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Use of otolith strontium:calcium ratios for hind-casting larval cod *Gadus morhua* distributions relative to water masses on Georges Bank

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ABSTRACT: The concentration ratios of strontium to calcium in laboratory-reared larval cod otoliths are shown to be related to the water temperature (T) at the time of otolith precipitation. This relationship is curvilinear, and is best described by a simple exponential equation of the form $(Sr/Ca \times 1000 = a \exp(-T/b)$. We show that when Sr/Ca elemental analyses are related to the daily growth increments in the larval otoliths, relative temperature histories of individual field-caught larvae can be reconstructed from the egg stage to the time of capture. We present preliminary examples of how such reconstructed temperature histories of Atlantic cod *Gadus morhua* larvae, collected on Georges Bank during April and May 1993, may be interpreted in relation to the broad-scale larval distributions and the hydrography of the Bank.

KEY WORDS: Cod · *Gadus morhua* · Georges Bank · Otolith · Sr/Ca ratios · Hydrography · Temperature histories

INTRODUCTION

Concentration ratios of strontium to calcium in some fish otoliths have been shown to be functionally related to the water temperature at the time of otolith precipitation (Radtke 1984, 1989, Radtke & Targett 1984, Townsend et al. 1989, 1992, Radtke et al. 1990). This is an important structural characteristic that, when coupled with daily otolith aging techniques, gives researchers the potential of using the otolith as an environmental chronometer of an individual fish's life history (e.g. Townsend et al. 1989). The Sr:Ca ratio thermometry technique does not appear to be universally applicable, unfortunately, and there are in the literature examples of failed attempts with some species to relate Sr:Ca ratios to water temperatures (e.g. Kalish 1989); these apparent differences in the physiological mechanism of Sr incorporation among fish species and environments are not well understood (Townsend et al. 1992).

Most fish otoliths are composed of the aragonite form of calcium carbonate which is precipitated within a protein matrix as the fish and otolith grow (Carlstrom 1963, Degens et al. 1969). Sr is one of a number of elements that can contaminate the carbonate crystal in trace amounts; because Sr has a similar ionic radius and the same +2 valence as Ca, it can substitute for Ca during the precipitation process (Kinsman 1969, Kinsman & Holland 1969). Work with corals (Smith et al. 1979) has shown that the Sr:Ca ratio in the coral aragonite was the same as that of the seawater from which it was precipitated, but there was evidence of a biological fractionation that acted to discriminate against the incorporation of Sr in a manner that appears to be related to temperature, beyond a purely physical chemical effect. Some workers have shown that, in general, calcifying organisms are able to modify the ionic composition of the fluid used in calcification, as compared with that in seawater, and that this modification may reflect changes in growth rate or environmental temperatures, or both (Lowenstam 1963, Pilkey & Goodell 1963, Milliman 1974, Lorens & Bender 1980).

The dependence of Sr:Ca ratios on temperature reported for otoliths of some fish species (e.g. Radtke 1984, 1989, Radtke & Targett 1984, Townsend et al. 1989, 1992, Radtke et al. 1990) appears to result from a reduced ability of a fish to physiologically discriminate against the incorporation of Sr at low environmental temperatures (Townsend et al. 1992). This temperature correlation with Sr:Ca ratios makes it possible, by measuring the Sr:Ca ratios along a transect from the core of the otolith to the outer edge, to reconstruct, in a correlative sense, the environmental temperature histories of individual fish larvae from the egg stage to the time of capture. The Sr:Ca ratio thermometry technique becomes a powerful research tool when used in conjunction with daily growth increments in fish otoliths, which provide a relatively precise chronometer for use in relating environmental temperatures to a particular date and period in the larva's life history.

Our preliminary experiments with larval Atlantic cod *Gadus morhua* otoliths reported here are part of a larger study of larval cod dynamics on Georges Bank that attempts to relate larval cod distributions to the physical and biological oceanographic conditions on the Bank; more detailed results of those studies will be presented elsewhere. Our specific purpose in this communication is to demonstrate the potential application of the Sr:Ca ratio technique in fisheries oceanographic studies by showing its use with Georges Bank cod larvae. In many ways, research questions concerning Georges Bank cod larvae are ideally suited to the application of the Sr:Ca ratio thermometry technique. Cod larvae are present on the Bank during the late winter and spring period when the water temperatures are still relatively cold (ca 3 to 6°C) and beginning to warm, and during their larval transport period around Georges Bank (Lough 1984, Buckley & Lough 1987, Lough & Bolz 1989, Lough et al. 1989) the larvae may experience a relatively broad range of water temperatures, indicating that they occupy various well-defined water masses in the region that impinge upon, and intrude onto, Georges Bank; those distributions may in turn hold important implications for larval survival (e.g. Wroblewski & Cheney 1984). Furthermore, cod otoliths exhibit relatively wide daily growth increments in their otoliths, from ca 2 to 4 µm (Bolz & Lough 1983, 1989), thus facilitating elemental analyses of Sr and Ca relative to the daily growth increments. We report in this communication our early laboratory and field experiments with larval cod, which show that Sr:Ca ratios in cod otoliths exhibit a temperature dependence, and we demonstrate the potential utility, and limitations, of the Sr:Ca ratio thermometry technique in tracking individual cod larvae on Georges Bank in the Northwest Atlantic.

MATERIALS AND METHODS

Eastern Atlantic cod *Gadus morhua* larvae were reared at the Flodevigen Biological Station in Arendal, Norway. The larvae were initially reared in a flow-through seawater system for ca 30 d, at which time they were transferred to temperature-controlled tanks and held for an additional 50 d at temperatures between ca 5 and 14°C. At the end of the 50 d period, 164 larvae were sacrificed and the outer portions of the otoliths, corresponding to the later temperature-controlled part of the experiment, were removed using a dental drill, and analyzed for Sr and Ca concentrations using atomic absorption spectroscopy. The Sr:Ca ratios and corresponding temperature data were fit to a number of equations using iterative least-squares techniques (using Table Curve 2D by Jandel Scientific, Inc.). The equation with the best fit was rearranged to solve for temperature, giving a standard curve, which we used to construct temperature history plots of individual larvae collected as part of our Georges Bank field survey program.

Larval cod and hydrographic data were collected during 2 research cruises on Georges Bank aboard the RV 'Columbus Iselin' in April and May 1993. Standard CTD (conductivity, temperature, depth recorder) casts and 60 cm Bongo net hauls were made at the stations shown in Fig 1. The Bongo frame was fitted with

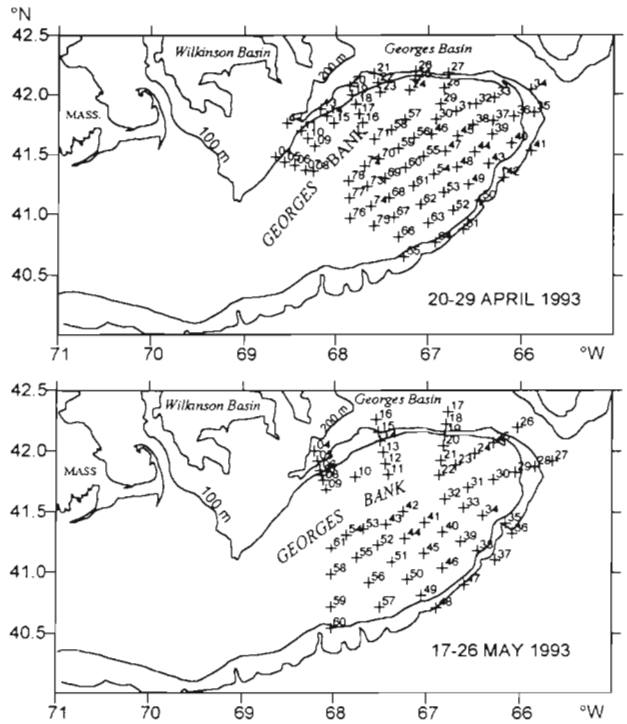

Fig. 1 Location of sampling stations on Georges Bank, for 2 RV 'Columbus Iselin' cruises. The 100 and 200 m isobaths are indicated

505 µm mesh nets and digital flow meters, and was hauled in a double oblique fashion at a speed of ca 2 knots, from the surface to ca 50 m, or, at shallower stations, to within ca 5 m of the bottom. Larvae from one side of the Bongo were sorted immediately upon collection and were preserved in ethanol; the other side of the Bongo sample was preserved in 5% formalin and sorted back at the laboratory for quantitative determinations of larval cod densities (no. of larvae per 100 m^3 filtered).

The larval otoliths from a number of the ethanol-preserved samples were later removed and prepared for electron microprobe analyses of the Sr:Ca ratios using a wave-length dispersive X-ray electron microprobe, as done in Townsend et al. (1989). Sagittae were mounted on 1 inch (2.5 cm) diameter glass disks using heat-setting petrological epoxy, and then ground using 600 grit grinding paper to reveal a sagittal section through the core region of the otolith. This surface was then polished further using 0.3 µm and 0.05 µm alumina paste, in order to dampen diffraction of resultant X-rays, rinsed with distilled water and ethanol, and given a carbon coating to conduct charge on the surface of the otolith. The larval otolith samples and standards were analyzed using a Cameca Camebax SX-50, fixed crystal, X-ray wavelength dispersive electron microprobe at the University of Hawaii. A series of data points was recorded for each larval otolith along a scan from the central core to the outer margin of the otolith. At each analysis point the sample was bombarded with an electron beam resulting in the emission of X-rays, which were then related to the elemental composition. Our analyses used an accelerating voltage of 15 kV, a beam current of 10 nA, and a 5 µm diameter focused beam. Characteristic X-rays for Ca and Sr were counted for 30 s and background measurements were recorded for 15 s at each sample location. We used standards of calcite for Ca calibration and strontianite for Sr calibration. Measurements of the Sr and Ca weight percents (wt %) in the standards were measured before and after each otolith sample was analyzed; those standards were averaged and compared to their known values to determine a correction factor which was applied to the Sr and Ca weight percents measured in the otolith samples. The crystals used in the X-ray detector were PET for Ca, and TAP for Sr. X-ray intensities were corrected and computed using the ZAF method (Reed 1975), and final elemental ratios were presented as ratios of Sr wt % to Ca wt %, and were multiplied by a factor of 1000 for presentation. Our measurement errors for Sr were typically in the range 3.5 to 3.9%, while errors for Ca were 0.5 to 0.6%; these errors were included along with regression errors in our resultant temperature history plots.

Following the microprobe analysis for Sr:Ca ratios, the otolith samples were cleaned with ethanol to remove the carbon coating, and were examined under 400× and 1000× magnification using transmitted- and reflected-light microscopy in order to relate the sample marks, or burn depressions left on the surface of the otoliths by the electron microprobe, to the corresponding number of daily growth increments in the otolith. By applying the laboratory-derived Sr:Ca ratio versus temperature relationship, we then constructed temperature-history plots for individual larvae, assigning each spot Sr:Ca ratio measurement of temperature to a larval age in days.

RESULTS

Laboratory experiments

The results of our measures of the Sr:Ca ratios as a function of temperature in reared cod larvae are given in Fig. 2, which shows an exponential relationship. Unlike our earlier results with herring larvae and juveniles (Townsend et al. 1989, 1992) our measures of Sr:Ca ratios in larval cod and corresponding temperature data did not fit the hyperbolic Michaelis-Menten equation as well as the more mathematically general exponential equation of the form:

$$\mathrm{Sr/Ca} = a\exp(-T/b) \quad (1)$$

where T is temperature (°C), the parameter a is the y-intercept, and b controls the function's curvature. The regression statistics are given in the figure legend (Fig. 2). This equation was rearranged to solve for temperature as:

$$T = -b\ln[(\mathrm{Sr/Ca})/a] \quad (2)$$

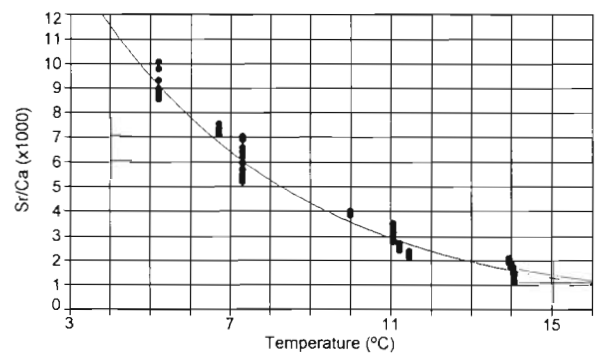

Fig. 2. *Gadus morhua*. Ratios of Sr to Ca as a function of temperature (T) for 164 otoliths from eastern Atlantic cod larvae reared at constant temperatures (see text). An exponential equation of the form $(\mathrm{Sr/Ca}) \times 1000 = a\exp(-T/b)$ was fit to the data using Table Curve 2d (Jandel Scientific, Inc.); a = 25.145 (SE = 0.609); b = 5.120 (SE = 0.076); coefficient of determination (r^2) = 0.967

and was used in reconstructing the temperature histories of a subsample of cod larvae collected on Georges Bank in April and May of 1993.

Larval distributions and hydrography on Georges Bank

The general results of our 2 survey cruises are given in Figs. 3 & 4 as areal contour plots of larval cod densities and surface water temperatures. We found 2 main patches of cod larvae in April, 1 on the Northeast Peak of Georges Bank and 1 on the Southwest flank (Fig. 3). These 2 patches were separated by a large mass of colder and less saline Scotian Shelf water that appears to have moved onto the eastern-most part of the Bank from the east; water colder than 3°C can be seen extending off the Bank to the east of our sampling grid. There was also an impingement of warmer and more saline slope water evident on the southeastern flank of the Bank, where surface water temperatures exceeded 12°C at Stn 51 (these warmer temperatures were not contoured in Fig. 3).

The May cruise results in Fig. 4 show how the system evolved in the 3 to 4 wk following the April cruise. Thermal stratification was underway in the deeper waters around the periphery of Georges Bank and in the Gulf of Maine. The larval cod patch on the Northeast Peak had moved to the south about 40 n miles, while the second patch on the Southwest flank moved to the north-northeast about 10 to 15 n miles. These larval cod transport patterns, and thus the presumed patch coherence between cruises, can be explained in terms of both topographic rectification of tidal currents around the periphery of Georges Bank (Loder & Wright 1985) and transport resulting from density-driven geostrophic currents. (A specific discussion of these transport processes is beyond the scope of this communication and will be presented elsewhere). The presence of cold Scotian Shelf water, which was obvious in April, remained evident in May as a tongue of colder (and less saline) water that appeared to be moving with the residual clockwise flow field around the periphery of the Bank. Also in May, there again was evidence of the warm, salty slope water that had impinged against the southern part of the Bank in April.

Temperature histories of larval cod on Georges Bank

Examples of temperature histories for 2 individual cod larvae collected from 1 of the larval patches in April (Stn 30; Fig. 3) are given in Fig. 5. The 2 larval temperature histories show coherence with one an-

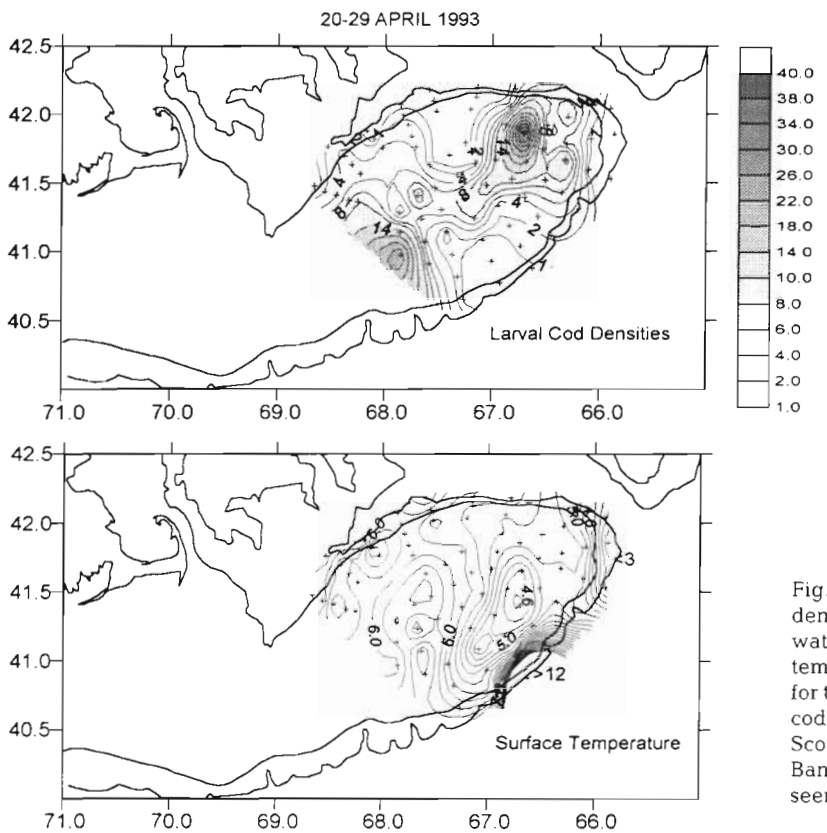

Fig. 3. *Gadus morhua*. Contours of larval cod densities, expressed as no. of larvae per 100 m^3 water filtered, and contours of surface water temperature (0.2°C intervals) on Georges Bank for the period 20 to 29 April 1993. Two patches of cod larvae are evident, as is an intrusion of cold Scotian Shelf water across the eastern half of the Bank. A mass of warmer slope water can also be seen impinging onto the southern part of the Bank (indicated by temperatures >12°C)

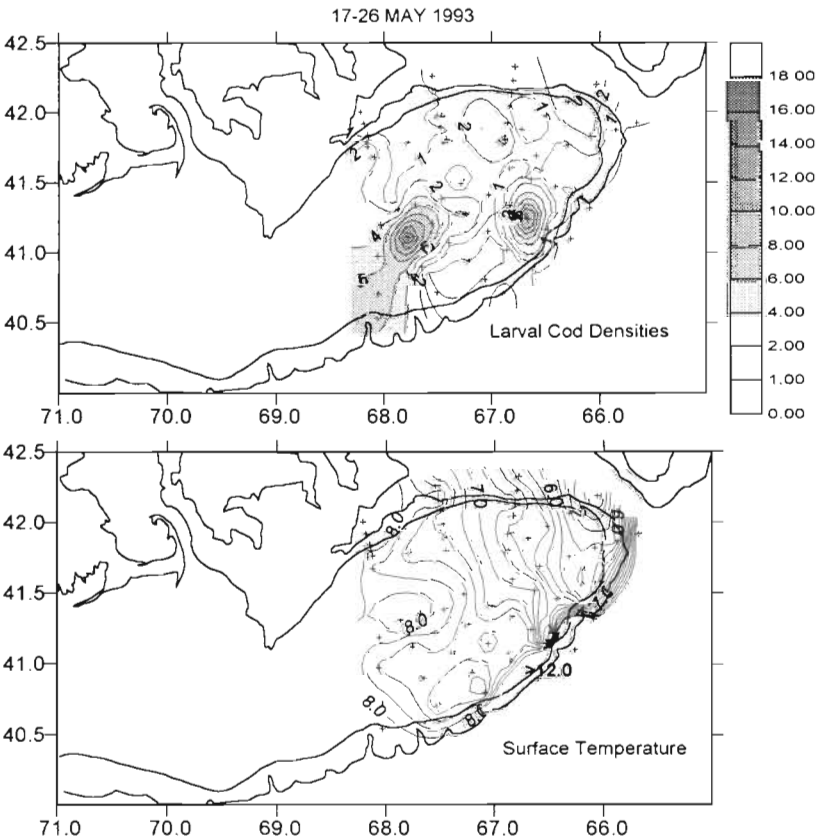

Fig. 4. *Gadus morhua*. Contours of larval cod densities and surface water temperature, as in Fig. 3, except for the period 17 to 26 May 1993. Note the differences in the positions of the 2 larval cod patches from those in April (Fig. 3), and that the remnant of the intrusion of cold Scotian Shelf water is still evident, as is the warm (>12°C) slope water to the south

other with respect to their general temperature trends, in that both larvae appear to have passed into relatively colder waters 5 to 15 d after hatching, and then each larva subsequently experienced fairly abrupt warming about 1 wk prior to capture. Similar plots of temperature histories are given in Fig. 6 for 3 individual cod larvae collected in May at Stn 55 (Fig. 3). There is less coherence among these 3 temperature-history plots, especially when comparing the younger specimens in the bottom panels with the specimen in the top panel (Fig. 6); the latter individual is an older fish and thus represents a longer temperature history. Each of the 3 larvae appears to have experienced cold water temperatures for a relatively brief period shortly after hatching; each was found in relatively warmer waters at the time of hatching.

Each of the temperature-history plots in Figs. 5 & 6, as reconstructed using Eq. (2) for our otolith Sr:Ca measurements, show temperatures at the time of capture that exceed those measured on each of our survey cruises by about 3°C, which would suggest to us that our laboratory-derived calibration is off. We have therefore applied a temperature-offset correction parameter equal to 3°C to Eq. (2) to partially account for this discrepancy between the calibration results from our laboratory-rearing experiments and the field observations of temperature at the time of collection; we have presented this correction as an additional temperature scale on the right sides of each panel in Figs. 5 & 6.

Basing our interpretations of the larval cod temperature histories on the corrected temperature scales (Figs. 5 & 6), we can begin to draw some preliminary inferences about the probable water mass associations of each of the larvae. Although the water column on Georges Bank in April 1993 was vertically well mixed and isothermal over most of the top of the Bank, we nonetheless can see evidence in the temperature histories in Fig. 5 of each larva having occupied relatively cold waters, perhaps as cold as 1 to 3°C, soon after hatching. This cold water episode may have been the result of the larvae having encountered the cold Scotian Shelf water mass, which remains clearly evident on the eastern half of the Bank during our April survey cruise when the fish were collected (Fig. 3). Stn 30, where the larvae were collected, is within the thermal frontal region that delimits the Scotian Shelf water mass (Fig. 3).

There was more hydrographic structure during May 1993 than in April, which reflects the vernal warming of the water column. The temperature histories of larvae collected during the May cruise (Fig. 6) also show evidence of the larvae having encountered relatively cold waters about 1 wk after hatching. These

larvae were most likely transported from the southwestern part of the Bank as part of the second larval patch (Fig. 4), and thus may have encountered a remnant cold water mass that can be seen in Fig. 7 as a cold water layer at intermediate depths (about 30 m) on the southern part of the Bank.

DISCUSSION

Our results suggest to us that Sr:Ca ratios in larval cod otoliths hold significant potential for use in hindcasting larval distributions in relation to water mass distributions on Georges Bank in spring. However, we caution that these results should be viewed as preliminary, and they are presented here only to illustrate the utility of the Sr:Ca ratio thermometry technique for larval cod research on Georges Bank. For example, our laboratory calibration of Sr:Ca ratios with temperature was conducted with reared cod larvae in Norway, and analyzed using atomic absorption spectroscopy, and although the Sr:Ca ratio versus temperature relationship in Fig. 2 is fairly tight, it clearly does not translate cleanly for application to electron microprobe measurements of Sr/Ca from larvae we collected on Georges Bank. We found that the Sr:Ca ratios at the outermost edges (i.e. the most recently deposited material) of the field-collected larval cod otoliths did not correspond well, when temperature was computed using the calibration expression from the rearing

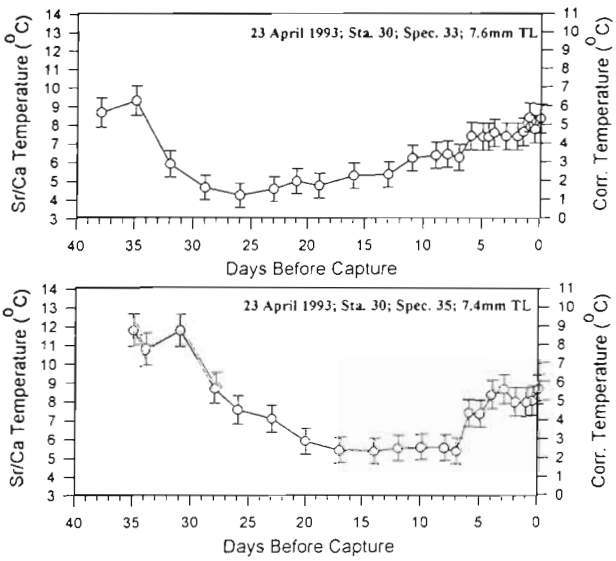

Fig. 5. *Gadus morhua*. Temperature-history plots of 2 cod larvae collected in April 1993 at Stn 30 (Fig. 1) on Georges Bank, based on otolith Sr:Ca ratio measurements as explained in the text. Error bars represent both the analytical error associated with Sr:Ca measurements using the electron microprobe (ca 5%), and the 95% confidence limits of the 2 exponential parameters, *a* and *b* in Eq. (1). The temperature scales on the left sides of the 2 panels represent the computed temperatures using the Sr:Ca versus temperature relationship in Fig. 2, rearranged to solve for temperature (Eq. 2); the corrected temperature scale on the right of each panel represents an offset of 3°C, which represents an adjustment to bring the temperature versus Sr:Ca relationship into agreement with the water temperatures at the time the larvae were collected (see text)

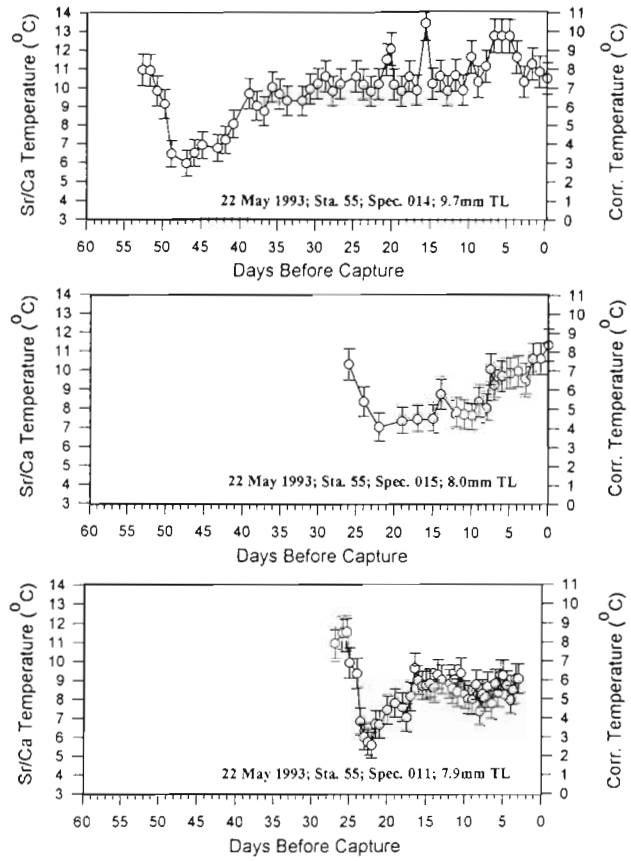

Fig. 6. *Gadus morhua*. Temperature-history plots, as in Fig. 5, except for 3 cod larvae collected in May 1993 at Stn 55

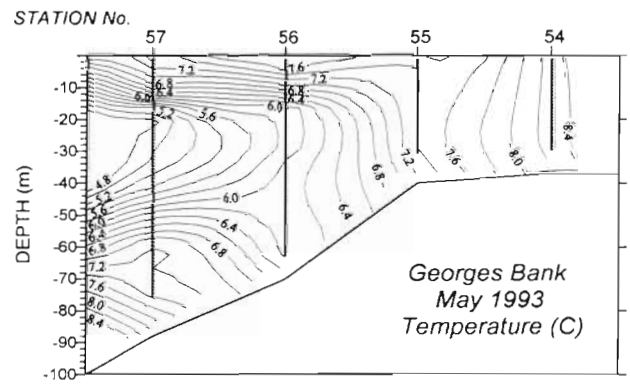

Fig. 7. Vertical section contour plot of temperature (°C) for the hydrographic transect from Stn 54 to Stn 57 (Fig. 1) in May 1993, based on CTD casts at those stations. Note the colder intermediate-depth water at the deeper end of the transect beginning at Stn 56

experiments, to the water temperatures on Georges Bank at the time of collection. The difference was on the order of 3°C, which we accounted for by adding an offset parameter to Eq. (2) and thus adjusting the temperature scales on our temperature-history plots. This adjustment made the calculated temperatures more realistic, although still not perfect, and allowed us to interpret qualitatively the probable water mass associations of the larvae.

The Sr:Ca ratio thermometry technique has been slow to develop as an acceptable research tool, and earlier efforts with the technique have encountered a number of problems. In our initial applications of the technique to a study of environmental histories of larval and juvenile herring (Townsend et al. 1989, Radtke et al. 1990), we used a linear regression model that related the Sr:Ca concentration ratios and temperature. That model was based on our preliminary field and laboratory calibration experiments, which we used to infer the distributions of fall-spawned herring larvae in relation to the known hydrographic regime in the Gulf of Maine, USA. We were able to reconstruct the temperature histories of the larvae and early juveniles and determine their overwintering distributions as well as identify the time at which they entered inshore waters in the spring (Townsend et al. 1989). In later laboratory experiments with juvenile herring (Townsend et al. 1992) we concluded that the Sr:Ca ratio versus temperature relationship is curvilinear, and that it could be described by a hyperbolic Michaelis-Menten function of the form: $(Sr/Ca) \times 1000 = aT/(b+T)$, where T is absolute temperature, the parameter a defines the asymptote and b defines the point halfway between the asymptote and the maximum, thus describing the degree of temperature sensitivity.

Regardless of the exact mathematical expression describing the Sr:Ca versus temperature relationship, demonstrating that relationship is curvilinear, and that it approaches an asymptote at higher temperatures, where there may be little, if any, dependence on temperature, is a significant step forward in developing the Sr:Ca ratio technique, because it may explain equivocal results of Kalish (1989). Kalish reported that he found no significant linear relationship between Sr:Ca ratios and temperature for juvenile Australian salmon at experimental temperatures between 13 and 22°C. However, he suggested that the indirect effect of temperature on the physiology of the fish might affect the Sr and Ca concentrations in the saccular endolymph. In turn, he reported that the endolymph Sr:Ca ratio was directly related to the otolith Sr:Ca ratio. We believe that Kalish was unable to discern a significant relationship between Sr:Ca and temperature because his experimental temperatures were not sufficiently low to affect significantly the fish's metabolism and thus retard the physiological discrimination against the passage of Sr into the fish's saccular endolymph and hence into the otoliths. Rather, his experimental temperatures may have been at the asymptote portion of a curvilinear relationship describing Sr:Ca versus temperature. Indeed, our earlier results with herring juveniles showed no clear temperature dependence of Sr:Ca ratios over the range from about 7 to 16°C, and the changes in Sr:Ca ratios did not appear to become significant until the temperatures decreased below about 7°C, which we also showed is the temperature below which growth of the fish becomes slowed, thus suggesting a reduced metabolism (Townsend et al. 1992). A closer examination of Kalish's (1989) Fig. 1 shows a slight positive correlation, where the Sr:Ca ratios may increase at higher temperatures between 19 and 22°C. Our laboratory results with cod larvae presented here would indicate that there is little change in Sr:Ca ratios with increasing temperatures above ca 12°C. Taken together, all of these results would suggest to us that Kalish's (1989) experimental temperatures were approaching the upper levels that might have been affecting the fish's ability to discriminate against the passage of Sr into the endolymph, which could be viewed as analogous to low temperature situations with cod and herring.

Our work with larval cod supports our earlier conclusion (Townsend et al. 1992) that the Sr:Ca ratio thermometry technique can be a useful tool to hindcast larval fish distributions with respect to environmental temperatures and hence to water mass distributions. This conclusion has some caveats: first, the technique apparently works only with fishes that experience environmental extremes, such as overwintering herring larvae and juveniles, and larval cod in the relatively cold waters of the Gulf of Maine and Georges Bank; second, careful attention must be paid to laboratory calibrations of the Sr:Ca versus temperature relationship, which should be cross-checked against Sr:Ca versus temperature measurements from field-collected material. More calibration experiments are needed to address the possibility that other factors, uncontrolled in the larval rearing experiments we report here, may alter Sr:Ca ratios in cod larvae. For example, the drop in Sr:Ca ratios which is evident shortly after hatching in each of the field-caught larvae in Figs. 5 & 6 could be related to physiological changes associated with yolk-sac absorption, which would be expected to occur at about that time in cod larvae; this possible effect would be in keeping with concerns expressed by Kalish (1989) of ontogenetic controls on Sr:Ca ratios. Although it is not likely that variable salinity, as seen on the outer continental shelf, would significantly affect source concentrations of Sr and Ca in seawater (river water is 2 orders of magnitude lower in Sr than

seawater; Riley & Chester 1971), the effects of variable pressure, as related to ontogenetic larval depth distributions, could potentially influence Sr:Ca ratios in some fashion. With continued laboratory and field calibration experiments, we maintain that the Sr:Ca technique holds the potential to be used beyond a simple qualitative interpretation of relative temperature histories, as reported here, to a more quantitative investigation of specific water masses experienced by individual fishes.

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