Somatic Growth Effects on the Otolith – Fish Size Relationship in Young Pond-reared Striped Bass, *Morone saxatilis*

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Somatic growth rate of pond-reared larval and juvenile striped bass, *Morone saxatilis*, influenced the relationship between otolith size and fish size. Slower growing groups of individuals had larger and heavier otoliths, relative to fish length, than did faster growing groups. Within each growth group, otolith and fish size were highly correlated. Daily increment formation was validated from 10 to 51 d after hatch. Significant interaction occurred between age and fish size effects on otolith size. We propose that otolith growth occurs by two interacting processes. Otoliths grow daily in an incremental manner which is independent of somatic growth. Growth also proceeds continuously within each daily cycle of increment deposition, probably in some proportion to daily somatic growth. Corollaries to the hypotheses are (1) somatic growth rate can influence the otolith – fish size relationship, (2) intraspecific variation in otolith scaling might be used to predict past differences in somatic growth rate, and (3) there is a biological rationale for the use of otolith size and fish size as predictors in age estimation.

Le taux de croissance somatique de larves et de juvéniles de bars rayés, *Morone saxatilis*, élevés en étangs influent sur la relation entre la taille des otolithes et celle du poisson. Les groupes de poissons à croissance plus lente présentaient des otolithes plus gros et plus lourds, par rapport à leur longueur, que les groupes de poissons à croissance plus rapide. La corrélation entre la taille des otolithes et celle des poissons était très élevée au sein des mêmes groupes de croissance. L’accroissement quotidien des otolithes a été démontré chez les individus âgés de 10 à 51 jours. Il y avait une interaction significative entre la dimension des otolithes et l’âge, d’une part, et la taille des poissons, d’autre part. Les auteurs émettent l’hypothèse que la croissance des otolithes a un origine deux processus interactifs. Les otolithes croissent quotidiennement par une formation de couches qui est indépendante de la croissance somatique. Il y a aussi une croissance continue, par dépôt au sein de chaque cycle quotidien, qui s’effectue probablement en proportion de la croissance somatique quotidienne. Ces hypothèses ont pour corollaires : 1) le taux de croissance somatique peut influer sur la relation entre la taille des otolithes et celle du poisson, 2) la variation intra-spécifique des anneau des otolithes pourrait servir à déterminer l’existence d’écarts antérieurs du taux de croissance somatique et 3) l’utilisation de la taille des otolithes et des poissons en tant que paramètres d’estimation de l’âge repose sur des fondements biologiques.

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Otoliths are calcium carbonate (CaCO₃) concretions which occur within the labyrinth systems of fishes. A pattern of ring-like increments is commonly observed within the microstructure of otoliths (Dean et al. 1983). Over the past decade, these increments (as defined by Tanaka et al. 1981 and Wilson et al. 1983) have been verified to form with a daily periodicity in many teleosts (Campana and Neilson 1985). Recent reports of the relationship between daily somatic growth and the incremental growth of otoliths (Brothers and McFarland 1981; Lough et al. 1982; Neilson and Geen 1982; Campana 1984a; Ralston and Miyamoto 1983; Volk et al. 1984; Bradford and Geen 1987) support the use of increment widths as measures of daily somatic growth because (1) increments form daily and (2) otolith size and fish size are highly correlated. An assumption of the second criterion is that a relationship between otolith size and fish size links otolith growth to somatic growth. In this report, we model a relationship between otolith and fish size and consider whether this relationship depends upon somatic growth rate.

The term "scaling" has been applied to body size relationships (Schmidt-Nielsen 1984). Here we define otolith scaling as comparisons between otolith size (e.g. otolith length, weight, area) and fish size (e.g. standard length, weight, head length). There have been several reports of intraspecific variation in otolith – fish size relationships (Table 1). Studies of the annular growth of otoliths indicate that otolith size depends upon both fish size and age (Templeman and Squires 1956; Blacker 1974; Frost and Lowry 1981; Wilson 1984; Boehrert 1985; Radtke et al. 1985). Hence, intraspecific variation in otolith scaling can be associated with varying growth rates. We hypothesize that the relationship between otolith and fish size is influenced by the daily, incremental manner in which otoliths grow.

Pond-reared larval and juvenile striped bass (life stage terms applied are those of Balon 1981) were used as a source of known-age otoliths. Pond systems were utilized to provide more natural conditions for the growth of otoliths and thus avoid the
TABLE 1. Reports of intraspecific variation in the scaling of otolith size to fish size. Type of relationship: A = allometric, where otolith size is a nonlinear function of SL; I = isometric, where otolith size is a linear function of SL. Period of life history studied is given in parentheses: L = larval period; J = juvenile period.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Species</th>
<th>Type of relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dean, unpubl. data</td>
<td>Leistomus xanthurus</td>
<td>A (L, J)</td>
</tr>
<tr>
<td>Geen et al. 1985</td>
<td>Oncorhynchus tshawytscha</td>
<td>A (L)</td>
</tr>
<tr>
<td>McGurk 1984</td>
<td>Clupea harengus harengus</td>
<td>A (L)</td>
</tr>
<tr>
<td>Marshall and Parker 1982</td>
<td>Oncorhynchus nerka</td>
<td>I (L)</td>
</tr>
<tr>
<td>Neilsow 1985</td>
<td>Sebastes spp.</td>
<td>I (L)</td>
</tr>
<tr>
<td>Rice et al. 1985</td>
<td>Coregonus hoyi</td>
<td>A (L), I (J)</td>
</tr>
<tr>
<td>Secor, unpubl. data</td>
<td>Pagoopsis major</td>
<td>A (J)</td>
</tr>
<tr>
<td>Taubert and Coble 1977</td>
<td>Lepomis macrochirrus</td>
<td>I (L, J)</td>
</tr>
</tbody>
</table>

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well-documented problems associated with otoliths from laboratory growth experiments (Campana and Neilson 1985).

Material and Methods

Experimental fish were from South Carolina’s Santee-Cooper striped bass population. Striped bass eggs were stripped and hatched at the Moncks Corner Striped Bass Fish Hatchery, South Carolina, by workers of the South Carolina Wildlife and Marine Resources Department from brood stock collected in the Cooper River. Eggs of two females were fertilized with sperm of six males and mixed (genetic effects were randomized). Two such batches of fertilized eggs were prepared for two sets of ponds: one set (seven ponds) stocked on April 15, 1984, and the other set (five ponds) 11 d later on April 26, 1984. As part of the Department’s fingerling production efforts, larvae were stocked without previous feeding at 250 000 per pond into twelve 1-acre (0.4-ha) earthen ponds. Ponds had been fertilized with organic and inorganic fertilizers and contained plankton blooms for the feeding larvae. No supplementary feeding occurred for any ponds.

Individuals, ages 10–55 d after hatch, were collected weekly. Larvae less than 20 mm standard length (SL) were collected at night with a strong light beam directed above a plankton net. Larger larvae and juveniles were seined. Due to low survival in certain ponds and collecting constraints, samples were unavailable or low in number for certain weeks (Table 2). Collected fish were put in ice water; they were then placed in 95% ethanol within 3 h to prevent degradation. Forty larvae and juveniles, sizes ranging from 12 to 30 mm, were measured before and after preservation to quantify shrinkage. Saccular otoliths (sagittae) were removed, cleaned, weighed, and measured along their longest axis under a dissecting microscope. As no difference could be demonstrated between the right and left otoliths, either was used (Table 3).

Preparation of otoliths for increment counts followed the procedure described by Haake et al. (1982). Otolith sections were further prepared for examination under a light microscope by gluing the polished face of the section to a thin (1 mm) plastic square (1 cm²) with a cyano-acrylic glue and again polishing to the core. For scanning electron microscopic (SEM) examination, otolith sections were decalcified for 4–10 min in 2% EDTA (pH at 7.4) or 3–4 h in 2% glutaraldehyde (EM grade). To calibrate technique for counting increments between investigators, SEM micrographs of six sections were examined for the following microstructural features: the primordium (initial site of calcium deposition), core (area of the otolith contained within the earliest deposited increment), and discontinuous and accretion zones which together comprise one increment (terminology from Tanaka et al. 1981; Mugiya 1987). The frontal plane (i.e. section) of the otolith was chosen for increment counts, since it contained microstructural features which were most consistently identified. Ring-like features described as “subdaily increments” (Campana and Neilson 1985) sometimes occurred along major growth axes of the otolith. These features did not meet the criteria for designation as an increment. By carefully following the course of these subdaily features, it was observed that they converged with discontinuous zones of properly identified increments in lateral and medial areas of the otolith.

To validate daily increment formation, 35 otoliths which represented all sample dates from a single pond were sectioned. Increments were counted three times each by two investigators with a compound microscope at 600× magnification (resolu-

TABLE 2. Numbers of fish sampled from ponds at various days after hatch. Sample numbers collected at each age (days after hatch) are listed. Dates with 0 samples indicate sample dates when no fish could be collected. Survival was estimated at harvest (50–55 d after hatch). FG = Pond Fast Growth; SG = Pond Slow Growth.

<table>
<thead>
<tr>
<th>Pond</th>
<th>Hatch date (April)</th>
<th>Survival (%)</th>
<th>Days after hatch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>8 10 14 17 19 20 22 24 28 31 35 38 41 45 48 51 53 54</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>15 3 0 0 0 0 0 10 0 10 0 0 0 0 0 0 0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>15 1 0 0 0 0 0 0 10 0 10 0 0 0 0 0 0 0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>15 2 0 0 0 0 0 0 10 0 10 0 0 0 0 0 0 0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FG</td>
<td>15 4 0 0 15 13 11 34 28</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>15 13 4 10 0 10 7 8 10 10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>30 48 6 0 6 10 6 9 0 0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>30 45 2 0 10 9 10 10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>15 33 0 0 4 10 10 10 10 0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SG</td>
<td>15 46 7 3 12 38 36 36</td>
<td></td>
<td></td>
</tr>
<tr>
<td>J</td>
<td>30 53 5 5 9 10 0 15</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K</td>
<td>30 69 4 11 0 10 0 5 10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>30 53 5 10 9 11 7 10</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TABLE 3. Precision estimates based on two repeated measurements of the same sample. No difference was found between repeated measurements for any of the variables (p < 0.05; paired t-test). \( N \) = number of paired comparisons; range = range in values of measurements.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Mean difference</th>
<th>Standard deviation</th>
<th>Precision of instrument</th>
<th>( N )</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard length (mm)</td>
<td>0.10</td>
<td>0.013</td>
<td>0.05</td>
<td>33</td>
<td>12-28</td>
</tr>
<tr>
<td>Otolith length (( \mu )m)</td>
<td>10</td>
<td>2.1</td>
<td>20</td>
<td>46</td>
<td>517-1433</td>
</tr>
<tr>
<td>Right vs. left otolith length</td>
<td>11</td>
<td>2.2</td>
<td>20</td>
<td>31</td>
<td>480-1200</td>
</tr>
</tbody>
</table>

Increment counts
- Between readers: 3.2, 0.63, 1, 29, 10-51
- Within reader A: 2.5, 0.42, 1, 29, 10-51
- Within reader B: 1.9, 0.33, 1, 29, 10-51

TABLE 4. Pond-by-pond regressions of standard length (SL, mm) on age (d after hatch) and otolith length (\( \mu \)m) on SL. All regressions were significant at \( p < 0.005 \). Estimated coefficients of variation are listed. \( N \) = sample size; Size 1 = predicted SL (mm) at 55 d; Size 2 = predicted otolith length (mm) at 25 mm SL; Size 3 = predicted otolith length at 40 mm SL (given for ponds where 40 mm was attained by time of harvest). FG = Pond Fast Growth; SG = Pond Slow Growth.

<table>
<thead>
<tr>
<th>SL vs. age</th>
<th>Otolith length vs. SL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatch date (April)</td>
<td>Intercept</td>
</tr>
<tr>
<td>A 15</td>
<td>-27.2</td>
</tr>
<tr>
<td>B 15</td>
<td>-1.93</td>
</tr>
<tr>
<td>C 15</td>
<td>-28.4</td>
</tr>
<tr>
<td>FG 15</td>
<td>-1.75</td>
</tr>
<tr>
<td>E 15</td>
<td>-6.00</td>
</tr>
<tr>
<td>F 30</td>
<td>5.17</td>
</tr>
<tr>
<td>G 30</td>
<td>6.58</td>
</tr>
<tr>
<td>H 15</td>
<td>4.04</td>
</tr>
<tr>
<td>SG 15</td>
<td>3.84</td>
</tr>
<tr>
<td>J 30</td>
<td>7.88</td>
</tr>
<tr>
<td>K 30</td>
<td>7.17</td>
</tr>
<tr>
<td>L 30</td>
<td>8.16</td>
</tr>
</tbody>
</table>

TABLE 5. Between-pond comparisons (\( F \)-statistic) of regressions of standard length (SL), otolith length, and weight on age (d after hatch), of otolith length and weight on SL, and of otolith weight on length. \( N \) = sample size for Pond Fast Growth (FG) and Pond Slow Growth (SG).

<table>
<thead>
<tr>
<th>Relationship</th>
<th>( N/FG )</th>
<th>( N/SG )</th>
<th>( F )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>SL vs. age</td>
<td>139</td>
<td>94</td>
<td>189.4</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Otolith length vs. age</td>
<td>59</td>
<td>39</td>
<td>114.1</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Otolith weight vs. age</td>
<td>23</td>
<td>25</td>
<td>61.8</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Otolith length vs. SL</td>
<td>59</td>
<td>39</td>
<td>96.9</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Otolith weight vs. SL</td>
<td>23</td>
<td>25</td>
<td>84.6</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Otolith length vs. otolith weight</td>
<td>23</td>
<td>25</td>
<td>4.9</td>
<td>0.03</td>
</tr>
</tbody>
</table>

* Cubed root of otolith weight compared.
* Cubed of otolith length compared.

Otolith sections were randomized between counts. Six otoliths, for which counts varied more than 15% between readers, were omitted. Samples from the hatchery (age < 6 d) were examined for first increment formation.

Precision of measured parameters was estimated as the mean of absolute differences among replicated measurements. Comparisons made between linear models used the \( F \)-test for common slope and intercept described by Ott (1977).

**Results**

All precision estimates were within the range of the precision of the instruments used (Table 3). SL was slightly affected by alcohol fixation (fresh SL = 0.34 + 1.037 \times \text{shrinkage SL}; \( n = 30; R^2 = 0.98 \)). Residuals for this relationship showed constant variance over the size range tested. Pertinent regressions were adjusted for shrinkage.

**Somatic Growth Differences**

Unaccounted differences occurred among the ponds with respect to their population's survival and growth rates. An event prior to stocking (e.g. handling stress, poor pond conditions) may have caused an initial mortality event in certain ponds and allowed a release from density-dependent growth for the few survivors (Secor and Dean 1986). Cannibalism might also explain some of the difference, but is not probable because all ponds were stocked at similar rates. Whatever the reason for pond-specific survival and growth rates, this fortuitous event enabled us to investigate somatic growth and age effects on otolith scaling. Pond-specific growth rates were estimated using linear regressions (Table 4). All regressions were significant (\( p < 0.001 \)). Low coefficients of determination for ponds B and C may have been due to small sample sizes (Table 2). Predicted sizes at age 55 d (approximate harvest time) ranged from 20.3 to 55.9 mm among the ponds and were inversely related to survival estimates (Table 2). Otolith size was significantly correlated with SL (\( p < 0.001 \)) (Table 4). To observe somatic growth effects on otolith scaling, predicted otolith sizes at 25 and 40 mm SL were calculated and arranged in descending order with respect to pond-specific growth rates (Table 4).
trend shown is that for populations experiencing slower growth rates, otolith size was greater in proportion to fish length. The following description of how the otolith scaled to fish size and the otolith's manner of growth is presented to further elucidate somatic growth effects on otolith scaling.

Otolith Size Relationships

To simplify analysis and avoid problems in comparing ponds of different parentage and stocking dates and of low sample sizes, examination of otolith scaling was limited to two ponds, both stocked on April 15; Pond Fast Growth (FG) and Pond Slow Growth (SG) (Tables 2 and 4). Somatic and otolith growth were estimated with linear models for both ponds to permit comparisons between regressions (Ott 1977). Other models did not fit the data significantly better (von Bertalanffy: Pond FG: \( R^2 = 0.72 \); Pond SG: \( R^2 = 0.69 \); logistic: Pond FG: \( R^2 = 0.79 \); Pond SG: \( R^2 = 0.77 \); but residual variance was age dependent for both logistic regressions). Differences in somatic growth rates and otolith – fish length relationships between the two ponds were significant (\( p < 0.0001 \)) (Table 5; Fig. 1 and 2). Otolith length inclined more steeply for Pond SG with increasing SL than for Pond FG. Hence, individuals of the same SL but from different ponds (i.e. with different growth rates) had different otolith lengths; the larger otoliths occurred for the slower growing group of fish. The change in otolith length with

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**FIG. 1.** Regressions of standard length (SL) on age for Pond Fast Growth (FG, plus signs) and Pond Slow Growth (SG, squares). Pond FG: SL = \(-1.7 + 0.83 \times \text{age} \); \( R^2 = 0.71 \); \( N = 94 \). Pond SG: SL = \( 3.8 + 0.41 \times \text{age} \); \( R^2 = 0.73 \); \( N = 138 \).

**FIG. 2.** Regressions of otolith length on standard length (SL) for Pond Fast Growth (FG, plus signs) and Pond Slow Growth (SG, squares). Pond FG: otolith length = \(-320 + 58.3 \times \text{SL} \); \( R^2 = 0.97 \); \( N = 39 \). Pond SG: otolith length = \(-391 + 70.6 \times \text{SL} \); \( R^2 = 0.97 \); \( N = 59 \).
Fig. 3. Regressions of otolith length on age for Pond Fast Growth (FG, plus signs) and Pond Slow Growth (SG, squares). Pond FG: otolith length = -830.5 + 61.3 × age; $R^2 = 0.89; N = 39$. Pond SG: otolith length = -184.5 + 30.3 × age; $R^2 = 0.81; N = 59$.

Fig. 4. Regression of average increment count on known-age of fish from Pond Slow Growth. Averages for each otolith were calculated for six repeated counts (two investigators each did three repeated counts). Prediction interval shown. Increment count = -2.97 + 0.95 × age; $R^2 = 0.99; N = 29$.

Assumptions for constant and independent variance of residuals were met for all regressions except for somatic and otolith growth relationships. Significant departures from constant variance occurred beyond 45 d and indicated that beyond this time, the rate of increase in SL or otolith length declined away from a linear relationship for both ponds.

Incremental Growth of Otoliths

First increment formation occurred between 4 and 5 d after hatch. Examination of the sagittae from older individuals with light microscopy and SEM showed distinct increments. Otolith material was taken from Pond SG, since some reports have indicated that nondaily increment formation occurs due to low growth rate (Geffen 1982; Lough et al. 1982; Jones 1986) although more recent reports have shown that nondaily increment formation is probably due to limited resolution (Jones and Brothers 1987; Campina et al. 1987). The number of incre-
ments counted for each otolith was not influenced by the order in which the otolith was read ($p = 0.61$), nor were they significantly different between readers ($p = 0.50$). Increment counts for each otolith were averaged and regressed against age (Fig. 4). The slope was not different from the expected rate of one increment per day, nor was the expected intercept significantly different than the modeled intercept based on observed first increment formation at 4-5 d after hatch (average number of increments $= -2.96 + 0.95 \times d$ after hatch; $F$-test for slope of 1 and intercept of $-4$, $p = 0.08$).

Otolith Scaling Model

To assess the generality of somatic growth effects on otolith scaling, otolith length was modeled with data pooled from all 12 ponds (Table 6). A model which used age and SL alone showed significant main effects and interaction for these variables (Table 6). Other models which included pond and hatch date effects showed significant main effects due to the additional variables but improved prediction of otolith length negligibly. Also, no significant interaction occurred between the variables SL, age, and pond or hatch date.

Age prediction models were fit using otolith length, SL, pond, and hatch date effects (Table 6). Main effects for SL were significant only when the model included hatch date or pond effects. Pond and hatch date effects, albeit significant, did little to improve the age prediction regression. Age prediction models using SL and the cube root of otolith weight were tested for combined data from Pond FG and Pond SG ($n = 48$). Main effects (cube root of otolith weight and SL) and interaction terms (cube root of otolith weight $\times$ SL and cube root of otolith weight $\times$ SL $\times$ pond) were significant at $p = 0.0001$ with a high determination coefficient ($R^2 = 0.91$).

Discussion

DIP Model

We show that differences in otolith scaling patterns were attributable to somatic growth differences. Since scaling differences occurred between ponds (Pond FG versus Pond SG) which were stocked with larvae from the same batch of fertilized eggs, temporal and genetic differences can be discounted. For pooled data, nonsignificant effects of pond and hatch date on the interaction term SL $\times$ age also suggest that location, genetic, and temporal influences can be ruled out. Based on the results, we propose a model for otolith size which considers both fish size and age effects. We believe that this model is appropriate, since daily increment formation (i.e. age effects) can occur independent of somatic growth. Because increment formation will always contribute to otolith growth in the model, we refer to it as the daily increment packing (DIP) model for otolith scaling.

Uncoupling Hypothesis

Evidence suggests that daily accretion of CaCO$_3$ and organic matrix onto the otolith is an endogenously defined rhythm (Mugiya et al. 1981; Radtke and Dean 1982; and many others, see Campana and Neilson 1985). Therefore it is possible for changes in otolith size to occur that are not synchronous with changes in fish size. In an extreme case, cessation of fish growth could occur and the increment growth of the otolith continue, resulting in dissociation or uncoupling of otolith and somatic growth. Uncoupling has been used to explain intraspecific variation in otolith scaling. Uncoupling may be due to differences in core size (Neilson et al. 1985b), experimental manipulation of photoperiod (Campana 1984b), metamorphic transition (Brothers and McFarland 1981; Nishimura and Yamada 1984), or cessation of growth (Brothers 1981; Marshall and Parker 1982; Campana 1984a). For this study, analysis of residuals for somatic and otolith growth regressions showed a declination from linearity after 45 d. But previous to the last week of the sampling period, somatic and otolith growth was continuous. A comparison between Pond FG and Pond SG with all samples older than 45 d omitted showed significant differences in the otolith length $\times$ SL relationship ($n = 79$; $F = 69.2$; $p = 0.0001$). Also, no inflection point in the otolith length $\times$ SL relationship was observed which corresponded to the shift in growth rate (Fig. 2). Our evidence suggests that fish growth need not be interrupted for differences in otolith scaling to occur. Uncoupling probably represents one extreme in a continuum of scaling relationships influenced by somatic growth rate.

Rationale for the DIP Model

A range of somatic growth effects on otolith scaling can be explained by two interacting components of increment deposition, a temporal component and an amplitude component.
Mugiya (1987) has shown through in vitro studies that otolith growth depends upon diurnal cycles of CaCO$_3$ and organic matrix deposition, each cycle occurring in opposite phase with the other (e.g., the peak of CaCO$_3$ deposition is simultaneous to the nadir of organic matrix deposition and vice versa). Since otoliths are primarily mineral (Degens et al. 1969), we will apply further arguments to CaCO$_3$ deposition only. Diurnal variation of CaCO$_3$ deposition onto the otolith and serum calcium were shown to be simultaneous (Mugiya et al. 1981; Mugiya 1987). Wagner et al. (1985) recorded variation in daily calcium uptake rates for rainbow trout (Salmo gairdneri) fry which cycled every 7–17 d. They indirectly related this variation to cycles in weight gain. Assuming that calcium uptake and serum calcium level are related (Taylor 1985; Wagner et al. 1985), there is biological rationale for relating changes in fish length (or weight) to otolith growth. Conceptually, daily changes in fish size are associated with the amplitude of a deposition period of CaCO$_3$ (i.e., the area under a peak). Otolith growth as defined by deposition period, and each period’s amplitude can thus be related to age and fish size.

The DIP model assumes that increment formation is only related to age. A few studies have concluded that somatic growth rate influences increment formation (Geffen 1982, 1983; McGurk 1984). In a recent study using SEM (Jones and Brothers 1987), daily increment formation was confirmed for larval striped bass reared in aquaria and starved intermittently. It has been suggested that resolution and otolith preparation may limit the ability to observe increments in instances of reduced fish growth (Campana and Neilson 1985; Jones and Brothers 1987; Campana et al. 1987).

Several reports of intraspecific variation in otolith scaling have suggested growth- and age-related causes. Based on a recent a priori test on age-related otolith – fish length differences, Reznick et al. (1989) concluded that although age-related differences in otolith size were small in magnitude, they were still statistically significant. In a similar experiment, Marshall and Parker (1982) found that fish on a lower ration level grew less and yielded larger otoliths at a given fish length. However, Rice et al. (1985) showed that variation in scaling was not attributed to somatic growth rate (ration). More descriptive field studies relate intraspecific variation in otolith scaling to year-class (Templeman and Squire 1956; Neilson et al. 1985a; Penny and Evans 1985), cohorts (Messieh 1972), sampling locations (Taubert and Coble 1977; Frost and Lowry 1981), and sex (Templeman and Squires 1956; Wilson 1984). It is feasible that these examples of intraspecific variation may have occurred due to somatic growth effects. For instance, Wilson (1984) provided strong evidence for a scaling – somatic growth relationship in adult billfishes. Sexual dimorphism in fish size resulted from discrete sex-related growth rates. Otoliths were significantly heavier for older males than for younger females at the same body weight. Templeman and Squires (1956) described similar results for adult haddock (Melanogrammus aeglefinus). Because the daily deposition of CaCO$_3$ and organic matrix determines otolith growth in adult fishes (Taubert and Coble 1977; Mugiya et al. 1981; Wilson 1984; Mugiya 1987), these cases of growth-related variation in otolith scaling for adults are relevant to the DIP model.

Age Prediction based on the DIP Model

Since otolith growth depends upon the period of CaCO$_3$ deposition as well as the amplitude of each deposition period, age and SL effects on otolith size were expected. By rearranging these variables, we were able to predict age based on otolith size and fish size. Conceptually, were growth rates not variable within a population, then otolith size would only depend upon age (period of deposition). But variable growth rates, manifested in SL, will affect daily deposition rates (period amplitude). Therefore, SL will influence the relationship between age and otolith length. Hence, the regression model for age had significant interaction between SL and otolith length. But SL main effects were not always significant. This may be due to colinearity between otolith length and SL.

Reznick et al. (1989) suggested that the residuals from the regression otolith length = SL may be used in age prediction models. We tested several combinations of this term and found that the best prediction equation was age = otolith length + (otolith length – residual). With $R^2 = 0.76$, it explained less variation than a model based on interaction between otolith and fish length.

Implications for Interpretation of Increment Widths

Several workers have used increment widths as estimators of age-specific growth rates (see the introduction). These studies assume a simple relationship between otolith and fish size which is species specific. Our results suggest a more complex relationship. (1) Within a species, there are population-specific otolith scaling patterns which are related to growth rates. Therefore for each population studied, an otolith – fish size relationship must be verified. (2) Among individual fish, increment widths will be a function of the period of deposition and that period’s amplitude. For instance on a day when somatic growth is negative, zero, or very slow, some minimum amount of CaCO$_3$ and organic matrix is deposited on the otolith (Marshall and Parker 1982; Jones and Brothers 1987). On a day when growth is fair to good, material additional to this minimum amount is deposited on the otolith. The actual relationship between increment width and somatic growth is much more complicated than this; beyond the minimum limit, increment width is probably a declining function of somatic growth rate (Baldeverona 1987). Therefore, one cannot assume that increment width and somatic growth are linearly related; minimum and maximum limits on increment widths will have to be integrated into any age-specific growth rate model. A further complication is that otoliths change shape throughout ontogenesis (Brothers and McFarland 1981; Campana 1984a; Nishimura and Yamada 1984). As otolith growth axes shift, so will the minimum and maximum limits.

Limitations of the DIP Model

Factors other than somatic growth rate can be associated with differences in scaling and may curtail prediction of somatic growth rate and age. These include factors which effect uncoupling (see previous discussion), the CaCO$_3$ to organic matrix ratio (Radkte et al. 1985), life history events (Brothers and McFarland 1981; Campana 1984a; Nishimura and Yamada 1984), temperature, genotypic variation, and variable growth rates. Radkte et al. (1985) suggested that the protein to CaCO$_3$ ratio may vary according to growth rate. Fast growing fish would deposit more protein relative to CaCO$_3$, resulting in less dense, lighter otoliths. This hypothesis is speculative, since protein content in otoliths has been rarely quantified. Degens et al. (1969) measured organic content for otoliths of 25 species which ranged from 0.25 to 10.14% and averaged 1.5%.
temperature will affect the amplitude of the deposition period (Y. Mugiya, Faculty of Fisheries, Hokkaido University, Minato-3, Hakodate, 041 Japan, pers. comm.). Should populations be exposed to variable temperatures, this factor may complicate predictions based on scaling. In this study, genotypic variation was randomized by mixing batches of eggs. Until genotypic variation is quantified, the use of otolith scaling should be confined to population studies.

Age and growth rate prediction on the basis of otolith scaling assumes a constant growth rate for both the fish and the otolith. Both of these assumptions limit application, since somatic growth rate is known to change throughout a fish’s life history due to such events as starvation or compensatory growth. Also, otoliths will undergo metamorphic shifts as they grow, resulting in shifts in growth axes. Therefore we do not propose otolith scaling as a precise measure, but rather as an index or an average of past growth rates. This index will be limited to population studies which consider discrete life stages and assume constant growth rates (D. Reznick et al. 1989).

Future Studies

In the future, it may be possible to predict relative differences in somatic growth between groups of young-of-the-year fishes with otolith size relationships (Secor and Dean 1986). Prediction intervals for the otolith length – SL relationship for Pond FG and Pond SG (not shown) overlapped due to the range in data for each growth group (Fig. 2). However, with further testing and modification, the DIP model may allow fishery workers to deduce that a larger otolith, from a comparison of fish of the same length, is indicative of slower growth. As we have demonstrated through a statistical and conceptual model, age prediction on the basis of otolith scaling is also feasible. Otolith weight may be a better dimension of otolith growth and hence allow better age prediction. Otolith – fish size relationships are easily measured, especially compared with the arduous tasks ofincrement counts and increment width measures. Comparisons could be made between hatchery and naturally produced fish, spawning sites, and year-classes.

Future studies need to establish a physiological link between fish anabolism and otolith growth. Mugiya (1986) has shown that the regulatory protein calmodulin (which is regulated by serum calcium) is involved in otolithic calcification; but a regulatory sequence from general anabolic activity to CaCO3 deposition remains to be elucidated. Integral problems to investigate include the role of organic matrix in CaCO3 deposition and the function of the pineal and pituitary glands and their hormones on the deposition of organic matrix and CaCO3.

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