

Elemental Patterns in Red Hind (*Epinephelus guttatus*) Otoliths from Bermuda and Puerto Rico Reflect Growth Rate, Not Temperature

Yvonne Sadovy^{1,2}

Fisheries Research Laboratory, P.O. Box 3665, Mayagüez, PR 00708

and Kenneth P. Severin³

Department of Geology and Geophysics, Box 755780, University of Alaska Fairbanks, Fairbanks, AK 99775-5780, USA

Sadovy, Y., and K.P. Severin. 1994. Elemental patterns in red hind (*Epinephelus guttatus*) otoliths from Bermuda and Puerto Rico reflect growth rate, not temperature. *Can. J. Fish. Aquat. Sci.* 51: 133-141.

Sodium, sulfur, calcium, and strontium concentrations were measured (with an electron microprobe) across sectioned wild red hind (*Epinephelus guttatus*) otoliths from Puerto Rico and Bermuda. A single inverse relationship between strontium/calcium (Sr/Ca) ratios and log body growth rate describes the data from both localities. Patterns in Sr/Ca ratios have been used to infer temperature histories of individual fish; our data indicate that there is not a single Sr/Ca-temperature relationship capable of yielding a plausible temperature history across a single otolith, nor is there one that could give reasonable temperature histories for both the Puerto Rico and Bermuda otoliths. Previous findings of Sr/Ca-temperature relationships could be the result of body growth rate being correlated with temperature.

Des chercheurs ont mesuré (au moyen d'une sonde électronique) les concentrations de sodium, de soufre, de calcium et de strontium dans des coupes transversales d'otolithes de mérou couronné sauvage (*Epinephelus guttatus*) de Puerto Rico et des Bermudes. Une relation inverse simple entre les rapports strontium/calcium (Sr/Ca) et le logarithme du taux de croissance corporelle décrit les données recueillies aux deux endroits. Les profils des rapports Sr/Ca ont été utilisés pour établir les antécédents thermiques dans la vie de chaque poisson; d'après les données que nous avons obtenues, il n'existe pas de rapport unique entre Sr/Ca et la température permettant d'établir des antécédents thermiques plausibles à partir de la coupe transversale d'un seul otolithe, ni même un seul rapport qui peut donner des données thermiques raisonnables pour les otolithes de poissons provenant de Puerto Rico et des Bermudes. Des résultats antérieurs sur le rapport entre Sr/Ca et la température pourraient être le résultat d'une corrélation entre le taux de croissance corporelle et la température.

Received February 20, 1992

Accepted July 29, 1993

(JB414)

Reçu le 20 février 1992

Accepté le 29 juillet 1993

Optical and chemical patterns in aragonitic otoliths are commonly used to age fish and have also been used to infer external environmental parameters, events, or changes in internal metabolism (Pannella 1980; Casselman 1982; Victor 1982; Brothers 1987; Radtke 1988; Kalish 1989, 1990). In corals and molluscs, strontium levels in inorganically precipitated aragonite are inversely related to temperature (Smith et al. 1979; Schneider and Smith 1982) and this relationship has likewise been suggested for the otoliths of fishes (Radtke and Targett 1984; Radtke 1987, 1989; Townsend et al. 1989). In an earlier study (Sadovy and Severin 1992), we found that strontium/calcium (Sr/Ca) ratios could not be used to infer environmental temperatures for white grunt (*Haemulon plumieri*) (Pisces: Haemulidae) taken from two areas with different temperature regimes, Puerto Rico in the Caribbean and the Carolinas on the east coast of the United States. However, a single relationship could describe Sr/Ca ratios and growth rate, as determined

by growth in length, for individuals from both locations, even though von Bertalanffy growth parameters (K and L_{∞}) (von Bertalanffy 1938) differed markedly between the two areas.

In the present study, we examine the relationships between Sr/Ca ratios, temperature, and somatic growth for two populations of the red hind (*Epinephelus guttatus*) (Pisces: Serranidae). Our aim is to test whether a Sr/Ca - growth rate relationship applies to this species, as it did to the unrelated white grunt, indicating that this relationship might apply more widely in the teleosts. We compared the hypotheses of temperature versus somatic growth determination of Sr/Ca ratios by examining the sagittal otoliths of two populations of wild red hind, one taken from Puerto Rico and the other from Bermuda. As a measure of somatic growth, we used mean annual growth rates in length calculated for each age class from individual growth curves.

Materials and Methods

Fish

Otoliths assessed for strontium and calcium abundance were taken from fish collected from western Puerto Rico,

¹Order of authorship is alphabetical, no seniority is implied.

²Present address: Department of Zoology, University of Hong Kong, Pok Fu Lam Road, Hong Kong.

³Author to whom correspondence should be addressed.

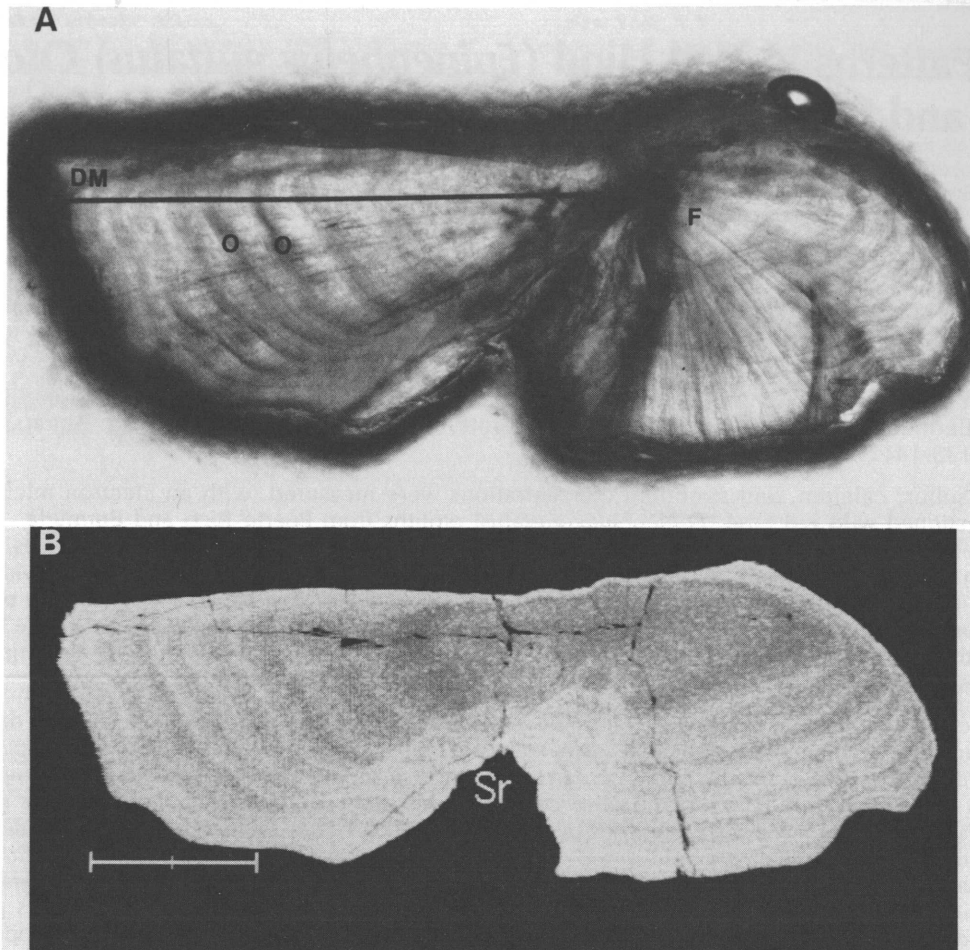


FIG. 1. Light photograph and X-ray map of an otolith section from red hind from Puerto Rico. Scale bar = 1 mm. Pixels are $10 \times 10 \mu\text{m}$. (A) Viewed under transmitted light showing focus (F), otolith dorsal margin (DM), and opaque zones (O); the line indicates the position of the microprobe traverse. (B) X-ray map; the bright areas indicate the highest concentrations of strontium.

by hook-and-line and fish trap, between June 17 and 23, 1988. Red hind from Puerto Rico selected for the present study measured between 201 and 314 mm fork length (FL) and were aged between 1 and 6 yr ($N = 10$). Otoliths from Bermuda were obtained from fish collected by hook-and-line and fish trap between August 6, 1972, and May 12, 1974 (Burnett-Herkes 1975). Fish from Bermuda measured 395–425 mm FL and were aged 7 yr ($N = 4$).

Otoliths for quantitative analyses were selected on the basis of their optical legibility following sectioning and to ensure inclusion of a wide size and age range of fish. The otoliths had initially been collected for age and growth work according to which growth parameters were similar for both populations (Burnett-Herkes 1975; Sadovy et al. 1992).

Temperature

Temperature data from surface waters and at depth are available from both Puerto Rico and Bermuda. Those for Puerto Rico indicate a range of 25–30°C at 2 m depth (Department of Marine Sciences, University of Puerto Rico) and 25–29°C at 18 m depth (P.L. Colin, Chuuk Atoll Research Laboratory, P.O. Box 70, Weno, Chuuk State, Federated States of Micronesia, 96942, personal communica-

tion). For Bermuda, the annual temperature range is 17–28°C for surface waters and 17–27°C at 25 m depth (Burnett-Herkes 1975).

Growth Rate Determination

To calculate growth rates from otoliths, sagittae were removed, washed, sectioned dorsoventrally to 0.36–0.43 mm, and mounted on glass slides. Size-at-age for each fish was determined using a back-calculation formula that allowed estimation of body length at the time of initiation of the formation of each opaque zone appearing in sample otoliths, i.e., at the proximal margin of each opaque zone along a scan line running from the focus to the dorsal margin (Fig. 1 and 2). Using the calculated size-at-age data, growth curves were constructed for each individual. The mean annual growth rate at each opaque zone was determined from the growth curves by calculating the tangent to the curve at each opaque zone. These calculated growth rates provided a single estimate of mean annual growth rate (millimetres per year) for each individual at each opaque zone which could be associated with Sr/Ca ratios measured within the corresponding opaque zone (arrows, Fig. 3 and 4).

The Lee proportional back-calculation formula was used

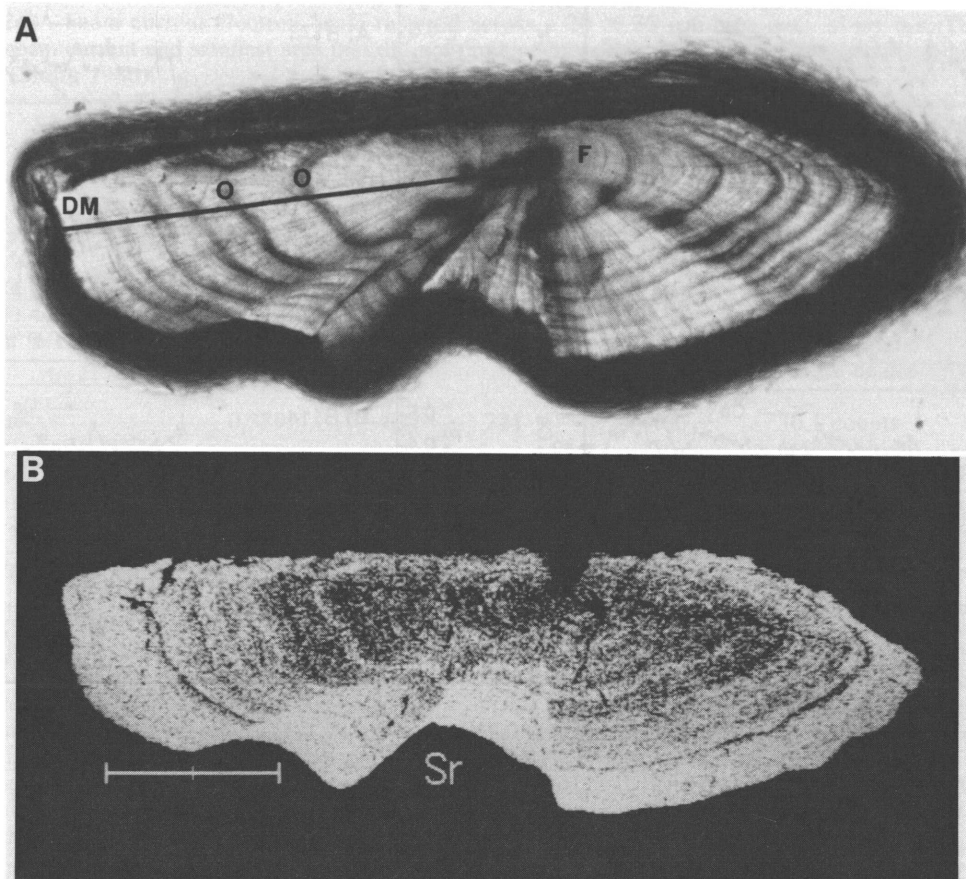


FIG. 2. Light photograph and X-ray map of an otolith section from red hind from Bermuda. Scale bar = 1 mm. Pixels are $10 \times 10 \mu\text{m}$. (A) Viewed under transmitted light showing focus (F), otolith dorsal margin (DM), and opaque zones (O); the line indicates the position of the microprobe traverse. (B) X-ray map; the bright areas indicate the highest concentrations of strontium.

for back-calculation of length-at-age (Carlander 1981). This equation requires knowledge of the relationship between otolith radius (OR) and FL in otoliths taken at the same time and location as individuals for which individual growth curves are calculated. For details of otolith preparation and analysis, see Sadovy et al. (1992). For Puerto Rico the FL/OR relationship was (Sadovy et al. 1992)

$$\text{FL} = 33.218 + 3.0743 \text{ OR}; N = 624; r^2 = 0.76$$

and for Bermuda the relationship was

$$\text{FL} = 64.43 + 2.95 \text{ OR}; N = 44; r^2 = 0.79$$

where FL is in millimetres and OR is in micrometre units (32 units = 1 mm).

Growth parameters for the populations from the two locations are similar as described by the von Bertalanffy growth function (von Bertalanffy 1938). For Puerto Rico, L_∞ (asymptotic length) = 515 mm FL and K (Brody growth coefficient, Ricker 1975) = 0.101 (Sadovy et al. 1992), as determined by otoliths. For Bermuda, L_∞ = 505 mm FL and K = 0.180 (Burnett-Herkes 1975) as determined by length-frequency data corroborated by otolith ring counts.

Otolith band pairs (one opaque + one translucent zone as viewed under transmitted light) 1–10 have been validated as annual for fish from Puerto Rico by marginal increment analysis and also in a field study using injected oxytetracycline as a time marker (Sadovy et al. 1992). The tempo-

ral nature of the band pairs has not been validated for Bermuda but is assumed to be the same as for Puerto Rico.

Because of problems inherent in back-calculation manipulations (Campana 1990), the relationship between Sr/Ca and age, which is independent of otolith measurements and back-calculation, was also determined. Analyses were not made by sex because the red hind is a protogynous hermaphrodite with many individuals functioning as both female and male in their lifetime: sexual maturation occurs between 2 and 3 yr (Sadovy et al. 1992).

Microprobe Analyses

Sagittal otoliths were sectioned transversely (dorsoventral) with a slow-speed saw. Sections were then mounted on glass slides with thermo-epoxy (Petropoxy 154, Palouse Petro Products, Palouse, Wash., USA), ground on a diamond lap wheel until the focus was exposed, and then polished flat with 0.05- μm alumina on silk. All samples were coated with approximately 25 nm of carbon before examination with the Cameca SX-50 microprobe at the Department of Geology, University of Puerto Rico, Mayagüez (one energy dispersive and three wavelength dispersive spectrometers). Investigations of wavelength spectral scans revealed no elements (atomic number >10) other than sodium, sulfur, calcium, and strontium in enough abundance (greater than about 0.1 weight %) to be analyzed quantitatively.

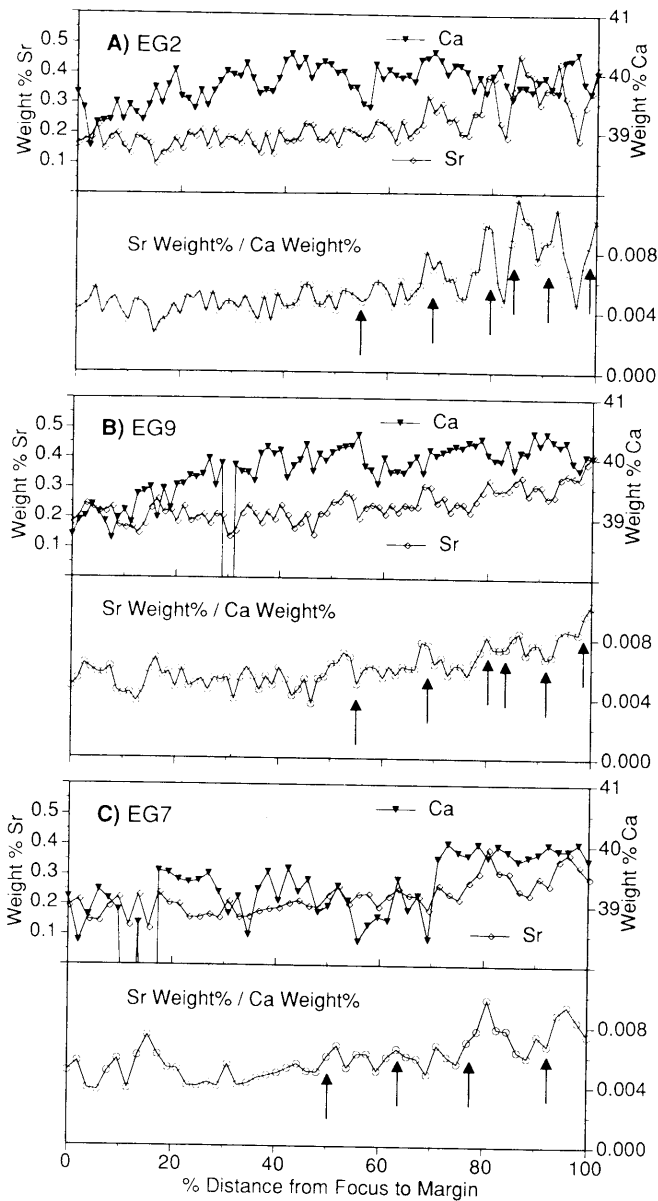


FIG. 3. Elemental concentrations across sectioned otoliths of Puerto Rico fish. Arrows indicate points at initiation of opaque zones, i.e., proximal margins, and associated Sr/Ca values used in the analyses. (A) EG2, caught June 23, 1988, FL = 277 mm, male, 6 yr old; (B) EG9, June 23, 1988, FL = 305 mm, male, 6 yr old; (C) EG7, June 23, 1988, FL = 278 mm, sexually transitional, 4 yr old.

Patterns in strontium and calcium abundance were measured along a traverse from the otolith focus to the otolith margin (Fig. 1A). Analytical conditions and precision for the calcium and strontium measurements reported here are summarized in Table 1. Digital X-ray maps of sectioned otoliths were produced on the Cameca SX-50 at the Laboratory for Microbeam Analysis, University of Alaska Fairbanks (one energy dispersive and four wavelength dispersive spectrometers). Detailed discussion of the acquisition and processing of X-ray maps may be found in Goldstein et al. (1992).

Measured variability in trace element abundance across a single otolith results from several factors. Some arise because of errors inherent in the microprobe's ability to

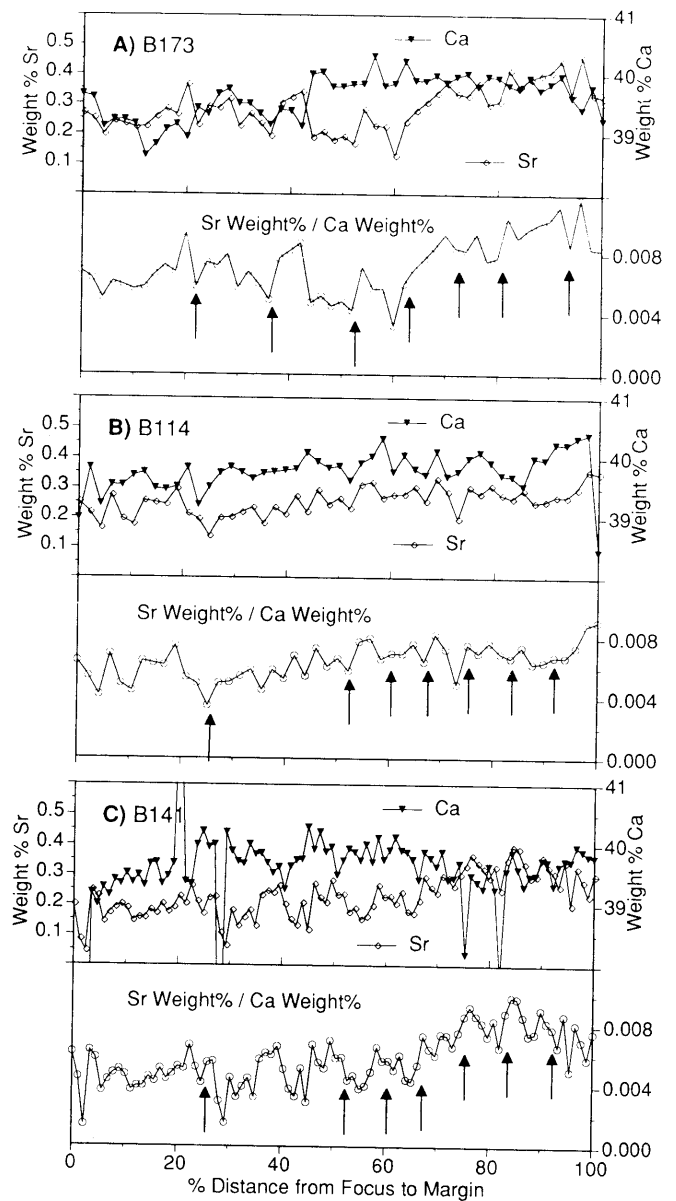


FIG. 4. Elemental concentrations across sectioned otoliths of Bermuda fish. Arrows indicate points at initiation of opaque zones, i.e., proximal margins, and associated Sr/Ca values used in the analyses. (A) B173, caught May 6, 1973, FL = 345 mm, female, 7 yr old; (B) B114, August 6, 1972, FL = 295 mm, sex unknown, 7 yr old; (C) B141, October 10, 1972, FL = 336 mm, sex unknown, 7 yr old.

detect low levels of trace elements, particularly when analyzing carbonates. Carbonates are sensitive to thermal decomposition caused during the electron beam/sample interaction (Smith 1986), and the usual techniques of increased beam current or increased counting times cannot be applied. Gunn et al. (1992) discussed various electron microprobe operating parameters as they pertain to otolith analysis.

We chose to use Sr/Ca ratios to compare with growth rate data because electron microprobe analyses of otoliths for strontium and calcium (and other minor cations) do not directly yield otolin concentrations (the organic matrix of otoliths, see Morales-Nin 1987 for summary). Otolin concentrations can only be estimated by assuming that the measured cations are contained in the aragonite and stoichio-

TABLE 1. Analytical conditions, standards, and relative errors due to counting. Data were collected with a 15-kV, 2-nA beam current electron beam rastered across a $20 \times 35 \mu\text{m}$ area once every 6 s. This was the highest beam current and smallest area that did not produce measurable thermal decomposition of the aragonitic otoliths (Smith 1986).

Element and standard	Weight %	Peak counts	Background counts	Net counts	σ_{net}^a	Relative precision, weight % (1σ) ^b
Calcium ^c	40.033	81 053	275	83 959	290.7 counts 0.35% of net	0.139
Calcite (USNM 13621) 40.09 weight % Ca	38.382	84 234	275	80 778	285.2 counts 0.35% of net	0.135
Strontium ^d	0.389	687	221	466	30.1 counts 6.47% of net	0.025
Strontianite (USNM R10065) 55.20 weight % Sr	0.156	446	258	188	26.5 counts 14.11% of net	0.022

^aStandard deviation due to counting statistics (σ_{net}) is calculated from $\sigma_{\text{net}} = (\sigma_{\text{peak}}^2 + \sigma_{\text{background}}^2)^{1/2}$. Because σ_{peak}^2 or $\sigma_{\text{background}}^2$ = the number of counts recorded for the peak or background, $\sigma_{\text{net}} = (N_{\text{peak}} + N_{\text{background}})^{1/2}$.

^b σ_{net} can be divided into the net number of counts to obtain a relative standard deviation. Data (from a traverse across EG7, June 23) for high and low concentrations are presented because relative precision is a function of elemental concentration. See Williams (1987) for more discussion of precision and accuracy of X-ray analyses.

^cCalcium K α X-rays were measured with a Kevex 8000 energy dispersive spectrometer. X-rays were collected for 100 s (live time); the peak was deconvoluted and quantified with Kevex-Quantex software.

^dStrontium L α X-rays were measured with a wavelength dispersive spectrometer (TAP crystal). X-rays were counted for 100 s at the emission peak, and the background was determined for a total of 100 s, 50 s on either side of the peak.

metrically estimating the amount of otolin. Implicit in this method is the assumption that the otolin does not contain significant amounts of cations. Under this assumption, Sr/Ca ratios are independent of the otolin/aragonite ratio and are measures of the relative amounts of strontium and calcium in the aragonite. If absolute strontium abundances were used, then it would not be possible to differentiate between analyses that yielded, for example, 1% strontium, 35% calcium, 5% otolin and 1% strontium, 40% calcium, 0% otolin.

Spatial resolution of trace element abundances across an otolith remains constant, but temporal resolution does not because otoliths do not grow at a constant rate. In the case of red hind, the analyzed area ($20 \times 35 \mu\text{m}$) spans about a 2-wk time period in the juvenile portion of an otolith and individual analyses are separated by approximately 1-mo intervals. In the adult portion of an otolith, because of slower otolith growth, each analyzed area covers about 1 mo and analyses are separated by approximately 2 mo. Thus, variability detected in the proximal, younger portions of otolith scans reflects a shorter time span than variability in more distal regions; the two should be compared with caution. Short-term growth rate fluctuations below the level of resolution of individual microprobe measurements could obscure Sr/Ca – growth relationships.

Results

General Distribution of Elements

The patterns of elemental abundance from the focus to the dorsal margin of sectioned otoliths of red hind from both locations approximated the optical banding pattern as viewed under transmitted light (compare Fig. 1A and 1B,

2A and 2B). Visual inspection indicated that concordance between optical bands and patterns of elemental abundance was closer in some otoliths (Fig. 3A, 3C, and 4A) than in others (Fig. 3B, 4B, and 4C). Strontium maxima and calcium minima coincided approximately with opaque zones (Fig. 3 and 4; arrows indicate the proximal border of successive opaque zones).

Relationship between Sr/Ca Ratios and Temperature

Several studies have suggested an inverse relationship between Sr/Ca ratios and temperature in fish otoliths. If this type of relationship exists for the red hind, then Sr/Ca maxima should represent times of temperature minima and vice versa. Interpreting our data under this hypothesis, the Sr/Ca ratios across otoliths of fish from Puerto Rico (Fig. 3 and 5) suggest that the fish spent the early portions of their lives (until about 1 yr old) in relatively warm water (compared with the rest of the life cycle) and then moved between, or encountered in their areas of residence, cycles of cold and warm water, with a net shift into cooler water with increasing age. While it is true that red hind juveniles generally settle inshore and move progressively offshore as they grow, large individuals are frequently found inshore and small individuals occur in deeper water (Burnett-Herkes 1975; Y. Sadovy, personal observation).

A similar interpretation is valid for Bermuda fish (Fig. 4), with the exception that they did not experience the same annual temperature extremes during their adult lives as the Puerto Rico fish. Furthermore, because the range of Sr/Ca ratios in otolith sections is similar in both locations (0.002–0.010), we would conclude that the annual temperature range in both locations is similar. Instead, the tem-

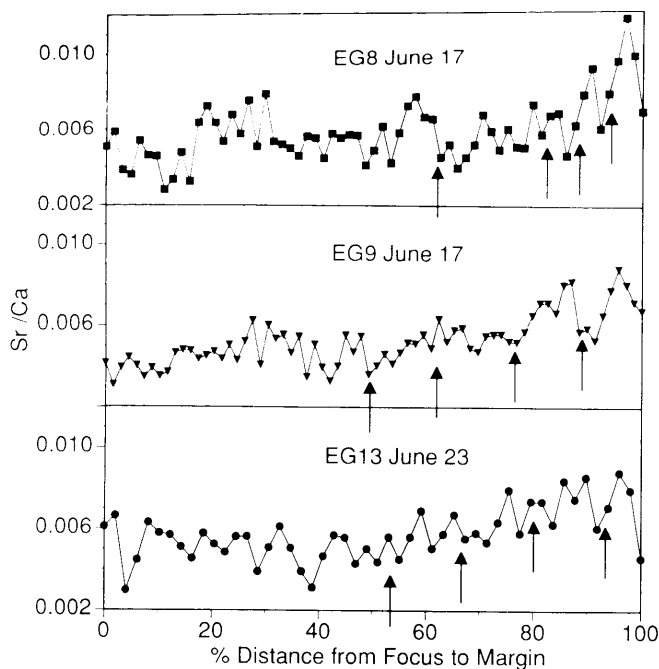


FIG. 5. Comparison of Sr/Ca ratios across EG8 (June 17, FL = 225 mm), EG9 (June 17, FL = 261 mm), and EG13 (June 23, FL = 235 mm), all 4-yr-old females taken in 1988. Although these individuals were caught within 1 wk of each other in the same location, the patterns of the Sr/Ca ratios differ.

perature range for the Puerto Rico fish is about 5°C and the range for the Bermuda fish is twice that, about 10°C.

A comparison of Sr/Ca ratios across the otoliths of similarly aged (4 yr old) individuals in Puerto Rico, collected from the same area at the same time, showed markedly different patterns (Fig. 5). If the Sr/Ca ratios were controlled by a single physical factor, such as temperature, then the Sr/Ca ratios in all these individuals should be similar. The fact that they differ indicates either that individual life-history temperature profiles vary substantially, which seems unlikely, or that temperature was not the principle factor determining Sr/Ca ratios.

Sr/Ca ratios at otolith margins showed no consistent pattern in either increase or decrease of Sr/Ca with season of capture. This observation was particularly striking in otoliths of Puerto Rico fish. First, Sr/Ca ratios at the otolith margins spanned much of the range seen across all the otoliths (0.004–0.010). Second, Fig. 3A and 3B show Sr/Ca ratios increasing at the margins of two fish captured on June 23, 1988, while in Fig. 3C and 5 they were decreasing at the margins of four fish caught at the same location between June 17 and 23, 1988. Again, based on the “temperature” hypothesis, we would conclude that two of these animals were experiencing decreasing temperatures at the time of capture, while four others were experiencing increasing temperatures. This interpretation is unlikely given that all fish were caught at the same location within 1 wk of each other.

Finally, if this hypothesized relationship holds, then Sr/Ca maxima should occur at the times of lowest temperature. However, despite some variability, strontium maxima were generally associated with opaque zones. In Puerto Rico, opaque zones in red hind otoliths are formed in the spring and summer (Sadovy et al. 1992), when water temperatures

are either rising or are at their annual maximum (Sadovy and Severin 1992). Sr/Ca maxima were thus more directly associated with high or rising, rather than low, environmental temperatures. While it is, perhaps, tempting to invoke some sort of time lag to make the Sr/Ca maxima match temperature minima, any such lag requires the abandonment of the inorganic precipitation model for this system. Moreover, opaque zone formation tends to occur earlier in the year in younger than in older fish (Sadovy et al. 1992). A similar intraspecific temporal variation in opaque zone formation has been reported in other species (Moe 1969; Casselman 1974). Such temporal variation is inconsistent with a single principal environmental variable being the major causative agent of opaque zone formation and associated high Sr/Ca ratios in red hind. Moe (1969) proposed that the different timing of annulus formation in older age groups in red grouper (*Epinephelus morio*) probably reflects a slower metabolic rate and a shorter annual growth period compared with younger age groups.

There does not appear to be a single, simple relationship consistent with an inverse Sr/Ca ratio – temperature correlation in the red hind, either for individuals from two different geographic locations or within a single location.

Relationship between Sr/Ca Ratios and Age

An ANCOVA showed that location ($F_{1,68} = 14.44$, $p = 0.0003$, $N = 71$) and age, as estimated by opaque zones ($F_{1,68} = 47.07$, $p = 0.0001$, $N = 71$), are significant predictors of Sr/Ca ratios and that the regressions between age and Sr/Ca values at the two localities are indistinguishable ($F_{1,67} = 0.59$, $p = 0.4437$, $N = 71$). The significance of location in predicting Sr/Ca ratios is probably due to the different-aged samples from the two localities, as indicated by location being not significant ($F_{1,68} = 1.19$, $p = 0.2802$, $N = 71$) when the age–location interaction term is included in the model. The regression of age and Sr/Ca ratios for the combined localities is

$$\text{Sr/Ca} = -0.000495 \text{ age} + 0.005101; F_{1,69} = 30.522; \\ p = 0.0001; N = 55; r^2 = 0.30.$$

Relationship between Sr/Ca Ratios and Growth Rate

Because of difficulties in the optical resolution of growth zones near the otolith margin of older fish, and in distinguishing the proximal margin of the innermost zone, only growth rates from opaque zones distal to the innermost zone and growth rates greater than 10 mm/band pair annually were used in the analyses. Sr/Ca ratios at each opaque zone were plotted against the back-calculated average annual growth rate for the age class designated by that zone. Inspection of the data suggested that relationships between growth rates and Sr/Ca ratios were best described by log-transforming the growth rate data.

The Sr/Ca values used were those that were optically determined to be at the proximal edge of each opaque zone (values indicated by arrows in Fig. 3, 4 and 5). The regression of log growth rate and Sr/Ca ratios was significant for fish from both Puerto Rico ($F_{1,30} = 9.74$; $p = 0.0040$; $N = 32$; $r^2 = 0.22$) and Bermuda ($F_{1,21} = 6.85$; $p = 0.0161$; $N = 23$; $r^2 = 0.21$) fish. An ANCOVA showed that location was not significant in predicting Sr/Ca ratios ($F_{1,21} = 1.98$; $p = 0.166$), that log growth rate was significant ($F_{1,52} = 16.78$; $p =$

0.0001), and that the regressions between Sr/Ca ratios and log growth rate at the two locations (interaction) were not distinguishable ($F_{1,51} = 0.10$; $p = 0.751$). The regression of log growth rate and Sr/Ca ratios for the combined localities is

$$\text{Sr/Ca} = -0.001856 \ln(\text{GR}) + 0.012933; F_{1,53} = 16.485; \\ p = 0.0001; N = 55; r^2 = 0.24.$$

Figure 6 shows the relationships between Sr/Ca and growth rate in fish from both locations separately and then combined. The three regressions do not differ substantially, and any one of them could be used to describe the data, again suggesting that a single relationship exists between growth rate and Sr/Ca ratios for fish from geographically separate locations.

Discussion

The patterns of strontium abundance and Sr/Ca ratios across sectioned otoliths of wild red hind from Bermuda and Puerto Rico do not support the hypothesis that a simple inverse relationship exists between Sr/Ca ratios and temperature. On the other hand, similar significant relationships between log body growth rate and Sr/Ca ratios were found for red hind from both Puerto Rico and Bermuda. The significant relationship between Sr/Ca ratio and age for both Puerto Rico and Bermuda is consistent with a Sr/Ca ratio – growth rate hypothesis and inconsistent with one invoking temperature because age and growth rate are related, while age and temperature are not. A direct Sr/Ca–age relationship would not account for results of other workers, however, nor for the interindividual variabilities in Sr/Ca ratios-at-age described in this study.

Although salinity has been implicated in affecting the Sr/Ca ratios in otoliths (Radtko et al. 1988), the red hind is a marine species characteristically found in offshore and reef habitats. Because red hind spend their entire life in well-mixed marine waters, there is no reason to expect that the populations in Puerto Rico and Bermuda experience different salinities or seawater strontium concentrations during their lives (Culkin and Cox 1966; Brass and Turekian 1972).

A Sr/Ca – growth rate relationship is a consistent alternative explanation for all other published experimental results on Sr/Ca ratios in fish otoliths for which a temperature relationship has been proposed, with the exception of one, the Hawaiian snapper (*Pristipomoides filamentosus*) (Radtko 1987), where Sr/Ca values decrease during the life of the fish. Kalish (1989) reported a significant relationship between Sr/Ca and age in blue grenadier (*Macruronus novaezealandiae*) and proposed that seasonal variations in otolith chemistry in both wild blue grenadier and Australian salmon (*Arripis trutta*) are partly due to seasonal changes in growth rates and/or reproductive investment. He found no Sr/Ca–temperature relationship for either species. In the bearded rock cod (*Pseudophycis barbatus*), Kalish (1991) found significant seasonal variation in otolith Sr/Ca ratios and was able to explain 52% of the Sr/Ca variability in male and female otoliths by considering six factors, including fish weight and gonad weight, but not temperature.

While gross seasonal changes in growth rate over the annual cycle probably account for a significant proportion of the variation in Sr/Ca levels across otolith sections for Puerto Rico fish, irregularities and interindividual variations in the pattern of the microprobe traverses clearly show that other

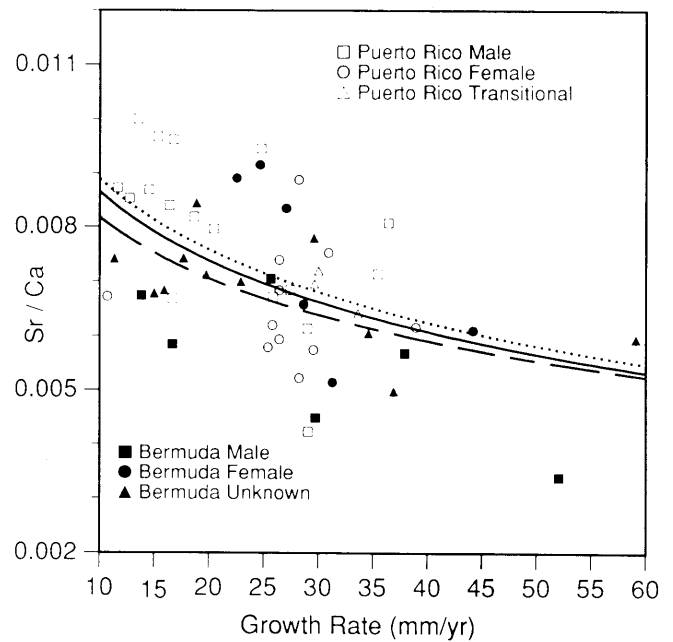


FIG. 6. Growth rate versus Sr/Ca ratios. The solid line is the regression based on data from Puerto Rico and Bermuda fish combined, the dotted line is based on data from Puerto Rico fish only, and the broken line is based on data from Bermuda fish only. The figured regressions describe the data equally well and suggest a significant relationship between log growth rate and Sr/Ca ratios.

factors are also involved. These factors include both errors associated with the measurement of Sr/Ca ratios (see section on Microprobe Analyses) and growth rates and irregular events that also impact growth. For example, Cailliet and Radtko (1987) attributed irregular fluctuations of calcium and phosphorus in the centra of gray reef sharks to life-history events such as temporarily decreased food supply, temperature changes, metabolic pauses, or injury-related phenomena.

The high variability of growth rate-at-age between individuals from a single location indicates that growth rate is influenced by many factors. Moreover, because data were analyzed for growth-in-length, rather than growth-in-weight, as an indicator of somatic growth, weight changes in larger fish are likely to be grossly underrepresented and may be considerable due to weight fluctuations caused by variations in food availability or reproductive condition (Moreau 1987). The most likely factors to influence growth rate in fish are food supply or rate of consumption, environmental temperature, ambient oxygen, salinity, reproductive activity, migrations, genetics, and age (Weatherley and Gill 1987). Reproductive activity is not likely to be a major cause of Sr/Ca variability in the red hind because there are no noticeable differences in Sr/Ca ratios for individuals in the male, versus the female, phase despite the fact that ripe ovaries attain four to five times the size of ripe testes. Moreover, despite the fact that the annual reproductive period is brief, lasting 2 mo at most, there is no discernible signal in Sr/Ca ratios that would suggest a direct correlation with such a well-defined period of spawning activity (Y. Sadovy, A. Rosario, and A. Román, unpublished data).

The results of the analyses of red hind otoliths from two geographic locations are similar to those for the white grunt

from Puerto Rico and the Carolinas (Sadovy and Severin 1992). The gradual rise and increasing variability in Sr/Ca ratios across otolith sections is similar to, although somewhat less extreme than, that observed in the white grunt in Puerto Rico, a fish that characteristically occupies a lesser maximum depth than the red hind (Sadovy and Severin 1992). In both studies, the Sr/Ca-temperature hypothesis was rejected, and a similarly significant relationship was found between Sr/Ca ratios and growth, with considerable variability still unexplained. For both species the overall form of the relationship for both geographic areas was similar. In Puerto Rico, Sr/Ca ratios in older white grunt showed markedly similar trends to those in the red hind but exhibited a more regular and marked oscillation than was observed for the red hind in this study, suggesting species-specific effects. For both species the elemental distribution patterns from the more northern locations were somewhat more irregular than for Puerto Rico. The reason(s) for these intra- and interspecific differences is not known.

If somatic growth proves to be a principal cause of Sr/Ca variation across fish otoliths, analysis of otolith Sr/Ca holds potential for understanding many aspects of life history that are virtually inaccessible using currently available methods. The possible role of the various factors likely to influence growth rate and, hence, Sr/Ca levels, would need to be examined by controlled laboratory experiments for all sizes, ages, seasons, and reproductive conditions to understand the extent of their effects on growth rate variation. It may be possible to estimate otolith Sr/Ca directly from living fish, as the Sr/Ca content of the saccular endolymph is reported to be linearly correlated with otolith Sr/Ca ratios (Kalish 1989). The effect of selecting different radii for traverses within otoliths should be evaluated (Gauldie and Nelson 1990), and any time lag involved between changes in growth rates and changes of otolith Sr/Ca ratios must be understood before these become the indicators they promise to be. Different measures of somatic growth would need to be evaluated.

Despite the possible value of Sr/Ca ratios in unraveling various aspects of life history, caution is needed in interpreting Sr/Ca ratios because of the many factors that may influence them (Kalish 1989, 1991). Indeed, since growth rate itself is often likely to be strongly temperature influenced, deconvolution of temperature and growth effects is particularly critical. However, if properly and carefully applied, Sr/Ca information eventually could become a valuable tool for refining our knowledge of growth history.

Acknowledgments

We thank R.S. Appeldoorn, P.L. Colin, M. Figuerola, C. Goenaga, G. Mitcheson, B.A.B. Severin, and V. Vicente for their assistance at various stages of this research. The comments of anonymous reviewers improved the presentation. The Department of Marine Sciences, University of Puerto Rico, provided access to daily water temperature records. Otolith samples in Puerto Rico were collected during an age and growth study funded by the Caribbean Fishery Management Council (NOAA). Special thanks go to J. Burnett-Herkes and J. Ward for providing otoliths from Bermuda.

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