The record of daily growth in otoliths of Atlantic silversides, *Menidia menidia*, from field and laboratory

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Otoliths were removed from field-collected silversides of age less than 3 months. Otolith diameter was highly correlated with total length of the fish. Daily growth ring counts for this species are known to be a function of age rather than size, so widths for the daily growth rings provide a record of daily increases in length of the fish. Measurement of ring widths showed that weekly specific growth rate was greater than 70% at age 1 week, but declined to about 30% at age 1 month and about 15% at age 2 months. A laboratory experiment in which temperature was changed on a weekly basis demonstrated that environmental variables can affect the width of rings. Nevertheless, the growth rate of field-collected fish, as calculated from otolith ring widths, was more highly correlated with size of fish, as measured by otolith radius, than with the environmental variables of temperature, salinity and plankton abundance. Back-calculation of growth rates from otolith ring widths of five fish collected at the end of the growing season yielded the same age-growth curves as were obtained from 203 fish collected biweekly during the season.

I. INTRODUCTION

Since Pannella's (1971) original observation that the otoliths of young fish possess daily growth rings, the presence of such rings has been noted in many species (see review in Ralston & Miyamoto, 1983). Daily growth rings have been used to age fish for construction of age–growth curves (Struhsaker & Uchiyama, 1976; Taubert & Coble, 1977; Methot & Kramer, 1979; Barkman *et al.*, 1981; Brothers, 1981; Brothers & McFarland, 1981; Methot, 1981; Townsend & Graham, 1981; Lough *et al.* 1982; Marshall & Parker, 1982; Wilson & Larkin, 1982; Crecco *et al.*, 1983; Nishimura & Yamada, 1984) and to identify the time of hatching or metamorphosis (Barkman *et al.*, 1981; Brothers & McFarland, 1981; Marshall & Parker, 1982).

The mechanisms involved in the formation of otolith ring increments and the effects of environmental variables on both formation and width of the increments have been studied but are not well understood. Taubert & Coble (1977) suggested that entrainment to a 24-h light–dark cycle was necessary for ring formation in *Tilapia mossambica* and noted that rings were not deposited by *Lepomis cyanellus* in cold temperatures that simulated winter conditions. The necessity of light cues for increment formation was also reported for *Fundulus heteroclitus* by Radtke & Dean (1982). Brothers (1981) found that temperature is the predominant factor in determining increment deposition in fish from a temperate stream although feeding and light have subordinate roles. Neilson & Geen (1982) showed experimentally that photoperiod and temperature affect increment width, but feeding frequency

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affects both increment number and width in *Oncorhynchus tshawytscha*. Volk *et al.* (1984) reported that increment width was correlated with daily ration level. However, other studies have demonstrated that deposition of daily rings by *Platichthys stellatus* is unaffected by photoperiod or temperature fluctuations (Campana & Neilson, 1982) and that foraging periodicity is not a significant factor in *Oncorhynchus nerka* (Marshall & Parker, 1982), *Salmo gairdneri* or *P. stellatus* (Campana, 1983). Tanaka *et al.* (1981) (working with *Tilapia nilotica*) and Townsend & Shaw (1982) (working with *Micromesistius poutassou*) concluded that otolith growth is endogenously controlled, synchronized by photoperiod or some yet-to-be-identified environmental variable. That conclusion was also adopted by Campana & Neilson (1985) in a recent review.

One advantage of studying daily ring widths is that the entire growth history of the fish should be recorded therein. If it were necessary to collect fish only at the end of a growing season and then analyse otoliths, that would obviate the need to sample a large number of fish over time to obtain length-frequency data. If environmental data were also available, a comparison of daily growth to environmental variables may yield information about the variables most important for growth. For example, Crecco & Savoy (1985) used otolith ring data to show that larval shad, *Alosa sapidissima*, growth and survival were correlated with temperature, river flow rate and zooplankton density.

This study was undertaken to: (a) determine whether otolith diameter is highly correlated to fish total length, and therefore reflects fish growth, for the Atlantic silverside, *Menidia menidia*; (b) demonstrate in the laboratory that variation in a single environmental variable can cause variation in fish growth that is recorded in the otolith; and (c) try to correlate growth, as recorded in rings of field-captured fish, with changes in the environmental variables of temperature, salinity and food abundance. Previous research has shown that this species deposits daily rings and that otolith ring counts are dependent on age of the fish, not on otolith size (Barkman, 1978).

II. METHODS

COLLECTION OF FISH AND ENVIRONMENTAL DATA

Fish were collected with a 2-mm mesh, 15·2 m long beach seine from the west shore of the upper Pettaquamscutt River, a long, narrow estuary in southern Rhode Island, U.S.A. Samples were taken biweekly from June to September 1977, and a single sample was taken on 17 July 1979. At least 10 fish were retained from each sample, their total lengths were measured, and their sagitta otoliths were removed.

Measurements of temperature, salinity and zooplankton abundance during the months of May–September were made five times per week in 1977 and three times per week in 1979 at the fish collection site. The data were then averaged for each week. Details of the sampling procedure and the data collected are presented elsewhere (Bengtson, 1984).

LABORATORY EXPERIMENTS

Menidia menidia postlarvae were reared through metamorphosis to the juvenile stage over a 1-month period in four temperature regimes. The four regimes were: 1, constant ambient Narragansett Bay water (A); 2, constant heated water, $8 \pm 1°$ C above ambient (H); 3, ambient during weeks 1 and 3, heated during weeks 2 and 4 (A1,H2); 4, heated during weeks 1 and 3, ambient during weeks 2 and 4 (H1,A2). Actual measured temperatures are given in Fig.1. Twenty fish were removed from each tank each week and killed; their total lengths and wet weights were recorded and the sagitta otoliths removed. The length and
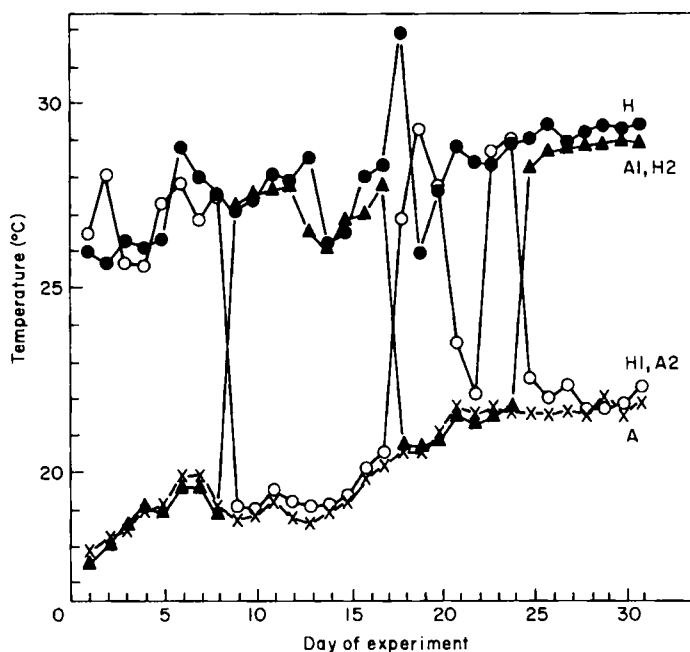
FIG. 1. Daily measured temperatures in the laboratory study of temperature effect on *Menidia menidia* otolith growth. A, ambient water; H, heated water; A1, H2, ambient during weeks 1 and 3, heated during weeks 2 and 4; H1, A2, heated during weeks 1 and 3, ambient during weeks 2 and 4.

weight data and additional information about the experimental methods are presented elsewhere (Bengtson & Barkman, 1981).

OTOLITH COUNTS AND MEASUREMENTS

Otoliths that were removed from field-collected fish were prepared for ring counts according to the methods of Barkman (1978). Sagitta diameter was measured along the longest dimension of the otolith by means of a microscope with a stage micrometer. The otoliths were photographed for ring counts through a Reichert* photo-automatic micro-scope at × 500 magnification. Number of rings was used as the independent variable in an equation (Barkman, 1978) to determine the age of each fish. Other procedural details and data on the fish collected during 1977 were given by Barkman *et al.* (1981).

Otoliths from five fish collected from the field on 1 September 1977, and five collected on 17 July 1979, were subjected to further analysis of their record of growth. These particular fish were chosen because they had hatched within days of each other; the hatching dates of the former group of fish fell within one day of each other and those of the latter group fell within 10 days of each other. A series of photographs was taken of each otolith along the longest dimension on the anterior-posterior axis, between the nucleus and the edge of the otolith. Ring widths (RW) were measured to the nearest micrometer from the photographs, using a photograph of a stage micrometer taken at the same magnification.

Otoliths removed from fish in the laboratory experiment were prepared and photo-graphed in the manner described above, but only the width of the outermost seven rings and the otolith radius were measured, to determine growth of fish during the previous week.

DATA ANALYSIS

Weekly specific growth rates (SGR) for the ten field-collected fish whose ring widths were measured were calculated from the measurements according to a formula used by Laurence (1974):

$$SGR = 100 \times (\ln R_1 - \ln R_0)/t,$$

*The use of trade names does not imply endorsement by the U.S. Environmental Protection Agency.
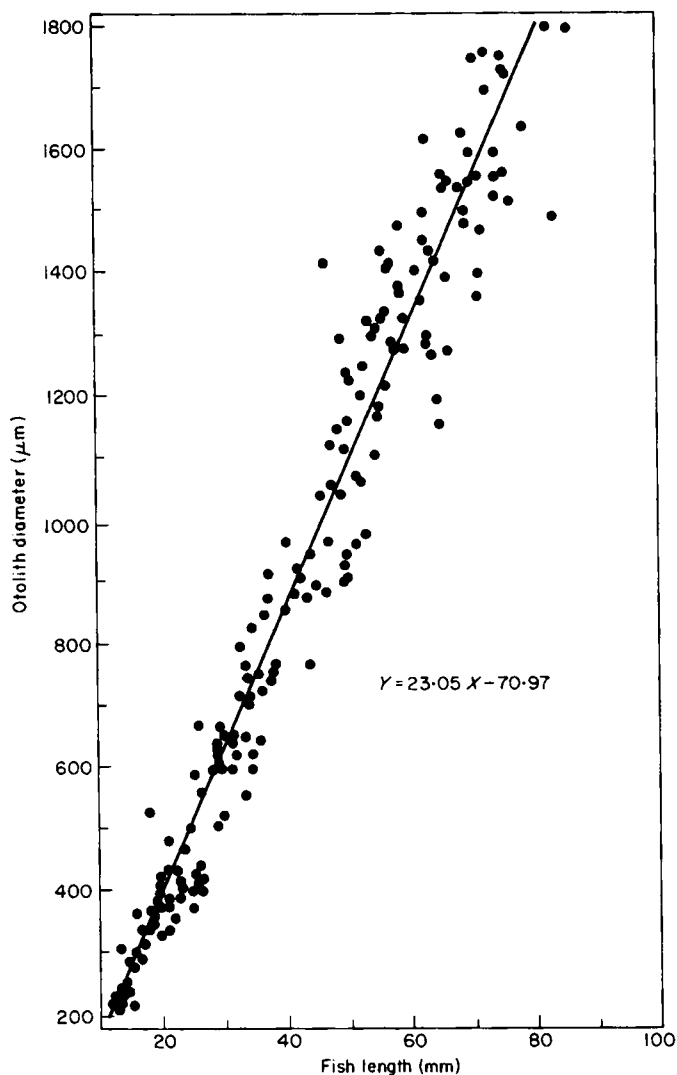
FIG. 2. Otolith diameter as a function of fish total length for 179 field-captured *Menidia menidia* collected during biweekly sampling in 1977.

where R_0 is the otolith radius at the beginning of a week, R_1 is the radius at the end of that week and t is the time increment (1 week). The average weekly SGRs and an assumed initial length at hatch of 5·0 mm were used to calculate the growth (i.e. reconstruct the growth history) of *M. menidia* during the first 10 weeks of life in 1977 and the first 8 weeks of life in 1979.

The relationships of the environmental variables to SGR and RW were determined by a stepwise regression procedure available in the Minitab statistical package.

III. RESULTS

The otolith diameter (OD) in μm is very highly correlated with fish total length (TL) in mm (Fig. 2), according to the formula
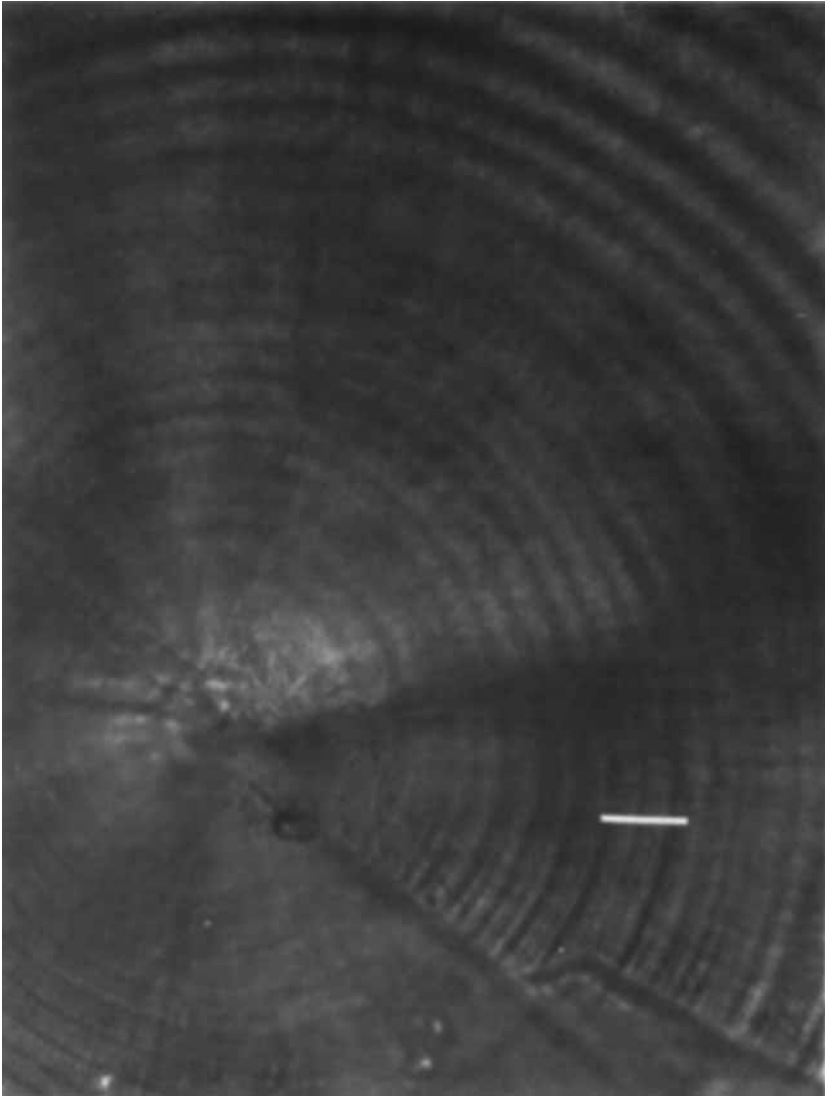
$$OD = 23·05 \, (TL) - 70·97 \, (r^2 = 0·95), \tag{1}$$

FIG. 3. Photomicrograph of an otolith from a 79-day-old *Menidia menidia*, showing the first 20 daily increments (× 300 magnification; scale = 10 µm).

thereby demonstrating that the otolith is an excellent representation of fish growth.

An otolith magnified × 500 (Fig. 3) shows the rings representing the record of growth for the first 20 days of life of a 79-day-old Atlantic silverside collected on 1 September 1977. The width of individual rings, each represented by a light and dark zone, varied between 1·8 and 9·1 µm. The variation in ring width is largely due to variation in the width of the dark zone (Fig. 4).

The results of the laboratory experiment (Fig. 5) demonstrate that temperature can affect growth of the otolith. The otoliths from fish that were raised in constantly heated water (H) showed consistently larger weekly increments than those
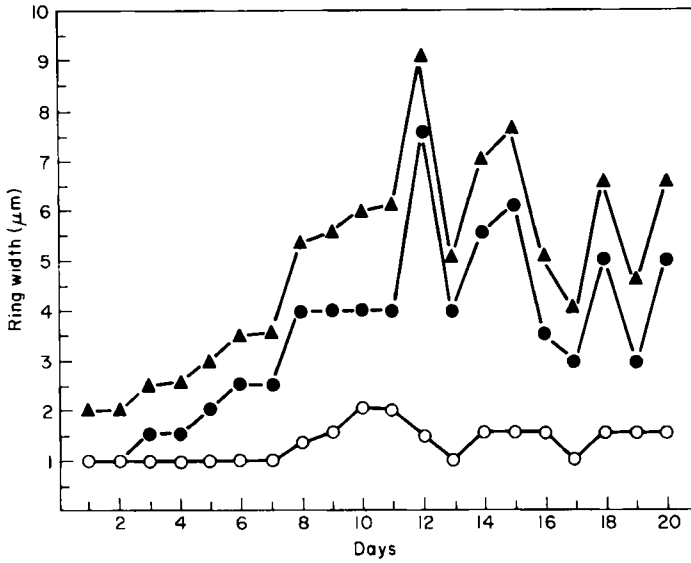
FIG. 4. Total width, ▲—▲, of each of the 20 increments shown in Fig. 3, along with separate measurements of the light, ○—○, and ●—●, dark zone within each increment.
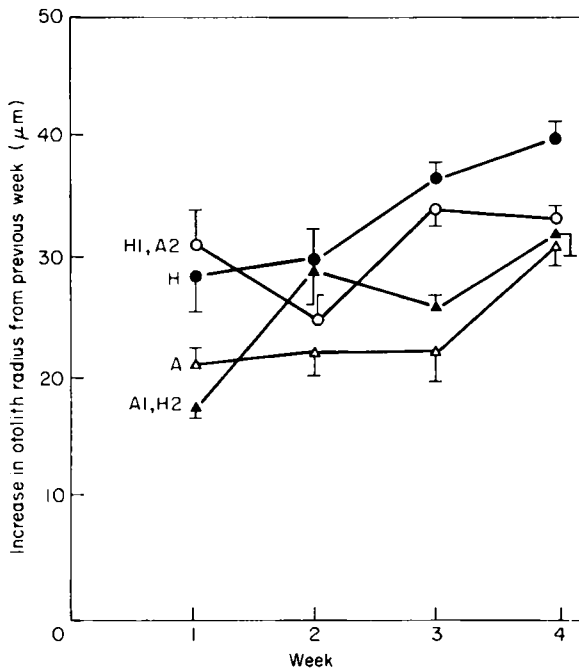

FIG. 5. Average increase in otolith radius during each week of the laboratory study of temperature effect on otolith growth. ($n = 5$ for each data point; error bars denote s.d.) See Fig. 1 for key to letters denoting treatment from which each group of fish was taken.
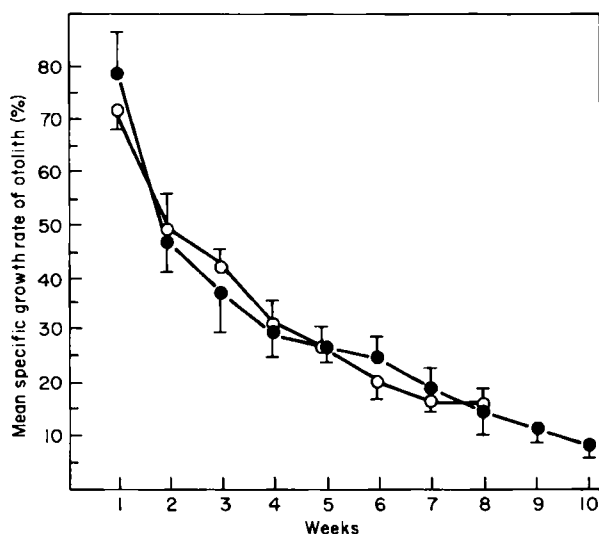
FIG. 6. Mean weekly specific growth rates calculated from otolith ring width measurements of five *Menidia menidia* collected from the field in September 1977, ●—●, and five collected from the field in July 1979, ○—○.

of fish raised in ambient water (A), and the size of the increments of both groups increased each week. Fish raised in water temperatures that fluctuated from week to week (A1, H2 and H1, A2) showed increased growth under heated conditions and decreased growth under ambient conditions.

The mean weekly specific growth rates for the first 10 weeks of life of the five fish collected in 1977 and for the first 8 weeks of life of the five fish collected in 1979 (Fig. 6) decrease monotonically and are nearly identical from year to year. When growth is expressed not as a rate but as an absolute amount (Fig. 7), we see that growth increases to a maximum sometime during weeks 5–7 and then stabilizes or declines.

We used the growth rate data in Fig. 6 and an assumed length at hatch of 5·0 mm to reconstruct age–length curves for the fish as they grew in 1977 and 1979 (Fig. 8). The linear regressions for total length (TL) in mm as a function of age (AGE) in days were

$$1977, TL = 0·905\,(AGE) + 0·294\,(r^2 = 0·99); \tag{2}$$

$$1979, TL = 0·862\,(AGE) + 1·035\,(r^2 = 0·99). \tag{3}$$

These regression lines are not significantly different (analysis of covariance; $P > 0·05$) from each other or from the age–length regression given by Barkman *et al.* (1981):

$$TL = 0·842\,(AGE) + 3·409\,(r = 0·90) \tag{4}$$

for 203 *M. menidia* (captured in the 1977 biweekly sampling) whose actual lengths were measured and whose actual ages were determined by otolith ring counts. Thus, a single sample of five fish taken at the end of the growing season yielded the same age-length information through counting of rings and measurement of ring widths as did the biweekly sampling, measuring and ring-counting of 203 fish.
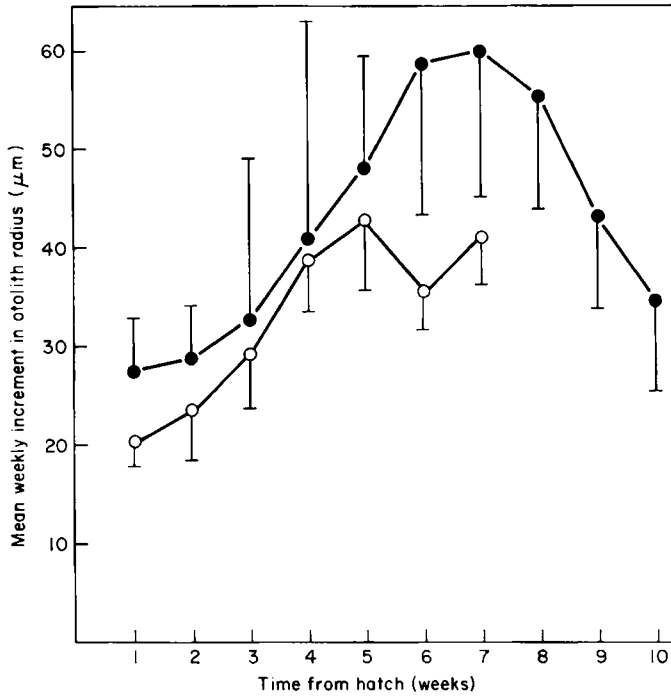
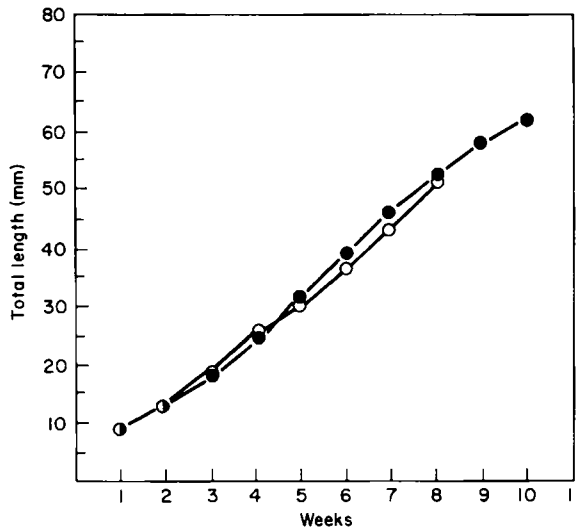FIG. 7. Mean weekly growth of the otolith radius for the same fish as in Fig. 6.

FIG. 8. Calculated length-at-age curves for the same fish as in Fig. 6, based on the growth rates shown in Fig. 6 and an assumed length at hatch of 5·0 mm.
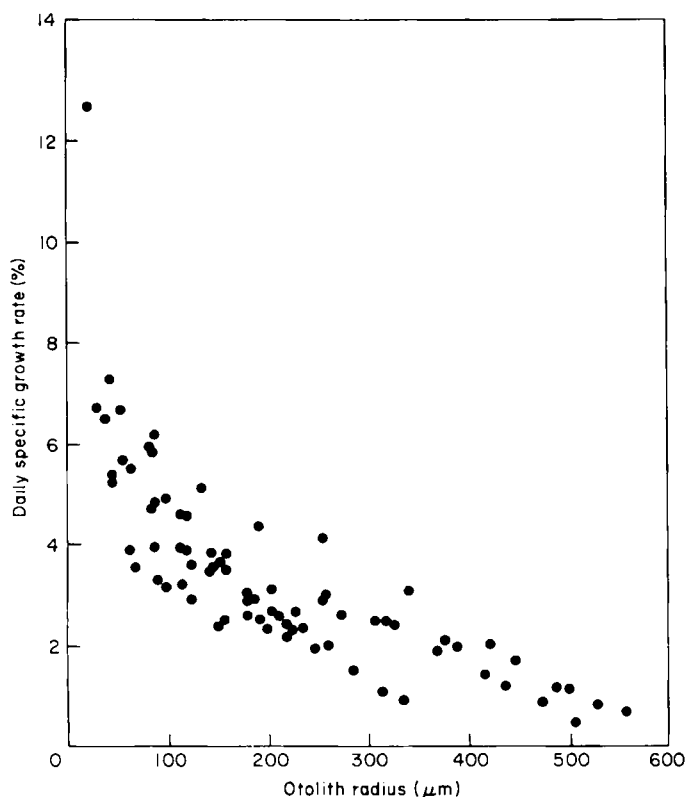
FIG. 9. Daily specific growth rate as a function of otolith radius for *Menidia menidia* collected from the field in 1977 and 1979 (same fish as in Fig. 6).

The stepwise regression procedure that related daily specific growth rate (DSGR, which equals weekly SGR divided by 7) to environmental variables of temperature in $^{\circ}$ C (T), salinity in ‰ (S), and plankton abundance in number 1^{-1} (P) yielded only a simple linear regression equation relating growth rate to salinity, but with poor correlation:

$$DSGR = 6{\cdot}080 - 0{\cdot}216(S) \, (r^2 = 0{\cdot}32). \qquad (5)$$

When the same procedure was used to relate ring width (RW) to the three environmental variables, a simple linear regression relating ring width to temperature was obtained, again with poor correlation:

$$RW = 3{\cdot}4 \, (T) - 40{\cdot}7 \, (r^2 = 0{\cdot}32). \qquad (6)$$

It appears, therefore, that the three environmental variables are poor predictors of both growth rate and ring width of field-collected fish.

One variable that is an excellent predictor of DSGR, however, is otolith radius (RAD) at the beginning of the week in which growth rate is measured (Fig. 9):

$$DSGR = 6{\cdot}062 - 0{\cdot}011 \, (RAD) \, (r^2 = 0{\cdot}82). \qquad (7)$$

Growth rate is more related to fish size than to any environmental variable measured.

IV. DISCUSSION

Our study has demonstrated that the widths of daily rings in the otolith provide an excellent record of the growth of *M. menidia* postlarvae and juveniles. The same age–length data were available from the ring widths in otoliths of a very small sample of fish at the end of the summer as were available from ring-counts/measured-fish-lengths from a series of large samples taken throughout the summer. Fishery biologists could potentially reduce substantially the number of specimens needed for analysis to obtain age–length curves if the ring-width approach could be shown to be applicable to other species.

Even though one can show a relation between a single environmental variable and otolith ring width in the laboratory, the relationship is not necessarily apparent in field populations where other variables also operate. Specifically, our study showed that fish size (expressed as otolith radius) overshadowed the other measured environmental variables in determining the growth rate of the fish. An inherent, presumably genetic, control of growth must be operating unaffected by environmental variation, at least within the boundaries of variation that exist in the estuary during summer months. It should be pointed out, however, that the fish sampled are the 'survivors' of the year class and that the majority of the year class probably does not survive to the end of the first growing season. Whether fish that did not survive were affected by the environment is, of course, unknown. Our data merely show that the surviving fish in two separate years exhibited almost identical growth rates despite environmental differences. It is noteworthy that the 1977 fish hatched in mid-June and were generally exposed to higher temperatures and salinities than the 1979 fish which hatched in mid-May. Lough *et al.* (1982) also observed a consistent pattern of growth in otoliths of herring larvae collected at different locations and at different times.

We suggest that investigators who wish to correlate environmental variables with growth rate must plan their sampling and analysis of field fish so that the fish to be analysed have had approximately the same hatching date. After plotting size-dependent DSGR (as in Fig. 9), the expected DSGR for a given size of radius can be calculated and compared with the actual DSGR observed for the radius during the next week (or whatever time period). The residuals (observed minus expected DSGR) might then be correlated with environmental variables to determine which, if any, variables may have altered DSGRs from their expected values.

One question about our analysis is whether we measure environmental variables in the same way that the fish do. That is, do our measurements in one place at one time of day accurately reflect the environment that the fish experiences? For example, if the fish feed exclusively in patches of plankton, our sampling, which was not designed to collect only patches, would not reflect the plankton abundance available to the fish.

The finding that changes in the increment width of *M. menidia* daily rings is due primarily to increased width of the dark zone agrees with Pannella's (1971, 1974) observation that the dark zone is associated with rapid growth. Degens *et al.* (1969) reported that the dark zone has a greater degree of calcification than the light zone. The changes in width of rings depicted in Fig. 7 indicate that actual growth of the fish is greatest in the weeks following metamorphosis, which occurs during week 2. The fact that actual growth declined abruptly in weeks 9 and 10 of

1977 coincides with the observation that growth of *M. menidia*, as measured by length–frequency diagrams, also slows in late summer (Bengtson, 1984).

Although the use of otolith daily rings for fish age and growth studies has recently become more widespread, many fishery biologists are inhibited by the labour-intensive aspect of the method. From our studies with *M. menidia*, we calculate the following costs and benefits for the different methods of measuring growth over time. Collection of a sample (~ 50–100 fish) requires about 2 h. Simply measuring lengths of fish on several dates for length–frequency diagrams requires about 15 s per fish; however, the growth estimate obtained with this method substantially underestimates actual individual fish growth (0.5 mm day^{-1} *v.* 0.8 mm day^{-1} actual) (Mulkana, 1966; Barkman *et al.*, 1981; Bengtson, 1984). The preparation of a single otolith for counts or measurements requires about 1 h. Accurately counting the rings requires about 1 h per otolith. Photographing an otolith and subsequently taking measurements of ring widths requires about 4–5 h per otolith. Thus, the total time required for generation of equation (4) above was about 430 h (24 h sampling, 203 h processing, 203 h counting), whereas that for equation (2) was about 30 h (2 h sampling, 5 h processing, 23 h photographing and measuring). At least for this species, labour can actually be reduced by using one-time, end-of-season sampling.

The fish selected each year for end-of-season ring width analysis were chosen solely on the basis of similarity of hatching date, which differed (mid-May *v.* mid-June) for the two years studied. The growth rates of fish in the two years were very consistent and the end-of-season survivors' back-calculated growth rates were consistent with those of the general population during the growing season. For other species, whose growth rates may not be so consistent, or who are subject to significant size-dependent selection pressure, end-of-season survivors may not represent well the growth rates of the general population. An analysis such as we have conducted is an essential verification step before end-of-season ring-width analysis can be routinely applied.

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