# Stable oxygen isotope reconstruction of ambient temperature during the collapse of a cod (*Gadus morhua*) fishery

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*Abstract.* Changing environmental conditions set against a backdrop of high exploitation can result in severe consequences for commercially harvested stocks. The collapse of the Eastern Scotian Shelf cod (Gadus morhua L.) off eastern Canada was primarily due to overexploitation but may have been exacerbated by a widespread temperature decline. Recent studies have called for accurate determination of ambient temperature (the actual temperature exposure history of the fish) before discarding environmental conditions as a factor in the collapse. We used the stable oxygen isotope composition of otoliths ( $\delta^{18}O_{oto}$ ) to reconstruct the ambient temperature history of Eastern Scotian Shelf cod from 1970 to 2000 in order to determine whether the stock experienced the temperature decline or shifted their distribution to avoid it. To correct  $\delta^{18}O_{oto}$  for seawater isotope content ( $\delta O_w$ ), we generated a new metaequation for the relationship between  $\delta^{18}O_w$  (per mil) and salinity (S, in psu) on the Eastern Scotian Shelf:  $\delta^{18}O_w = 0.539 \times S - 18.790$ . The ambient temperature series revealed that the large-scale geographic distribution of mature cod remained constant through the cooling period, although their ambient temperature was cooler than expected in warmer periods and warmer than expected in cooler periods, indicating small-scale thermoregulatory movement. Although the mean hydrographic temperature was 4°C, mature cod usually inhabited the coldest available waters (mean ambient temperature  $= 3^{\circ}$ C), while the juveniles usually inhabited warmer waters (mean ambient temperature  $= 5.5^{\circ}$ C). Length-at-age was significantly related to ambient temperature, especially in the early years of growth, and therefore declining ambient temperatures were at least partially responsible for declines in asymptotic length (up to age 8 yr). The most active thermoregulatory movement occurred during a moderate warming period; therefore extreme warming events (such as those predicted under climate change) may force large-scale northward latitudinal shifts in this historically sedentary stock. Retroactive stable isotope chronologies can be an important tool in sustainable management strategies under the shifting climate conditions predicted for years to come.

Key words: ambient temperature; Atlantic cod; back-calculated length-at-age; Eastern Scotian Shelf; Gadus morhua; growth; stable oxygen isotopes.

## INTRODUCTION

Climate change is expected to significantly alter the distribution of many terrestrial and aquatic organisms (Parmesan and Yohe 2003). Marine fish species unable to shift their distribution to avoid temperature changes could be forced to suffer the consequences (Perry et al. 2005), such as the costly metabolic process of acclimation to new temperature regimes (Claireaux et al. 1995, Pörtner et al. 2001). Alternatively, movement away from otherwise favorable conditions could also negatively affect a stock by altering feeding patterns (e.g., Welch et al. 1998, Castonguay et al. 1999), mismatching predator and prey populations (Murawski 1993, Drinkwater

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2005, Perry et al. 2005), or excluding spawners from favorable larval retention and nursery areas (de Young and Rose 1993). When the effects of climate change are set against a backdrop of high exploitation, such as that faced by many groundfish in the Northwest Atlantic, the consequences for commercially harvested stocks and the ecosystems they inhabit can be severe. The collapse of the Eastern Scotian Shelf cod (Gadus morhua L.) off the coast of eastern Canada was likely due to fishing mortality (Fu et al. 2001), but a debate has arisen in the literature as to the influence of a coincident and widespread temperature decline that may have exacerbated the collapse (Choi et al. 2004). We used otoliths (ear stones) to reconstruct a 30-yr temperature exposure and growth history of the Eastern Scotian Shelf cod and to determine whether the large-scale distribution of the Eastern Scotian Shelf cod remained constant during the widespread temperature decline.

The massive decline of fish stocks has become commonplace in the North Atlantic over the last 50

Manuscript received 18 December 2007; revised 9 September 2008; accepted 16 September 2008; final version received 19 January 2009. Corresponding Editor (ad hoc): G. A. Rose.

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FIG. 1. The Eastern Scotian Shelf includes the continental shelf south of 46° N, extending roughly from 63° W to the middle of the Cabot Strait. Overlaid polygons (except 6 and 13) show the sampling areas for hydrographic measurements from the Climate Database (Gregory 2004). The main banks in the northeastern section are Banquereau (4), Misaine (5), and Middle (7).

years (Christensen et al. 2003). The Eastern Scotian Shelf off Nova Scotia, Canada (Fig. 1), was characterized by significant and sharp declines in groundfish biomass between the 1970s and early 1990s (Choi et al. 2004). Growth overfishing (in which exploitation levels damage growth potential) caused sharp declines in spawning-stock biomass before the imposition of the 200-mile (322-km) Exclusive Economic Zone (EEZ) in 1977, after which the spawning-stock biomass peaked in 1986 and subsequently collapsed (Fu and Fanning 2004). This final collapse was primarily due to both growth and recruitment overfishing (damaging growth and reproductive potential; Zwanenburg et al. 2002), but coincided with a prolonged temperature decline.

Beginning in the mid-1980s and through the early 1990s, water temperatures over an unusually large area of the Eastern Scotian Shelf (Page and Losier 1994) dropped below the long-term mean (Drinkwater 1996; Fig. 2). Latitudinal shifts in response to climate warming over several decades were noted in 15 of 36 marine fish species in the North Sea (Perry et al. 2005) and 12 of 36 marine fish and squid species in the Northwest Atlantic Ocean (Murawski 1993) and were predicted in association with future climate change for several Atlantic cod stocks (Drinkwater 2005). Climate cooling might produce similar latitudinal shifts. Since the new colder water covered many shallow banks favorable to spawning (Gagné and O'Boyle 1984), migration in response to the intrusion would have excluded cod from their traditional spawning grounds and favorable retention and nursery areas (de Young and Rose 1993). Spawning in other regions lacking these favorable conditions could result in reduced spawner condition (Begg and Marteinsdottir 2002) and therefore decreased reproductive potential (Marteinsdottir and Begg 2002).

If the cod did not migrate in response to the coldwater intrusion, they would have suffered the consequences of remaining in cooler waters. For cod populations above the southernmost limits of the species range (i.e., acclimated to relatively cool water temperatures), moderate temperature increase is positively related to productivity (Dutil and Brander 2003), growth (Campana 1996, Myers et al. 1997, Shackell et al. 1997), and recruitment (Planque and Fredou 1999). Several field studies have examined the effects of temperature on cod size-at-age (Campana et al. 1995*b*,



FIG. 2. The increased spatial coverage of cold temperatures at depth with Atlantic cod abundance (indicated by circle size) from research vessel surveys in spring of (A) 1984 and (B) 1987. Spawning-stock biomass peaked near 150 000 Mg in 1985 and was reduced to 50 000 Mg by the closure of the stock in 1993 (Fu et al. 2001).

Dutil et al. 1999, Sinclair et al. 2002b) or distribution (Perry and Gavaris 1985, Smith and Page 1995, Castonguay et al. 1999). Unfortunately, the best measure of ambient temperature (the actual temperature experienced by a fish; Brander 1995) used in these studies was either temperature-at-catch or hydrographically measured temperature linked to location-at-catch. Although associating the distribution of a stock with hydrographically measured temperature is a valid technique under some circumstances, Brander (2000) noted that otolith microchemistry could more precisely determine ambient temperature.

There are few retroactive methods capable of providing good estimates of ambient temperature, but wellpreserved otoliths can provide an accurate temperature history over the entire lifetime of many teleost fish (Campana 1999). Pairs of translucent and opaque zones of aragonitic carbonate form continuously within an otolith on an annual basis (together each pair is called an "annulus"; Casselman 1983). Like the rings of a tree, the width of these annuli can provide an estimate of age and growth history (Campana 1990) when length-atcatch is known.

When the isotopic composition of the ambient water can be determined, the mean annual ambient temperature can be calculated from the stable oxygen isotope composition of an otolith. The fractionation of <sup>18</sup>O as it is deposited into otolith aragonite increases relative to <sup>16</sup>O as temperature decreases, thus the change in <sup>18</sup>O of otolith aragonite ( $\delta^{18}$ O, in per mils [‰]) is negatively related to water temperature (Kim and O'Neil 1997). The stable oxygen isotope ratios in otoliths are metabolically inert and vary closely with the ambient seawater to provide a highly accurate reconstruction of ambient temperature (Thorrold et al. 1997, Campana 1999). Stable isotope reconstruction is also reliable because otolith formation is continual and persistent through time (Campana and Thorrold 2001), such that stable oxygen isotope ratios of otoliths have also been used to determine prehistoric temperature conditions (e.g., Patterson et al. 1993, Ivany et al. 2000, Andrus et al. 2002). Since otoliths have been collected by the Department of Fisheries and Oceans since the 1970s, the necessary materials were already available to reconstruct the ambient temperature history of the Eastern Scotian Shelf stock.

The objective of this study was to determine whether the distribution of the spring spawning cod from the Eastern Scotian Shelf remained constant during the cold-water intrusion in the mid-1980s. We expected to see a cold signal in the reconstructed ambient temperature history after 1986 if the cod did not shift their distribution to avoid the cold-water intrusion. We also examined the effects of ambient temperature on backcalculated length-at-age through the reconstructed period (1970–2000) to assess the implications of the cold-water intrusion for the subsequent stock collapse.

## METHODS

## Study area

The Eastern Scotian Shelf (ESS) extends roughly 200 km off the coast of Nova Scotia with bank surfaces ranging between 30 and 200 m depth. Middle, Misaine, and Banquereau comprise the main banks in the northeastern portion of the ESS (Fig. 1). The ESS bank surface typically intercepts the cold intermediate layer (CIL) at or above 90 m depth (Page and Losier 1994). First described by Hachey (1942), the CIL is usually at least 40 m thick and  $<5^{\circ}$ C (McLellan 1954), with little seasonal variation (Loder et al. 1997), and was the source of the cooling period from 1986 to 1992 (Page and Losier 1994). The CIL water is heavily influenced by

input from the Gulf of St. Lawrence and southern Newfoundland shelves (Loder et al. 1997).

The ESS is occupied by two substocks of Atlantic cod, delineated by their spawning season: the spring spawning component spawns on or near the surface of banks found in the northeastern region of the ESS, especially Banquereau Bank, while fall spawning occurs primarily on the more southwestern banks (Gagné and O'Boyle 1984). Banquereau Bank is also an important nursery area (Sinclair 1992). Eastern Scotian Shelf cod usually exhibit limited migrations, maximizing their proximity to favorable conditions (such as retentive gyres; Loder et al. 1997) that may help to increase the survivorship of eggs and larvae (Robichaud and Rose 2004). Stock mixing occurs in the winter as cod from the Gulf of St. Lawrence and north of Cape Breton enter the shelf region (Campana et al. 1995*a*).

The productivity of ESS cod is relatively low (Dutil and Brander 2003), with estimated rates of growth falling between the Gulf stocks to the north and Georges Bank to the south, positively related to an estimated bottom temperature gradient (Myers et al. 1997, Shackell et al. 1997). Eastern Scotian Shelf cod are currently listed by the Committee on the Status of Endangered Wildlife in Canada as a species of special concern (COSEWIC 2003).

#### Environmental conditions

Hydrographic timelines (1970-2004 inclusive) were generated from the Climate Database (Gregory 2004) using 1360 temperature and 551 salinity measurements collected in at least seven months per year (most frequently March and July) from offshore areas of the ESS (at least 20 km from the Nova Scotian coast, extending northeast from 63°W to the Cabot Strait; Fig. 1). The temperature and salinity measurements in the Climate Database were collected primarily by conductivity-temperature-depth recorder casts (CTD; 42.6%) and bathythermographs (39.6%), with hydrographic bottles (16.3%) and minilog temperature recorders (1.5%) accounting for the remainder. The 30-yr temperature and salinity series were derived from the estimated marginal means of generalized linear models with month and year as factors to account for irregular annual sampling frequency (Fig. 3).

The most applicable preexisting equation estimating the isotopic content of seawater was produced by Fairbanks (1982) for surface waters on the Scotian Shelf. The function of that pilot study was to determine water composition in the New York Bight and Gulf of Maine using isotopic signatures, but use of their equation was inappropriate for our study because of its low resolution in space and time ( $\delta^{18}$ O of the seawater was recorded in a single year along a single transect off of Halifax, Nova Scotia). The  $\delta^{18}$ O of surface water differs from waters at depth because the oxygen isotope composition of marine surface water fluctuates seasonally based on the oxygen isotope



FIG. 3. Annual mean salinity (in practical salinity units, psu) and temperature for the Eastern Scotian Shelf at depth (50–80 m) with 95% CIs (dashed lines).

composition of input meltwater, precipitation, and evaporative processes (Strain and Tan 1993). As well, seasonal stratification of the water column on the ESS prevents mixing (McLellan 1954), so the bottom-water  $\delta^{18}$ O composition (ambient waters for the demersal cod) would likely have differed markedly from the surface.

Since the Fairbanks equation was unsuitable for ESS water at depth, we generated a new equation based on salinity and  $\delta^{18}$ O seawater data sets from Khatiwala et al. (1999) and the NASA GISS Global Seawater Oxygen-18 Database (Schmidt et al. 1999) that provided more relevant relationships between  $\delta^{18}$ O and salinity for ESS water at depths between 50 and 100 m. Samples were taken at multiple points covering the offshore areas of the ESS in 1975, 1976, 1985, and 1995, increasing the likelihood of accurate temporal and spatial resolution of seawater  $\delta^{18}$ O (n = 86). A simple linear regression through these points (Fig. 4) produced the following seawater oxygen isotope relationship:

$$\delta^{18} O_w = 0.539 \times S - 18.790 \tag{1}$$

where  $\delta^{18}O_w$  is the oxygen isotope content of seawater (in per mils) and *S* is salinity (in practical salinity units [psu]). Our  $\delta^{18}O_w$  correction for the ESS cod was accurate due in part to their relatively limited migrations (Jean 1964) and the low seasonal variation in salinity in this region (Loder et al. 1997), but other marine fish stocks may experience greater seasonal variation in ambient salinity. In such cases, estimation of  $\delta^{18}O_w$  using a regression equation may be inappropriate.

# Sampling

Sagittal otoliths (see Plate 1) were collected by the Department of Fisheries and Oceans (DFO) from commercial fisheries in the Maritimes region through the International Observer and the National Port Sampling Programs from 1975 to 2001. Otoliths were selected for aging based on season (April to July) and region (Banquereau, Middle, and Misaine Banks, NAFO subdivision 4Vs) of catch in order to minimize stock mixing concerns and isolate the spring spawning cod (Campana et al. 1995*a*; Table 1).

Some otoliths were already embedded, sectioned, and mounted, while others were stored dry in envelopes. Unprepared otoliths were embedded in opaque black resin and sectioned through the core to ~1 mm thickness using a table-mounted grinder with a diamond wheel after Strong et al. (1985) to ensure uniform preparation. All embedded sections were polished using a Gesswein hand drill (Gesswein, Bridgeport, Connecticut, USA) with a silicate head to reveal fine detail and imaged using a Firewire Insight Spot12 digital camera (Diagnostic Instruments, Sterling Heights, Michigan, USA) mounted on a Nikon SMZ1000 binocular scope (Nikon Canada, Mississauga, Ontario, Canada). These high-resolution digital images ( $2048 \times 2048$  pixels) were aged along the short and long axes of growth (n = 460).

A randomly selected subsample (n = 131) of imaged otoliths aged 4–12 yr was used to construct an otolith chronology from 1970 to 2000 for isotope assay. To avoid contamination, any resin in contact with aragonite was removed to 750 µm depth using a Merchantek micromill (New Wave Research, Fremont, California,



FIG. 4. The relationship between the oxygen isotope content ( $\delta^{18}O_w$ ) of seawater and salinity (in practical salinity units, psu) for the Eastern Scotian Shelf at depth (50–100 m; *P* < 0.001,  $R^2 = 0.89$ , slope = 0.539).

USA). Sample vials were rinsed once in 95% ethanol and air dried, then sonified for a minimum of 3 min and rinsed in Super Q water (Millipore, Billerica, Massachusetts, USA) three times. Otoliths were rinsed with ethanol and then each of the eighth to second annuli were milled inwards along the short axis of growth (from the ventral edge to the core) to 450  $\mu$ m depth. To prevent contamination between samples, otoliths, sampling tweezers, and the micromill bit were cleared with clean compressed air and rinsed in ethanol between sampling events. Two to four sampling paths following transects parallel to annual translucent boundaries (to maximize sample precision after Dettman and Lohmann 1995) were usually adequate to collect the minimum of 15  $\mu$ g required for assay.

Carbonate samples were assayed for oxygen and carbon isotope content at the Woods Hole Oceanographic Institute (Woods Hole, Massachusetts, USA) using a Finnigan MAT 253 mass spectrometer with a Kiel III carbonate device (Thermo Fisher Scientific, Waltham, Massachusetts, USA). The measurements were calibrated to PeeDee Belemnite (PDB) standard,  $\pm 0.07$  precision for  $\delta^{18}$ O samples between 15 and 300 µg.

Ambient temperature was calculated using the following equation:

$$T(^{\circ}C) = -(\delta^{18}O_{oto} - \delta^{18}O_{w}) \times 0.206^{-1} + 18.010 \quad (2)$$

where  $\delta^{18}O_{oto}$  is the oxygen isotope composition of otolith aragonite (enriched 0.6% relative to calcite) and  $\delta^{18}O_w$  is the oxygen isotope composition of the ambient seawater (adapted from Kim and O'Neil 1997). A recently published update to the aragonite fractionation equation (Kim et al. 2007) was virtually identical to the equation used above, with a parallel slope and an offset of about 0.19‰, corresponding to only 0.04°C. All isotope ratios were reported relative to PDB standard (seawater values were corrected from standard mean ocean water [SMOW] by subtracting 0.22‰).

Image analysis software (Image Pro Plus, version 5.1; Media Cybernetics 2004) was used to measure otolith and annulus width from the otolith images. The widths of each annulus (to the edge of the translucent zone) and long axis (from the core to the edge of each otolith) were measured to the nearest hundredth of a millimeter. A scatter plot of total radius length (long axis) vs. fish length-at-catch was comparable to Sinclair et al. (2002*a*). Therefore, their intercept values of 0.44 mm (otolith radius,  $O_o$ ) and 2.44 cm (fish length,  $L_o$ ) were used to back-calculate length-at-age using the biological intercept equation:

$$L_i = L_c + (O_i - O_c)(L_c - L_o)(O_c - O_o)^{-1}$$
(3)

where  $L_i$  was the length of fish *i* (in centimeters),  $L_c$  was fish length-at-catch (in centimeters), and  $O_c$  was otolith radius-at-catch (in millimeters; Campana 1990).

TABLE 1. Sample information for assayed Atlantic cod otoliths.

| Sample | Original sample code | Source | Date collected | п  | Gear |
|--------|----------------------|--------|----------------|----|------|
| 1      | 19770526             | NSP    | 26 July 1977   | 5  | SOT  |
| 2      | LC182                | IOP    | 4 April 1980   | 11 | SOT  |
| 3      | MC183                | IOP    | 2 April 1980   | 10 | TOT  |
| 4      | BM143                | IOP    | 21 Âpril 1984  | 1  | TOT  |
| 5      | RC151                | IOP    | 9 May 1984     | 2  | TOT  |
| 6      | KS180                | IOP    | 26 June 1984   | 5  | TOT  |
| 7      | 860132               | NSP    | 12 April 1986  | 3  | SOT  |
| 8      | 860287               | NSP    | 9 June 1986    | 9  | TOT  |
| 9      | DJohnson             | IOP    | 22 May 1989    | 2  | SOT  |
| 10     | DJohnson             | IOP    | 8 June 1989    | 6  | TOT  |
| 11     | MP121                | IOP    | 25 June 1989   | 8  | TOT  |
| 12     | PGray                | IOP    | 22 July 1989   | 1  | TOT  |
| 13     | 920174               | NSP    | 14 April 1992  | 15 | TOT  |
| 14     | PSmale               | IOP    | 28 May 1992    | 3  | TOT  |
| 15     | 950102               | NSP    | 7 April 1995   | 7  | TOT  |
| 16     | B95-0166             | IOP    | 23 Âpril 1995  | 1  | TOT  |
| 17     | 980255               | NSP    | 9 May 1998     | 26 | LL   |
| 18     | 20010389             | NSP    | 18 June 2001   | 16 | LL   |
|        |                      |        |                |    |      |

*Notes:* The samples (*n* is the number of fish) were collected from between  $60^{\circ}$  and  $56^{\circ}$  W and between  $45^{\circ}$  and  $44^{\circ}$  N as part of the International Observer Program (IOP) or National Sampling Program (NSP). Gear types were side otter trawls (SOT), stern otter trawls (TOT), or longline (LL).

#### Data analysis

Examination of otolith isotope timelines or length-atage data between individuals involved the comparison of repeated otolith measures from many different fish. Since the age-at-catch of assayed otoliths could be as low as 4 yr, the number of annuli sampled from each individual varied from three to seven and produced an unbalanced data series. A mixed-effects model best accounted for the unbalanced data (Pinheiro and Bates 2000), and the relationship between the variable under investigation and age (annulus) was determined in order to choose between the linear and nonlinear mixed-effects forms. These relationships were determined by examining curves of the dependent variables ( $\delta^{18}O_{oto-w}$  or backcalculated length-at-age) with annulus and then fitting a variety of parsimonious least squares models to each (linear, logistic, and asymptotic; Pinheiro and Bates 2000).

Temperature (Campana et al. 1995b, Shackell et al. 1997), density dependence (Swain et al. 2003), and interannual differences in natal conditions, as represented by year class (Campana 1996), have been shown to influence body size in Atlantic cod. Therefore, ambient temperature, year class, and spawning-stock biomass (DFO 2003) through the period from 1970 to 2000 were examined for inclusion in the length-at-age model after Pinheiro and Bates (2000).

Since the number of samples divided by the number of parameters was generally <40 for both the generalized linear and nonlinear mixed-effects models, Akaike's Information Criterion (AIC; Akaike 1973) was corrected using Hurvich and Tsai's (1989) second-order bias adjustment,  $AIC_c$ :



FIG. 5. The oxygen isotope composition of otolith aragonite  $(\delta^{18}O_{oto})$  corrected for seawater  $(\delta^{18}O_{oto-w})$  with annulus (age) (mean and 95% CI).

$$AIC_{c} = AIC + 2K(K+1) \times (n-K-1)^{-1}$$
 (4)

where K is the number of model parameters and n is the sample size. These bias-corrected  $AIC_c$  values were compared using AIC weights (w):

$$w_{i} = \exp(-1/2\Delta_{i}) \times \left[\sum_{r=1}^{R} \exp(-1/2\Delta_{r})\right]$$
$$\Delta_{i} = \operatorname{AIC}_{ci} - \operatorname{AIC}_{c \min}$$
(5)

where AIC<sub>ci</sub> is the AIC<sub>c</sub> of model *i* and AIC<sub>cmin</sub> is the relative minimum AIC<sub>c</sub> (Burnham and Anderson 2002). Models with the highest *w* provide the most parsimonious explanation of the data, while additional models with w > 0.5 merit consideration (Burnham and Anderson 2002). When *w* is < 0.5 for the best-fit model, additional models should be shown (as in Calvert et al. 2005).

Statistical analysis and graphical outputs were produced using R 2.5.1 (Ihaka and Gentleman 1996) and SPSS 11.5 (SPSS 2002).

## RESULTS

#### Environmental conditions

The 30-yr hydrographic temperature timeline for the ESS (Fig. 3) illustrated the cold-water intrusion between 1986 and 1991. Although mean temperatures for the entire series never dropped below  $2^{\circ}$ C (ranging between 2.37° and 5.43°C), the minimum recorded temperatures were consistently below  $-1^{\circ}$ C for five consecutive years (1986–1991). These mean minimum temperatures were at the lower tolerance limits of cod in the North Atlantic (Page and Losier 1994) and had only been recorded consecutively in 1980 and 1981 in the 50-yr record before this mid-1980s decline.

The salinity timeline was much less variable, ranging between 32.3 and 33.3 psu. Since the salinity tolerance in Scotian Shelf cod is relatively wide compared to other species (Scott 1982), the small salinity range likely had little effect on distribution (Smith and Page 1996) or growth. The mean standard error in the salinity timeline was low (0.071 psu), thereby minimizing the error surrounding the estimation of  $\delta^{18}O_w$  (Fig. 4). According to Eq. 1, a change in salinity of 1.04 psu (the maximum range in the 30-yr timeline) would change  $\delta^{18}O_w$  by 0.56‰. The mean change in salinity from year to year was 0.19 psu (±0.03 psu), resulting in a 0.10‰ change annually in  $\delta^{18}O_w$ . Converting to ambient temperature using Eq. 2, the annual change in  $\delta^{18}O_w$  corresponds to a 0.50°C adjustment.

## Otolith isotopes

The assayed annuli had an average  $\delta^{18}O_{oto}$  of 1.49 ( $\sigma$ = 0.51). Once the  $\delta^{18}O_{oto}$  timeline was corrected for  $\delta^{18}O_w$  ( $\delta^{18}O_{oto-w}$ ), the relationship between  $\delta^{18}O_{oto-w}$ and annulus appeared curvilinear (Fig. 5), with the second and third annuli consistently more depleted in  $\delta^{18}O_{oto-w}$  than the fourth to eighth annuli. The correction for seawater isotope content displaced the series by roughly 1.5‰ (Fig. 6). The variance associated with the juvenile  $\delta^{18}O_{oto-w}$  timeline supports a wider temperature range for juveniles compared to adults, while the intermittent overlap between juveniles and adults throughout the  $\delta^{18}O_{oto-w}$  series suggests some common temperature experience (Fig. 6). The separation between juvenile and adult timelines increased after 1978, suggesting that juveniles occupied warmer waters than adults after that year.

The warmer waters occupied by juvenile cod may not have been available within the CIL: the highest hydrographically measured temperatures for the ESS between



FIG. 6. Original otolith isotope timelines (gray symbols and lines) and seawater-corrected timelines (black symbols and lines) for juvenile (2–3-yr-olds; open circles) and adult (4–8-yr-olds; squares) Atlantic cod (means and 95% CIs).



FIG. 7. Calculated ambient cod temperature (black squares, mean with 95% CIs) and estimated marginal means of hydrographic measurements (gray circles) for 4–8-yr-old Atlantic cod.

50- and 100-m depth averaged 5.30°C, while the mean ambient temperature of the juveniles was 5.48°C. In the laboratory, juvenile cod exhibited a significantly higher thermal preference compared to adults (Lafrance et al. 2005), and, in the wild, they are known to spend at least part of the year in shallower, warmer waters than adults (Jean 1964, Sinclair 1992); therefore their higher mean ambient temperature may be due to this alternate habitat. Unfortunately, the association between water temperature and salinity implies that the juveniles experienced alternate salinity conditions as well, which could have interacted with the estimation of  $\delta^{18}O_w$  to alter their ambient temperature series. The relatively flexible migration history of juveniles with respect to temperature and depth makes their salinity timeline more difficult to approximate than the more sedentary adults, so in order to investigate the relationship between hydrographic and ambient temperature, the second and third annuli were removed from consideration. The fourth annulus was included with the mature timeline because 4-yr-old cod tend to inhabit similar waters to adults (Smith et al. 1991).

Examination of the remaining timeline (adults only; Fig. 6) shows that  $\delta^{18}O_{\text{oto-w}}$  in the 1970s was relatively depleted. This depletion contributed to a significant overall trend of enrichment through the 30-yr series for each annulus (P < 0.001), but with the exclusion of  $\delta^{18}O_{\text{oto-w}}$  from annuli formed in the 1970s, the apparent increase in  $\delta^{18}O_{\text{oto-w}}$  became nonsignificant (P > 0.05). Calculated ambient temperatures fell within the range of measured temperatures (mean ambient temperature =  $3.01^{\circ}$ C; Fig. 7), suggesting that the seawater isotope correction was reasonable for mature cod in the ESS region.

Although warmer temperatures were present on the bank surfaces, the cod consistently inhabited the coldest available waters. In the 1970s, ambient temperatures were at or above the mean hydrographic temperatures, but after 1979, ambient temperatures generally fell below this series, except for an overlap period from 1987 through 1990 (Fig. 7).

With the exclusion of the second and third annuli from analysis, the relationship between  $\delta^{18}O_{oto-w}$  and annulus became linear. The relationship between  $\delta^{18}O_{oto-w}$  and the hydrographically measured temperatures could therefore be described by the linear mixed effects model for  $\delta^{18}O_{oto-w}$  otolith *i* at age *t*:

$$\delta^{18}O_{it} = (\alpha + \alpha_i) + (\beta 1 + b_i) \times \gamma_{it} + \beta 2 \times C_{it} + \beta 3 \times C.Z_{it} + \varepsilon_{it}$$
(6)

where  $\alpha$  and  $\beta$  are the fixed effects coefficients,  $\alpha_i$  and  $b_i$ are the random effects,  $\gamma$  is annulus or age, C is the hydrographic temperature in degrees Celsius, C.Z denotes the temperature vs. time (a binary variable for year before or after 1986) interaction term, and  $\varepsilon_{it}$  is error (P < 0.001; Table 2). The random effects were assumed to have a normal distribution with zero mean and a variance–covariance matrix  $\sigma_i^2 \mathbf{N}$ . The random error associated with annulus  $(\varepsilon_{ii})$  was also assumed to have a normal distribution with zero mean and a variance–covariance matrix  $\sigma_i^2 \mathbf{B}$ . Removing the fixed and random effects of the binary variable did not alter the model significantly, so they were excluded. Examination of the residuals vs. the fitted values showed that the assumption of constant variance was met (inset in Fig. 8), suggesting that the model sufficiently accounted for autocorrelation.

The  $\delta^{18}O_{oto-w}$  (ambient temperature) of the ESS cod was significantly related to hydrographically measured temperature, implying that the ESS cod showed the cooling signal after 1986 (the beginning of the cooling period) and, therefore, that the large-scale geographic distribution of the spring spawning cod remained constant. The magnitude of the temperature effect on  $\delta^{18}O_{oto-w}$  was not large (Table 2), but significant and negative. This negative coefficient was consistent with Kim and O'Neil's (1997) fractionation relationship. There was a significant weakening in the relationship between ambient and hydrographically measured temperatures after 1986, indicated by the significant interaction between the hydrographic temperature and the binary calendar year variable (before and after 1986). This interaction does not imply a change in the fractionation relationship, rather that ambient temper-

TABLE 2. Fixed effects of the linear mixed-effects model for oxygen isotope composition of otolith aragonite ( $\delta^{18}O_{oto}$ ) corrected for seawater ( $\delta^{18}O_{oto-w}$ ).

|                  |             |        | 95% CI |       |
|------------------|-------------|--------|--------|-------|
| Model term       | Coefficient | Р      | Lower  | Upper |
| (Intercept)      | 2.93        | < 0.00 | 2.74   | 3.11  |
| Annulus          | 0.06        | < 0.00 | 0.04   | 0.08  |
| Temperature      | -0.07       | < 0.00 | -0.10  | -0.03 |
| Interaction term | 0.03        | < 0.01 | 0.01   | 0.05  |



FIG. 8. Residuals of the linear mixed-effects model for oxygen isotope composition of otolith aragonite ( $\delta^{18}O_{oto}$ ) corrected for seawater ( $\delta^{18}O_{oto-w}$ ) (solid line) with the temperature anomaly (dashed line) for the Eastern Scotian Shelf cod. The two timelines are roughly aharmonic, except for the period from 1983 to 1990. Standardized residuals vs. fitted values are shown in the inset.

atures differed more from hydrographically measured temperatures after 1986.

Splitting the time series at 1986 groups a wide range of year-to-year variability into only two blocks; therefore, more in-depth consideration of the entire series was necessary. Closer examination of the residual time series illustrated that the relationship between ambient and hydrographic temperatures began to weaken before 1986 (Fig. 8). The largest residuals were present in the 1970s (positive) and years surrounding 1986 (positive before and negative after). The residuals through the 1980s mimicked rather than opposed the temperature anomaly series, implying that the ambient cod temperature was cooler than expected in warmer periods and warmer than expected in cooler periods. The  $\delta^{18}O_{oto-w}$ residuals from 1983 and 1985 are roughly twice the magnitude of the residuals from 1986 through 1989, implying that ambient cod temperatures differ more from the hydrographic temperatures before 1986 than after.

## Back-calculated length-at-age

Length-at-age was back-calculated for only 126 of 131 otoliths (Table 3) because length-at-catch was not recorded in association with otolith information for the 1977 sample.

A three-parameter logistic growth curve significantly modeled the relationship between back-calculated length and age (P < 0.0001; Table 4). After the logistic model was fit to the back-calculated length-at-age data,  $\delta^{18}O_{oto-w}$ , annulus, spawning-stock biomass, calendar year, and year class were examined for inclusion as covariates. The final nonlinear mixed-effects model (P < 0.0001) was of the following form:

$$y_{ij} = L_{\infty} \times \{1 + \exp[(x_{mid} - x_{ij})]/s\}^{-1} + \varepsilon_{ij},$$
  

$$L_{\infty} = \beta_1 + tx_{1i} + \gamma x_{2i} + t : \gamma x_{1i} x_{2i} + b_{1i},$$
  

$$x_{mid} = \beta_2 + b_{2i},$$
  

$$s = \beta_3 + tx_{3i} + b_{3i}$$
(7)

where x is back-calculated length-at-age *i* for otolith *j* (in centimeters),  $L_{\infty}$  is asymptotic length (in centimeters),  $x_{\text{mid}}$  is the inflection point (annulus), *s* is the scale,  $\varepsilon_{ij}$  is within-otolith error,  $\beta$  are the fixed effects coefficients, *b* are the random effects, *t* is  $\delta^{18}O_{\text{oto-w}}$ ,  $\gamma$  is annulus, and *t*: $\gamma$  is the interaction between  $\delta^{18}O_{\text{oto-w}}$  and annulus (w > 0.9999). The scale parameter corresponds to the distance on the *x*-axis between  $x_{\text{mid}}$  and where  $y_{ij}$  is  $L_{\infty} \times (1 + \omega)$ 

TABLE 3. Descriptive statistics of the back-calculated lengthat-age data calculated by annulus (year of growth; n is the number of otoliths).

|         |     | Length-at-age (cm) |         |       |      |
|---------|-----|--------------------|---------|-------|------|
| Annulus | п   | Minimum            | Maximum | Mean  | SE   |
| 2       | 126 | 7.46               | 39.80   | 19.22 | 0.61 |
| 3       | 126 | 14.36              | 58.02   | 29.89 | 0.72 |
| 4       | 126 | 20.11              | 64.86   | 39.56 | 0.75 |
| 5       | 124 | 32.32              | 72.92   | 48.18 | 0.75 |
| 6       | 117 | 37.50              | 79.56   | 55.39 | 0.82 |
| 7       | 101 | 41.05              | 82.58   | 61.36 | 0.97 |
| 8       | 78  | 43.18              | 91.35   | 65.90 | 1.23 |

TABLE 4. Fixed effects of the nonlinear mixed-effects model for length-at-age.

| Coefficient                                    | SE  | Р  |
|--|---|--|
| 50.38<br>1.06<br>-3.48<br>0.76<br>2.56<br>1.06 | 4.05<br>0.70<br>1.11<br>0.20<br>0.08<br>0.10                          | <0.00<br>0.13<br><0.00<br><0.00<br><0.00<br><0.00  |
|  | Coefficient<br>50.38<br>1.06<br>-3.48<br>0.76<br>2.56<br>1.06<br>0.07 | Coefficient         SE           50.38         4.05           1.06         0.70           -3.48         1.11           0.76         0.20           2.56         0.08           1.06         0.10           0.07         0.03 |

*Note:* Abbreviations are:  $\delta^{18}O_{oto}$ , oxygen isotope composition of otolith aragonite;  $\delta^{18}O_{oto-w}$ ,  $\delta^{18}O_{oto}$  corrected for seawater.

 $e^{-1}$ )<sup>-1</sup> (Pinheiro and Bates 2000). The random effects were assumed to follow a normal distribution with zero mean and 3 × 3 variance–covariance matrix  $\sigma^2 \mathbf{D}_i$ (diagonal elements  $\sigma_{\beta_1}^2$ ,  $\sigma_{\beta_2}^2$ ,  $\sigma_{\beta_3}^2$ ). The random error associated with length-at-age ( $\varepsilon_{ij}$ ) was also assumed to have a normal distribution with zero mean and a variance–covariance matrix  $s^2 \mathbf{B}_i$ . The asymptote × annulus term ( $\gamma x_{2i}$ ) was nonsignificant, but was retained since the effect of annulus on asymptotic length ( $L_{\infty}$ ) was involved in a significant interaction with  $\delta^{18}O_{oto-w}$ .

Overall, the nonlinear mixed-effects model showed that asymptotic length was negatively related to  $\delta^{18}O_{\text{oto-w}}$  (P < 0.002) and therefore positively related to ambient temperature. The interaction between annulus and  $\delta^{18}O_{\text{oto-w}}$  accounted for a significant amount of the variation in asymptotic length, suggesting that differing ontogenetic temperature associations had some ultimate cumulative effect on length-at-age. The scale of the logistic model (s) was significantly positively related to  $\delta^{18}O_{\text{oto-w}}$ , but this was likely an artifact of the negative relationship between the asymptote and  $\delta^{18}O_{\text{oto-w}}$ . It is important to note that sampled annuli were a maximum of 8 yr old, and therefore the actual asymptotic length of the wild population was likely higher than the values reported here.

There was a significant decrease in asymptotic length through the 30-yr time series (Fig. 9). This decrease began prior to 1986, continued after the end of the cooling period, and was significantly related to ambient temperature. A model similar to the nonlinear mixed-effects model above with calendar year in place of annulus was significant (P < 0.046), but inferior to the annular model ( $\Delta_i > 50$ ).

#### DISCUSSION

We reconstructed the ambient temperature history of the spring spawning cod from the Eastern Scotian Shelf, predicting that we would find a cold signal in the late 1980s if the distribution of these fish remained constant in response to the cold-water intrusion. Our oxygen isotope values were comparable to those found by Weidman and Millner (2000) for wild North Atlantic cod and revealed a significant relationship between hydrographic and ambient temperature for this 30-yr period. Length-at-age was significantly related to ambient temperature, especially in the early years of growth, and therefore declining ambient temperatures through the 30-yr series were at least partially responsible for overall declines in asymptotic length.

The isotope timeline for mature cod indicated that they usually occupied the coldest available water within the cold intermediate layer. The hydrographic temperature timeline demonstrated the persistence of coolerthan-average waters at depth after 1986, and although ambient cod temperatures were slightly higher than predicted by the average hydrographic timeline during this period, they were not beyond the temperature range available within the CIL. Although there was no superficial synchrony between the hydrographic and adult cod ambient temperature timelines, removal of between-individual variation by the linear mixed-effects model revealed a significant relationship between the two series. Catch data support the overall CIL association of mature cod: Smith and Page (1996) found that older ESS cod were likely to be associated with the CIL and that variation in cod abundance was generally associated with the proportion of sea bottom that intercepted this layer. Our results indicated that mean ambient temperatures directly overlapped mean hydrographic temperatures from 1986 to 1989, and it is therefore unlikely that the spring spawning component of the ESS cod migrated out of the region to avoid the cold-water inclusion after 1986 (although they may have selected warmer waters within the CIL).

Large-scale migrations in response to climate warming have frequently been found in cod stocks close to the northern limits of their distribution (Perry et al. 2005), but contradictory large- and small-scale distribution shifts have been reported for some cold-acclimated stocks. Hutchings (1996) used stock density aggregate models and weight-at-age data to conclude that northern cod remained relatively stationary in response to a



FIG. 9. Nonlinear least-squares fitted asymptotic length by mean otolith year of formation fit with a LOWESS 35% smoother. Mean otolith year refers to the mean year of annulus formation for each otolith.

cold-water intrusion. In contrast, Rose et al. (2000) noted that neither physiological nor morphometric characteristics were consistent with a stationary distribution for northern cod and that they were much more consistent with a large-scale southward migration in response to colder temperatures. On the ESS, Fu et al. (2001) noted that a lack of increased abundance in regions close to the ESS pointed away from a large-scale distribution shift in the spring spawning cod. Therefore, it is possible that large-scale migrations in response to environmental conditions are only likely when the population in question routinely undertakes large-scale seasonal migrations, as is the case with northern cod (Rose 1993).

Since the ambient temperature series remained within the range of CIL temperatures after 1986 (implying relatively constant distribution during the cold-water intrusion), the post-1986 residuals from the relationship between hydrographic and ambient temperature may be explained by the small-scale migration history of the fish. Cod transplanted from the ESS to a laboratory setting performed small-scale depth migrations (<10 m) to maintain stable ambient temperatures (Claireaux et al. 1995). Claireaux et al. (1995) theorized that thermoregulatory movement helped individuals avoid the high bioenergetic costs of acclimation to temperature changes of 2.5°C. Catch data from the ESS were consistent with this small-scale migration hypothesis. Page et al. (1994) found cod in unusually warm waters in 1989 (the only year in the ambient temperature series of mature cod that overlapped hydrographic temperatures since the 1970s), but at depths consistent with other survey years, suggesting that the cod selected warmer waters within their historic distribution limits. If these smaller scale migrations were responsible for the residuals of the linear mixed-effects model, synchrony between  $\delta^{18}O_{oto-w}$ and the temperature anomaly series (opposition between ambient and hydrographic temperatures) would indicate active thermoregulatory movement starting before the 1986 cooling period.

If cold-adapted stocks are more likely to alter their distribution in response to a warming event, it is perhaps unsurprising that our otolith-derived ambient cod temperatures differed more from hydrographically measured temperatures during a warming period than during the cold-water inclusion after 1986. This warming period peaked in 1984 (when the temperature anomaly was 1°C warmer than the 30-yr mean), as did the residual series, implying that ESS cod used thermoregulatory movement during the warming period to select cooler waters that differed more from the CIL temperature anomaly than at any other time in the 30-yr series.

Juvenile cod did not exhibit the same cold-temperature associations as the adults, but consistently inhabited warmer waters. Since depleted  $\delta^{18}O_{oto-w}$  readings were consistent with the association of juveniles with warmer waters than adults, the separation between the  $\delta^{18}O_{oto-w}$  of juveniles and adults may be related to their separate life histories. In general, the temperature tolerance range of juvenile cod was wider than that of adults, and consequently juveniles have a more flexible geographic range (Brander 1996). Juveniles also performed wide diel vertical migrations and experienced a wider range of temperatures in stratified summer waters than the range projected for adult cod in a laboratory study by Clark and Green (1991). This wider range was supported by survey data, as juvenile cod were often found in warmer, shallower water than older cod on the ESS (Sinclair 1992).

Overall, back-calculated length-at-age was significantly related to ambient temperature. Before the cold-water inclusion in the mid-1980s, the ESS cod exhibited less yearly growth than more southerly stocks (Shackell et al. 1997), and declines in mean length were becoming apparent even in the late 1970s (Beacham 1982). Since ambient temperature can determine the temperature history of an individual more precisely than temperature-at-catch (Brander 2000), previous studies linking growth to hydrographically measured temperature (e.g., Campana et al. 1995b, Shackell et al. 1997, Dutil et al. 1999, Swain et al. 2003) may have under- or overestimated the influence of temperature on growth. Since Krohn et al. (1997) found that growth rates in two of three northern cod stocks were not physiologically limited by cold water, the effects of hydrographic temperature on cod growth in the ESS may have been overestimated.

Smith and Page (1996) found that cod became more abundant in trawls with increased CIL abundance, and thus the catchability of cod in warmer temperatures (i.e., those moving slightly further down bank slopes to take advantage of warmer waters) may have been reduced, increasing differences between the average temperatureat-catch and ambient temperature. These differences could have significantly altered estimations of average temperature-at-catch. Declines in length-at-age after 1986 were almost certainly temperature related, but small-scale thermoregulatory movements would have reduced the negative effects of the cooling period after 1986 as well as the positive effects of the warming period before 1986. These year-to-year changes in small-scale migration based on random environmental conditions highlight the importance of determining an accurate ambient temperature series.

Our significant relationship between ambient temperature and asymptotic length is the first to link an accurate measure of ambient temperature to length-atage of wild cod over a multi-decadal timescale. This relationship adds to the findings of previous studies that significantly related length-at-age (Campana et al. 1995b, Shackell et al. 1997) or distribution (Page et al. 1994) to hydrographically measured temperature. Additionally, calendar year, year class, and spawning-stock biomass were significant covariates of alternate models in our study, although they did not minimize model



PLATE 1. (Left) Paired sagittal otoliths from a cod (*Gadus morhua*). Although the cod uses the otoliths for balance and hearing, they are an important source of age and environment information for science. (Right) Transverse section of a cod otolith showing annual growth bands (annuli). Since the year of collection (corresponding to the edge of the otolith) is known, each annulus can be assigned a year of formation. Photo credits: S. E. Campana.

selection criteria. These results are consistent with the findings of Swain et al. (2003) that temperature variations were more important than abundance when modeling growth on the ESS.

Temperature in this region may soon be altered for an extended duration. Drinkwater (2005) noted that northward range expansion would be likely for many stocks, but suggested that climate warming would result in an abundance increase in ESS cod, as local warming produced increased productivity. Although we did find a positive relationship between ambient temperature and asymptotic length, our findings present another, less optimistic possibility. Extrapolation of the moderate thermoregulatory movement of the ESS cod under moderate warming to larger scale thermoregulatory migration under climate change scenarios could suggest a northward latitudinal shift in the stock, as exhibited by cod in the North Sea (Perry et al. 2005). Since the warming anomaly pre-1986 of ~1°C produced relatively large differences between ambient and hydrographic temperatures (indicative of the most active thermoregulatory movement in the 30-yr series), temperature change predicted under climate warming scenarios (2°-4°C; Drinkwater 2005) could completely exclude cooler waters from bank surfaces and induce large-scale migration in the ESS cod, despite their sedentary history. Exclusion of the cod from these favorable spawning grounds could result in negative consequences to larval retention and nursery habitat, as proposed in de Young and Rose's (1993) cold-water exclusion scenario. Future work should seek to determine whether there is some warm temperature threshold beyond which small-scale thermoregulatory movements become largescale latitudinal shifts.

Future work could also extend the scope of the annulus time series. The 1970s presented results contrary to other years in a number of different instances: (1) the overlap between  $\delta^{18}O_{oto}$  of juvenile and mature cod, (2) the lack of harmony between the  $\delta^{18}O_{\text{oto-w}}$  residual series and the temperature anomaly series, and (3) the only instance in which the ambient temperature timeline for mature cod was warmer than the hydrographic timeline for more than a single year. Indeed the decline in ambient temperature throughout the series was significant only when the 1970s were included. Swain and Kramer (1995) also found cod in the Gulf of St. Lawrence occupying warmer waters from 1972 to 1979 (except 1977), suggesting that this phenomenon persisted over a wider geographic region than just the ESS. As with their study, our interpretation of the 1970s was restricted by the truncation of the ambient temperature timeline at 1970, which begs the question: were the thermoregulatory movements of the period after 1980 consistent with the long-term history of the ESS cod or some aliased anomaly? Pauly (1995) cautioned that populations under heavy exploitation were unlikely to provide reliable baseline data. Since otolith collection and preservation began after commercial fishing on the ESS, archaeological reconstruction may be the only sure method of determining the true baseline in this region.

Our study has demonstrated that  $\delta^{18}$ O can provide an accurate reconstruction of the ambient temperature of a fish population over many years. To our knowledge, this 30-yr chronology is the largest and longest continuous multi-otolith isotope chronology developed to date. While the practice of chronology building (using a series of subjects to extend annular characteristics beyond the life span of an individual) is commonplace in dendrochronology, it is just beginning to gain popularity in the

field of otolith research (Black et al. 2005). Retroactive chronologies that reach beyond the beginnings of commercial exploitation could provide important baseline data for the growth and migratory history of a stock, especially in species for which the  $\delta^{18}$ O fractionation temperature relationship can be confirmed. Our use of a salinity– $\delta^{18}O_w$  relationship specific to our study site, in conjunction with a salinity time series, provided an accurate correction for seawater isotope composition for every year of our study. Such a correction may not always be possible, especially in cases in which accurate records of ambient salinity conditions are not available or for species or stocks with a migratory history through multiple water masses. In such cases, temperature reconstructions can be estimated assuming a constant seawater isotope content (e.g., Ivany et al. 2000), albeit with an attendant loss in precision and accuracy. Accurate temperature reconstructions require both a local salinity– $\delta^{18}O_w$  relationship and a salinity time series.

Monitoring the ambient stock temperature represents a crucial step in responsible ecological management in several ways. First, the "noise" produced by the effects of environmental conditions on a stock are best removed in order to determine the effects of commercial exploitation (Rothschild 1992). Second, small-scale thermoregulatory movements may indicate a response to unusual environmental conditions. Monitoring for these changes could be achieved by more frequent assay of otoliths and seawater to monitor the ambient temperature of a stock relative to hydrographic conditions.

In summary, the spring spawning component of ESS cod remained on their traditional spawning grounds throughout the cooling period from 1986 to 1991, but responded to temperature extremes within the 30-vr series using small-scale thermoregulatory movements from 1980 onwards. Overall declines in asymptotic length could be at least partially attributed to ambient temperature, although the greatest effects of temperature act upon early juvenile growth. Ambient temperature significantly influenced length-at-age on the ESS. Long-term stable isotope series are a powerful tool for reconstructing past conditions to form the basis of sustainable management strategies in the future. Our ambient temperature reconstruction has shown that although future climate warming could increase the productivity of the ESS cod in the long term, an extreme temperature increase could result in decreased recruitment and further decline.

#### Acknowledgments

Many thanks to Warren Joyce, Raouf Kilada, Linda Marks, Coilin Minto, Romney McPhie, Anna Calvert, Dylan Fraser, Tania Davignon-Burton, Shelley Bond, Mark Showell, Doug Gregory, Brian Petrie, Paul Bentzen, Jeff Hutchings, Martin Castonguay, Mark Johnston, Sandra Walde, Dalhousie University, the Bedford Institute of Oceanography, and the reviewers of this manuscript for their helpful suggestions. Financial support was generously provided by NSERC, the Department of Fisheries and Oceans Canada, the Clemens-Rigler travel fund, and the Patrick Lett Fund.

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