in accurately counting and identifying menhaden food items, though new insights were gained. Chipman ('59) and June and Carlson ('71) examined the stomachs of post-metamorphic juveniles and observed phytoplankton and zooplankton in the diet, noting that juveniles consumed smaller zooplankton than younger larval menhaden. Jeffries ('75) used biochemical methods to characterize zooplankton contribution to the diet of juveniles. Lewis and Peters ('94) demonstrated the utilization of refractory cellulose by menhaden feeding near marsh habitats. Lacking quantitative inference about menhaden diet, attention turned to experimental work measuring the filtration efficiency of the fish.

An ontogenetic continuum of menhaden filtering ability was confirmed by two sets of clearing rate experiments that characterized their ability to filter over an ecologically relevant size spectra of plankton. One of the clearing rate experiments was done with a group of large migratory adults whereas the other was done with a group of fish of a transitional size between juvenile and adult. The experiment with adults was conducted with fish averaging  $\approx 260$  mm fork length (FL) and showed that larger, older menhaden had a minimum size threshold of  $13 \mu\text{m}$  diameter particles (Durbin and Durbin, '75). However, the clearing rate data for these fish also suggest that significant retention (10% efficiency) does not occur for particles less than  $30 \mu\text{m}$  in diameter. At the larger end of the prey size spectra, the adults were highly efficient when filtering zooplankton. The clearing rate experiments with the transitional juvenile fish were conducted with  $\approx 138$  mm FL fish, which considering when the fish were collected, were most likely age-1 fish that over-wintered in Chesapeake Bay. These fish were shown to have dramatically different filtering ability from that of large adults, retaining particles as small as  $5\text{--}7 \mu\text{m}$  and showing significant retention efficiencies on  $7\text{--}9 \mu\text{m}$  sized particles (Friedland et al., '84). With the helping effect of detritus and other plankton

particles, menhaden can retain food particles smaller than the effective filtering efficiencies suggested by experiments with uniformly sized cells (Friedland et al., '84). Thus, juvenile menhaden can graze bacteria and flagellates less than  $5 \mu\text{m}$  in diameter at some low rate. However, when feeding at the larger end of the prey size spectrum, the transitional juveniles filtered some zooplankton at a lower efficiency than phytoplankton, suggesting the fish have maximum filtration efficiency at a size intermediate between phytoplankton and zooplankton. We are faced with the dilemma of whether it is appropriate to extrapolate the results of these two studies to post-metamorphic juveniles (30–100 mm FL) that concentrate in estuarine nurseries or to young adults (15–20 cm FL) that migrate between estuaries along the coast. Both of these population segments form critical filtering components of their respective food webs.

Many estuarine and oceanic processes are governed by the production and utilization of plankton particles so it is easy to see where incorporating menhaden into ecosystem models is essential. Estuaries face increasing threats from nutrient loading and the distribution of hypoxic conditions (Hagy et al., 2004). Atlantic menhaden are among a suite of filter-feeding organisms resident in estuaries and the coastal ocean that collectively exert a controlling effect on both living and detrital particles and the nutrients and pollution they carry (Breitburg, 2002; Jung and Houde, 2003, 2005). The large number of menhaden occurring in neritic waters represents a significant filtering capability (Oviatt et al., '72), which in addition to removing phytoplankton from the water column, may also utilize detrital material to a significant degree (Lewis and Peters, '94). Menhaden feeding may accelerate the deposition of material to anoxic bottom sediments through the formation of fecal pellets thus affecting the consumption of oxygen and the sequestration of nutrients in the benthos (Lane et al., '94). Since the discovery that cyanobacteria appear viable after gut passage through menhaden (Friedland et al., 2005), the observed shift in estuarine plankton communities may in part be attributed to changes in grazing pressure on the plankton (Davis et al., '97). Understanding the grazing dynamics of the full-size range of menhaden is essential to understanding the workings of estuarine and coastal food webs.

Relating feeding structure functional morphology to feeding selectively has been used effectively

in understanding resource partitioning in congener menhadens (Castillo-Rivera et al., '96), among other species, and in studying ontogenetic shifts in feeding (MacNeill and Brandt, '90). A range of approaches has been used to characterize the functional morphology of feeding structures ranging from direct measurement of structure spacings to less functional measurements such as sieving structures per standard distance. From analyses of the functional morphology of menhaden feeding structures, it is clear that branchiospinules, the secondary structures off gill raker blades, form the physical sieve that retains plankton particles (Monod, '61; Friedland, '85). These structures are arrayed in parallel and lend themselves to measurement with image processing.

The goal of this investigation was to describe the ontogenetic changes in the functional morphology of the menhaden feeding apparatus. We report on the ontogenetic change in the physical dimension of the branchial basket and the dimensions of structures related to the filtration and retention of food particles. The ontogenetic series for the adult portion of the analysis represents the mixed-origin stock occurring in marine waters. We assessed the effect of differences in regional juvenile rearing areas by comparing juvenile populations from a latitudinal cline.

## MATERIALS AND METHODS

We measured a suite of morphological attributes of the branchial baskets and gill rakers of an ontogenetic series of Atlantic menhaden. Menhaden samples were recovered from various locations along the East Coast of the United States. All material was fixed in 10% buffered formalin and transferred to 95% ethanol for storage. Juveniles,

for the purposes of our study fish less than 104 mm FL, were collected from estuarine locations in North Carolina, New York, Massachusetts, and New Hampshire (Table 1). Juvenile fish from North Carolina ranged in size from 32 to 103 mm FL and were the only juveniles used in the ontogenetic analysis. The analysis of the other nursery areas was limited to 5 fish per location and restricted to a size range of 74–92 mm FL. The adult fish ranged in size from 109 to 326 mm FL and were assumed to represent fish from various rearing areas along the coast. In total, measurements were made on 62 animals.

The suite of morphologic attributes consisted of measurements of the gill arches, raker blades, and branchiospinule spacings. Branchiospinules are the secondary processes on the raker blades of menhaden and the spacing between them form the sieve apertures of the branchial basket. Menhaden have five pairs of gill arches, which we refer to as arches I–V going from the anterior-lateral arch to the posterior-interior arch of the basket, respectively. We made measurements only for arches I–IV; arch V is highly reduced and proved too difficult to measure. Measurements of arches I and II were divided into three subsections following the branchial bones of the arch and are referred to as the superior, middle, and inferior, associated with the epi-branchial, cerato-branchial, and hypobranchial bones, respectively (Fig. 1). This yielded eight arch sections for measurement. For each arch or arch subsection, we measured the length of the associated branchial bone, which we refer to as base length; the length of the raker blades in the middle of the arch or arch subsection, and the mean spacing between branchiospinules.

Macro measurements of base and raker lengths were made with calipers. The first two anterior

TABLE 1. Location, year of collection, and size range of Atlantic menhaden samples used in the analysis of branchial basket functional morphology

Location	Year							Total	Range FL (mm)
	1978	1985	1995	2000	2001	2002	2004		
Hampton Harbor, NH							5	5	74–92
Childs River, MA	5							5	78–89
Peconic River, NY		5						5	77–87
Beaufort, NC				8	1	2		11	109–314
Drum Inlet, NC				6				6	243–287
Hatteras, NC				2				2	272–302
Neuse River, NC			14			2		16	34–326
Salter Path, NC				12				12	116–179
Total	5	5	14	28	1	4	5	62	

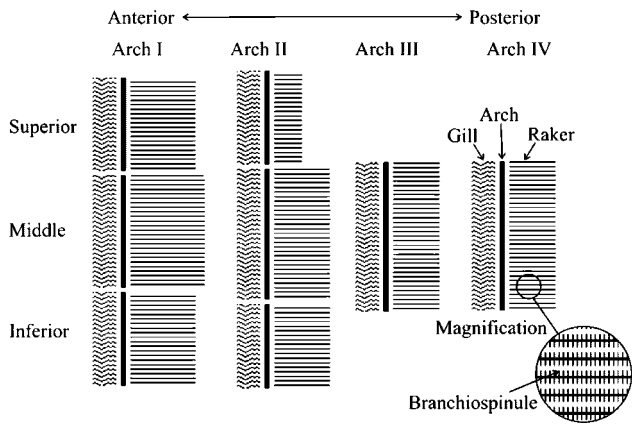


Fig. 1. Gill arch and arch subsections used to characterize the morphology of Atlantic menhaden branchial baskets.

arches were dissected at the epi-ceratobranchial and cerato-hypobranchial joints before the base lengths of the three subsections were measured. The base lengths were measured to the closest 0.1 mm. Since menhaden gill rakers are often damaged, most often by parasites, at least eight complete raker blades were dissected from each arch section and used to determine a mean raker length.

Branchiospinule spacings are submillimeter distances requiring microscopic examination. Menhaden produce copious amount of mucus that is integral to food handling in the branchial basket (Friedland, '85). When the brachial basket tissues are fixed in formalin, mucus on the branchial basket is also fixed, encapsulating the rakers and branchiospinules, thus making it difficult to make measurements. The fixed mucus was stripped from the raker blade with a solution of pancreatin, a common digestive enzyme. A pancreatin solution was made by dissolving the contents of a Twinlab<sup>1</sup> pancreatin capsule containing 500 mg of enzyme in 10 ml of water. The raker blades were soaked in the solution for 0.5–5 hr. Mucous stripping was imprecise so it was necessary to adjust pancreatin solution concentration and soak times accordingly. Cleaned raker blades were stained with alcian blue stain to improve the visibility of the raker structures. The rakers were wet mounted on a glass slide and observed with transmitted light microscopy; branchiospinule spacings were measured with image processing as illustrated in Figure 2. We evaluated the within-blade variability of branchiospinule spacing by taking measurements at three locations along the length of the blade: at the base of the blade or closest to the

<sup>1</sup>Reference to trade names does not imply endorsement.

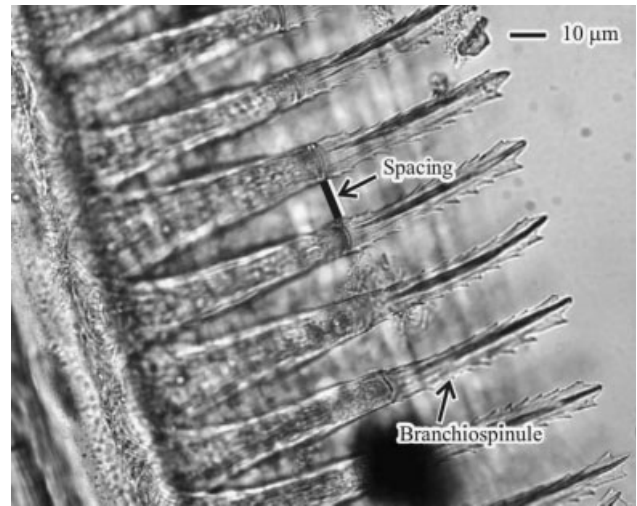


Fig. 2. Micrograph of arch IV raker blade for a 121 mm FL Atlantic menhaden specimen. Spacing bar illustrates distance measured to represent branchiospinule spacing.

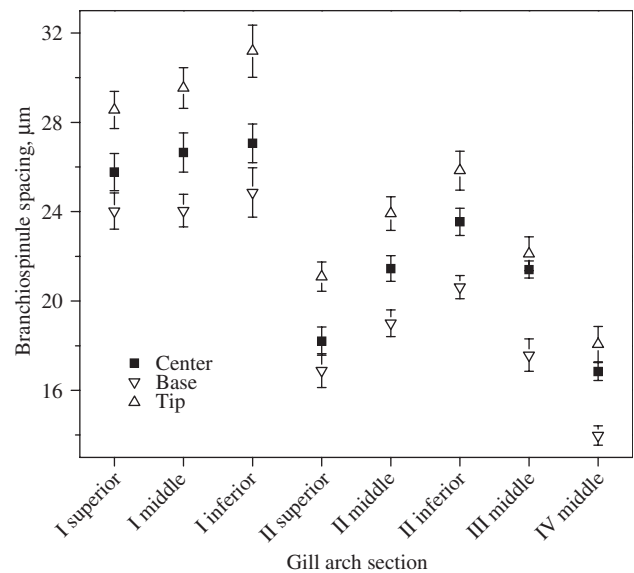


Fig. 3. Branchiospinule spacing at three locations along the gill raker by arch section for a 156 mm FL Atlantic menhaden. Error bars are 95% confidence intervals.

attachment to the gill arch; at the center of the blade; and at the distal tip. Twenty-five spacings were measured from a minimum of three raker blades at each location. Within-blade spacing variability was significant with the narrowest spacings occurring at the base and widest at the tip (Fig. 3, note 95% confidence intervals). We considered the center location representative of the spacings of an individual blade and used that location for all spacing measurements.

Ontogenetic change in branchial basket morphology was evaluated by comparing linear

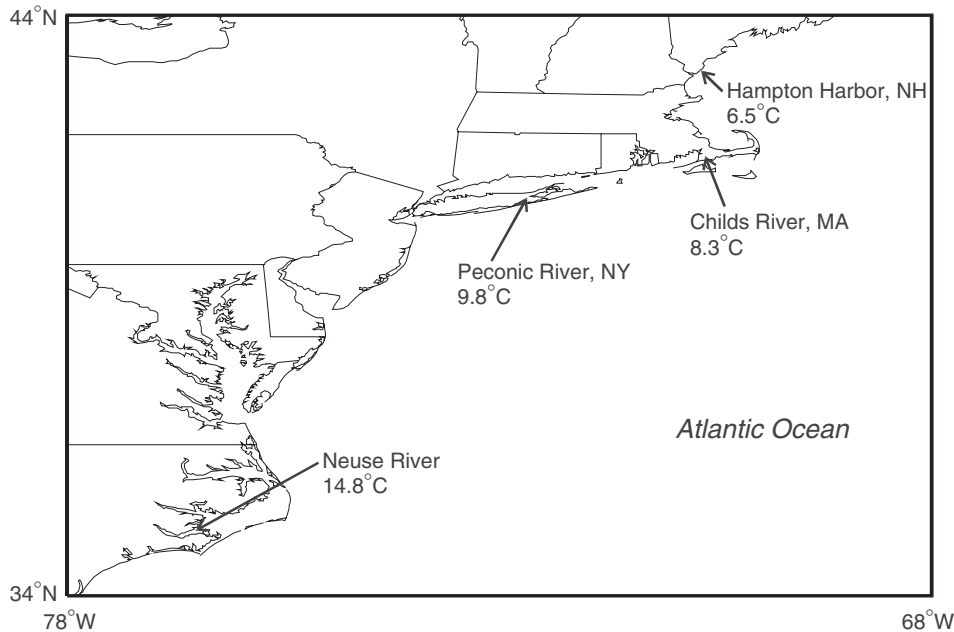


Fig. 4. Map showing location of juvenile sample sites. Average spring low air temperature shown for each location.

and nonlinear model fits. The series of morphology data for juveniles from North Carolina and all adult fish were regressed against fish length. Linear fits were considered indicative of isometric growth and non-linear fits were considered diagnostic of growth allometry (Osse and Van den Boogaart, 2004).

Branchiospinule spacing between juvenile collections was compared to test if there is a geographic gradient in the development of branchial basket traits. The gradient reflects the latitude of the sample location and the assumed differences in thermal regime experienced by juvenile fish (Fig. 4). The four juvenile samples were compared with analysis of covariance over the size range of 74–92 mm FL.

## RESULTS

Base length of menhaden gill arches increased linearly with FL. Base length of the three subsections of arch I are all less than 5 mm in the smallest juvenile fish and increased to over 40 mm in the largest adults (Fig. 5A). The base lengths for the middle sections were longest whereas base lengths of the superior sections averaged 80% of the length of the middle section. The base lengths of the inferior sections averaged 76% of the middle section lengths. The same pattern was observed for the base lengths of arch II (Fig. 5B). The middle section base lengths were

longest, the superior section lengths averaged 74% of the lengths of the middle section, and the inferior section lengths averaged 61% of the middle section. The base lengths for arches III and IV ranged from 5 to 47 mm and 50 mm, respectively (Figs. 5C and D). The most likely sources of error were the dissections separating the arch from the glossohyal and separation at the epi-ceratobranchial joint. Dissection at the glossohyal often resulted in an underestimation of the length of the inferior section. Likewise, dissection at the epi-ceratobranchial joint often caused underestimation of the middle section.

Raker length of menhaden increased linearly with FL. The rakers of arch I were longest of any arch ranging in size from 1.8 to 25.9 mm (Fig. 6A). The raker lengths for the middle section were longest whereas raker lengths of the superior and inferior sections averaged 84% and 91% of the length of the middle section, respectively. A slightly different pattern was observed for the raker lengths of arch II (Fig. 6B). The superior section raker lengths were longest, the middle section lengths averaged 99% of the lengths of the superior section, and the inferior section lengths averaged 59% of the superior section. The raker lengths for arches III and IV had similar ranges of 1–17 mm (Figs. 6C and D).

Branchiospinule spacing showed a non-linear response to increasing FL, suggesting that this anatomical feature was allometric to the growth

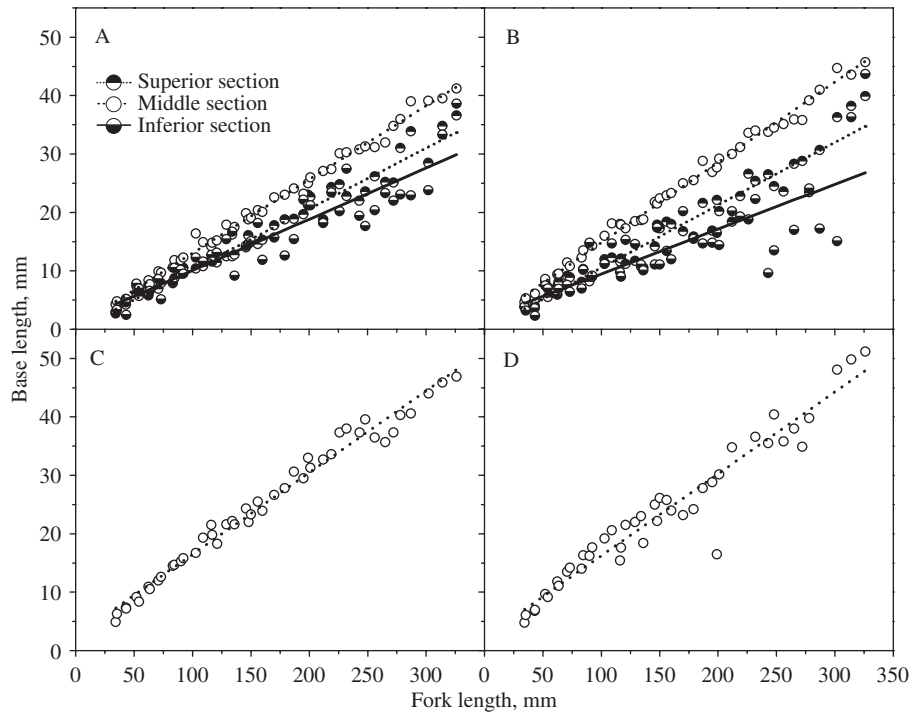


Fig. 5. Base length vs. fork length for arches I (A), II (B), III (C), and IV (D). All curves are linear fits.

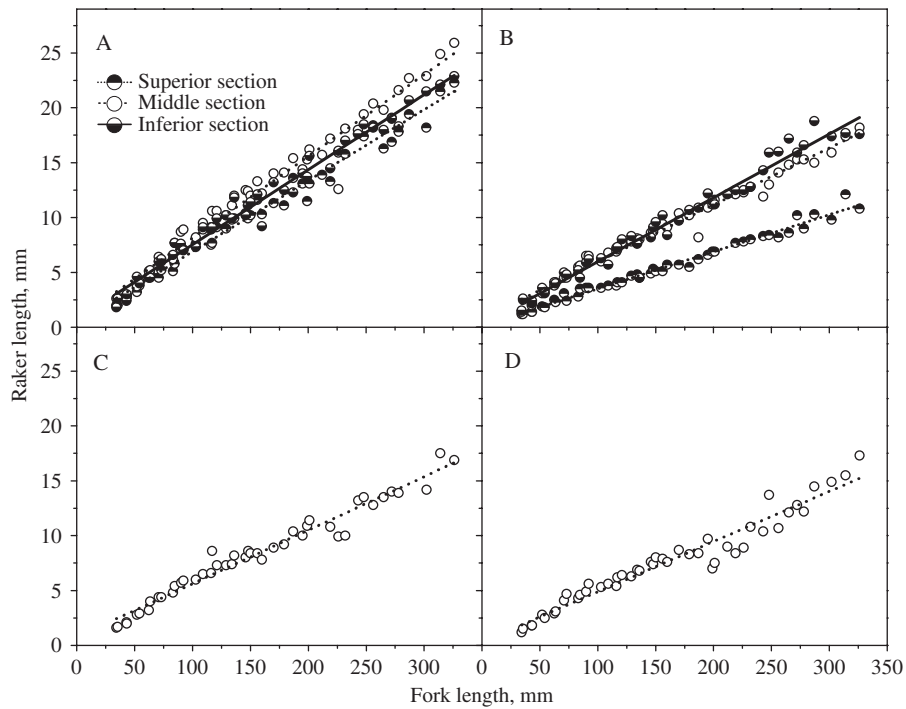


Fig. 6. Raker length vs. fork length for arches I (A), II (B), III (C), and IV (D). All curves are linear fits.

of other parts of the branchial basket. The spacings of arch I were widest of any arch, ranging in size from 12 to 69  $\mu\text{m}$  (Fig. 7A). The spacings for the inferior section were widest, whereas spacings

of the superior and middle sections averaged 83% and 92% of the spacing of the length of the inferior section. The same pattern was observed for the spacings of arch II (Fig. 7B). The inferior section

spacings were widest, the superior section spacings averaged 77% of the spacings of the inferior section, and the middle section spacings averaged 89% of the inferior section. The branchiospinule spacing for arches III and IV have similar ranges of 7–38  $\mu\text{m}$  (Figs. 7C and D). The non-linear responses of branchiospinule spacing to fish length were modeled with Boltzmann curves which provided better fits than linear models (Table 2). The Boltzmann fits also provided estimates of the two inflection points of the

allometry, suggesting the lower transition occurred at approximately 100 mm FL and the upper at approximately 200 mm FL.

From these data we computed two derived parameters related to the feeding dynamics of menhaden. First, we computed mean branchiospinule spacing, weighted by the physical area of respective arch subsections (area as the product of base and raker lengths). The allometry in spacing is preserved in the weighted mean data (Fig. 8). The mean spacing in juveniles was found

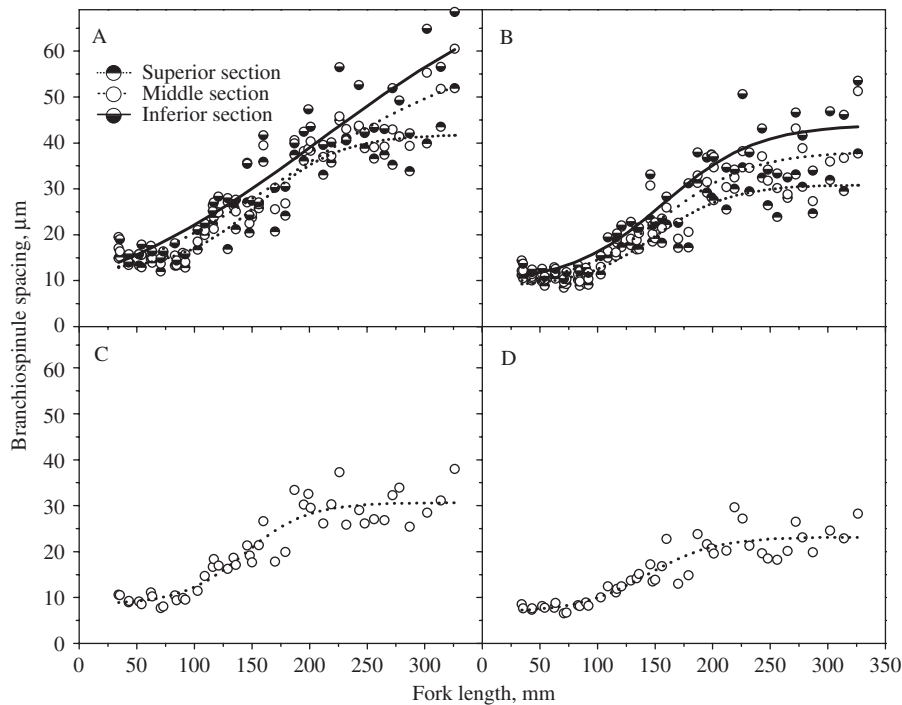


Fig. 7. Branchiospinule spacing vs. fork length for arches I (A), II (B), III (C), and IV (D). All curves are Boltzmann nonlinear fits.

TABLE 2. Regression results for linear and Boltzmann models used to estimate branchiospinule spacing as a function of menhaden fork length

Gill arch section	Linear model $R^2$	Boltzmann model $R^2$	Lower inflection point	Upper inflection point
I superior	0.851	0.881	112	204
I middle	0.885	0.887	54	NE
I inferior	0.877	0.882	64	NE
II superior	0.841	0.883	109	194
II middle	0.836	0.855	104	207
II inferior	0.866	0.883	104	211
III middle	0.819	0.881	109	180
IV middle	0.799	0.846	105	183
Mean			95	196
Mean <sup>1</sup>			107	

Lower and upper inflection points refer to the slope inflections of the Boltzmann curves.

<sup>1</sup>Mean calculated without data for arch sections I middle and I inferior.

NE—no estimate of inflection point within range of data.

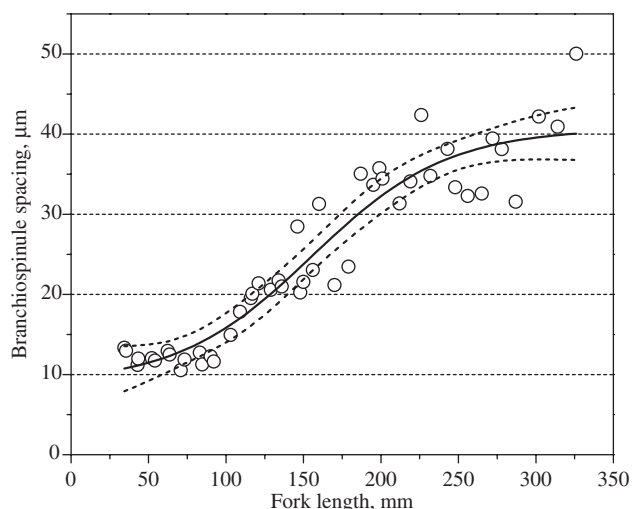


Fig. 8. Mean weighted branchiospinule spacing vs. fork length. Curve is Boltzmann non-linear fit with 95% confidence limit:

$$\text{Spacing} = 40.685 + \frac{-31.806}{1 + e^{(FL-155.507)/43.626}}, R^2 = 0.9$$

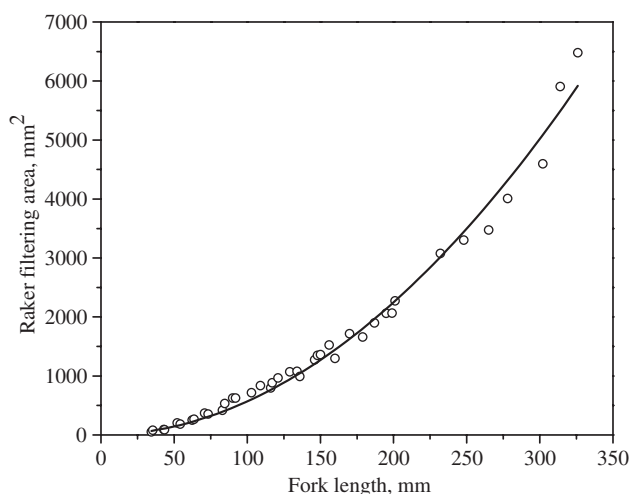


Fig. 9. Raker filtering area vs. fork length. Curve is allometric fit:  $\text{area} = 0.062 \times FL^{1.982}$ ,  $R^2 = 0.986$ .

to be between 10 and 15 µm and increased to an approximate range of 35–45 µm as suggested by the range of the raw data and the confidence interval on the model fit. This provides an integrated depiction of the potential ontogenetic change in filtration efficiency. The second derived parameter is raker filtering area or the sum of the filtering areas of the arch subsections. Not surprisingly, this parameter increases by a power of two and was best fit with an allometric equation (Fig. 9).

TABLE 3. Analysis of covariance results comparing four regional samples of menhaden juvenile, probability (P) of accepting hypothesis of homogeneity of slope and differences in adjusted means

Gill arch section	Treatment by covariate interaction <sup>1</sup>	Treatment adjusted for covariate <sup>2</sup>
I superior	<b>0.170</b>	< <b>0.001</b>
I middle	<b>0.428</b>	< <b>0.001</b>
I inferior	<b>0.819</b>	< <b>0.001</b>
II superior	<b>0.177</b>	< <b>0.001</b>
II middle	0.026	<b>0.003</b>
II inferior	<b>0.269</b>	< <b>0.001</b>
III middle	<b>0.816</b>	<b>0.001</b>
IV middle	<b>0.115</b>	<b>0.002</b>

<sup>1</sup>Bold in this column indicates assumption of homogeneity of slopes is plausible.

<sup>2</sup>Bold in this column indicates treatment adjusted for the covariate is significant.

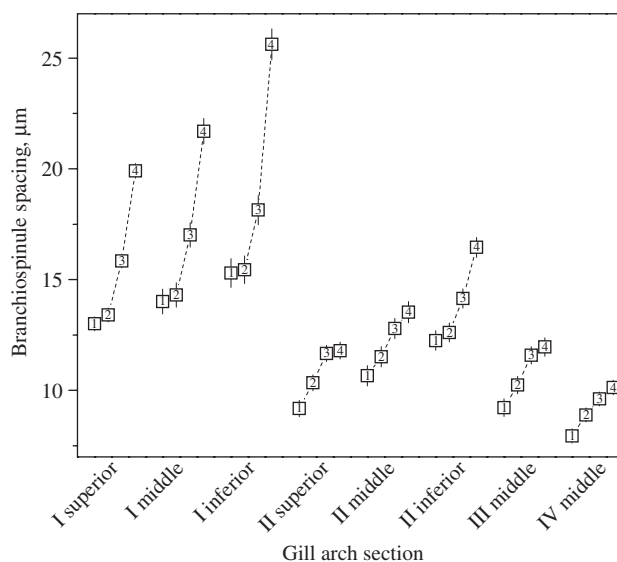


Fig. 10. Adjusted least square mean branchiospinule spacing for each arch section from analysis of covariance. Groups: 1, Neuse River, NC; 2, Peconic River, NY; 3, Childs River, MA; 4, Hampton Harbor, NH. Error bars are standard error of the means.

Branchiospinule spacing in juvenile samples varies spatially with wider spacings associated with more northerly rearing areas and narrower spacings associated with more southerly areas. Spacing was significantly different for all eight raker subsections, with only one subsection, II middle, failing the test for homogeneity of slopes (Table 3). The North Carolina samples had the narrowest spacings with each more northerly



location having progressively wider spacings (Fig. 10).

## DISCUSSION

Menhaden filter feeding efficiency changes allometrically with menhaden size reflecting adaptations related to juvenile and adult resource utilization. Our data suggest that juvenile menhaden retain the ability to filter the smallest fraction of the plankton community during their period of estuarine residency. It is only after the fish emigrate to the ocean and join the adult migratory population that their filtering efficiencies change. The increase in branchiospinule spacing that occurs in the gill rakers must be pivotal to this transition. Plankton communities in the coastal waters are typified by lower concentrations of phytoplankton biomass and a general shift to larger-sized particles, including higher concentrations of zooplankton, than those occurring in estuaries (Hulbert, '63; Malone and Chervin, '79; Muylaert and Sabbe, '99; Sin et al., 2000; Kimmel et al., 2006). Hence, as migratory adults the fish must be able to filter more water to concentrate food, which would be hydrodynamic and energetic burdens if they retained the branchiospinule spacing they had as juveniles.

The second allometric transition is associated with young vs. older adults, which also reflects the range of migration potential between small and large menhaden. Large menhaden migrate earlier in the year and venture farther north than the smaller size components of the population (Ahrenholz, '91). As a consequence, large menhaden are more often feeding in waters in direct competition with other cold-water clupeid filter feeding fish such as American shad, *Alosa sapidissima* (Munroe, 2002), and Atlantic herring, *Clupea harengus* (Gibson and Ezzi, '92). These species particulate and filter feed and are thus less likely to make much use of phytoplankton by direct filtration. The second allometric transition results in menhaden retaining branchiospinule spacing that will filter large phytoplankton, thus it appears to be an adaptation that serves to avoid niche overlap with other filter feeding species. These data suggest that the sequence of morphological development adaptive to the intermediate eco-morphology needs of the species is not limited to allometric change during the early history stages (Keeley and Grant, '97; Gisbert, '99).

Our predictions of filter feeding efficiency from functional morphology are dependent on the

expectation that the morphological measurements we made will correlate with menhaden diet. Key to that assumption is the prerequisite that the anatomical features measured can be interpreted in a functional context (Wainwright and Richard, '95). Parallel arrays of menhaden gill rakers will result in the formation of a sieve by the interdigitations of branchiospinules, thus water being filtered by menhaden will have to pass through some part of the sieve array formed by the branchial basket. We have two benchmarks to compare form and function, those being the two clearing rate experiments on transitional juvenile- and adult-sized menhaden. The interior arches, arches III and IV, have the most closely spaced rakers so they should provide an indication of the minimum size of plankton the fish could retain. With the adults, the branchiospinule spacing should be on the order of 27  $\mu\text{m}$ , thus the detection of significant filtration efficiency by Durbin and Durbin ('75) at this size correlates very well. The transitional juveniles studied by Friedland et al. ('84) would be assumed to have branchiospinule spacings on the order of 16  $\mu\text{m}$  for the interior arches; however, these fish start to show significant particle retention at a threshold just below 10  $\mu\text{m}$ . There are a number of potential explanations for this poor correlation including a reduction in effective pore size of the menhaden feeding sieve caused by a crowding effect of other particles (Friedland et al., '84) or significant retention of particles by means of other than dead-end sieving, such as aerosol filtration of particles on mucus aggregates and crossflow filtration (Drenner et al., '87; Sanderson et al., 2001). This discrepancy should be taken into account if these data are used to develop feeding efficiency curves for a size spectrum of menhaden.

Filtration efficiency has been modeled by a number of researchers using ontogenetic filtration efficiency functions at variance to the findings in this study. Most notable are the studies by Luo et al. (2001) and Brandt and Mason (2003) which use an exponential curve to model a change in filtration efficiency with size in juvenile menhaden. Our data negate this assumption and suggest filtration efficiency may be best considered constant over the span of juvenile-sized fish. However, the allometric changes in filtration efficiency would be an important feature to capture in grazing models of adult fish (Durbin and Durbin, '98; Macy et al., '99), especially if they model feeding around the size range associated with the second allometric inflection.

Juvenile menhaden residing in estuaries may have a more dominant influence on the succession of various phytoplankton species and size distributions along estuarine gradients than previously considered. The effect of filter feeding fish on plankton communities (Drenner et al., '84) and the trophic cascade effects when filter feeding fish not only compete with other filter feeding species but also prey upon them (Lu et al., 2002) can be significant. The branchiospinule spacing data suggest that juvenile menhaden have feeding sieve apertures that are on the order of one half the size of the transitional juveniles characterized with clearing rate data (Friedland et al., '84). What does this portend about the filtration efficiency on various plankton size fractions for juvenile fish? Over the size range of nanoplankton, transitional juveniles retained plankton particles at efficiencies as high as 40%; on face value, the functional morphology relationship between juveniles and transitional juveniles suggests that the juveniles may be able to retain nanoplankton with efficiencies twice as high as the transitional juveniles and may be able to retain significant amounts of picoplankton.

The latitudinal cline in branchiospinule spacing shows that this morphological trait can vary among regional groups of menhaden; however, we cannot conclude if this is due to regional genetic divergence or an environmentally induced difference in a meristic trait. Though Atlantic menhaden is viewed as a single biological population, the appearance of meristic and morphometric variation has suggested that more than one population may exist (June, '58; Epperly, '89). Alternatively, the spacing of branchiospinules is a function of the rate of their formation along the gill raker as it increases in length. It is generally recognized that environmental factors such as temperature can influence meristic characters and that the traits are often sensitive to environmental effects during restricted periods of development (Barlow, '61). We recognize that our samples were inadequate to fully test these competing hypotheses. But in either case, the variation in the trait serves to locally adapt feeding among regional juvenile populations.

If the trait is adaptive, it would be expected to confer a locally adapted feeding advantage to the juvenile menhaden recruited to estuaries found at differing latitudes, thus we would expect that filter feeding in northern estuaries is keyed to larger cell size phytoplankton and perhaps higher concentrations of zooplankton. The summer nur-

tery season in northern estuaries will be shorter; therefore, as has been seen with other species, northern populations often have to maintain higher growth rates in the northern part of their range to successfully recruit (Conover and Present, '90). The general trend in the plankton communities ordered by latitude suggests they are less species rich (Jeffries, '64; Dolan and Gallegos, 2001; Woodd-Walker et al., 2002), but it is not clear whether phytoplankton and zooplankton follow Bergmann's rule of larger body size with increasing latitude (Casanova, '81; Stelzer, 2002).

A consequence of recent shifts in juvenile recruitment of Atlantic menhaden may be a concomitant shift in the feeding ability of adult fish and thus a population level change in foraging and habitat preferences along the coast. Recent assessments of Atlantic menhaden (ASMFC, 2004) show that with the decline in juvenile recruitment to the estuaries of Virginia and North Carolina, there has also been an increase in recruitment to estuaries in the northern part of the range. Juvenile recruits from northern estuaries would be expected to have wider spaced branchiospinules through their lifetime, and thus would be expected to forage and distribute differently than recruits reared in southern estuaries. Assessment of spawning patterns and local distribution should take into account the effect foraging may have on habitat selection by the fish.

## ACKNOWLEDGMENTS

We thank M. Dionne for the provision of samples and the NOAA Chesapeake Bay Office for supporting this research.

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