Abstract. – Age, growth, and mortality of larval Atlantic bumper *Chloroscombrus chrysurus* were compared between cruise samples collected during August–September 1986 and September 1987 off the Louisiana–Mississippi barrier islands. Calcein-marked Atlantic bumper otoliths (sagitta) were used for age validation. The first growth increment formed on the sagitta approximately 2 days after spawning, and daily increments formed thereafter. Length at hatching was estimated at 0.7–0.9 mm SL. Growth rates were determined from sagitta and length-frequency data. Highest growth rates occurred in August 1986 (0.40 mm/day) and were associated with highest mean temperature and zooplankton standing stock estimates. The length exponent for Atlantic bumpers' dry weight-length relationship was 3.25. Instantaneous daily mortalities (M) ranged from 0.62 in August 1986 to 0.17 in late September 1987.

Age validation, growth, and mortality of larval Atlantic bumper (Carangidae: *Chloroscombrus chrysurus*) in the northern Gulf of Mexico

Deborah L. Leffler

Florida Marine Research Institute, Florida Department of Natural Resources
3 Jackson Street, Fort Walton Beach, Florida 32548

Richard F. Shaw

Coastal Fisheries Institute, Center for Wetland Resources
Louisiana State University, Baton Rouge, Louisiana 70803-7503

Atlantic bumper *Chloroscombrus chrysurus*, a carangid, is an abundant coastal pelagic fish that is widely distributed in the western Atlantic and Gulf of Mexico (Leak 1977). Exploratory fishing surveys indicate that Atlantic bumper may be abundant enough in the northern Gulf of Mexico to harvest commercially (Juhl 1966, Bullis and Carpenter 1968, Bullis and Thompson 1970, Klima 1971). Presently, Atlantic bumper is mainly a commercial bycatch, marketed primarily for petfood, with little potential as a food fish in the United States (Klima 1971, Leak 1977). It, however, may be an important food source for many predatory fish (Reintjes 1979).

Atlantic bumper spawn primarily in nearshore coastal waters, especially off Louisiana and Mississippi (Boschung 1957, Perret et al. 1971, Christmas and Waller 1973, Ditty 1986, Shaw and Drullinger 1990), and the larvae of this species were most abundant during surveys off the Louisiana–Mississippi (LA–MS) barrier islands (Stuck and Perry 1982, Leffler 1989). Larvae have been collected from June to October, with abundance peaks usually occurring in July or August (Sabins 1973, Stuck and Perry 1982, Williams 1983, Ditty 1986).

Very little early-life-history work has been conducted on Atlantic bumper (Shaw and Drullinger 1990). Early-life-history information is a critical component in estimating future year-class strength (Cushing 1975, Leak and Houde 1987). For example, slow larval growth rates influence mortality by extending the duration of vulnerable larval stages (Bannister et al. 1974, Houde 1987), while a fast growth rate can possibly increase interaction with predators (Pepin 1991), thereby influencing recruitment. Early-life-history data are needed for Atlantic bumper to determine their ecological role and to assist in the prudent development of any directed fishery.

The abundance of Atlantic bumper over a wide geographic range, their perceived potential as a commercial resource, and their probable ecological importance as a forage fish, provided the impetus for conducting this larval age-and-growth study. The goals of this ichthyoplankton study were to (1) validate the periodicity of growth increments on larval and juvenile Atlantic bumper otoliths, (2) estimate Atlantic bumper length at hatching, (3) estimate the age structure of the sample population, (4) describe larval growth and mortality rates, and (5) relate larval growth

and mortality rates to environ-
mental parameters and food
availability.

Materials and methods

Sampling procedure

Atlantic bumper larvae were col-
lected during five cruises off the
Louisiana–Mississippi barrier
islands in the Gulf of Mexico
(Chandeleur Is., Ship I., and
Horn I.; 29°50′–30°15′N and
88°40′–89°00′W; Fig. 1). Three
cruises were completed in 1986
(5–7 Aug., 8–9 Sept., and 22–24
Sept.) and two in 1987 (8–10 and
24–26 Sept.). Adverse weather
conditions canceled the sched-
uled August 1987 cruise.

The sampling design consisted
of a 4×4 grid of stations (N 16)
randomly sampled on two con-
secutive nights, and a 3×3 grid
of stations (N 9) randomly sam-
pled during daylight, starting 12
hours after the initiation of the
first nocturnal sampling. The
sampling grid had a fixed com-
pass orientation with respect to
three windowshade, subsurface
current drogues (five drogues were used in 1987) which
were released at the beginning of each cruise (Shaw
et al. 1988). The change to five drogues in 1987 allowed
for a more defined sampling grid. Surface-water
temperature and salinity, as well as water depth, were
recorded for each ichthyoplankton tow.

Three-minute surface tows were taken at ~1.0 m/s
using a 60 cm "bongo-type" plankton sampler fitted
with a flowmeter (General Oceanics model 2030). In
1986, samples were collected using a 202 μm mesh net,
while in 1987 a 333 μm mesh net was used. During the
two cruises in September 1987, the bongo sampler was
fitted with one 202 μm mesh net and one 333 μm mesh
net for comparisons of daytime collections. Atlantic
bumper collected using the two mesh sizes were placed
into 1 mm size-classes and tested for differences using
a Median test (α 0.05; SAS Inst. 1985). Ichthyoplank-
ton samples used for age determination were preserved
with 95% ethanol, stored in ice water, and later trans-
ferred to 70% ethanol in the lab.

Live larval and juvenile Atlantic bumper were col-
lected for an age-validation experiment and length-
weight measurement analysis by dipnetting the jelly-
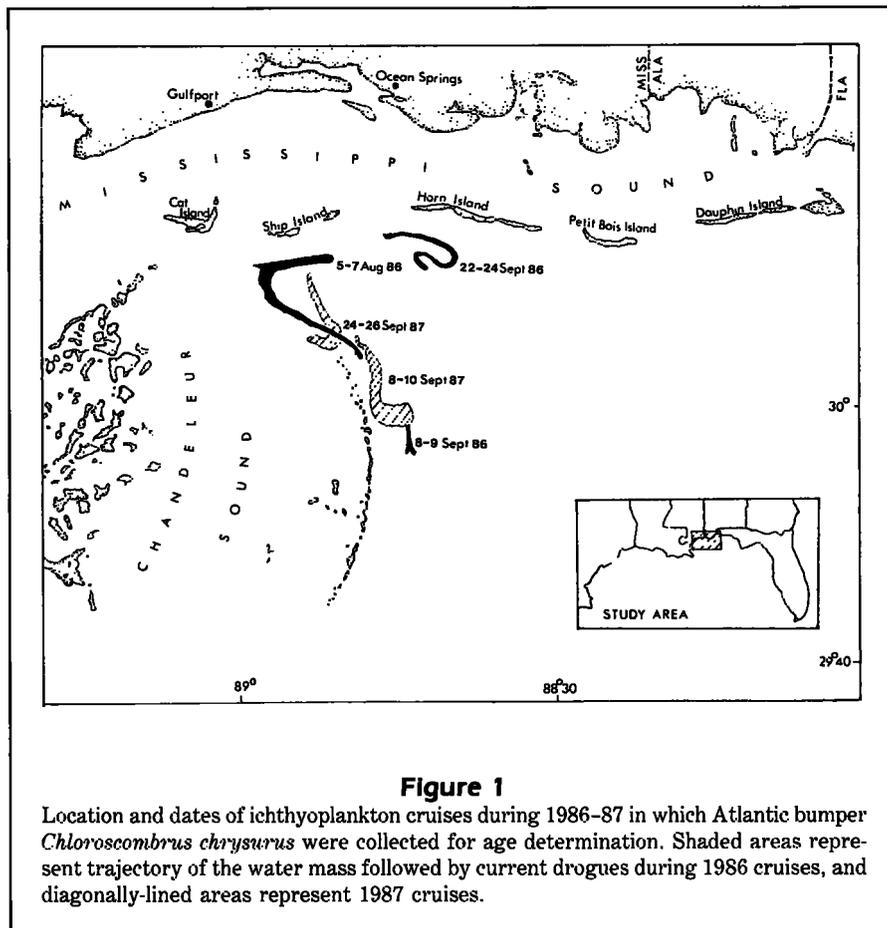
Figure 1
Location and dates of ichthyoplankton cruises during 1986–87 in which Atlantic bumper
Chloroscombrus chrysurus were collected for age determination. Shaded areas repre-
sent trajectory of the water mass followed by current drogues during 1986 cruises, and
diagonally-lined areas represent 1987 cruises.

fish *Aurelia aurita* with which the fish are often
associated (Reid 1954, Franks 1970). Fish were then
transferred to a cooler containing 100 ppm calcein
(2,4-bis-[N,N′-di(carbomethyl)aminomethyl]fluorescein)
in 13 L of aerated ambient seawater to create a fluores-
cent mark in their otoliths using the method described
by Wilson et al. (1987). Fish were held between 6 and
12 h in the seawater-calcein solution and then trans-
ferred into a 127 L aquaria. Fish were held under a
12 h/12 h photoperiod in 23°C and 25 ppt water and fed
ad libidium on brine shrimp. Fish were sacrificed 2,
7, and 10 days after marking.

Lab analysis

Ichthyoplankton samples from the bongo net collections
were split once with a Folsom plankton splitter (Van
Guelpin et al. 1982). *Chloroscombrus chrysurus* larvae
were sorted, counted, and measured to the nearest
0.1 mm standard length (SL). Preflexion larvae were
measured to the end of their notochord, otherwise
larvae were measured to the posterior tip of the
hypural plate. When more than 52 fish were present,

a random subsample of 50 fish were measured, as well as the shortest and longest. Ethanol-related shrinkage was assumed to be uniform for each fish collected and preserved (3-min tow, alcohol preservation; see Radtke 1989).

Validation, age, and growth

Sagittal otoliths were removed from each Atlantic bumper larvae using a dissection microscope equipped with polarized light. The sagitta from nine postlarval and juvenile Atlantic bumper (8.3–25.0 mm SL) that were immersed in the calcein-seawater solution were prepared and viewed using the method described by Wilson et al. (1987). Growth increments, following the fluorescent mark, were counted at 400× and verified at 1000×. The number of growth increments counted from the calcein mark to the otolith edge were compared with the number of days fish were held in captivity after marking.

Age estimation of larval Atlantic bumper was performed using sagitta that were air-dried and mounted in S/P Accu-mount 60 on a glass microscope slide. Most larval otoliths were thin enough that only viewing under a compound microscope was necessary to make total increment counts and otolith radius measurements. A few larger otoliths were ground with 600 WetorDry grit sandpaper and polished using 0.3μ Alumina 2 Alpha Micropolish until growth rings were countable. The counting and measurement procedure was enhanced by using a digital imaging system which produced images on a video monitor at 400× or 1000×. Independent increment counts were made twice by the same person without knowledge of fish length or previous otolith count. Only otoliths for which replicate counts were identical were used in the analysis. Eleven of the 170 otoliths prepared were discarded.

Separate linear growth equations of standard length on increment number were developed for fishes collected on the five cruises. These five equations were compared using analysis of covariance (ANCOVA, α 0.05; SAS Inst. 1985). Exponential and other nonlinear models (e.g., Laird-Gompertz) used to describe larval growth were also tested (Campana and Neilson 1985). A General Linear Model ANOVA, followed by a multiple comparisons test (Duncan, α 0.05; SAS Inst. 1985), were used to detect differences in surface-water temperature between years, months, and cruises.

Zooplankton biomass

Zooplankton displacement volumes (mL/m^3) were determined (Yentsch and Hebard 1957) for each net tow. A mean zooplankton standing stock value was then calculated for each cruise and net mesh type. A simple regression of zooplankton standing-stock values (202 vs. 333μm mesh nets) was developed for both September 1987 cruises. ANCOVA (α 0.05) was used to test for differences between the two cruises. The data from the two cruises were combined into one zooplankton standing-stock regression to standardize the values from the two mesh sizes.

Dry weight-length relationship

Larval and juvenile Atlantic bumper (N 120, 8.0–32.0 mm SL) collected by dipnetting for jellyfish, were measured to the nearest 0.1 mm SL, oven dried for 6 h at 62°C, and then weighed to the nearest 1.0 mg. A log-log dry weight-length relationship was established and described by the equation $W = aL^b$, where $W = \log_{10}$ dry weight (mg), and $L = \log_{10}$ standard length (mm). A 95% confidence interval placed around the estimated slope (b) was used to test for differences in the estimated length power term (b) and the classical b estimate of 3.0 for adult fish (LeCren 1951) and 4.0 for larval fish (Power 1989).

Mortality

Atlantic bumper densities for each 1 mm SL category were converted into mortality estimates following the length-frequency method described by Essig and Cole (1986). Sampling with respect to the windowshade drogues allowed us to monitor larval densities from the same mass of water for an entire collecting period. Only nighttime collected larvae >2.0 mm or <5.0 mm were utilized in our mortality estimates to minimize biases from net avoidance by larger larvae or extrusion through the mesh openings by the smallest larvae. The descending limb of each age-frequency distribution corresponding to a length range of 2.0–5.0 mm SL was described by the equation $Dt = D_o \exp^{(-Mt)}$, where $M =$ the instantaneous daily mortality coefficient, $Dt =$ larval fish density at time t, $D_o =$ larval fish density in the first fully recruited group (i.e., time = 0), and $t =$ time in days (Peebles and Tolley 1988). Mortality estimates were tested for statistical differences between cruises and years using ANCOVA (α 0.05).

Results

Validation, age, and growth

Daily increment formation on Atlantic bumper sagitta was validated using calcein. Each otolith from the nine fish treated had distinct growth increments between the green fluorescent calcein mark and the edge of the otolith (Fig. 2). On each sagitta examined, the number of increments counted after the calcein mark was
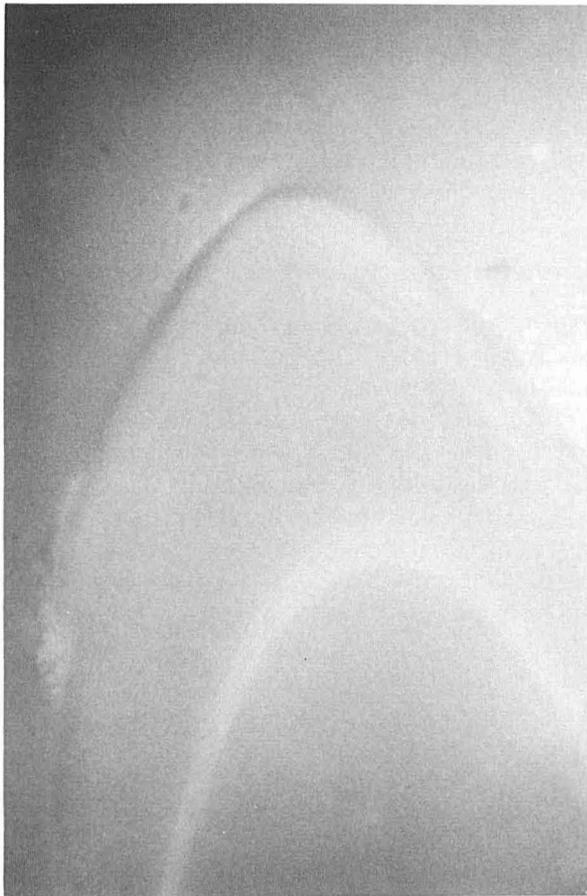
Figure 2
Photomicrograph (400×) of the transverse-sectioned sagittal otolith of a 23.5 mm SL juvenile Atlantic bumper *Chloroscombrus chrysurus* observed under ultraviolet light. The lower light band displays the uptake of calcein during the immersion process.

Figure 3
Regression of the number of otolith growth increments subsequent to the fluorescent calcein mark on the number of days each fish was held in captivity before sacrificing. Numbers associated with points represent overlapping values.
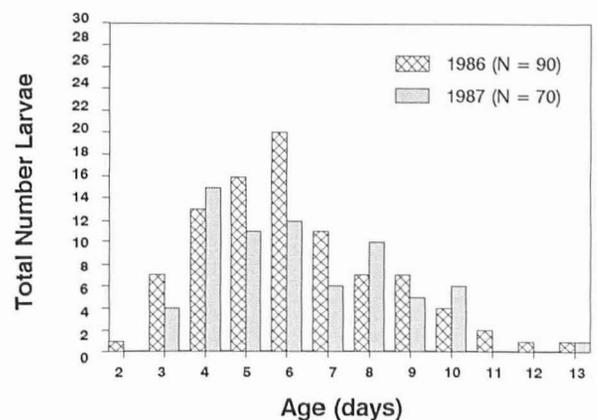
Figure 4
Age distribution of Atlantic bumper *Chloroscombrus chrysurus* larvae captured off the Louisiana–Mississippi barrier islands, 1986–87.

equivalent to the number of days the fish was held in captivity. The slope (1.02) of a least-squares linear regression (Fig. 3) was not significantly different from 1.0 (t-test, $p > 0.05$), confirming daily increment formation in otoliths of larval and juvenile Atlantic bumper.

Larval Atlantic bumper have circular sagitta, with a central core. Yolksac larvae (0.8 mm SL, preserved length) lacked increments. However, all other aged fish between 1.0 and 5.0 mm (preserved length; N 158) had countable increments (i.e., 1–11 increments or 3–13 days old; Fig. 4). Growth models were based only on 2–13 day-old fish.

Larval Atlantic bumper growth rates during the first two weeks of life were best described using a linear model. A separate growth curve was estimated for the 5–7 August 1986 data (Table 1). Growth curve com-

parisons for the two cruises in September 1986 (days 8–9 and 22–24) showed no significant differences within month (intercept, p 0.44; slope, p 0.48). Similarly, no significant difference was found between the two September cruises in 1987 (days 8–10 and 24–26; intercept, p 0.07; slope, p 0.42). Therefore, the paired September data sets were combined into a single regression for each year (1986 and 1987; Table 1). Atlantic bumper length-frequencies displayed no significant differences (p 0.93) between the two different mesh sizes (202 vs. 333 μm) during the 1987 daytime

Table 1

Estimates of three linear growth equations used to describe the growth rate (mm/day) of larval *Chloroscombrus chrysurus* (0.8–4.8 mm) collected off the Louisiana-Mississippi barrier islands during 1986 and 1987, and the associated mean surface-water temperatures (°C) including ranges. R^2 is the coefficient of determination for the respective models; L = standard length (mm); X = age (days).

Sampling date	Number fish aged	Size (range)	Equations	R^2	Growth rate (mm/day)	Mean surface-temperature (°C) (range)
5–7 August 1986	9	0.8–3.7	L=0.40X−0.13	0.94	0.40	29.6 (29.0–30.8)
8–9, 22–24 Sept. 1986	81	1.2–4.8	L=0.26X+0.70	0.61	0.26	28.4 (28.0–29.0)
8–10, 24–26 Sept. 1987	69	1.3–4.5	L=0.31X+0.71	0.72	0.31	27.8 (26.5–30.0)

Figure 5

Regression of larval standard length (mm) on sagittal otolith radius (µ) for Atlantic bumper *Chloroscombrus chrysurus* larvae collected off the Louisiana-Mississippi barrier islands, 1986–87.
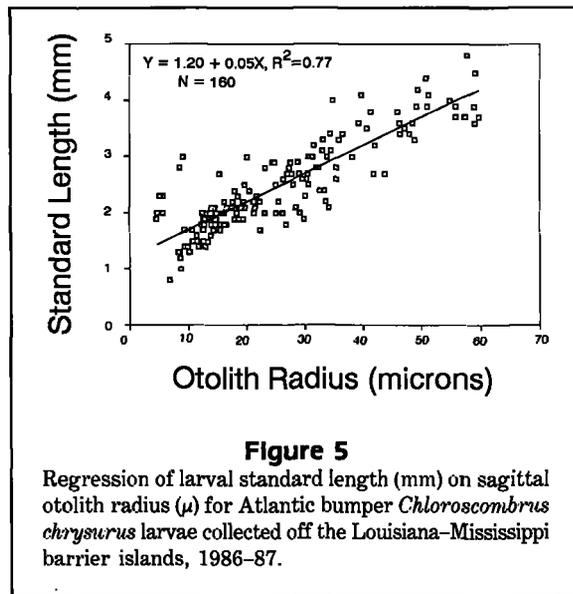
Table 2

Zooplankton standing-stock estimates (mL/m^3±SE) with 1987 values converted to equivalent 202µm mesh net values, based on the conversion study done during both September cruises in 1987. The number of samples taken during each cruise is indicated in parentheses. The following equation was used in the conversion: Y = 0.785X − 0.054 (R^2 0.86).

Month	1986 (202µm)	1987 Converted	1987 (333µm)
August	0.83±0.17 (34)	—	—
early Sept.	0.61±0.13 (25)	0.57±0.04 (40)	0.39±0.04 (40)
late Sept.	0.32±0.05 (41)	0.39±0.03 (40)	0.25±0.03 (40)

collections. Comparisons of the growth curves for September 1986 and 1987 and August 1986 indicated a significant difference in both the August intercept ($p<0.04$) and slope ($p<0.03$) of the regressions. Even though the sample size (N 9) was small, the observed growth rate for August (0.40 mm/day) was significantly higher than for September (0.26 mm/day in 1986 and 0.31 mm/day in 1987). The higher August growth rate occurred at a higher mean surface-water temperature, 29.6°C (Table 1). In September of 1987, the water temperature range (26.5–30.0°C) was wider than the other sampling periods due to a cold front passing through before the late-September cruise. There was, however, no significant difference (p 0.11) in temperature between months because of the low number of cruises.

Atlantic bumper standard lengths were regressed on the otolith radius (measured in microns; Fig. 5). The coefficient of determination (r^2) for the relationship

was 0.77 and the equation is L = 120 + 0.05R, where L = standard larval length (mm) at the otolith radius, R (Fig. 5). The relationship between the age and otolith radius explained less variability (r^2 0.68) and fit the following equation A = 2.96 + 0.13R, where A = age in days at the otolith radius, R. Otolith radius was observed to increase with both larval length and age.

Zooplankton biomass

Zooplankton mean biomass values for 1986 were similar to the converted 1987 values. The 202 vs. 333µm mesh regression equation Y = −0.054 + 0.785X (r^2 0.86), where Y = the 333µm zooplankton standing-stock value, and X = the 202µm zooplankton value, was used to establish a correction factor to convert the 1987 zooplankton values into estimates comparable to the 1986 values. The highest mean zooplankton biomass estimate (0.83 mL/m^3) was found in August 1986 (Table 2). The mean standing-stock estimates declined throughout the September cruises within each year (Table 2).

Dry weight-length relationship

The dry weight-length relationship for postlarval and juvenile Atlantic bumper (Fig. 6) is described by the exponential model Weight = 0.0016 Length$^{3.25}$ (r^2 0.94), where weight = dry weight of the fish (mg) and length = standard length (mm). The dry weight-length power term for larval and juvenile Atlantic bumper, 3.25, is significantly different from the classical standard length-weight power term of 3.0 for adult fish (LeCren 1951) and 4.0 for larval fish (Power 1989) at the 95% confidence level ($p > 0.05$).

Mortality

Instantaneous daily mortality (M) for larval Atlantic bumper was significantly higher during August 1986 (F 13.8, p 0.03) than in either September 1986 or 1987, with September values decreasing during successive cruises each year (Table 3). As a whole, however, the M values for all cruises in 1986 and 1987 were similar (F 0.74, p 0.45).
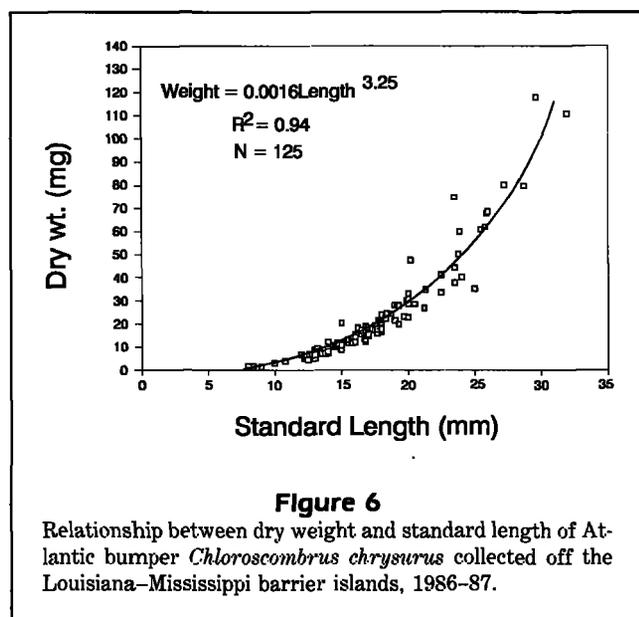
Discussion

The age of larval and juvenile Atlantic bumper was estimated from counts of growth increments on sagittal otoliths. One growth increment formed daily on each sagitta of Atlantic bumper between 8 and 25 mm SL. We, like others (Pritcher 1988, Fowler 1989, Parsons and Peters 1989), assumed that this relationship held true for smaller larvae (1–8 mm). We validated the periodicity of otolith growth increments and established an otolith age-and-growth analysis for larval Atlantic bumper in the northern Gulf of Mexico.

Growth increments were not visible in the otoliths of yolksac Atlantic bumper larvae (0.8 mm NL), but at least one increment was visible in 1.0 mm SL larvae. The length at hatching appears to be between 0.7 and 0.9 mm SL (after preservation) based on the larval length measurements. Atlantic bumper larvae, therefore, appear to begin otolith increment deposition after yolksac absorption, approximately 2 days after spawning (allowing 1 day each for egg incubation and yolksac absorption). Pelagic species, such as Atlantic bumper, often begin growth increment formation on their sagitta at the time of yolksac absorption (Radtke 1984).

An isometric or linear relationship between the size of otolith radius and standard length was revealed for Atlantic bumper larvae. The variation observed in our otolith radius–fish size relationship could be influenced by growth- and age-related factors. For example, under unfavorable environmental conditions the fish may not continue to experience an increase in otolith radius or fish size, while daily increment formation may continue (Lyczkowski-Shultz et al. 1988, Secor and Dean 1989).

Figure 6
Relationship between dry weight and standard length of Atlantic bumper *Chloroscombrus chrysurus* collected off the Louisiana–Mississippi barrier islands, 1986–87.

Table 3
Estimates of instantaneous daily mortality of larval *Chloroscombrus chrysurus* (2.0–5.0 mm SL) off the Louisiana–Mississippi barrier islands were calculated using the length-frequency method. Total larval Atlantic bumper densities and total larval fish densities were included for each cruise in 1986 and 1987. R^2 is the coefficient of determination for the respective models.

Sampling dates	Number of fish	Instantaneous daily mortality estimates (M)	R^2	Atlantic bumper total densities (#fish/100 m³)	Total larval fish density (#fish/100 m³)
5–7 August 1986	1912	0.62	0.82	608.9	1838.1
8–9 Sept. 1986	576	0.35	0.98	121.7	799.8
22–24 Sept. 1986	291	0.18	0.86	227.9	599.9
8–10 Sept. 1987	573	0.30	0.90	62.2	262.4
24–26 Sept. 1987	122	0.17	0.92	42.4	298.2

Temperature (Laurence 1978, Laurence et al. 1981, Houde 1989) and food availability (Methot and Kramer 1979, Laurence et al. 1981, Lyczkowski-Shultz et al. 1988, Warlen 1988) play important roles in larval growth and survival. Atlantic bumper growth rates were highest in August 1986, when mean surface-water temperatures and zooplankton biomass estimates were greatest.

The Atlantic bumper growth rate calculated over the two cruises in September 1987 may have been higher than the September 1986 growth rate because of the increase in zooplankton availability (Tables 1 and 2). Zooplankton displacement volume values calculated from the samples taken in 1986 declined from August to September. Relative zooplankton biomass values have peaked, however, as late as October off the Chandeleur Is. within Chandeleur Sound (102,000 animals/100 m^3; Gillespie 1971; Fig. 1). Our zooplankton standing-stock estimates were high compared with values obtained from Mississippi River plume fronts during July 1987 (0.04–0.43 mL/m^3; R.F. Shaw, unpubl. data).

Atlantic bumper larvae had a dry weight-length exponent value of 3.25 which is similar to that of 3.32 determined for larval northern anchovy *Engraulis mordax* (Lasker et al. 1970). This power term, however, is lower than values determined for seven laboratory-reared, cold-water marine larval species (3.76–4.77; Laurence 1979), or the hypothesized standard value for developing larval fish (4.0; Power 1989).

The highest Atlantic bumper instantaneous daily mortality estimate (M 0.62), observed during August, was similar to that reported for estuarine larval spotted seatrout *Cynoscion nebulosus* (0.64; Peebles and Tolley 1988) and, to some extent, another carangid, jack mackerel *Trachurus symmetricus* (0.80; Hewitt et al. 1985). Mortality estimates, which declined throughout September 1986 (0.35–0.18) and 1987 (0.30–0.17), were similar and were within the reported range for several larval marine species (Essig and Cole 1986, Houde 1987 and 1989, Pepin 1991). The highest daily mortality rate was associated with highest temperatures, highest macrozooplankton displacement volumes, and highest larval Atlantic bumper densities (Tables 1–3). In late September 1986, however, there was a low mortality rate during a time of relatively high Atlantic bumper densities, lower zooplankton biomass estimates, and lower temperatures. Two factors—larval size and lower water temperatures—may have influenced this lower mortality rate (Weinstein and Walters 1981). Mean larval Atlantic bumper standard lengths (1.2 mm) were similar for all the cruises. Lower surface-water temperatures, therefore, may have enhanced survival,

reducing the Atlantic bumper mortality estimate. Larval growth (i.e., daily development) and mortality rates have been reported to increase with temperature (Houde 1989, Pepin 1991). The high growth-rate and mortality estimate observed in August 1986 is consistent with these findings.

The high natural mortality observed in August is probably related to predation, based on two existing theories. Larval Atlantic bumper are usually aggregated in patches (Leffler 1989) and, therefore, may offer exceptional feeding opportunities to any predator that encounters them (McGurk 1987). Pepin (1991) suggested that increased mortality rates were associated with increasing growth rates, resulting from increased encounters with predators. These higher growth rates require a higher intake of food, causing increased activity which leads to increased predator encounters.

Another possible cause for the high August mortalities may be associated with competition for limited food resources, i.e., density-dependent mortality (Cushing 1974). Food availability as indexed by the zooplankton biomass estimate was highest during August, but the high total larval fish density may have rapidly depleted the food source, causing elevated mortalities. Larval Atlantic bumper density was high during the August cruise (608.9 larvae/100 m^3) as was the total larval fish density (1838.1 larvae/100 m^3; Leffler 1989).

This study provides preliminary information on the early life history of larval Atlantic bumper. Further studies need to be conducted on larval Atlantic bumper to determine the relationship between these early-life-history parameters and fluctuating temperatures and food availability.

Acknowledgments

Citations

Bannister, C.A., D. Harding, and S.J. Lockwood
1974 Larval mortality and subsequent year-class strength in the plaice (*Pleuronectes platessa* L.). *In* Blaxter, J.H.S. (ed.), The early life history of fish, p. 21–37. Springer-Verlag, NY.

Boschung, H.T.
1957 The fishes of Mobile Bay and the Gulf Coast of Alabama. Ph.D. diss., Univ. Alabama, Tuscaloosa, 626 p.

Bullis, H.R. Jr., and J.S. Carpenter
1968 Latent fisheries resources of the central West Atlantic region. *In* de Witt, G. (ed.), The future of the fishing industry of the United States, p. 61–64. Univ. Wash. Publ. Fish., New Ser. 4, Seattle.

Bullis, H.R. Jr., and J.R. Thompson
1970 Bureau of commercial fisheries exploratory fishing gear research base, Pascagoula, Mississippi—July 1, 1967 to June 30, 1969. U.S. Fish Wildl. Serv., Circ. 351, 29 p.

Campana, S.E., and J.D. Neilson
1985 Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014–1032.

Christmas, J.Y., and R.S. Waller
1973 Estuarine vertebrates, Mississippi. *In* Christmas, J.Y. (ed.), Cooperative Gulf of Mexico estuarine inventory and study-Mississippi, p. 320–439. Gulf Coast Res. Lab., Ocean Springs.

Cushing, D.H.
1974 The possible density-dependence of larval mortality and adult mortality in fishes. *In* Blaxter, J.H. (ed.), The early life history of fish, p. 103–112. Springer-Verlag, NY.
1975 Marine ecology and fisheries. Cambridge Univ. Press, Cambridge, 278 p.

Ditty, J.G.
1986 Ichthyoplankton in neritic waters of the northern Gulf of Mexico off Louisiana: Composition, relative abundance and seasonality. Fish. Bull., U.S. 84:935–946.

Essig, R.J., and C.F. Cole
1986 Methods of estimating larval fish mortality from daily increments in otoliths. Trans. Am. Fish. Soc. 115:34–40.

Fowler, A.J.
1989 Description, interpretation and use of the microstructure of otoliths from juvenile butterfly fish (family Chaetodontidae). Mar. Biol. (Berl.) 102:167–181.

Franks, J.S.
1970 An investigation of the fish population within the inland waters of Horn Island, Mississippi, a barrier island in the northern Gulf of Mexico. Gulf Res. Rep. 3:3–104.

Gillespie, M.C.
1971 Analysis and treatment of zooplankton of estuarine waters of Louisiana. *In* Cooperative Gulf of Mexico estuarine inventory and study, Louisiana Phase IV, Biology, p. 108–175. La. Wildl. Fish. Comm., New Orleans.

Hewitt, R.P., G.H. Theilacker, and N.C.H. Lo
1985 Causes of mortality in young jack mackerel. Mar. Ecol. Prog. Ser. 26:1–10.

Houde, E.D.
1987 Fish early life dynamics and recruitment variability. *In* Hoyt, R.D. (ed.), 10th annual larval fish conference, p. 17–29. Am. Fish. Soc. Symp. 2, Bethesda.
1989 Comparative growth, mortality, and energetics of marine fish larvae: Temperature and implied latitudinal effects. Fish. Bull., U.S. 87:471–495.

Juhl, R.
1966 Experimental trawling survey along the Florida west coast. Commer. Fish. Rev. 28(6):1–5.

Klima, E.F.
1971 Distribution of some coastal pelagic fishes in the Western Atlantic. Commer. Fish. Rev. 33(6):21–34.

Lasker, R., H.M. Feder, G.H. Theilacker, and R.C. May
1970 Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345–353.

Laurence, G.C.
1978 Comparative growth, respiration, and delayed feeding abilities of larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as influenced by temperature during laboratory studies. Mar. Biol. (Berl.) 50:1–7.
1979 Larval length-weight relations for seven species of Northwest Atlantic fishes reared in the laboratory. Fish. Bull., U.S. 76:890–895.

Laurence, G.C., A.S. Smigielski, T.A. Halavik, and B.R. Burns
1981 Implications of direct competition between larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in laboratory growth and survival studies at different food densities. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178:304–311.

Leak, J.C.
1977 Distribution and abundance of carangidae (Pisces, perciformes) larvae in the eastern Gulf of Mexico, 1971–1974. M.S. thesis, Univ. Miami, Coral Gables, 83 p.

Leak, J.C., and E.D. Houde
1987 Cohort growth and survival of bay anchovy, *Anchoa mitchilli*, larvae in Biscayne Bay, Florida. Mar. Ecol. Prog. Ser. 37:109–122.

LeCren, E.D.
1951 The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca flavescens*). J. Anim. Ecol. 20(2):201–219.

Leffler, D.L.
1989 Composition, abundance, and small-scale distribution of ichthyoplankton off the Louisiana–Mississippi barrier islands, with special emphasis on the age, growth, and mortality of *Chloroscombrus chrysurus*. M.S. thesis, Louisiana State Univ., Baton Rouge, 151 p.

Lyczkowski-Shultz, J., J.P. Steen Jr., and B.H. Comyns
1988 Early life history of red drum (*Sciaenops ocellatus*) in the north central Gulf of Mexico. MASGP-88-013, Gulf Coast Res. Lab., Ocean Springs, MS, 147 p.

McGurk, M.D.
1987 Natural mortality and spatial patchiness: Reply to Gulland. Mar. Ecol. Prog. Ser. 39:201–206.

Methot, R.D. Jr., and D. Kramer
1979 Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish Bull., U.S. 77:413–423.

Parsons, G.R., and K.M. Peters
1989 Age determination in larval and juvenile sheepshead, *Archosargus probatocephalus*. Fish. Bull., U.S. 87:985–988.

Peebles, E.B., and S.G. Tolley
1988 Distribution, growth, and mortality of larval spotted seatrout, *Cynoscion nebulosus*: A comparison between two adjacent estuarine areas of southwest Florida. Bull. Mar. Sci. 42(3):397–410.

Pepin, P.
1991 Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquat. Sci. 48:503–518.

Perret, W.S., W.R. Latapie, J.F. Polland, W.R. Mock, G.B. Adkins, W.J. Gaidry, and C.J. White
1971 Fishes and invertebrates collected in trawl and seine samples in Louisiana estuaries, Section I. *In* Cooperative Gulf of Mexico estuarine inventory and study, Louisiana, Phase IV, Biology, p. 39–105. La. Wildl. Fish. Comm., New Orleans.

Power, J.H.
1989   Sink or swim: Growth dynamics and zooplankton hydro-mechanics. Am. Nat. 133(5):706–721.

Pritcher, C.R.
1988   Validation of a technique for reconstructing daily patterns in the recruitment of coral reef damselfish. Coral Reefs 7:105–111.

Radtke, R.L.
1984   Formation and structural composition of larval striped mullet otoliths. Trans. Am. Fish. Soc. 113:186–191.

1989   Larval fish age, growth, and body shrinkage: Information available from otoliths. Can. J. Fish. Aquat. Sci. 46: 1884–1894.

Reid, G.K.
1954   An ecological study of the Gulf of Mexico fishes in the vicinity of Cedar Key, Florida. Bull. Mar. Sci. Gulf Caribb. 4:1–94.

Reintjes, J.W.
1979   Coastal herrings and associated species: A profile of species or groups of species, their biology, ecology, and current exploitation with economic and social information. Prepared for Gulf of Mexico Fish. Manage. Counc. by NMFS Southeast Fish. Sci. Cent., Beaufort NC, 170 p.

Sabins, D.S.
1973   Diel studies of larval and juvenile fishes of the Caminada Pass area, Louisiana. M.S. thesis, Louisiana State Univ., Baton Rouge, 163 p.

SAS Institute Inc.
1985   SAS User's Guide: Statistics, 1982 Edition. SAS Inst. Inc., Cary NC, 584 p.

Secor, D.H., and J.M. Dean
1989   Somatic growth effects on the otolith—fish size relationship in young pond-reared striped bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. 46:113–121.

Shaw, R.F., and D.L. Drullinger
1990   Early-life-history profiles, seasonal abundance, and distribution of four species of carangid larvae off Louisiana during 1982 and 1983. NOAA Tech. Rep. NMFS 89, 37 p.

Shaw, R.F., D.L. Drullinger, K.A. Edds, and D.L. Leffler
1988   Fine-scale spatial distribution of red drum, *Sciaenops ocellatus*, larvae. Contrib. Mar. Sci. 30(suppl.):109–116.

Stuck, K.C., and H.M. Perry
1982   Ichthyoplankton community structure in Mississippi coastal waters. In Fishery monitoring and assessment completion report, 1 Jan. 1977 to 31 Dec. 1981, p. VI-I-1 thru VI-I-53. Proj. 2-296-R, Gulf Coast Res. Lab., Ocean Springs, MS.

Van Guelpin, L., D.F. Markle, and D.J. Duggan
1982   An evaluation of accuracy, precision, and speed of several zooplankton sampling techniques. J. Cons. Perm. Int. Explor. Mer 40:226–236.

Warlen, S.M.
1988   Age and growth of larval gulf menhaden, *Brevoortia patronus*, in the northern Gulf of Mexico. Fish. Bull., U.S. 86:77–90.

Weinstein, M.P., and M.P. Walters
1981   Growth, survival and production in young-of-year populations of *Leiostomus xanthurus* Lacepede residing in tidal creeks. Estuaries 4(3):185–197.

Williams, L.W.
1983   Larval fish assemblages of lower Mobile Bay. M.S. thesis, Univ. South. Alabama, Mobile, 55 p.

Wilson, C.A., D.W. Beckman, and J.M. Dean
1987   Calcein as a fluorescent marker of otoliths of larval and juvenile fish. Trans. Am. Fish. Soc. 116:668–670.

Yentsch, C.S., and J.F. Hebard
1957   A gauge for determining plankton volume by the mercury immersion method. J. Cons. Cons. Int. Explor. Mer 22(2):184–190.