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Comparison of otolith growth and somatic growth in larval and juvenile fishes based on otolith length/fish length relationships

David H. Secor, John Mark Dean, and Rodolfo B. Baldevarona

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The use of otolith daily increment widths to estimate somatic growth rates has relied on single and highly correlated otolith-fish length relationships. For three species of fishes *Morone saxatilis*, *Pagrus major*, and *Leiostomus xanthurus*, the ratio of otolith size to fish size increased with starvation or decreased somatic growth rate. Based on microstructural examination of the otoliths of *Leiostomus xanthurus*, it was shown that short-term otolith growth was not linearly related to somatic growth and varied according to previous growth conditions. The results suggest that a more complex relationship exists between otolith growth and somatic growth than has been previously reported.

David H. Secor, John Mark Dean, and Rodolfo B. Baldevarona: Belle W. Baruch Institute for Marine Biology and Coastal Research, Biology Department, and Marine Science Program, University of South Carolina, Columbia, South Carolina 29208, USA. Rodolfo B. Baldevarona (current address): College of Fisheries, University of the Philippines in the Visayas, Iloilo City 5000, Philippines.

Introduction

Otolith microstructure investigations have provided a wealth of information to larval fish ecologists. Increments within the microstructure of otoliths, originally described by Pannella (1971), have been verified to form at daily rates in dozens of fishes (Campana and Nielson, 1985). Enumeration of daily increments has allowed workers to estimate early growth rates (size at age) (Struhsaker and Uchiyama, 1976; Lough *et al.*, 1982; Ralston and Miyamoto, 1983; Beckman and Dean, 1984; Penny and Evans, 1985; Natsukari *et al.*, 1988), spawn-date frequencies (Radtke and Dean, 1982; Beckman and Dean, 1984; Solomon *et al.*, 1985; Victor, 1986; Peters and McMichael, 1987; Rice *et al.*, 1987; Warlen, 1988), and mortality rates (Crecco *et al.*, 1983; Essig and Cole, 1986). Quantification of these life history parameters is essential in the evaluation of life history paradigms such as Hjort's (1914) critical period concept, Lasker's (1981) match-mismatch hypothesis, and Iles and Sinclair's (1982) larval retention hypothesis.

To obtain measures on individual larval growth rates, Pannella (1971) proposed back-calculating age-specific

growth rates using daily increment widths. By measuring successive increment widths, it should be possible to completely reconstruct a juvenile's growth history. Recent studies, however, have shown several confounding characteristics of otolith growth which can limit comparisons between somatic growth and otolith microstructure. (1) Measures of an individual's daily and weekly somatic growth rates correlate poorly to increment widths for corresponding time periods (Bradford and Geen, 1987). (2) Otolith growth continues during periods of starvation and negative somatic growth (Marshall and Parker, 1982; Baldevarona, 1987; Jones and Brothers, 1987). (3) There can be a maximum asymptotic limit to daily otolith growth in fast growing fish (Baldevarona, 1987). (4) Temperature affects the relationship between somatic and otolith growth (Eckman and Rey, 1987; Mosegaard *et al.*, 1988). (5) Intra-specific variation in the manner in which otoliths scale to body size is influenced by somatic growth rate, where slower growing fish have relatively larger otoliths than fast growers of the same somatic size (Reznick *et al.*, 1989; Secor and Dean, 1989). These results indicate that the manner in which otolith growth is related to fish growth is complex.

In this paper, the effects of growth rate, food deprivation, and feeding regime on the otolith-fish size relationship for three different species are described. Species include larval and juvenile striped bass, *Morone saxatilis* (effect of growth rate); larval and juvenile red-sea bream, *Pagrus major* (effect of food deprivation); and juvenile spot, *Leiostomus xanthurus* (effect of feeding regime). The resolution of increment widths as a measure of daily somatic growth rate in juvenile spot is examined. Somatic growth rates for wild populations of juvenile striped bass are also predicted based on a previous study which quantified somatic growth rates and otolith length/fish length relationships in pond-reared juvenile striped bass (Secor and Dean 1989).

Materials and methods

The possible effect of somatic growth on the otolith length/fish length relationship are examined using several data sets from three species. Two published data sets, those on spot (Baldevarona, 1987) and pond-reared striped bass (Secor and Dean, 1989) are used and two additional data sets, on food deprivation in red seabream and population growth rates of wild striped bass juveniles are presented here for the first time. It is convenient to categorize methodology and results by species.

Striped bass

In the spring and summer of 1984, larvae from the Monks Corner Striped Bass Hatchery (South Carolina) were sampled from 5 to 55 d (days post-hatch) in twelve earthen ponds as described in Secor and Dean (1989). Pond-specific regressions of SL on age and otolith length on SL were performed (Table 4 in Secor and Dean, 1989). Juveniles from the Santee-Cooper population (South Carolina) were seined from Lake Marion in June and July of 1986 and 1987. Otoliths from juveniles were sectioned and the juveniles were aged using daily increments. Daily increment formation for larval and juvenile striped bass has been validated in pond studies (Secor and Dean, 1989).

Preparation of otoliths for increment counts and microstructural measures followed those of Haake *et al.* (1982) and Beckman and Dean (1984). A thin section through the core of the sagitta, in the frontal plane, is obtained by (1) embedding the sagitta in Spurr's low viscosity medium; (2) gluing the block of Spurr onto a glass slide with a thermoplastic glue; (3) polishing the block and otolith with wet 200–1200 grit sandpaper and polishing alumina to the core in frontal plane; (4) heating the glue, turning the section over and gluing it down on its polished face; (5) polishing the section down to the core. Otolith section thickness averages about 25 μm ; sections are examined under high intensity light at 400–1000 \times .

For each Santee-Cooper juvenile's otolith (right or left sagitta) daily increments were counted twice each by two investigators and the resultant four counts were averaged. Estimated ages ranged from 30 to 62 d for 1986 and 35 to 73 d for 1987. Year-specific regressions of SL on age and otolith length on SL were performed.

Red seabream

Eggs were obtained from the Azuma-cho Fishing Cooperative Hatchery in Kagoshima Prefecture, Japan. Larvae were fed rotifers and reared at Kagoshima University's Fishery Research Center in a metric-ton tank according to standard protocol (Keitake and Kogane, 1981). As controls, 20–30 fish were collected from the stock culture at 22, 34, and 42 d for SL measurement and otolith removal and measurement. On these same days, groups of fish were also obtained for starvation experiments. SL was first measured and the fish then placed in 30-l aquaria for varying periods of starvation: 22 d larvae were starved for 4 d; 34 and 42 d juveniles were starved for 9 and 8 d respectively. Following starvation, SL was measured, the sagittae and lapilli were sampled and measured and otolith length/fish length regressions fitted. Somatic growth during starvation was estimated from measurements taken at the experiments' beginning and end. Initial otolith size for each experiment was estimated from the control groups' otolith length/fish length regressions.

Spot

Juvenile spot were collected from the North Inlet Estuary (South Carolina) and subjected to three feeding regimes. Each feeding regime was three weeks long and comprised three feeding transitions (Table 1). Each three-week-long feeding regime was replicated in four 30-l aquaria each containing 10 spot. Otoliths were marked by oxytetracycline (OTC) immersion (250 ppm for 2 h) 1 d prior to the initiation of the feeding regimes. Each week in the experiment was comprised of 6 d of feeding (Table 1) followed by one day of food deprivation. Food deprivation resulted in a check in the otolith's microstructure which permitted later identification of each week's otolith growth. Juveniles were weighed on the sixth day of each week and then again

Table 1. Feeding rate (percent body weight fed per day) treatments for each week for juvenile spot.

	Week 1 %	Week 2 %	Week 3 %
Cycle 1	1	10	5
Cycle 2	5	1	10
Cycle 3	10	5	1

on the seventh day just prior to the next week's feeding treatment to determine somatic growth resulting from each feeding treatment.

Following the experiment the sagittae were removed and prepared for microstructural analysis as described above. The OTC mark was recognized in each section under incidental epifluorescence. Likewise the two checks in each section, marking the feeding transitions, were identified. These three points and the otolith margin were digitized appropriately so that linear measures associated with each feeding transition could be quantified. Measurements of daily increment widths within these weekly measures were not always possible due to irregularities in the way the otolith grew ("overlapping increments"), or because increment widths approached the resolution limit of the microscope (1.2 μm). Therefore, "weekly" (6 d) somatic growth was only compared to weekly (6 d) otolith growth.

Results

Striped bass

Somatic growth rate was shown to significantly affect the relationship between otolith length and fish length among populations of pond-reared juvenile striped bass (Secor and Dean, 1989). For any two ponds with different somatic growth rates, otolith length at a given SL was greater for the site with slower growing fish. A direct comparison between somatic growth rate and the otolith length/fish length relationship was made by plotting slopes of these relationships for each site (Fig. 1). The plot clearly showed that otolith length declined proportionally to SL with increased growth rate.

Despite the pond-specific variation shown in both the otolith length/SL ratio and somatic growth rate, the combination of data from all pond samples resulted in overall high correlation between otolith length and SL ($R^2 = 0.95$).

Juveniles collected from the wild showed similar growth rates between years (1986: 1.0 mm/d; 1987: 1.1 mm/d) and were adequately modelled using a linear regression (Fig. 2). As expected, the otolith length/SL ratios between the populations were also similar (1986: otolith length (μm) = $396 + 44.0 \times \text{SL}$ (mm); $N = 199$; $R^2 = 0.82$; 1987: otolith length = $26.2 + 50.1 \times \text{SL}$; $N = 487$; $R^2 = 0.93$). When plotted among pond-derived values of growth rates versus otolith length/SL ratios (Fig. 1), they fell within the 95% prediction intervals.

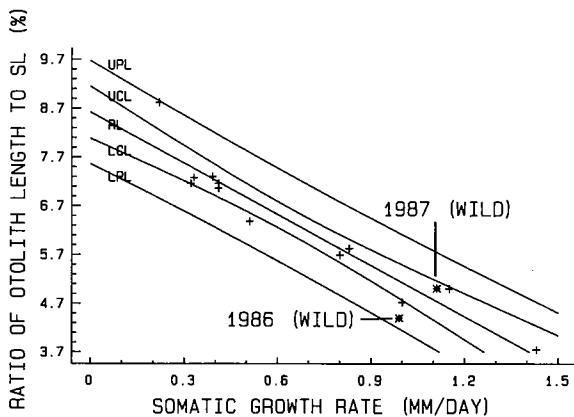


Figure 1. Somatic growth rate vs. otolith length/SL ratio for groups of pond-reared (+) and wild striped bass (*). Regression was fitted for pond samples only. Otolith length/SL = $86.2 - 34.9 \times \text{somatic growth rate}$; $N = 12$; $p < 0.0001$; $R^2 = 0.92$. UPL: upper 95% prediction limit; UCL: upper 95% confidence limit; RL: regression line; LCL: lower 95% confidence limit; LPL: lower 95% prediction limit.

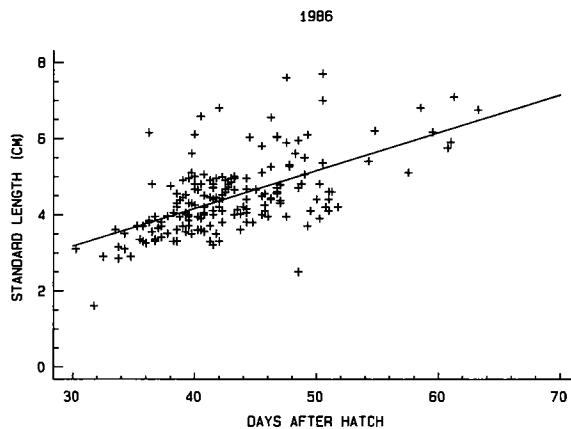


Figure 2a. Estimated age vs. standard length for juvenile striped bass collected from Lake Marion in May and June 1986. $\text{SL} = 0.19 + 0.99 \times \text{age}$; $N = 182$; $p < 0.001$; $R^2 = 0.36$.

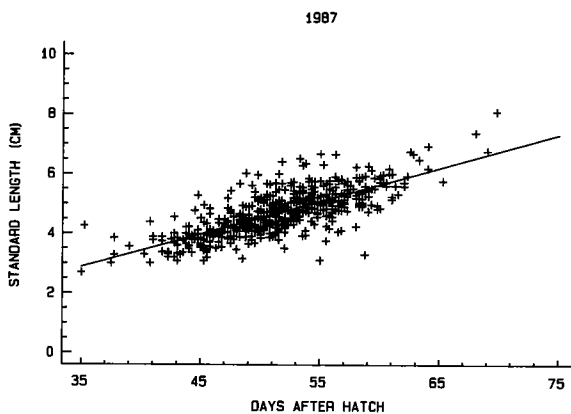


Figure 2b. Estimated age vs. standard length for juvenile striped bass collected from Lake Marion in May and June 1987. $\text{SL} = -1.01 + 1.11 \times \text{age}$; $N = 489$; $p < 0.0001$; $R^2 = 0.56$.

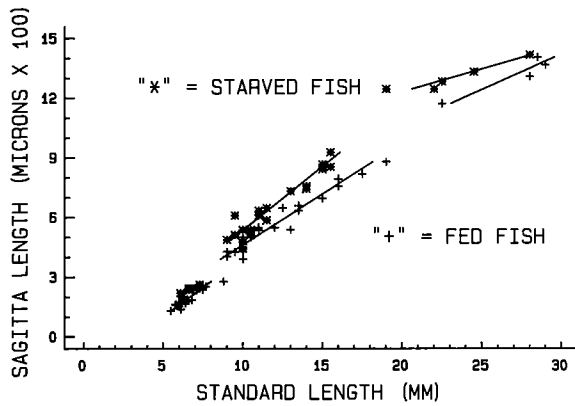


Figure 3. Standard length vs. sagitta length for fed (control) and starved larval and juvenile red seabream. The smallest group of fish were sampled at 22 d after hatch and starved until 26 d. The intermediate group was sampled at 34 d and starved until 43 d. The largest group of fish were sampled at 42 d and starved until 50 d. When all fed and starved treatments were combined the overall regression was: sagitta length = $-135 + 58.5 \times SL$; $p < 0.0001$; $R^2 = 0.95$.

Red seabream

For each group of experimental fish, otolith length at a given fish length was significantly greater for the starvation treatment than that of the control treatment (Fig. 3, Table 2). No somatic growth occurred during starvation but both the sagittae and lapilli continued to grow (Table 2). When data for all starved and control groups were combined, otolith and fish size were highly correlated (sagitta: $R^2 = 0.95$; lapillus: $R^2 = 0.92$). These trends in otolith length/fish length relationships taken together with those for striped bass suggest that small deviations in the ratio of otolith length to SL can be the result of large somatic growth differences or episodic starvation.

Spot

The effects of time, feeding rate, and feeding cycle on weekly somatic and otolith growth were investigated using multiple range tests (Table 3). Weekly somatic

Table 2. Comparison of sagitta, lapillus, and SL between fed (control) and starved red seabream larvae and juveniles. Juveniles which were starved from 42 to 50 d were not included because of low sample size.

	22 day-old fed (control) vs. 26 day-old starved (4 days' starvation)				34 day-old fed (control) vs. 43 day-old starved (9 days' starvation)			
	Increase	s.d.	N	P	Increase	s.d.	N	P
SL (mm)	0.03	0.08	14	0.22	-0.22	0.43	18	0.04
Sagitta (μm)	31.2	15.2	7	0.002	82.1	25.1	16	0.0001
Lapillus (μm)	21.0	4.9	5	0.0001	24.8	24.1	16	0.0001

Table 3. Multiple range tests for means of "weekly" somatic and otolith growth of juvenile spot using 95% confidence intervals. Weekly growth refers to six days' growth (see Materials and methods). Treatments with different groups (A, B, or C) are significantly different at $\alpha = 0.05$.

	Weekly somatic growth			Weekly otolith growth	
	Average (g)	Groups	Average (μm)	Groups	
Week:	1	3.18	A	4.50	A
	2	4.02	A	4.92	AB
	3	3.84	A	5.46	B
Feeding rate:	1%	-2.70	A	3.36	A
	5%	5.22	B	5.34	B
	10%	8.46	B	5.76	C
Feeding cycle:	1	1.92	A	5.76	C
	2	3.30	BC	4.98	B
	3	5.76	C	4.14	A

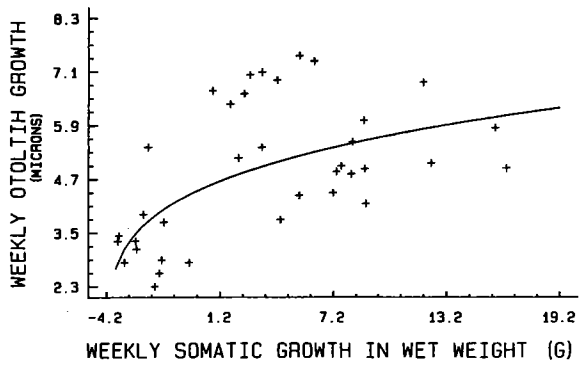


Figure 4. Weekly somatic growth (g wet weight) vs. weekly otolith growth (μm) for juvenile spot reared under various feeding regimes. Weekly otolith growth = $3.97 \times (\text{weekly somatic growth} + 4.21)^{0.114}$; $N = 36$; $p < 0.001$; $R^2 = 0.31$.

growth was different between 1% and 10% feeding rate, and cycles 1 and 3. Weekly otolith growth was different for each level of feeding rate and cycle. The relationship between weekly otolith and somatic growth was variable (Fig. 4) but appeared to be related to feeding cycle (Fig. 5). The greatest otolith growth rates were observed for cycle 1 where ration level was raised from 1% body weight to 10% over the first two weeks. Very little relationship occurred between increment width and somatic growth rate for cycle 2 where feeding ration was decreased and then increased again. Cycle 3, where

there was a succession of decreases in ration over three weeks resembled the overall relationship (Fig. 4), where the rate of otolith growth decreased relative to somatic growth with increased somatic growth rates. All cycles showed positive otolith growth during periods of negative somatic growth.

Discussion

Somatic growth effects on the otolith length/fish length relationship were observed among the three species studied. Daily increment formation has been validated for larval and juvenile striped bass (Jones and Brothers, 1987; Secor and Dean, 1989), red seabream (Tsuji and Aoyama, 1982; Secor, unpubl. data) and spot (Beckman and Dean, 1984; Baldevarona, 1987). Because daily increment formation causes positive otolith growth, otoliths continue to grow during periods of negative somatic growth. This has been confirmed by Jones and Brothers (1987) through scanning electron microscopy. This positive daily growth of the otolith also results in otoliths that are large with respect to somatic size in individuals experiencing low somatic growth rates.

Somatic growth and age prediction

The otolith length/fish length relationship can be used to infer previous somatic growth rates. Somatic growth rates for the 1986 and 1987 populations of wild striped bass, estimated from daily increment enumeration, fell

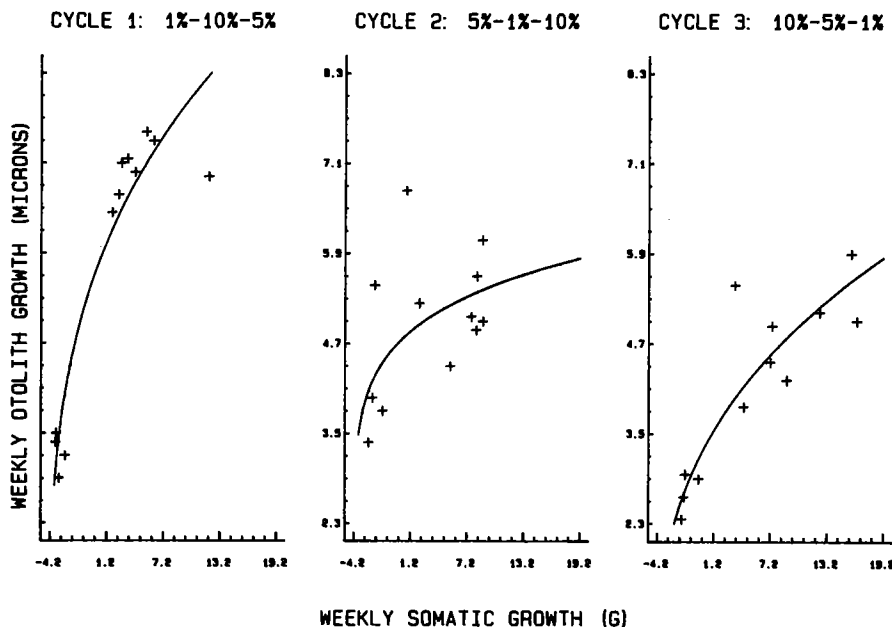


Figure 5. Weekly somatic growth (g wet weight) vs. weekly otolith growth (μm) for juvenile spot reared under each feeding regime. Cycle 1: feeding regime was 1%, 10%, and 5% (% body weight fed per day) for three successive weeks. Cycle 2: feeding regime was 5%, 1%, and 10%. Cycle 3: feeding regime was 10%, 5%, and 1%. All axes among the cycles are scaled the same.

within the 0.85–1.35 mm/d range predicted by their otolith length/SL ratios (Fig. 1). Further data on otolith length/SL relationships for the Santee-Cooper population is expected to improve somatic growth rate prediction.

Because daily increment formation always contributes to otolith growth, it has been hypothesized that age prediction based on the relationship between otolith and fish size is possible (Reznick *et al.*, 1989; Secor and Dean, 1989). We tested age prediction models for the 1987 field-collected sample. The only significant predictor of age was otolith length ($p < 0.001$); neither SL ($p = 0.8$) nor the interaction between SL and otolith length ($p = 0.6$) was significant. These other variables were significant for an age prediction model for pond-reared larvae and juveniles (Secor and Dean, 1989). The coefficient of determination for field collected juveniles ($R^2 = 0.63$) was substantially lower than for pond-reared fish ($R^2 = 0.81$). This might be due to the greater variability in both the somatic growth rate and the otolith length/fish length relationship for field-collected fish as compared to pond-reared fish (Fig. 2, Secor and Dean, 1989).

Estimation of daily somatic growth rates from daily increment widths

It has been assumed that if otolith length is highly correlated to fish size, then daily otolith and somatic growth rates are directly linked (Rosenberg and Haugen, 1982; Penny and Evans, 1985; Nielson *et al.*, 1985; Barkman and Bengston, 1987; Post and Prankevicus, 1987). Under this assumption, negative otolith growth is predicted for periods of negative somatic growth. And during very rapid somatic growth, a similar magnitude in otolith growth is predicted.

Results shown here suggest that establishing high correlation between otolith length and fish length does not prove a direct link between daily otolith and somatic growth rates. Determination coefficients are affected by sample size and the range and distribution of data. Indeed, when pond samples were combined in the striped bass study and control and starved groups combined for the red seabream study, the determination coefficients inflated due to increased sample sizes. Subpopulation otolith length/fish length data, when grouped into one sample may thus artificially inflate the correlation coefficient. Outliers in the otolith length/fish length relationship may be significant and indicative of individuals growing at rates that are very different from the rest of the sampled population. In striped bass and red seabream, it was observed that small deviations in the otolith length/fish length relationship were the result of large somatic growth differences or episodic periods of starvation.

Bradford and Geen (1987) branded chinook salmon juveniles and found that known growth histories cor-

related poorly with growth calculated from increment widths over a 7–15 d period. Significant correlations occurred when longer segments of time were considered. They concluded that otolith growth was “conservative” relative to somatic growth. Conservative otolith growth might explain the results shown here as well. Volk *et al.* (1984) observed a log-linear relationship between daily otolith growth and somatic growth, which showed a decline in the rate of increase in otolith growth relative to somatic growth. Comparison between weekly rates of somatic and otolith growth in spot showed a similar trend. We have hypothesized that there are physiological constraints on daily otolith growth which are independent of somatic growth (Secor and Dean, 1989). Such constraints would result in a log linear relationship between otolith and fish length over short time intervals.

Feeding regime effects confounded the relationship between daily otolith growth and somatic growth. Cycling feeding rate seemed to throw otolith growth out of phase with somatic growth, especially in cycle 2 (Fig. 5), where feeding rate was decreased and then increased. The results suggest a lagged effect of feeding rate on increment width. Campana (1984a) observed a lag between feeding and otolith growth in starry flounder, and Eckman and Rey (1987) showed that a feeding or temperature transition changed the thickness and contrast qualities of increments over several days beyond the shift in bloater. If feeding transitions or cycling potentially occur in natural populations of fish, application of the otolith growth record becomes more difficult.

Otolith increment widths are affected by somatic growth rate (Wilson and Larkin, 1982; Volk *et al.*, 1984; Bradford and Geen, 1987; Reznick *et al.*, 1989; Secor and Dean, 1989) feeding transitions and cycling (Eckman and Rey, 1987; Baldevarona, 1987), stage of development (Brothers and McFarland, 1981; Campana, 1984b; Nishimura and Yamada, 1984), temperature (Campana, 1984a; Eckman and Rey, 1987; Mosegaard *et al.* 1988), and the endogenous rhythm of daily increment formation (Mugiya, 1987). The magnitude and interactions of biological and environmental effects on otolith growth will be difficult to interpret in field collected fish and verification experiments are essential.

In verification studies, laboratory-reared fish should be exposed to similar ranges and fluctuations in temperature and feeding regimes to those expected to occur in nature. Experimental fish should be sampled frequently for direct comparisons between short-term otolith growth and fish growth. Back-calculation techniques should be applied to the fish collected at the end of the experiment and tested against the direct comparisons. Because otolith microstructure from fish reared in aquaria often has different visual contrast qualities than those collected from wild fish (Radtke and Dean, 1982; Beckman and Dean, 1984), pond or enclosure veri-

fication studies are advisable. Such studies can provide an intermediate step between experimental and field studies, where predictions based on measured environmental parameters can be tested.

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