FOOD OF YOUNG ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*, IN RELATION TO METAMORPHOSIS

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ABSTRACT

To rear this species in captivity required knowledge of the kinds of organisms it ate. Larvae ate zooplankton (copepods), but prejuveniles and juveniles fed chiefly on phytoplankton. There were similarities as well as differences between the alimentary tract contents of the fish and the composition of the plankton community. Changes in food habits during metamorphosis were accompanied by gross morphological changes in the alimentary tract and related structures. Laboratory studies of larvae disclosed that their failure to feed at low light intensities, their digestion rate, and their defecatory response to capture and preservation probably contributed to the high incidence of empty alimentary tracts in field collections.

Laboratory research is needed to determine how specific environmental factors affect the distribution, behavior, and survival of young Atlantic menhaden (*Brevoortia tyrannus*) after their entry as larvae into estuarine nurseries from oceanic spawning grounds (June and Chamberlin, 1959). Before these young fish can be successfully maintained in the laboratory, it is necessary to know their diet requirements.

Previous investigators established that young Atlantic menhaden feed on plankton. Peck (1894) observed that stomach contents of juveniles (60 and 100 mm. long) collected near Woods Hole, Mass., closely agreed with the plankton in the surface waters. He also described the specialized gill rakers that this fish uses to strain minute organisms from the water. Using radioisotope techniques, Chipman (1959) determined that larvae were unable to filter phytoplankton, but fed on larval brine shrimp and on copepods. Juveniles (averaging 188 mm. long), on the other hand, could filter phytoplankton cells (*Nannochloris*) as small as 2 μ. Richards (1963a, 1963b) found crustaceans (chiefly *Balanus* larvae, *Neomysis*, and the copepods *Centropages, Paracalanus, Acartia*, and *Temora*) to be the principal food of 29 specimens (16–120 mm. long) from Long Island Sound, N.Y. She reported no differences in stomach contents of fish of different sizes.

None of the earlier investigators clearly identified the changes in composition of diet associated with the transformation of Atlantic menhaden larvae into juveniles.[3] Because our principal aim was to establish techniques for rearing laboratory stocks of these young fish through metamorphosis for experimental purposes, we needed to know their food requirements at the different developmental stages and the suitability of substitute foods. Moreover, in connection with studies of the estuarine ecology of young menhaden in progress in Indian River, Del. (June, 1957), it was essential to know their natural foods so as to assess the relevant components of the plankton. Finally, changes in morphology of the digestive system that enable juveniles to feed on smaller

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[3] We follow the definitions of Mansueti and Hardy (1967). Larva: The stage of development between hatching and attainment of the adult fin-ray complements; our specimens ranged from 13 to about 30 mm. fork length. Prejuvenile: The intermediate stage between larval and juvenile form; these ranged from about 30 to 40 mm. fork length. Juvenile: Young fish after attainment of full adult counts and before sexual maturation; the stage begins when the body form closely approximates that of the adult and in our specimens occurred at about 40 mm. fork length.

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plankters than larvae had not been previously described. Most of our research on these subjects was done at the former Field Station of the BCF (Bureau of Commercial Fisheries) at Millville, Del., in 1960 and 1961.

STUDIES OF ALIMENTARY TRACT CONTENTS AND PLANKTON COMPOSITION

We determined the natural foods of young Atlantic menhaden by examining the alimentary tract contents of wild specimens. Analysis of concomitant plankton samples enabled us to compare the organisms available and those actually ingested.

MATERIALS AND METHODS

Alimentary tracts of 738 young menhaden were examined for food. Of this number, 592 came from larvae chosen at random from catches made with 1-m.-diameter nylon plankton nets (mesh aperture 0.90 mm.) in the mouth of Indian River, Del., between November 1960 and May 1961 (table 1). The rest came from larvae, prejuveniles, and juveniles captured by haul seines within this estuary from April to June 1961 (table 2).

Preservation techniques varied with the size of the fish and character of the alimentary tract contents. Larvae were preserved intact in 5 percent Formalin[4] buffered with borax. The alimentary tract from most prejuveniles and juveniles was removed, slit longitudinally, and preserved in a chrom-osmic mixture (Gray, 1954); some tract contents were only chilled prior to examination.

The fraction and portion of the tract contents examined also varied with the developmental stage of the fish. The alimentary tract of larvae was opened, the percentage fullness estimated, and the location of contents within the tract noted. Organisms were removed, identified, counted, and measured; and the relative volume of each item was estimated. With prejuveniles and juveniles, only the contents of the esophagus and anterior stomach were examined, because we could recognize few organisms

[4] The use of trade names in this publication does not imply endorsement of commercial products.

TABLE 1.—*Samples of Atlantic menhaden larvae for food studies collected in plankton nets at Indian River Inlet, Del., November 1960 to May 1961*

Date	Time of collection	Larvae examined	Alimentary tracts containing food		Mean number of organisms per tract containing food	Fork length of larvae with food		Sky condition at time of collection
						Range	Mean	
		Number	*Number*	*Percent*	*Number*	*Mm.*	*Mm.*	
1960								
November 7	0855–0955	30	18	60	4	19–25	22.3	Clear
29	0325–0425	11	0	0	0			Obscured by dense fog
December 2	1810–1910	11	1	9	3	32		Clear (dark); followed by rising full moon
6	0840–0940	2	2	100	5	26–28	27.0	Obscured by clouds
8	2155–2255	5	1	20	2	30		Partly cloudy
12	1325–1505	56	46	82	2	24–32	28.3	Do.
16	1725–1825	40	18	45	2	23–30	27.3	Clear (dark)
19	1910–2010	54	32	59	5	24–29	26.8	Do.
20	0155–0255	53	9	17	2	24–30	26.6	Clear
20	0730–0840	14	0	0	0			Partly cloudy
22	2140–2240	9	7	78	3	26–34	28.6	Clear; ¼ moon
28	0235–0335	50	14	28	3	23–29	27.4	Clear; ¾ moon
28	0910–1010	3	2	67	2	26–28	27.0	Partly cloudy
28	1517–1617	21	13	62	5	23–29	26.0	Do.
28	2130–2230	18	6	33	3	23–27	25.7	Do.
30	1730–1830	55	35	64	3	23–28	26.2	Clear; full moon
1961								
January 2	1900–2000	46	22	48	3	22–28	26.0	Do.
3	0040–0140	5	1	20	2	21		Do.
3	0655–0755	48	7	14	1	23–28	25.7	Clear
16	1755–1855	5	2	40	1	27–29	28.0	Clear (dark)
16–17	2355–0055	6	1	17	1	25		Clear
17	0630–0730	7	2	28	2	24	24.0	Do.
May 9	0235–0335	43	4	9	1	28–30	29.0	Do.
Total		592	243		3	19–34		

TABLE 2.—*Samples of Atlantic menhaden larvae, prejuveniles, and juveniles for food studies collected in haul seines within the Indian River estuary, Del., April to June 1961*

Date	Number of alimentary tracts examined	Alimentary tracts containing food	Fork length of fish with food	
			Range	Mean
		Number	*Mm.*	*Mm.*
April 27	20	7	30–37	33.7
June 5	45	44	28–46	35.9
20	10	10	65–94	81.0
23	27	27	33–75	57.7
23	10	10	75–90	83.8
30	26	15	68–75	71.9
30	8	4	68–78	73.5
Total	146	117	28–94	

in the pyloric stomach (gizzard) and intestine. Identifiable contents were treated in the same manner as the contents of the alimentary tracts of the larvae. Diatoms were cleared by the Van Der Werff (1955) method and mounted in hyrax before examination.

Concomitant plankton samples were usually taken for each fish collection. Zooplankton was collected with a high-speed sampler described by Miller (1961) and monofilament nylon net (mesh aperture 0.24 mm.). Most samples were preserved in 5 percent buffered Formalin. Phytoplankton was collected in a 140-ml. water sampler and preserved with the chrom-osmic mixture used for contents of alimentary tracts. Some zooplankton and phytoplankton samples were only chilled prior to examination. Organisms in aliquots of preserved and fresh plankton samples were identified, counted, and measured. Diatoms, when present, were cleared (Van Der Werff, 1955) and mounted in hyrax.

FOOD OF MENHADEN AND RELATIONS TO ESTUARINE PLANKTON

We took samples at the inlet and within the estuary.

Samples at the Inlet

The contents of the alimentary tracts of larvae consisted of zooplankton. Of 592 tracts examined, 349 (59 percent) were empty. Of the 243 that contained food, 52 percent were less than one-quarter full, 28 percent were about half full, and 20 percent were over half full. The contents were 99 percent copepods, of which *Centropages* was the most common of those identified (table 3). The number of food organisms averaged 3 per alimentary tract, but varied between 1 and 12. Composition of tract contents showed no apparent changes during the sampling period.

The size of copepods ingested varied widely (0.65–2.00 by 0.16–0.65 mm.) but generally increased with fish length (fig. 1). *Pseudodiaptomus* was the only copepod found in larvae under 23 mm. long. *Centropages* occurred in larvae 23 mm. and longer, whereas *Acartia* and *Temora* were found in specimens from 24 to 30 mm. long.

TABLE 3.—*Alimentary tract contents of 243 Atlantic menhaden larvae collected at Indian River Inlet, Del., November 1960 to May 1961*

Food item	Alimentary tracts containing organisms	Mean number of organisms per tract	Total tract contents	Size of organisms			
				Range		Mean	
				Length	Width	Length	Width
	Number	*Number*	*Percent*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Zooplankton							
Copepoda							
Centropages	72	<1	18.7	0.85–2.00	0.30–0.65	1.29	0.41
Acartia	26	<1	9.5	0.85–1.58	.24–.60	1.28	.38
Pseudodiaptomus	15	<1	6.7	0.65–1.20	.16–.35	1.07	.31
Temora	6	<1	1.6	1.20–1.48	.48–.52	1.34	.50
Tortanus	2	<1	0.2	1.70	.54	1.70	.54
Unidentified copepods	189	2	62.3				
Total copepods	238	3	99.0				
Pelecypoda	7	<1	0.8	0.37–0.46	.30–.37	0.40	.34
Phytoplankton							
Centrales							
Coscinodiscus	1	<1	0.1	0.22			
Unidentified organic material	2						

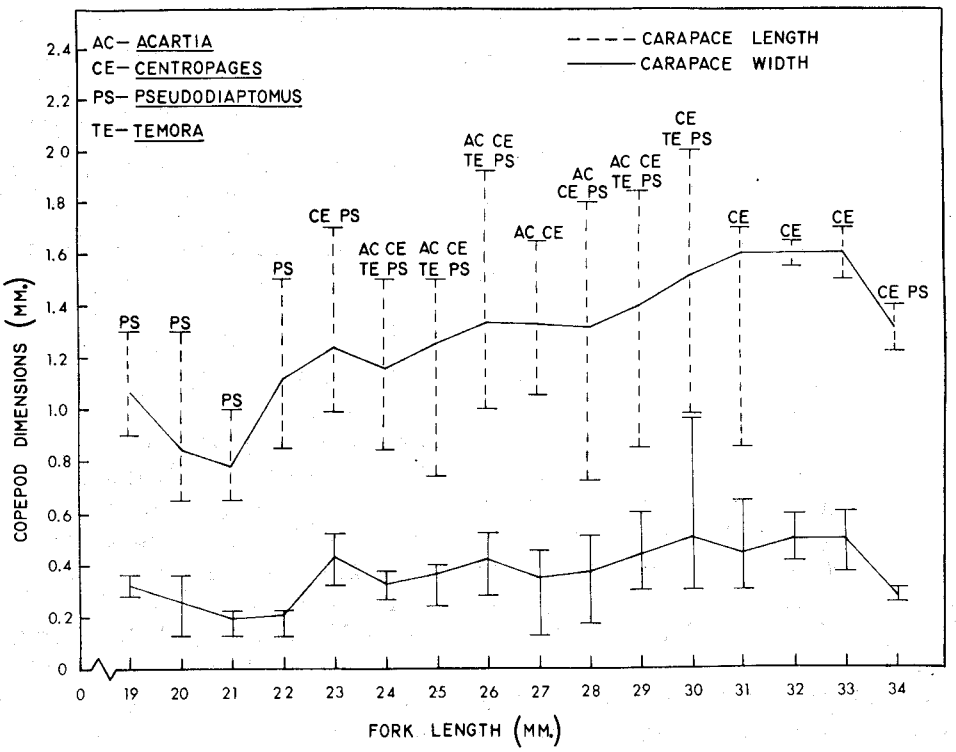

FIGURE 1.—Size of copepods ingested in relation to fork length of Atlantic menhaden larvae. Range of copepod dimensions shown by vertical lines; mean length and width shown by trend lines.

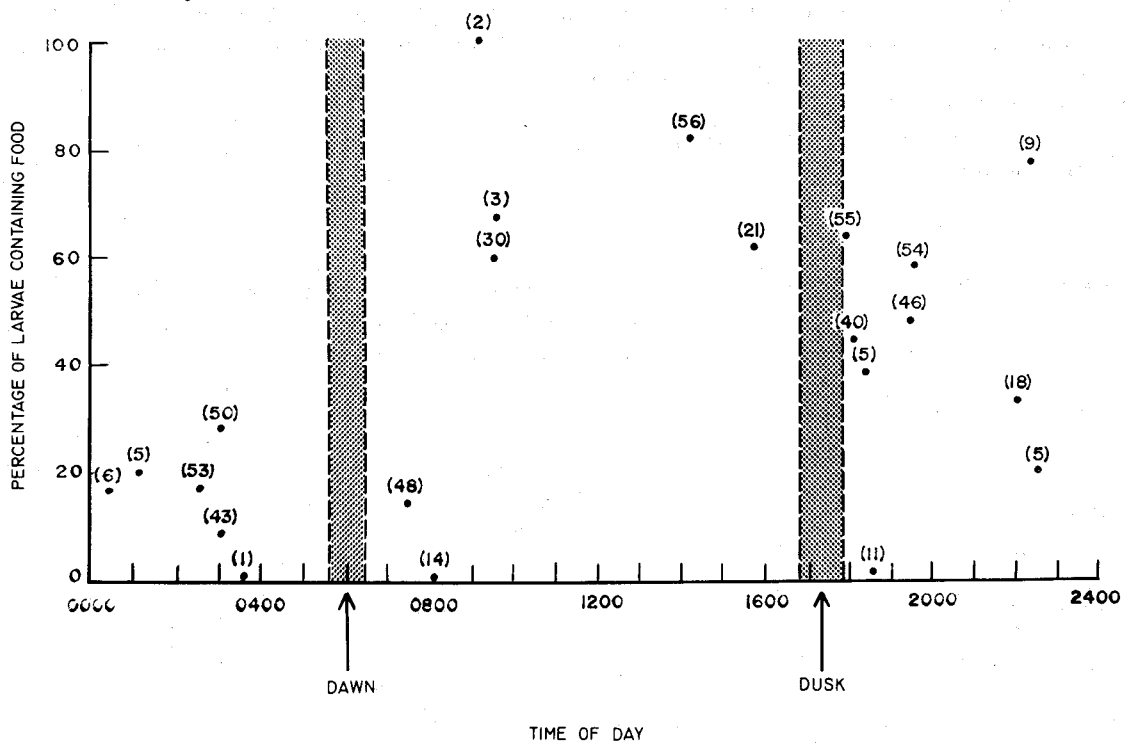

FIGURE 2.—Scatter diagram showing the relation between the number of alimentary tracts of Atlantic menhaden larvae containing food and time of collection. Number of larvae examined shown above each dot.

Percentages of larvae with food organisms in the alimentary tracts were generally higher in daylight and evening (fig. 2). Feeding activity tended to be higher on moonlit nights than on dark nights (50 percent of the larvae caught on moonlit nights contained food compared with 31 percent on dark nights).

The composition of the net plankton and the alimentary tract contents of larvae showed similarities and differences. For example, copepods accounted for 98 percent of the net zooplankton and 99 percent of the tract contents (table 4). Four genera, *Centropages, Acartia, Pseudodiaptomus,* and *Temora,* were common to both the net zooplankton and the alimentary tract contents, but their order of rank differed. With the exception of the single sample collected in May, in which the genus *Temora* predominated, *Acartia* consistently was the most abundant organism in the net zooplankton. Pelecypods were rare in both the net samples and the alimentary tracts.

Centrate diatoms dominated the phytoplankton numerically in 10 samples taken at random throughout the sampling period (table 5). Of all larval alimentary tracts examined, only one contained a single phytoplankter, *Coscinodiscus.*

Samples Within the Estuary

The contents of the alimentary tracts of larvae and smaller prejuveniles consisted of zooplankton, but changed to phytoplankton and unidentifiable material in larger prejuveniles and juveniles. Only 29 (20 percent) of the tracts examined were empty. As was found in the inlet collections, the tract contents of larvae consisted exclusively of copepods (chiefly *Acartia*). The contents of progressively larger prejuveniles gradually shifted from copepods to a mixture of greenish brown amorphous material, diatoms, and flagellates (fig. 3), and at least 80 percent (by volume) of the tract contents of juveniles consisted of these latter items. Diatom genera identified, in order of their frequency of occurrence, were *Pleurosigma, Navicula, Nitzschia, Cyclotella, Melosira, Amphora, Gyrosigma,* and *Surirella.* Flagellates identified included *Peridinium, Gymnodinium,* and *Polykrikos.*

The composition of the plankton resembled the contents of the alimentary tracts examined for the size range of fish sampled. Copepods, chiefly *Acartia,* accounted for nearly 100 percent (by volume) of the net zooplankton after

TABLE 4.—*Composition of fauna in 23 tow-net samples taken concomitantly with collections of Atlantic menhaden larvae at Indian River Inlet, Del., November 1960 to May 1961*

Organisms	Samples containing organisms	Mean number of organisms per cubic meter	Percentage of total organisms	Size of organisms			
				Range		Mean	
				Length	Width	Length	Width
	Number	*Number*	*Percent*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Chaetognatha	19	3	<0.1	4.50–14.60	0.22–0.75	9.41	0.46
Copepoda							
Acartia	23	2,228	55.6	0.89– 1.55	0.26–0.37	1.20	.33
Temora	10	2,194	23.8	1.40– 1.76	0.40–0.59	1.49	.50
Centropages	23	457	11.4	0.88– 1.92	0.30–0.58	1.51	.43
Pseudodiaptomus	20	312	6.8	1.09– 1.85	0.28–0.68	1.36	.40
Tortanus	4	3	<0.1	1.68– 1.96	0.44–0.65	1.85	.51
Labidocera	4	23	0.1	2.07– 2.75	0.45–0.74	2.43	.64
Rhincalanus	2	1	<0.1	3.03	0.52		
Eucalanus	1	<1	<0.1	2.25	0.60		
Unidentified nauplii	2	4	<0.1	0.81	0.30–0.37		.33
Ostracoda	3	1	<0.1	0.63– 1.18	0.37–0.48	0.85	.43
Malacostraca							
Mysidacea	21	92	2.1	2.55– 6.75	0.30–1.50	5.87	.63
Isopoda	7	1	<0.1	1.80–21.00	0.68–7.00		
Decapoda	13	3	<0.1	1.32–52.00	0.30–1.80		
Amphipoda	9	3	<0.1	1.32– 5.70	0.31–1.50	3.55	.63
Pelecypoda	8	6	<0.1	0.36– 1.20	0.20–0.60	0.65	.38
Miscellaneous	13	5	<0.1	0.36– 5.25	0.35–0.90		

TABLE 5.—*Composition of phytoplankton in 10 water samples taken concomitantly with collections of Atlantic menhaden larvae at Indian River Inlet, Del., November 1960 to May 1961*

Organisms	Samples containing organisms	Estimated mean number of organisms per liter	Percentage of total
	Number	*Number*	*Percent*
Pennales			
Nitzschia	2	372	0.4
Pleurosigma	6	559	1.9
Gyrosigma	1	293	0.2
Navicula	3	398	0.7
Diploneis	2	186	0.2
Cocconeis	2	132	0.2
Achnanthes	3	657	1.1
Thalassiotrix	8	1,310	6.1
Asterionella	7	783	3.2
Centrales			
Bellerochea	1	483	0.3
Biddulphia	1	500	0.3
Corethron	1	426	0.2
Rhizosolenia	1	2,909	1.7
Actinoptychus	6	775	2.7
Coscinodiscus	9	3,403	17.8
Thalassiosira	7	2,560	10.4
Cyclotella	5	942	2.7
Skeletonema	8	8,689	40.3
Melosira	7	672	2.7
Diatoms other than above genera	6	1,525	5.3
Peridiniales			
Peridinium	2	1,525	0.3
Prorocentrales			
Gyrodinium	2	459	0.3
Prorocentrum	1	237	0.1
Exuviella	1	237	0.1
Unidentified flagellates	2	604	0.7

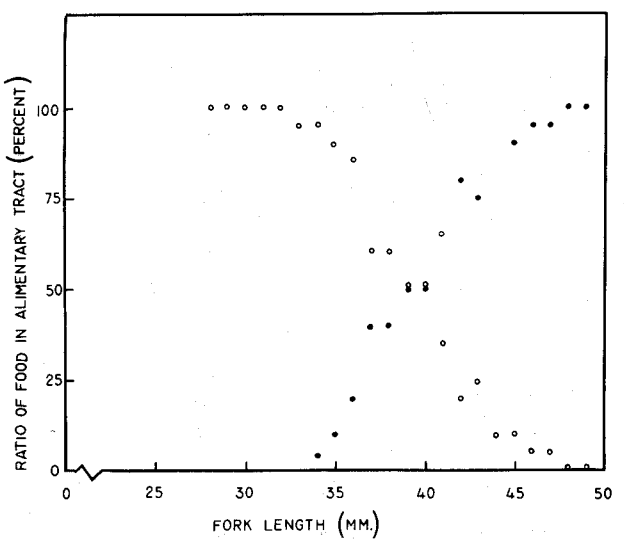

FIGURE 3.—Volume ratio of copepods and amorphous food material (chiefly phytoplankton) in alimentary tracts of young Atlantic menhaden in relation to fork length. Open circles represent copepods and solid circles amorphous material.

removal of the ctenophores, *Pleurobrachia* and *Mnemiopsis*, from the samples. Phytoplankton consisted of naked and thecate flagellates (mainly *Polykrikos*, *Peridinium*, and *Gymnodinium*), and diatoms (chiefly *Pleurosigma* and *Coscinodiscus*). Similarities between the color and form of the greenish brown materials found in the alimentary tracts of the fish and the fragile flagellates in water samples suggested to us that the amorphous residue was the remnants of these organisms.

Our studies of the natural food of young Atlantic menhaden confirmed that they are plankton feeders. As larvae they feed only on zooplankton but during metamorphosis they increase their capability to retain smaller phytoplankters. During its early life stages, this fish directly utilizes the abundant standing crops of both phytoplankton and zooplankton in estuaries. No other marine fish now occupies this ecological role in Atlantic Coast estuaries.

The occurrence of young Atlantic menhaden within the Indian River estuary appeared to be associated with the seasonal cycle of plankton production. Our highest catches of larvae at the inlet were made in December and January (69 and 66 larvae per tow, respectively, as compared with 0 to 9 per tow in other months) and coincided with the maximum monthly catches of each of the four dominant copepods represented in our net samples (*Centropages*, *Acartia*, *Pseudodiaptomus*, and *Temora*). Metamorphosis of menhaden larvae began in April 1961 and followed a phytoplankton flowering in this estuary in late March. Jeffries (1964) also found that the occurrence of Atlantic menhaden larvae in Raritan Bay coincided with the seasonal peak of *Acartia tonsa* in that locality. Apparently, seasonally abundant estuarine populations of copepods (Deevey 1956, 1960) provide an available food supply for the carnivorous larvae when they enter the estuary, and high standing crops of phytoplankton (Riley, 1967) are available during and following the metamorphosis of larvae into juveniles within the estuary.

STUDIES OF MORPHOLOGICAL CHANGES DURING METAMORPHOSIS OF YOUNG MENHADEN

As Atlantic menhaden larvae transform into juveniles, they acquire scales, fin-ray complements, and the deep body form characteristic of adults (Mansueti and Hardy, 1967). The shift from a carnivorous to an omnivorous diet during metamorphosis suggests that changes also take place in structures directly concerned with feeding and digestion.

MATERIALS AND METHODS

Changes in the morphology of structures associated with feeding and digestion were described from counts or measurements as a function of fish length. The counts or measurements were made on 196 specimens, 19 to 75 mm. long, from the samples of fish used for the food studies and included the following:

Dentary teeth: Total along margin of left dentary.

Fork length: Distance (1.0 mm.) from tip of mouth to end of median rays in caudal fin.

Gape height: Distance (0.1 mm.) between inner margins of premaxillary and dentary symphyses with jaws opened to a 65° angle.

Gape width: Distance (0.1 mm.) between inner margins of jaw angles opened to a 65° angle.

Gill rakers: Total, including rudiments, along first left gill arch.

Length of the anterior alimentary tract: Distance (0.1 mm.), with tract extended, between posterior margin of pharynx and the pylorus.

Length of the posterior alimentary tract: Distance (0.1 mm.), with tract extended, between the pylorus and anus.

Maxillary teeth: Total along margin of left maxillary.

Pyloric caeca: Total evaginations at juncture of anterior and posterior alimentary tracts.

DEVELOPMENT OF THE DIGESTIVE SYSTEM IN RELATION TO DIET

We studied morphological changes in the mouth, teeth, gill rakers, alimentary tract, and pyloric caeca during metamorphosis and related these changes to the diet.

Mouth

The terminal mouth of the Atlantic menhaden larva has an elliptical opening and is relatively large through later stages of development (fig. 4). A median notch is present on the upper jaw of larvae over 19 mm. long, and the lower jaw is included in the upper one. The mouth opening in 19-mm. larvae is about 1 mm.^{2}; it increases to a maximum of about 7 mm.^{2} in prejuveniles and reaches about 20 mm.^{2} in 75-mm. juveniles. Because gape height and width increase linearly with length of the fish (fig. 5), the maximum dimension

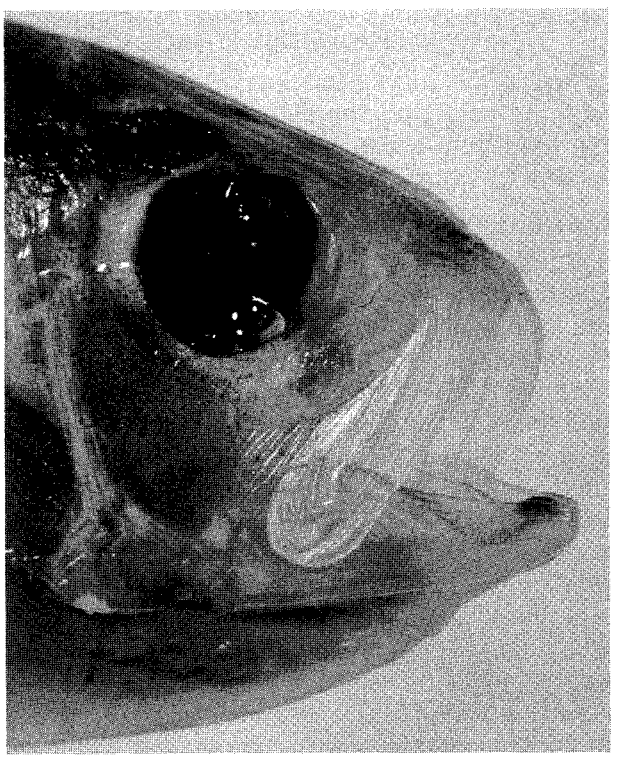

FIGURE 4.—Lateral view of the head of a 75-mm. (fork length) juvenile Atlantic menhaden showing the gape and the median notch on the upper jaw.

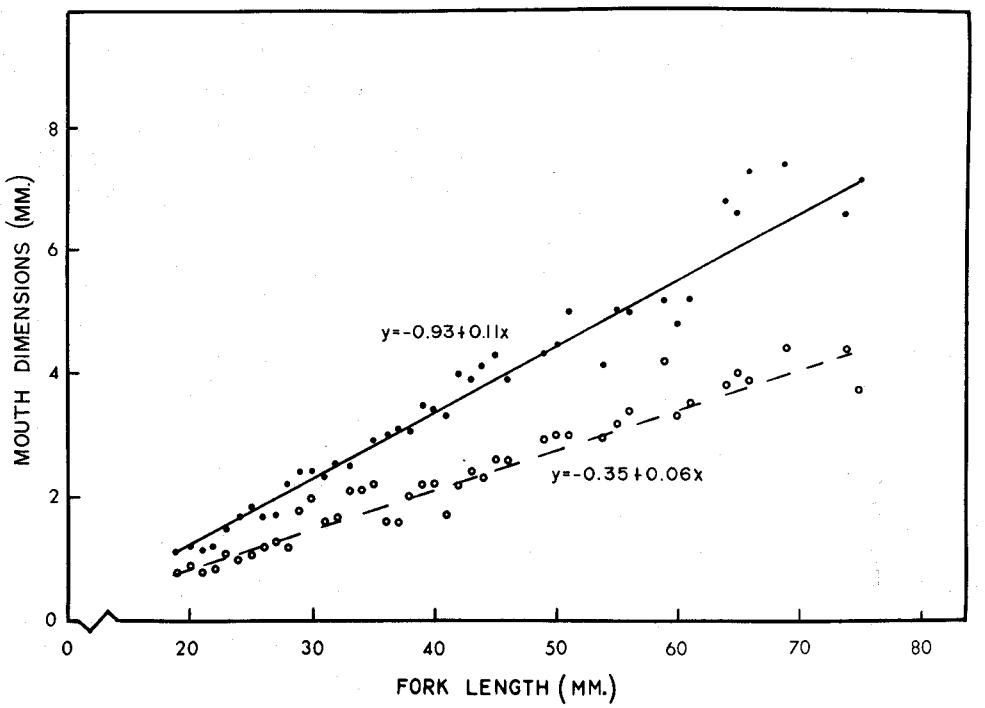

FIGURE 5.—Regression of gape height (solid circles) and gape width (open circles) on fork length of young Atlantic menhaden. Circles represent means of a group of measurements; regression lines were computed from measurements of 124 fish.

of organisms that the fish might ingest would increase from about 0.6 mm. in a 19-mm. larva to about 7.0 mm. in a 75-mm. juvenile.

Teeth

Teeth are prominent in larvae but largely absent in juveniles. Maxillary teeth of larvae are in a single row on the anterior margin of the bone (table 6). Each tooth is 30 to 40 μ long, irregularly shaped, but usually pointed, and has a wide base (fig. 6). These teeth increase in number in prejuveniles, become partially embedded in tissue, and form two or three overlapping rows on the flank of the maxillary. After metamorphosis, maxillary teeth apparently are nonfunctional and eventually disappear.

Dentary teeth occur as slightly recurved conical projections, each 25 to 30 μ long, on the medial anterior edge of the bone (fig. 7). These teeth are conspicuous in larvae and prejuveniles but disappear in juveniles (table 6).

Specialization of the mouth structures in relation to actual food consumed by young Atlantic menhaden is indicated. The large terminal mouth and recurved marginal teeth in larvae are adapted for the capture and retention of zooplankters. Dentition would seem to be

TABLE 6.—*Tooth counts of young Atlantic menhaden*

Fork length	Teeth on left side	
	Maxillary	Dentary
Mm.	*Number*[1]	*Number*[1]
19	12	4
20	13	4
21	16	4
22	16	4
23	20	4
24	20	4
25	16	4
26	18	4
27	17	4
28	22	4
29	21	4
30	24	4
31	25	4
32	25	4
33	27	4
34	25	4
35	24	4
36	26	3
37	28	2
38	24	2
39	23	2
40	25	1

[1] Average of counts on two specimens.

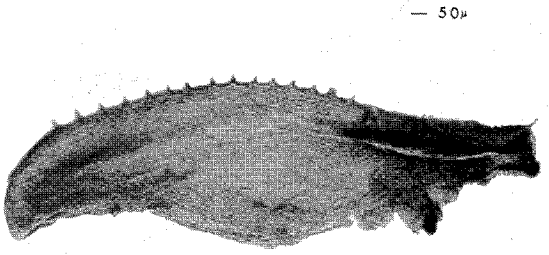

FIGURE 6.—Exterior view of left maxillary bone of a 22-mm. (fork length) Atlantic menhaden larva showing the single row of teeth; posterior end on left.

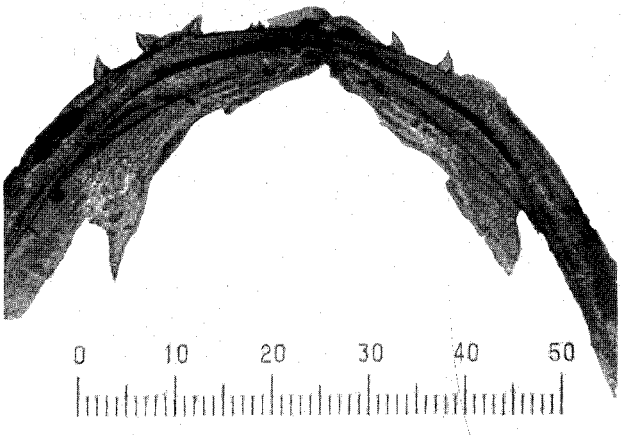

FIGURE 7.—Top interior view of dentary bones of a 22-mm. (fork length) Atlantic menhaden larva showing the single row of teeth (1 division=50 μ).

superfluous for ingesting the smaller organisms that compose the phytoplankton; dentition becomes nonfunctional after metamorphosis.

Gill Rakers and Accessory Structures

During metamorphosis the gill rakers increase in length, number, and complexity. In larvae under 25 mm. long the lower limb (consisting of the hypobranchial and the ceratobranchial segments) and the upper limb (epibranchial segment) are slightly curved. Rakers initially form as rounded protuberances at the angle between the upper and lower limbs (fig. 8); those of the lower limb appear first. Two

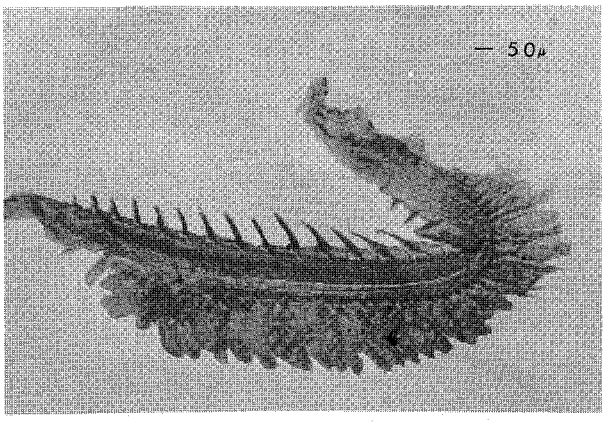

FIGURE 8.—First left gill arch of a 20-mm. (fork length) Atlantic menhaden larva showing the rudimentary rakers on the upper and lower limbs.

rows of barbs appear along the longitudinal axis of individual rakers. As fish increase in length, the rakers become distinctly elongate. Barbs increase in number, become slightly curved, and ultimately develop a serrate tip (fig. 9). The hypobranchial segment of the first gill arch becomes more curved anteriorly; rakers continue to form at the anterior ends of the epibranchial and hypobranchial segments, while those near the angle on the upper

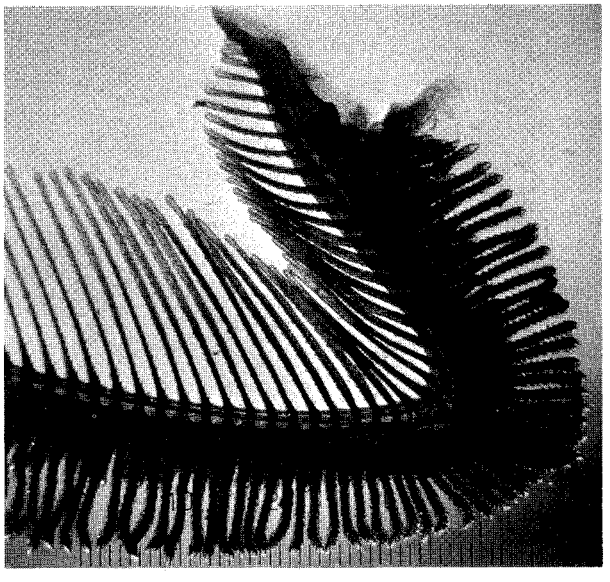

FIGURE 9.—Photomicrograph showing the barbs on the rakers of the first left gill arch of a 32-mm. (fork length) Atlantic menhaden prejuvenile (1 division = 50 μ).

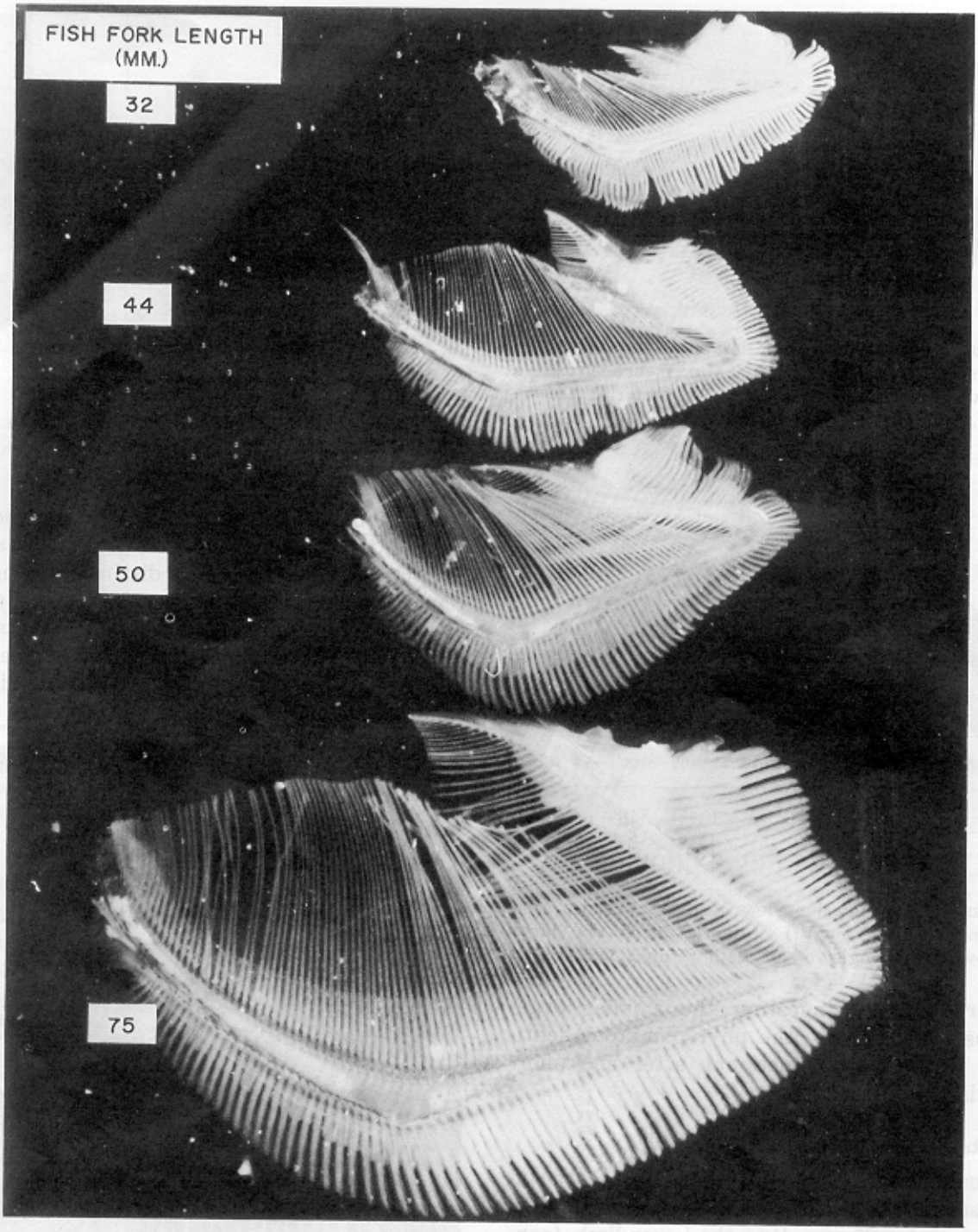

FIGURE 10.—Photomicrograph showing the structure of the gill rakers and the increase in relative size of the first left gill arch of young Atlantic menhaden.

limb extend downward and lie over those on the upper part of the lower limb (fig. 10). The number of rakers on the first left gill arch is variable and a nonlinear function of length

over the range examined (table 7). The number of rakers progressively decreases on the second, third, fourth, and fifth arches.

TABLE 7.—*Gill-raker counts of young Atlantic menhaden*

Fork length	Specimens examined	Range of gill-raker counts: Upper limb	Lower limb	Total	Mean total count
Mm.	*Number*	*Number*	*Number*	*Number*	*Number*
20–24	14	0–10	10– 22	12– 29	20
25–29	13	7–17	17– 35	24– 52	35
30–34	10	15–26	30– 48	47– 69	60
35–39	11	24–40	44– 58	69– 87	75
40–44	12	29–40	47– 63	79–103	89
45–49	5	36–44	57– 63	93–117	103
50–54	5	42–48	64– 79	106–127	118
55–59	5	45–55	68– 78	113–133	121
60–64	5	48–61	73– 81	121–136	129
65–69	5	54–64	86– 96	145–150	149
70–74	5	59–62	93–101	152–160	155

The fold of mucous membrane, which forms a groove along the bone of the gill rakers in adult Atlantic menhaden (Peck, 1894), appears as a transparent ridge in larvae (fig. 8). In prejuveniles the ridge becomes a distinct pigmented groove with an opening at the juncture of each branch of the gill arch (fig. 10). The function of this structure is not clear, but it may aid channeling food organisms posteriorly.

Pharyngeal pockets, described in clupeids by Hyrtl (1855) and in *Brevoortia* by Monod (1961), are first evident in larvae 25 mm. long. These structures appeared as two slight swellings, one on each side of the longitudinal plane, above the pharynx and anterior to the fifth gill arch. In prejuveniles the pockets become pigmented and kidney-shaped; their size increases as the length of the fish increases. Lagler and Kraatz (1945) postulated that the pharyngeal organ in the gizzard shad, *Dorosoma cepedianum,* is accessory to the digestive tract, rather than to the respiratory system as suggested by Hyrtl (1855). The presence of fresh food organisms in these structures in Atlantic menhaden suggests that the pharyngeal pockets are part of the digestive system and may accumulate the plankton prior to swallowing.

The change from a zooplankton to a phytoplankton diet in young Atlantic menhaden is thus associated with developmental changes in the gill-raker complex. Peck (1894) described the gill rakers of adults as being ". . . so complete as to render the whole pharyngeal cavity capable of filtering large quantities of water . . ." The gill rakers of larvae, however, are rudimentary and have no obvious function. So the incorporation of phytoplankton into the diet of prejuveniles and juveniles seems to be largely a function of the straining capacity of the gill rakers.

Alimentary Tract

Like the gill arch complex, the alimentary tract undergoes remarkable changes during development. In larvae the tract is nearly a straight tube connecting the pharynx and the anus. At about one-third its length, a constriction marks the junction of the stomach and intestine. The length of the anterior tract changes relatively little as the fish grows longer, but the posterior tract (intestine) changes markedly (fig. 11). When linear relations are assumed, the regression lines in figure 11 show that the length of the alimentary tract in larvae increases by about 0.3 mm. for each 1-mm. increase in length of fish; but in prejuveniles and juveniles, the length of the tract increases about 10 mm. for each 1-mm. increase in fish length.

In prejuveniles the stomach folds on itself; a blind sac develops posteriorly, forming the tail of a Y, with the pneumatic duct leading from its tip; and the lower part of the stomach (gizzard) enlarges and develops a muscular wall. Pyloric caeca are first evident in larvae 28 mm. long. Their number is variable and reaches a maximum in juveniles (table 8). In recently metamorphosed juveniles, the intestine folds on itself and forms two or three coils, the pyloric caeca lengthen, and fat is deposited among the caeca and coils of the intestine (fig. 12).

The simple straight gut of Atlantic menhaden larvae is characteristic of early clupeid development (Harder, 1958, 1960) and generally associated with a carnivorous diet in fishes (Barrington, 1957; Nikolsky, 1963). The change in food habits during metamorphosis of young menhaden is linked with changes in the digestive tract. Development of the gizzardlike pyloric stomach probably aids in the crushing of diatoms, while development of pyloric caeca

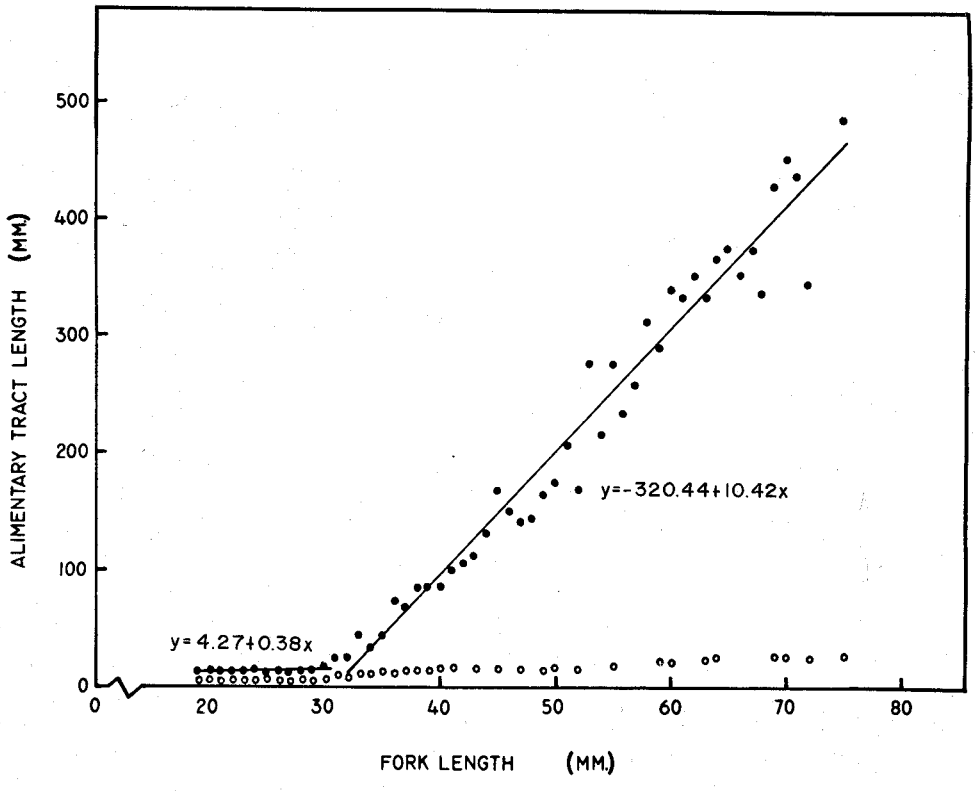

FIGURE 11.—Length of anterior alimentary tract and of total tract in relation to fork length of young Atlantic menhaden. Open circles represent group means of anterior tract measurements of 138 specimens; solid circles represent group means of the total tract length. The regression line for the 19- to 30-mm. fork length range was computed from measurements of 48 specimens and that for the 31- to 75-mm. fork length range from measurements of 90 specimens.

and the long coiled intestine increases the surface area for secretion and absorption.

LABORATORY STUDIES

We demonstrated that qualitative differences in the diet of young Atlantic menhaden were associated with changes in the gill raker-alimentary tract complex during metamorphosis, but we still did not know the quantities of food they needed for growth. The high incidence of empty or partially filled alimentary tracts in larvae captured in Indian River, Del., suggested that these quantities were small. Peck (1894) and Breder (1959) had described the feeding behavior of juveniles sufficiently for our needs, but we still did not know how larvae and prejuveniles fed nor if they could

TABLE 8.—*Pyloric caeca counts of young Atlantic menhaden*

Fork length	Pyloric caeca
Mm.	*Number*
28	241
29	277
30	446
31	312
32	299
33	303
34	254
35	372
37	288
40	355
42	368
43	299
45	440
50	357
55	351
60	323
65	437
70	411
75	436

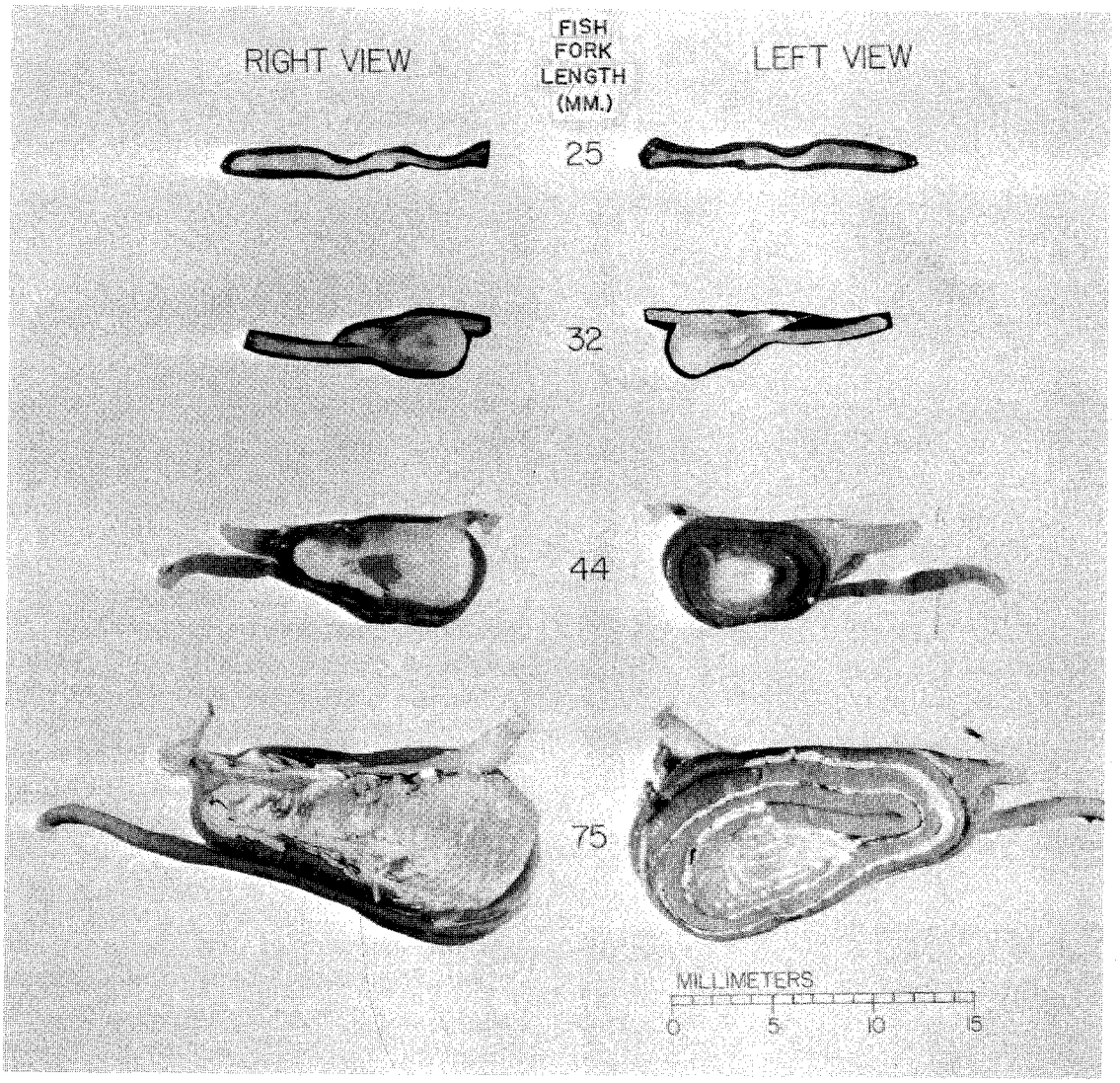

FIGURE 12.—Lateral views of the alimentary tract of young Atlantic menhaden.

be maintained in captivity with substitute foods. Through limited experiments, we sought answers to these questions.

MATERIALS AND METHODS

Atlantic menhaden larvae used in the laboratory studies were caught in the mouth of the Newport River, N.C. The experiments were made at BCF Biological Laboratory, Beaufort, N.C., in January and February 1961.

Capture and Establishment of Larvae

Our proposed experiments hinged on our capability in collecting and establishing viable Atlantic menhaden larvae in the laboratory. Larvae were caught with 1-m.-diameter nylon plankton nets (mesh aperture 0.90 mm.) suspended in flooding tidal currents. A wooden pen (1.4 by 0.9 by 0.4 m.), lined with plastic window screen (mesh aperture 1.50 mm.), was attached to the cod end of the net. This arrangement reduced the mortality sometimes associated with capture of fish larvae (Marr, 1956). The catches were dipped from the pen with 9-liter plastic buckets and transported therein to the laboratory (fig. 13). Menhaden larvae were removed, one or two at a time,

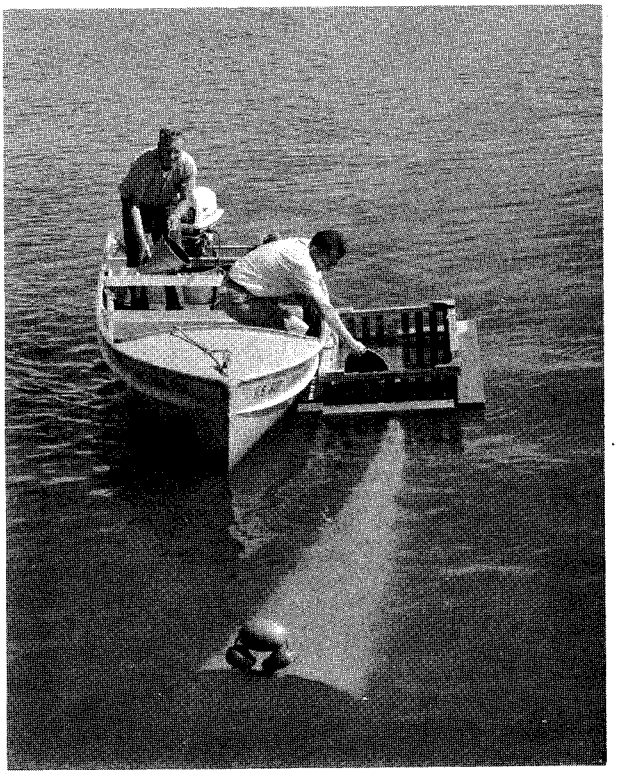

FIGURE 13.—Capture of Atlantic menhaden larvae.

from the buckets in 100-ml. beakers and placed in laboratory aquariums. By these techniques menhaden larvae were kept immersed at all times and could easily be separated from larvae of other species.

Two porcelain bathtubs served as laboratory aquariums. To minimize the bumping of the newly captive larvae against the tub walls, the interior was painted black and illuminated continuously by pink fluorescent lamps mounted 2 m. above the water. Filtered sea water was continuously supplied to each aquarium and the level controlled by a 10-mm.-diameter standpipe to provide a volume of 180 liters for about 300 larvae, 13 to 28 mm. long. During the establishment period, salinity varied between 28 and 33 p.p.t. (parts per thousand) and temperature, between 16.0° and 19.0° C.

The larvae were left undisturbed for at least 12 hours after transfer to the laboratory aquariums. Dead or dying larvae were removed daily. Total mortality during establishment was less than 5 percent.

Experimental Procedures

Experiments were begun 3 to 5 days after larvae were established in the aquariums. Individual tests were made in 100-ml. beakers, 250- and 500-ml. bowls, or 8-liter battery jars, all painted black, and filled with sea water from the aquarium supply. Larvae were transferred to the test container with a 100-ml. beaker, one or two specimens at a time. From 1 to 10 larvae were placed in each beaker or bowl and as many as 20 larvae in each battery jar.

Procedures differed for specific studies. They are described separately.

Light and feeding.—Larvae were transferred to 250-ml. bowls, eight larvae to a bowl, and left unfed in total darkness for 24 hours before the experiments were started. *Artemia* nauplii in suspension were dropped into the bowls (*Artemia* were used in preference to copepods because their pink color made them readily distinguishable after ingestion by the larvae). Light intensity of a 500-watt, tungsten filament lamp suspended 75 cm. above the water was varied by a transformer and measured with a light meter at the surface. We used penlight illumination periodically to detect the presence of food in larvae kept in darkness or exposed to low light intensities.

Food passage and digestion.—Food ingestion and digestion times were determined visually and with a radioactive tracer. For the visual observations, several lots of eight larvae each were placed in 500-ml. bowls. They were left unfed for 24 hours before the start of the experiments and then fed *Artemia* nauplii. When they had stopped feeding, the larvae were transferred to separate 100-ml. beakers for observation. Rate of food passage was estimated from the time that feeding stopped until the alimentary tract of each larva was completely empty.

For the radioactive tracer tests, several lots of eight larvae each were placed in 500-ml. bowls and fed 10 to 50 copepods (*Centropages* and *Acartia*) that had been immersed in sea water containing 0.001 μc./ml. (microcurie per milliliter) of Zn^{65} and rinsed in fresh sea water before they were fed to the larvae. When the

larvae had stopped feeding (usually within 20 minutes), they were siphoned from the bowls, rinsed in fresh, nonradioactive sea water, and placed in separate 100-ml. beakers of fresh sea water. The radioactivities of each lot of copepods, of each larva (after rinsing), and of the sea water in each 100-ml. beaker were measured with a gamma-ray scintillation detector and a well-type 76-mm. sodium iodide crystal. The number of copepods ingested by an individual larva was estimated by dividing its net activity gain (counts per minute) after feeding by the mean count per copepod for the lot fed (attempts to feed an individual larva a single, radioactive copepod were unsuccessful). The presence of copepods in the alimentary tract was also verified visually at the time a larva was transferred to a 100-ml. beaker. Uptake and initial distribution of Zn^{65} in the body of larvae were followed over a 3½-day period. When a larva was killed (or died), the entire alimentary tract was removed, and its activity level and that of the remaining body tissues were determined.

Capture and preservation of larvae.— Three lots, each with eight larvae, were transferred to separate 500-ml. bowls and fed *Artemia* nauplii. After the larvae had stopped feeding, four of them were individually removed from one bowl with a 50-mm.-diameter nylon mesh dip net and placed in solutions of 0.4, 10, and 50 percent Formalin and saturated chloral hydrate respectively. The remaining four were first anesthetized by adding a solution of tricaine methanesulfonate (0.25 g./l.) to the bowl and then transferred in a similar manner. Larvae in the second and third bowls were divided and transferred to the same four solutions from bowl two by siphoning with a 25-mm.-bore plastic tube and from bowl three by dipping with a 100-ml. beaker.

FEEDING BEHAVIOR AND RESPONSES OF LARVAE TO SELECTED STIMULI

Feeding

Atlantic menhaden larvae are selective carnivores and voracious feeders. On transfer to a bowl, they schooled and began to swim slowly around the container. When an aqueous suspension of copepods was added to the bowl, the larvae scattered, but within 1 or 2 minutes they reformed in a tighter school and swam around the container at a faster rate than previously. Feeding began when an individual larva swam away from the school, slowed down, oriented slightly below and about 10 mm. away from a suspended copepod, flexed its body in an S-shaped position (fig. 14), and drifted within 2 to 5 mm. of the prey; then, with a sudden flip of its tail, the larva straightened out as it lunged forward and upward to engulf the copepod. After the "strike," momentum carried the larva a few millimeters beyond the point of capture, from whence it swam vigorously downward, completing an arc, and then returned to the original swimming depth before finally rejoining the school. The time required for an individual feeding act and return to the school was 3 to 5 seconds. If the copepod were missed, or only partly engulfed on the first try, the larva made several violent lunges in an attempt to seize it. If these attempts were unsuccessful, the larva swam

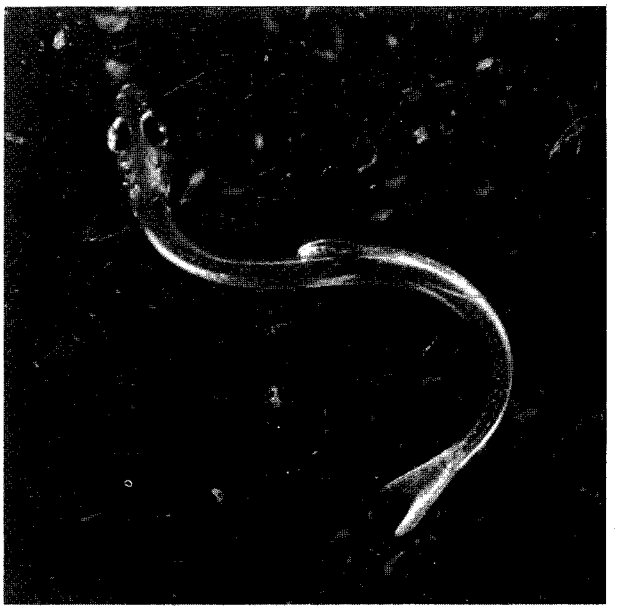

FIGURE 14.—Atlantic menhaden larva in the act of capturing a copepod. The body is flexed in an S-shaped attitude about 10 mm. from the prey and ingestion accomplished by a forward darting movement.

rapidly toward the school and rejoined it. Some larvae ingested as many as 15 copepods (average 10) before they stopped feeding. They ignored or rejected *Artemia* or *Balanus* nauplii, dead copepods, chopped clams, and finely ground particles of fish meal when introduced with copepods, but readily ingested *Artemia* or *Balanus* nauplii alone. Unsuccessful attempts at feeding and the occurrence of larvae with empty alimentary tracts during our observations suggest that some individuals may be inefficient feeders when the food supply is limited. Atlantic menhaden larvae thus appear to select preferred foods visually but will accept substitutes when no preferred foods are present.

Prejuveniles and juveniles reacted differently than larvae to the introduction of food. A school of fish suddenly reduced its forward swimming speed and turned in the direction of the food. Individuals differentially increased their swimming speed until they were in contact with the food; then, with mouth agape, they swam slowly upward and downward through the water as they appeared to suck in the food particles. Throughout feeding, their opercula were flared and their bright red gill filaments were clearly visible. At times some of the prejuveniles pursued individual copepods, but, in general, their feeding behavior was the same as that of juveniles. During feeding the fish spread out, but as the food supply diminished they gathered in small groups. These groups, enlarged by the addition of individuals, eventually joined to reestablish the school.

Our observations generally agree with those of Breder (1959), but indicate that filter feeding, rather than particulate feeding, is the principal means by which both prejuvenile and juvenile Atlantic menhaden obtain food.

Influence of Light on Feeding

Larvae fed at a minimal light intensity of 25 lux (table 9). At lower intensities, the larvae remained inactive and randomly distributed near the bottom of the bowl. At higher light intensities, the rate of feeding was increased and maximum intensity (about 500 lux) had no apparent adverse effect. We did not study the possible effects of the changes in wave length that accompanied reduction of light intensity on the feeding response.

Our laboratory observations thus indicate that Atlantic menhaden larvae do not feed at low intensities of artificial light; however, results of our field studies suggested that larvae fed more actively on moonlit nights than on dark nights. The incident light intensity of moonlight probably does not exceed 0.5 phototopic lux (Urey, 1961), but this natural light level may be sufficient for larvae to capture swimming copepods silhouetted at or near the water surface.

TABLE 9.—*Numbers of larvae feeding at different light intensities*

[Light intensities in parentheses]

Elapsed time following introduction of food	Larvae with food in alimentary tract					
	Lot 1		Lot 2		Lot 3	
Minutes	*Number*	*Lux*	*Number*	*Lux*	*Number*	*Lux*
0	0	(0)	0	(25)	0	(8)
15	0	(0)	8	(25)	0	(8)
30	0	(0)	----------		[1]3	(25)
45	0	(0)	----------		[2]8	(25)
60	0	(4)	----------		----------	
70	0	(4)	----------		----------	
80	0	(8)	----------		----------	
160	0	(15)	----------		----------	
195	[1]6	(25)	----------		----------	
210	[2]8	(25)	----------		----------	

[1] Feeding began.
[2] Alimentary tract full or nearly full.

Digestion Time

Artemia nauplii passed through the esophagus to the posterior alimentary tract—where they often could be seen wriggling—within 1 to 3 seconds. At water temperatures ranging from 16.8° to 17.5°C., 80 percent of the larvae with apparently full posterior tracts had voided all contents between 8 and 10 hours after feeding; those estimated to be one-quarter to three-quarters full, between 6 and 7 hours. One larva retained food for 14 hours.

Rapid uptake of radioactive zinc (Zn^{65}) by the body tissues of larvae fed labeled copepods indicated that assimilation of food began almost immediately. Nearly two-fifths of the radioactivity was in the body tissues within 1½ hours; three-fourths, after 8½ hours; and

nine-tenths, after 34 hours (table 10). The total radioactivity decreased rapidly during the first day after the larvae were transferred to nonradioactive sea water (fig. 15). Between 17 and 19 percent of the Zn^{65} was retained within the body 14 days after feeding (no correction was made for Zn^{65} decay).

These findings suggest to us that digestion rate in relation to time since last feeding probably contributed to the low incidence of food found in larvae captured at Indian River Inlet during dark nights, and especially in those captured toward dawn.

TABLE 10.—*Distribution of Zn^{65} in Atlantic menhaden larvae after feeding on copepods labeled with this radionuclide*

[Levels represent the mean of individual lots of larvae, adjusted for the dosage given]

Elapsed time since feeding	Activity level	
	Alimentary tract	Remainder of body
Hours	*Percent*	*Percent*
0.0	98	2
1.5	59	41
8.5	24	76
34.0	10	90
89.0	1	99

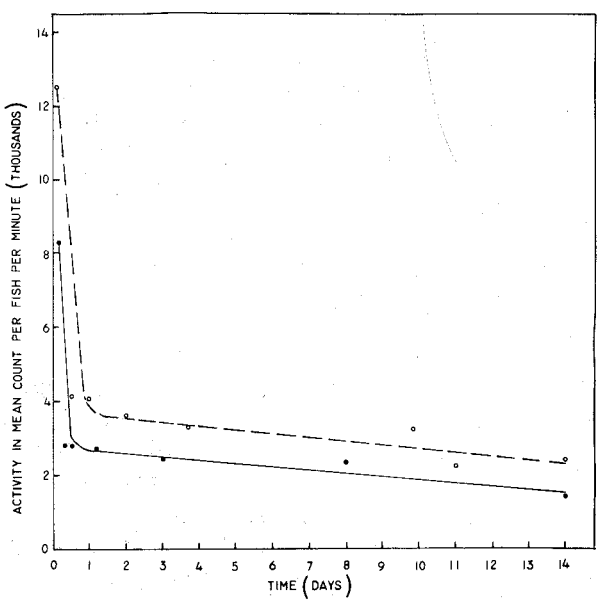

FIGURE 15.—Activity level of Zn^{65} in the body of Atlantic menhaden larvae fed labeled copepods and returned to nonradioactive sea water. Solid and open circles represent two larvae.

Effects of Capture and Preservation of Larvae on Their Alimentary Tract Contents

All larvae transferred by the dip net defecated all or a portion of their alimentary tract contents when removed from the water, but none transferred in sea water defecated any of their tract contents.

Active larvae placed in the various Formalin solutions had violent spasms, accompanied by complete or partial defecation of their tract contents. If defecation were incomplete, the remaining organisms were restricted to the end of the posterior alimentary tract. Sometimes the entire contents were ejected in a single, violent spasm. Generally, larvae voided their tract contents violently and completely in 10 and 50 percent Formalin and died within 10 to 30 seconds. In 0.4 percent Formalin they quivered for as long as 10 minutes and often defecated all or part of their tract contents.

Larvae placed in the chloral hydrate solution reacted as in the stronger Formalin concentrations, although they voided only about one-fourth to one-half of the tract contents.

Larvae in the tricaine methanesulfonate gradually lost equilibrium in 3 to 5 minutes and had no spasms. They did not defecate any portion of their alimentary tract contents during transfer by net or immersion in Formalin or chloral hydrate.

These observations suggest that larvae may defecate much of their alimentary tract contents during capture with a net or at the time of preservation, thereby leading one to the erroneous conclusion that they feed little or digest their food rapidly. So both the high incidence of empty alimentary tracts and the low numbers of food organisms per tract which we found in larvae collected at Indian River Inlet probably was largely due to the harsh treatment to which larvae were subjected during retrieval of the net from the water onto a bridge (about 10 m. above the surface) and their preservation in Formalin. Capturing larvae with a net attached to a floating pen and anesthetizing them prior to preservation should provide specimens with alimentary tract contents that reflect actual conditions at the time of capture.

REARING YOUNG MENHADEN IN THE LABORATORY

The foregoing field and laboratory studies provided the necessary technical information for us to establish and successfully rear Atlantic menhaden larvae through and beyond metamorphosis in captivity. Feeding was begun about 12 hours after larvae were established in an aquarium. The maintenance ration was varied according to the developmental stage of the fish. Larvae were fed a daily ration of 15 to 20 copepods (chiefly *Centropages* and *Acartia*, 0.5 to 1.3 mm. greatest dimension) or 30 to 50 *Artemia* nauplii per larva. At the onset of metamorphosis, the animal diet was supplemented with natural phytoplankton pumped into the aquarium from nearby intertidal waters. The pumping rate was adjusted to provide a daily minimum of 17 liters of water per fish. After metamorphosis was completed, a slurry consisting of 10 parts menhaden meal and 1 part pureed clam (*Mercenaria mercenaria*) was substituted for the copepod-*Artemia* nauplii component and fed at a ratio of 1 to 20, based on the total estimated weight of the fish in an aquarium.

The handling and feeding procedures described in this paper can provide healthy stocks of young menhaden in different developmental stages for laboratory research.

SUMMARY

This paper covers the food of young Atlantic menhaden, changes in the alimentary tract and related body structures during their metamorphosis from larvae to juveniles, and laboratory studies of feeding, digestion, and associated responses of the young fish.

The alimentary tracts in 592 Atlantic menhaden larvae collected at Indian River Inlet, Del., were examined for food. More than half of the tracts were empty. Contents of 243 tracts that contained food consisted almost entirely of copepods, chiefly *Centropages*. Generally, larger larvae fed on larger copepods, and greater numbers of copepods in tract contents were associated with daylight and evening hours. Food items generally reflected the composition and relative abundance of individual copepod genera in the plankton. Although phytoplankters were abundant at the Inlet, larvae did not eat them.

Young menhaden changed their food habits during metamorphosis within the estuary. Alimentary tract contents of 20 larvae and 31 early-stage prejuveniles consisted almost entirely of copepods, chiefly *Acartia*. Tract contents of late-stage prejuveniles and juveniles consisted mostly of pennate and centrate diatoms, dinoflagellates, and amorphous plant materials. In general, major food items identified in the alimentary tracts also were the more abundant organisms in the water.

Metamorphosis of Atlantic menhaden is distinguished by the development of a highly specialized gill raker-alimentary tract complex. The mouth is relatively large at all stages of development. Prominent maxillary and dentary teeth are present in larvae. The teeth become nonfunctional during late metamorphosis and eventually disappear. Gill rakers are rudimentary in larvae, but increase in length, number, and complexity during metamorphosis. Pharyngeal pockets appear during metamorphosis. The alimentary tract of larvae is nearly a straight tube. In prejuveniles the tract begins to fold forward, the muscularized stomach (gizzard) starts to develop, and many pyloric caeca become evident. In juveniles the intestine forms several coils, pyloric caeca increase in number and length, and fat deposits usually surround the caeca and lie between the folds of the intestine.

Observations on Atlantic menhaden in captivity confirmed that larvae and early-stage prejuveniles feed selectively on living prey. They capture their prey by flexing and striking like a snake. An individual larva may ingest as many as 15 copepods, but the average was 10. Larvae preferred copepods, but also fed on *Artemia* and *Balanus* nauplii. Late-stage prejuveniles and juveniles feed mainly by filtering plankton in the water. They disperse while feeding, but reassemble in a tight school when they have exhausted the food supply.

Laboratory studies of selected responses of Atlantic menhaden larvae suggest that the absence or low numbers of food organisms found

in the alimentary tracts of larvae collected at Indian River Inlet may have been largely due to their defecating all or part of the contents during capture and preservation. Proper capture devices for larvae and their anesthetizing prior to preservation should reduce loss of their alimentary tract contents. Other factors which may have contributed to the paucity of food in alimentary tracts were lower feeding rate during dark nights and digestion rate in relation to elapsed time since last feeding.

Information obtained from our studies enabled us to establish and successfully rear Atlantic menhaden from larvae to juveniles in captivity. The work also provided insight into some aspects of the estuarine ecology of young Atlantic menhaden.

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