

Evaluation of periodic and aperiodic otolith structure and somatic-otolith scaling for use in retrospective life history analysis of a tropical marine goby, *Bathygobius coalitus*

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ABSTRACT: Daily increment formation in sagittal otoliths, scaling between otolith and somatic growth, and the temporal link between settlement and formation of a settlement mark in otolith structure were evaluated for their use in reconstructing aspects of the early life history of the basalt goby *Bathygobius coalitus*. Formation of daily increments was validated in sagittae of fish ranging in life history stage from new recruits to sexually differentiated males and females. Total length (TL) was proportional to other measures of body length, width, and depth, and linearly proportional to sagitta radius for fish between 8 and 40 mm TL. Somatic-otolith scaling became more curvilinear in larger fish due to declining growth rate of otoliths relative to TL, especially in fish collected during warmer sea surface temperatures. For fish 8 to 40 mm TL, somatic-otolith scaling was not affected by differential somatic growth rates nor by seasonal water temperature. A settlement mark, clearly identifiable as a distinct and abrupt shift in optical focal plane, contrast, and width of daily increments, was verified to coincide with settlement. Wider post-settlement increments abruptly followed narrower pre-settlement increments across the settlement mark. These results support the use of daily increments, somatic-otolith scaling, and a settlement mark for reconstruction of hatch and settlement dates, mean daily pre- and post-settlement growth rates, size and age at settlement, and post-settlement size-at-age histories for the basalt goby.

KEY WORDS: Gobiidae · Hawaiian reef-fish · Daily increments · Settlement mark

INTRODUCTION

Understanding processes that underlie the dynamics of local, open populations of reef fishes has profound theoretical and applied importance (e.g., Sale 1980, Doherty 1983, Caley 1996). Growing interest and debate over the influence of early life history events on population dynamics has popularized the use of retrospective otolith-based techniques for reconstructing aspects of an individual's early life history (Pannella 1971, Victor 1982, 1986b,c Brothers et al. 1983, Campana & Neilson 1985, Wellington & Victor 1989, Cowen

1991, McCormick 1994). Interpretation of otolith structure as a chronological record of fish life history relies on numerous assumptions about how otolith structure and growth are influenced by endogenous daily biological rhythms, ontogeny, eco-physiology, and somatic growth; however, these assumptions are rarely critically evaluated.

Interpretation of otolith structure as a chronological record is based primarily on the assumption that increment formation is periodic and regular. For many fishes, formation of daily increments in otoliths is a relatively common and robust occurrence (Gauldie & Nelson 1988, Gauldie et al. 1990); however, a variety of environmental and physiological factors can produce increments other than daily ones (Campana & Neilson 1985). Moreover, interpretation of daily increment

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structure can be confounded by cessation of otolith growth or changing growth axis, the appearance of subdaily increments or aperiodic checks, and resolution limitations or methodological artifacts (Campana & Neilson 1982, 1985, Victor 1986b, Campana et al. 1987, Jones & Brothers 1987). Consequently, before otolith structure can be interpreted as a chronological record, the regular periodicity of increment formation must be determined, and appropriate analytical techniques to visualize and analyze increments must be developed.

Back-calculation of somatic size-at-age from otolith size-at-age is a powerful retrospective tool for estimating growth rates and reconstructing size at specific dates or life history events. Proportional- (Campana 1990, Francis 1990) and regression- (Secor & Dean 1992) based back-calculation techniques rely on stanzas of consistent correlation between somatic and otolith growth. Whereas somatic and otolith dimensions are inherently correlated due to the positive nature of growing structures (e.g., Shea 1985), and many studies have reported significant correlation (Wilson & Larkin 1982, Volk et al. 1984, Campana & Neilson 1985, Neilson et al. 1985, Barkman & Bengtson 1987, Gleason & Bengtson 1996), departures from constant proportionality can occur during variable environmental, ontogenetic, and growth conditions (e.g., Mosegaard et al. 1988, Hare & Cowen 1995). Specifically, because otolith growth is an extracellular chemical process, whereas somatic growth is primarily a function of metabolism, somatic and otolith growth can proceed independently (Mosegaard et al. 1988, Casselman 1990, Lombarte & Lloenart 1993), and can demonstrate different responses or response times to environmental or metabolic changes (e.g., Molony & Choat 1990).

A common allometry resulting from the disparate nature of somatic and otolith growth is that relative to fish size, slower growing individuals may have larger and/or heavier otoliths than faster growing conspecifics (Templeman & Squires 1956, Boehlert 1985, Mosegaard et al. 1988, Reznick et al. 1989, Secor & Dean 1989, Hovencamp 1990, Francis et al. 1993, Hare & Cowen 1995). Because shifts in proportional somatic-otolith scaling can bias back-calculated estimates of somatic size (Campana 1990), the interaction of somatic-otolith scaling with age, temperature, growth rate, and ontogeny must be explored.

Formation of a discontinuity in otolith structure associated with settlement (i.e., a settlement mark, Victor 1982) provides a useful reference for estimation of larval duration and size at settlement (Bailey et al. 1977, Pannella 1980, Sale 1980, Brothers & McFarland 1981, Victor 1982, 1986a,b,c, Brothers et al. 1983, Doherty 1987, Cowen 1991, Hare & Cowen 1994, Wilson &

McCormick 1997, 1999). Settlement marks have been observed to occur in the otoliths of a variety of fishes, and are presumed to result from changes in a fish's morphology, physiology, and environment during settlement and metamorphosis. The structure of settlement marks appears to be taxon-specific, however, and may be subject to spatial and temporal variation (Wilson & McCormick 1997, 1999). Settlement may also occur with no coincidence of disruption to regular otolith structure, or may result in the deposition of settlement marks varying in composition from 1 to 2 increments to a wide multi-incremental transitional zone (Brothers & McFarland 1981, Victor 1982, Pitcher 1988, Radtke et al. 1988, Fowler 1989, Hare & Cowen 1994, Sponaugle & Cowen 1994, Wilson & McCormick 1997, 1999). As a result, the species-specific structure of settlement marks must be investigated, and the temporal link between formation of a settlement mark and settlement must be verified.

As the first step in a larger effort to understand the early life history dynamics of the basalt goby *Bathygobius coalitus*, a common and abundant shoreline gobiid in Hawai'i, the present study evaluates assumptions critical to the interpretation of patterns in otolith structure as a chronological record of fish life history. Specifically, this study examines whether (1) daily increments are formed in sagittae, (2) somatic-otolith scaling is proportional during early life history, and (3) a settlement mark forms in sagittae during settlement and metamorphosis.

METHODS

Taxonomy. Classification of gobiids has frequently undergone dramatic revisions, due in part to difficulties associated with high taxonomic diversity and small adult sizes (Hoese & Gill 1993). The basalt goby *Bathygobius coalitus*, was previously taxonomically lumped with another similar *Bathygobius* species (the brown goby *B. fuscus*, Gosline & Brock 1976, Tinker 1982), but recently has been identified as *B. coalitus* (D. F. Hoese, The Australian Museum, Sydney, Australia, pers. comm.).

Collection and handling of specimens. Juvenile and adult basalt gobies were collected by hand-net from tidepools at Sandy Beach Park on O'ahu, Hawai'i (21° 17' 25" N, 157° 40' 16" W) at monthly intervals between July 1990 and September 1992 and quarterly intervals between October 1992 and October 1993. A total of 2300 *Bathygobius coalitus* was collected, ranging in size from 8.7 to 113.8 mm total length (TL). In Hawai'i, seasonal minima of sea surface temperature (SST) typically occur before or during March/April and maxima occur before or during October (K. Bigelow &

C. Boggs unpubl. dataset cited in Shafer 1998). Specimens were selected from collections made during periods of cool (March 1991, April 1991, 1992, 1993), warm (October 1991, 1992, 1993, November 1991), and intermediate (January 1991 and June 1991) SST for somatic-otolith scaling and settlement mark analyses. Morphological differentiation of external genitalia was used to define the ontogenetic onset of maturity (e.g., Cole 1990). Differentiation of external genitalia could be discerned in fish as small as 20 mm TL (consistent with 18 mm standard length [SL] in Cole 1990), when genitalia became more slender and elongate in males and rounded and truncate in females, as in other gobiids (Tavolga 1954, Akihito et al. 1984).

Increment periodicity. A total of 21 basalt gobies, ranging in size from 12.7 to 32.1 mm TL, was collected in May 1995 from the intertidal zone at Sandy Beach. Fish were transported to the laboratory and held in complete darkness for 24 h in an alizarin complexone solution (30 mg of alizarin-3-methylamine-N,N-diacetic acid per liter of 9:1 distilled water:seawater solution). Alizarin complexone readily becomes incorporated into the growing margin of calcified tissues, and fluoresces under ultraviolet (UV) illumination (Tsukamoto et al. 1989).

Following immersion in alizarin complexone solution, fish were washed with seawater for 10 min to remove residual alizarin complexone from their external surfaces, then transferred to seawater (35 ppt salinity) aquaria with 12 h light:12 h dark illumination cycles and fed live *Artemia* nauplii *ad libitum*. Average water temperature during captivity was 20.5°C, and all marking, transfer, and sacrifice procedures occurred at approximately 10:00 h. Two individuals were sacrificed and measured every second day from Days 5 to 25. Left and right sagittae were dissected, cleaned of extraneous tissue with needles and a nylon brush, and stored dry on modified paleoslides in complete darkness to prevent degradation of the fluorescent reference mark (Fargo & Chilton 1987).

Right sagittae were mounted sulcus-side down onto glass slides with the heat-setting thermoplastic Crystal Bond (Aremco Products, USA), and viewed with transmitted light at 160× and 400× magnifications using a Zeiss Axioskop compound microscope. Images were digitized using a computer-interfaced digitizing card and a Hitachi KP-160 CCD digital camera, and enhanced using image analysis software (Image 1.47, National Institutes of Health, USA). Otoliths were blindly selected (i.e., duration of captivity following marking was unknown to the counter) and viewed at 160× and 400× magnifications with a Zeiss epifluorescent compound microscope. The location of the fluorescent reference mark was identified and noted on each digital image.

Daily increments following the fluorescent reference mark were enumerated and individually noted on digitized images. The confidence of each blind count was coded, ranging from 0 (not confident) to 5 (very confident), and counts assigned a confidence code of 3 or lower were recounted. If the second count differed from the first, then images of both counting transects were compared, and areas along the transect where counting discrepancies occurred were identified. Areas with discrepant counts were re-evaluated using different magnification, light polarization, and focus to best resolve increment structure, then assigned new confidence levels. The count with the highest confidence level was accepted as the best estimate.

Widths of the 5 daily increments immediately preceding (wild) and following (laboratory) the fluorescent reference mark were measured using image analysis software. Daily increment widths were compared between wild and laboratory growth intervals with a paired *t*-test (Sokal & Rohlf 1981). The null hypothesis of no difference in width was tested versus a 1-tailed alternative that wild increments were wider than laboratory increments. A 1:1 relationship between increment number and days following alizarin complexone marking was tested by regression analysis of number of increments on elapsed days.

Growth isometry. Scaling between somatic and otolith growth was investigated by cross-sectional analysis of somatic and otolith dimensions measured at capture, with different-sized individuals representing progressive positions along a generalized life history size continuum. Models were chosen to best describe somatic-otolith scaling according to standard regression criteria (as outlined in Hare & Cowen 1995), including (1) simplicity (i.e., the model with fewest parameters), (2) residuals from the model were normally distributed (Kolmogorov-Smirnov test, $\alpha = 0.05$), (3) residuals had a constant variance with respect to the independent variable, and were independent of each other (by visual inspection of the bivariate plot of residuals on predicted values), and (4) a significant amount of the variation in somatic size was explained by otolith size in the model (using the *F*-statistic and r^2). Because of the positive correlation inherent between positively growing structures (Shea 1985), a significance level $p < 0.01$ was chosen as the criterion for evaluating regression coefficients.

Morphometry. Body size: Choosing an appropriate somatic dimension as a representative indicator of overall somatic growth is an often overlooked, but important component in back-calculation procedures (Hare & Cowen 1995). Scaling among somatic dimensions and TL was examined to evaluate how well changes in TL reflected overall somatic growth. TL

was regressed on SL, wet weight, body depth and width at the opercula and urogenital vent, least caudal-peduncle depth, head length, and relative gape for arbitrarily selected subsamples. All length measurements were made with an optical micrometer in the eyepiece of a Zeiss dissecting microscope for fish smaller than about 12.5 mm TL and with a dial caliper for larger measurements. Fish wet weight was measured to 0.01 g with an electronic balance. Depth and width at the opercula and urogenital vent were measured at positions bisecting the mid-plane of these structures. Relative gape was measured as the maximum clearance between upper and lower teeth when the maxillary and dentary bones were extended orthogonally.

Otolith size: The postero-ventral corner (terminology from Hecht 1987) of *Bathygobius coalitus* sagittae consisted of a rounded lobe that demonstrated only slight variation in marginal sculpture and changed little in shape and direction of growth axis with ontogeny. Because of these conservative morphological properties, the growth axis traversing from the core to the postero-ventral corner of sagittae was selected for use in increment counts and measurements. Hereafter, otolith radius (OR) refers to measurements along this growth axis.

Calculation of average growth rate. Embryonic duration for *Bathygobius coalitus* was assumed to be approximately 3 d based on the embryonic duration determined for the congeneric frillfin goby *B. saporator* (Tavolga 1954). Assuming that the first otolith increment was formed at hatch (Miller & Storck 1982, Nishimura & Yamada 1984, Victor 1986a,b, Eckmann & Rey 1987, Kingsford & Milicich 1987, Radtke et al. 1988, Sponangle & Cowen 1994), age estimates were adjusted to account for embryonic duration by adding 3 d to daily increment counts. This correction procedure reduced the overestimation of mean daily growth rate (i.e., $TL_{\text{capture}}/\text{age}$), by accounting for embryonic growth as a component of TL at capture.

Somatic-otolith scaling. Somatic-otolith scaling was modeled by linear and quadratic models for fish grouped to sizes between 8 and 70 mm TL (the largest fish examined in this study was 68.43 mm TL) and sizes between 8 and 40 mm TL (the postero-ventral sagittae growth axis was observed to begin to change direction in some fish larger than about 46 mm TL).

Effects of sexual differentiation on somatic-otolith scaling were explored by comparing scaling between TL and OR for undifferentiated versus differentiated fish using an ANCOVA (analysis of covariance) model (Sokal & Rohlf 1981). A significant interaction between OR and developmental stage ($\alpha = 0.05$) was interpreted to indicate an effect of maturity on somatic-otolith scaling.

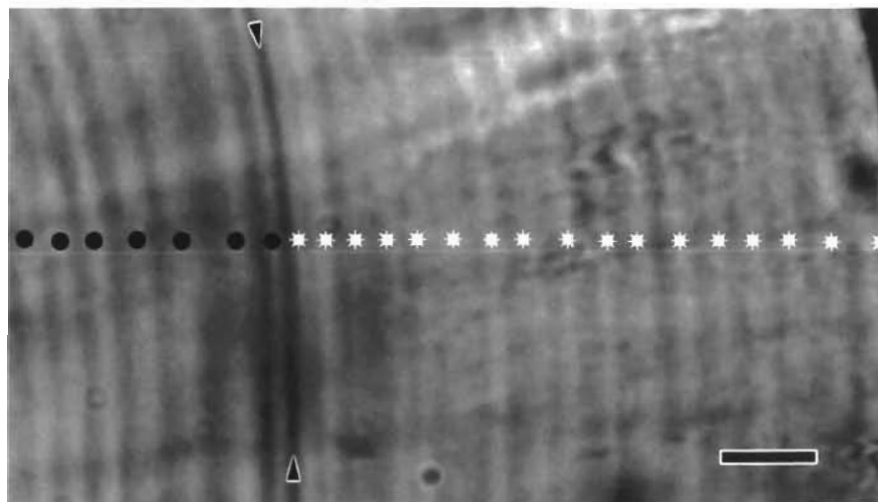
Effects of seasonal water temperature on somatic-otolith scaling were investigated by comparing scaling between TL and OR for fish collected during months associated with cool SST versus scaling for those collected during warm SST using an ANCOVA model. A significant interaction ($\alpha = 0.05$) was interpreted to indicate a seasonal temperature effect on somatic-otolith scaling.

The robustness of somatic-otolith scaling to variation in growth rate was evaluated by a procedure adapted from Hare & Cowen (1995), whereby (1) sagitta radius and fish age were modeled with regard to TL, then (2) the relationship between residuals from the sagitta radius on TL (somatic-otolith scaling) and age on TL (growth rate) models was evaluated by correlation analysis. For these analyses, linear models were chosen as best fits to the relationships of sagitta radius on TL and age on TL. Heteroscedasticity (i.e., increasing variance with increasing magnitude of the independent variable, TL) in the linear models of sagitta radius on TL and fish age on TL was reduced by natural log transformation of independent and dependent variables. Ln-transformed models had high coefficients of determination (r^2), and residuals demonstrated independence and near constant variance. Residuals from ln-transformed sagitta radius on TL and fish age on TL models were standardized to the predicted value for each model, then compared using the Pearson's correlation coefficient, r (Sokal & Rohlf 1981).

If somatic-otolith scaling was unaffected by growth rate, then the standardized residuals of somatic-otolith scaling (from ln sagitta radius on ln TL) and standardized residuals of growth rate (from ln age on ln TL) were expected to demonstrate no correlation (i.e., H_0 : Pearson's $r = 0$). Alternatively, if faster growing fish (negative standardized residuals from ln age on ln TL) had smaller otoliths for their size (negative standardized residuals from ln sagitta radius on ln TL), then the standardized residuals of somatic-otolith scaling and standardized residuals of growth rate were expected to be positively correlated (i.e., 1-tailed, $H_a: r > 0$). Analysis included only fish smaller than 40 mm TL, for which composite somatic-otolith scaling was determined to be linear.

Settlement mark. To determine the temporal link between settlement and formation of a settlement mark in otoliths, sagittae of metamorphosing gobies ($n = 18$) and metamorphosed gobies ($n = 263$) were compared for presence of a settlement mark. Metamorphosing *Bathygobius coalitus* were scaleless, transparent, and presumed to have just settled. If formation of a settlement mark coincides with settlement, a settlement mark was expected to be visible circumscribing an interior portion of sagittae of all settled individuals, whereas no settlement mark, or one immediately form-

Fig. 1 *Bathygobius coalitus*. Transmitted light micrograph of daily increments in the right sagitta from a 17.5 mm TL *B. coalitus* immersed for 1 d in alizarin complexone solution, then held in a seawater aquarium for 17 d. The experimental reference mark (see arrowheads), formed during immersion in alizarin complexone, separates increments formed during wild (black circles) and laboratory (white stars) growth. Scale bar = 10 μ m



ing at the otolith margin, was expected to be visible in sagittae of just-settled metamorphosing individuals.

To further examine the timing of settlement mark formation, back-calculated sizes at settlement for metamorphosed fish smaller than 40 mm TL were compared to sizes of just-settled metamorphosing fish by ANOVA. If settlement marks coincide with settlement, back-calculated sizes at settlement of metamorphosed fish (using the settlement mark as a reference) were not expected to differ from known sizes at settlement (sizes of metamorphosing fish). Size at settlement of metamorphosed fish was back-calculated using the location of the settlement mark in otolith structure, somatic-otolith scaling determined at capture, and the Dahl-Lea equation (Lea 1910, reviewed in Francis 1990): $TL_s = (TL_c \times OR_s) / OR_c$, with subscripts c and s denoting time at capture and settlement, respectively. Because metamorphosing fish were collected during periods of cool SST, and because larval duration and size at settlement in *Bathygobius coalitus* are inversely related to temperature (Shafer 1998), size at settlement of metamorphosing fish was compared to back-calculated size at settlement for metamorphosed fish also settling during periods of cool SST.

RESULTS

Increment periodicity

When viewed with UV illumination, all sagittae from *Bathygobius coalitus* immersed in alizarin complexone solution demonstrated a distinct continuous fluorescent mark circumscribing an interior portion of the otolith. When viewed with transmitted light, a dark structural disruption coincided with the fluorescent

mark, although it was not always continuous around the otolith. Coincidence of the disruption and fluorescent mark enabled otolith carbonate accreted during laboratory growth to be structurally identified in the absence of UV illumination (Fig. 1). A slope of near unity for the linear regression of number of increments on elapsed days (increment number = days $[0.989] + 0.111$, $F = 16760$, $p < 0.0001$, $r^2 = 0.99$; or with the intercept constrained to 0: increment number = days $[0.996]$, $F = 16882$, $p < 0.0001$, $r^2 = 0.99$) indicated that increment formation occurred with daily periodicity. Daily increments formed in sagittae during laboratory growth were slightly less distinct and narrower (paired t -test, $df = 20$, $t = 7.49$, 1-tail $p < 0.0001$) than those formed during wild growth (mean \pm SD, $4.15 \pm 1.02 \mu$ m [laboratory] vs $5.40 \pm 1.22 \mu$ m [wild]), but could still be distinguished confidently (Fig. 1).

Growth isometry

TL was determined to be a good representative measure of overall somatic growth, as SL, head length, relative gape, caudal-peduncle depth, and body depth and width at the opercula and urogenital vent were all proportional to TL, resulting in approximate cubic scaling between TL and fish wet weight (Table 1). Among these measures of body size, TL and SL were the most highly correlated with sagitta radius (Pearson's correlation coefficient $r = 0.99$, $p < 0.0001$, for both). TL was chosen over SL for analysis of somatic-otolith scaling because it has greater ecological significance and could be measured with greater precision.

Composite somatic-otolith scaling (TL on OR) for fish grouped to sizes between 8 and 40 mm TL was best described by a linear model (Fig. 2a, solid line).

Table 1. *Bathygobius coalitus*. Scaling of somatic dimensions. Dimensions include total length (TL), standard length (SL), head length (HL), relative gape (RG), caudal-peduncle depth (CD), body depth and width at the opercula (OD and OW, respectively), body depth and width at the urogenital vent (UD and UW, respectively), and fish wet weight (FWt). All measurements are in millimeters except fish weight (g).

All $p < 0.0001$

Somatic dimensions	n	Model	r^2
SL on TL	2236	$SL = 0.189 + 0.742(TL)$	0.99
FWt on TL	2218	$FWt = 7.01E^{-6}(TL)^{3.12}$	0.99
HL on TL	250	$HL = 0.304 + 0.206(TL)$	0.99
RG on TL	100	$RG = -0.164 + 0.096(TL)$	0.97
OD on TL	550	$OD = 0.200 + 0.154(TL)$	0.97
OW on TL	550	$OW = -0.220 + 0.169(TL)$	0.98
OD on OW	550	$OD = 0.417 + 0.910(OW)$	0.98
UD on TL	330	$UD = 0.108 + 0.158(TL)$	0.98
UW on TL	330	$UW = 0.165 + 0.117(TL)$	0.97
UD on UW	330	$UD = -0.049 + 1.338(UW)$	0.98
CD on TL	250	$CD = -0.258 + 0.111(TL)$	0.99

Linear models also provided the best fit for somatic-otolith scaling for fish 8 to 40 mm TL grouped to all monthly collections (except January 1991), and grouped to collections associated with warm and cool seasonal SST (Table 2), with no difference in scaling between seasons (ANCOVA, $F_{interaction} = 0.17$, $p > 0.680$). Small differences in scaling were detected between sexually undifferentiated and differentiated individuals (Fig. 2b; 8 to 40 mm TL: ANCOVA, $F = 5.61$, $p < 0.019$; 8 to 70 mm TL: ANCOVA, $F = 62.88$, $p < 0.0001$), with no difference in scaling between differentiated males and females (8 to 40 mm TL: ANCOVA, $F = 1.62$, $p > 0.208$; 8 to 70 mm TL: ANCOVA, $F = 0.45$, $p > 0.504$).

Residuals from a linear fit to somatic-otolith scaling for fish 8 to 70 mm TL were observed to depart from the model for fish sizes greater than about 46 mm TL, resulting in a better fit to the data by a quadratic model (Fig. 2a, dashed line). The postero-ventral growth axis of sagittae commonly began to change direction in fish older than 200 d (also approximately 46 mm TL), resulting in a change in shape of the postero-ventral lobe (Fig. 3). For individuals 8 to 70 mm TL grouped to monthly collections, somatic-otolith scaling was best described by linear models for March, April, and June collections, and by curvilinear models for October, November, and January collections (Table 2). Curvilinearity in somatic-otolith scaling of fish 8 to 70 mm TL occurred predominately in collections during or just following periods associated with warm SST maxima. Specifically, scaling was best described by a linear model for fish collected during periods associated with

cooler SST (March and April), and by a curvilinear model for those collected during periods associated with warmer SST (October and November), with a slightly significant difference in somatic-otolith scaling for fish 8 to 70 mm TL between seasons (Table 2, ANCOVA, $F_{interaction} = 5.56$, $p < 0.019$).

Somatic-otolith scaling for fish 8 to 40 mm TL was robust over the natural range of growth rates. There was no correlation between the standardized residuals of somatic-otolith scaling (from \ln sagitta radius on \ln TL) and the standardized residuals of growth rate (from \ln age on \ln TL) (Fig. 4; Pearson's $r = 0.027$, $p > 0.341$), indicating no growth rate effect on somatic-otolith scaling.

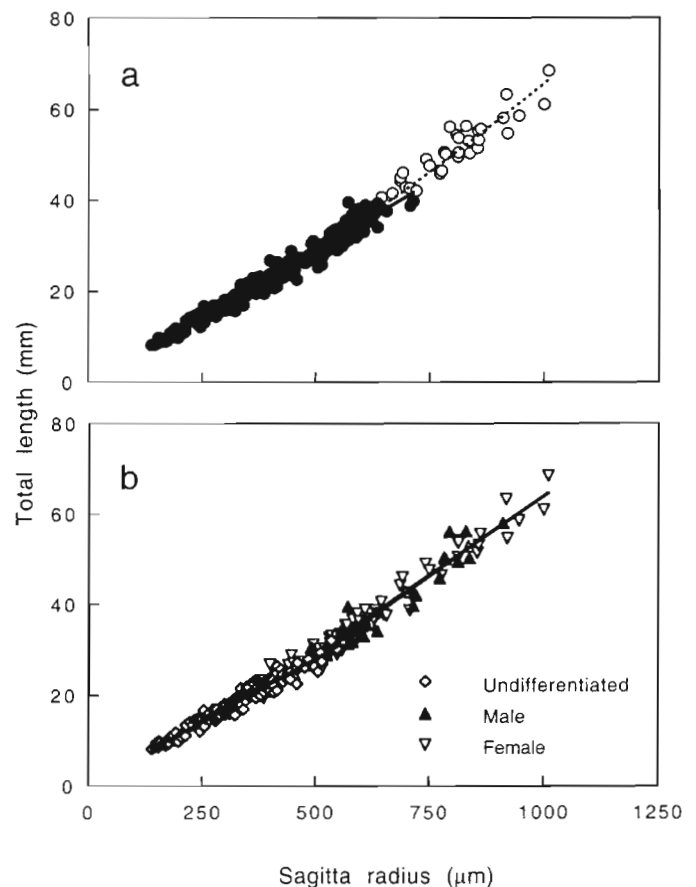


Fig. 2. *Bathygobius coalitus*. Scaling between TL (mm) and sagitta radius (OR, μm) for (a) the grand population of *B. coalitus*, see Table 2 for linear (fish 8 to 40 mm TL, shaded circles, solid line) and quadratic (fish 8 to 70 mm TL, open circles, dashed line) regression equations; and for (b) sexually undifferentiated and differentiated males and females, regression equations: sexually undifferentiated males and females, $TL = 0.27 + 0.06(OR)$, $r^2 = 0.95$, $p < 0.0001$; sexually differentiated males, $TL = -7.58 + 0.07(OR)$, $r^2 = 0.93$, $p < 0.0001$; and sexually differentiated females, $TL = -5.56 + 0.07(OR)$, $r^2 = 0.96$, $p < 0.0001$.

Settlement mark

All sagittae of metamorphosed gobies (ranging in size from 9.0 to 68.43 mm TL and age from 39 to 277 d, n =

263) exhibited an abrupt discontinuity in structure (see arrows in Fig. 5) located at a mean (\pm SD) radial distance of $146.05 \pm 12.59 \mu\text{m}$ from the core center (range, 119.26 to $185.00 \mu\text{m}$). Increments immediately predat-

Table 2. *Bathygobius coalitus*. Comparisons of regression models for scaling between otolith radius (OR, μm) and total length (TL, mm) for *B. coalitus* grouped to sizes between 8 and 70 mm TL and 8 to 40 mm TL. Fish were grouped to monthly collections and to cool- (March 1991, April 1992, 1993) and warm- (October 1991, 1992, 1993, November 1991) seasonal temperature collections. Statistically significant regression coefficient values are indicated: ***p < 0.0001, **p < 0.001, *p < 0.01, non-significant p-values in parentheses. The exponent E is base 10 and r^2_1 and r^2_2 are coefficients of determination for linear and quadratic models, respectively

Date	n	Models:		TL ₂ = a + b (OR) + c (OR ²)			r ² ₁ /r ² ₂
		TL ₁ = a + b (OR)		a	b	c	
Fish 8 to 40 mm TL							
Jan 91	46	0.30	0.057***	7.04	0.018 (0.04)	5.10E ⁻⁵ ***	0.96/0.97
Mar 91	27	-0.46	0.058***	-0.40	0.058***	5.1E ⁻⁷ (0.97)	0.98/0.97
Jun 91	22	-2.70	0.067***	-3.35	0.071***	-4.28E ⁻⁶ (0.74)	0.99/0.99
Oct/Nov 91	41	-4.19	0.066***	-1.84	0.054*	1.24E ⁻⁵ (0.54)	0.97/0.97
Apr 92	28	-2.67	0.063***	2.01	0.040 (0.11)	2.69E ⁻⁵ (0.12)	0.96/0.96
Oct 92	24	-2.17	0.062***	2.64	0.037 (0.02)	2.91E ⁻⁵ (0.10)	0.98/0.98
Apr 93	27	-0.33	0.060***	-4.29	0.082***	-2.77E ⁻⁵ (0.05)	0.96/0.96
Oct 93	25	-0.33	0.055***	1.83	0.043***	1.52E ⁻⁵ (0.15)	0.98/0.98
Cool	82	-0.84	0.060***	-1.16	0.062***	-2.34E ⁻⁶ (0.77)	0.97/0.97
Warm	89	-1.84	0.060***	0.98	0.045***	1.78E ⁻⁵ (0.03)	0.97/0.97
Totals	238	-0.94	0.060***	0.49	0.052***	9.73E ⁻⁶ (0.07)	0.96/0.96
Fish 8 to 70 mm TL							
Jan 91	49	-1.57	0.063***	3.81	0.035***	3.18E ⁻⁵ **	0.98/0.99
Mar 91	29	-1.34	0.061***	0.42	0.052***	8.58E ⁻⁶ (0.05)	0.99/0.99
Jun 91	24	-2.51	0.067***	-3.36	0.071***	-4.42E ⁻⁶ (0.55)	0.99/0.99
Oct/ Nov 91	46	-6.19	0.070***	0.17	0.045***	2.22E ⁻⁵ **	0.98/0.99
Apr 92	30	-3.39	0.065***	0.46	0.048***	1.61E ⁻⁵ (0.07)	0.97/0.98
Oct 92	28	-3.05	0.065***	0.84	0.047***	1.68E ⁻⁵ *	0.99/0.99
Apr 93	38	-1.88	0.065***	-1.92	0.065***	-1.68E ⁻⁷ (0.98)	0.98/0.98
Oct 93	28	-3.78	0.067***	5.16	0.021*	4.61E ⁻⁵ ***	0.97/0.99
Cool	97	-2.23	0.064***	-0.27	0.055***	8.46E ⁻⁶ (0.03)	0.98/0.98
Warm	102	-4.35	0.067***	2.38	0.037***	2.88E ⁻⁵ ***	0.98/0.99
Totals	272	2.78	0.065***	1.27	0.046***	1.79E ⁻⁵ ***	0.98/0.98

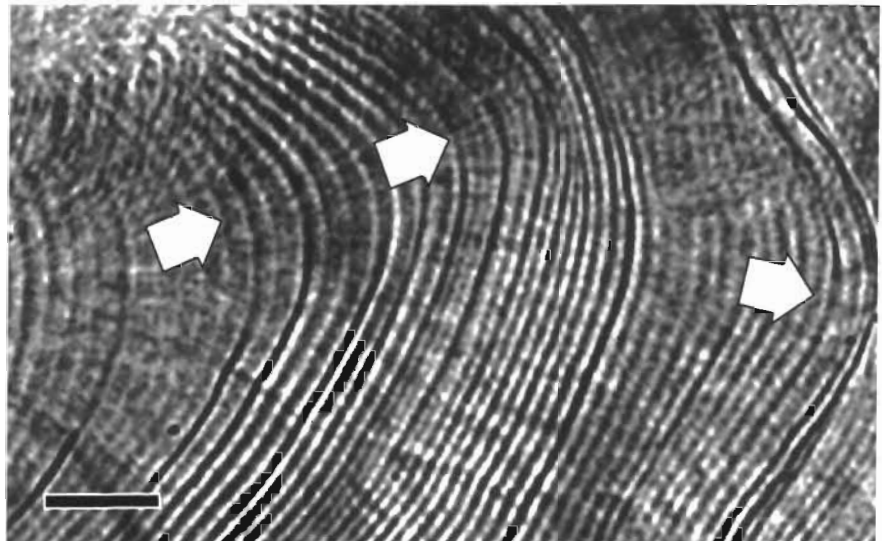


Fig. 3. *Bathygobius coalitus*. Transmitted light micrograph illustrating directional shifts in growth axis (see arrows) near the postero-ventral corner of the right sagitta from a 54 mm TL *B. coalitus*. Scale bar = 30 μm

ing the discontinuity were often narrower, of reduced contrast, and situated in a different optical focal plane than increments following the discontinuity (Fig. 5). No

comparable discontinuity was observed in sagittae from metamorphosing individuals (ranging in size from 8.25 to 9.75 mm TL and in age from 32 to 50 d).

Back-calculated sizes at settlement of metamorphosed fish settling during periods of cooler temperatures (23 to 25°C, $n = 75$, 8.70 ± 0.82 mm TL) did not differ (ANOVA, $F = 3.346$, $p > 0.07$) from sizes of metamorphosing fish collected during similar periods of cooler SST ($n = 18$, 9.06 ± 0.42 mm TL).

DISCUSSION

Increment periodicity

Daily increments formed in sagittae of *Bathygobius coalitus* ranging in life history stage from relatively new recruits to sexually differentiated males and females as large as 32 mm TL (~140 d old, Shafer 1998). Stress resulting from capture, transport, disruption of the natural light cycle, and temperature and salinity changes, including immediate transfer from full-strength seawater to mostly freshwater-based alizarin complexone solution, likely contributed to the distinctiveness of the experimental reference mark separating wild and laboratory growth (e.g., Campana 1983, Volk et al. 1984, Boehlert & Yoklavich 1985, Karakiri & von Westernhagen 1989). Narrowed widths and reduced optical contrast of daily increments deposited during laboratory growth probably resulted from sub-optimal rearing conditions and reduced somatic growth rates, as has been observed for other species (Barkman et al. 1981, Radtke & Dean 1982, Campana & Neilson 1985, Rice et al. 1985, Hovenkamp 1990). In particular, mean aquarium water temperature (20.5°C) during laboratory growth was slightly colder than the minimum water temperature encountered in the wild (seasonal range of daily SST, 22 to 27°C, K. Bigelow & C. Boggs unpublished dataset cited in Shafer 1998), and cooler water temperatures have been implicated in slower otolith and somatic growth rates in *B. coalitus* (Shafer 1998) and in other species (Mosegaard et al. 1988, Karakiri & von Westernhagen 1989, Tzeng & Yu 1989).

Accretion of daily increments following presumably stressful capture and marking procedures suggests that daily increment formation in *Bathygobius coalitus* is robust and biologically entrained (e.g., Gauldie & Nelson 1988, Gauldie et al. 1990). In contrast, immediate changes in

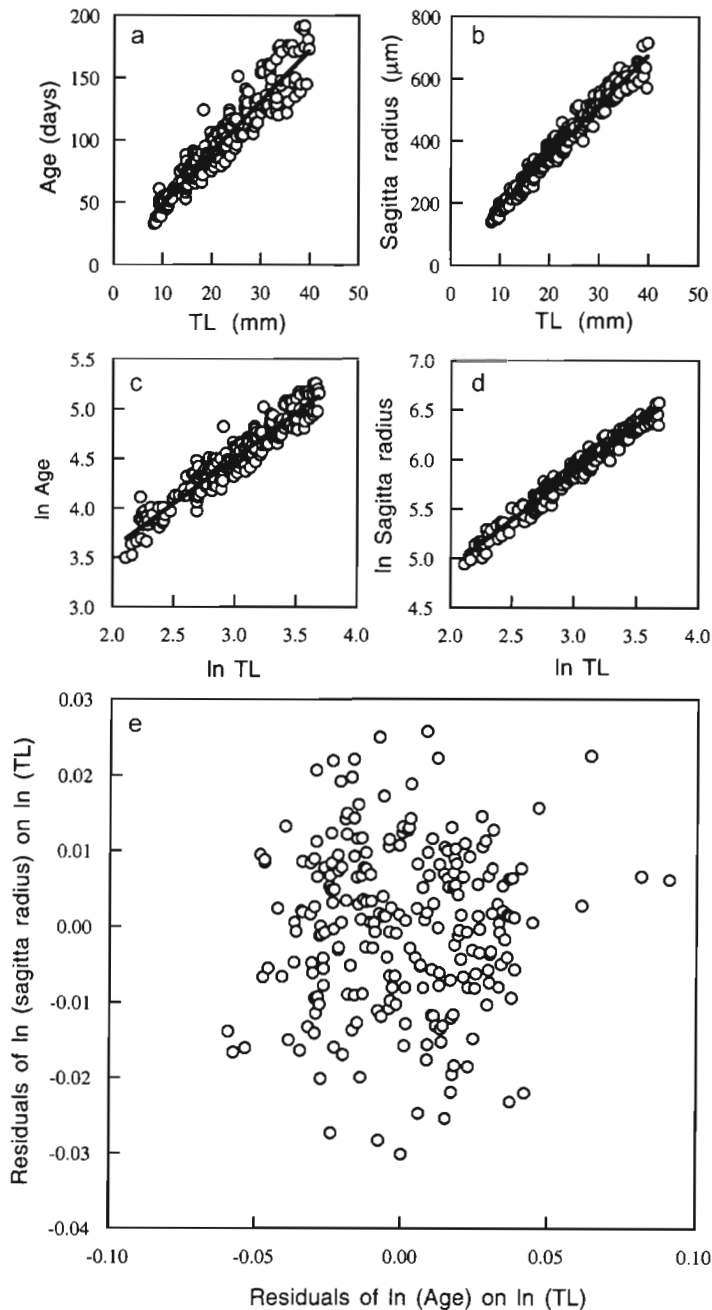


Fig. 4. *Bathygobius coalitus*. Regressions of (a) age on TL and (b) sagitta radius on TL for fish 8 to 40 mm TL, with total length (TL, mm), age (days), and sagitta radius (μm). Heteroscedasticity in a & b was reduced by natural log (ln) transformations of both axes (c & d, respectively). Standardized residuals of somatic-otolith scaling (from d) and standardized residuals of growth rate (from c) were compared in a bivariate plot (e), indicating no correlation between variables (Pearson's $r = 0.09$, $p < 0.01$) and thus no effect of growth rate on somatic-otolith scaling

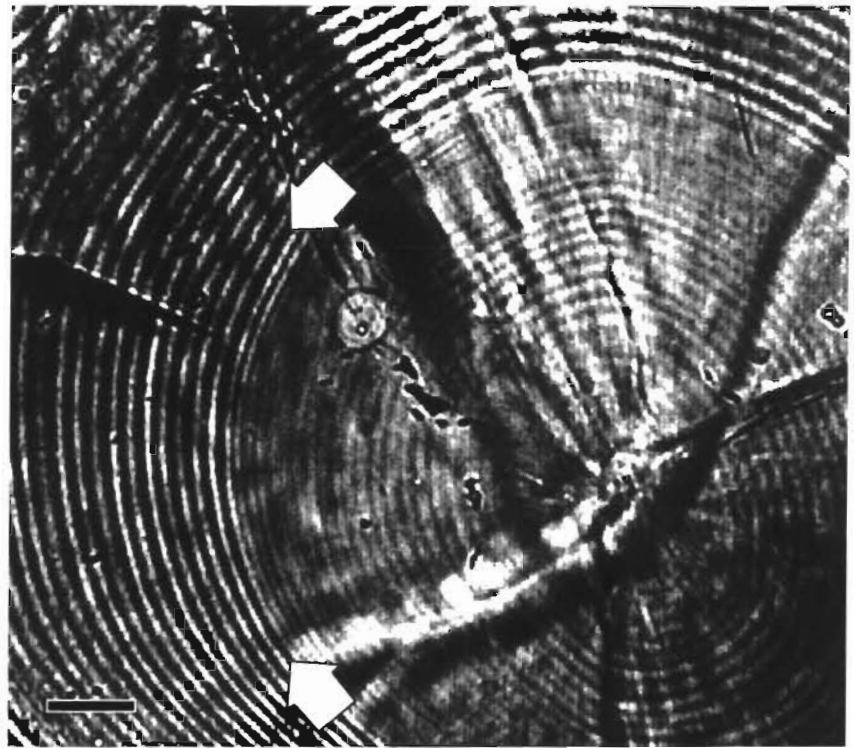


Fig. 5. *Bathygobius coalitus*. Transmitted light micrograph illustrating characteristics of the settlement mark (see arrows) in the sagitta from a 22.37 mm TL *B. coalitus*. Scale bar = 20 μ m

width and optical contrast of daily increments between wild and laboratory growth intervals illustrate the capability of *B. coalitus* otoliths to record significant shifts in environmental and metabolic conditions on a daily basis. Formation of daily increments in fish otoliths is likely an obligatory result of circadian-driven physiological control of plasma calcium levels and calcium uptake rates by otoliths (e.g., Mugiya et al. 1981, Mugiya 1987). Otoliths from fish as large as 70 mm TL (~307 d old, Shafer 1998) featured increments comparable in optical properties and widths to increments shown to be daily in experimental fish. *B. coalitus* is a relatively fast growing tropical reef fish with large, fast growing otoliths. Increments forming a continuous series in wild *B. coalitus* otoliths, accreted during early life history and comparable in width and optical properties to the daily increments observed in this study, are also likely to be daily.

Growth isometry

Accuracy of proportional back-calculation procedures depends on selection of representative measures of somatic and otolith growth and on the consistency of proportional scaling of somatic and otolith dimensions throughout targeted somatic and otolith size ranges (Campana 1990, Francis 1990). TL of *Bathygobius coalitus* was proportional to other measures of body length,

width, and depth, and proportional to sagitta radius for fish between 8 and 40 mm TL. For fish 8 to 40 mm TL, somatic-otolith scaling did not differ between sexually differentiated males and females, nor between fish collected during warm- or cold-water temperature seasons. Small shifts in scaling may begin to occur in *B. coalitus* as early as the onset of sexual maturity (~25 mm TL); however, second order terms were not significant in models of somatic-otolith scaling for fish 8 to 40 mm TL.

Curvilinear fits to somatic-otolith scaling for fish 8 to 70 mm TL resulted from declining otolith growth rate with respect to somatic growth rate in fish larger than about 46 mm TL. Directional changes in the postero-ventral growth axis probably contributed to measures of declining otolith growth rates, as daily increments became narrower or sometimes disappeared from view in areas adjacent to the main axis of otolith growth in fish larger than about 46 mm TL. Curvilinear somatic-otolith scaling in larger fish was also predominately associated with warmer SST. Warmer SST typically results in faster somatic growth rates in *Bathygobius coalitus* (Shafer 1998), which may not be accompanied by proportionally faster otolith growth rates in larger fish.

Allometry in somatic-otolith scaling due to growth effects has been well documented for other fishes, where faster growing individuals tend to have disproportionately smaller otoliths than equal-sized, slower

growing individuals (Templeman & Squires 1956, Boehlert 1985, Neilson et al. 1985, Mosegaard et al. 1988, Reznick et al. 1989, Secor & Dean 1989, Secor et al. 1989, Hovencamp 1990, Francis et al. 1993, Hare & Cowen 1995, Gleason & Bengtson 1996). Growth effects (Secor & Dean 1992) on somatic-otolith scaling may result from the conservative nature of daily increment formation, resulting in continuous otolith growth irrespective of somatic growth (Jones & Brothers 1987). This study found no evidence for a growth effect on somatic-otolith scaling in *Bathygobius coalitus*. Negligible growth effects on somatic-otolith scaling have also been reported for bloater (Rice et al. 1985) and chinook salmon (Neilson & Geen 1982).

Proportional somatic-otolith scaling for *Bathygobius coalitus* between 8 and 40 mm TL supports reconstruction of post-settlement size-at-age using a simple back-calculation model (e.g., the Dahl-Lea equation, see 'Methods') for fish smaller than 40 mm TL. Back-calculation of size-at-age for fish larger than 40 mm TL requires a more complicated model (e.g., Laidig et al. 1991) to accommodate for curvilinearity in somatic-otolith scaling. Curvilinear proportional back-calculation techniques rely on the assumption that individual inflection points in curvilinear somatic-otolith scaling occur at the same otolith or somatic size (e.g., Campana & Jones 1992). Because ontogenetic shifts in post-settlement somatic-otolith scaling probably occur at variable sizes and ages in *B. coalitus*, estimates of size-at-age derived from curvilinear proportional back-calculation models may contain significant error.

A more refined understanding of somatic-otolith scaling may lead to improved accuracy in species-specific back-calculation methods. This investigation relied on analysis of composite somatic-otolith scaling for various groupings of individuals, with different individuals representing positions along a 'generalized' life history continuum. Such cross-sectional treatment of somatic-otolith scaling aggregates information at a level higher than the individual, and limits resolution of subtle scaling dynamics in the individual. In contrast, longitudinal investigation of somatic-otolith scaling can provide resolution of dynamics at the level of the individual (see arguments for longitudinal analyses in studies of growth, Chambers & Miller 1995; and somatic-otolith scaling, Hare & Cowen 1995), and will lead to more accurate individual-based proportional back-calculation models.

Back-calculation techniques may also be improved by careful selection of representative measures of somatic and otolith growth. Measures of somatic and otolith growth should be chosen to optimize the strength of their correlation. Among measurements of somatic growth considered in this study, TL and SL were most highly correlated with sagitta radius; how-

ever, length may not always provide the best correlation with otolith size. For example, in bluefish *Pomatomus saltatrix*, body area was most highly correlated with otolith radius (Hare & Cowen 1995). Furthermore, measurements of otolith size should be defined for an otolith growth axis that is least biased by ontogenetic changes in shape. For example, many studies have measured otolith size as the longest otolith diameter (Rice et al. 1985, Gleason & Bengtson 1996) or reported otolith size as the average of left and right sagitta diameters (Reznick et al. 1989). Because sagittae are rarely perfectly round, averaged measurements of sagitta diameter (e.g., Reznick et al. 1989) may result in a 2-dimensional convolution of otolith growth, which may not be an appropriate measure to compare with a linear measure of somatic growth (i.e., SL or TL).

Settlement mark

A settlement mark, clearly identifiable as a distinct and abrupt shift in optical focal plane, contrast, and width of daily increments, was a consistent feature in sagittae of all metamorphosed fish. Because no settlement marks were visible in otoliths of metamorphosing basalt gobies, and because settlement is probably a rapid (i.e., < 1 d) event for *Bathygobius coalitus*, the settlement mark probably formed some time between settlement and the first day of post-settlement. Most likely, the settlement mark was present at the growing otolith margin of metamorphosing fish at settlement, but its presence could not be discerned without a contrasting optical reference provided by further otolith accretion (e.g., Brothers et al. 1983, Fowler 1989).

Changes in growth, physiology, metabolism, and environment during metamorphosis and settlement all likely contribute to changes in regular otolith accretion (Mugiya et al. 1981, Gauldie et al. 1995), resulting in the formation of a settlement mark (e.g., Gauldie 1988). At the end of larval life, transparent/silver *Bathygobius* spp. larvae undergo a series of morphological changes, including development of darker pigmentation more suited to camouflage on benthic substrates, and increases in density due to bone ossification, scale formation, and loss of the larval swim bladder, resulting in negative buoyancy (Tavolga 1950, Peters 1983). In addition, abrupt shifts in water temperature and chemistry, and in abundance and type of prey items occur during settlement in the shallow nearshore benthic habitat. Changes in skull shape during metamorphosis (e.g., for *B. soporator*, Peters 1983) and in hearing requirements (direction of sound source, etc.) during settlement may also be accompanied by ontogenetic changes in the functional design of *B. coalitus* otoliths. Small shifts in growth axes, effecting changes in otolith

shape, may further contribute to the observed contrast between pre- and post-settlement otolith structure.

Settlement marks occur in the otoliths of a variety of fishes, including both amphidromous (*Stenogobius hawaiiensis*, *Awaous guamensis*, Radtke et al. 1988) and marine (*Coryphopterus glaucofraenum* and *Gnatholepis thompsoni*, Sponaugle & Cowen 1994) gobies. They occur with a broad range in width and distinctiveness among various fishes, which may result from phylogenetic, biological, or environmental factors (Brothers & McFarland 1981, Victor 1983, Radtke et al. 1988, Fowler 1989, Sponaugle & Cowen 1994, Wilson & McCormick 1997, 1999). Wilson & McCormick (1999) classified settlement marks of tropical reef fishes into 3 categories: Type I shows abrupt marks characterized by a rapid decrease in increment width over settlement; Type II, zonal marks characterized by a band of increments that are wider than pre-settlement increments; and Type III, gradual marks characterized by a gradual decrease in increment width during settlement. Settlement marks from all species examined in their study plus those described in the literature could be classified according to their system, with 2 exceptions: the Caribbean gobies *Gnatholepis thompsoni* and *Coryphopterus glaucofraenum* (Sponaugle & Cowen 1994). Otoliths from these gobies demonstrated abrupt settlement marks with narrower pre-settlement increments, followed by wider post-settlement increments. The present study provides further evidence for the existence of a fourth type of settlement mark, also demonstrated by a marine goby.

For most reef fishes examined to date (see Wilson & McCormick 1999), daily increments immediately following the settlement mark are generally narrower than those preceding it, which is the converse of the pattern found for *Bathygobius coalitus*. Slower post-settlement growth rates in other species were suggested to result from energy conservation or poor energy acquisition during early post-settlement life history (Wilson & McCormick 1999). Immediately following settlement of *B. coalitus*, the somatic growth rate (and increment widths) may increase due to changes in food availability in the benthos and higher intertidal temperatures (Shafer 1998). Somatic-otolith scaling for larval *B. coalitus* and the effects of metamorphosis and settlement on otolith growth are unknown, however, and comparative changes in increment widths across the settlement mark may not translate into equivalent changes in somatic growth.

High abundance and widespread distribution of the basalt goby along Hawaii's coastlines suggest that it may be important to the ecology of nearshore marine ecosystems. This study confirms that the regular and aperiodic structure of *Bathygobius coalitus* otoliths preserves a rich chronology of fish age, size, and

growth rates during early life history. Robust daily increment formation provides a valid basis to determine age and growth at capture and to reconstruct chronological and calendar references to early life history events, including hatch and settlement dates. Proportional somatic-otolith scaling in *B. coalitus* smaller than 40 mm TL forms a reliable basis for back-calculation of somatic sizes from otolith radii, and consistent formation of a settlement mark in otoliths provides a permanent chronological reference for settlement. Retrospective analyses of the dynamics and interactions among variable growth rates, larval duration, size at settlement, and environmental conditions will provide important insight into recruitment, survival to maturity, and, ultimately, the ecology of the basalt goby.

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