

Stable $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopes in otoliths of haddock *Melanogrammus aeglefinus* from the northwest Atlantic Ocean

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ABSTRACT: Analyzing stable isotopes deposited in fish otoliths can provide insights into the environmental variation that individual fish experience throughout their life history which, in turn, can indicate their home range, movements, and underlying stock structure. We investigated the use of stable $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopes in haddock *Melanogrammus aeglefinus* otoliths as indicators of environmental variation and stock structure in the northwest Atlantic Ocean. Samples were collected between 1995 and 1998 from individual spawning components on Georges Bank, the Gulf of Maine, and along the Scotian Shelf. Samples from 1 yr- and 4 yr-old haddock were analyzed from an integrated and chronological life history perspective, respectively. Annual, seasonal, and ontogenetic variation in otolith isotopes indicated that haddock undergo shifts in distribution throughout their life history, possibly as a means of compensating for variable environmental conditions; this underlines the difficulty of temperature reconstructions from mobile organisms with optimal temperature ranges.

KEY WORDS: Otolith isotopic composition · Carbon · Oxygen · Georges Bank · Retrospective environmental regimes · Stock identification · Fisheries management

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INTRODUCTION

The stable isotope chemistry of biogenic carbonates, such as fish otoliths, can provide information on the environmental variation (i.e. habitat, diet, temperature and depth) that a marine organism has experienced throughout its life history (Radtke et al. 1987, Kalish 1991a,b, Gauldie et al. 1994, Schwarcz et al. 1998). The environmental variation recorded in fish otoliths can subsequently be used as an indicator of the home range and spatial distribution of a fish species, which can have implications for stock structure and fisheries

management (Campana et al. 1995, Edmonds & Fletcher 1997, Roelke & Cifuentes 1997). In this study, we investigated the use of stable $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopes in haddock *Melanogrammus aeglefinus* otoliths as indicators of environmental variation and stock structure in the northwest Atlantic Ocean, with particular emphasis on the Georges Bank ecosystem (see Fig. 1).

Differences in the stable isotope chemistry of otoliths between geographically separate groups of fish suggest that distinct environmental regimes are occupied throughout their life history, providing an indirect measure of stock separation (Thorrold et al. 1998, Campana 1999, Edmonds et al. 1999, Newman et al. 2000). Stock separation derived from stable isotope chemistry is based upon the metabolically inert nature of otoliths (Campana & Neilson 1985), and the assumption that the calcium carbonate and isotopic composition of otoliths is mainly derived from the water in

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which the fish reside, as modified by ambient temperature (Campana et al. 1995).

Carbon isotope ($\delta^{13}\text{C}$) data derived from fish otoliths may provide information on growth and metabolic rates, diet, and productivity levels of the ecosystem in which the fish reside (DeNiro & Epstein 1978, Fry 1988, Hesslein et al. 1991, Kalish 1991b, Gauldie 1996, Thorrold et al. 1997). However, interpretation of $\delta^{13}\text{C}$ data can be complicated because of the inherent biological and metabolic effects that can influence otolith $\delta^{13}\text{C}$, besides ambient environmental conditions (Grossman & Ku 1986). In contrast, aragonite of fish otoliths has been demonstrated to precipitate in isotopic equilibrium with $\delta^{18}\text{O}$ of ambient environmental conditions (Devereux 1967, Degens et al. 1969, Kalish 1991a,b, Patterson et al. 1993, Thorrold et al. 1997). Consequently, fish otoliths can be used to reconstruct temperature regimes because they enable the estimation of $\delta^{18}\text{O}$ values for ambient environmental conditions in which the fish have resided (Kalish 1991a, Patterson et al. 1993). Furthermore, because of the rhythmic banding pattern found in fish otoliths, retrospective environmental temperature regimes can be reconstructed on both an annual and seasonal basis (Radtke et al. 1987, Patterson 1998). Reconstruction of environmental regimes is desirable for fisheries management because it can provide insights into relationships between the ambient environmental conditions that a fish has experienced and its subsequent stock structure, migration patterns, and life history events (Mountain & Murawski 1992).

We investigated the use of stable isotope chemistry to determine if there were differences in the isotopic

composition of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in haddock otoliths sampled throughout the northwest Atlantic Ocean. Particular emphasis was placed on the depleted haddock resource in the Georges Bank ecosystem, where stock rebuilding plans are currently being implemented and where individual spawning components of haddock have been identified over eastern and western Georges Bank (Smith & Morse 1985, Gavaris & van Eenennaam 1998, Begg et al. 1999, 2001, Page et al. 1999, Begg & Brown 2000) (see Fig. 1). Differences in the isotopic composition of haddock otoliths sampled from the different geographic regions were assumed to be indicative of site-specificity and a phenotypic measure of stock separation. In addition, we examined the isotopic composition of haddock otoliths on an annual and seasonal basis to determine the potential for stable $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopes to reflect metabolic and ambient environmental conditions experienced by haddock throughout their life history.

MATERIALS AND METHODS

Sample collection. Samples of *Melanogrammus aeglefinus* were collected in spring 1995, 1996, 1997 and 1998 during Northeast Fisheries Science Center (NEFSC) stratified random bottom-trawl surveys, when the fish were assumed to be on or near their spawning grounds (Table 1). Samples were collected from survey stations throughout eastern Georges Bank (EGB), western Georges Bank (WGB), the Gulf of Maine (GOM), and the Scotian Shelf (ScS) (Fig. 1, Table 1). At sea, haddock samples were measured (fork length, FL, to the nearest cm), and sagittal otolith pairs were removed from each fish. In the laboratory, 1 otolith from each pair was transverse-sectioned and assigned an age following standard methods for northwest Atlantic finfish species (Penttila & Dery 1988). Haddock samples of 1 and 4 yr of age were then selected for isotopic analysis. The 1 yr-old samples were analyzed from an integrated life history perspective, while the 4 yr-old samples were analyzed from a chronological life history perspective.

Isotope analysis. Otoliths were prepared for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotope analysis in different ways, depending on their age. For the 1 yr-old samples, thin (~200 μm) transverse sections of the otoliths were crushed into a fine powder using a mortar and pestle. The resulting powdered carbonate samples

Table 1. *Melanogrammus aeglefinus*. Sampling details and mean (\pm SD) otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of haddock samples. n = number of samples. FL = fork length

Region, Year class	Age group (yr)	(n)	FL range (cm)	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
Eastern Georges Bank (EGB)					
1994	1	(10)	20–26	-1.022 (0.330)	1.520 (0.229)
1995	1	(10)	20–28	-0.498 (0.264)	1.317 (0.277)
1996	1	(10)	23–26	-0.789 (0.383)	1.263 (0.159)
1997	1	(8)	20–27	-1.439 (0.402)	1.531 (0.329)
1993	4	(3)	51–58		
Western Georges Bank (WGB)					
1994	1	(10)	23–28	-0.687 (0.373)	1.480 (0.131)
1995	1	(10)	20–27	-0.808 (0.433)	1.305 (0.129)
1996	1	(10)	22–28	-0.524 (0.216)	1.072 (0.121)
1997	1	(7)	20–25	-1.463 (0.501)	1.160 (0.325)
1993	4	(3)	49–53		
Gulf of Maine (GOM)					
1996	1	(10)	19–25	-0.844 (0.448)	1.008 (0.258)
Scotian Shelf (SS)					
1996	1	(9)	15–20	-1.277 (0.370)	1.334 (0.131)

(each weighing ~1 mg) represented the integrated 1 yr life history of each sample. In contrast, preparation of otoliths for the 4 yr-old samples was more involved. The transverse sections of these otoliths were mounted with epoxy resin onto glass slides to make petrographic thin sections (~100 μm). Seasonal growth increments were then identified from magnified images of these sections, and digitized as navigational input to an automated micro-sampling system. The micro-sampling was accomplished by milling sequential layers (~30 μm in width) along a given growth increment of each otolith section, from the distal edge of the otolith (most recent growth) to the center of the otolith (earliest growth). Each layer, or combined set of adjacent layers, comprised a single sample (weighing ~40 μg). Consequently, a continuous time-series with seasonal resolution (2 or more samples per annum) was obtained for each 4 yr-old sample.

All stable isotope analyses were carried out at the National Ocean Sciences Accelerator Mass Spectrometer Facility at the Woods Hole Oceanographic Institution using a VG Prism stable isotope mass spectrometer with an on-line hydrolysis extraction system. The analytical precision (1 s) reported for this instrument, based on daily analysis of powdered NIST carbonate standards, was ± 0.05 s for carbon and ± 0.08 s for oxygen. All isotopic values are reported using the international standard delta notation for carbonates (i.e. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$).

Metabolic and environmental variation. Age- and year class-specific growth rates were examined in relation to otolith $\delta^{13}\text{C}$ content to determine the use of this isotope as an indicator of metabolic variation. Mean length (cm) of 1 yr-old haddock for each year class (1994 to 1997) from eastern and western Georges Bank respectively, were estimated from combined NEFSC spring and autumn survey data (range = 106 to 239 aged samples), and used as a measure of growth and metabolism throughout the first year of life. Otolith $\delta^{13}\text{C}$ values of the 1 yr-old samples were then compared to the respective mean-length-at-age data to determine the use of $\delta^{13}\text{C}$ as a measure of metabolic variation.

The temperature and salinity of the ambient waters in which haddock reside were then examined in relation to otolith $\delta^{18}\text{O}$ values to determine the use of this

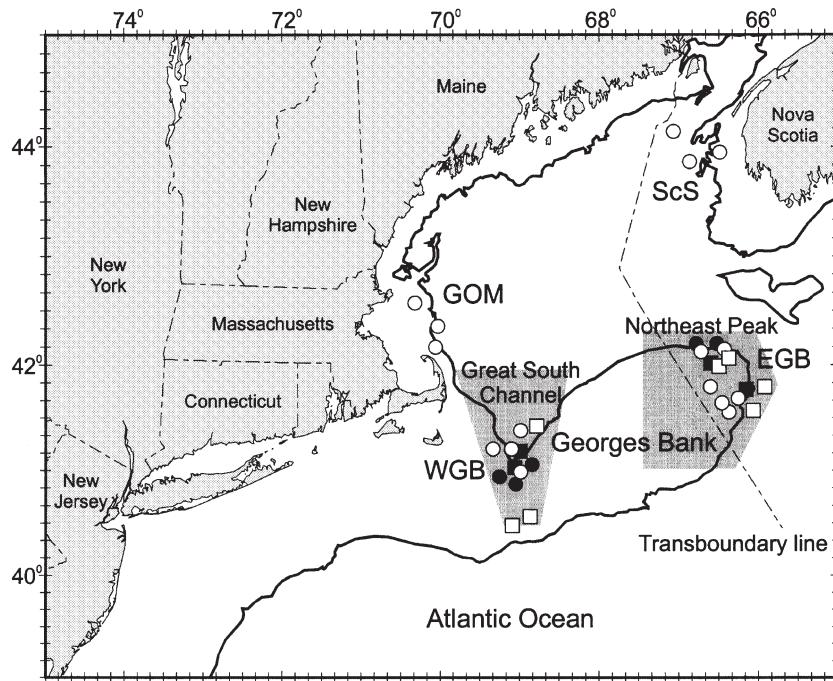


Fig. 1. Northeast Fisheries Science Center stratified random survey stations from where haddock samples were collected in 1995 (●), 1996 (■), 1997 (○), and 1998 (□) for stable $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotope analysis. EGB: eastern Georges Bank; GOM: Gulf of Maine; ScS: Scotian Shelf; WGB: western Georges Bank; shaded areas: regions used in estimation of areal mean environmental data

isotope as an indicator of retrospective environmental regimes. Only eastern and western Georges Bank haddock samples were analyzed in relation to environmental variation because of sample limitations, although it was assumed the use of stable isotopes as environmental indicators would be similar for haddock in other regions of the northwest Atlantic Ocean. Areal mean bottom temperature ($^{\circ}\text{C}$) and salinity (psu) values were estimated from NEFSC surveys (1993 to 1998) using the methods described in Mountain & Holzwarth (1989), for eastern and western Georges Bank, respectively (Fig. 1). These values were calculated for the mid-date (calendar day) of each survey, and averaged within each year to provide annual mean estimates of the environmental variation. Consequently, the final temperature and salinity values were the resultant means of environmental data collected from several (range = 3 to 9) surveys in any given year. These values were then used in the Kim & O'Neil (1997) revised calcite equation based on inorganic aragonite to estimate ambient seawater temperature at the time of carbonate deposition (Campana 1999):

$$T = \frac{\partial A(\text{VPDB}) - \partial W(\text{VSMOW}) - 3.71}{-0.206}$$

where T = ambient seawater temperature ($^{\circ}\text{C}$), ∂A (VPDB) = $\delta^{18}\text{O}$ of otolith aragonite, and ∂W (VSMOW) = ambient $\delta^{18}\text{O}$ seawater. VPDB and VSMOW refer to the international standard measurement scales for reporting the $\delta^{18}\text{O}$ compositions of carbonate and water, respectively. Ambient $\delta^{18}\text{O}$ seawater, ∂W (VSMOW), was estimated using the Fairbanks (1982) salinity- $\delta^{18}\text{O}$ seawater equation for the Gulf of Maine and Scotian Shelf, which was assumed to be applicable to Georges Bank:

$$\partial W (\text{VSMOW}) = -14.66 + 0.421(S)$$

where S = areal mean salinity values estimated for eastern and western Georges Bank, respectively.

Data analysis. Analyses were structured to account for the effects of fish length, age, and year class which could have biased our interpretations of environmental variation and stock structure based on the stable isotope values of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. Analysis of covariance (ANCOVA) was initially used to examine the effect of fish length on the value of each isotope, only for the 1 yr-old samples. Either isotope found to be signifi-

cantly correlated with fish length from the ANCOVAs was adjusted using the respective common within-group slope (b). Multivariate analysis of variance (MANOVA) was then used to examine potential confounding year-class differences among 1 yr-old samples in their otolith isotopic composition, from eastern and western Georges Bank, respectively. One-way, fixed effects, unbalanced analyses of variance (ANOVA) and Tukey's honestly significant difference (HSD) tests were further used to examine $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data to interpret any significant differences detected by the MANOVAs. The same multi- and univariate tests were then used to examine the otolith isotopic composition of 1 yr-old samples from the different regions to determine if there was any evidence for stock structure of haddock in the northwest Atlantic Ocean based on stable isotope values. The 4 yr-old samples were examined to determine the potential of stable isotopes to reconstruct metabolic and temperature histories of individual fish, although no statistical analyses were conducted on these data because of sample limitations.

RESULTS

Individual ANCOVAs for otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data for 1 yr-old *Melanogrammus aeglefinus* samples indicated that there were no significant interactions between fish length and sample region and year class (homogeneity of slopes test, $p > 0.05$), although both isotopes were significantly correlated with fish length ($p < 0.01$) (Fig. 2). Consequently, prior to further statistical analysis, the values of each isotope measured in the 1 yr-old samples were adjusted for variable fish length using their respective within-group regression coefficient ($\delta^{13}\text{C}$: $b = 0.04865$; $\delta^{18}\text{O}$: $b = -0.02865$).

Temporal isotopic differences were observed in the values of both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ deposited in haddock otoliths; indicative of annual metabolic and environmental variability experienced by haddock throughout their first year of life (Table 1). The integrated otolith isotopic composition of 1 yr-old haddock samples varied significantly between year classes for haddock on eastern Georges Bank (MANOVA: $F = 4.59$; $df = 6, 68$; $p < 0.0006$), and western Georges Bank (MANOVA: $F = 9.73$; $df = 6, 66$; $p < 0.0001$), respectively. Individual otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values also varied significantly between year classes (Fig. 3). Eastern Georges Bank haddock samples indicated a decline in $\delta^{13}\text{C}$ since 1995 (linear regression: $F = 24.05$; $df = 1, 26$; $p < 0.0000$), which was significantly more enriched than the other year classes, except in 1996 (HSD, $p < 0.05$). In contrast, otolith $\delta^{18}\text{O}$ remained fairly stable between samples from the different year classes (Fig. 3). West-

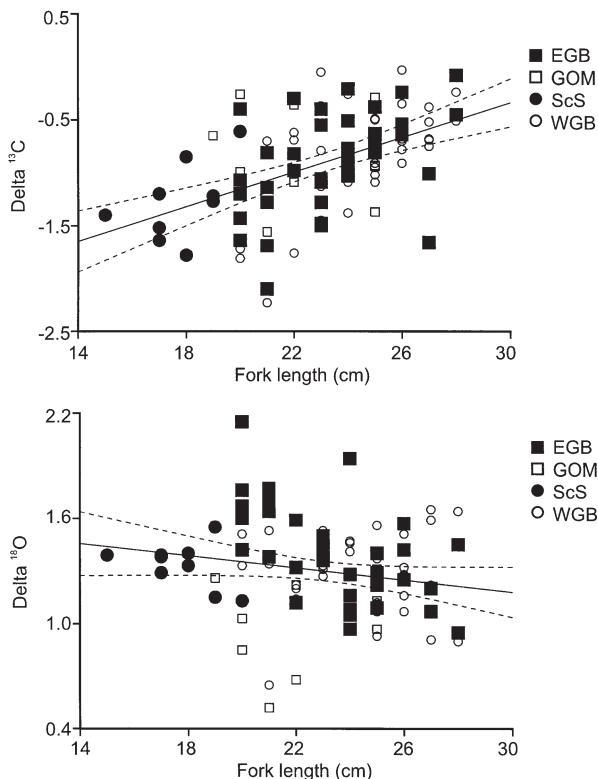


Fig. 2. *Melanogrammus aeglefinus*. Otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ as a function of increasing fork length (cm) of 1 yr-old haddock samples. Dashed lines represent 95 % confidence intervals of mean regression line. EGB: eastern Georges Bank; GOM: Gulf of Maine; ScS: Scotian Shelf; WGB: western Georges Bank

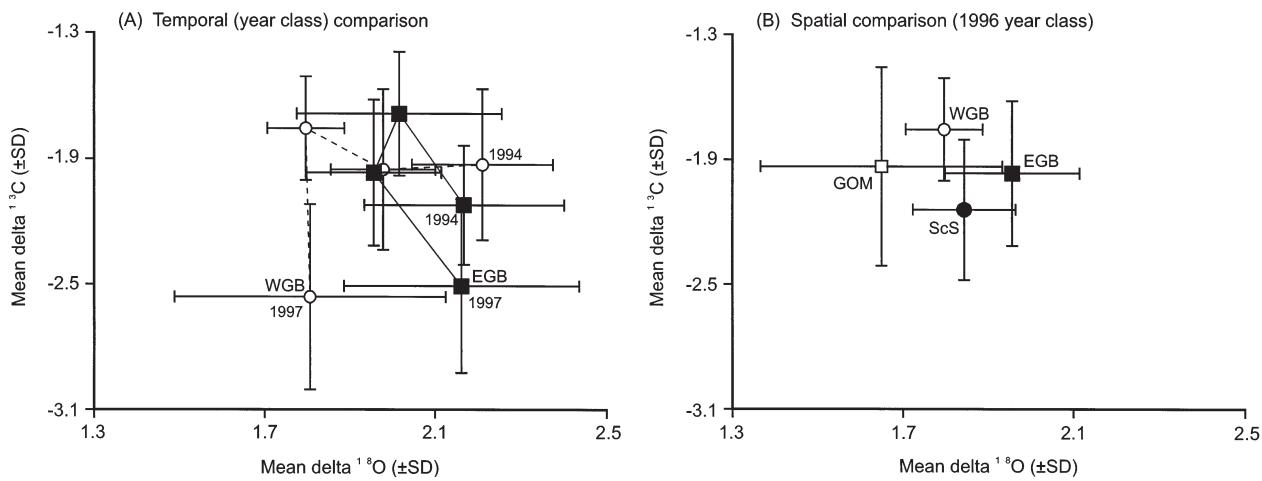


Fig. 3. *Melanogrammus aeglefinus*. Temporal and spatial comparisons of mean (\pm SD) length-adjusted otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values between 1 yr-old haddock samples from different regions in the northwest Atlantic Ocean for each year class, 1994 to 1997. EGB: eastern Georges Bank; GOM: Gulf of Maine; ScS: Scotian Shelf; WGB: western Georges Bank

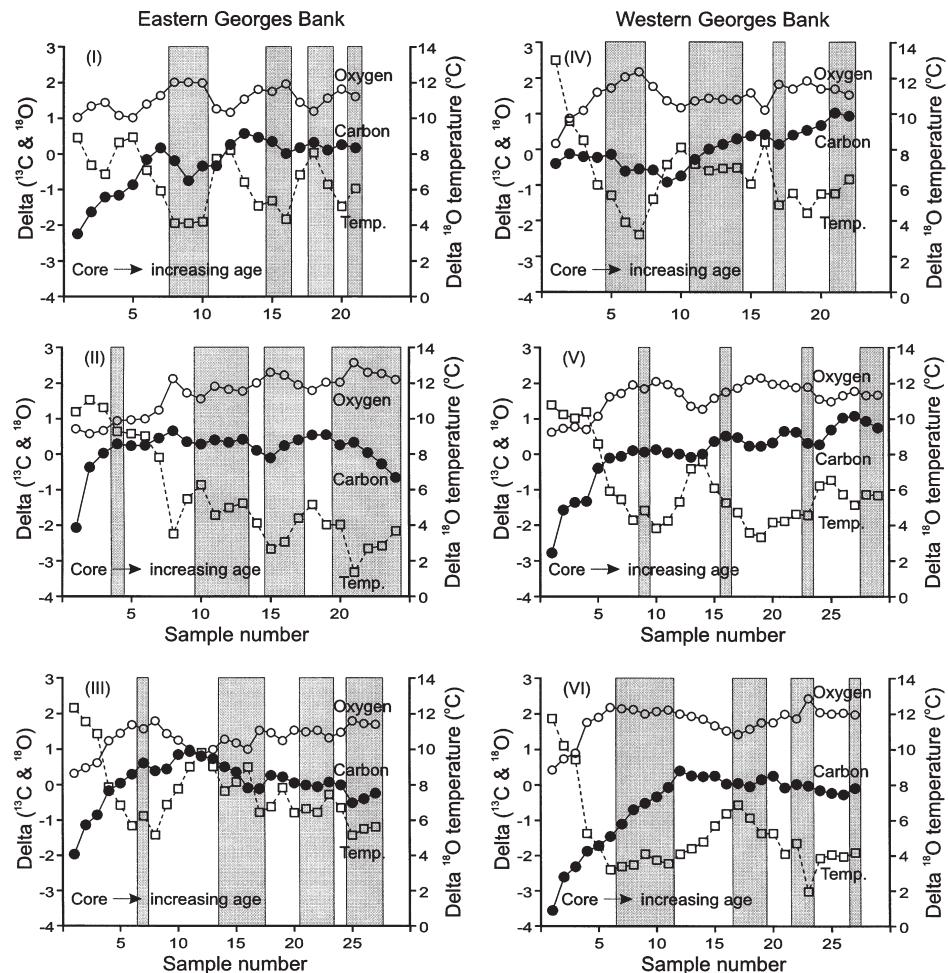


Fig. 4. *Melanogrammus aeglefinus*. Temporal variation in otolith $\delta^{13}\text{C}$ (●) and $\delta^{18}\text{O}$ (○) values, and otolith $\delta^{18}\text{O}$ predicted temperatures (°C, □) of individual 4 yr-old haddock samples from eastern (EGB) and western (WGB) Georges Bank. Otolith $\delta^{18}\text{O}$ predicted temperatures were based on mean salinity (psu) values for each region (1993 to 1996: EGB = 32.80 psu; WGB = 32.76 psu). Bars represent approximate winter growth zones

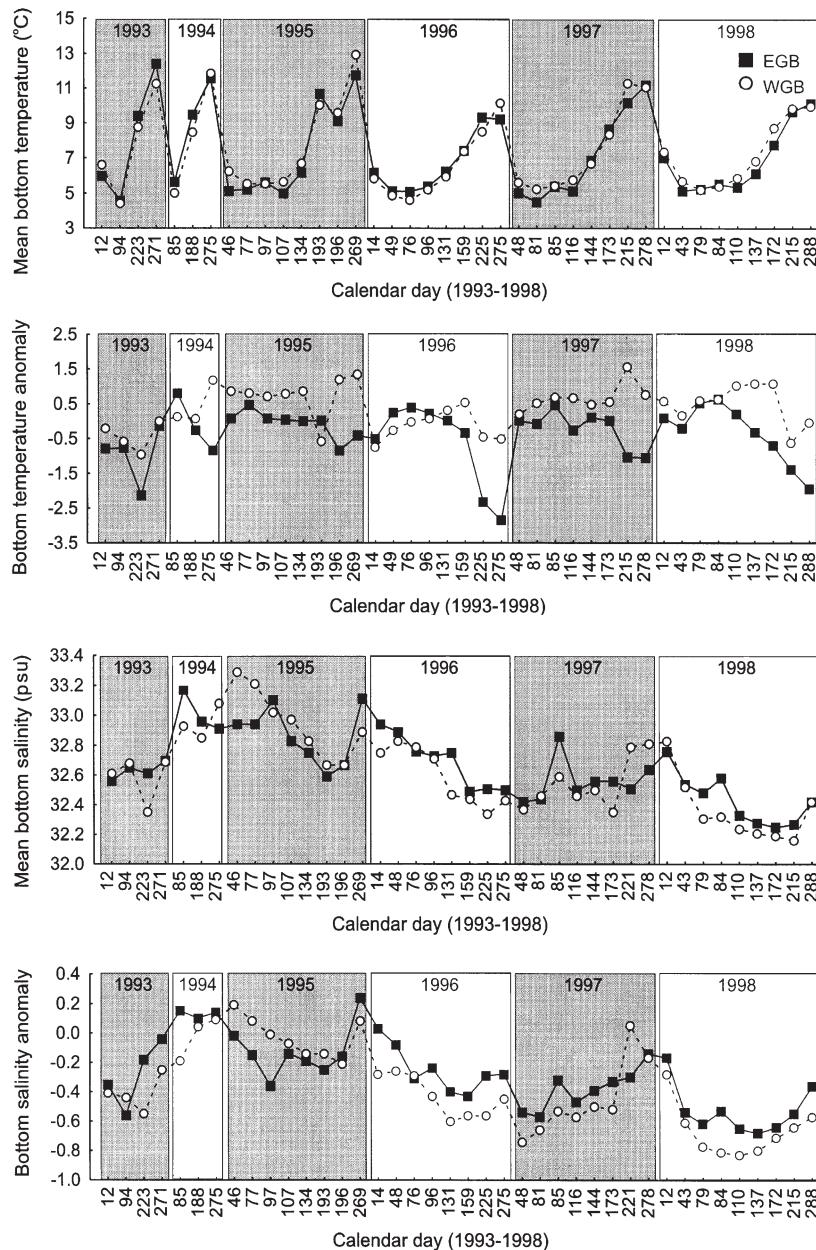


Fig. 5. Areal mean bottom temperature, salinity, and anomaly values for mid-date (calendar day) of each survey on eastern (EGB) and western (WGB) Georges Bank, 1993 to 1998

ern Georges Bank haddock samples indicated a decline in $\delta^{13}\text{C}$ in 1997 (linear regression: $F = 23.23$; $df = 1, 15$; $p < 0.0002$), which was significantly lower than the other year classes (HSD, $p < 0.05$). Similarly, otolith $\delta^{18}\text{O}$ declined throughout the study period (linear regression: $F = 26.93$; $df = 1, 35$; $p < 0.0000$), whereby the 1994 year class was significantly more enriched than the other year classes (HSD, $p < 0.05$) (Fig. 3).

Otolith $\delta^{18}\text{O}$ content of individual 4 yr-old haddock samples tended to show cyclical (i.e. seasonal) varia-

tion with age, as well as considerable variation between individual fish, particularly in their first year of life (Fig. 4). Likewise, predicted temperatures based on these otolith $\delta^{18}\text{O}$ data tended to be highly variable, although the isotope peaks (and corresponding cooler temperatures) tended to coincide with winter growth zones. In addition, all individual haddock samples appeared to inhabit warmer waters (3.2 to 13.0°C) during their initial summer growth phase, following which they remained within a cooler predicted temperature range of 1.4 to 9.8°C. Furthermore, all individual samples were characterized by greater otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enrichment with increasing age (Fig. 4).

Spatial isotopic differences were also observed between haddock samples throughout the northwest Atlantic Ocean (Table 1). Differences in isotopic values between haddock samples from different geographic regions indicated that variable metabolic and environmental conditions were experienced by haddock throughout their spatial distribution (Fig. 3). The integrated otolith isotopic composition of 1 yr-old haddock samples from the 1996 year class varied significantly between regions (MANOVA: $F = 3.36$; $df = 6, 70$; $p < 0.0057$), mainly due to differences in $\delta^{18}\text{O}$ values (ANOVA: $F = 4.94$; $df = 3, 35$; $p < 0.0058$). Eastern Georges Bank haddock were significantly more enriched in otolith $\delta^{18}\text{O}$ than Gulf of Maine haddock (HSD, $p < 0.05$). Likewise, eastern Georges Bank haddock tended to be more enriched in otolith $\delta^{18}\text{O}$ than western Georges Bank haddock (except in 1994), with significant differences detected in 1997 (ANOVA: $F = 5.39$; $df = 1, 13$; $p < 0.0372$) (Fig. 3).

Eastern and western Georges Bank were characterized by slightly different environmental conditions (Fig. 5). Typically, bottom conditions over eastern Georges Bank tended to be cooler and more saline than those over western Georges Bank. In addition, observed otolith $\delta^{18}\text{O}$ values suggested a predicted temperature range of 0.2 to 6.0°C (1994 to 1997, mean \pm SD = $3.8 \pm 1.2^\circ\text{C}$) experienced by eastern Georges Bank haddock, and 2.3 to 7.3°C ($4.3 \pm 1.0^\circ\text{C}$) by western Georges Bank haddock (Fig. 6). These temperature dif-

ferences may have been partly responsible for lower growth, and hence, metabolic rates of eastern versus western Georges Bank haddock (Fig. 6). One yr-old haddock from eastern Georges Bank tended to be smaller in mean length (1994 to 1997, mean \pm SD = 24.5 ± 7.3 cm) than those from western Georges Bank (26.7 ± 8.8 cm). Likewise, otolith $\delta^{13}\text{C}$ values tended to reflect spatial differences in metabolic rates, with a significant relationship detected between $\delta^{13}\text{C}$ and mean-length-at-age 1 (linear regression: $F = 8.37$; df = 1, 73; $p < 0.005$) (Fig. 6). Furthermore, the predicted otolith $\delta^{18}\text{O}$ temperatures related to the typically more enriched otolith $\delta^{18}\text{O}$ of eastern Georges Bank haddock, where cooler bottom temperatures were experienced, than otoliths from haddock on western Georges Bank. However, bottom temperatures on Georges Bank may not fully characterize the home range occupied by haddock throughout their life history because their pre-

dicted otolith $\delta^{18}\text{O}$ temperatures appeared to decline while overall bottom temperatures on Georges Bank increased (Fig. 6).

DISCUSSION

The stable isotope chemistry of *Melanogrammus aeglefinus* otoliths provided information on the metabolic and ambient environmental conditions that individual fish in the northwest Atlantic experienced throughout their life history. We found otolith isotopic values of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ to vary on both a temporal and spatial basis, suggestive of ontogenetic differences in diet, distribution, movements, and/or stock structure. Otolith $\delta^{18}\text{O}$ values indicated that haddock modify their distribution in response to shifts in temperature regimes, most likely in order to remain in habitats optimal for growth and survival; this underlines the difficulty of temperature reconstructions from mobile organisms with optimal temperature ranges.

Annual and seasonal variation in otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ indicated that haddock undergo temporal shifts in distribution and home range throughout their life history, as well as ontogenetic shifts in diet. Declining otolith $\delta^{13}\text{C}$ in 1 yr-old haddock across Georges Bank suggested reductions in trophic levels and/or metabolic rates throughout the study period (Fig. 3). Wainright et al. (1993) found that temporal declines in scale $\delta^{13}\text{C}$ values of Georges Bank haddock were in response to reductions in trophic levels that reflected changes in prey availability, and/or a shift towards lower trophic level invertebrates. Otolith $\delta^{13}\text{C}$ values also appeared to reflect similar variation in growth and metabolic processes of haddock, where lower $\delta^{13}\text{C}$ values were associated with lower mean-lengths-at-age (Fig. 6). Furthermore, declining otolith $\delta^{18}\text{O}$ values in 1 yr-old haddock on western Georges Bank suggested warmer ambient conditions, whereas otolith $\delta^{18}\text{O}$ in haddock on eastern Georges Bank suggested more stable conditions during the study period. However, these trends were in contrast to declining temperatures on Georges Bank (Fig. 5). Consequently, haddock may be compensating for variable environmental conditions by modifying their distribution throughout their life history to reside in habitats with optimal temperature ranges (Fig. 6).

Environmental conditions often define the biological limits and distribution range of a fish stock (Iles & Sinclair 1982), where most fish reside in habitats optimal for growth and survival (Swain & Wade 1993, Maravelias 1999). Haddock undergo seasonal movements in the northwest Atlantic Ocean, presumably in response to shifts in environmental conditions (Needler 1930, McCracken 1960, Halliday & McCracken 1970).

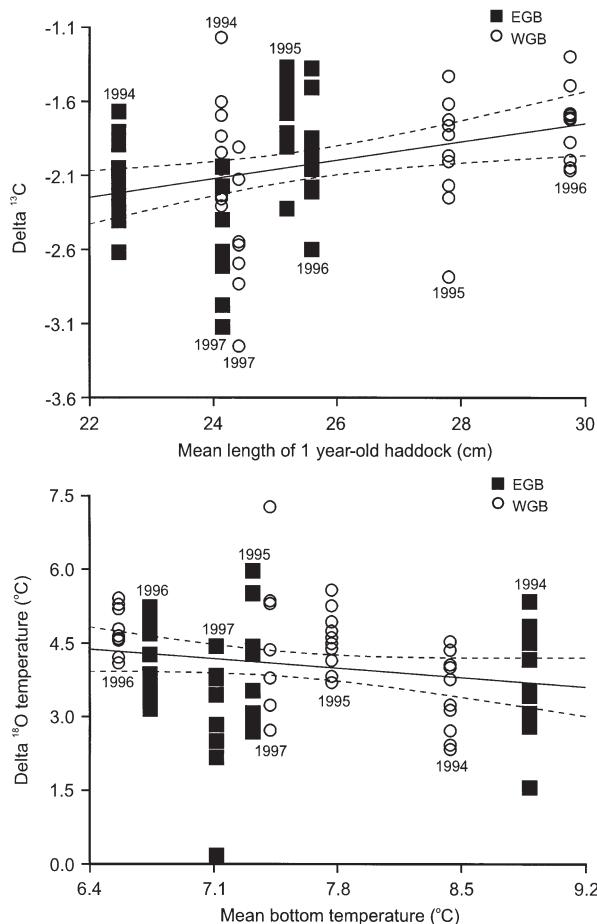


Fig. 6. *Melanogrammus aeglefinus*. Otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ predicted temperatures for 1 yr-old haddock versus mean length and mean areal bottom temperatures, respectively, for eastern (EGB) and western (WGB) Georges Bank, 1994 to 1997. Dashed lines represent 95% confidence intervals of mean regression lines

For example, on Georges Bank, haddock are generally more dispersed in shallow waters across the top of the Bank during spring when temperatures are cooler, withdrawing to deeper waters along the edge of the Bank and in the Gulf of Maine during summer and early autumn when temperatures on the Bank are warmer (Bigelow & Schroeder 1953, van Eeckhaute et al. 1999). Our results concurred indirectly with these seasonal movements, as the predicted ambient temperatures derived from the otolith $\delta^{18}\text{O}$ values relative to the actual temperatures on Georges Bank suggested that haddock were not staying on the Bank for their entire life history. Mountain & Murawski (1992) estimated haddock compensated for nearly two-thirds of the interannual changes in shelf water temperatures on Georges Bank by shifting their distribution either north-south along the shelf, or between shallow and deep waters across the shelf, to maintain some optimum or preferred temperature range. Hence, temperatures on Georges Bank alone do not fully characterize the complete range of habitats occupied by haddock throughout their life history, unlike the environmental signal recorded in the $\delta^{18}\text{O}$ values of their otoliths.

The inability of $\delta^{18}\text{O}$ in otoliths of haddock to accurately reconstruct the actual bottom-water temperatures derived from research survey data during the study period emphasizes the difficulties associated with environmental reconstructions of geographic regions from otoliths of fish that are highly mobile and capable of seeking out optimal temperature environments. Alternatively, it may also reflect the inability of research survey data to detect small variations in ambient environmental conditions. The areal mean temperature and salinity data we used in this study to characterise the physical environment may have been too coarse for detecting subtle changes in the distribution and environmental conditions experienced by haddock that were recorded in the $\delta^{18}\text{O}$ values of their otoliths. Research survey data only provides 'snapshots' of mean environmental conditions over broad spatial and temporal scales, that are usually further confounded by interannual variations in the timing of the surveys (Murawski & Mountain 1990). Finer spatial and temporal scales of the environment are needed if we are to reconstruct environmental conditions of specific geographic regions from otolith $\delta^{18}\text{O}$ values, particularly for organisms such as haddock that are highly mobile with optimal temperature ranges (Bigelow & Schroeder 1953, Mountain & Murawski 1992, Begg 1998). Moreover, temperature reconstructions from otolith $\delta^{18}\text{O}$ values can be further confounded by variation in seawater $\delta^{18}\text{O}$ composition that may result from ontogenetic changes in spatial and depth-related seasonal movements (Campana 1999).

Cyclical patterns in the otolith $\delta^{18}\text{O}$ values indicated that haddock also experience seasonal variations in their ambient environmental conditions, and demonstrated the chronological time-keeping properties of otolith stable isotopes (Fig. 4). The general cyclical pattern in otolith $\delta^{18}\text{O}$ values of the 4 yr-old haddock samples from eastern and western Georges Bank presumably corresponded with the seasonal heating cycle, albeit with significant variability between individual fish. Typically, the winter growth zones in the otoliths tended to coincide with more enriched otolith $\delta^{18}\text{O}$ or cooler environmental conditions, further suggesting that haddock undergo seasonal movements throughout their life history. In contrast, the otolith $\delta^{13}\text{C}$ values did not exhibit any clear seasonal signal, although deposition of this isotope is influenced more by metabolic processes than by ambient environmental conditions (i.e. Kalish 1991b, Gauldie 1996, Thorrold et al. 1997, Schwarcz et al. 1998).

Ontogenetic variation was also observed in the isotopic composition of haddock otoliths (Fig. 4). Greater enrichment with age of otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ suggested that higher trophic levels and cooler conditions were experienced by haddock as they got older, related to ontogenetic changes in contribution of metabolic $\delta^{13}\text{C}$ and differences in location or depth characterised by variable seawater $\delta^{18}\text{O}$ composition. Supporting this suggestion is that haddock undergo a shift in diet with age (1 to 2 yr; 20 to 30 cm), from one of small invertebrate generalists to one of larger invertebrate detritivores (Wainright et al. 1993, Garrison & Link 2000, NEFSC unpubl. data). Moreover, enrichment in otolith $\delta^{13}\text{C}$ appeared to reach an asymptotic or maximum value, followed by a decline, in almost all the individual samples. Similar results have been found in other studies where maximum $\delta^{13}\text{C}$ values corresponded with age at sexual maturation, while subsequent declines corresponded with slower age-related metabolism coupled with attainment of maximum trophic levels (Mulcahy et al. 1979, Gauldie 1996, Schwarcz et al. 1998). This scenario was certainly plausible for haddock on Georges Bank, which tend to reach sexual maturity around 2 yr of age (Begg et al. 1999), corresponding to when the asymptotic or maximum $\delta^{13}\text{C}$ values were generally observed in the individual haddock samples. Furthermore, enrichment in otolith $\delta^{18}\text{O}$ with increasing age, is due to haddock undergoing age-dependent shifts in habitat use, with juveniles tending to reside in shallower, warmer waters, and adults in deeper, cooler waters (Brown 1998, van Eeckhaute et al. 1999). Mulcahy et al. (1979) found age-related enrichment in otolith $\delta^{18}\text{O}$ for another groundfish species (*Coryphaenoides acrolepis*), and suggested that it was also due to migrations to deeper, cooler waters as the fish got older. Likewise, Edmonds

& Fletcher (1997) and Newman et al. (2000) found that pilchards *Sardinops sagax* and goldband snapper *Pristipomoides multidens*, respectively, residing in cooler waters, were more enriched in otolith $\delta^{18}\text{O}$ than those in warmer waters.

Spatial variation in the otolith isotopic composition of the 1 yr-old haddock samples suggested differences in the ambient environmental conditions experienced throughout their life history, providing an indirect measure of stock structure. However, these differences were not as pronounced as the temporal and ontogenetic differences, and distributions of both the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values demonstrated significant overlap between haddock from some of the regions, limiting the use of whole-otolith stable isotope analysis for discrimination of individual haddock to their stock of origin (Fig. 3).

Throughout the northwest Atlantic Ocean, individual spawning components of haddock have been identified on Georges Bank, in the Gulf of Maine, and along the Scotian Shelf, but uncertainty exists as to the degree of connectivity and interchange between them (Begg 1998). On Georges Bank, individual spawning components of haddock have been identified over eastern and western Georges Bank (Smith & Morse 1985, Gavaris & van Eeckhaute 1998, Begg et al. 1999, 2001, Page et al. 1999, Begg & Brown 2000), although the clockwise gyre on the Bank enables the potential for interchange of individuals between spawning components during the planktonic egg and larval stages (Begg et al. 1999, Page et al. 1999). Eastern Georges Bank haddock are more influenced by southward-flowing cooler, Scotian Shelf waters, in contrast to western Georges Bank haddock which are more influenced by warmer, Gulf of Maine waters (Drinkwater & Mountain 1997). These circulation patterns were reflected in the otolith $\delta^{18}\text{O}$ values, whereby haddock from eastern Georges Bank and the Scotian Shelf were more similar in their $\delta^{18}\text{O}$ values than those from western Georges Bank and the Gulf of Maine (Fig. 3). Furthermore, eastern Georges Bank tends to be cooler and more saline than western Georges Bank, providing a basis for the development of differences in otolith $\delta^{18}\text{O}$ as well as in growth, metabolism and, indirectly, otolith $\delta^{13}\text{C}$ values between haddock from these 2 regions. However, the apparent temperature compensation exhibited by haddock in their seasonal movements, and/or any mixing that occurs throughout their life history, may reduce the effect of environmental differences between eastern and western Georges Bank, which in turn, may account for reduced differences in their otolith isotopic compositions. Consequently, finer spatially and temporally resolved sampling of both the fish and their otoliths than that derived from whole-otolith analysis, coupled with equally resolved

environmental conditions are required for more accurate stock discrimination of haddock throughout the northwest Atlantic based on stable isotope chemistry.

Stable isotope chemistry of haddock otoliths enables insight into the retrospective environmental conditions that individual fish experience throughout their life history. Combined with life history characteristics, the use of stable $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopes can provide chronological relationships on metabolism, home range, dispersal patterns, and ambient environmental conditions. However, otolith $\delta^{18}\text{O}$ is only indicative of the external conditions about a fish, and cannot by itself be used to differentiate whether a fish has moved into cooler/warmer waters, or whether the waters around the fish have changed. Future studies could incorporate depth, temperature and location information derived from recently developed electronic data storage tags (i.e. Thorsteinsson & Eggertson 1998) to confirm these relationships and enable a more realistic means of comparing ambient environmental conditions with otolith isotopic compositions. Moreover, stable isotope chemistry may enable movements of individual haddock larvae to be back-calculated to quantify the degree of interchange between spawning components, while reconstruction of long-term environmental regimes that individual fish have experienced via fine-scale sampling of archived biological material may provide insights into stock collapses and subsequent rebuilding strategies.

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