

Image-enhanced burnt otoliths, bomb radiocarbon and the growth dynamics of redfish (*Sebastes mentella* and *S. fasciatus*) off the eastern coast of Canada

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Abstract. Many past attempts to age deep-water redfish (*Sebastes mentella*) and Acadian redfish (*S. fasciatus*) in the north-west Atlantic have been stymied by inappropriate ageing methods, the absence of age validation and the failure to differentiate among species. Herein we report substantial improvements in methods for ageing *Sebastes* spp. by linking the established ‘crack and burn’ method to modern sectioning and image-enhancement protocols. Bomb radiocarbon assays of the otolith core and monitoring of year-class progression confirmed the accuracy of the resulting age determinations to an age of 46 years. The use of microsatellite DNA to confirm species identity eliminated past confusion caused by species mixtures. Age determinations of 1252 redfish from the eastern coast of Canada demonstrated the presence of significant differences in growth rate and longevity both between the two redfish species and among populations and stocks, with a maximum observed longevity of 70 years. Even within species and stocks, an individual fish with a fork length of 38 cm could be anywhere between 15 and 50 years of age, highlighting a near cessation of somatic growth after sexual maturation. In keeping with other deep-water species, sustainable management will require more attention to the low productivity expected of redfish stocks, rather than the high initial biomass that can support short-term but high catch rates.

Additional keywords: age validation, annuli, break and burn, ¹⁴C, false check.

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Introduction

Although most deep-water fisheries have a shorter history of exploitation than those in shallower waters, their record shows a disproportionately high level of overexploitation (Roberts 2002). It has been recognised only recently that deep-sea fishes tend to be slow growing, long lived and characterised by a late age of sexual maturation, making them particularly sensitive to overfishing and slow to recover from depletion (Clarke *et al.* 2003). Some high-profile examples of serious overfishing have occurred, at least in part, because of overly optimistic impressions of growth and productivity brought on by age underestimation. For example, the orange roughy (*Hoplostethus atlanticus*) off New Zealand was fished intensively on the basis of a presumed longevity of 20–30 years (Tracey and Horn 1999). By the time it was realised that the species grew extremely slowly and could live to an age of more than 100 years (Smith *et al.* 1995; Andrews *et al.* 2009), the damage had been done and

many populations had already been fished almost to the point of collapse. It is possible that roundnose grenadier (*Coryphaenoides rupestris*) in the north-west Atlantic will never recover from its fishery, in part because of slow growth rates and longevities of 60 years, which are much greater than previously suspected (Clarke *et al.* 2003). Indeed, longevities exceeding 100 years become increasingly frequent as habitat depth increases (Cailliet *et al.* 2001; Roberts 2002), an observation that would have been ridiculed some 30 years ago (Campana 2001).

The speciose genus *Sebastes* supports commercial fisheries in both the Pacific and Atlantic oceans, where they are known as rockfish and redfish respectively. Many of the species are deep-water species and some are now known to reach ages of over 75 (in the Atlantic) and 200 years (in the Pacific) (Campana *et al.* 1990; Munk 2001), making them less capable of supporting an intensive fishery. Indeed, overexploitation leading to fisheries closures has already occurred in some areas (Department of

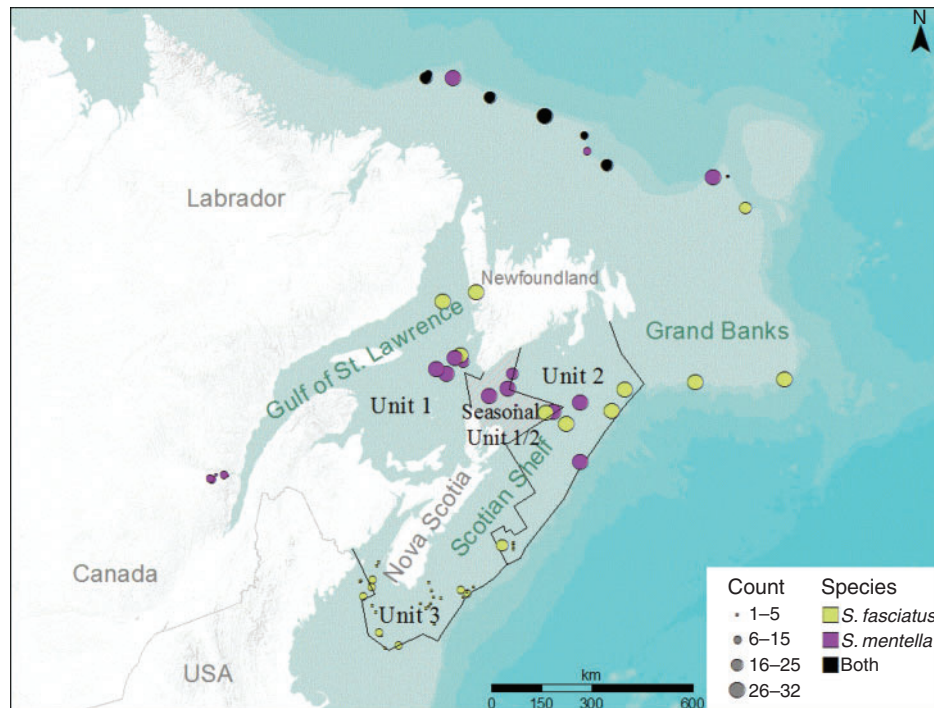


Fig. 1. Map of the north-west Atlantic showing the location of *Sebastes* spp. sampled for age determination. Symbol size is scaled according to the number of fish sampled. Redfish management units are shown. Depth contours are in 1000-m intervals.

Fisheries and Oceans Canada, DFO 2012). The problem has been exacerbated by difficulties in age determination and controversy over the appropriate ageing method (Campana *et al.* 1990; Nedreaas 1990; Stransky *et al.* 2005a). Early attempts at redfish age determination using scales (Perlmutter and Clarke 1949) persisted until recently in some regions of the north-east Atlantic, but appear to grossly underestimate the ages of older fish (Nedreaas 1990). Most redfish are now aged using either the ‘crack and burn’ (C&B) method or with otolith thin sections, two methods that appear to give roughly comparable results (Stransky *et al.* 2005b). The accuracy of the C&B method has been validated in two independent radiometric studies (Campana *et al.* 1990; Stransky *et al.* 2005a). Nevertheless, growth parameters reported in different studies have varied widely, in part because of the difficulty of distinguishing among the three redfish species *Sebastes marinus*, *S. mentella* and *S. fasciatus* (Saborido-Rey *et al.* 2004). As a result, it has been difficult to know whether there are real differences in growth trajectories among regions and species, or whether the reported differences are due to differences in otolith interpretation or errors in species identification.

The objectives of the present study were to: (1) improve the accuracy and precision of existing methods of redfish age determination and age validation; (2) remove uncertainty in species identification by using microsatellite DNA to identify individual fish; and (3) apply standardised ageing methods and interpretation criteria to large sample sizes of *S. mentella* and *S. fasciatus* across a broad region of the north-west Atlantic in order to test current perceptions of redfish growth.

Material and methods

Samples of redfish were collected with otter trawls aboard research vessels in 2001 and 2002, mostly during routine annual groundfish surveys. Specimens were sampled from large aggregations of redfish (i.e. >100 kg by set) in the Gulf of St Lawrence and along the Laurentian Channel (North Atlantic Fisheries Organization (NAFO) Units 1 and 2), on the southern slope of the Grand Banks (NAFO 30), the eastern Grand Banks (NAFO 3LN) and in the Labrador Sea (NAFO 2J3K). Individuals were also sampled in the Saguenay fjord (far western Gulf of St Lawrence) using handlines during ice-fishing in winter 2003, as well as in the east arm of the Bonne Bay fjord (west coast of Newfoundland) in spring 2002 (Fig. 1). The specimens were frozen immediately after capture. After thawing in the laboratory, fork length, sex and maturity were recorded, and a piece of muscle tissue was preserved in 95% ethanol awaiting genetic analyses. The sagittal otolith pair was then removed from each fish and stored dry in paper envelopes until the time of processing for age determination. Additional otoliths (stored dry in paper envelopes) were sampled from the archived otolith collection housed at the Northwest Fisheries Science Centre in St John’s (Newfoundland, Canada). These additional otoliths belonged to redfish sampled during routine multispecies trawl surveys conducted in 2011 in the Labrador Sea and for which fork length, sex and maturity were recorded at sea. In all cases, the species identity of individual fish was unknown at the time of collection, but was subsequently assigned on the basis of the genotype at 13 microsatellite loci. DNA extraction and microsatellite amplification were performed as described by Valentin

et al. (2014). DNA was extracted from the muscle tissue preserved in ethanol or, for the 2011 sample, from the material adhering to the archived otoliths. The extraction procedure was slightly modified for the otolith samples, adding a step where the extracted DNA (eluted in a volume of 400 μL) was concentrated to 50 μL using a Microcon centrifugal filter YM-100 (EMD Millipore, Billerica, MA, USA) and the standard Microcon protocol. Specimens with an incomplete genotype at more than three loci were discarded from the database. After species identification was completed, individuals were assigned to population based on genotype (Valentin *et al.* 2014).

Samples of Unit 3 (see Fig. 1) redfish were collected in the summer of 2013 as part of routine annual groundfish surveys of the Scotian Shelf. Otoliths were collected as described above, but muscle tissue was not collected for subsequent genetic identification. Rather, it was assumed that most or all of the samples were from *S. fasciatus* based on previous genetic and meristic surveys of the region (Roques *et al.* 2001; Valentin *et al.* 2006, 2014).

In order to compare recent growth rates with those collected and aged several decades earlier, historic samples of what were probably *S. mentella* (based on depth of collection) were collected from Unit 2 in 1982 and 1986, and then aged using traditional C&B methods for use in another study (Campana *et al.* 1990). Those lengths at age were then compared with those of other samples from Unit 2, collected and aged in 2002.

Protocol for age determination

One sagittal otolith from each fish was cut transversely through the core (perpendicular to the longest axis of the otolith) with a single blade of an Isomet saw so as to ensure a flat, smooth surface for the subsequent burning (Charles *et al.* 2013). The otolith was not embedded in epoxy, but was firmly pressed into plasticine (modelling clay) on the IsoMet chuck (Buehler World Wide Headquarters, Lake Bluff, IL, USA) during sectioning. To ensure that the saw blade was precisely aligned with the otolith core, the blade was first lowered so as to press lightly into the putty on the saw chuck, leaving an impression against which the pencil-marked otolith core could be aligned when the otolith was pressed into the putty. Cuts were made at slow-medium speed with relatively little weight on the cutting arm to avoid breakage. Using forceps, the cut surface of the otolith half that best showed the core and annuli was held perpendicular to (and over) the flame of an alcohol burner for 2–10 s, or until the surface was chestnut brown in colour. The sulcus side was left facing up so as to avoid excessive charring along the sulcus edge. Otoliths with a particularly thin dorsal edge were tilted with the edge up and away from the flame. After cooling, the charred otolith half was pressed into putty such that the cut surface was exactly parallel to the surface of the microscope lens and thus parfocal across the otolith surface. After coating the cut surface with a light layer of mineral oil, the surface was imaged with a digital video camera (Olympus DP-72, see <http://www.olympus-ims.com/en/microscope/dp72/>) working at a 14-bit colour depth per channel through a dissecting microscope under reflected light at a resolution of 4000×3000 pixels. The resulting image was then digitally enhanced with Adobe Photoshop CS2 (see <http://www.adobe.com/products/photoshop.html>) through grey level expansion to fill the entire grey level

space with the levels spanning that of the otolith, followed by an unsharp mask filter using a radius of 10–20 pixels and amounts of 100%–200%. Two images were captured: one using a microscope objective magnification of $\sim 13\times$ to view the entire cut surface and a second zoomed into the dorsal region between the core and the proximal surface where older growth bands were most likely to form. Images were captured within 1 h of burning, before the burn clarity had decreased.

Comparison between ageing methods

In order to determine the optimal method for otolith interpretation, a matched pair comparison was made between ageing methods, whereby one sagittal otolith from each fish was cut transversely through the core with a single blade of an Isomet saw. One-half of each otolith was subsequently sent to a laboratory (Pacific Biological Station (PBS), Nanaimo, BC, Canada) with expertise in ‘break and burn’ ageing (MacLellan 1997) for burning and ageing under reflected light, whereas the remaining unburnt half of the same otolith was imaged under reflected light and aged by a second laboratory (Bedford Institute of Oceanography (BIO), Dartmouth, NS, Canada) with expertise in image enhancement. Therefore, each otolith was aged using two methods and two laboratories. As a second part of the study, the image-enhanced, unburnt half of the aged otolith was subsequently and independently burned and re-aged by the second laboratory (BIO), thus providing a matched-pair comparison of image-enhanced and burnt otoliths by the same laboratory.

Age interpretations at both PBS and BIO were made without knowledge of fish length or of the age estimates of the other laboratory, with both using a 1 January birth date. Systematic ageing differences between the methods and between the laboratories were evaluated with age bias plots, whereas precision was quantified using the CV.

Samples from 51 *Sebastes* otoliths were used in the comparison study. The fork lengths of *S. mentella* ($n = 30$) ranged from 30 to 40 cm (mean 35.8 cm), whereas the fork lengths of *S. fasciatus* ($n = 21$) ranged from 23 to 36 cm (mean 29.6 cm). Both sexes were equally represented in the samples.

Bomb radiocarbon assays for age validation

Otolith cores ($n = 13$) for bomb radiocarbon age validation were isolated from a 1-mm transverse section through the otolith core made using paired blades on the Isomet saw. Otolith cores representing the first 2–3 years of life were isolated from the section as a solid piece with a Merchantek computer-controlled micromilling machine (ESI, Portland, OR, USA) using 300- μm diameter steel cutting bits and burrs. The date of sample formation was calculated as the year of fish collection minus the number of growth increments from the edge of the otolith to the midpoint of the range of growth increments present in the extracted core. After sonification in ultrapur water and drying, the sample was weighed to the nearest 0.1 mg in preparation for the ^{14}C assay with accelerator mass spectrometry (AMS). AMS assays also provided $\delta^{13}\text{C}$ (‰) values, which were used to correct for isotopic fractionation effects and provide information on the source of the carbon. Where there was insufficient sample material for the $\delta^{13}\text{C}$ assay, mean values were used for correction of $\Delta^{14}\text{C}$ values. Radiocarbon values were

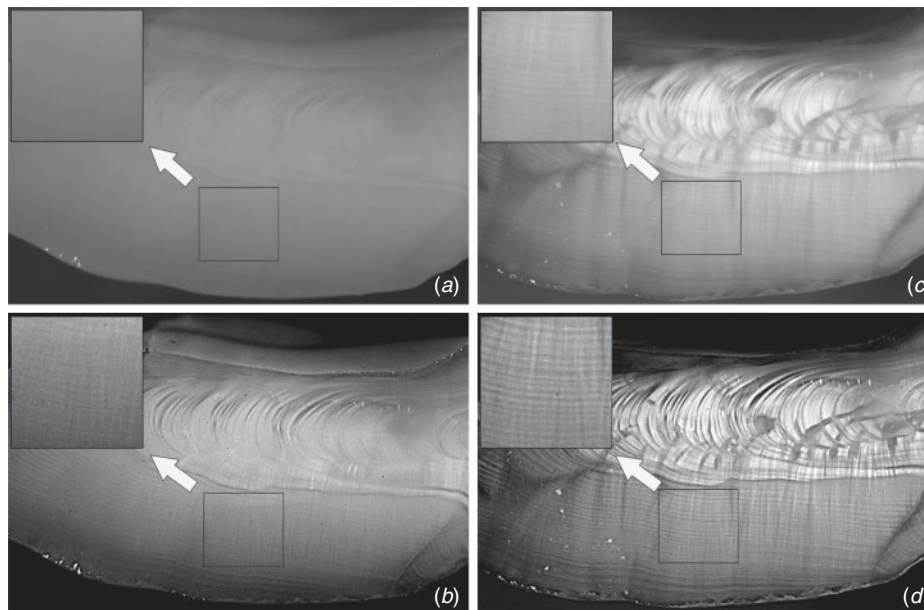


Fig. 2. Matched comparison of high-resolution images from a single *Sebastes mentella* otolith section prepared using different methods and varying levels of image enhancement. The insets in each panel show magnified views of a portion of the growth sequence, as indicated. (a) Unburnt, unenhanced image as it would be seen through the microscope; (b) unburnt but enhanced image; (c) burnt, unenhanced image; (d) burnt and enhanced image. Both burning and image enhancement substantially improved the visibility of the growth sequence, but the combination of the two provided the best results.

subsequently reported as $\Delta^{14}\text{C}$, which is the per mille (‰) deviation of the sample from the radiocarbon concentration of 19th century wood, corrected for sample decay before 1950 according to methods outlined by [Stuiver and Polach \(1977\)](#). The mean s.d. of individual radiocarbon assays was $\sim 3\%$.

The reference $\Delta^{14}\text{C}$ carbonate chronology for the north-west Atlantic (NWA) was derived from 73 otoliths of young, known-age fish of various species (including *Sebastes* spp.) whose cores were formed between 1949 and 2000 ([Campana *et al.* 2008](#)). Differences in $\Delta^{14}\text{C}$ among species are neither expected nor observed if the species inhabit marine waters of similar water mass characteristics.

The feature of a bomb radiocarbon chronology that best serves as a stable dated reference mark is the year of initial increase above pre-bomb levels in response to the period of atmospheric testing of nuclear weapons. Comparison of this year of initial increase in the reference chronology with that of the species being tested (in this case redfish) provides a good measure of the accuracy of age estimation, because consistent over- or underestimation of age will shift the calculated year of initial increase in the test chronology to earlier or more recent years ([Francis *et al.* 2010](#)). The year of initial appearance of bomb $\Delta^{14}\text{C}$ (Y_T) was defined as described by [Campana *et al.* \(2008\)](#).

Growth analyses

The von Bertalanffy growth function was fitted to the length-at-age data by species, stock and decade:

$$L_t = L_\infty(1 - e^{-K(t-t_0)})$$

where L_t is the fork length of redfish (cm) at age t (years), L_∞ is the asymptotic length, K is a growth coefficient (year^{-1}) and t_0 is the age at zero length. Non-linear regression was used to estimate the parameters of the model using SPSS software (ver. 23, IBM Corporation, Armonk, NY, USA). Growth model comparisons were made between stocks, species and sexes by using the sum of squares reduction test, calculating the F statistic from a full model that estimates model parameters for each group and a reduced model that combines groups in a single set of model parameters ([Haddon 2001](#)). The same growth comparisons were subsequently made between genetic populations of each species.

Results

Presumed annual growth bands were visible in all otoliths, although interpretability varied among otoliths. In general, otoliths were clear and relatively easy to read (for *Sebastes*), although the presence of multiple checks formed during the first few years of life sometimes complicated the interpretation of young fish. Growth bands formed after ~ 20 years of age were sometimes extremely narrow or faint, making them challenging to identify.

Comparison between ageing methods

The visibility and interpretability of growth bands differed noticeably with the mode of sample preparation ([Fig. 2](#)). For any given otolith, the visibility of the growth increment sequence improved markedly after either image enhancement or burning. However, the combination of burning followed by image enhancement almost always produced the clearest growth

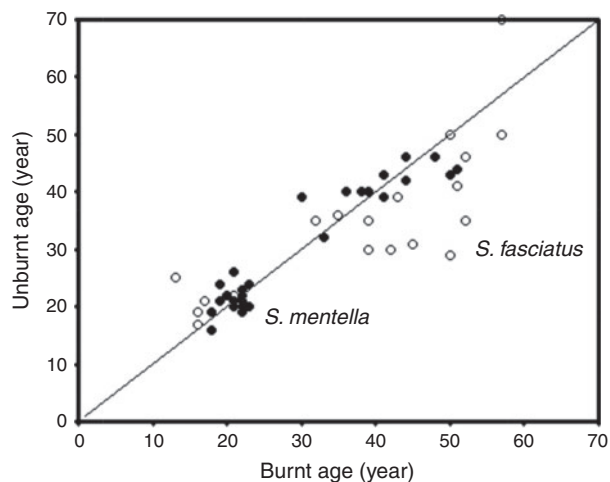


Fig. 3. Age bias plot comparing unburnt and burnt age estimates for *Sebastes mentella* (solid circle) and *S. fasciatus* (open circle) as interpreted by the same age readers. Both forms of preparation were image enhanced. The two sets of ages are very similar for *S. mentella*, but burning seems to reveal more annuli in *S. fasciatus* older than ~40 years.

pattern. In contrast, the growth sequence in otolith sections that were neither burned nor enhanced tended to be indistinct in all but young fish.

The matched-pair age comparisons for *S. mentella* demonstrated that comparable ages were obtained independent of the method or the laboratory. Ages ranged from 16–43 years using unburnt image enhancement to 18–50 years with burning by either laboratory. There was no obvious bias across the methods or the laboratories for *S. mentella* (Fig. 3). The CV between burnt and unburnt images within a laboratory was 6.5%. The CV between unburnt (BIO) and burnt (PBS) was 5.9%, whereas the CV between laboratories for burnt preparations was 7.3%.

The matched-pair age comparisons for *S. fasciatus* indicated that the preparation method could affect the quality of the results, and that interpretations were being made differently between the laboratories. Ages ranged from 10–70 years using unburnt image enhancement to 11–62 years after burning by PBS to 13–50 years after burning by BIO. There was obvious bias between both the methods and the interpretation of the laboratories such that more increments were visible in older fish (>40 years) after burning than before burning (Fig. 3). However, the method alone did not explain all the difference in interpretation between laboratories. Older *S. fasciatus* could be interpreted as having either many fine narrow annuli or fewer broad ‘split’ annuli (Fig. 4), and both laboratories reported having difficulty deciding which interpretation to make. In the end, one laboratory elected to interpret the otoliths as old, whereas the other laboratory elected to interpret them as younger. However, both laboratories were capable of ageing them either way, and there were no significant differences in ages if both laboratories used similar ageing criteria. The younger ages were later entered into the statistical analyses.

Bomb radiocarbon assays and age validation

The date of formation of the redfish otolith cores was estimated in two ways: (1) through age determination of the fish based on

otolith growth increment counts; and (2) through comparison of otolith core $\Delta^{14}\text{C}$ values with the values known to be present in surface marine waters of the NWA at the time (the NWA reference chronology). Agreement between the increment- and $\Delta^{14}\text{C}$ -based dates confirms that the annuli were interpreted correctly for age estimation, at least on average.

In all, 13 otolith cores were assayed for radiocarbon, and the resulting range of $\Delta^{14}\text{C}$ values (–82 to +57) was that expected of pre- to post-bomb radiocarbon in the NWA (Table 1). However, there was no overlap between the NWA reference chronology and the chronology derived from the redfish otolith cores, even when uncertainty in the growth increment count was considered by using the entire plausible age range (Fig. 5a). Somewhat surprisingly, there was a close correspondence between the reference and redfish core chronologies if it is assumed that one or the other of the chronologies was offset by 9 years (Fig. 5b). This correspondence indicates either that all the redfish ages were underaged by 9 years, regardless of whether the fish was young or old, or that the NWA reference chronology representative of surface marine waters was inappropriate for use on deep-water redfish. As discussed later, if it was determined that a reference chronology phase lagged by 9 years was appropriate for use with redfish, this would indicate that the age determinations based on growth increment counts were accurate up to an age of at least 46 years.

Deep-water redfish recruitment in the Gulf of St Lawrence is known to be strongly episodic and various stock assessments have commented on the record size of the 1980–81 year-classes since 1983 (DFO 2010). To determine whether the age assignments based on growth increment counts were consistent with the presence of these strong year-classes, the year of birth was calculated for all Unit 1 and 2 redfish (Fig. 6). The calculated 1980 and 1981 year-classes based on age reading dominated all other year-classes of *S. mentella* in both Units 1 and 2, indicating that the age reading must have been accurate up to at least an age of 22 years. In contrast, relative year-class strength was much more dispersed in *S. fasciatus*, a species not known for the same level of episodic recruitment in Units 1 and 2.

Growth analyses

In all, 470 *S. fasciatus* and 470 *S. mentella* from six management units were aged to develop growth curves, with maximum observed ages of 44 and 50 years respectively for the two species. Both species showed similar growth patterns, with relatively rapid growth to an age of 10–15 years, after which growth slowed markedly (Fig. 7). The growth of *S. fasciatus* appeared to be fairly similar across stocks, with the exception of the Scotian Shelf stock (Unit 3), which appeared to grow somewhat more quickly. *Sebastes mentella* also appeared to grow similarly in all stocks, with the exception of the NAFO 2J3KL stock, where it may have grown more quickly; however, the scarcity of NAFO 2J3KL individuals with ages >15 years made it difficult to determine whether their absolute growth rate was actually higher than that of other stocks. Within the best-sampled management unit, the growth of the two species appeared to follow similar trajectories, with *S. mentella* growing to slightly larger asymptotic lengths and ages (Fig. 8). The von Bertalanffy growth models fit to each species and stock resulted in estimates

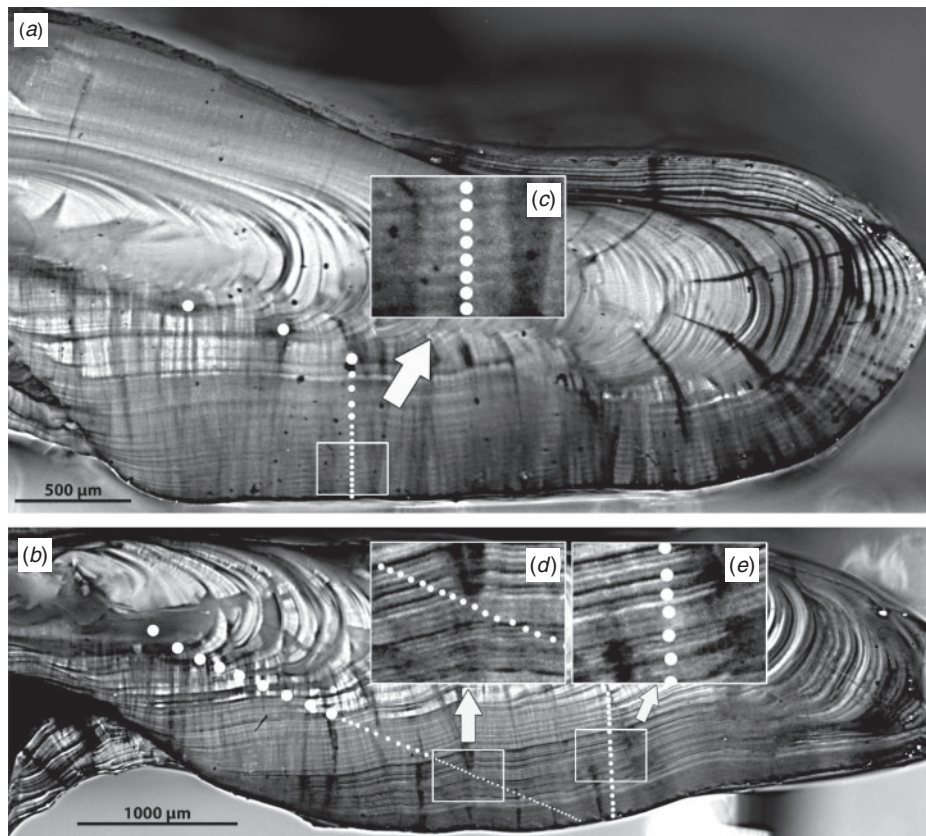


Fig. 4. Enhanced images of burnt otolith sections from (a) *Sebastes mentella* and (b) *S. fasciatus* with symbols indicating annuli. The two species show similar growth increment patterns for the first 15–20 years. Annuli in older *S. mentella* became very narrow, but were often straightforward to interpret (c). In contrast, annuli in many older *S. fasciatus* often showed considerable splitting (d, e), which could either be interpreted as fewer well-demarcated annuli (e) or many very narrow annuli (d).

Table 1. Summary of $\delta^{13}\text{C}$ and $\Delta^{14}\text{C}$ assay results for otolith cores (2–3 years of growth) microsampled from redfish for age validation. Year of core formation is that based on the number of growth increments. FL, fork length; men, *Sebastes mentella*; fas, *S. fasciatus*; ND, not determined

Year collected	Species	Unit area	FL (mm)	Annulus-based age (years)	Age range (years)	Core age (years)	Annulus-based year of core formation	$\delta^{13}\text{C}$ (‰)	$\Delta^{14}\text{C}$
2002	men	Unit 1	370	46	44–46	3	1957.5	–2.0	–73
2002	fas	Unit 1	353	44	41–47	3	1959.5	–3.0	–72
2002	men	Unit 1	365	44	40–44	3	1959.5	–3.0	–64
2002	fas	Unit 1	326	42	30–42	2	1961.0	ND	–58
2002	men	Unit 1	369	41	41–48	3	1962.5	–7.0	–70
2002	fas	Unit 1	360	39	36–49	3	1964.5	–3.0	–82
2002	fas	Unit 1	293	38	36–48	3	1965.5	–2.0	–72
2002	men	Unit 2	387	37	37–42	3	1966.5	ND	–62
2002	men	Unit 2	353	32	32–41	2	1971.0	–5.3	–46
2002	men	Unit 2	323	32	31–32	2	1971.0	–5.6	49
2002	men	Unit 1	331	29	22–29	3	1974.5	–7.0	19
2002	men	Unit 2	311	27	26–27	2	1976.0	–5.4	37
2001	fas	Unit 1	338	26	25–26	2	1976.0	ND	57

of asymptotic length that tended to be <400 mm for *S. fasciatus* and >400 mm for *S. mentella* (Table 2; Fig. 7). With the exception of redfish from NAFO 2J3KL, all estimates of the growth coefficient K were <0.1 year⁻¹, indicating slow growth.

Likelihood ratio tests indicated that the growth coefficients of *S. fasciatus* in Unit 3 and NAFO 2J3KL were significantly greater than those in other stocks ($P < 0.05$). Small but significant differences were evident in some other stocks as well, but

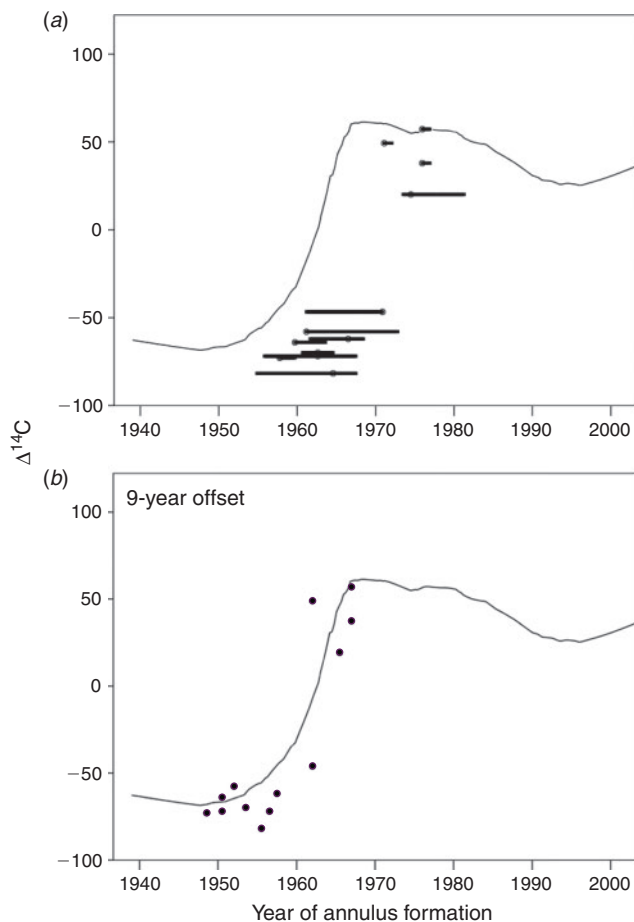


Fig. 5. Bomb radiocarbon chronology of *Sebastes* spp. otolith cores (circles) compared with the reference carbonate chronology for the north-west Atlantic (curved line). (a) Otolith core radiocarbon values appear offset from the reference chronology, even when ageing error uncertainty bars are placed around the ages determined from annulus counts. (b) Otolith core radiocarbon values provide a close fit to the reference chronology, with no evidence of age-related bias, if the chronology is offset by 9 years because of delayed penetration of the bomb signal to the depth of the fish.

those results were associated with small sample sizes and may not be biologically important. For all stocks and both species, there were very few samples with lengths <180 mm, implying that modelled lengths below this size were solely a function of the K and t_0 growth parameters. Indeed, some of the t_0 values reported in Table 2 differ considerably from zero, highlighting the growth uncertainty of very small redfish. For *S. mentella*, samples from NAFO 2J3KL grew significantly faster and those in Unit 2 significantly slower than those in other stocks ($P < 0.05$). The growth rate differed significantly between sexes for both species in almost all stocks, whereby females grew more rapidly and to larger sizes than males, at least after ages 7–10 years (likelihood ratio test, $P < 0.01$).

The growth curves of 430 *S. fasciatus* and 467 *S. mentella* from the genetically identified populations of Valentin *et al.* (2014) suggested that some or all of the observed differences in length at age could be attributed to environmental rather than

genetic differences (Fig. 9). Environmental effects were most evident in *S. mentella*, where there were large and significant differences ($P < 0.01$) in growth rate between the Gulf of St Lawrence population and the genetically identical sink population in the Saguenay fjord. Slower growth was also observed in the Bonne Bay population of *S. fasciatus*, but because this population is both environmentally and genetically distinct, it was not possible to disentangle the effects. For all other populations of both species, it appeared that there was little evidence of differences in length at age; significant differences were evident in some cases, but those differences were probably due to very different length or age differences among samples.

A comparison of the recent length at age of *S. mentella* in Unit 2 with that evident in 1982 and 1986 suggested that there had been no visible change in growth trajectory over a 20-year interval (Fig. 10). Large changes in age composition were evident, with maximum ages of ~ 70 years observed in 1986 compared with 42 years in 2002. However, it is not clear whether that difference represents a true change in age composition or merely reflects non-routine sampling from deep-water stations in the 1980s.

Discussion

Otolith transverse thin sections have become the standard method for age determination of fishes around the world, particularly for long-lived species (Beamish and McFarlane 1987). Thus, it is somewhat curious that C&B otolith preparations have persisted as the preparation of choice for *Sebastes* spp. and a small number of other species in both the Pacific and Atlantic oceans (Stransky *et al.* 2005b; CARE 2006). To some extent, this may reflect convention, because Beamish's (1979) first report on the longevity of Pacific *Sebastes* was based on C&B otoliths. However, subsequent comparative research on various *Sebastes* species has demonstrated that C&B and otolith thin sections provided comparable age estimates up to an age of over 100 years (Andrews *et al.* 2002; Stransky *et al.* 2005b). Early ageing studies recognised the advantages of working with cross-sectional views of otoliths, even if their methods were sometimes cruder (otoliths broken by hand; Kelly and Wolf 1959; Sandeman 1969; Mayo *et al.* 1981), presumably because the methods avoid the age underestimation bias associated with either scales or whole otoliths at ages >30 years (Campana *et al.* 1990; Nedreaas 1990). The results reported herein extend the findings of Stransky *et al.* (2005b), demonstrating comparability between C&B and image-enhanced sections to an age of ~ 40 years. However, annual increments in old *Sebastes* spp. are known to be both narrow and difficult to interpret (Nedreaas 1990; Stransky *et al.* 2005b), which probably explains why image-enhanced C&B preparations using cut surfaces provided superior visibility to even image-enhanced sections at ages >40 years. Given the relative ease of preparing a cut transverse surface without embedding, the ability to capture and archive a high-quality digital image before fading of the burnt surface and the significant benefits of rapid image enhancement, a slight reduction in productivity would appear to be an acceptable limitation of the method. Thus image-enhanced C&B otoliths using cut surfaces are highly recommended for routine age determination of *Sebastes* spp. at least in older fish.

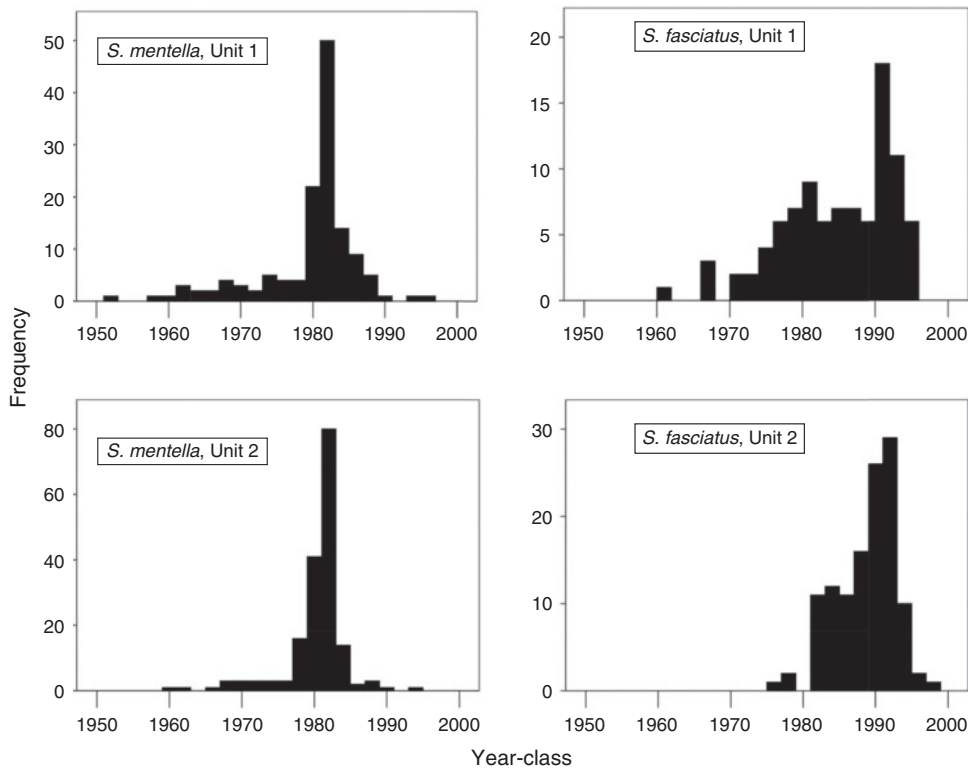


Fig. 6. Frequency histograms of redfish year-class by species (*Sebastes mentella* and *S. fasciatus*) and management unit based on collections made in Units 1 and 2 after 2000.

Bomb radiocarbon is well established as an effective method of age validation for long-lived species, often with a precision of as little as 1–2 years (Kalish 1993; Campana 2001). Given that two previous radiochemical studies have confirmed the overall accuracy of C&B preparations and sections for determining the age of *S. mentella* and *S. marinus* in the Atlantic (albeit with low precision; Campana *et al.* 1990; Stransky *et al.* 2005a), and in light of another two studies that have confirmed the accuracy of these methods for ageing *S. mentella* to an age of 10 years (Mayo *et al.* 1981; Saborido-Rey *et al.* 2004), the bomb radiocarbon results in the present study were initially puzzling. The consistent offset of 9 years between the NWA reference chronology and the redfish core chronology indicates that either our growth increment counts were underaged by 9 years in every fish that we aged or the NWA surface marine chronology was inappropriate for use on *Sebastes* spp. off eastern Canada. There is no $\Delta^{14}\text{C}$ reference chronology available for the Gulf of St Lawrence at depths of ~ 400 m, although the surface water chronology shows a 3-year delay relative to the NWA (Morin *et al.* 2013). A 3-year delay is insufficient to explain the assay results in the present study. However, several lines of evidence suggest it was the delayed penetration of the bomb radiocarbon signal to the 390–450 m living depth of the redfish that produced the offset and thus made the NWA surface chronology inappropriate for use. It is well known that the bomb signal in dissolved inorganic carbon (DIC) was initially confined to the surface marine layers, but has penetrated to increasingly deeper waters over time. Through ^{14}C assays of both the core and edge of the otoliths of deep-dwelling fish species, Horn *et al.* (2010) were

able to demonstrate that there was a delay of 10–15 years in the penetration of the ^{14}C signal to depths of 300–600 m in the south-west Pacific. Independent and more detailed otolith radiocarbon assays by Grammer *et al.* (2015) documented a 5–10-year delay in radiocarbon penetration to a depth of 400–500 m in the Tasman Sea. In the north-east Atlantic, the $\Delta^{14}\text{C}$ penetration depth increased by 1000 m over a period of 18 years (Nydal 1993); assuming a linear increase in depth through time, starting from the base of the 200-m mixed layer, this would imply that it would take 4.5 years for the signal to penetrate to the mean 450-m depth of the redfish in the present study. Similarly, the bomb signal took 14 years to penetrate to a depth of 800 m in the Indian Ocean (Rubin and Key 2002); given the same calculations described above, this would imply a 6-year penetration time to a depth of 500 m. Friess and Sedberry (2011) also observed a 5-year lag between surface and otolith $\Delta^{14}\text{C}$ values at depths of 450–600 m, although they attributed this to otolith ageing error. Therefore, it not only appears inevitable that the bomb signal would be delayed in reaching the depth of redfish in the present study, but the length of the delay is consistent with the 9-year delay we observed, suggesting that our redfish ages were, indeed, accurate.

Although the bomb radiocarbon results were consistent with our ages based on growth increment counts, uncertainty about the exact magnitude of the delay in the bomb signal meant that we could not validate our ages with the 1–2-year precision normally expected of the method. However, the dominance of the 1980–81 year-classes of *S. mentella* in Units 1 and 2 confirmed the accuracy of our ages for redfish up to an age of

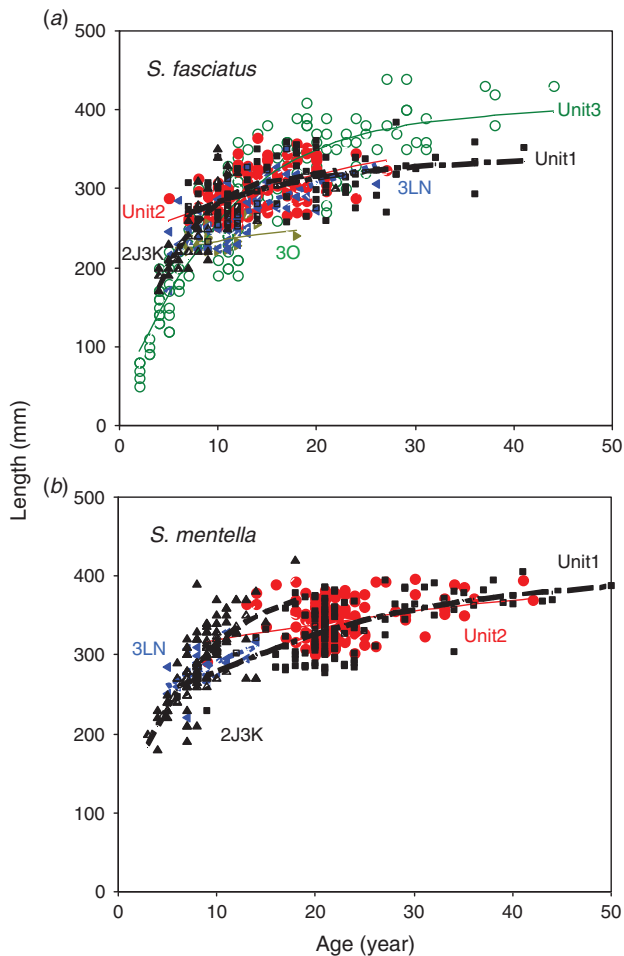


Fig. 7. Von Bertalanffy growth models fit to redfish length at age data by North Atlantic Fisheries Organization (NAFO) management area and species. (a) *Sebastes fasciatus* and (b) *S. mentella*.

22 years, because inaccurate ages would not have identified the correct birth years in fish collected in 2003. Age determination of dominant year-classes is a valid means of age validation (Campana 2001) but is only useful when recruitment is periodic and highly variable in strength. Fortunately, this is the case with many of the *Sebastes* populations in the Atlantic, and several previous studies have used it to validate their age interpretations of younger redfish (Mayo *et al.* 1981; Nedreaas 1990; Saborido-Rey *et al.* 2004). In the present study, the youngest fish assayed for bomb radiocarbon was ~20 years old. Given that the dominant year-class method validated our age interpretations to an age of 22 years, this suggests that our bomb radiocarbon results (with a 9-year delay) were also accurate, extending our age validation to an age of 46 years.

The results of the present study indicate that *S. mentella* grows to a larger size and with a lower growth coefficient than *S. fasciatus*, but that the growth trajectories and longevities of the two species can be quite similar. Few other studies have attempted to compare the growth of these two *Sebastes* species, in part because of their problematic species identification. In comparing the growth and longevity of *S. fasciatus*, *S. mentella* and *S. marinus* on the Flemish Cap, Saborido-Rey *et al.* (2004)

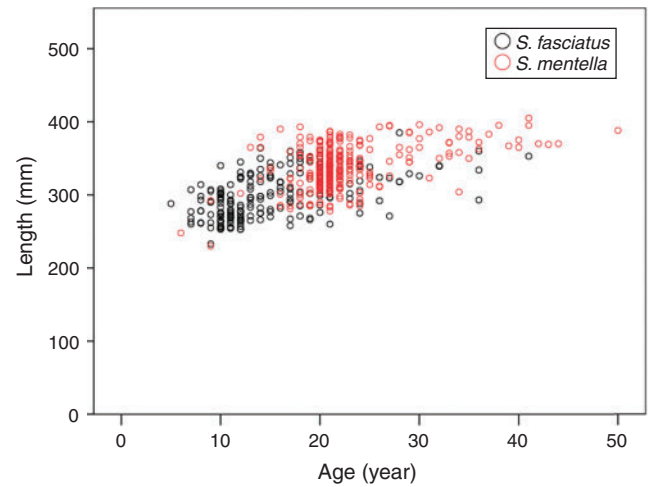


Fig. 8. Comparison of length at age by species (*Sebastes mentella* and *S. fasciatus*) for redfish collected after 2000 in Units 1 and 2.

commented on the difficulty of distinguishing between the first two species, but then neglected to state how they identified the species. They concluded that *S. marinus* grew fastest, *S. mentella* grew slowest and that longevities ranged from 32 to 34 years for *S. mentella* and *S. fasciatus* (Table 3). None of the other published studies considered *S. fasciatus*. However, most of these studies reported that *S. mentella* grew slower and to smaller size than *S. marinus*, with longevities on the order of 40–56 years (Sandeman 1969; Nedreaas 1990; Stransky *et al.* 2005b). The von Bertalanffy parameters in the present study are relatively similar to those that have been published (Table 3), with the possible exception of those published by Saborido-Rey *et al.* (2004). To our knowledge, the present study is the only age determination study that has unequivocally differentiated between Atlantic redfish species on the basis of genetic markers.

The genus *Sebastes* is extremely speciose in the north-east Pacific, where there at least 72 reported species (Love *et al.* 2002). Across these species, longevities ranging from 18 to 205 years (mean 62 years) have been reported, with mean concomitant K and L_{∞} values of 0.15 (0.03–0.62 year⁻¹) and 42 cm (15–86 cm) respectively (Love *et al.* 2002). These mean values of longevity and asymptotic length are reasonably similar to those we report here for the well-sampled Gulf of St Lawrence–Scotian Shelf (Unit 1–3) stocks (mean longevity 41 years; L_{∞} = 39 cm), although the mean Pacific K value is somewhat higher than the Units 1–3 mean K value of 0.06 year⁻¹. *Sebastes* spp. in Alaskan waters appear to grow more slowly (Malecha *et al.* 2007) and are thus more similar to those in the NWA, presumably reflecting the colder ambient waters.

Although there were clear differences in growth and longevity between redfish species, it was difficult to determine whether there were biologically meaningful differences among stocks within a species. Certainly, there were significant differences among many of the stocks, but low sample sizes and limited size ranges of the *S. fasciatus* samples from NAFO 3LN, 3O and 2J3KL may have affected accurate estimation of growth parameters in those regions. However, for the better-sampled Unit 1–3 stocks, the results suggest that there is relatively little difference within species for Units 1 and 2, but that *S. fasciatus*

Table 2. von Bertalanffy growth model fits to redfish length at age data by species and North Atlantic Fisheries Organization (NAFO) stock. Standard errors are bootstrapped estimates. men, *Sebastes mentella*; fas, *S. fasciatus*. L_{∞} , asymptotic length; K , growth coefficient; t_0 , age at zero length. NAFO stock: 2J3K, Labrador Sea; 3LN, eastern Grand Banks; 3O, southern slope of the Grand Banks

Species	Stock	<i>n</i>	Age range (years)	L_{∞} (cm) (s.e.)	K (year ⁻¹) (s.e.)	t_0 (s.e.)
fas	2J3K	37	4–22	328 (36)	0.196 (0.051)	0 (1)
	3LN	59	5–26	404 (54)	0.044 (0.030)	-12 (5)
	3O	32	6–18	271 (15)	0.057 (0.040)	-25 (51)
	Unit1	91	7–41	341 (15)	0.076 (0.045)	-13 (8)
	Unit2	121	5–27	380 (27)	0.046 (0.035)	-20 (7)
	Unit3	126	2–44	402 (15)	0.101 (0.014)	0 (1)
men	2J3K	126	3–18	396 (63)	0.138 (0.061)	-2 (2)
	3LN	30	5–14	406 (28)	0.047 (0.017)	-17 (4)
	Unit1	132	6–50	402 (20)	0.054 (0.016)	-11 (6)
	Unit2	176	9–42	431 (25)	0.020 (0.007)	-57 (9)

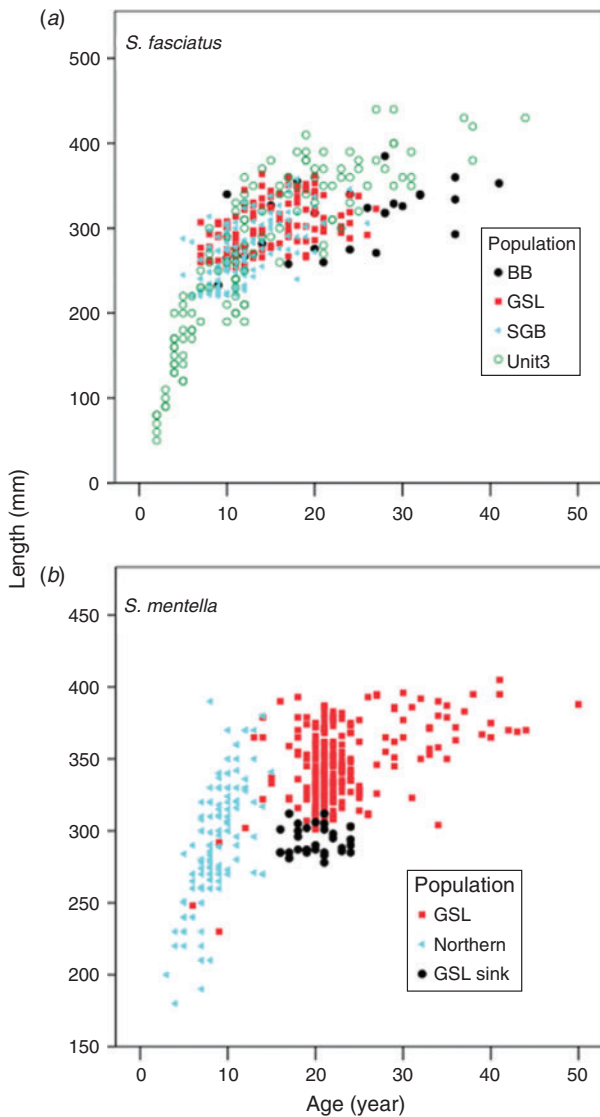


Fig. 9. Comparison of length at age by species for genetic populations of redfish. (a) *Sebastes fasciatus* and (b) *S. mentella*. BB, Bonne Bay; GSL, Gulf of St Lawrence; SGB, southern Grand Banks.

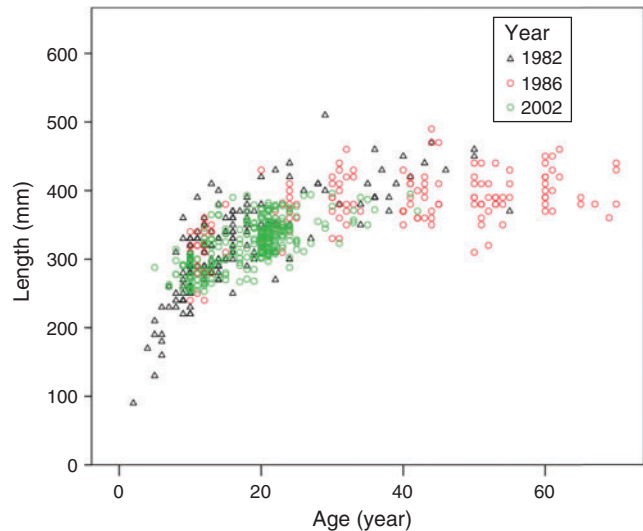


Fig. 10. Comparison of length at age of redfish (mainly *S. mentella*) in Management Unit 2 over a 20-year collection period. Although differences in age composition are evident, there was no obvious change in growth rate between 1982 and 2002.

grew faster in the warmer slope waters of Unit 3. Examination of growth rates by genetic population, rather than management unit, clearly highlighted some of the growth heterogeneity that was present. In particular, the genetically identical sink population (Saguenay fjord) of the Gulf of St Lawrence population indicated that environmental effects could affect growth rate, even in a deep-water species such as *Sebastes*. Nevertheless, the overall perspective was one of a consistent growth trajectory for each species in the area of southern Newfoundland and the Gulf of St Lawrence, with growth differences evident only for isolated populations (Bonne Bay) or sink populations (Saguenay fjord).

Given the relative constancy of water temperature at the ambient depth of the redfish, it is perhaps not surprising that there was little evidence of long-term (20-year) changes in growth rate within Unit 2 redfish, despite marked changes in age composition. Whether the reduced apparent longevity in Unit 2 in recent years represents a real change, perhaps

Table 3. von Bertalanffy growth model parameters reported in previous studies that used otolith sections or the 'crack and burn' method for age determinationmen, *Sebastes mentella*; fas, *S. fasciatus*; mar, *S. marinus*; viv, *S. viviparous*; NE, north-east; NF, Newfoundland; GoSL, Gulf of St Lawrence; L_{∞} , asymptotic length; K , growth coefficient

Study	Species	Region	Longevity (years)	L_{∞} (cm)	K (year ⁻¹)
Nedreaas (1990)	men	NE Atlantic	48	49.0	0.06
	mar		44	50.2	0.11
	viv		39	27.2	0.10
Sandeman (1969)	men	NF	40	30.6–44.8	0.06–0.17
		GoSL	46	36.0–38.4	0.06–0.13
	mar	Flemish Cap	40	34.4–38.5	0.15–0.17
		NF	42	55.0–60.0	0.05–0.10
		Flemish Cap	40	45.0–47.8	0.07–0.13
Saborido-Rey <i>et al.</i> (2004)	men	Flemish Cap	34	43.2–45.8	0.096–0.107
	fas		32	40.3–44.0	0.103–0.119
	mar		42	46.4–58.1	0.069–0.104
Stransky <i>et al.</i> (2005b)	mar	Iceland	30	46.4–52.7	0.095–0.121
	men	NE Atlantic	56	38.8–40.1	0.066–0.117

because of increased fishing mortality, is unclear. However, it likely represents more intensive sampling of deep-water stations in the 1980s, at locations that have not been sampled since. Similar longevity and von Bertalanffy growth parameters were reported for *S. mentella* in the only other study that has looked at redfish growth in and around the Gulf of St Lawrence (Sandeman 1969).

Examples of the successful management of deep-water fisheries are few and far between (Roberts 2002). In part, the failures are because of the slow growth, delayed age at maturation and infrequent recruitment characteristic of many deep-sea species (Musick 1999). High initial biomass often leads to unsustainably high catch rates, which then plummet as the virgin stock is exploited. This pattern has been repeated in many deep-sea fisheries around the world (Devine *et al.* 2006) and it has the potential to develop with *Sebastes* in the Atlantic Ocean as well. Musick (1999) noted that von Bertalanffy growth coefficient (K) values $<0.10 \text{ year}^{-1}$ are often associated with stocks that are particularly vulnerable to rapid and unsustainable overexploitation, and most of the *Sebastes* stocks in the NWA fall into this category. Both *S. mentella* and *S. fasciatus* in and around the Gulf of St Lawrence are characterised by growth curves that show a virtual cessation of somatic growth after an age of 10–15 years, corresponding to the approximate age of sexual maturation. Thus, it is of concern to see that recent stock assessments have placed the biomass of Unit 1 *S. mentella* at $<10\%$ of its value in 1990 (DFO 2010). Given the intrinsically lower growth and productivity of *S. mentella* compared with *S. fasciatus*, and in light of the apparent inevitability of mixed species catches in Units 1 and 2, it appears that at least some of the continued decline in *S. mentella* abundance and biomass can be attributed to the impact of fishing mortality on a multispecies mixture containing stocks of differing productivities (Kell *et al.* 2004).

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