Can changes in length-at-age and maturation timing in Scotian Shelf haddock (*Melanogrammus aeglefinus*) be explained by fishing?

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Abstract: Factors affecting size-at-age in fish populations include temperature and fishing where the latter can represent a strong selective force on size-at-age variation through changes in population growth and maturation. Over the past three decades, Scotian Shelf haddock (*Melanogrammus aeglefinus*) exhibited declines in maturation timing and mature fish length-at-age. Here, we examine these declines with respect to temperature, stock biomass, and fishing. We employ the thermal integral (growing degree-day, GDD, °C·day) to examine the variation in length-at-age (length-at-day, LaD, cm) and maturity (age-at-50%-maturity) that is attributable to temperature. Unexplained variation in LaD and age-at-50%-maturity remains and is characterized by declines in the LaD-at-GDD regression parameters and the thermal constant for maturity with increasing year-class. We find no significant correlation between the temperature-independent declines in LaD and stock biomass. The combination of high fishing mortality (favouring early maturation) and sustained harvesting of large fish (fast-growing, late-maturing individuals) offers the simplest explanation for the systematic decline in inferred growth and age-at-maturity for Scotian Shelf haddock. These results are consistent with other exploited populations and recent laboratory experiments quantifying the effects of fishing on size-at-age and age-at-maturity.

Résumé : Les facteurs qui affectent la taille en fonction de l'âge dans les populations de poissons comprennent, entre autres, la température et la pêche; cette dernière représente une importante force de sélection sur la variation de la taille en fonction de l'âge par les modifications de la croissance et de la maturation de la population. Au cours des trois dernières décennies, les aiglefins (*Melanogrammus aeglefinus*) de la Plate-forme néo-écossaise ont connu un déclin dans le moment de la maturation et dans la longueur en fonction de l'âge des poissons adultes. Nous examinons ici ces déclins en fonction de la température, de la biomasse du stock et de la pêche. L'intégrale thermique (degrés-jours de croissance, GDD, °C·jour) nous sert à examiner la variation de la longueur en fonction de l'âge (longueur à un jour donné, LaD, cm) et de la maturité (âge de 50 % de maturité) attribuable à la température. Il reste de la variation inexpliquée de LaD et de l'âge de 50 % de maturité et elle est caractérisée par des déclins dans les paramètres de la régression de LaD à CDD et dans la constante thermique pour la maturité dans les classes d'âge supérieures. Il n'existe aucune corrélation significative entre les déclins de LaD indépendants de la température et la biomasse du stock. La combinaison d'une mortalité élevée due à la pêche (qui favorise une maturation hâtive) et de la récolte continue de poissons de grande taille (individus à croissance rapide et à maturation tardive) semble présenter l'explication la plus simple du déclin systématique de la croissance et de l'âge à la maturité obtenus chez les aiglefins de la Plate-forme néo-écossaise. Ces résultats s'accordent avec ceux provenant d'autres populations exploitées et avec des expériences de laboratoire récentes qui mesurent les effets de la pêche sur la taille en fonction de l'âge et sur l'âge à la maturité.

[Traduit par la Rédaction]

Introduction

Fishing mortality can affect population maturation and growth (e.g., Rijnsdorp 1993; Law 2000; Heino and Gødo 2002) and can result in declines in observed size-at-age (Sinclair et al. 2002*a*; Engelhard and Heino 2004; Hutchings 2005). High fishing mortality can induce changes in maturity timing, as late-maturing fish are more prone to being harvested before first-spawning (e.g., Roff 1992; Heino and Kaitala 1999; Conover 2000). This is of particular concern for species that mature at a relatively large size resulting in high cumulative fishing mortality prior to first-spawning (Heino and Gødo 2002; Armstrong et al. 2004). In addition, the nature of fishing gear and the use of minimum size limits can result in size selectivity in many fisheries that preferentially harvest large fish (Heino and Gødo 2002; Sinclair et al. 2002*a*; Shin et al. 2005). Thus, fishing mortality removes large fish and can result in a population disproportionately

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represented by maturation at a younger age and smaller size such that the size-at-age of mature fish is expected to decline (Rijnsdorp 1993; Heino and Gødo 2002). Evidence of these changes in growth and life history dynamics is often associated with periods of exploitation (e.g., Olsen et al. 2004; Hutchings 2005; Conover et al. 2009) and may have a genetic link (e.g., Swain et al. 2007, 2008; Heino et al. 2008). Variation in growth and maturation affects population size and recovery rates through recruitment via fecundity and egg size (Ratner and Lande 2001; Hutchings 2005). Consequently, evaluating fishing pressure and its effects on fish size and maturity is instrumental in assessing the production capabilities of a population, determining sustainable exploitation rates, and predicting recovery in overexploited stocks.

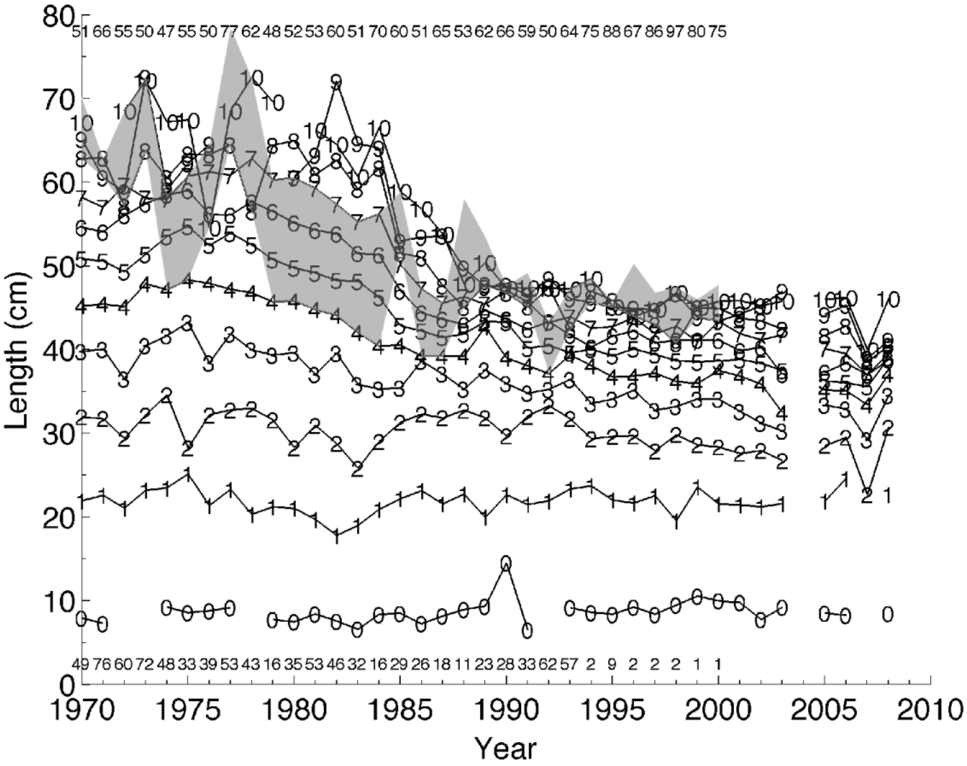
Management strategies differ depending on the source(s) of variation in size-at-age (e.g., length-at-age) and thus require the sources to be identified before successful strategies can be implemented (Sinclair et al. 2002*b*; Hsieh et al. 2006). The ability to assess the effect of fishing pressure on the variation in population length-at-age lies in the ability to disentangle the different factors that can contribute to length-at-age variation. The predominant fishing-independent factors include temperature, food consumption, food quality, phenotype, and genotype. Of these, it is temperature that governs growth via reaction rates at the cellular (metabolic) level (Fry 1971) and the effect of temperature on length-at-age variation must be examined foremost (Brander 1995). The effects of temperature changes on metabolism are near instantaneous and these effects are integrated over time to produce observed length-at-age (i.e., a growth integral). Thus, examining temperature effects on length-at-age variation requires a temperature metric that is also integrated over time. For over two centuries in other areas of ectotherm research (e.g., agriculture and entomology: Seamster 1950; Atkinson 1994; Bonhomme 2000), the thermal integral (i.e., the growing degree-day, GDD, °C·day) has been successfully employed to explain temperature-dependent size-at-age variation in a physiologically meaningful manner. The GDD is a simple estimate of the time integral of daily temperature measured above a given temperature threshold. Recently, it has been shown to explain >90% of variation in fish length-at-age among 41 different data sets representing a range of species, stocks, environments, temperature regimes, and laboratory and field studies with strong linear relationships between length-at-age and GDD within a developmental stage (i.e., while the energy budget of the fish remains unchanged; Neuheimer and Taggart 2007). When life history transitions (e.g., smoltification, maturation) are marked by a change in energy allocation from growth to other physiological demands (e.g., in the case of maturation, to allow for gonad production, spawning behaviour, etc.: Jobling 1982; Lambert and Dutil 2000), an abrupt change in the relationship between length-at-age and GDD occurs. Such a change identifies a thermal constant: the amount of heat (GDD) needed to achieve some aspect of development (Campbell et al. 1974). The thermal constant has been employed to determine development time to stage (e.g., emergence, maturation) in agriculture and entomology (e.g., Trudgill et al. 2005) and is equally applicable to fish development timing (Lange and Greve 1997) including egg hatching time and smoltification (Neuheimer and Taggart 2007), and maturation. Thus, the GDD is the "correct" measure for examining length-at-age and maturation time variation among fishes, allowing one to disentangle effects of temperature from those of other factors (food availability, genetic predisposition, fishing effects, etc.) by examining growth and development on a physiologically relevant time scale.

Scotian Shelf haddock (*Melanogrammus aeglefinus*) (Northwest Atlantic Fisheries Organization (NAFO) statistical divisions 4VW) demonstrate marked declines in length-at-ages 3+ over the period 1970 through 2008 (Frank et al. 2001; Mohn and Simon 2004; R. Mohn, Population Ecology Division, Fisheries and Oceans Canada, 1 Challenger Drive Dartmouth, NS, B2Y 4A2, Canada, unpublished data). These declines were coincident with declines in length- and age-at-maturity, changing temperature, population biomass, and high fishing pressure (Frank et al. 2001). Neuheimer et al. (2008) used GDD to estimate year-class-specific thermal histories for Scotian Shelf haddock and its relation to length-at-age variation from 1970 through 2003. The results demonstrated that the thermal integral explained a surprisingly small portion of the length-at-age variation, even when stock distribution changes and associated varying thermal histories were incorporated into the analyses. Here, we expand on Neuheimer et al. (2008) to identify and quantify sources of variability in haddock length-at-age and maturation schedules and we include more recent data (2005 through 2008) concerning the thermal environment and stock metrics. We quantify temperature-dependent length-at-age variation using year-class-specific thermal histories (GDD) over the period 1970 through 2008. We then determine how much of the unexplained variation may be attributable to density dependence effects estimated via stock biomass and consider what role fishing mortality may have had in generating the long-term decline in length-at-age. Finally, we estimate the thermal constant of maturation over the study period and assess the roles that temperature versus other factors may play in explaining the decline in age-at-maturity found in this stock.

Materials and methods

Haddock length-at-age data (described as length-at-day, LaD, cm, for consistency with the GDD metric) from the Scotian Shelf, eastern Canada (NAFO division 4VW), for 1970 through 2008 were obtained from Fisheries and Oceans Canada research vessel (RV) surveys conducted annually in July across the Scotian Shelf following standardized sampling protocols using depth-stratified random sampling (Frank et al. 2001; Mohn and Simon 2004; R. Mohn, Population Ecology Division, Fisheries and Oceans Canada, 1 Challenger Drive Dartmouth, NS B2Y 4A2, Canada, unpublished data) (Fig. 1). We examined year-classic-specific LaD for all ages but restrict our further analyses to mature haddock (ages 5 through 10, with age 11+ too sparse to include; Mohn and Simon 2002) to avoid the change in LaD-at-GDD parameterization that occurs upon maturation (see Introduction and Neuheimer and Taggart 2007). Year-class-specific time series of LaD were examined for the 1965 through 2001 year-classes for ages 5 through 10 for comparison with GDD analysis (below) as linear regression according to

Fig. 1. Temporal variation in length-at-age (cm) (symbols: 1970 through 2000, Frank et al. 2001; 2001 through 2008, R. Mohn, Fisheries and Oceans Canada, Population Ecology Division, Bedford Institute of Oceanography, 1 Challenger Drive, Dartmouth, NS B2Y 4A2, Canada, unpublished data) and lengths associated with highest fishing mortality (gray shading, see Materials and methods section; derived from data in Frank et al. 2001). Proportion of exploitation pressure on lengths-at-highest-fishing-mortality (%) is shown in text at the top of the figure. Also shown is annual exploitation pressure on ages 5 through 10 (text at the bottom of the figure).



(1) $\text{LaD} = \beta' \times \text{Time} + \alpha'$

where β' is the slope, cm·day^{-1}, and α' is the intercept, cm, of the LaD-at-time relation and "Time" is in days.

Following Neuheimer et al. (2008), monthly mean temperature data were obtained from the Bedford Institute of Oceanography hydrographic database for 1960 through 2008 and the 75 ± 25 m depth stratum over the area of the Scotian Shelf associated with the highest haddock abundance (Neuheimer et al. 2008). Mean monthly temperature estimates were interpolated (month-to-month) where necessary and then at day to provide daily estimates for GDD calculation.

GDD at day n, °C·day, was calculated for each year-class as

$$(2) \qquad \text{GDD}(n) = \sum_{i=1}^{n} (T_i - T_{\text{Th}})\Delta d, T_i \geq T_{\text{Th}}$$

where T_i is the interpolated mean daily temperature at day i, i = 1 at spawning (i.e., 16 May or day-of-year 136, representing the midpoint of the April–June peak in spawning: Page and Frank 1989; Waiwood and Buzeta 1989), T_{Th} is the predetermined threshold temperature (T_{Th} = 0 °C; Neuheimer and Taggart 2007), and Δd is a set time step (sampling frequency, i.e., 1 day). Variation in LaD and GDD for the fish aged 5 through 10 of each year-class was compared and quantified through linear regression according to

(3) $\text{LaD} = \beta \times \text{GDD} + \alpha$

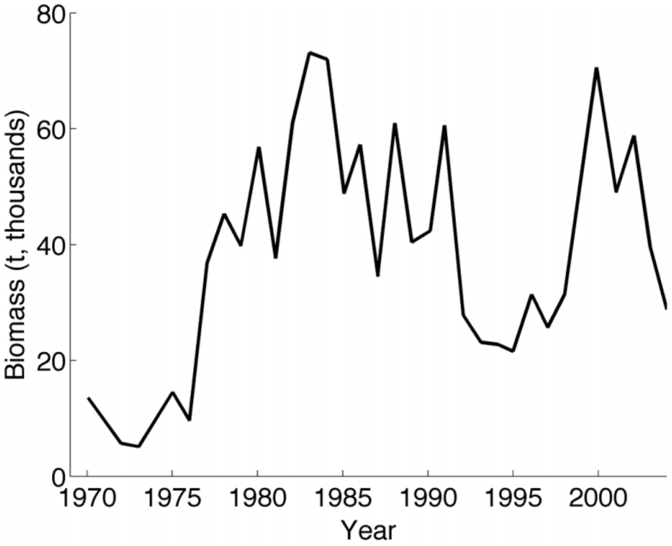
where β is the slope, cm·(°C·day)$^{-1}$, and α is the intercept, cm, of the LaD-at-GDD relation. Variability in β and α among year-classes was assessed for trends that would indicate temperature-independent variability in LaD among year-classes.

Concurrent with the changes in size-at-age for this stock are changes in the total biomass estimates, tonnes (t), demonstrating increases in biomass over the late 1970s, declines in the early 1990s, and increases again in the late 1990s (Fig. 2). To assess the relation between stock biomass (density) and variation in LaD, biomass was averaged over the years corresponding to ages 5 through 10 for each year-class and the resulting averages were compared with the β and α of the LaD-at-GDD relations.

Measures of fishing intensity and size selection were estimated using annual fishing-mortality-at-age (F_{A}) for 1970 through 2000 derived from a standard age-based sequential population analysis (SPA; Frank et al. 2001; see Appendix A) with estimated trends in fishing-mortality-at-age in agreement with the known exploitation history for the stock as well as mortality rates estimated from annual surveys (Frank et al. 2001). Annual exploitation pressure (E, %) on ages 5 through 10 was estimated for each year over 1970 through 2000 as

$$(4) \qquad E = \left(1 - e^{\overline{F}_{\text{A}}}\right) \times 100$$

Fig. 2. Total 4VW haddock biomass. Data extracted from fig. 1 in Mohn and Simon (2004).



where $\overline{F}_A$ is the mean instantaneous fishing-mortality-at-age for ages 5 through 10. Fishing-mortality-at-age was employed to determine the ages at which fishing mortality was highest and was converted to fishing-mortality-at-length (F_L) using the length-at-age estimates. The length-at-highest-fishing-mortality (L_{high}) was determined for each year and the proportion of total fishing mortality concentrated on the length-at-highest-fishing-mortality ($\%F_{L_{high}}$) was calculated as

$$(5) \qquad \%F_{L_{high}} = \frac{\sum F_{L_{high}}}{\sum F_L} \times 100$$

where $\sum F_{L_{high}}$ is the sum of F_L at the lengths-at-highest-fishing-mortality and $\sum F_L$ is the sum of F_L for all lengths.

Variability in the thermal constant of maturity was examined among year-classes. Age-at-50%-maturity was obtained from the annual RV survey for 1978 through 2000 (Mohn and Simon 2002). Average age-at-50%-maturity was estimated for each year-class where data were available (i.e., 1975 through 1997) and the thermal constant of maturity, °C·day, was estimated for each year-class using integrated temperature from spawning to age-at-50%-maturity.

All statistical analyses were performed using MATLAB (version 6.5; MathWorks Inc., Natick, Massachusetts). Statistical significance was evaluated at 0.05 unless otherwise stated.

Results

Following Neuheimer et al. (2008), Scotian Shelf haddock demonstrate significant declines in length-at-ages 3+ from 1970 through 2008 with the highest rates of decline occurring over the period ~1975 through 1990 for ages 4 through 6 and ~1982 through 1989 for ages 7 through 10 (Fig. 1; Table 1). Length-at-ages 0+ and 1 show no trend over time ($P > 0.18$), while length-at-age 2 shows a marginal decline, as time explains only 26% of the variation in length-at-age in comparison with >75% for older ages (Table 1).

Table 1. Parameters of linear regression for length-at-age (cm) of Scotian Shelf haddock as a function of year from 1970 through 2008.

Age (years)	Slope (cm·year^{-1})	Intercept (cm × 10^3)	r^2	P
0				0.18
1				0.62
2	–0.11	2.3	0.26	0.0011
3	–0.26	5.9	0.75	<0.001
4	–0.38	8.7	0.86	<0.001
5	–0.49	11.0	0.87	<0.001
6	–0.62	13.7	0.88	<0.001
7	–0.68	14.9	0.86	<0.001
8	–0.72	16.0	0.82	<0.001
9	–0.71	15.8	0.76	<0.001
10	–0.82	19.1	0.79	<0.001

Year-class-specific length-at-day as a function of calendar time shows significant variation among year-classes (Fig. 3*a*) with decreases in intercept (α', cm; linear regression: $\alpha' = -0.21$ year-class – 454 cm; $r^2 = 0.28$, $P = 0.0078$; Fig. 4*a*) and slope (β', cm·day^{-1}; linear regression: $\beta' = -0.0019$ year-class – 0.38 cm·day^{-1}; $r^2 = 0.54$, $P < 0.0001$; Fig. 4*c*) with increasing year-class. These trends remain when LaD is assessed on a GDD time scale (Fig. 3*b*) where declines in the intercept (α, cm; linear regression: $\alpha = -0.30$ year-class – 634 cm; $r^2 = 0.52$, $P < 0.0001$; Fig. 4*b*) and the slope (β, cm·(°C·day)$^{-1}$; linear regression: $\beta = -2.2 \times 10^{-5}$ year-class – 0.045 cm·(°C·day)$^{-1}$; $r^2 = 0.40$, $P = 0.0011$; Fig. 4*d*) occur with increasing year-class. All results were similar when temporal variability in haddock distribution was incorporated into temperature measures (see Neuheimer et al. 2008).

There was no correlation between the intercepts (α; $P = 0.45$; Fig. 5*a*) or slopes (β; $P = 0.11$; Fig. 5*b*) of the LaD-at-GDD relations and the year-class-specific average biomass. Fishing mortality on mature fish (ages 5 through 10) was two- to threefold greater than the management target up until the closure of the fishery in 1993 (Frank et al. 2001) with annual exploitation rates on ages 5 through 10 averaging 39% (Fig. 1). Instantaneous fishing mortality (F) was systematically targeting the larger fish in the stock each year throughout the study period (Figs. 1 and 6*a*) with the exploitation on the lengths-at-highest-fishing-mortality constituting between 47% and 77% of the total (Fig. 1). Over the same period, lengths-at-ages 3 through 12 declined such that the lengths associated with the highest annual fishing mortality paralleled the decline in length of the largest fish in the stock (Fig. 1). This pattern is consistent with temporal changes in the exploitation-rate-at-length as the fishery targeted individuals ≥50 cm length (ages 5+) until those sizes virtually disappeared near 1990. At this time, the fishery continued targeting the age 5+ fish, now in the 40–50 cm size range (Fig. 6*b*), and continued to do so following the closure of the fishery in 1993, although at a much reduced exploitation rate (Figs. 1 and 6*b*).

Maturity timing decreased from an age-at-50%-mature of ~3.5 years in the late 1970s to 2.5–3 years in the late 1990s (Mohn and Simon 2002). Year-class-specific age-at-maturity (year) demonstrates a significant decline with increasing year-class (age-at-maturity = –0.025 year-class – 53 years;

Fig. 3. Length for Scotian Shelf haddock ages 0 through 10 as a function of (*a*) calendar time and (*b*) growing degree-days. Lines indicate a significant linear relationship among length of ages 5 through 10 and time or GDD ($P < 0.05$). The shaded area is variability in maturity timing (see Materials and methods). Data labels denote year-class decade and year.

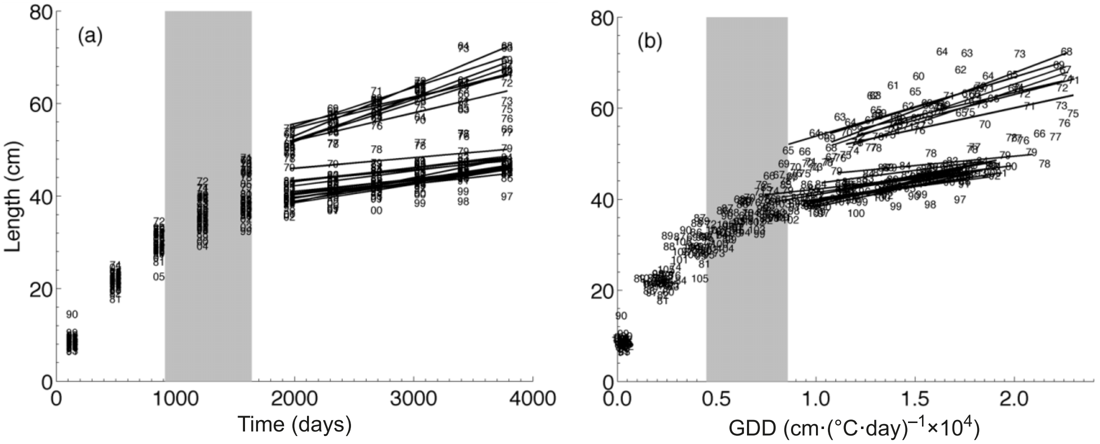


Fig. 4. Parameters of the (*a* and *c*) LaD-at-time and (*b* and *d*) LaD-at-GDD linear relations for Scotian Shelf haddock year-classes. Intercepts of the (*a*) LaD-at-time and (*b*) LaD-at-GDD relations demonstrate significant declines with increasing year-class (solid line, linear regression; broken lines, 95% confidence intervals around the prediction: (*a*) $r^2 = 0.28$, $P = 0.0078$; (*b*) $r^2 = 0.52$, $P < 0.0001$). Slopes of the (*c*) LaD-at-time and (*d*) LaD-at-GDD relations demonstrate a significant decrease with increasing year-class (solid line, linear regression; broken lines, 95% confidence intervals around the prediction: (*c*) $r^2 = 0.54$, $P < 0.0001$; (*d*) $r^2 = 0.40$, $P = 0.0011$).

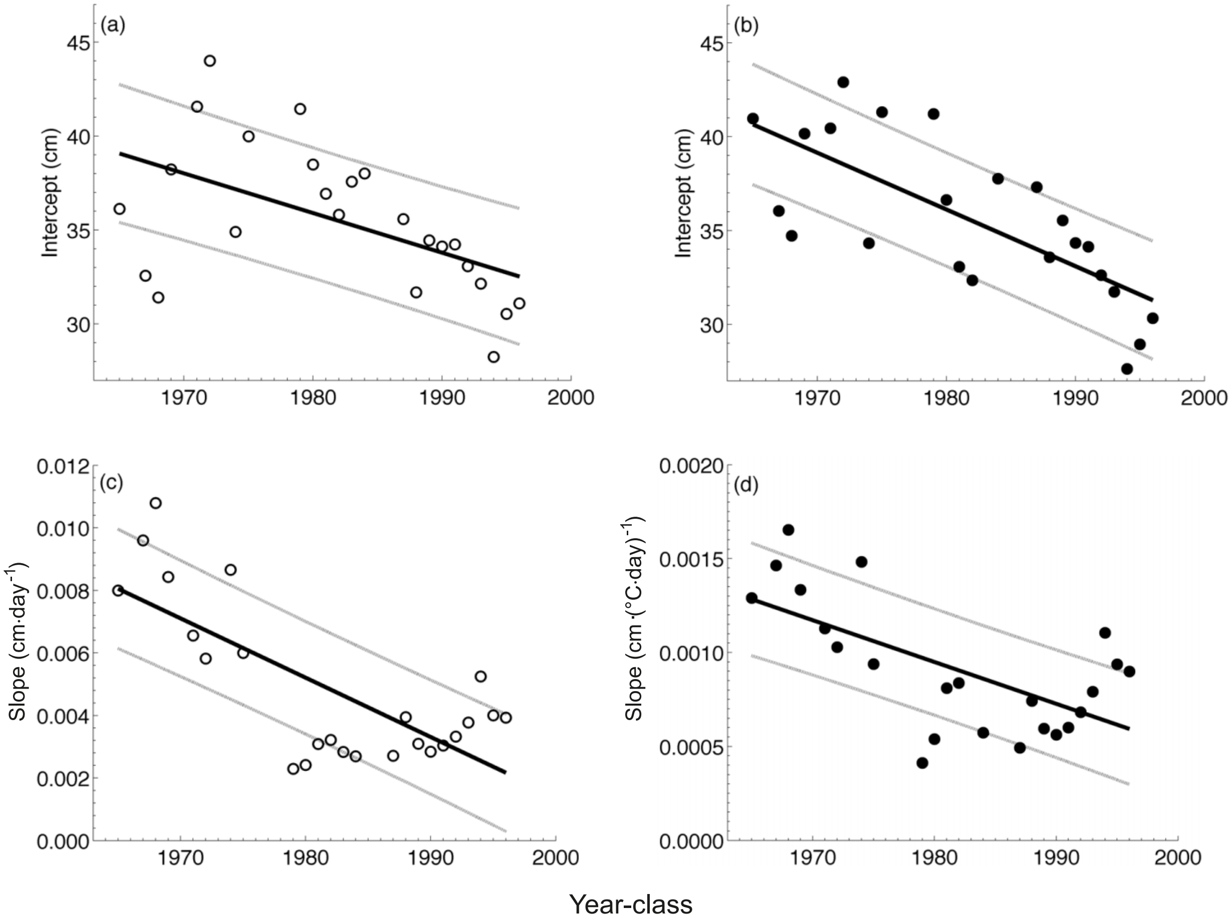


Fig. 5. (*a*) Intercepts (no significant relation, $P = 0.45$) and (*b*) slopes (no significant relation, $P = 0.11$) of LaD-at-GDD relations as a function of year-class-specific mean annual biomass from Fisheries and Oceans Canada summer RV surveys. Data labels denote year-class decade and year.

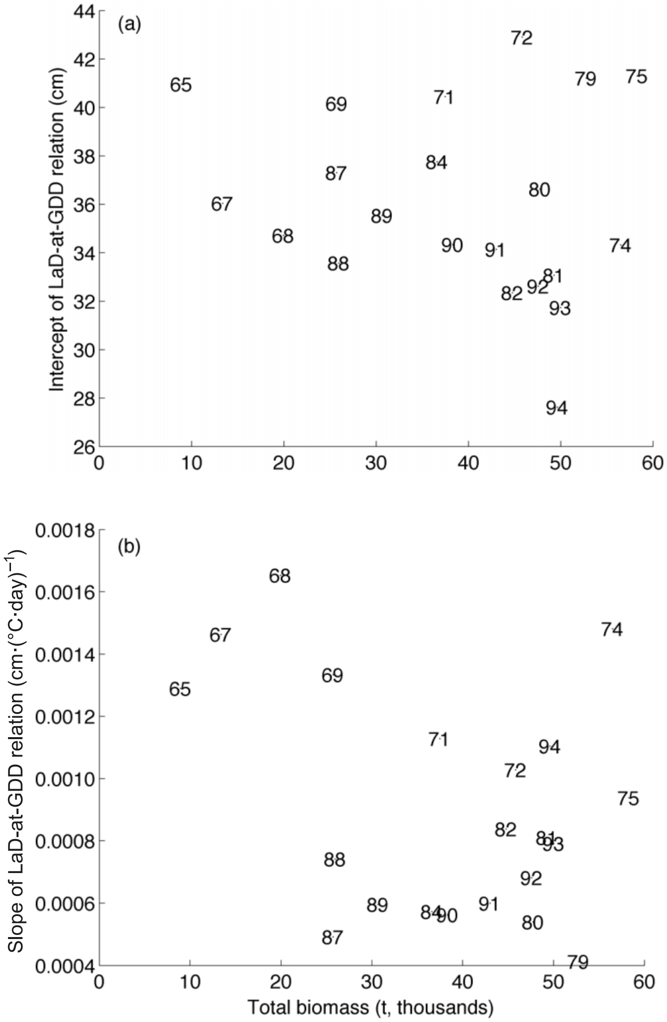
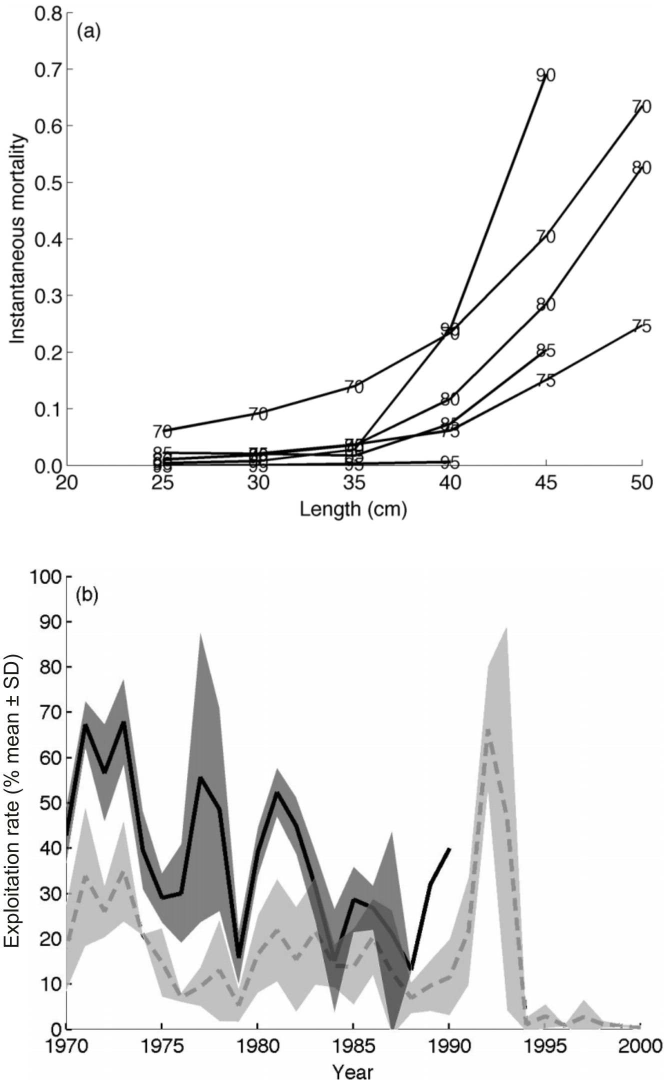


Fig. 6. (*a*) Variation in mean instantaneous fishing mortality (Frank et al. 2001) as a function of 4VW haddock length grouped into 5-year periods: 70, 1970 through 1974; 75, 1975 through 1979; 80, 1980 through 1984; 85, 1985 through 1989; 90, 1990 through 1994; 95, 1995 through 1999; (*b*) exploitation rate for fish of length >50 cm (solid line, dark grey shading) and 40–50 cm (broken line, light grey shading).



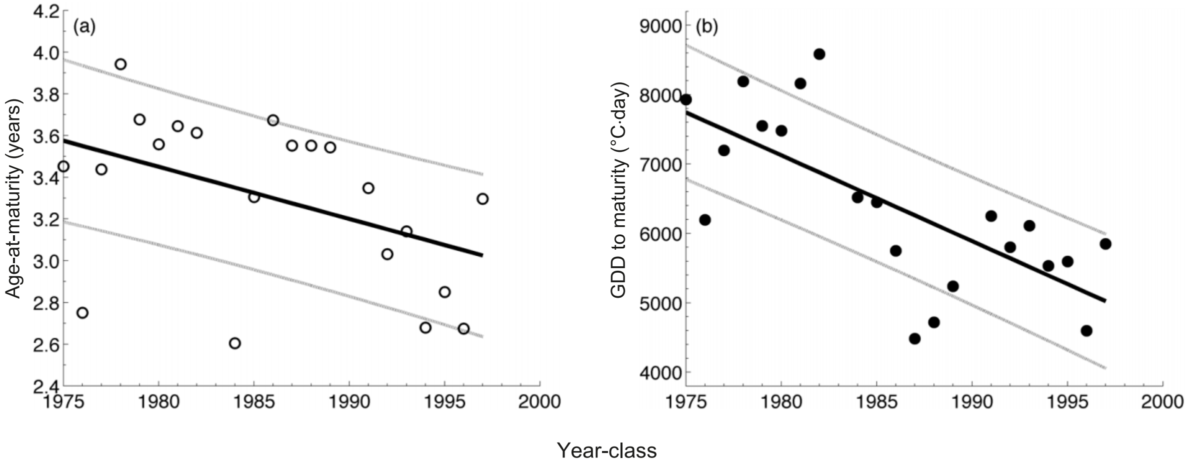
$r^2 = 0.20$, $P = 0.04$; Fig. 7*a*). Similarly, the thermal constant for maturity (°C·day) demonstrates a significant decline with increasing year-class (thermal constant of maturity = -124 year-class + 2.5×10^5 °C·day; $r^2 = 0.50$, $P < 0.0001$; Fig. 7*b*).

Discussion

The Scotian Shelf haddock decline in LaD over the last three decades (noted here as declines in slope and intercept of the LaD-at-time relations) was coincident with changes in a number of factors that affect fish growth as inferred in population size-at-age, factors that include temperature, food resources, and fishing effort (e.g., Zwanenburg 2000). While the decline in size-at-age has been described previously using the von Bertalanffy growth function (Frank et al. 2001), quantifying temperature effects on size-at-age is not possible due to the von Bertalanffy growth function being formulated for endotherms (von Bertalanffy 1938) using calendar time. Here, we accomplish this task by examining year-class-specific LaD as a function of variation in year-class thermal history (GDD) over 1970 through 2008. As in Neuheimer et al. (2008) for 1970 through 2003, year-class LaD-at-GDD relations demonstrate declines in slope and intercept with increasing year-class that are unrelated to variation in temperature (also see Neuheimer et al. 2008).

The decline in intercepts of the LaD-at-GDD relations among the year-classes can be explained by two different and testable hypotheses. The first is slower growth prior to maturation and thus maturation occurs at a smaller size but at the same thermal constant (Fig. 8*a*). The second is unchanged growth prior to maturation where maturation occurs at a smaller size and is associated with a lower thermal constant (Fig. 8*b*). As the LaD for the immature fish age 0 and 1 show no change over time (linear regression: age 0, $P = 0.18$; age 1, $P = 0.62$), we reject the first hypothesis. The

Fig. 7. Time to maturity as (*a*) age-at-maturity (solid line, linear regression; broken lines, 95% confidence intervals around the prediction: $r^2 = 0.20$, $P = 0.04$) and (*b*) the thermal constant of maturity (i.e., GDD to maturity; solid line, linear regression; broken lines, 95% confidence intervals around the prediction: $r^2 = 0.50$, $P < 0.0001$).

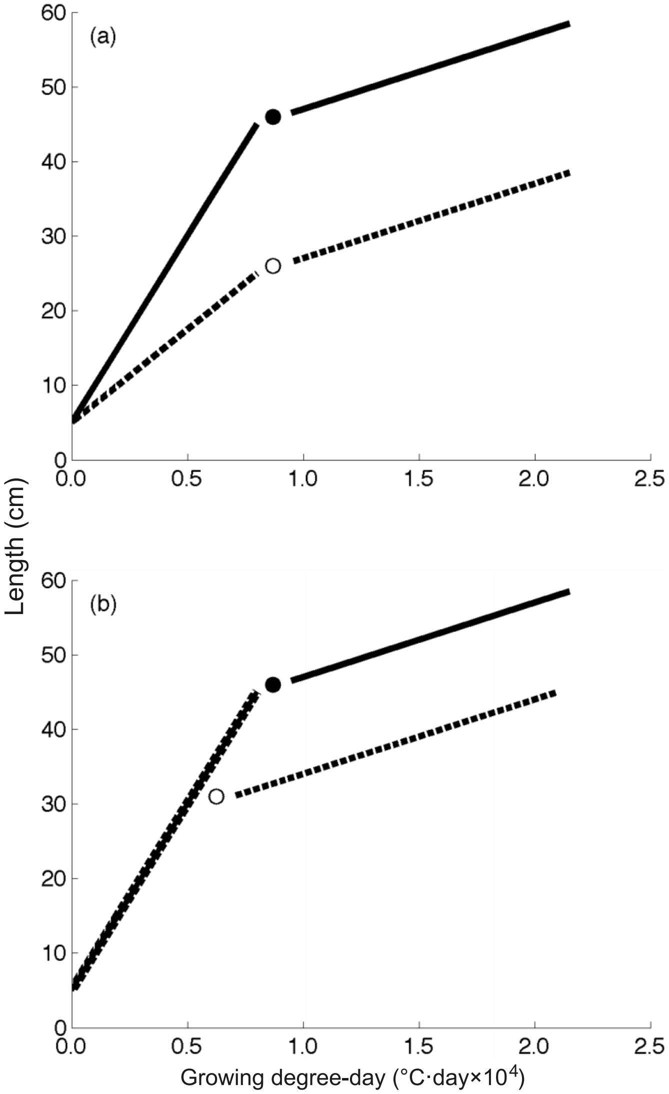


same is somewhat true for age 2 ($P = 0.0011$, $r^2 = 0.26$) relative to all other ages where $P < 0.001$ and $r^2 > 0.75$. Conversely, the haddock year-classes show a decline in age-at-50%-maturity ($P = 0.04$) that is maintained when examined in thermal time ($P < 0.001$). Variability in maturation timing among year-classes is unexplained by temperature — the thermal history associated with maturation has changed — and we cannot reject the hypothesis that the decline in intercepts results from maturation that is now occurring at a smaller size and is associated with a lower thermal constant. Therefore, maturation occurring at increasingly younger ages and smaller sizes (decrease in LaD-at-GDD intercepts among year-classes) combined with slower growth in mature fish (decrease in LaD-at-GDD slopes among year-classes) appears to be the most parsimonious explanation for the decrease in LaD in this stock. Having isolated temperature-independent changes in the haddock growth and maturation, we now go on to explore other factors that may explain these trends.

While density dependence is thought to influence growth rates by predicting decreased growth at high population abundance due to competition for food or habitat, etc. (Lizaso et al. 2000; Sinclair et al. 2002*a*), evidence for correlations of population size and size-at-age is mixed (Melvin and Stephenson 2007; Swain et al. 2007) and such a relationship is not de facto a causal one (i.e., we fail to directly measure resource limitation; Millner and Whiting 1996). In our analyses, there are no significant correlations between the haddock biomass estimates and the LaD-at-GDD parameters (slope or intercept, $P > 0.11$). The difficulty of identifying meaningful density effects has been recognized in other areas of ecology and is of particular concern when addressing populations under natural conditions at realistic densities (i.e., intermediate population size) where other factors (e.g., climate, fishing) influence the demographics (Strong 1984). Density-dependent relationships are most likely observed at "artificially high densities under controlled and experimentally homogenous conditions, where influences of variables that are normally important in nature are kept low. Density-explicit relationships are common in homogenous, crowded laboratory cultures" (Strong 1984, p. 317). In field situations, correlations between density and demographic rates (e.g., growth) may be spurious or the result of an independent cause by a third factor, making it difficult to distinguish between causal versus statistical density dependence (Royama 1981).

Similar problems arise when employing size-based condition metrics (e.g., Fulton's condition, relative condition) to describe variation in growth. First, morphometric condition indices include fish size in their calculation, making correlations between variation in size (e.g., length) and size-based condition indices expected and arguably meaningless: an artefact (i.e., a product of human conception as opposed to an inherent element) rather than an estimate of resource limitation. This is further exacerbated for Scotian Shelf haddock, as the timing of the survey (July) can overlap with the end of spawning (May to August; Waiwood and Buzeta 1989) and observed weight-at-length variability may be due to variation in proportion of spawned versus spawning fish sampled each year, particularly as spawning time can be a function of thermal history (not calendar time). Thus, explaining variability in size-at-age with condition indices that include weight measures should be interpreted with caution. Second, like density dependence, condition metrics do not directly estimate resource limitation and changes in condition are not de facto indicative of a change in resource availability. Morphometric condition measures are not necessarily indicative of energy reserves (Marshall et al. 2004) and have been shown to diverge from other, more direct, measures of condition such as liver weight and hepatosomatic index (e.g., Pardoe et al. 2008). Thus, while declines in size-based condition have been calculated in this stock over the study period (Fisheries and Oceans Canada 2003; Choi et al. 2004), the metric is insufficient to conclude resource limitation as the direct cause of the declines in LaD and maturity timing. Indeed, as growth-related variables have been favourable for increased growth in the latter period of our study (e.g., low inter- and intra-specific groundfish abundance, warmer temperatures, high prey abundance since ~1990), "the persistent reduced condition of a variety of groundfish species...is perplexing to say the least" (Fisheries and Oceans Canada 2003, p. 20). As stated by Mar-

Fig. 8. Illustrations of the possible mechanisms resulting in a decrease in the intercept of the LaD-at-GDD relation for mature fish. The onset of maturation induces a decrease in growth rate as a portion of the energy previously allocated to growth is redirected toward reproduction (Jobling 1982; Lambert and Dutil 2000). Thus, the slope of the LaD-at-GDD relation for mature fish is typically lower than that of immature fish with a change in slope occurring at maturation (circles). A decrease in the intercept of the LaD-at-GDD relation for mature fish (i.e., from broken line to solid line) may result from either (*a*) slower growth prior to maturity, i.e., the slope of the LaD-at-GDD relation for immature fish is lower, while maturation (open circle) occurs at the same physiological time (versus solid circle, same thermal constant; Neuheimer and Taggart 2007) or (*b*) earlier maturation, i.e., the slope of the LaD-at-GDD relation for immature fish remains the same, while maturation (open circle) occurs earlier in physiological time (versus solid circle, a different thermal constant).

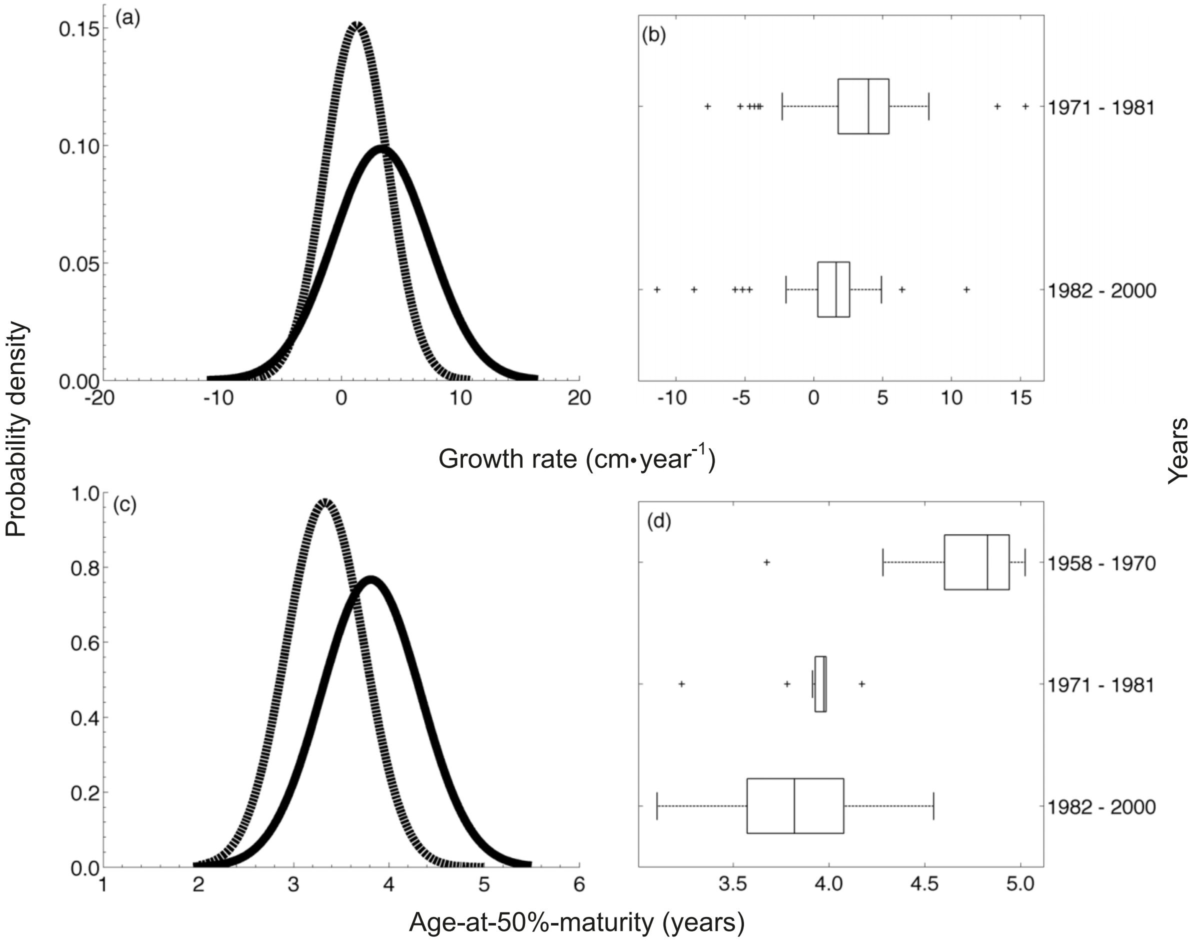


shall et al. (2004, p. 1913), “it is unwise to assume a priori that morphometric condition indices are sensitive indices of condition without independent and preferably bioenergetic evidence supporting this assumption.” Such evidence (e.g., energy density or liver weights) is not available for Scotian Shelf haddock but would be a valuable addition to the annual RV survey protocol.

In contrast with the indirect measures of density dependence and condition, we have direct evidence of the consistent, strong, and directional force of fishing (Law and Grey 1989) on the Scotian Shelf haddock, evidence that is independent of other biological and environmental factors. Prior to 1993, Scotian Shelf haddock were subject to an extensive and intensive fishery with fishing pressure concentrated on the largest haddock throughout the study period. Preferential harvesting of large fish in a stock is typical of many fisheries where minimum limits, hook- or mesh-size, etc., are employed to allow the smallest fish to escape (Sinclair et al. 2002*a*). The effect that differentially harvesting large fish might have on the life history characteristics of a stock can be explored by first identifying the factors that allow an individual fish to be larger at age relative to its cohort average. These are (*i*) faster growth overall and (*ii*) later maturation with more time spent at the faster, immature growth rate (Fig. 8). The preferential removal of the largest fish (fast-growing and older fish; Ratner and Lande 2001) within a stock effectively represents a preferential removal of those individuals predisposed to a faster than average growth rate and later (or larger) than average maturation (Conover 2007). Moreover, high fishing pressure in general will encourage earlier maturation, as fish risk being harvested before first-spawning (Heino and Gødo 2002). If we provide the variation in growth rate and time to maturation for the Scotian Shelf haddock population using normal probability density functions (Figs. 9*a* and 9*c*), we can illustrate that removing the late-maturing and fast-growing fish results in the growth and maturation distributions being forced toward the left and thus a population that is disproportionately represented by slower-growing (smaller size-at-age) and earlier-maturing (or maturation at smaller size) fish, as seen in Scotian Shelf haddock (Figs. 9*b* and 9*d*). Similarly, Choi et al. (2004) identified the two primary factors that could explain the widespread declines in body size of groundfish species on the Scotian Shelf over the same period as cumulative biomass removal from fishing and abiotic change (Choi et al. 2004). Here, we go a step further for haddock by employing GDD to disentangle possible temperature (abiotic) effects on growth and life history changes. We are left with sustained exploitation of large fish combined with high exploitation pressure overall as a simple mechanism that would favour a systematic decline in inferred growth (expressed as length-at-age and slope of the LaD-at-GDD relation) and in age-at-maturity (intercept of the LaD-at-GDD relation) over time, precisely as observed for Scotian Shelf haddock.

Very similar responses to intensive and/or size-selective fishing are found elsewhere in the literature (e.g., Anderson et al. 2008; Fenberg and Roy 2008) including declines in size-at-age in Atlantic salmon (*Salmo salar*) (Schaffer and Elson 1975), Atlantic cod (*Gadus morhua*) (e.g., Trippel 1995; Sinclair et al. 2002*a*; Hutchings 2005), European plaice (*Pleuronectes platessa*) (Rijnsdorp 1993; Grift et al. 2003), and brook trout (*Salvelinus fontinalis*) (Magnan et al. 2005) and greater reductions in size-at-age are found among fishing-target species relative to nontarget species (Zwanenburg 2000; Ratner and Lande 2001; Hsieh et al. 2006). Most recently, Shackell et al. (2009) showed that size-selective

Fig. 9. Schematic normal probability density functions for (*a*) inferred growth rate (solid line, 1971 through 1981; broken line, 1982 through 2000; parameterised from length-at-age (cm) data in Frank et al. 2001) and (*b*) age-at-50%-maturity (solid line, 1958 through 1981; broken line, 1982 through 2000; parameterised from age-at-50%-maturity data in Frank et al. 2001) along with box and whisker illustrations of (*c*) inferred growth rate for 1971 through 1981 and 1982 through 2000 (from length-at-age (mm) data in Frank et al. 2001) and (*d*) age-at-50%-maturity for 1958 through 1970, 1971 through 1981, and 1982 through 2000 (from Mohn and Simon 2002 and Frank et al. 2001). Vertical lines are lower quartile, median, and upper quartile and whiskers denote the extent of data with outliers as “+”.



fishing has reduced size-at-age across a whole suite of fisheries and species on the Scotian Shelf and influenced a substantial change in local trophic structure. The literature also documents trends toward earlier maturation among several exploited populations including European plaice, Atlantic halibut (*Hippoglossus hippoglossus*), and Atlantic cod, (e.g., Sinclair et al. 2002*a*; Barot et al. 2004; Olsen et al. 2005). Recent evidence for similar responses exist for northern pike (*Esox lucius*) (Carlson et al. 2007) and for Atlantic silverside (*Menidia menidia*) where size-selective mortality harvesting the largest fish reduced the mean size-at-age under controlled conditions within five generations (Conover et al. 2009), equivalent to ~20–25 years for Scotian Shelf haddock.

Questions of recovery time for overexploited populations require the differentiation of genetic versus phenotypic changes in growth and life history characters. We are not able to assess how genetically based and heritable or “plastic” and readily reversible the declines in haddock size and maturation timing may be (Baccante and Reid 1988; Grift et al. 2003). However, such changes can result from genetic shifts in a population (Trippel 1995; Grift et al. 2003) and may not be readily reversible, unlike phenotypic changes such as those resulting from the influence of temperature or food availability (Grift et al. 2003), particularly considering the low strength of natural selection relative to fishing selection (Sinclair et al. 2002*a*; Jørgensen et al. 2007; Swain et al. 2007). Such shifts can act on time scales of decades (Reznick and Ghalambor 2005; Conover et al. 2009) and may reduce the population’s capacity to recover from high exploitation, as the overall effect of fishing is to remove individuals with those traits that allow for the conversion of energy into population growth (Walsh et al. 2006; Fenberg and Roy 2008). For example, it was estimated that a shift in Atlantic cod age-at-maturity from 6 to 4 years could reduce annual population growth by 25% to 30% (Hutchings 2005). Conover et al. (2009) estimated the recovery time of a fisheries-induced decline in size-at-age as 12 generations, ~50–60 years for Scotian Shelf haddock. This estimate is conservative and will be influenced by the severity of harvesting (and corresponding magnitude of genetic change), life history, and environment such as prey abundance, temperature, etc. (Conover et al. 2009). Subsequent to the closure of the Scotian Shelf haddock fishery in

1993, there has been no increase in size-at-age, consistent with the possibility of a fisheries-induced genetic shift in the population. Evidence for the recovery potential of the Scotian Shelf haddock will begin to become apparent as the monitoring of size-at-age continues, especially if GDD is employed to explain temperature-dependent variation in size-at-age and to make year-class comparisons using a physiologically relevant time scale.

We cannot, with absolute certainty, reject the possibility that other factors (e.g., food availability and quality) contributed to the observed changes in size-at-age in this stock. We can argue, at this time and until demonstrated otherwise, that intensive and size-selective fishing provides the most parsimonious mechanism for the observed changes in length-at-age and age-at-maturity that are observed in this stock. These trends strongly caution against proposals for reopening of the Scotian Shelf haddock fishery, particularly where reduced minimum-size restrictions are considered (Mohn and Simon 2004).

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Appendix A

Table A1. Fishing-mortality-at-age of Scotian Shelf haddock estimated from standard age-based population analysis (reproduced from Frank et al. 2001).

Age (years)	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
1	0.04	0.07	0.04	0.07	0.01	0.01	0.02	0.01	0.02	0	0.01
2	0.03	0.12	0.1	0.22	0.04	0.02	0.04	0.01	0.02	0.01	0.03
3	0.11	0.26	0.17	0.32	0.29	0.12	0.06	0.08	0.05	0.02	0.1
4	0.29	0.62	0.36	0.71	0.2	0.42	0.09	0.17	0.3	0.09	0.28
5	0.47	1.05	0.58	0.83	0.51	0.36	0.29	0.25	0.34	0.13	0.39
6	0.61	0.98	0.8	1.4	0.88	0.39	0.43	0.45	0.68	0.2	0.56
7	0.48	1.21	0.87	1.48	0.88	0.45	0.54	0.52	0.69	0.28	0.54
8	0.74	1.41	0.88	1.52	0.84	0.61	0.51	0.74	0.58	0.1	0.43
9	0.72	3.04	0.72	0.77	0.25	0.32	0.32	0.56	0.49	0.08	0.38
10	0.91	0.83	1.54	1.62	0.52	0.19	0.86	1.96	0.49	0.23	0.21
11	0.43	5.25	1.32	2.9	1.63	0.05	0.21	3.99	2.9	0.21	0.45
12	0.79	1.76	1.05	1.31	0.54	0.37	0.56	1.09	0.52	0.14	0.34

Age (years)	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
1	0.01	0	0.01	0	0.01	0	0.01	0.02	0.08	0.01	0
2	0.01	0.01	0.01	0.01	0	0.01	0.02	0.01	0.06	0.03	0.01
3	0.03	0.07	0.02	0.02	0.01	0.01	0.02	0.01	0.02	0.05	0.07
4	0.34	0.12	0.2	0.12	0.09	0.11	0.02	0.04	0.1	0.04	0.29
5	0.62	0.78	0.52	0.21	0.22	0.28	0.04	0.06	0.15	0.11	0.13
6	0.8	0.51	0.56	0.4	0.22	0.32	0.7	0.08	0.1	0.14	0.24
7	1	0.92	0.25	0.25	0.27	0.25	0.08	0.11	0.2	0.27	0.39
8	0.68	0.48	0.44	0.06	0.33	0.4	0.07	0.14	0.33	0.4	0.42
9	0.75	0.53	0.11	0.09	0.26	0.35	0.14	0.11	0.35	0.64	0.52
10	0.57	0.45	0.38	0.02	0.7	0.17	0.12	0.15	0.39	0.4	0.67
11	0.37	0.17	0.64	0.07	0.34	0.22	0.04	0.13	0.61	0.53	0.49
12	0.66	0.48	0.31	0.06	0.43	0.31	0.11	0.13	0.36	0.48	0.54

Age (years)	1992	1993	1994	1995	1996	1997	1998	1999	2000
1	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0
3	0.01	0	0	0	0.01	0	0	0	0
4	0.26	0.01	0	0	0.01	0.01	0	0	0
5	0.92	0.11	0	0.01	0.01	0	0	0	0
6	0.31	0.5	0.01	0.01	0.01	0	0.01	0.01	0
7	1.85	0.08	0.05	0.02	0.01	0	0	0	0.01
8	0.86	1.82	0	0.06	0.01	0.01	0.01	0	0
9	0.86	1.31	0.02	0	0.06	0.02	0.02	0.01	0
10	0.87	1.17	0.04	0.41	0	0.06	0.06	0.01	0.01
11	1.05	0.56	0.1	0.19	0.04	0.01	0.47	0.01	0.01
12	0.86	1.43	0.02	0.16	0.02	0.03	0.03	0.01	0.01

Reference

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