

Parasites and Cyclopoid Predators of Age-0 Fish in the Roanoke River, North Carolina

JOHN E. COOPER¹

*Institute for Coastal and Marine Resources
East Carolina University
Greenville, North Carolina 27858*

ABSTRACT: Altered river flow has been suggested as a cause for the low recruitment of striped bass, *Morone saxatilis*, in the Roanoke River (North Carolina) because of its effect on the proximity of zooplankton and larval striped bass. This results in unsuccessful feeding and subsequent starvation, which was considered to be a major mortality factor. Other mortality factors, such as parasitism and copepod predation on age-0 fish, may also be regulated to some extent by changes in river flow. The relationship of cestode plerocercoids, trematode metacercariae, mussel glochidia, and cyclopoid copepod predators with age-0 fish was evaluated in the lower Roanoke River and western Albemarle Sound from plankton net collections made in 1984 to 1986 and 1988. Plerocercoid prevalence was higher under low river flow conditions than under high flow conditions in darters (*Percidae*; 16.7% vs. 9.2%), minnows (*Cyprinidae*; 28.8% vs. 4.7%), and *Morone* (1.9% vs. 0%). Gut analysis of the age-0 fish revealed that copepods (source of the plerocercoids) were a major diet component of *Morone* and darters but not of minnows or herring (*Clupeidae*). Decreases in river flow were associated with increases in copepod density (Pearson $r = -0.62$; $p = 0.0001$) and plerocercoid prevalence in *Morone* (Pearson $r = -0.29$; $p = 0.03$). The low correlation value for *Morone* may be quite strong considering the complexity of the variables associated with prevalence. Metacercariae were found only in *Morone* and minnows, and prevalence and mean intensity were less than that found for plerocercoids. Mussel glochidia prevalence was less than 0.5% for all affected taxa, an order of magnitude less than that found in other studies. The low value may indicate that the mussel population in the Roanoke River is declining. Prevalence of attacks by the predatory copepod *Mesocyclops edax* on age-0 fish was similar to that in Chesapeake Bay, and striped bass was the primary prey. Spatial and temporal proximity of copepods and fish prey may be the key factors in regulating copepod attacks. The low prevalence of parasites and copepod predators seen in this study would suggest that mortality from these sources may not be a major factor in age-0 recruitment in this system. Confirmation of these conclusions would require a more controlled experimental approach.

Introduction

Altered river flow has been suggested as a cause for the low recruitment of striped bass, *Morone saxatilis*, juveniles in the Roanoke River due to its effect on the temporal and spatial juxtaposition of zooplankton and larval striped bass (Rulifson et al. 1988). This temporal and spatial asynchrony of predator and prey was hypothesized to result in larval fish starvation. Alterations in river flow and its effect on water temperature may lower the production of zooplankton prior to the initial feeding period of striped bass. Stevens et al. (1985) attributed reduced zooplankton production in the nursery areas as one factor in the decline of juvenile striped bass in the Sacramento-San Joaquin Estuary.

Parasitism and copepod predation on age-0 fish may be an additional source of mortality that would add to the decline in recruitment of striped bass juveniles, as well as juveniles of other fish taxa. Marine and freshwater age-0 fish are host to nu-

merous parasitic taxa (Govoni 1983; Fischer and Kelso 1990) that can affect the physiology and survival of fish hosts through competition for nutrients (Rosenthal 1967) and by subsequently reducing host body condition (Gordon and Rau 1982; Lemly 1982; Moles 1983; Lemly and Esch 1984; Cunjak and McGladdery 1991). Predatory cyclopoid copepods are known to attack larval fish (Lillelund and Lasker 1971; Smith and Kernehan 1981) and have been suggested as a significant, although sporadic, mortality factor for larval fish (Hartig et al. 1982).

This study had three objectives: first, to determine the prevalence and intensity of plerocercoid larvae (Cestoidea), metacercarian larvae (Trematoda), mussel glochidia (Unionacea), and predatory cyclopoid copepods (Crustacea) in age-0 fishes; second, to determine at what size fish were susceptible to parasitism and copepod predation; and third, to determine if parasitism and copepod predation were associated with river flow.

Study Area

The Roanoke River delta encompasses the main channel of the Roanoke River and two distributar-

¹ Present address: Environmental Science and Forestry, State University of New York, Syracuse, New York 13210.

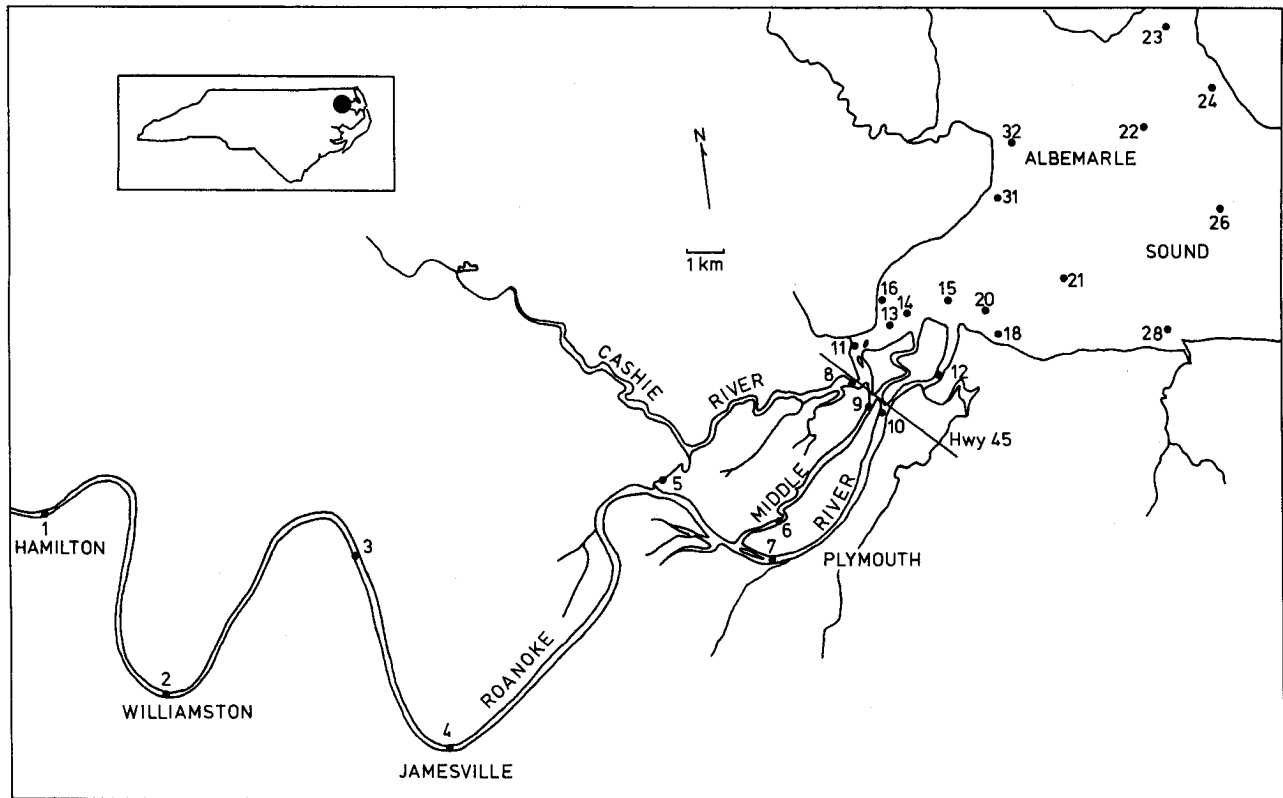


Fig. 1. Map of the lower Roanoke River delta and Western Albemarle Sound with locations of sampling stations used from 1984 to 1988. Not all stations were sampled in each year. Tidal effects extend upstream to Hamilton.

ies—the Middle and Eastmost rivers, and the Cashie River (Fig. 1). Flow rate in the Roanoke River is determined primarily by water releases by three upstream dams. There are no large backwater areas, although the forest surrounding the river can be flooded during periods of extreme river discharge and may function as a backwater area under this condition.

The Roanoke River and western Albemarle Sound are primarily fresh water because of three factors: a relatively high freshwater inflow; flow regulation of the Roanoke River by upstream dams, particularly low flow augmentation, which greatly reduces saltwater intrusion (Geise et al. 1979); and the only ocean access to eastern Albemarle Sound is through a single, restricted opening, Oregon Inlet, 125 km from the Roanoke River mouth. Salinity in Albemarle Sound generally reaches a maximum of 2‰ in December (50 km east of the Roanoke River mouth) and is minimal in March (Geise et al. 1979). Saltwater intrusion has been recorded in the Roanoke ($\geq 0.39\text{‰}$) during July through November 1981 (Zincon and Rulifson 1992); on two days (May 15, June 8) in 1986 (up to 1‰), and sporadically in 1988 ($\leq 0.3\text{‰}$; Rulif-

son et al. 1992). Water circulation is primarily due to wind, with ocean tides secondary; tidal amplitude is approximately 15 cm and tidal effects extend upstream to Hamilton (Geise et al. 1979).

Materials and Methods

The age-0 fish examined in this study were collected from 1984 to 1986 and in 1988 in a series of striped bass distribution and feeding studies (Rulifson 1984; Rulifson et al. 1992) in the lower Roanoke River and western Albemarle Sound. Fish data from 1987 was excluded because only five striped bass were collected. Ichthyoplankton and zooplankton collections were made on alternate nights May 18 to June 18, 1984; April 26 to June 10, 1985; May 1 to June 8, 1986; April 14 to June 15, 1988). Fifteen stations were sampled on each date (weather permitting), which required about five hours. Water temperature, salinity, and dissolved oxygen were measured at surface, mid-depth, and bottom with each plankton collection. River flow rates were taken from the United States Geological Survey gauge at river km 214.9 located 4.5 km downstream from the Roanoke Rapids

Dam. The gauge is approximately 129 river km upstream from the study area.

Age-0 fish were collected with paired 0.5 m dia, 505- μ m mesh plankton nets towed in an oblique manner for 6 min. Zooplankton collections were made with a single 0.5 m dia 250- μ m mesh plankton net towed just below the surface for 2 min. The fish and zooplankton samples were preserved in 10% borax-buffered formalin containing rose bengal dye. Fish were identified (Lippson and Moran 1974; Auer 1982; and Olney et al. 1983) and measured to the nearest 0.5 mm total length (TL). At lengths between 8 mm TL and 15 mm TL and at other lengths where no species determination could be made, white perch, *Morone americana*, and striped bass were identified as *Morone*. These three taxa have been combined as *Morone* for analysis. Gut analysis was done only on those fish capable of feeding and those fish were characterized as having developed jaws and an inflated gas bladder. Alimentary tracts (esophagus to anus) were dissected from *Morone* from all stations sampled from 1984 to 1986 and 1988 and from other fish taxa collected at stations 1, 4, 7, 8, 10, 13, 14, and 15 in 1984 and 1985. Prey organisms from dissected tracts and collected zooplankton were identified (copepods were segregated into cyclopoid, calanoid, and harpacticoid; Pennak 1978; McCafferty 1981; Merritt and Cummins 1984) and zooplankton density was determined by a standard subsampling method (Rulifson et al. 1992). The prey organisms were counted in total.

Plerocercoids, metacercaria, and glochidia in *Morone* were recorded from all stations sampled in each year and in other fish taxa at stations 1, 4, 7, 8, 10, 13, 14, and 15 in 1984 and 1985. Predatory copepod attacks on fish were recorded for all taxa in 1986 and 1988. The stations sampled and number of samples are summarized in Table 1.

Plerocercoids were differentiated from metacercaria using the characteristics given by Yamaguti (1959): scolex unarmed with four apical suckers, a fifth sucker sometimes present, no evidence of a ventral or oral sucker and parasites not enclosed by a cyst (identifications verified by David Zwerner, Virginia Institute of Marine Science). Plerocercoids were dehydrated in a graded ethanol series and slide-mounted in Euparal. Metacercaria were passed through a graded ethanol series (70% and 50%) and then stained for 24 h in Grenacher's alcoholic borax carmine, destained in 50% ethanol and 70% acid alcohol, washed in 70%, 95%, and 100% neutral ethanol, cleared in xylene and slide-mounted in Preservaslide. Specific identification was not attempted because of the limited development of the plerocercoid and metacercaria larvae. Glochidia were not identified but their iden-

TABLE 1. Number and location of samples examined for parasites and predatory copepods. Plerocercoids (P), metacercaria (M), and glochidia (G) in *Morone* were recorded from all stations sampled in each year and from other fish taxa at stations 1, 4, 7, 8, 10, 13, 14, and 15 in 1984 and 1985. Predatory copepod attacks (PC) were recorded for all fish taxa in 1986 and 1988. Station numbers refer to locations shown in Fig. 1; stations 1 through 12 are "river," all others are "sound."

Station	<i>Morone</i> (P M G)				Other Fish Taxa (P M G)		(P C)	
	1984	1985	1986	1988	1984	1985	1986	1988
1	14	14	22	32	13	13	22	32
2	14	14	22	30			22	30
3	14	14	22	22			22	20
4	14	14	22	28	14	14	22	28
5	22	30	34	22			34	22
6	22	40	34	30			34	30
7	22	38	34	3	22	37	34	30
8	28	40	34	30	28	36	34	32
9	28	40	34	26			34	36
10	28	40	34	36	24	37	34	40
11	28	40	34	24			34	24
12	28	40	34	34			34	24
13	28	36	30	22	27	36	28	22
14	26	36	30		21	32	30	
15	28	36	30	32	25	33	32	32
16	6	2		28				28
18	6			12				12
20			6	2			6	
21			6	12			6	12
22			6	8			6	8
23			4	6			4	6
24			6	6			6	6
26			6	8			6	8
28			6	8			6	8
31				12				12
32				12				12
Total	356	474	490	502	174	238	490	504

tity was inferred by the presence or absence of adult mussels. Searches for adult mussels were made along the banks of each tributary in water up to 0.5 m in depth and in muskrat middens. Adult mussels were identified using Burch (1973) and Shelley (1987) (verified by William Adams, United States Army Corps of Engineers, Wilmington, North Carolina; and Arthur Bogan, Freshwater Molluscan Research, Sewell, New Jersey). Copepods were softened and stained in a solution of lactic acid and a few drops of picro acid fuchsin in chloral hydrate, rinsed in chloral hydrate, dissected in Hoyers mounting medium, and sealed with ringed cement. Several copepods were also slide-mounted as whole mounts in Pro-Texx mounting medium after dehydrating in 100% isopropyl alcohol. Predatory copepods were identified using the methods described for zooplankton.

Plerocercoids, metacercaria, and predatory copepods were counted and the site of occurrence in the host's body recorded using a numbered grid (Fig. 2). The grid dimensions were proportionally scaled to fish size so that each grid square would

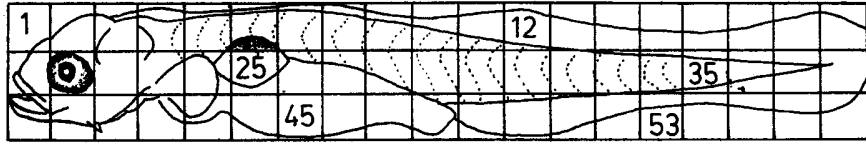


Fig. 2. Schematic grid used for categorizing host body sites for parasites and predators. Each square was proportionately modified to accommodate changes in fish body length.

remain at its respective morphological position. Attacks by predatory copepods were defined as an attached copepod having possession of part of the host's tissue. This definition was used to avoid recording apparent attacks induced by the unnatural

proximity of copepods and fish in the collecting nets. The terms prevalence (percentage of host taxa infested by parasite taxa), mean intensity (number of individuals of a single parasite taxa per infested host taxa), and site (part of host in which parasite was found) follow Margolis et al. (1982).

All statistical analyses were made using SAS version 6.03 (SAS Institute, Inc. 1988). Analysis of variance was used to examine differences in mean water temperature by year; plerocercoid prevalence at stations common to *Morone*, minnows (Cyprinidae), herring (Clupeidae), and darters (Percidae); plerocercoid prevalence in these four fish taxa; plerocercoid prevalence and mean intensity in *Morone* at all stations sampled in 1985 and 1986 and in Albemarle Sound stations in 1986 and 1988. The nonparametric Kruskal-Wallis χ^2 approximation (NPAR1WAY) was used where distributions were considered to be non-normal: plerocercoid prevalence in river and sound; plerocercoid prevalence among the Roanoke and Cashie distributaries and Albemarle Sound; mean plerocercoid intensity at stations common to *Morone*, minnows, herring, and darters; and mean intensity among these four fish taxa in 1984 and 1985. The distributions of parasitized fish were compared using the Kolmogorov-Smirnov test.

Pearson correlations were calculated between the percent of copepods in fish diets and plerocercoid prevalence; plerocercoid prevalence and fish total length; plerocercoid prevalence and river flow; plerocercoid prevalence and copepod density; river flow and copepod density; and fish density and copepod attacks.

Results

PHYSICAL FACTORS

The average river flow rates (April to June) were higher in 1984 ($392 \text{ m}^3 \text{ s}^{-1}$) and 1987 ($555 \text{ m}^3 \text{ s}^{-1}$) than in any other year of this study. The flow rates in 1984 were the seventh highest on record for 1912–1990 and those in 1987 were the highest ever observed in the April–June period (Fig. 3). Flow during the April–June period in 1985 was the lowest on record and remained low during 1986 (but higher than 1985) and was moderate in 1988. The licensed regulation of the river flow by Roanoke Rapids Dam requires a minimum flow of 56.6 m^3

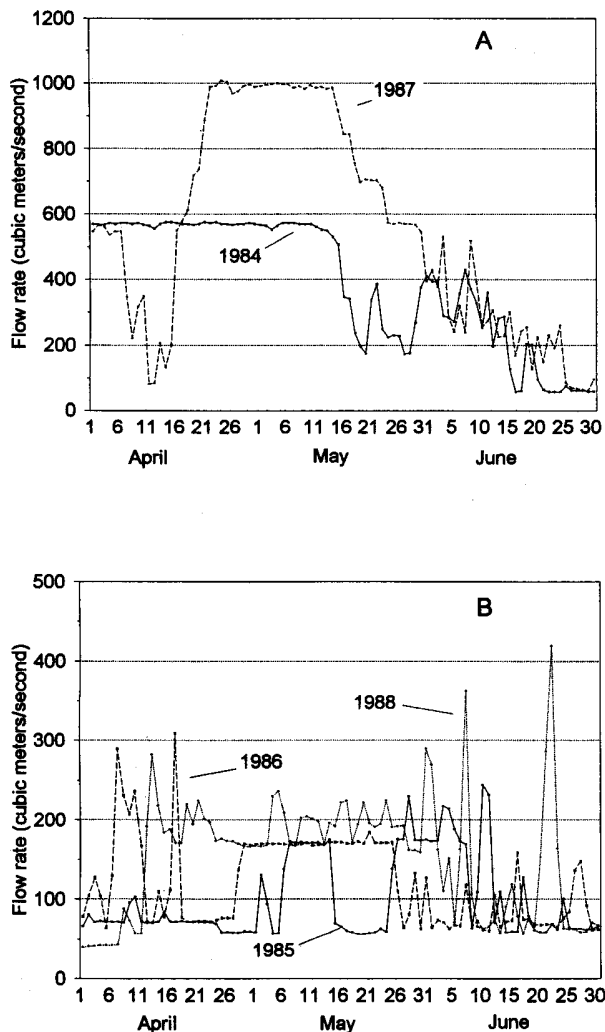


Fig. 3. Average daily rates of discharge from the Roanoke Rapids Dam for April through June measured at the United States Geological Survey gauge at river km 214.9. A) high flow years of 1984 and 1987; B) low to moderate flow in 1985, 1986, and 1988. Sharp spikes are water releases for hydropower generation.

s^{-1} during the striped bass spawning season (Rulifson and Manooch 1990), but maximum flow rates were not regulated. This can result in relatively stable flows (e.g., April 26 to May 26, 1986; Fig. 3) and in rapidly increasing-then-decreasing flows during periods of hydroelectric generation.

River water temperature in April ranged from a low of 15°C (1988) to a high of 23.4°C (1985) and generally increased about 1°C per week to between 24°C and 28°C by the second week of June. Water temperature decreased to 17°C (a 5°C decline) in the first week of June, 1984, before increasing to 27°C at the end of June. This was the only year in which a decrease of this magnitude was seen and was most likely brought about by an increase of 226.6 $m^3 s^{-1}$ in river flow over a 4-d period. River water mean temperature was significantly higher in 1985 (ANOVA, $F = 7.47$, $df = 3, 72$, $p = 0.05$; Tukey) than in 1984 or 1988 but was not significantly different than that in 1986.

Salinity was less than 0.46‰ during April to June in each year except for two dates in 1986: May 15 and June 8, when it was 1.0‰. Salinity was not considered as a factor in the distribution of parasites or predatory copepods.

Dissolved oxygen saturation was rarely below 45% and was most often in the 70–75% range. Flooding of the blackwater swamp areas can result in depressed dissolved oxygen when swamp water is mixed with river water.

PLEROCERCOIDS

Plerocercoids varied in shape from triangular to oblate spheroid. Individuals ranged in size from 0.08 mm to 0.56 mm across the longest axis (mean = 0.20, SD = 0.08, $n = 59$) and from 0.08 mm to 0.48 mm across the shortest axis (mean = 0.20, SD = 0.08, $n = 59$). The developing scolex, characterized by four apical suckers (Fig. 4), generally occupied one-half of the parasite's body. Calcareous-like deposits, characteristic of *Proteocephalus*, were present but could not be differentiated from possible crystalline deposits from the formalin.

Eleven of the 17 fish taxa examined were parasitized by plerocercoids. In those taxa where 10 or more fish were examined, the highest prevalence was found in darters (10%), followed by minnows (9.4%) (Table 2). Prevalence increased from 1984 to 1985 in herring (0.3% to 1.4%), Atlantic menhaden, *Brevoortia tyrannus* (0% to 3.5%), and yellow perch, *Perca flavescens* (0% to 3.8%) as the number of fish examined increased, and decreased in centrarchids (Centrarchidae; 8.7% to 0%) as the number of fish examined decreased. Prevalence increased in minnows from 1984 to 1985 (4.7% to 28.8%), and darters (9.2% to 16.7%) as the number of fish examined decreased. *Morone* had a prev-



Fig. 4. Proteocephalid plerocercoid (0.36 mm \times 0.56 mm) with four apical suckers in the developing scolex. This plerocercoid was taken from a 8.5-mm TL *Morone*.

alence of 0% in 1984, 1.9% in 1985, 0.2% in 1986, and 1.8% in 1988, but the changes in prevalence did not follow the number examined.

The highest mean intensity was found in minnows (4.5), followed by centrarchids (2.0), and Atlantic menhaden (2.0; Table 2). Although the overall mean intensity was 2.5, several individual fish larvae harbored a much greater number of plerocercoids (>90 in a 13 mm TL minnow, 12 in a 4.0 mm TL centrarchid, 12 in a 23 mm TL white perch). Mean intensity did not vary greatly between years by taxa. Mean intensity decreased from 1984 to 1985 in herring (1.7 to 1.2), darters (1.9 to 1.2), minnows (5.2 to 4.0), and centrarchids (2.0 to 0), and increased in Atlantic menhaden (0 to 2.0) and yellow perch (0 to 1.0). Mean intensity in *Morone* was 1.1 in 1985 and 1986 and increased to 1.6 in 1988.

In this study, 96% of the plerocercoids were located in the gut cavity (sites 24 to 28 and 42 to 48; Fig. 2) attached to the intestine, liver, gas bladder, or mesenteries, which is characteristic of *Proteocephalus*. The remainder were found in the tissue of the lower jaw (1.6%), head (<1.0%), tail (<1.0%),

TABLE 2. Prevalence and mean intensity of plerocercoid and metacercarian parasites in fish taxa examined in 1984 to 1986 and 1988. *Morone* were examined in all years and all other taxa were examined in 1984 and 1985.

Taxa ^a	n	Mean TL (mm)	Range TL (mm)	Plerocercoids		Metacercaria	
				Prevalence	Mean Intensity	Prevalence	Mean Intensity
All Stations							
<i>Morone</i>	12,989	5.9	3.0–26.5	0.9	1.3	0.1	1.0
Stations 1, 4, 7, 8, 10, 13, 14, 15							
Herring ^b	3,530	13.8	2.5–41.5	1.1	1.3	0	0
Minnow ^b	1,151	17.7	4.5–38.5	9.4	4.5	0.5	1.7
Centrarchids ^b	245	5.7	3.0–26.0	0.8	2.0	0	0
Atl. Menhaden ^b	203	39.2	27.0–61.0	3.4	2.0	0	0
Darters ^b	110	12.5	5.0–25.0	10	1.8	0	0
Yellow perch	30	18.7	10.0–31.0	3.3	1.0	0	0
Pirate perch	6	11.6	5.5–20.0	16.7	9.0	0	0
E. mudminnow	3	31.4	6.5–34.0	33.3	3.0	0	0
Total	18,424	9.0		1.6	2.5	0.04	1.6

^a Taxa (and number examined) that did not harbor plerocercoid or metacercarian parasites were carp (56), brown bullhead (51), American eel (26), suckers (11), white catfish, *Ictalurus catus* (7), and Atlantic needlefish, *Strongylura marina* (6).

^b Taxa with 10 or more fish parasitized with plerocercoids.

and dorsal body (<0.5%). Plerocercoids that occurred in the gut cavity were either attached directly to the host tissue (97%) or were free within the cavity, attached only by a slender thread.

All plerocercoid parasites found in *Morone*, Atlantic menhaden, American eel (*Anguilla rostrata*), yellow perch, pirate perch (*Aphredoderus sayanus*), and eastern mudminnow (*Umbra limi*) were located within the gut cavity. This was not true for minnows, centrarchids, darters, or herring, but the number of plerocercoids outside the gut cavity was low. The plerocercoids outside of the gut cavity may have been recently acquired and had not yet migrated. The distribution of plerocercoids was more diverse in minnows than in any other taxa. The body sites of plerocercoids in all parasitized fish taxa are summarized in Table 3.

Gut analysis revealed that copepods were a major component of the diet of *Morone*, darters, At-

lantic menhaden, and brown bullhead (*Ictalurus nebulosus*), but not of herring, minnows, centrarchids, carp (*Cyprinus carpio*), American eel, or yellow perch (Table 4). The majority of *Morone* and darters with empty guts occurred over a narrower length range than did herring or minnows: *Morone* (5.5–6.5 mm, 94%); darters (5.0–8.0 mm, 58%); herring (3.0–13.0 mm, 79%) and minnows (4.5–12.5 mm, 66%). All taxa examined had consumed copepods, but there was no significant correlation between the percent of copepods in the diet and plerocercoid prevalence for all taxa combined (Pearson $r = 0.147$, $p = 0.70$). There was a weak but significant correlation between these two variables for *Morone* (Pearson $r = 0.33$, $p = 0.01$) and minnows (Pearson $r = 0.33$, $p = 0.01$). Eighty percent of those taxa that were examined at first-feeding lengths had been parasitized: *Morone* at 4.5–6.0 mm, herring at 4.0 mm, darters at 5.5 mm, min-

TABLE 3. Percent occurrence of plerocercoid parasites in various body sites in age-0 fish in 1984–1986 and 1988. Numbers separated by a hyphen refer to body sites as numbered in Fig. 2.

Taxa	Body Site										Total Parasites	
	Head		Dorsal		Tail	Pelvic	Gut Cavity		Lower Jaw	Ventral Finfold		
	1–3	20–22	Body	Finfold			24–28	42–48	39–41	49–57	n	Percent
Minnows		0.4	0.4		1.6	0.2	18.0	76.7	2.4		488	65.6
<i>Morone</i>							11.0	89.0			155	20.8
Herring							16.0	82.0	2.0		50	6.7
Darters						5.0	5.0	90.0			20	2.7
Centrarchids		25.0					25.0	50.0			4	0.5
Atlantic menhaden								100			14	1.9
Pirate perch								100			9	1.2
E. mudminnow								100			3	0.4
Yellow perch								100			1	0.1
Percent of total	0	0.4	0.4	0	1.1	1.3	15.3	80.8	1.7	0	744	

TABLE 4. Primary diet components of selected fish taxa. Data for *Morone* were derived from all stations sampled in 1984 to 1986 and 1988. Values for other fish taxa were taken from stations 1, 4, 7, 8, 10, 13, 14, and 15 in 1984 and 1985. The number of fish examined in each taxon is given in Table 1.

Fish taxa ^a	Diet Component (percent)						Percent Empty Stomachs
	<i>Bosmina</i>	Copepods	Other Cladocerans	Diptera Larvae	Amphipods	Rotifers	
<i>Morone</i>	29.8	33.9	17.8	0.7	0.6	0	56.5
Herring	21.3	8.7	11.5	4.0	0	38.2	58.0
Minnows	0.9	12.1	33.6	1.1	0	42.2	18.4
Darters	0.6	34.4	38.7	2.7	0	2.9	6.1
Centrarchids	6.0	5.9	21.2	1.7	0	36.6	84.4
Atl. Menhaden	21.6	34.9	12.6	0.7	0	11.8	0
Carp	21.4	15.4	20.2	0	0	4.7	67.8
Br. bullhead	0.1	23.9	24.4	24.0	2.4	0.9	4.3
American eel	0	3.6	18.4	33.9	21.2	0	23.1
Yellow perch	9.0	36.2	12.0	0.1	0.6	0.3	0

^a Taxa (and percent copepods in diet) collected in low numbers and only in 1984 were white catfish (23.8%), eastern mudminnow (16.7%), suckers (26.2%), and pirate perch (50%). Six Atlantic needlefish (77.8%) were collected from 1984 and 1985.

nnows at 5.0 mm, eastern mudminnow at 6.5 mm, and pirate perch at 6.0 mm. Suckers (Catostomidae) and carp were not parasitized. Fifty percent of all parasitized fish were 15.0 mm TL or less and 90% were 21.0 mm TL or less.

Copepods constituted a higher percentage of the diet at sound stations (stations 13–32) than at river stations (stations 1–12) for *Morone* (73.9% vs. 10%), herring (39.5% vs. 3.4%), and minnows (4.3% vs. 1.1%) but not for darters (6.5% vs. 32.7%). Minnows and darters were rarely collected as larvae at sound stations and only at those stations near the mouths of the Roanoke and Cashie rivers.

Four taxa *Morone*, herring, darters, and minnows, were analyzed for the percentage of copepods consumed as fish lengths increased. The distributions fell into two types: a high percentage of copepod consumption at first-feeding (*Morone* and darters), which remained high throughout the fish lengths examined (Fig. 5); and a lower percentage at first-feeding (herring and minnows) that did not increase rapidly until the fish had reached approximately 13 mm, and then the percentage decreased to a relatively low percentage at greater lengths.

Prevalence and mean intensity by fish length class were compared for the same taxa analyzed for copepod consumption. The smallest length class (3.0–7.0 mm) was chosen to segregate first-feeding fish from larger fish (Table 5). Prevalence increased through all length classes only for *Morone*. Prevalence in the other three taxa first increased and then decreased in larger length classes. Mean intensity varied little in *Morone* (the value of 7.0 was for one fish), darters, and herring but steadily increased in minnows.

The distribution of percent cumulative *Morone*, herring, darters, and minnows examined were plotted against the percent cumulative fish parasit-

ized in each respective taxa by total length (Fig. 6). The departure from the x-axis of the line that represents cumulative parasitized fish represents that fish length at which parasitism first occurred. White perch accounted for all parasitized fish at lengths less than 5.5 mm in the plot for *Morone*. The steep slope in the plots for *Morone* and darters reflects the high percentage of copepod consumption by these fish larvae and relatively high prevalence in first-feeding fish. In contrast, the plots for herring and minnows show a delay in plerocercoid parasitism corresponding to a delay in copepod consumption until the fish reach a length of approximately 13 mm TL. The line representing cumulative parasitized fish is steeper in the plot for minnows than for herring, which reflects the higher percentage of copepod consumption by minnows; both minnows and herring consumed a higher percentage of rotifers and cladocerans than did *Morone* or darters. The crossing of the two lines in the plot for minnows corresponded to a shift in diet from rotifers and cladocerans to copepods and cladocerans.

The cumulative distribution of parasitized *Morone* was significantly different ($\alpha = 0.01$) than the distribution of parasitized minnows (Kolmogorov-Smirnov $D = 21.4$, maximum difference = 44.0) and the distribution of parasitized herring ($D = 29.6$; maximum difference = 53.1). *Morone* acquired parasites at a faster rate at shorter body lengths than either herring or minnows. The distribution of parasitized minnows was not significantly different than the distribution of parasitized herring ($D = 30.2$, maximum difference = 12.7).

There was a strong correlation between prevalence and total length in *Morone* (Pearson $r = 0.67$; $p = 0.0001$), a weak, significant correlation of these variables in herring in fish lengths up to 16 mm (Pearson $r = 0.43$; $p = 0.03$) but a nonsignif-

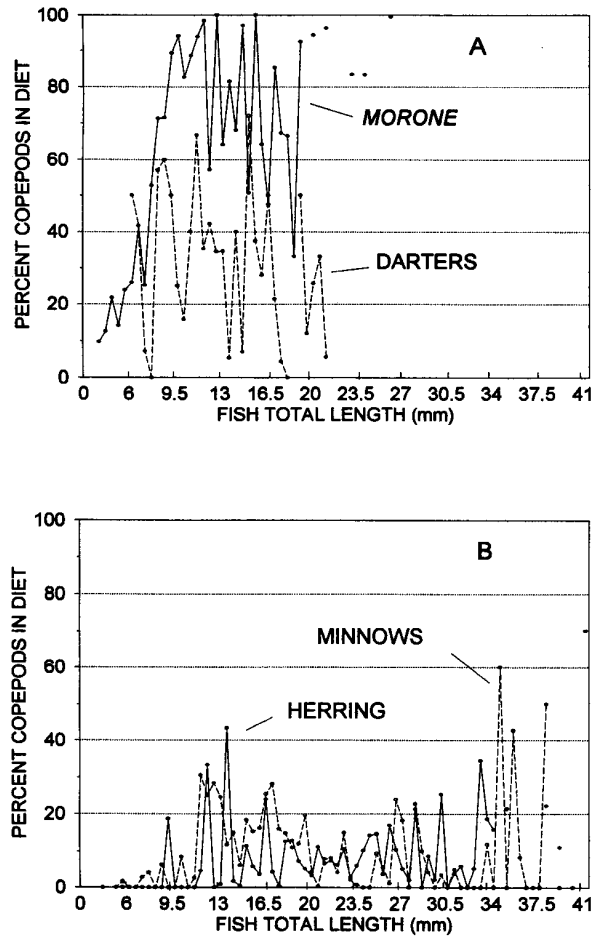


Fig. 5. Distributions of mean percent copepods in diets by 0.5-mm length class of four fish taxa that were parasitized by plerocercoids. Breaks in value lines indicate length classes in which no fish were examined. A) generally high copepod consumption that remained high throughout the length classes examined; B) low copepod consumption that remained low in most length classes.

icant correlation at greater lengths (Pearson $r = 0.14$; $p = 0.46$). There was a weak correlation in darters (Pearson $r = -0.37$; $p = 0.05$). The distributions for minnows were dissimilar where the cumulative percentage of parasitized larvae increased faster than the cumulative percent examined in the 13 mm to 25 mm length classes. This resulted in a positive correlation of prevalence with total length up to fish lengths of 15.5 mm (Pearson $r = 0.62$; $p = 0.01$) and a negative correlation (Pearson $r = -0.68$; $p = 0.0006$) at lengths of 16 mm and greater.

Twenty-one of the 26 stations sampled had parasitized fish. Eighty percent of those stations where no parasitized fish were collected were located in Albemarle Sound; however, prevalence at six of the 14 sound stations was higher than at any station in the river. Average plerocercoid prevalence was significantly higher in Albemarle Sound (11.7%) than in the river (1.4%; Kruskal-Wallis $\chi^2 = 4.18$; $p = 0.04$), but there were 73% fewer fish examined at the sound stations and 10 of the 15 sound stations had fewer than 10 parasitized fish. The 10 stations at which 10 or more parasitized fish were collected were evenly distributed between river and sound and nearly so between the Roanoke and Cashie rivers. There were no significant differences in prevalence among the Roanoke and Cashie rivers or Albemarle Sound (Kruskal-Wallis $\chi^2 = 1.62$; $p = 0.44$). The two stations in Middle River had fewer than 10 parasitized fish. The highest prevalence of plerocercoid parasitism in the sound did not occur at stations that had the highest overall copepod density. In the river, two of four (8, 11) stations with high prevalence also had high copepod density.

The differences in sampling effort by station for *Morone* and the other fish taxa reduced the possible station-by-station comparisons for prevalence and intensity. Three prevalence comparisons were made for *Morone*, minnows, herring, and darters:

TABLE 5. Plerocercoid prevalence (upper number of couplet) and mean intensity (\pm SD) (lower number of couplet) of four taxa of age-0 fish. *Morone* values are from all samples taken in 1984 to 1986 and 1988. Values for the other taxa are from stations 1, 4, 7, 8, 10, 13–15 in 1984 and 1985. Dash (—) indicates no fish were collected in that length class.

Taxa	Length Class (mm)					
	3.0–7.0	7.5–11.5	12.0–16.0	16.5–20.5	21.0–25.0	>25.5
<i>Morone</i> ^a	0.3	9.1	38.1	57.4	71.4	100
	1.0 \pm 0.2	1.1 \pm 0.3	1.2 \pm 0.4	1.4 \pm 0.7	2.6 \pm 1.7	7.0
Darters	11.1	21.4	4.6	5.9	0	—
	2.0	1.5 \pm 1.2	2.5 \pm 2.1	2.0	0	—
Minnows	1.9	5.8	25.0	13.8	7.6	1.2
	1.0	2.8 \pm 2.4	3.4 \pm 5.7	4.6 \pm 8.1	6.3 \pm 9.2	12.5 \pm 7.1
Herring	0.1	0.1	1.3	2.4	1.8	1.3
	1.0	3.0 ^b	1.0 \pm 0.4	1.3 \pm 0.7	1.4 \pm 1.1	1.0

^a One *Morone* was examined in the >25.5 mm length class.

^b Intensity value from one herring.

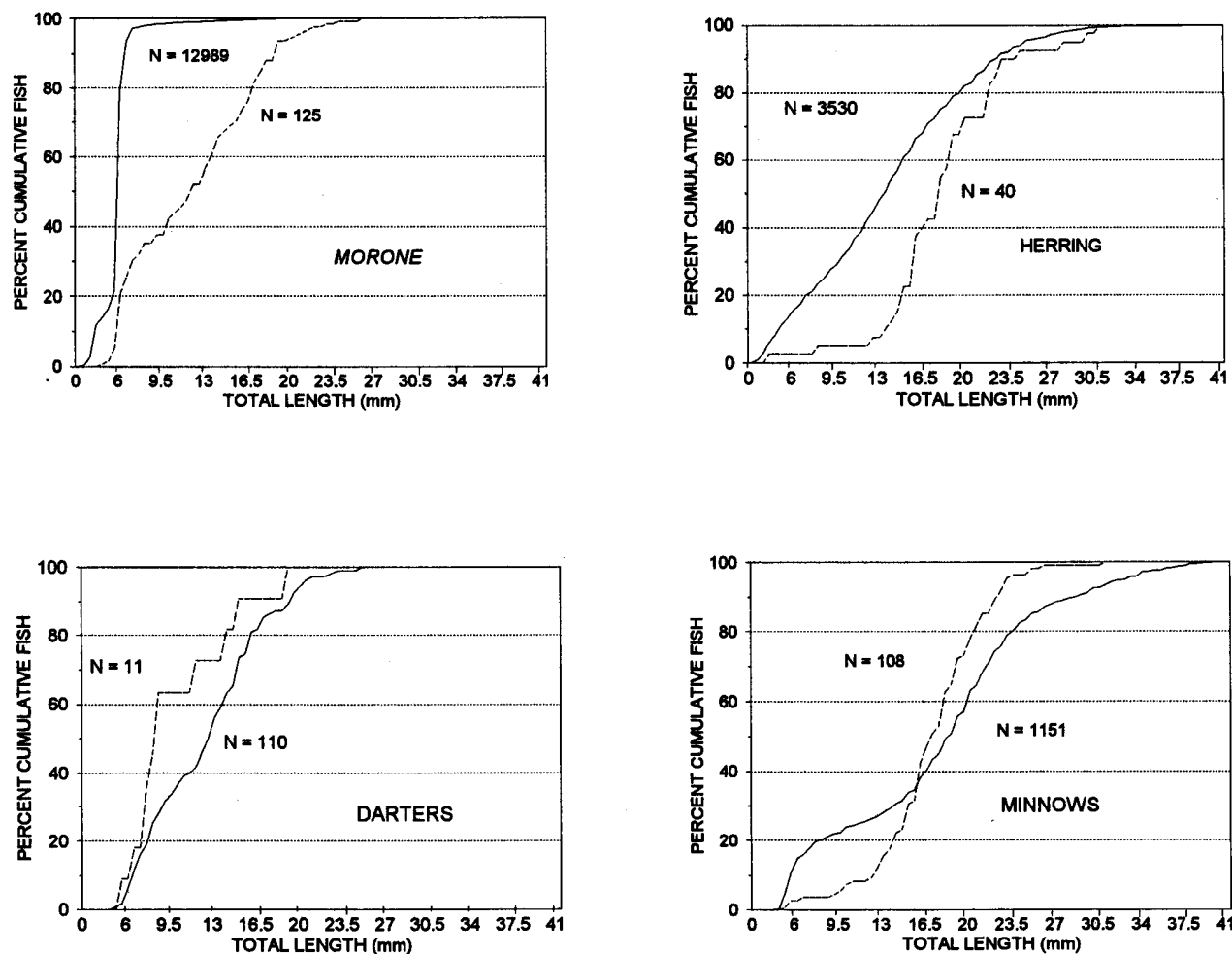


Fig. 6. The percent cumulative number of fish examined (solid line) and percent cumulative number of parasitized fish (dashed line) plotted against total length for the four most heavily parasitized fish taxa.

among stations common to all four taxa (1, 4, 7, 8, 10, 13, 14, 15) in 1984 and 1985; for *Morone* at all stations sampled in 1985 and 1986 (there was no parasitism of *Morone* in 1984 and all parasitism in *Morone* in 1988 was at sound stations); and for *Morone* at sound stations sampled in 1986 and 1988. There was a significant difference in prevalence in 1984 and 1985 among taxa at the common stations (ANOVA; $F = 3.06$; $df = 10, 21$; $p = 0.01$). The average prevalence for each taxa was compared using the Tukey multiple comparison ($\alpha = 0.05$, $df = 21$): average prevalence (7.6) in darters was significantly higher than that in minnows (6.5), *Morone* (1.9), or herring (0.9); average prevalence in herring was significantly lower than in the other taxa and average prevalence in minnows and *Morone* did not differ. There were no significant differences among stations. There were no significant differences among stations in the comparisons of

Morone in 1985 and 1986 (ANOVA, $F = 0.85$; $df = 13, 14$; $p = 0.61$) or in 1986 and 1988 (ANOVA, $F = 0.99$; $df = 6, 7$; $p = 0.49$). High variability (coefficient of variation ranged from 146.7 to 289) characterized all of these comparisons, some stations had low or no parasitized fish in one year and either no parasitized fish, a similar number of parasitized fish, or a high number of parasitized fish the following year. The only apparent trend was that station 8 was among the stations with higher prevalence in three of the four years.

Mean intensity in the river was highest at station 7 (5.9) and highest in the sound at station 24 (4.0). Ten of the 26 stations had a mean intensity of one, seven of which were in the river and three in the sound. There was no significant difference in mean intensity between the sound and river (Kruskal-Wallis $\chi^2 = 0.67$; $p = 0.41$) and no significant difference among the Roanoke and Cashie rivers

or Albemarle Sound (Kruskal-Wallis $\chi^2 = 0.48$; $p = 0.78$). There were no significant differences in mean intensity among the common stations for *Morone*, minnows, herring, and darters in 1984 and 1985 (Kruskal-Wallis $\chi^2 = 11.5$; $p = 0.12$) or among the four fish taxa at these stations (Kruskal-Wallis $\chi^2 = 0.06$; $p = 0.99$). There were no significant differences in *Morone* mean intensity among stations (1985 and 1986 combined; ANOVA, $F = 1.87$; $df = 14, 15$; $p = 0.12$) or among sound stations (1986 and 1988 combined; ANOVA, $F = 0.72$; $df = 11, 12$; $p = 0.70$). River and sound stations with high mean intensity in each year did not have high copepod density for the same year except for station 8 (highest in copepod density but third in mean intensity).

Plerocercoid prevalence for all taxa across all years was weakly correlated with river flow (Pearson $r = 0.22$; $p = 0.06$). There was a weak but significant correlation (Pearson $r = -0.29$; $p = 0.03$) between prevalence in *Morone* (all years) and river flow and a weak, significant correlation (Pearson $r = 0.36$; $p = 0.007$) between prevalence in *Morone* and copepod density. Copepod density was negatively correlated with river flow (Pearson $r = -0.41$; $p = 0.0006$) over all years, but the association was stronger in 1985 ($r = -0.69$; $p = 0.0007$) and 1986 ($r = -0.83$; $p = 0.0001$).

METACERCARIA

Metacercaria exhibited little internal development and were not identified. Metacercaria were spheroid and ranged in size from 0.12 mm to 0.5 mm across the long axis (mean = 0.29, $SD = 0.19$, $n = 10$) and from 0.08 mm to 0.28 mm across the short axis (mean = 0.19, $SD = 0.02$, $n = 10$). Metacercaria were found in the gut cavity (64.3%), tail (28.6%), and head (7.1%).

Metacercaria were found only in *Morone* (one parasite) and minnows (10 parasites). Prevalence and mean intensity were less than that found for plerocercoids (Table 2). Parasitized fish ranged from 8.0 mm TL to 21.5 mm TL, and 42.8% were less than 15 mm TL (mean TL = 15.6 mm).

Three stations (4, 7, and 8) of 26 sampled had fish parasitized by metacercaria: stations 7 and 8 in 1984 and stations 4 and 7 in 1985. Mean intensity was equal at stations 4 and 7 (1.7) and lowest at station 8 (1.0).

GLOCHIDIA

Thirteen hooked glochidia were collected from five age-0 fish taxa from 1984 through 1986 and 1988. *Morone* and herring accounted for 76.9% of all glochidia attacks. Only one multiple attack was found; a minnow with a glochidium on each of the upper and lower jaw. Prevalence was less than 0.5%

TABLE 6. Fish taxa that harbored glochidia in 1984–1986 and 1988. The mean total length and range of total length for each taxon was the same as in Table 2.

Taxa	n	Mean Host Length (mm)	Number of Glochidia	Prevalence	Mean Intensity
All Stations					
<i>Morone</i>	11,433	5.5	6	0.05	1.0
Stations 1, 4, 7, 8, 10, 13, 14, 15					
Herring	3,530	12.7	4	0.11	1.0
Minnows	1,151	6.2	2	0.17	1.0
Centrarchids	245	5.0	1	0.41	1.0
Total	16,359		13	0.07	1.0

in all affected taxa (Table 6). Mussel collections yielded one species of Anodontinae, *Anadonta implecata*, that could be the source of the collected glochidia. Other mussels found were *Lampsilis cariosa* (Lampsilinae, one empty shell), *Elliptio roanokensis* (Pleurobleminae, one empty shell, one living individual), and numerous live specimens of *Rangia cuneata*, *Sphaerium* sp., *Pisidium* sp., and *Corbicula fluminea*.

Glochidia were most prevalent in those age-0 fish less than 7.0 mm TL (69%); the mean total length of all affected taxa was 7.8 mm. Average prevalence was higher in the Cashie River (23.1%, stations 8 and 13) than in the Roanoke River (15.4%, stations 1 and 10), Middle River (15.4%, station 6), or Albemarle Sound (7.7%, station 15). All glochidia attacks occurred in the head region, divided between brain area (30.8%), lower jaw (30.8%), upper jaw (23.1%), and opercle (15.4%), including gill filaments when present.

PREDATORY COPEPODS

Four age-0 fish taxa were attacked by *Mesocyclops edax* in the samples examined from 1986 and 1988 (Table 6). *Morone* was the primary prey, accounting for 81.5% of the attacked fish, including six multiple attacks of two copepods each. One centrarchid also had a multiple attack. The mean total length of all attacked fish was 6.2 mm ($n = 81$, $SD = 2.5$, range 3.0–18.5 mm). Attacks were directed at the gut cavity (or yolk sac, 22.7%), tail (20.4%), lower jaw (13.6%), and head (10.2%). The remainder (33%) was distributed over the body. Forty-four percent of the attacks were made at the terminal ends of the fish. The majority of attacks (47.8%) were made from a lateral angle to the fish. Ventral attacks were 32.9% of the total, with the remainder coming at a dorsal angle.

Prevalence of *M. edax* attacks was only 1% or less for each attacked taxa and the highest intensity was 1.2% in centrarchids. Fish less than 8.0 mm TL accounted for 95% of the recorded attacks. The other 5% was comprised of three herring (mean

TABLE 7. Summary of attacks on age-0 fish by *Mesocyclops edax* in 1986 and 1988. Fish were examined from all stations.

Taxa ^a	Fish Examined			Number of Attacks		Prevalence	Mean Intensity
	n	Mean TL	Range	1986	1988		
<i>Morone</i>	22,710	5.5	2.0–26.5	27	39	0.3	1.1
Herring	12,434	6.7	2.5–38.0	8	6	0.1	1.0
Centrarchids	621	5.6	4.5–9.0	1	4	0.6	1.2
Suckers	93	15.2	10.0–17.5	0	1	1.0	1.0
Total	35,858	6.0		38	50	0.2	1.1

^a Taxa (and number examined) that were not attacked were minnows (4,307), darters (657), carp (107), yellow perch (32), Atlantic silverside (32), brown bullhead (30), pirate perch (23), and channel catfish (13).

TL = 16.2 mm) and one sucker (16.5 mm). Two genera of parasitic copepods (*Ergasilus* and *Argulus*) and one predatory cladoceran (*Leptodora*) were collected in zooplankton samples, but there was no evidence of parasitism or predation on age-0 fish by these genera. These copepods were, in general, larger than the majority of the fish examined.

In 1986, 52.6% of the attacks occurred at station 12, more than twice the percentage at any other station. Forty-two percent of the attacks occurred within a single sample (station 12; May 13, 1986). Attacks occurred over a 1-mo period (May 1 to June 4), with a peak of attacks on May 15 (23.7%) and on May 31 (42.1%). In 1988, 38% of the attacks occurred at station 11 and 30% at station 13. Attacks occurred over only a 9-d period (May 28 to June 5, 1988), with 88% of the attacks occurring between May 30 and June 1. The period of May 30 to June 5 over both years accounted for 68.2% of all *M. edax* attacks. Stations 6, 11, 12, and 13 accounted for 81% of the attacks over both years. The highest percentage of attacks was found in the Cashie River and at those sound stations in immediate proximity to the Cashie (52.3%); only 27.3% were from the Roanoke River and 20.4% from Middle River. There were no attacks at sound stations that were not directly adjacent to the river mouths.

Correlation analysis indicated that there was no association between *Morone* density and cyclopoid attacks by date in 1986 (Pearson $r = 0.06$; $p = 0.80$) or in 1988 (Pearson $r = 0.10$; $p = 0.64$), and no association between *Morone* density by station and cyclopoid attacks in either year (1986: Pearson $r = 0.09$; $p = 0.71$; 1988: Pearson $r = 0.16$; $p = 0.56$). There was no association between herring density and cyclopoid attacks by date in either year (1986: Pearson $r = -0.16$; $p = 0.51$; 1988: Pearson $r = -0.34$; $p = 0.11$) or between herring density by station and cyclopoid attacks (1986: Pearson $r = 0.29$; $p = 0.17$; 1988: Pearson $r = -0.39$; $p = 0.14$). Attacks on other taxa were not analyzed since there were so few of them.

Discussion

PLEROCERCOIDS

Procercooids of *Proteocephalus* parasitize copepods as a primary host and become established in age-0 fish as plerocercoids after the fish have ingested the infested copepods or an infested fish (Cheng 1973). Plerocercoids were the primary parasite found in age-0 fish in this study. Although these plerocercoids had not developed to where they could be specifically identified, the general characteristics of the scolex and the body sites of infestations suggested that they were *Proteocephalus*. This putative identification is supported by the fact that no fish were found to be parasitized by plerocercoids that had not begun feeding and by the relatively high percentage of copepods in the larval fish diets.

FOOD HABITS

Differing food habits of *Morone*, minnows, herring, and darters were reflected in plerocercoid prevalence. High copepod consumption led to high plerocercoid prevalence and declining consumption was similarly followed by declining prevalence. *Morone* and darters had higher copepod consumption and prevalence at first-feeding lengths than did minnows or herring. The latter two taxa delayed copepod consumption, perhaps due to smaller mouth gape. This was more evident in herring than in minnows. Prevalence increased rapidly in minnows and herring in the 13–25 mm length range as their diet included progressively greater proportions of copepods. Prevalence then declined at greater fish lengths as copepod consumption declined. In contrast, *Morone* copepod consumption remained high and prevalence increased throughout the length classes examined. Prevalence in darters was initially high but decreased as fish length increased even though copepod consumption remained similar. This decrease in prevalence may have been due to having examined progressively fewer fish as total length

increased caused by net avoidance as darters became more benthic.

The correlations of plerocercoid prevalence and total length followed the observed changes in copepod consumption. The strongest correlation was in *Morone* as would be expected since prevalence increased with fish length at all lengths examined. The correlation of total length and prevalence in darters was negative, although prevalence was significantly higher than the other three fish taxa. The pattern of prevalence in minnows and herring was similar: an increase up to intermediate fish lengths coinciding with a low but steady increase in copepod consumption and then both decreased at greater fish lengths. This resulted in a positive correlation in minnows up to 15.5 mm TL but a negative correlation at greater lengths. The correlation in herring was positive but not significant up to 15.5 mm TL, and significant and positive at greater fish lengths.

This relationship of plerocercoid prevalence and copepod consumption is similar to that found by Govoni (1983) and Fischer and Kelso (1990). Govoni found increasing prevalence of the cestode *Scolex pleuronectis* as fish length and copepod diet increased in age-0 Gulf menhaden (*Brevoortia patronus*) and Atlantic croaker (*Micropogon undulatus*). Fischer and Kelso found that prevalence of *Proteocephalus ambloplites* plerocercoids in age-0 largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) was positively correlated with the percent of copepods in the diets.

Prevalence computed over the entire range of fish lengths examined may underestimate the true impact of parasitism. Although overall prevalence for minnows and darters was relatively high, it was considerably less than that found in specific length classes. Overall prevalence in *Morone* was two orders of magnitude less than in intermediate and large length classes, probably as a result of the high number of first-feeding fish examined. If copepods were the source of the plerocercoids then changes in copepod consumption should be reflected in the correlation of prevalence with total length, and this was true for the four fish taxa examined by correlation.

Infestation in age-0 fish may be due to random encounters with infested copepods since there were no significant differences in prevalence among stations for any of the fish taxa and no significant differences in prevalence among the Roanoke and Cashie rivers or Albemarle Sound. The highest plerocercoid prevalence in the sound was not related to copepod density and only half of the river stations with high prevalence also had high copepod density.

Mortality of age-0 fish caused by plerocercoids

would be related to the time of exposure and, if the migrating plerocercoids did not damage a vital organ, the intensity of parasites. The fish in this study were no more than 2 mo old and the majority were about 2 wk old. This amount of time may not be sufficient to be able to detect mortality attributable to plerocercoids. The intensity values may only indicate an initial level of parasitism that would be within the fish's tolerance for plerocercoids. Only one fish had more than one taxon of parasite or predator so vulnerability to new parasites or predators may not increase with the acquisition of a low number of parasites in the time period covered in this study.

Paperna and Zwerner (1976) found that age-0 striped bass and white perch (ca. 47 mm TL) were parasitized by proteocephalid plerocercoids as well as *Scolex pleuronectis*. Liver lesions, caused by the encapsulation of the parasite, led to extensive fibrosis of the visceral organs, but these lesions did not appear until the fish were from 4 mo old to 5 mo old.

METACERCARIA

Metacercariae do not follow the same strategy as plerocercoids in that this parasite actively penetrates the host tissue, thus the host does not need to have feeding capability to become infested. The only requirement is physical contact between the metacercarian and a suitable fish host.

Metacercariae were not abundant in any of the taxa examined in this study. Prevalence was less than that reported by Paperna and Zwerner (1976) for age-0 striped bass from upper tributaries of Chesapeake Bay and less than that in larval inland silverside (*Menidia beryllina*), bluegill, and shad (*Dorosoma*) (Fischer and Kelso 1988). Lemly (1982) found that metacercarial prevalence of *Uvulifer ambloplitis* was about 8% in ≤ 30 mm bluegill and that prevalence increased as bluegill length increased over the summer months. Similar results were found for *Allocanthochasmus* sp. (Fischer and Kelso 1990) in all length classes of bluegill greater than 15 mm TL and for *Diplostomulum* sp. and *Posthodiplostomum* sp. in age-1 bluegill (Davis and Miller 1989).

Metacercarial mean intensity in this study was generally less than that in age-0 bluegill and largemouth bass (Lemly and Esch 1984; Fischer and Kelso 1990) and age-1 bluegill (Davis and Miller 1989). These latter studies reported variation in intensity of different genera of metacercarial trematodes in these fish species. Mean intensity was seasonal, increasing from winter to summer (Davis and Miller 1989) and peaking in October in all length classes except 15 mm TL (Fischer and Kelso 1990). The relatively younger fish in this study

would have had a shorter time of exposure to become infested than those in the other studies. Lemly (1982) suggested that smaller bluegill (<30 mm) had too short of an exposure to become infested with metacercaria.

The low prevalence and intensity of metacercaria in this study may be due, in part, to the time and location of sample collection. The seasonal trends shown in Lemly (1982) and Fischer and Kelso (1990) indicate that metacercarial prevalence and intensity was lowest in spring when fish were small (<35 mm) and that the greatest prevalence and intensity was associated with quiet water in vegetated areas (habitat of the snail host). My samples were collected in the spring in mid-river in relatively strong current and were not associated with vegetation. The relatively higher prevalence and intensity in minnows in this study may indicate that they had been associated with the vegetated shoreline habitats prior to collection. *Morone* and herring would be less likely to become infested than minnows or darters in the Roanoke River since *Morone* and herring do not utilize the vegetated areas (Cooper et al. in press) but move through the river delta into Albemarle Sound. The collection areas of Paperna and Zwerner (1976) were most similar to this study, but the mean length (47 mm) of their age-0 striped bass (collected in July) were nearly twice the maximum length of *Morone* in this study.

The penetration of the host by the metacercaria can cause pathological changes in the internal organs (Paperna and Zwerner 1976), and these changes may be more acute in developing fish where the size of the parasite is much larger in relation to the size of the host. Deaths may be due to mechanical tissue damage resulting from parasite migration as well as their release of proteolytic enzymes (Millemann and Knapp 1970). Lemly (1982) found that heavily infested bluegill had significantly lower weight and body condition than did lightly infested individuals of the same length class. Heavily infested fish may have impaired swimming and feeding ability if metacercaria became concentrated in the caudal peduncle and isthmus. These characteristics were not addressed in this study.

GLOCHIDIA

The initial attachment of glochidia to its host has been characterized as random and relies only on physical contact to stimulate closure of the valves (Pennak 1978). In this study, all of the attacks were in the head region (including gills), which may indicate that these fish were attacked while foraging, perhaps while attempting to capture the glochidia. Mozley (1984) reported finding glochidia in age-0 fish stomachs in Albemarle Sound. The presence

of glochidia on a fish, however, does not necessarily indicate that the fish is a proper host. Glochidia of many mussel species are host-specific (Neves et al. 1985), and glochidia that become attached to an unsuitable host may release it voluntarily or be sloughed off by the host (Weaver et al. 1991).

Prevalence of glochidia in this study was one to two orders of magnitude less than that of age-0 striped bass (Paperna and Zwerner 1976), bluegill, and largemouth bass (Fischer and Kelso 1990), and intensity was half as much (Fischer and Kelso 1990). The short time of exposure for fish in this study may account for the differences in prevalence and intensity.

Glochidia may increase the metabolic expenditure of larval fish by increasing drag of swimming larvae and preventing the efficient capture of prey, particularly if the glochidia are attached to the fish's jaws. Carbine (1942) suggested that the sphaeriid clam *Musculium securis* attached to the jaws of northern pike fingerlings may remain there long enough to cause the death of the pike. This clam-northern pike interaction was proportionately the same as the glochidia attached to fish in this study. Moles (1983) experimentally infested coho salmon *Oncorhynchus kisutch* fry with glochidia of *Anadonta oregonensis*. Those fish with less than 50 attached glochidia showed reduced growth and fat content and those fish with 50 or more glochidia died within 30 d. Cunjak and McGladdery (1991) found that the mean condition factor of Atlantic salmon (*Salmo salar*) young-of-year was significantly lower in those fish that had a greater prevalence of glochidium.

Little is known about the mussel species inhabiting the lower Roanoke River system (Shelley 1987), but the unionid mussel population has been characterized as decreasing (Clarke 1983). Only two potential sources of hooked glochidia have been reported to date, *Anodonta implicata* found in the present study and *Alasmodonta* sp. (Cooper and Rulifson 1993). The relatively low number of glochidia found attached to age-0 fish may indicate a low population level of unionid mussels in the Roanoke River.

PREDATORY COPEPODS

The prevalence of attacked *Morone* in this study was similar to that of Smith and Kernehan (1981) but less overall than the 3.7% reported by Hartig et al. (1982) for alewife (*Alosa pseudoharengus*) larvae. Individual sample values can be much greater (21%; Hartig and Jude 1984). Smith and Kernehan (1981) did not report any multiple attacks in contrast to the low percentage found in this study, in Hartig et al. (1982), and in Hartig and Jude (1984). The majority of attacks were directed at the

head and tail areas in all of these studies except Smith and Kernehan (1981) where the majority of larvae were attacked at the yolk-sac.

Predatory copepods are more limited in the size selection of their prey, concentrating, for the most part, on smaller, less robust fish larvae (Smith and Kernehan 1981; Hartig et al. 1982; Hartig and Jude 1984). In the above studies, the majority of attacked fish was less than 9 mm TL, similar to the size distribution found in this study, but larger larvae can be attacked (14–18.5 mm, this study; 21–25 mm, Hartig et al. 1982; 10–14 mm, Hartig and Jude 1984).

Morone were attacked at a much greater rate than any other taxa in this study. The density of *Morone* was much higher than any other fish taxa in this study and their rate of encounter would probably be higher. *Morone* have limited swimming ability at the attacked lengths (7.0 mm and less); however, they would be vulnerable only for a short time as the water they are moving with would pass through the river in a few days and their swimming ability would quickly develop to afford an escape. Attacks were confined to the river stations and one sound station immediately adjacent to the river. This would indicate that *Morone* in the sound were either too large or too scattered for successful capture by copepods.

Hartig and Jude (1984) suggested that the attacks by the copepods *Diacyclops thomasi* and *Acanthocyclops vernalis* on larger larvae were in contrast to the findings of Kerfoot (1977) that cyclopoid copepods avoided attacking larger prey. Kerfoot was referring to *Diaptomus bicuspidatus* avoiding larger *Bosmina* but this was not just a response to size but to shape as well. The increased difficulty in manipulating the round, hard carapace of larger *Bosmina* would make escape more likely. This may not be as much a factor with soft-bodied fish larvae that have limited swimming ability or an attenuated body shape (e.g., herring) that facilitates grasping by the copepod. Li and Li (1979) suggested that narrow body shape, carapace hardness, and swimming mode were the major factors in prey selection by *Acanthocyclops vernalis*.

The data of Hartig et al. (1982), Hartig and Jude (1984), and that of this study clearly show that cyclopoid copepods will attack prey at least 15 times larger in length than themselves but these attacks occurred at a low percentage, which may indicate that successful attacks are few. These larger fish may have been in poor condition and therefore more vulnerable to attack. Williamson (1980) has found that the type of motion by potential prey through the water influenced the probability of attack by *Mesocyclops edax*: the smooth movement of rotifers and ciliates reduced the attack probability,

but the jerky motion of the cladoceran *Bosmina* increased the attack probability. Attacked *Bosmina* will fold the antennae flush with the carapace and passively sink in the water column after being attacked and this lack of movement was apparently insufficient to stimulate the mechanoreceptors of the attacking copepod and the cladoceran could escape (Kerfoot 1977). Rapid vibration of the tail by fish larvae, particularly recently-hatched larvae with limited swimming ability, increases their probability of being detected and attacked by copepods (Lillelund and Lasker 1971).

Spatial and temporal proximity were the key factors in copepod attacks on larval fish examined by Hartig et al. (1982) and Hartig and Jude (1984), but the likelihood of encounters and attacks was higher in areas of high abundance of either predator or prey. The data in this study suggested that spatial and temporal proximity may be more important than densities as there was no correlation between *Morone* density and copepod attacks.

Hartig et al. (1982) concluded that cyclopoid predation was a significant mortality factor of larval fish, in contrast to Smith and Kernehan (1981), and stated that their estimates of predation might be low because the addition of formaldehyde causes the copepods to release their prey (Lillelund and Lasker 1971). Predation estimates in the present study might also be low because of formalin additions but also because of the sinking behavior of *Mesocyclops* when handling large prey (Williamson 1980). This behavior may have prevented the collection of some attacked fish.

RIVER FLOW

Altered river flow was suggested as a cause for low recruitment of striped bass because of its effect on temporal and spatial timing of zooplankton and larval striped bass. Stevens et al. (1985) attributed reduced zooplankton production, caused by water flow variations, as one factor in the decline of striped bass in the Sacramento-San Joaquin River. Most fish larvae rely on chance encounters with appropriately-sized zooplankton for successful feeding and depend upon drift to reach their nursery areas (Marcy 1976). Changes in river flow, particularly during the spawning season, may alter the developmental timing of fish and zooplankton populations. River flow may indirectly regulate parasitism by the same effect it has on the spatial and temporal proximity of zooplankton and fish larvae, that is, controlling the juxtaposition of infested copepods with feeding age-0 fish. There is evidence from my study that suggest that this may be true: 1) a lower plerocercoid prevalence in *Morone*, darters, minnows, and herring under high flow conditions than under moderate or low flow condi-

tions; 2) a negative correlation between copepod density and river flow; 3) increased copepod consumption under low flow conditions; and 4) a weak but significant positive correlation between prevalence in *Morone* and copepod density. The low values of some correlations are not surprising since factors that operate over a large area are being correlated with specific results. There are other factors entering into these observed effects that were not measured. These conclusions are based on observational data and the resulting correlations must be viewed cautiously. Flow rates were measured near the dam and may not reflect the exact conditions at the study site, but there is evidence that links river flow with striped bass recruitment in the Roanoke River (Rulifson and Manooch 1990) and in California (Stevens et al. 1985). Confirmation of these conclusions would require a more controlled experimental approach.

ACKNOWLEDGMENTS

I would like to thank David Zwerner for the examination of parasites and predators, William Adams and Arthur Bogan for examination of mussels, and William Bell, Kay Evans, Donna Hardee, Nancy Hobbs, Marsha Shepherd, and Scott Wood (East Carolina University) for their ideas and assistance. Photographic assistance was given by Tim Charles (East Carolina University). The valuable suggestions by two anonymous reviewers were appreciated. Sample collection and gut analysis were done under contract F27-4 from the North Carolina Wildlife Resources Commission to Roger A. Rulifson.

LITERATURE CITED

- AUER, N. (ed.). 1982. Identification of larval fishes of the Great Lakes Basin with emphasis on the Lake Michigan drainage. Great Lakes Fisheries Commission, Ann Arbor, Michigan. Special publication 82-3.
- BURCH, J. B. 1973. Freshwater Unionacean Clams (Mollusca: Pelecypoda) of North America. Biota of Freshwater Ecosystems, Identification Manual No. 11. Environmental Protection Agency, Washington, D.C.
- CARBINE, W. F. 1942. Sphaeriid clams attached to the mouth of young pike. *Copeia* 1942:187.
- CHENG, T. C. 1973. General Parasitology. Academic Press, New York.
- CLARKE, A. H. 1983. Status survey of the Tar River spiny mussel. Final Report to United States Fish and Wildlife Service for contract 14-16-0004-82-014. Asheville, North Carolina.
- COOPER, J. E. AND R. A. RULIFSON. 1993. Benthic biocriteria assessment of the lower Roanoke River, North Carolina. Final Report to Weyerhaeuser Paper Company. East Carolina University Institute for Coastal and Marine Resources, Greenville, North Carolina. Contribution Series No. ICMR 93-03.
- COOPER, J. E., S. F. WOOD, AND R. A. RULIFSON. in press. Extent of water lily (*Nuphar lutea*) beds and their use by larval fish in the Roanoke River, NC. *Journal of the Elisha Mitchell Scientific Society*
- CUNJAK, R. A. AND S. E. MCGLADDERY. 1991. The parasite-host relationship of glochidia (Mollusca: Margaritiferidae) on the gills of young-of-the-year Atlantic salmon (*Salmo salar*). *Canadian Journal of Zoology* 69:353-358.
- DAVIS, S. R. AND G. C. MILLER. 1989. Parasites of some fishes from B. Everett Jordan Reservoir, North Carolina. *Journal of the Elisha Mitchell Scientific Society* 105:97-114.
- FISCHER, S. A. AND W. E. KELSO. 1988. Potential parasite-induced mortality in age-0 bluegills in a floodplain pond of the lower Mississippi River. *Transactions of the American Fisheries Society* 117:565-573.
- FISCHER, S. A. AND W. E. KELSO. 1990. Parasite fauna development in juvenile bluegills and largemouth bass. *Transactions of the American Fisheries Society* 119:877-884.
- GEISE, G. L., H. B. WILDER, AND G. G. PARKER, JR. 1979. Hydrology of major estuaries and sounds of North Carolina. United States Geological Survey Water Resources Investigations 79-46. Reston, Virginia.
- GORDON, D. M. AND M. E. RAU. 1982. Possible evidence for mortality induced by the parasite *Apatemon gracilis* in a population of brook stickleback (*Culea inconstans*). *Parasitology* 84: 41-47.
- GOVONI, J. J. 1983. Helminth parasitism of three larval fishes in the northern Gulf of Mexico. *Fishery Bulletin* 81:895-898.
- HARTIG, J. H., D. J. JUDE, AND M. S. EVANS. 1982. Cyclopoid predation on Lake Michigan fish larvae. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1563-1568.
- HARTIG, J. H. AND D. J. JUDE. 1984. Opportunistic cyclopoid predation on fish larvae. *Canadian Journal of Fisheries and Aquatic Sciences* 41:526-532.
- KERFOOT, W. C. 1977. Implications of copepod predation. *Limnology and Oceanography* 22:316-325.
- LEMLY, A. D. 1982. Effects of a larval parasite on the growth and survival of young bluegill. *Proceedings, Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 34: (1980)263-274.
- LEMLY, A. D. AND G. W. ESCH. 1984. Effects of the trematode *Uvulifer ambloplitis* on juvenile bluegill sunfish, *Lepomis macrochirus*: Ecological implications. *Journal of Parasitology* 70:475-492.
- LI, J. L. AND H. W. LI. 1979. Species-specific factors affecting predator-prey interactions of the copepod *Acanthocyclops vernalis* with its natural prey. *Limnology and Oceanography* 24:613-626.
- LILLELUND, K. AND R. LASKER. 1971. Laboratory studies of predation by marine copepods on fish larvae. *Fishery Bulletin* 69: 655-667.
- LIPPSON, A. J. AND R. L. MORAN. 1974. Manual for the identification of early developmental stages of fishes of the Potomac River Estuary. Martin Marietta Corporation, Baltimore, Maryland.
- MARCY, B. C., JR. 1976. Planktonic fish eggs and larvae of the lower Connecticut River and the effects of the Connecticut Yankee Plant including entrainment. *American Fisheries Society Monograph* 1:115-140.
- MARGOLIS, L., G. W. ESCH, J. C. HOLMES, A. M. KURIS, AND G. A. SCHAD. 1982. The use of ecological terms in parasitology. *Journal of Parasitology* 68:131-133.
- MCCAFFERTY, W. P. 1981. Aquatic Entomology. The Fishermen's and Ecologists' Illustrated Guide to Insects and Their Relatives. Jones and Bartlett Publishers, Inc. Boston, Massachusetts.
- MERRITT, R. W. AND K. W. CUMMINS. 1984. An Introduction to the Aquatic Insects of North America. Second edition. Kendall/Hunt Publishing Co., Dubuque, Iowa.
- MILLEMANN, R. E. AND S. E. KNAPP. 1970. Pathogenicity of the "salmon poisoning" trematode, *Nanophyetus salmincola*, to fish. *American Fisheries Society Special Publication* 5:209-217.
- MOLES, A. 1983. Effect of parasitism by mussel glochidia on growth of coho salmon. *Transactions of the American Fisheries Society* 112:201-204.
- MOZLEY, S. C. 1984. Zooplankton and diets of juvenile blueback herring in the Chowan River and Albemarle Sound, 1982-1983, p. 81-105. In S. E. Winslow, N. S. Sanderlin, S. C. Mozley, and R. A. Rulifson (eds.), North Carolina Anadromous

- Fisheries Management Program, Progress Report for Project AFCS 22-1. Morehead City, North Carolina.
- NEVES, R. J., L. R. WEAVER, AND A. V. ZALE. 1985. An evaluation of host fish suitability for glochidia of *Villosa vanuxemi* and *V. nebulosa* (Pelecypoda: Unionidae). *American Midland Naturalist* 113:13-19.
- OLNEY, J. E., G. C. GRANT, F. E. SCHULTZ, C. L. COOPER, AND J. HAGEMAN. 1983. Pterygiophore-interdigitation patterns in larvae of four *Morone* species. *Transactions of the American Fisheries Society* 112:525-531.
- PAPERNA, I. AND D. E. ZWERNER. 1976. Parasites and diseases of striped bass, *Morone saxatilis* (Walbaum), from the lower Chesapeake Bay. *Journal of Fish Biology* 9:267-281.
- PENNAK, R. W. 1978. Freshwater Invertebrates of the United States. Ronald Press, New York.
- ROSENTHAL, H. 1967. Parasites in larvae of the herring (*Clupea harengus* L.) fed with wild plankton. *Marine Biology* (Berlin) 1: 10-15.
- RULIFSON, R. A. 1984. Food and feeding of young striped bass in western Albemarle Sound, North Carolina. Completion report for Contract No. C-1366 to North Carolina Department of Natural Resources and Community Development. Greenville, North Carolina.
- RULIFSON, R. A., J. E. COOPER, AND D. W. STANLEY. 1988. Larval striped bass and the food chain: Cause for concern? p. 213-224. In W. L. Lyke and T. J. Hoban (eds.), Proceedings Symposium on Coastal Water Resources. American Water Resources Association, Bethesda, Maryland.
- RULIFSON, R. A., J. E. COOPER, D. W. STANLEY, M. E. SHEPHERD, S. F. WOOD, AND D. D. DANIEL. 1992. Food and feeding of young striped bass in Roanoke River and Western Albemarle Sound, North Carolina, 1984-1991. Completion Report for Project F-27, Striped Bass Investigations to North Carolina Wildlife Resources Commission, Greenville, North Carolina.
- RULIFSON, R. A. AND C. S. MANOOCH, III. 1990. Recruitment of juvenile striped bass in the Roanoke River, North Carolina, as related to reservoir discharge. *North American Journal of Fisheries Management* 10:397-407.
- SAS INSTITUTE, INC. 1988. SAS/STAT User's Guide, Release 6.03 Edition. Cary, North Carolina.
- SHELLEY, R. M. 1987. Unionid molluscs from the Upper Cape Fear River Basin, North Carolina, with a comparison of the faunas of the Neuse, Tar, and Cape Fear drainages (Bivalvia: Unionacea). *Brimleyana* 13:67-89.
- SMITH, R. E. AND R. J. KERNEHAN. 1981. Predation by the free-living copepod *Cyclops bicuspidatus thomasi*, on larvae of the striped bass and white perch. *Estuaries* 4:81-83.
- STEVENS, D. E., D. W. KOHLHORST, L. W. MILLER, AND D. W. KELLEY. 1985. The decline of striped bass in the Sacramento-San Joaquin Estuary, California. *Transactions of the American Fisheries Society* 114:12-30.
- WEAVER, L. R., G. B. PARDUE, AND R. J. NEVES. 1991. Reproductive biology and fish hosts of the Tennessee clubshell *Pleurobema oviforme* (Mollusca:Unionidae) in Virginia. *American Midland Naturalist* 126:82-89.
- WILLIAMSON, C. E. 1980. The predatory behavior of *Mesocyclops edax*: Predator preferences, prey preferences, and starvation-induced changes. *Limnology and Oceanography* 25:903-909.
- YAMAGUTI, S. 1959. Systema Helminthum. Vol. 2. The Cestodes of Vertebrates. Interscience, New York.
- ZINCONI, L. H., JR. AND R. A. RULIFSON. 1992. Reply to the comments of Thomas M. Leahy, III. *Rivers* 3:114-121.

Received for consideration, December 2, 1992

Accepted for publication, June 23, 1995