AGE AND GROWTH OF LARVAL GULF MENHADEN, *BREVOORTIA PATRONUS*, IN THE NORTHERN GULF OF MEXICO

STANLEY M. WARLEN[1]

ABSTRACT

Experiments on laboratory-spawned and -reared larval gulf menhaden, *Brevoortia patronus*, showed that they formed one otolith growth increment per day and that the increments could be used to estimate their age. Wild larvae from collections in the northern Gulf of Mexico along three transects (Cape San Blas, Florida; Southwest Pass, Louisiana; and Galveston, Texas) were aged. Gompertz growth equations were used to describe the relationship between age and standard length for larvae collected at various locations, and in different seasons and years. MANOVA tests and subsequent pairwise tests were used to test for differences among these growth curves. For the most extensive data set (Southwest Pass, Louisiana), there were significant differences in growth between early season (December) and late season (February) larvae. Early season larvae grew faster than late season larvae. Growth of larvae also differed among December collections and among February collections. The growth model for the pooled data for all wild larvae predicted that they grew from 2.4 mm SL at hatching to 20.4 mm SL at 62 days.

Gulf menhaden, *Brevoortia patronus*, is the most abundant commercial finfish in the Gulf of Mexico and, with 883,500 metric tons (t) landed in 1985 (U.S. National Marine Fisheries Service 1986); it constitutes the largest fishery in the United States. Some aspects of the oceanic early life history of this clupeid are known and are reviewed by Turner (1969), Christmas and Waller (1975), Lewis and Roithmayr (1981), Govoni et al. (1983), and Shaw et al. (1985a). However, virtually nothing is known about the age and growth of the larvae, much less how these parameters vary spatially and temporally. Daily growth increments on otoliths of larval fishes can be used as an indicator of their age, and once the use of this technique, first described by Pannella (1971), is validated for the larvae of an individual species, their ages can be estimated with confidence and growth rates can be determined. Intraspecific growth may be compared for larvae from different areas and seasons (Lough et al. 1982), and from this it may be possible to ascertain how biotic and abiotic environmental variables affect larval growth and survival. The objectives of this study are to 1) validate the periodicity of increment formation in otoliths of larval gulf menhaden, 2) estimate larval growth rates, 3) compare growth rates of larvae from different locations and times, 4) estimate spawning times, and 5) examine possible relationships between larval growth and surface water temperature. This work was part of a larger project designed to investigate the early life history of several economically important fishes and the marine planktonic food webs that support their growth and survival in the northern Gulf of Mexico.

METHODS

Spawning and Larval Rearing

Adult gulf menhaden were collected near Gulf Breeze, FL, and transported to the Beaufort Laboratory, Beaufort, NC (Hettler 1983). After a period of acclimation, adults were induced to spawn in the laboratory. The resultant larvae were used in experiments to validate the periodicity of increment formation on their otoliths and the age at first increment formation.

Beginning February 1983, several thousand newly spawned gulf menhaden eggs were transferred to a tank containing 90 L of filtered seawater. The static water in this tank, kept at 20.5° ± 0.5°C throughout the experiment, was continuously aerated and the salinity maintained at 31 ± 1‰. Photoperiod was 12 hours light:12 hours dark. A food concentration of 25 rotifers (*Brachionus plicatilis*) mL^{-1} was maintained. A green alga, *Nanochloris* sp., was added periodically as food for the rotifers and to aid in removing toxic metabolites. The otoliths of larvae sam-

[1]Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.

Manuscript accepted September 1987.
FISHERY BULLETIN: VOL. 86, NO. 1, 1988.

pled at 10-, 17-, 24-, and 31-d posthatch were examined.

In January 1984 additional larvae were reared to compliment results of the earlier experiment. Smaller tanks with 60 larvae in 10 L of filtered water were used. Experimental conditions were the same as for the first experiment. The otoliths of larvae sampled at 7-, 14-, and 20-d posthatch were examined.

Larval Collections

Larval gulf menhaden were collected in the northern Gulf of Mexico during six cruises of the RV *Oregon II*. Sampling stations (Fig. 1) along transects LA (off Louisiana) and FL (off Florida) were occupied during 11–19 December 1979, 5–15 February 1980, and 2–12 December 1980 and along transects LA, FL, and TX (off Texas) during 9–24 February 1981, 2–13 December 1981, and 4–16 February 1982. Transect LA is near the Mississippi River outflow off Southwest Pass, LA; transect FL is southwest of Cape San Blas, FL; and transect TX is located off Galveston Bay, TX. Sampling stations were in water depths of 18, 91, and 183 m except off Texas where only the 18 and 91 m depths were sampled.

A multiple opening-closing net and environmental sensing system (MOCNESS) as described by Wiebe et al. (1976) were the primary sampling gear used to capture larvae. Additional samples were taken in oblique tows with a 60 cm bongo frame also fitted with 505 μm mesh nets. Samples were collected day and night and were preserved in 95% ethanol (final concentration ≈75%) within 5 minutes of collection. The ethanol was changed in all samples at least once after initial preservation to prevent dissolution of otoliths in fish from any samples that may have been inadequately preserved. Data from larvae collected at all stations within a transect were combined for that transect.

Estimating Age and Growth

All gulf menhaden larvae were measured to the nearest 0.1 mm standard length (SL). The largest otolith pair (sagittae) was teased from the surrounding tissue, cleaned in distilled water, and then placed on a glass microslide under a thin layer of Flo-Texx[2] mounting medium.

Otoliths were viewed with a compound microscope fitted with a television camera. Growth increments were counted from otolith images on a video monitor at magnifications of at least 400×. An increment appeared as a light, wide incremental band and a dark, narrow, discontinuous band (Tanaka et al. 1981). Increments were generally clearly discernable and easily counted (Fig. 2). Estimated age was the number of increments counted plus an empirically derived value for the

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

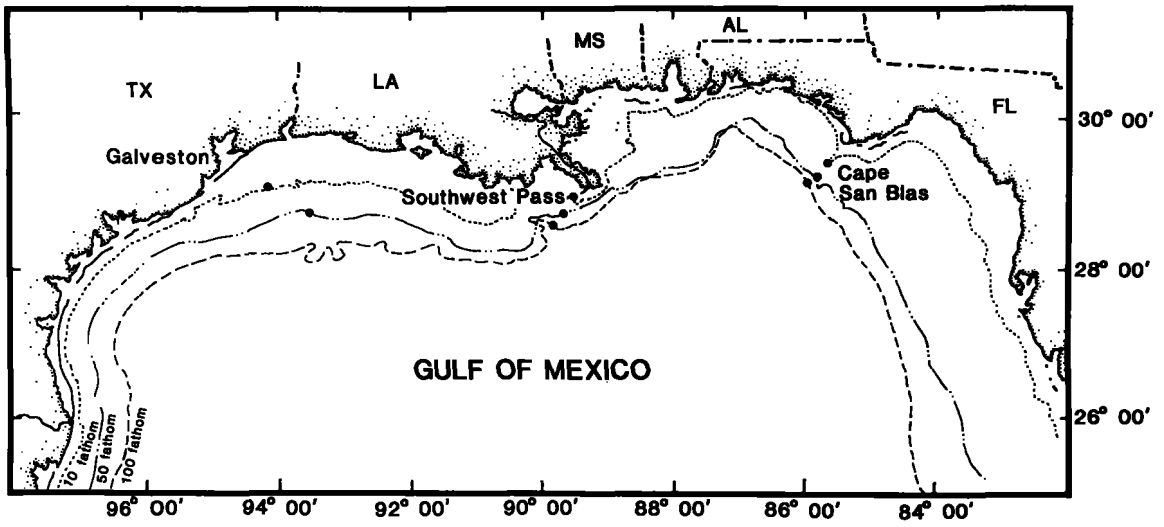

FIGURE 1.—Location of sampling sites from which larval gulf menhaden were collected during cruises of the RV *Oregon II* in December 1979–81 and February 1980–82.

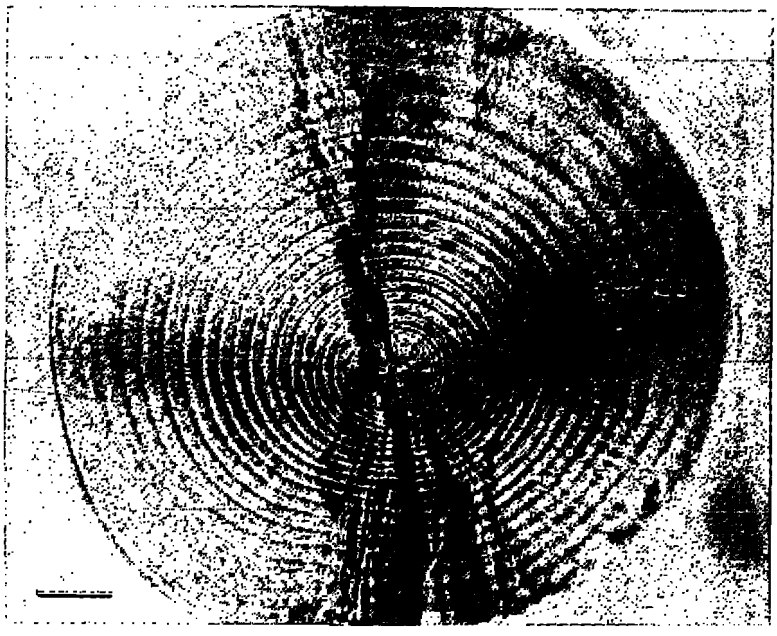

FIGURE 2.—Photomicrograph of a saggital otolith with 22 increments from a 17.4 mm SL field collected larval gulf menhaden. Scale bar represents 10 μm. Growth increments appear as pairs of wide incremental and narrow discontinuous bands.

number of days from spawning to first increment formation. Results of the laboratory experiments established the periodicity of otolith increment formation.

A spawning date was assigned each ageable larva by using the estimated age of the fish in days to back-calculate from the date of capture. It was assumed that there were no differences in either the age at initial increment deposition or the otolith increment deposition rate between locations and seasons and that the rate was not a function of temperature, food, or photoperiod.

Average growth of larvae was described by the Laird version (Laird et al. 1965) of the Gompertz growth equation (Zweifel and Lasker 1976) fitted to estimated age and size at time of capture for fish from all cruises and transects. To stabilize the variance of length over the observed age interval, length data were log-transformed and model parameters were estimated from the log-transformed version of the growth equation. The model was fit to data for each transect within each cruise and for pooled data from all cruises.

Potential differences in the overall growth curves among years and between seasons for larvae caught off Louisiana and between years (1981 and 1982) for larvae caught off Louisiana and Texas were examined by treating the parameters of the Gompertz equation as dependent variables in two-way multivariate analysis of variance (MANOVA) designs. A one-way MANOVA design was used to test for differences among transects (LA, FL, TX) within one season (February 1982). Following significant MANOVA results, prespecified pairwise Hotelling's T^2 test comparisons (Bernard 1981, as modified by Hoenig and Hanumara 1983) were made using the Bonferroni procedure (Harris 1975) to provide conservative tests of statistical significance. Bonferroni critical values for these individual tests were equal to the overall error rate (significance level = 0.05) divided by the number of possible comparisons in the particular MANOVA design. The emphasis in the comparisons was to look for overall differences in the growth of larvae using these statistics as a guide and not to look for differences in individual parameters of the growth models.

Hotelling's T^2 test and MANOVA both require that the data fit a multivariate normal distribution and that the variance-covariance matrices of the populations are not different (Harris 1975). These assumptions are difficult to test and are almost certainly not valid for real data sets (par-

ticularly field data), but they may be nearly valid for many sets of data (Harris 1975). No direct test of normality in a trivariate, joint probability distribution is available (Bernard 1981), but bias arising from nonnormal, multivariate, joint distributions is minimized with large sample sizes (Bernard 1981). While methods are available to test the hypothesis of equal variance-covariance matrices (e.g., Box's modification of Bartlett's test), these methods are very sensitive and even minor differences between group dispersions will likely be discovered (Pimentel 1979). In any event, the use of MANOVA in this paper relies on variance-covariance matrices estimated from nonlinear regressions, and these are not amenable to testing. However, both MANOVA and Hotelling's tests are extremely robust even under violation of the assumptions of homoscedasticity and multivariate normality (Harris 1975).

RESULTS

Increment Formation

The age of gulf menhaden at formation of the first otolith growth increment was estimated from laboratory-reared larvae. The intercept (2.6 days) of the regression of the number of growth increments on known posthatch age of 36 larval gulf menhaden (Fig. 3) was used to estimate posthatch age at formation of the first increment. This value was added to the time from spawning to hatching which at 20°C is 2 days (Powell[3]). This sum (4.6 days) is the estimated time from spawning to formation of the first increment. Hence, it was necessary to add 5 days to each increment count to estimate the age of larval gulf menhaden from spawning.

The periodicity of increment formation was ascertained from the regression of the number of growth increments on the known age (Fig. 3). The slope did not differ significantly (t-test, $P < 0.05$) from 1.0, and thus, on the average, one otolith growth increment was formed per day in laboratory-reared larvae up to 31 days after hatching. Results of a second experiment (Table 1) confirmed this periodicity. The age of gulf menhaden larvae estimated from otolith increment counts (+5) closely approximated the known ages of 51 laboratory-reared larvae. Mean estimated age of larvae differed by <1 day from the known

[3]A. B. Powell, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722, pers. commun. February 1986.

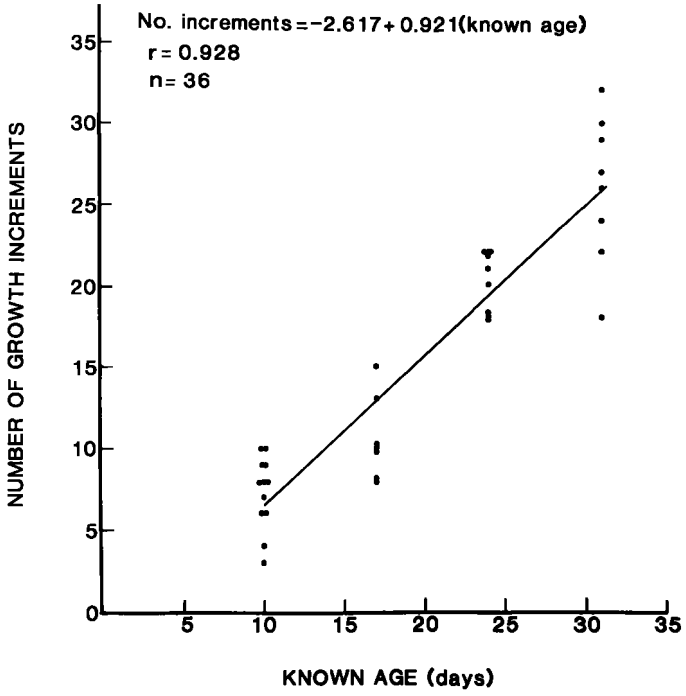

FIGURE 3.—Regression of the number of growth increments on the known posthatch age of 36 laboratory-reared gulf menhaden. Standard error of the slope is 0.108.

TABLE 1.—Standard length (mm) and estimated age (number of otolith growth increments +5) of laboratory-reared larval gulf menhaden. Values in parentheses are 95% interval estimates.

Known age (days)	Number of fish	Mean estimated age	Mean SL
7	13	7.8 (±0.38)	4.7 (±0.28)
14	16	13.2 (±1.14)	6.4 (±0.38)
20	22	19.3 (±0.77)	8.0 (±0.42)

ages and the 95% confidence intervals included the known age in each of the three groups. Some of the variation in the number of growth increments observed in known age larvae (Fig. 3, Table 1) may have been due to 1) poor growing conditions during rearing that could have resulted in reduced growth in underfed larvae, 2) variation in the inception of increment formation as has been observed in other species (Laroche et al. 1983; Fives et al. 1986), and 3) faintness of growth increments in some larvae. In contrast, increments on otoliths of field collected larvae (Fig. 2) were usually very regular and distinct and were more easily observed than those on otoliths of laboratory-reared larvae. I assumed that the growth increment deposition rate was also daily in wild larvae examined in this study.

Age and Growth of Larvae

Average growth of larval gulf menhaden during their first two months of life was described by the Gompertz growth model for pooled length at age data for 2,003 fish representing collections from all six RV *Oregon II* cruises (Table 2, Fig. 4). Larvae ranged in age from 5 to 62 days ($\bar{x}$=24.4 days) and in SL from 3.4 to 28.0 mm ($\bar{x}$=12.6 mm). In the log-transformed model, age accounted for 82% of the variation in length. Gulf menhaden were predicted to have grown from 2.4 mm SL at hatching to 20.4 mm at age 62 days. The size at hatching estimated from the Gompertz equation was only slightly less than the hatching size, 2.6–3.0 mm SL, observed in the laboratory (Hettler 1984). Age-specific growth rates declined from ≈7%/day at age 10 days to <0.4%/day at age 60 days. Maximum absolute growth rate occurred when gulf menhaden larvae were 7.9 mm SL and 13 days old.

The asymptotic length of larvae (21.5 mm SL), determined from the variables of the growth equation, is approximately the size when larvae begin to transform into juveniles. This transformation, described by Lewis et al. (1972) for the closely related Atlantic menhaden, *B. tyrannus*, apparently ends when the fish reach 28–30 mm SL (Suttkus 1956).

In all instances except one transect (TX December 1981, where there was no convergence in the parameter values in the computer fitting procedure and the model would not fit the data), the Gompertz growth model could be used to describe the growth of gulf menhaden larvae from each cruise and transect (Figs. 5-7, Table 2). The growth model for the FL December 1980 larvae approximates an exponential form because of the exceptionally low value for α. This may be due to the preponderance of small, young larvae.

GROWTH COMPARISONS

Louisiana - Seasons and Years

There were statistically significant differences (MANOVA, $P < 0.001$) in the growth curves for larvae caught off Louisiana for two seasons (December, February) and three years (1979-80, 1980-81, 1981-82). To determine if differences existed between seasons in each year and among any two years within each season, I selected 9 of the possible 15 pairwise comparisons for testing. The Bonferroni critical value in these tests was 0.0033 (0.05/15). The inability to fit a Gompertz growth model to the TX December 1981 data precluded a comparison with the larvae collected off Texas in February 1982.

Pairwise comparisons for within years data for Louisiana larvae showed significant differences ($P < 0.003$) in growth curves between early season (December) and late season (February) for each year. Faster growth of early season larvae is evident if the respective curves (Figs. 5; 6a, c; 7a, c) are compared. For any age, the predicted size is greater for early season than for late season larvae. Only for the third year did the length at age 40+ days of February-caught larvae exceed that for December-caught larvae.

In similar comparisons for larvae caught off Louisiana in December of all three years, there were significant differences ($P < 0.003$) in the growth curves (Figs. 5a, 6a, 7a) for any two years. As judged by the predicted size at any age, larvae appeared to grow faster in 1979 than in either 1980 or 1981. While the curves for the 1980 and 1981 larvae overlapped, larvae from 1980 were larger at 30+ days than were the 1981 larvae. Significant differences were also found among the curves (Figs. 5b, 6c, 7c) for larvae caught in

TABLE 2.—Estimates of Gompertz growth model parameters and mean age (days) and mean SL (mm) for larval gulf menhaden collected in the northern Gulf of Mexico during the winters 1979-80, 1980-81, and 1981-82. R^2 is the coefficient of determination for the respective models.

Date	Transect[1]	Number fish aged	R^2	Growth model parameters[2] $L_{(0)}$	$A_{(0)}$	α	Mean estimated age (d)	Mean SL (mm)
Winter 1979-80								
Dec. 1979	LA	42	0.863	2.768 (1.270)	0.1701 (0.0711)	0.0809 (0.0190)	28.1	17.4
Feb. 1980	LA	324	0.954	2.131 (0.138)	0.1592 (0.0105)	0.0710 (0.0031)	30.2	12.7
Winter 1980-81								
Dec. 1980	LA	191	0.931	2.888 (0.188)	0.1125 (0.0097)	0.0496 (0.0044)	22.0	11.8
Dec. 1980	FL	80	0.701	3.418 (0.994)	0.0561 (0.0370)	0.0001 (0.0407)	14.9	7.9
Feb. 1981	LA	338	0.849	2.702 (0.231)	0.1159 (0.0120)	0.0577 (0.0049)	24.6	11.7
Feb. 1981	TX	223	0.526	5.839 (0.579)	0.0305 (0.0088)	0.0125 (0.0110)	21.5	10.3
Winter 1981-82								
Dec. 1981	LA	370	0.921	0.384 (0.076)	0.4780 (0.0433)	0.1240 (0.0054)	21.7	13.3
Dec. 1981	TX	114	—	—[3]	—[3]	—[3]	25.4	11.9
Feb. 1982	LA	191	0.736	0.807 (0.337)	0.2729 (0.6093)	0.0851 (0.0090)	31.2	15.5
Feb. 1982	FL	88	0.624	2.278 (0.824)	0.1067 (0.0454)	0.0394 (0.0205)	17.6	8.9
Feb. 1982	TX	42	0.946	1.798 (0.392)	0.1276 (0.0340)	0.0500 (0.0142)	22.5	10.0
All years								
All data pooled		2,003	0.822	2.355 (0.098)	0.1345 (0.0059)	0.0608 (0.0020)	24.4	12.6

[1]LA=Mississippi River Delta (Southwest Pass Louisiana); FL=Cape San Blas, FL; TX=Galveston, TX.
[2]$L_{(0)}$=length at hatching, $A_{(0)}$=specific growth rate at hatching, α=exponential decline in $A_{(0)}$. Values in parentheses are estimated standard errors from the nonlinear regressions.
[3]Gompertz growth model did not fit the data.

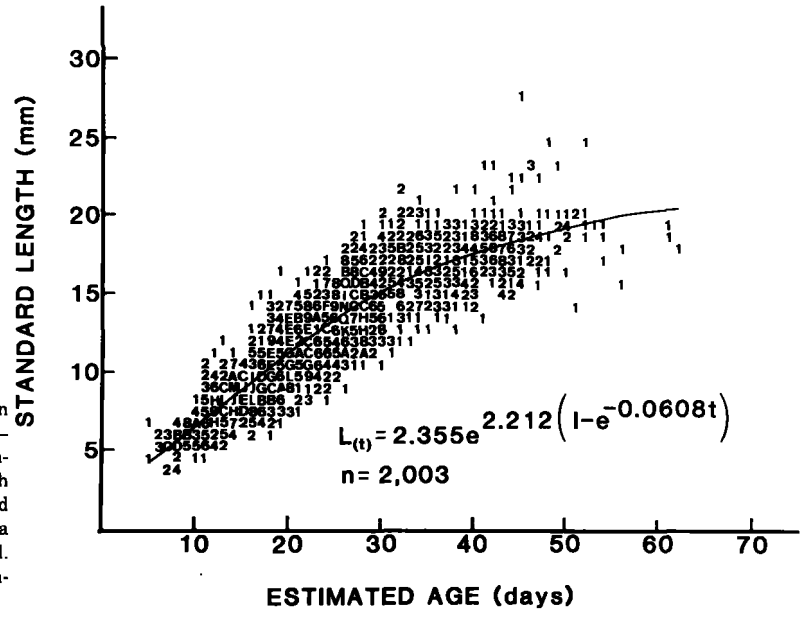

FIGURE 4.—Growth of gulf menhaden larvae collected in the winters of 1979–80, 1980–81, and 1981–82 in the northern Gulf of Mexico. The Gompertz growth model was used to describe the pooled data. Two through nine coincident data points are labelled with their numeral. Coincident points of 10 and above are labelled A, B, etc.

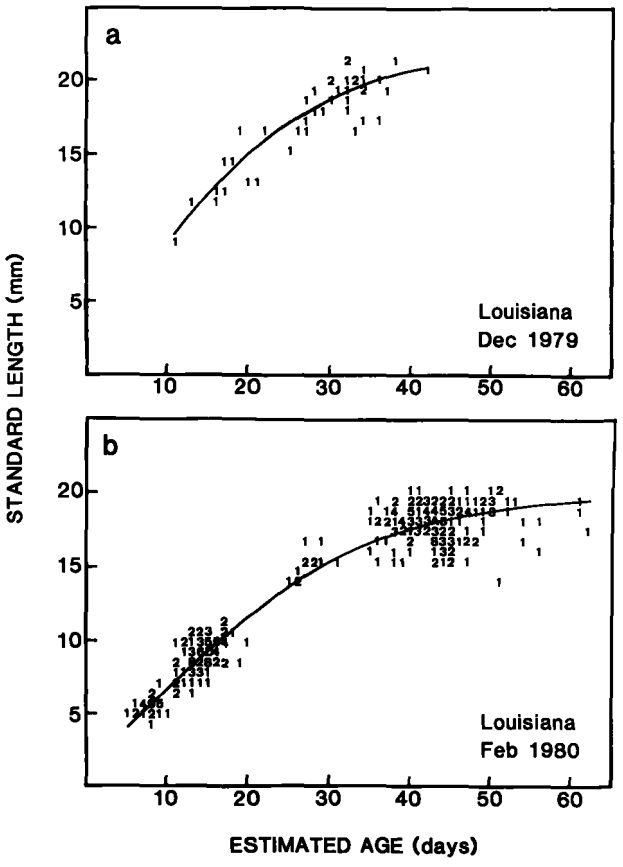

FIGURE 5.—Growth of larval gulf menhaden collected in the winter 1979–80 in the northern Gulf of Mexico. The Gompertz growth model was used to describe the data. Coincident data points are labelled as in Figure 4.

February in three years. Larvae caught in 1980 grew faster than larvae caught in 1981 and larvae caught in 1982 up to 25 days, thereafter 1980 and 1982 had very similar size at age estimates.

Louisiana vs. Florida vs. Texas - February 1982

There were no significant differences (MANOVA, $P = 0.212$) among the growth curves for larvae caught in February 1982 off Louisiana, Texas, and Florida (Figs. 7c, d, e), and hence no pairwise comparisons were necessary.

Louisiana vs. Texas - February 1981–82

Statistically significant differences (MANOVA, $P < 0.002$) in larval growth were observed in the LA and TX transects from February 1981–82. Pairwise comparisons indicated significant differences ($P < 0.008$) in the growth of larvae collected off Texas in 1981 (Fig. 6d) and 1982 (Fig. 7e) and in growth between LA 1981 (Fig. 6c) and TX 1981 collections. The earlier pairwise comparisons had already shown a significant difference in growth of larvae from LA February 1981 and February 1982 collections (Fig. 7c), but none for growth of larvae caught in the LA February 1982 and TX February 1982 collections. Two other potential tests, between transects of different areas and different years, were not considered to be meaningful.

Larvae caught off Louisiana in February 1981 were larger at age 18+ days than were larvae caught off Texas in February 1981, and might be considered to be faster growing fish. There was a

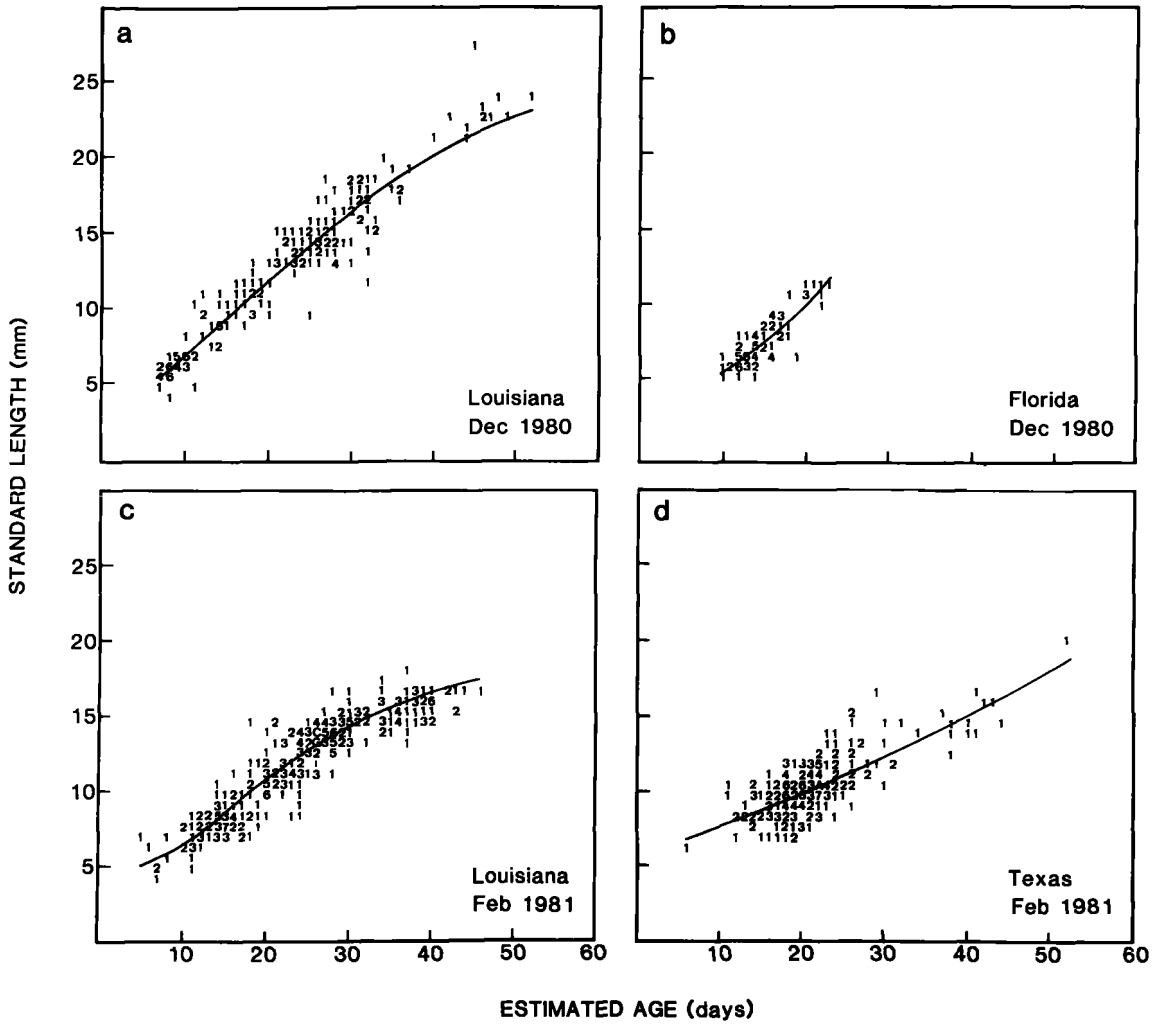

FIGURE 6.—Growth of larval gulf menhaden collected in the winter 1980–81 in the northern Gulf of Mexico. The Gompertz growth model was used to describe the data. Coincident data points are labelled as in Figure 4.

statistical difference in growth of larvae caught off Texas in February 1981 and 1982, and it appears that the 1982 larvae grew at a faster rate. Conclusions from these statistical differences involving TX February 1981 larvae collections should be viewed with caution because of the relatively poor fit ($r^2 = 0.526$) of the model. Inadequacies, such as the lack of larvae <13 or >31 days old, in that data set probably resulted in the relatively poor parameter estimates (Table 2). Additional sampling would be necessary to further test the hypotheses of differences in growth between geographic areas in the northern Gulf of Mexico and between years for Texas larvae.

Estimated Spawning Times

Gulf menhaden larvae observed in this study were estimated to have been spawned from mid-October to mid-February (Fig. 8). The limited extent of seasonal sampling precluded estimation of the probable total range of the spawning season. Most larvae captured in December and February had been spawned in November and January respectively (Fig. 8). The considerable overlap in spawning times of larvae caught the same month in different years is a reflection of the similarity of sampling dates. The relatively narrow distribution of spawning dates for larvae caught off Flor-

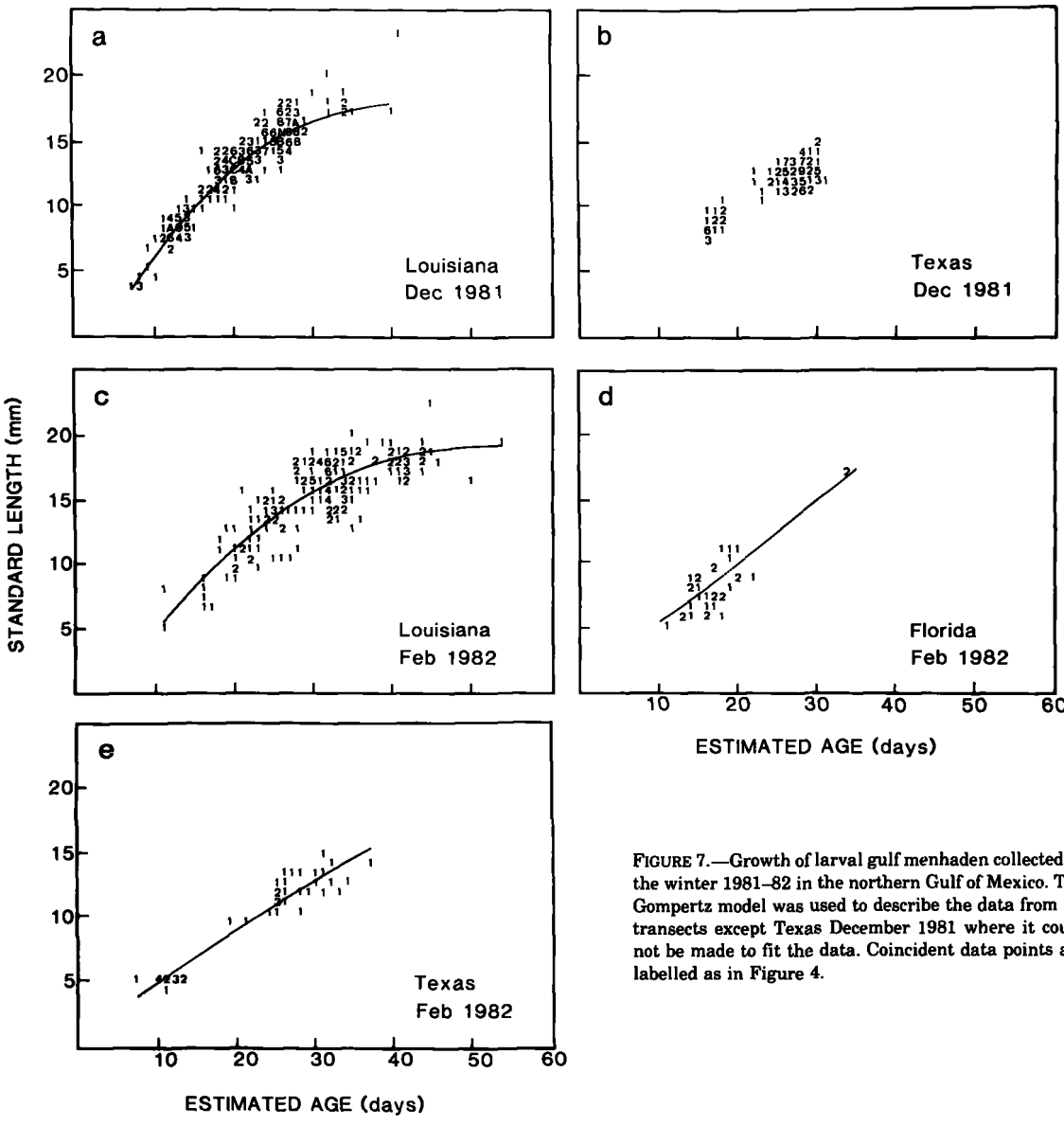

FIGURE 7.—Growth of larval gulf menhaden collected in the winter 1981–82 in the northern Gulf of Mexico. The Gompertz model was used to describe the data from all transects except Texas December 1981 where it could not be made to fit the data. Coincident data points are labelled as in Figure 4.

ida in both December 1980 (Fig. 6b) and in February 1982 (Fig. 7d), off Louisiana in February 1982 (Fig. 7c), and off Texas in February 1981 (Fig. 6d) represent larvae from fewer cohorts.

DISCUSSION

Laboratory observations indicate that larval gulf menhaden on the average form one growth increment per day on their otoliths and that counts of these increments can be used to estimate age. Otoliths of larval gulf menhaden are thin and round, and the increments are generally easily counted and consequently are ideally suited for ageing. The most closely spaced increments, those occurring near the focus, were at least 1.5 μm wide and were above the 0.2 μm resolution of the light microscope (Campana and Neilson 1985). First increment formation occurs about 5 days after spawning and probably coincides with first exogenous feeding. This is supported by Hettler (1984) who found that gulf menhaden eggs hatched at about day 1.7 at 19°-20°C. Four days after hatching larvae had functional

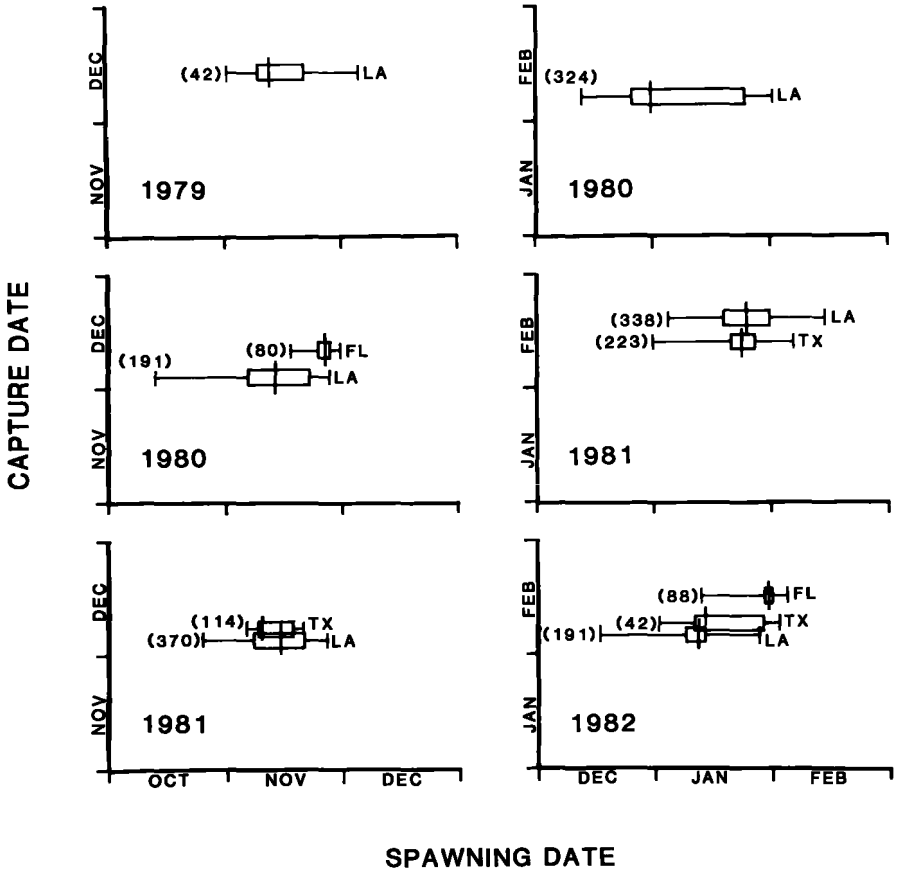

FIGURE 8.—Schematic plots of the spawning times of larval gulf menhaden collected in the northern Gulf of Mexico during 6 cruises of the RV *Oregon II* from December 1979 to February 1982. In each distribution the vertical line is the median value and 50% of the data points fall within the block. Lines beyond the boxes represent the range of data points. The value in parentheses to the left of each distribution is the number of fish.

mouths and were 4.5 mm SL. However, developmental rates are probably temperature dependent (Powell and Phonlor 1986), and hence larvae at lower temperatures would be older at first feeding.

The Gompertz growth model appears to adequately describe the growth of larval gulf menhaden in most cases. Except where data are somewhat limited (Figs. 6b, d; 7b, d) the fit of the model is relatively good and the r^2 is >0.73 for each transect (Table 2). Gompertz growth models have been used (Zweifel and Lasker 1976; Methot and Kramer 1979; Laroche et al. 1982; Warlen and Chester 1985) to describe growth of larval fishes where the length-age plots are nonlinear and upper asymptotes were apparent.

Average growth rate of larval gulf menhaden to day 60 was 0.30 mm/day throughout its oceanic existence. This rate was very similar to that, 0.28 mm/day (estimated from figure 2 of Hettler 1984), for larvae reared in the laboratory at 20° ± 2°C for 60 days. However, wild-caught larvae were from wider extremes in water temperature, with mean early season (December) temperatures from 17.4° to 21.2°C and late season (February) 12.9° to 16.4°C. The growth rate of larval Atlantic herring, *Clupea harengus*, up to 50 days old was similar and varied between 0.23 and 0.30 mm/day (Lough et al. 1982). However, gulf menhaden larvae grew slower than the fast growing but relatively short-lived engraulids—bay anchovy, *Anchoa mitchilli* (Fives et al. 1986) and northern anchovy, *Engraulis mordax* (Methot and Kramer 1979).

Only a small number of larvae from all the collections were ≥50 days old. Larvae of this age

were either not in the sampling area or were inaccessible to the fishing gear used. Although the latter cannot be fully discounted, the former possibility is most likely, since larvae as they grow are known to be transported (Shaw et al. 1985b) toward estuaries. Larvae are about 15–25 mm SL (estimated from Suttkus 1956) when they enter estuaries in Louisiana, and the smallest immigrating larvae are estimated from the growth model (Fig. 4) to have been at least 30 days old. Larvae then are probably 30–70 days old when they enter Gulf of Mexico estuaries. This range is very similar to that for Atlantic menhaden, *B. tyrannus*, entering North Carolina estuaries (S. M. Warlen, unpubl. data). The so-called "larval drift" period for gulf menhaden is probably closer to 4–10 weeks than the 3–5 weeks surmised by Reintjes (1970).

Growth of larval gulf menhaden in the northern Gulf of Mexico varied both spatially and temporally. For three consecutive years there were significant differences in growth for early season (December) and late season (February) larvae caught off the Mississippi River Delta. The increase in length for early season larvae was greater than for larvae hatched in late season. Environmental conditions in this area differed between early season and late season. Mean water temperature measured during the December 1979, 1980, and 1981 cruises were 17.4°, 19.4°, and 21.2°C, respectively, while in February 1980, 1981, and 1982 the temperatures were 13.8°, 15.7°, and 14.7°C, respectively. Although not shown experimentally for gulf menhaden larvae, there is evidence that larvae of some marine fishes grow faster at higher temperatures (Laurence 1978; Laurence et al. 1981). Jones (1985) also associated higher water temperatures with higher growth of larvae and found that increase in length of Atlantic herring larvae hatched early in the season was greater than for larvae hatched late in the season.

Growth rate of larvae caught in the same season but in different years was inversely related to mean water temperature. Larvae caught in December off Louisiana showed a trend of higher growth (1981 < 1980 < 1979) at lower respective mean water temperatures (21.2°, 19.4°, 17.4°C); similarly, the growth rates for larvae caught in February (1981 < 1982 < 1980) was higher at lower respective mean water temperatures (15.7°, 14.7°, 13.8°C). Other environmental factors in addition to temperature may also affect the growth rate of larval menhaden. Food availability that can be an important growth-limiting factor for larval fishes, may be determining the relative growth rates at the lower temperatures in February. On the basis of limited data on the zooplankton (pelecypod larvae, copepod nauplii, copepodites, and adult copepods) that could serve as food for gulf menhaden larvae (Govoni et al. 1983), food availability (number/100 m^3) is highest in February 1980, lower in 1982, and lowest in 1981. Analogous food abundance data is not available for the December cruises, but levels would probably need to be higher on a per fish basis to support the higher metabolism concomitant with the higher December mean water temperatures (17.4°–21.2°C). The main and interaction effects of growth-limiting (food abundance) and growth-regulating (temperature) factors on larval gulf menhaden growth still must be determined experimentally, preferably using laboratory-spawned and -reared larvae.

The apparent growth advantage enjoyed by menhaden larvae spawned early in the season (November) is only typical for a small part of the population. The largest segment of the population, those spawned in the peak months of January and February (Christmas and Waller 1975) and that immigrated to estuaries in February–April, typically had slower growth. Although slower growing, larvae spawned later in the season may be more successful in reaching estuaries. Guillory et al. (1983) found a negative relationship between temperature and gulf menhaden recruitment into Louisiana estuaries. The larger estuarine recruitment later in the season may be related to winter-early spring (January-April) predominant west-northwest longshore flow of coastal water within and just outside the coastal boundary front producing longshore advective transport and of lesser importance by episodic, short-term cross-shelf advection associated with cold fronts (Shaw et al. 1985b). They hypothesized that longshore currents facilitated the movement of larvae toward shore. Only for December did they note a reverse flow (eastward) that would not allow larvae to be transported toward estuaries west of the Mississippi delta.

The between transect comparisons of growth rate of larvae caught off Texas and Louisiana in February showed a difference in 1981 but not in 1982. Again higher growth rates were associated with higher mean water temperatures. Larvae from the LA February 1981 sample ($\bar{x}$ water temperature = 15.7°C) grew faster than larvae from the TX February 1981 sample ($\bar{x}$ water tempera-

ture = 12.0°C). Where no significant differences in growth were found, i.e., between LA and TX February 1982 samples, the respective mean water temperatures were 14.7° and 14.4°C. Neither of those growth curves were significantly different from the curve for larvae from the FL February 1982 sample where the mean water temperature was 16.4°C. However, the paucity of larvae >23 days old caught off Florida in February 1982 (Fig. 7d) suggests that comparisons of that data set with the data sets for larvae caught off Louisiana and Texas in February 1982 would be of little value.

The estimated spawning period for gulf menhaden extended from mid-October to mid-February (Fig. 8). These results agree with Fore (1970) and Christmas and Waller (1975) who, using the occurrence of eggs and larvae, estimated that gulf menhaden spawned from mid-October through March. Gonad weight-body weight ratios of adults (Lewis and Roithmayr 1981) and morphological and physiological features of ovarian tissue (Combs 1969) also indicate that spawning extends from October to early March. Based on the movement of late larvae into Lake Pontchartrain, Suttkus (1956) presumed that gulf menhaden spawning began in October and ceased in February. He suggested that the beginning and end of the spawning period fluctuates from year to year, and that there is no spawning activity during the spring and summer months as Higham and Nicholson (1964) have reported for the closely related Atlantic menhaden.

Most larvae caught in December were spawned in November (Fig. 8) regardless of the year. Larvae caught in February were spawned mostly in January but estimated spawning dates extended from mid-December to mid-February. For any given cruise, larvae from off Texas and Louisiana were spawned at about the same time. There was also considerable overlap in the spawning dates in any cruise off Florida and the other areas. The distribution of the central 50% of spawning dates from the Louisiana sample in February 1980 extended over a 29-d period and was wider than for any other data set. This unusually wide distribution may have been due to the presence of two distinct cohorts, one spawned in late December and one in late January, collected on the February 1980 cruise. Combs (1969) found that this species had intermittent total spawning. Lewis and Roithmayr (1981) inferred that gulf menhaden were intermittent, or fractional spawners. Christmas and Waller (1975) noted a modal temporal distribution of eggs in the region from the Mississippi delta to east of Cape San Blas. Baldauf[4] sampled young menhaden in the lower Neches River, TX, from November through April and found two incoming populations from which he suggested that there may have been two spawning peaks. Only in the larval collections of December 1981 did spawning date distribution appear to be bimodal; 7 and 20 November for Louisiana and 8 and 19 November for Texas. Future sampling throughout the spawning season will be necessary to determine the seasonal periodicity and peaks of gulf menhaden spawning. Relative numbers of larvae in cohorts within the spawning season could then be compared with measurements of environmental conditions as a test of the match-mismatch hypothesis (Cushing 1975) and to further test, as Methot (1983) has done, whether larvae spawned during favorable environmental periods constitute the greatest percentage of the year class.

ACKNOWLEDGMENTS

I thank the following persons of the Beaufort Laboratory: M. Boyd who extracted, mounted, and aged otoliths, W. Hettler who spawned gulf menhaden and furnished eggs for the laboratory experiments, A. Chester who advised on statistical procedures and problems, D. Ahrenholz and A. Powell who reviewed early drafts of the manuscript, and the crew and scientists on the RV *Oregon II* cruises. P. Ortner of the Atlantic Oceanographic and Meteorological Laboratories, NOAA, Miami, FL, provided raw data from which zooplankton counts were summarized. This research was supported by a contract from the Ocean Assessments Division, National Ocean Service, NOAA.

LITERATURE CITED

BERNARD, D. R.
1981. Multivariate analysis as a means of comparing growth in fish. Can. J. Fish. Aquat. Sci. 38:233–236.

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.
1975. Location and time of menhaden spawning in the

[4]Baldauf, R. J. 1954. Survey and study of surface and subsurface conditions in and around Beaumont, Texas. Biological survey of the Neches River in the region of Beaumont, Texas. Texas A&M Res. Found., Mimeo. Rep., 184 p.

Gulf of Mexico. Gulf Coast Res. Lab., Ocean Springs, MS, 20 p.

COMBS, R. M.
1969. Embryogenesis, histology, and organology of the ovary of *Brevoortia patronus*. Gulf Res. Rep. 2:333–434.

CUSHING, D. H.
1975. Marine ecology and fisheries. Cambridge Univ. Press, Cambridge, Eng., 278 p.

FIVES, J. M., S. M. WARLEN, AND D. E. HOSS.
1986. Aging and growth of larval bay anchovy, *Anchoa mitchilli*, from the Newport River estuary, North Carolina. Estuaries 9(4B):362–367.

FORE, P. L.
1970. Eggs and larvae of the Gulf menhaden. *In* Report of the Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C., p. 11–13. U.S. Fish Wildl. Serv. Circ. 341.

GOVONI, J. J., D. E. HOSS, AND A. J. CHESTER.
1983. Comparative feeding of three species of larval fishes in the northern Gulf of Mexico: *Brevoortia patronus*, *Leiostomus xanthurus*, and *Micropogonias undulatus*. Mar. Ecol. Prog. Ser. 13:189–199.

GUILLORY, V., J. GEAGHAN, AND J. ROUSSEL.
1983. Influence of environmental factors on gulf menhaden recruitment. La. Dep. Wildl. Fish. Tech. Bull. 37, 32 p.

HARRIS, R. J.
1975. A primer of multivariate statistics. Acad. Press, N.Y., 332 p.

HETTLER, W. F.
1983. Transporting adult and larval gulf menhaden and techniques for spawning in the laboratory. Prog. Fish-Cult. 45:45–48.
1984. Description of eggs, larvae, and early juveniles of gulf menhaden, *Brevoortia patronus*, and comparisons with Atlantic menhaden, *B. tyrannus*, and yellowfin menhaden, *B. smithi*. Fish. Bull., U.S. 82:85–95.

HIGHAM, J. R., AND W. R. NICHOLSON.
1964. Sexual maturation and spawning of Atlantic menhaden. Fish. Bull., U.S. 63:255–271.

HOENIG, N. A., AND R. G. HANUMARA.
1983. Statistical considerations in fitting seasonal growth models for fishes. Cons. Int. Explor. Mer, C.M. 1983/D:25, 25 p.

JONES, C.
1985. Within-season differences in growth of larval Atlantic herring, *Clupea harengus harengus*. Fish. Bull., U.S. 83:289–298.

LAIRD, A. K., S. A. TYLER, AND A. D. BARTON.
1965. Dynamics of normal growth. Growth 29:233–248.

LAROCHE, J. L., S. L. RICHARDSON, AND A A. ROSENBERG.
1982. Age and growth of a pleuronectid, *Parophrys vetulus*, during the pelagic larval period in Oregon coastal waters. Fish. Bull., U.S. 80:93–104.

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.

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. Réun. Cons. int. Explor. Mer 178:304–311.

LEWIS, R. M., AND C. M. ROITHMAYR.
1981. Spawning and sexual maturity of gulf menhaden, *Brevoortia patronus*. Fish. Bull., U.S. 78:947–951.

LEWIS, R. M., E. P. H. WILKINS, AND H. R. GORDY.
1972. A description of young Atlantic menhaden, *Brevoortia tyrannus*, in the White Oak River estuary, North Carolina. Fish. Bull., U.S. 70:115–118.

LOUGH, R. G., M. PENNINGTON, G. R. BOLZ, AND A. A. ROSENBERG.
1982. Age and growth of larval Atlantic herring, *Clupea harengus* L., in the Gulf of Maine-Georges Bank region based on otolith growth increments. Fish. Bull., U.S. 80:187–199.

METHOT, R. D., JR.
1983. Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. Fish. Bull., U.S. 81:741–750.

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.

PANNELLA, G.
1971. Fish otoliths: Daily growth layers and periodical patterns. Science (Wash., D.C.) 173: 1124–1127.

PIMENTEL, R. A.
1979. Morphometrics, the multivariate analysis of biological data. Kendell/Hunt Publ. Co., Dubuque, IA, 276 p.

POWELL, A. B., AND G. PHONLOR.
1986. Early life history of Atlantic menhaden, *Brevoortia tyrannus*, and gulf menhaden, *B. patronus*. Fish. Bull., U.S. 84:991–995.

REINTJES, J. W.
1970. The gulf menhaden and our changing estuaries. Proc. Gulf Caribb. Fish. Inst. 22:87–90.

SHAW, R. F., J. H. COWAN, JR., AND T. L. TILLMAN.
1985a. Distribution and density of *Brevoortia patronus* (gulf menhaden) eggs and larvae in the continental shelf waters of western Louisiana. Bull. Mar. Sci. 36:96–103.

SHAW, R. F., W. J. WISEMAN, JR., R. E. TURNER, L. J. ROUSE, JR., R. E. CONDREY, AND F. J. KELLY, JR.
1985b. Transport of larval gulf menhaden *Brevoortia patronus* in continental shelf waters of western Louisiana: A hypothesis. Trans. Am. Fish. Soc. 114:452–460.

SUTTKUS, R. D.
1956. Early life history of the gulf menhaden, *Brevoortia patronus*, in Louisiana. Trans. N. Am. Wildl. Conf. 21:390–407.

TANAKA, R., Y. MUGIYA, AND J. YAMADA.
1981. Effects of photoperiod and feeding on daily growth patterns in otoliths of juvenile *Tilapia nilotica*. Fish. Bull., U.S. 79:459–466.

TURNER, W. R.
1969. Life history of menhadens in the eastern Gulf of Mexico. Trans. Am. Fish. Soc. 98:216–224.

U.S. NATIONAL MARINE FISHERIES SERVICE.
1986. Fisheries of the United States, 1985. U.S. Natl. Mar. Fish. Serv. Curr. Fish. Stat. 8380, 121 p.

WARLEN, S. M., AND A. J. CHESTER.
1985. Age, growth, and distribution of larval spot, *Leiostomus xanthurus*, off North Carolina. Fish. Bull., U.S. 83:587-599.

WIEBE, P. H., K. H. BURT, S. H. BOYD, AND A. W. MORTON.
1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. J. Mar. Res. 34:313–326.

ZWEIFEL, J. R., AND R. LASKER.
1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609–621.