Abstract.—Laboratory analyses were conducted on age-0 weakfish, *Cynoscion regalis*, to determine if deposition rate of otolith increments was daily and to examine the relation among otolith increment growth, daily feeding rate, specific growth rate, and condition factor. Tetracycline-marked juveniles (n=58) had a mean deposition rate of 0.98 (0.03 SE) increments/d. Feeding rate significantly affected increment width and was positively correlated with somatic growth rate and condition factor. Increment width response to changes in ration level was immediate, significant differences occurring between day 7 and 14. Mean increment width and specific growth rate were positively correlated (r=0.86). The continuation of otolith growth during periods of negative fish growth reflects the conservative nature of otolith growth and the lack of otolith resorption. An established relation between known growth rates of juvenile weakfish in the laboratory and otolith increment width will allow otolith increment widths to be applied to field samples. Such analyses could be used to examine closely factors affecting growth, survival, and recruitment.

Daily growth increments in otoliths of juvenile weakfish, *Cynoscion regalis*: experimental assessment of changes in increment width with changes in feeding rate, growth rate, and condition factor

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Growth rates in fishes can be determined by using scales, otoliths, modal analysis, RNA-DNA ratios, and assorted skeletal structures (Bagenal, 1978; Campana and Neilson, 1985; Summerfelt and Hall, 1987). Interpretations from these structures are based upon assumptions that increments within otoliths are added periodically and that the change in thickness of consecutive rings is proportional to fish length (Campana and Neilson, 1985). Otoliths have also proven to provide an accurate record of fish growth because there has been no evidence of resorption (Degens et al., 1969; Dunkelberger et al., 1980; Watabe et al., 1982; Mugiya, 1987), except under extreme physiological stress (Mugiya and Uchimura, 1989).

The periodicity of increment addition has been shown to be daily in larval and juvenile fishes (Campana and Neilson, 1982; Hettler, 1984; Schmitt, 1984; Tsukamoto, 1985; Wilson et al., 1987; Tzeng and Yu, 1989; Monaghan, 1993). Otolith microstructure has more recently been used to compare growth of different cohorts within a year class (Townsend and Graham, 1981; Warlen, 1982; Methot, 1983; Jones, 1985), examine life history transitions (Brothers and McFarland, 1981; Laroche et al., 1982; Powell, 1982; Miller and Storck, 1982; Victor, 1986; Thresher and Brothers, 1989), estimate mortality and survival (Crecco et al., 1983; Graham and Townsend, 1985; Neilson and Geen, 1986; Essig and Cole, 1986; Dalzell et al., 1987; Post and Prankevicius, 1987; Rice et al., 1987), and determine the effects of biotic and abiotic factors on microstructure

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(Taubert and Coble, 1977; Tanaka et al., 1981; Campana and Neilson, 1982; Neilson and Geen, 1982, 1985; Neilson et al., 1985; Maillet and Checkley, 1991; Moksness, 1992).

Growth histories of fish are determined primarily through back calculation by using either a direct proportion or some nonlinear relation between otolith size and fish age (Maciena et al., 1987; Thorrold and Williams, 1989). Recent studies have used the relation between increment width (IW) and growth rate to show growth histories (Maillet and Checkley, 1990; Molony and Choat, 1990; Wright et al., 1990). Key assumptions for this use are that distance between increments is proportional to growth rate and that the increments are produced daily (Beamish and McFarland, 1983).

The objectives of this study were to validate the daily periodicity of otolith increments in juvenile weakfish, *Cynoscion regalis*, and to describe the relation between otolith IW and changes in feeding rate, specific growth rate, and condition factor.

Materials and methods

Experiment 1 (daily otolith increment validation)

Juvenile weakfish were captured in Delaware Bay in August, 1987, maintained in the laboratory in a recirculating seawater system under a photoperiod of 14 h light/10 h dark at 22°C (0.20 SE), 20‰, and fed ad libitum on squid. Fifty-eight fish were injected with a 200-mg oxytetracycline hydrochloride/0.1 mL saline solution and held in recirculating seawater for 26 days. Throughout the 26-d period, between 1 and 5 fish were removed and measured (SL), and their otoliths were removed for analysis. Fish sizes ranged from 68 to 150 mm SL.

Experiment 2 (effect of ration level on increment width and specific growth rate)

Weakfish were reared from eggs fertilized in the laboratory and raised to the juvenile stage in recirculating seawater (photoperiod=14L/10d at 22°C, 20‰). Individual fish were held in 20-L circular containers and fed ad libitum for two days to determine maximum ration (pretreatment period). Each day, fish were fed a known weight of live mysid shrimp (*Neomysis americana*) in excess of what they could consume. Fish were allowed to feed for 24 hours whereupon uneaten mysids were collected and weighed. Maximum ration was determined to be approximately 20% body weight/d.

Experimental treatment rations were randomly assigned on the third day of the experiment. Fish were weighed to the nearest 0.1 g and randomly assigned one of six daily rations: 100% maximum ration (MR, n=5), 90% MR (n=4), 80% MR (n=4), 60% MR (n=4), 40% MR (n=4), 20% MR (n=4, Table 1). Feeding levels were also calculated as percentages of body weight for individual fishes. For 14 days, fish were fed daily at these assigned levels; that is to say, they were allowed to feed for 24 h whereupon uneaten mysids were removed and collectively weighed. Fish were reweighed on day 7, and final weights and lengths were measured on day 14. The absolute weight of the daily feeding level offered (as a percentage body weight) was adjusted on day 7 to account for growth and maintain ration levels as a function of fish weight. Specific growth rate (SGR) was calculated for each fish as

$$SGR = \left[(\ln W_{14} - \ln W_0)/14\right] \times 100,$$

where W_{14} = the wet weight (g) on day 14;
W_0 = the initial wet weight (g); and
14 = the duration of the treatment period in days.

Mean specific growth rates were calculated for each treatment. Fulton's condition factor (K) at the end of the experiment was calculated for each fish as

$$K = W/L^3 \times 10{,}000,$$

where W = the wet weight (g); and
L = the standard length (mm).

Daily ration (percentage body weight/d) was calculated for each fish for each day on the basis of the

Table 1

Summary of ration levels. Actual treatment feeding levels and daily ration calculated based on calculated daily fish weights.

Feeding levels (% of maximum ration)		Daily ration (% body weight/day)		
Estimated feeding level	Actual feeding level	Mean	Week 1	Week 2
100	100	23.8	26.4	21.3
90	66	15.6	16.1	15.0
80	58	13.9	14.6	13.3
60	46	11.0	11.1	10.9
40	32	7.6	7.7	7.5
20	17	4.1	4.1	4.1

weight of mysids consumed (weight of mysids offered minus weight of mysids not eaten) and estimated fish weights (assuming exponential growth between weighing). Mean daily ration was calculated for each feeding level treatment (Table 1). Henceforth, feeding will refer to daily ration, whereas treatment levels will continue to be referred to as percentage of maximum ration (MR).

Because measurements of feeding depended upon the reliability with which uneaten mysids were collected, retrieval efficiency was determined. Live mysids, in amounts comparable to the feeding levels described above, were weighed to the nearest mg and placed in all ten containers with recirculating seawater. After 24 hours, the mysids were retrieved and reweighed. Mean weight of retrieved mysids was 89% (0.017 SE) of initial weight. Therefore, differences between the weight of mysids provided and the weight retrieved was considered to be a useful estimate of feeding.

Otolith preparation and analysis

Otoliths were ground by hand following modified procedures of Neilson and Geen (1981) and Volk et al. (1984). Both sagittal otoliths were embedded in EPON resin. Otoliths were attached to a glass slide with thermoplastic and ground to half their thickness across a transverse plane by using a series of 400–600 grit carborundum paper. Otoliths were polished with 0.3 μm alumina oxide paste, reattached to a glass slide with the polished side down, then ground and polished to produce a thin section through the nucleus. All counts and measures were made from the origin along the dorsal edge of the neural groove to the otolith margin. All other transects lacked precision.

Tetracycline-marked otoliths were examined with UV light at 400× magnification. Increment counts were made from the fluorescent mark to the edge of the otolith. Each otolith was counted twice, without knowledge of the previous measurement, and confirmed by an independent counter. Otoliths from experiment 2 were examined under 400× magnification with transmitted light. Mean IW was calculated from three "blind" measurements. We made all counts and measurements with an Olympus Cue 2 Image Analysis System. One pair of otoliths from the 66% ration treatment was not readable and was subsequently discarded.

Statistical analyses

Experiment 1—daily otolith increment validation To validate the daily nature of otolith increment, the regression slope of increment count on day was tested to determine if it differed from one (Students' t-test). Outliers were detected by calculating the leverage coefficients and by computing the standard residuals from the regression equation line. Only 2% of the otoliths were reexamined because the leverage coefficient was greater than $4/n$ and the standard residual was greater than the t-value for a sample size of n (Sokal and Rohlf, 1981).

Experiment 2—effect of ration level on increment width and specific growth rate Mean IW among ration treatments for increments formed during the pretreatment period was compared with ANOVA (α =0.05), followed by Tukey's multiple comparison tests (Zar, 1984). Mean IW among ration treatments for weeks 1 and 2 and between weeks within ration treatments was analyzed with two-way ANOVA (α =0.05). Mean specific growth rate for each treatment was regressed against mean increment width following confirmation of normality (Kolmogorov-Smirnov test) and homogeneity of variances (Cochran's C test) with α=0.05 for all treatment levels. Increment width was compared with SGR, daily ration, and Fulton's K at the end of the experiment for each fish (Pearson product-moment). Regression analysis was used to determine the relation between IW and SGR (log{G+1}) for each fish. Regression lines were fitted by using a second-order regression against daily ration (Zar, 1984).

Results

Experiment 1—daily otolith increment validation

The slope of the regression increments on days after injection was not significantly different from one (y=0.975x + 0.825, P>0.05), thus supporting the daily periodicity of otolith increment formation in this species (Fig. 1).

Experiment 2—effect of ration level on increment width and specific growth rate

No differences were found in mean IW among treatments during the 2-d pretreatment period. Initially, IW narrowed in the lower feeding levels: 17%, 32%, and 46% maximum MR (Fig. 2). Mean daily IW ranged from a low of 2.3 μm (17% MR or 4.1% body weight/d) during week 2 to a high of 4.5 μm (66% MR or 15.6% body weight/d) during week 1 (Table 2).

Mean IW was significantly lower for the 17%, 32%, and 46% MR treatments during the entire 14-d period as compared with the higher ration treatment

(Table 2; Fig. 3). Increments in the higher ration treatments remained relatively wide throughout the experimental period. Narrowing of increment width in the 17% and 32% MR treatments ensued immediately and continued to decrease after the first week of the experiment (Fig. 2). For all treatments, mean IW was lower during week 2 than week 1; significant differences occurred between weeks in the 17%, 32%, and 66% MR treatments (Table 2). By week 2, there were significant among-treatment differences in mean IW among the 46% MR and the 32% and 17% MR treatments. Mean IW among the higher feeding levels did not differ throughout the entire experiment except for the 66% MR level. During several days of the first week, this group had a significantly higher mean IW compared with other treatments (Table 2). Daily variability in IW was high in all treatments (Fig. 2).

There was a positive correlation ($IW = 2.58 + 1.49(\log\{G+1\})$, r=0.86, $P<0.05$) between mean daily IW and mean specific growth rate for each treatment (Fig. 4). Although some fish lost weight at the lowest ration level, daily increments continued to be produced. There was a positive correlation between mean IW and mean daily feeding rate and between mean specific growth rate and K at day 14 (Table 3; Figs. 3 and 4). This relation ($P<0.05$) developed during week 1 of the experiment and strengthened during week 2 (Table 3).

Table 2

Results of two-way analysis of variance and multiple-range tests from comparisons of mean weekly increment width from different ration treatments and one-way analysis of variance between weeks. MR is the maximum ration. * = $P<0.05$, ns = not significant; letters indicate the results of Tukey's HSD comparison among treatments. SE is the standard error associated with treatment means.

Treatment feeding levels (% MR)	Week 1	SE	Week 2	SE	Treatment means
17	3.042	0.0243	2.310	0.0378*	2.68[a]
32	3.021	0.0465	2.616	0.1203*	2.82[ab]
46	3.121	0.1402	3.027	0.1495ns	3.07[b]
58	3.823	0.7427	3.817	0.5864ns	3.82[c]
66	4.514	0.2835	3.766	0.8348*	4.14[c]
100	3.864	1.2942	3.755	0.6493ns	3.81[c]
Overall	3.538		3.215*		3.38

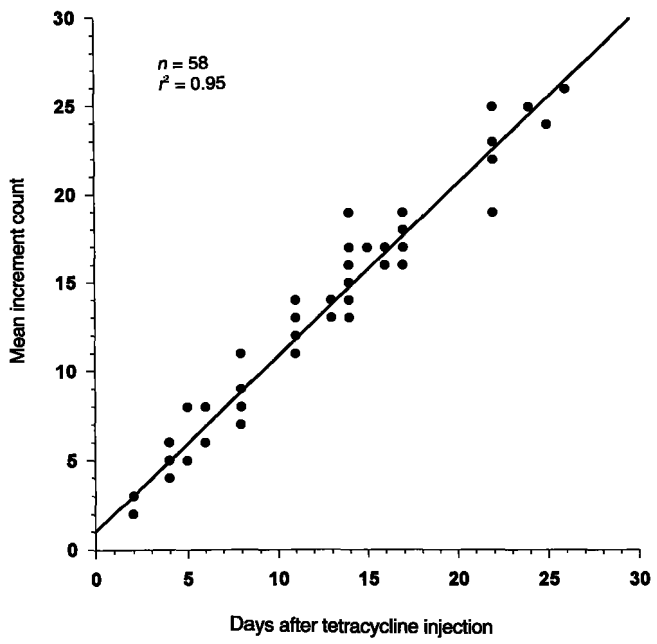

Figure 1

Relation between otolith increments distal to the fluorescent mark and days after tetracycline injection in juvenile weakfish, *Cynoscion regalis*. Symbols may represent more than one observation.

Discussion

Injection of oxytetracycline hydrochloride solution produced clear fluorescent bands in the otoliths of juvenile weakfish, and increment deposition occurred daily. Several other juvenile sciaenids have shown daily increments: spot (*Leiostomus xanthurus*), red drum (*Sciaenops ocellatus*), spotted seatrout (*Cynoscion nebulosus*), and silver perch (*Bairdiella chrysoura*) (Gjosaeter et al., 1984; Hettler, 1984; Peters and McMichael, 1987; McMichael and Peters, 1989; Hales and Hurley, 1991). The present study provides validation for ageing juvenile weakfish, thus enabling estimates of growth and providing, in combination with abundance data, a means of estimating accurate age specific mortality rates during this life history stage.

The rapid response of IW to changes in ration and the strong relation with SGR suggest that IW's may be used to infer growth history. Furthermore, significant differences in IW between high (58–100% MR) and low (17–46% MR) feeding levels suggests that IW may be used to approximate feeding history. Because of approximately a one-week lag time prior to stabilization of IW among treatments, the full magnitude of the change in IW cannot be assessed by examining just a few increments. At

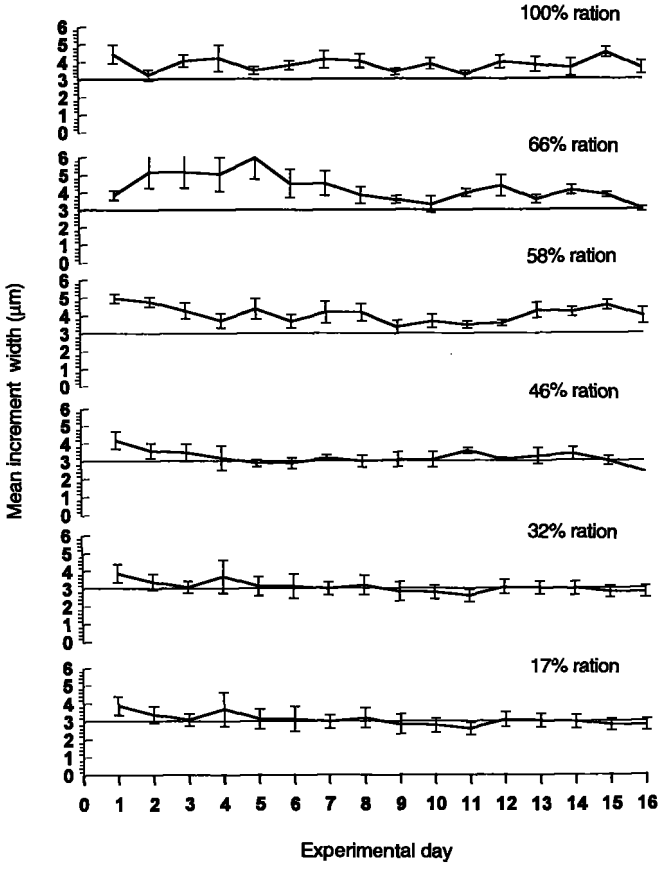

Figure 2

Relation between mean daily otolith increment width and experimental day for all feeding levels. Feeding levels are expressed as a percentage of maximum daily ration. Error bars represent ± SE.

least one week is required before IW responses to feeding and growth are statistically detectable although the physiological processes that result in IW differences begin acting sooner (Molony and Choat, 1990). Therefore, mean IW taken over several consecutive days would be most useful for making inferences regarding recent feeding and growth history for small sample sizes.

The magnitude of variability in IW observed in this study, particularly for the higher rations, has been documented for other species (Volk et al., 1984; Neilson and Geen, 1985; Maillet and Checkley, 1991). The reduced variability under the stress of lower ration may be related to reduced growth and utilization of food and stored reserves for maintenance (Molony and Choat, 1990). Continuation of otolith increment formation during periods of negative fish growth suggests that otolith growth is conservative and otolith resorption is not likely (Campana and Neilson, 1985; Secor et al., 1989).

Table 3

Results of Pearson product-moment correlation analysis (r) between daily increment width, daily feeding rate, and specific growth rate.

	Increment width		
	r	n	$P<0.05$
Daily feeding rate			
Week 1	0.5100	168	0.000
Week 2	0.6552	168	0.000
Specific growth rate			
Week 1	0.3961	168	0.000
Week 2	0.6232	168	0.000
Condition factor	0.3576	336	0.000

Otolith increments of spot, like those of weakfish, were found to have an immediate response to changes in ration (Govoni et al., 1985), although deposition

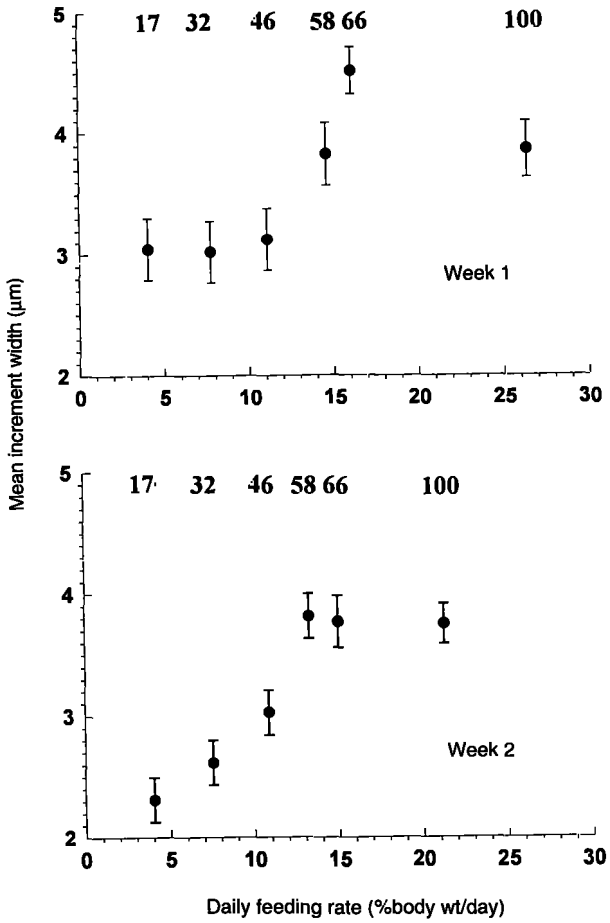

Figure 3

Relation between mean daily otolith increment width and daily feeding rate in juvenile weakfish, *Cynoscion regalis*, during week 1 and week 2. Error bars represent 95% Tukey's multiple comparison intervals. Values along the top of each panel are treatment feeding levels expressed as a percentage of maximum daily ration.

was found to be less than daily under low ration conditions (Siegfried and Weinstein, 1989). However, for the bloater (*Coregonus hoyi*) there was a loss of contrast between the hyaline and opaque bands and no effect on relative increment width (Rice et al., 1985). Maillet and Checkley (1990) found that starved Atlantic menhaden (*Brevoortia tyrannus*) larvae produced narrower increments with IW, increasing during a 3–6 day recovery period. In contrast to these examples of rapid otolith response to ration, changes in IW in juvenile chum salmon (*Oncorhynchus tshawytscha*) and the tropical glass fish (*Ambassis vachelli*) do not become discernible for three weeks and two weeks, respectively (Neilson and Geen, 1985; Molony and Choat, 1990). Recent experimental data suggest that the IW-growth relation may be more complex than originally thought (Reznick et al., 1989; Secor et al., 1989; Francis et al., 1993; Jenkins et al., 1993). The result of these studies suggests that the IW response to feeding and growth is variable, may be of limited use in some species, and needs to be evaluated on a species by species basis.

For species in which the relation of IW to growth has been established, otolith increment analysis can provide a means by which an investigator may relate recent environmental conditions to recent growth history during the important early life stages. Thus, a more complete understanding of the role of the environmental conditions relating to feeding, growth, and ultimately survival may be obtained.

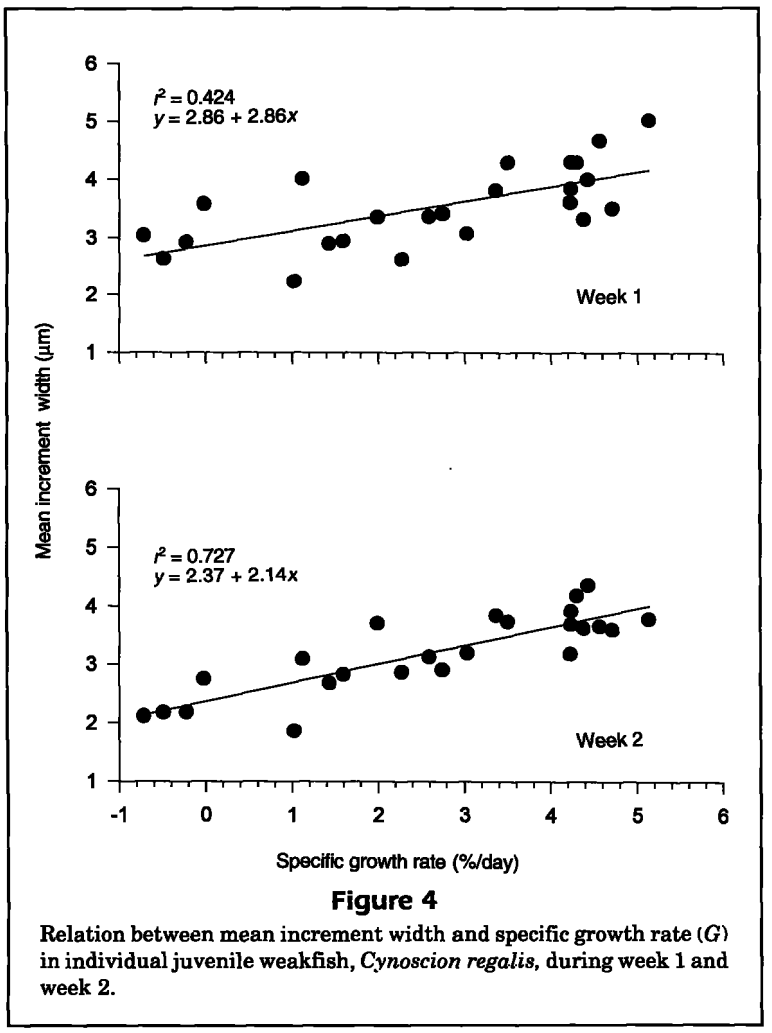

Figure 4

Relation between mean increment width and specific growth rate (G) in individual juvenile weakfish, *Cynoscion regalis*, during week 1 and week 2.

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