

Age and growth of redfish (*Sebastes marinus*, *S. mentella*, and *S. fasciatus*) on the Flemish Cap (Northwest Atlantic)

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Age determination of redfish is difficult. In this paper, the ages of *Sebastes mentella* on the Flemish Cap are validated by following year classes from 1991 to 2000. The criteria used for *S. mentella* are consistent and coherent. The growth of different year classes is described and compared, and density-dependence is demonstrated to influence the growth rate of the strong 1990 year class, growth of that year class being the slowest of those followed. The slow rate of growth prevented that year class from maturing at the anticipated age. Growth is also compared between sexes, of *S. mentella*, *S. marinus*, and *S. fasciatus*, revealing that females grow faster than males. Finally, growth rate is compared among species. *S. marinus* grows fastest and *S. mentella* slowest, although the influence of density-dependent growth in *S. mentella* needs to be taken into consideration.

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Introduction

Redfish (genus *Sebastes*) are distributed and targeted by fisheries throughout the North Atlantic. On the Flemish Cap there are three species: *S. marinus* (Linneo, 1758), *S. mentella* Travin, and *S. fasciatus* Storer, 1856. The morphological resemblance between them has precluded some good biological research, and not only on the Flemish Cap, despite their commercial importance.

Age determination is one of the most important yet unresolved questions in research on redfish in the North Atlantic. Controversy rages around the most appropriate means of age determination (Nedreaas, 1990), and several attempts have been made to create common criteria (ICES, 1983, 1984, 1991, 1996). Although such criteria have not yet been established, agreement has been reached on the use exclusively of otoliths for redfish age determination. Many different methodologies have been used. For instance, Russian scientists have read scales under ordinary light (ICES, 1991); German, Danish, and Icelandic scientists have read scales under polarized light after treatment with silver nitrate (Kosswig, 1980); North Americans have used the broken and burnt otolith technique, also used by Norwegian scientists (Nedreaas, 1990). In contrast, some Spanish scientists use otoliths, but

with a slightly different technique (Saborido-Rey, 1993). Norwegians and other Spanish scientists have used scales routinely in past years, but it is known that, after a certain age, there is little or no scale growth and, therefore, the age of older fish tends to be underestimated when scales are used (ICES, 1996).

The slow growth and longevity of North Atlantic redfish have made the issue of accurate age determination particularly difficult to resolve. The prevalence of inaccurate age determinations and its impact on the accuracy of population dynamics studies was reported by Campana (2001, and references therein). Errors in assignment of age may contribute to serious overexploitation of a stock or species, often through underestimating true age and producing optimistic estimates of the rates of growth and mortality. Therefore, validation of age readings is a crucial requirement for managing stocks, particularly for those being assessed by means of age-structured models, such as Flemish Cap redfish (Ávila de Melo *et al.*, 2003). Common validation techniques include direct methods such as tag/recapture (including marking with chemicals such as oxytetracycline and calcein) or the use of known-age fish, and indirect techniques such as back-calculation, marginal increment analysis, edge progression analysis, frequency year-class progression analysis, radiometric isotope

analysis, and element analysis. Direct methods are difficult to implement in *Sebastes* owing to the low rate of survival when fish are caught. Frequency year-class progression analysis has been successfully used in North Atlantic *Sebastes*: Svalbard *S. mentella* (Nedreaas, 1990) and Gulf of Maine *S. fasciatus* (then known as *S. marinus*; Mayo et al., 1981).

It is difficult to identify redfish accurately to species, so in many areas two or more species are considered as a single stock (Saborido-Rey, 1993), precluding the comparison of growth among species. For Flemish Cap redfish, Saborido Rey (1995) validated age readings and compared growth rates. However, the short time-series available for that study prevented accurate interpretation of the data, resulting in the necessity for the current revised and improved analyses. In this study, we first validate the age of *S. mentella* by following the strong 1990 year class or cohort over time. We follow this with analyses and comparisons of the growth rates of different *S. mentella* cohorts and both sexes, and of the three species found on the Flemish Cap.

Material and methods

Since 1988, the European Union (EU) has supported an annual summer groundfish survey of the Flemish Cap (Saborido-Rey and Vázquez, 2001). Otoliths of *S. marinus* have been collected routinely since the 1990 survey, but because prior to 1991 *S. mentella* and *S. fasciatus* were not distinguished in the catches owing to their morphological similarity, otoliths from those two species have only been available since 1991.

Owing to difficulties in identification to species, redfish <13–15 cm have not been identified routinely to species level, so they have been grouped in the survey results as redfish juveniles. *S. mentella* is the most abundant of the three species on the Flemish Cap, accounting for >80% of the redfish catch numerically on each survey, except in 1994 when adult *S. marinus* were unusually abundant. It may therefore be assumed that the redfish juvenile group has a high proportion of *S. mentella*. This and the absence of strong year classes of *S. marinus* and *S. fasciatus* explain why the validation exercise was conducted only on *S. mentella*, for which the 1990 year class was clearly strong.

Catch composition, length frequency distributions, and biological data were recorded during each survey. Length and age frequencies of *S. mentella* were estimated for the total population by means of the swept area method and as explained in Ávila de Melo et al. (2003). Sagittal otoliths were removed, brought ashore in envelopes, broken through the nucleus, baked for 1 h in an oven at 200 °C, mounted individually in black plasticine, and read under transmitted light. A 50:50 mixture of ethanol and glycerine was used to clean the surface of the otolith halves. The

birthdate of *Sebastes* is assumed to be 1 January, so because samples were taken in summer, annuli only were counted. The incomplete summer zone was not considered. All age readings were made by the same reader. The numbers of otoliths analysed per species, sex, and year are listed in Table 1, and the number per length class per species in Table 2.

To analyse the evolution of a year class over time, it should be borne in mind that redfish are totally recruited to the survey gear at some 15–18 cm, but that total recruitment to the fishery is only achieved at a length of some 20 cm. This means that the relative abundance of each age class in the catch will increase year on year until ±18 cm, before declining as a consequence of natural and fishing mortality.

The mean lengths at ages 1–10 were estimated for each *S. mentella* cohort for which sufficient data were available, i.e. 1985–1999. Differences between the 1990 cohort and others were evaluated at each age by means of a *post hoc* Tukey HSD test within an analysis of variance, using the statistical package Statistica (StatSoft, Inc., 1995); this test is considered more robust than a simple t-test.

To compare growth rates between sexes and species, data from the 1991–2000 surveys were used, except for *S. marinus*, for which the 1990 data were also included. For each species and sex, data were pooled for the entire period, and a von Bertalanffy growth equation was fitted to length-at-age data using the iterative quasi-Newton non-linear regression method, as implemented in the statistical package Statistica (StatSoft, Inc., 1995).

Differences in von Bertalanffy growth curves were tested by means of the Chow test (Chow, 1960). This test is an application of the F-test, commonly used to test for structural change in a regression model attributable to variations in some of or all the parameters. In the case of two groups, it requires the sum of squared errors from three

Table 1. Number of fish aged in the EU surveys on the Flemish Cap from 1990 to 2000.

Year	<i>S. marinus</i>		<i>S. mentella</i>		<i>S. fasciatus</i>	
	Females	Males	Females	Males	Females	Males
1990	226	242				
1991	188	274	260	257	83	132
1992	288	350	485	452	376	367
1993	187	216	184	225	239	242
1994	307	320	361	364	287	316
1995	381	459	367	366	399	349
1996	510	554	607	661	448	425
1997	196	223	243	279	49	78
1998	24	27	257	234	182	194
1999	314	369	458	517	459	487
2000	88	70	232	233	37	38
All years	2 823	3 215	3 454	3 588	2 559	2 628

Table 2. Number of redfish otoliths aged per species, sex, and length class.

Length (cm)	<i>S. mentella</i>		<i>S. marinus</i>		<i>S. fasciatus</i>	
	Females	Males	Females	Males	Females	Males
8				1		
9		2				
10				3	3	1
11	1	2	1	2	4	6
12	10	34	10	14	25	30
13	28	35	33	37	45	48
14	36	39	45	61	51	56
15	65	57	53	87	62	73
16	76	84	105	117	95	98
17	88	89	152	187	122	148
18	80	123	97	111	148	173
19	129	160	133	131	184	239
20	136	166	150	153	236	257
21	161	159	148	167	213	260
22	168	171	128	153	221	254
23	138	183	141	158	174	222
24	171	159	130	145	182	164
25	184	165	146	151	135	159
26	180	184	139	147	125	114
27	182	168	132	148	105	84
28	159	158	107	153	82	67
29	149	160	126	139	69	69
30	142	153	109	135	55	41
31	112	156	107	118	52	29
32	116	158	107	112	43	17
33	123	163	83	101	33	7
34	145	156	65	105	29	5
35	108	137	57	93	22	3
36	98	148	47	69	12	2
37	115	78	37	65	9	1
38	92	63	37	44	10	
39	84	33	35	31	4	1
40	66	17	39	24	4	
41	46	8	15	13	3	
42	34	10	16	9	2	
43	17	4	15	12		
44	7	3	9	7		
45	6	1	9	7		
46	2	1	13	3		
47		1	4	1		
48			8			
49			7			
50			6			
51			5	1		
52			6			
53			6			
54			1			
55			2			
56			1			
57			1			
Total	3 454	3 588	2 823	3 215	2 559	2 628

regressions, one for each group (SS_i) and one for the pooled data (SS_{pool}). Thus,

$$\text{Chow} = \frac{SS_{\text{within}}/d.f.}{SS_{\text{error}}/d.f.} = \frac{SS_{\text{pool}} - \sum SS_i/3}{\sum SS_i / \sum n_i - 2k} \approx F_{k, n_1 + n_2 - 2k}$$

Results

Age validation of *S. mentella*

Over the study period, it is possible to identify ten modes between 8 and 27 cm, corresponding to the lengths 8–9, 11–12, 15, 17–19, 20, 21–22, 24, 25, and 26–27 cm (Figure 1). However, a single strong mode was present every year, from some 8 cm in 1991 to 27 cm in 2000. It can be tracked easily throughout, and we assume it to correspond to the same cohort. The age frequencies derived from otolith readings for the same period are shown in Figure 2. Every year, one age class dominates the frequency distribution, each one year older than in the previous year. The 8–9 cm modal group is assigned as age 1, so age frequencies are consistent with length frequencies year on year, and the age can be concluded to be correct or, at least, consistent. This is taken to be independent evidence that the length modes represent age classes moving through up to age 10, in this case the 1990 year class, because, as discussed below, we assume that redfish reach 8 cm in summer at age 1.

Figure 3 shows the mean length at ages 1–10 for the different cohorts of *S. mentella* present during the study period (1985–1999 cohorts). Comparison of the mean length at age for the 1990 cohort with the modal lengths at the putative age (e.g. age 1 in 1991 to age 10 in 2000) leads to the same conclusion of correct age and, hence, the age is validated. In 1991 there were three clear year classes, those of 1986, 1987, and 1990. The 1986 and the 1987 year classes were mixed (but still visible) in 1991, where their length ranged from 18 to 22 cm, and 1992 (20–24 cm; Figure 1). Subsequently, they were apparently fished out, because it was difficult to identify them.

Growth of *S. mentella*

The mean lengths at ages 1–10 for the different cohorts of *S. mentella* present during the study period (Figure 3) reveal a similar growth pattern for each cohort at ages 1 and 2. At age 1, mean length was around 9 cm for all cohorts, with less than 1 cm variation in the mean length. However, at ages 3 and older, the mean length of each cohort differs, the variation being greater in older fish. Most noticeable, though, is that the mean lengths of the 1990 cohort were the smallest in the record, at all ages, but particularly at ages 6–10, when the length difference from the preceding cohorts exceeds 3 cm (Figure 3), suggesting slower growth of that 1990 cohort. The other two strong year classes, those of 1986 and 1987 (ages 4 and 5 in 1991; Figure 2) had similar mean lengths at ages 1–5, but larger mean lengths than that of the 1990 year class at ages 6–10, suggesting a different growth pattern.

Comparison of the mean lengths at age of the 1990 cohort with those of the other 13 cohorts (1985–1999) by means of a *post hoc* (or multiple comparison) Tukey HSD

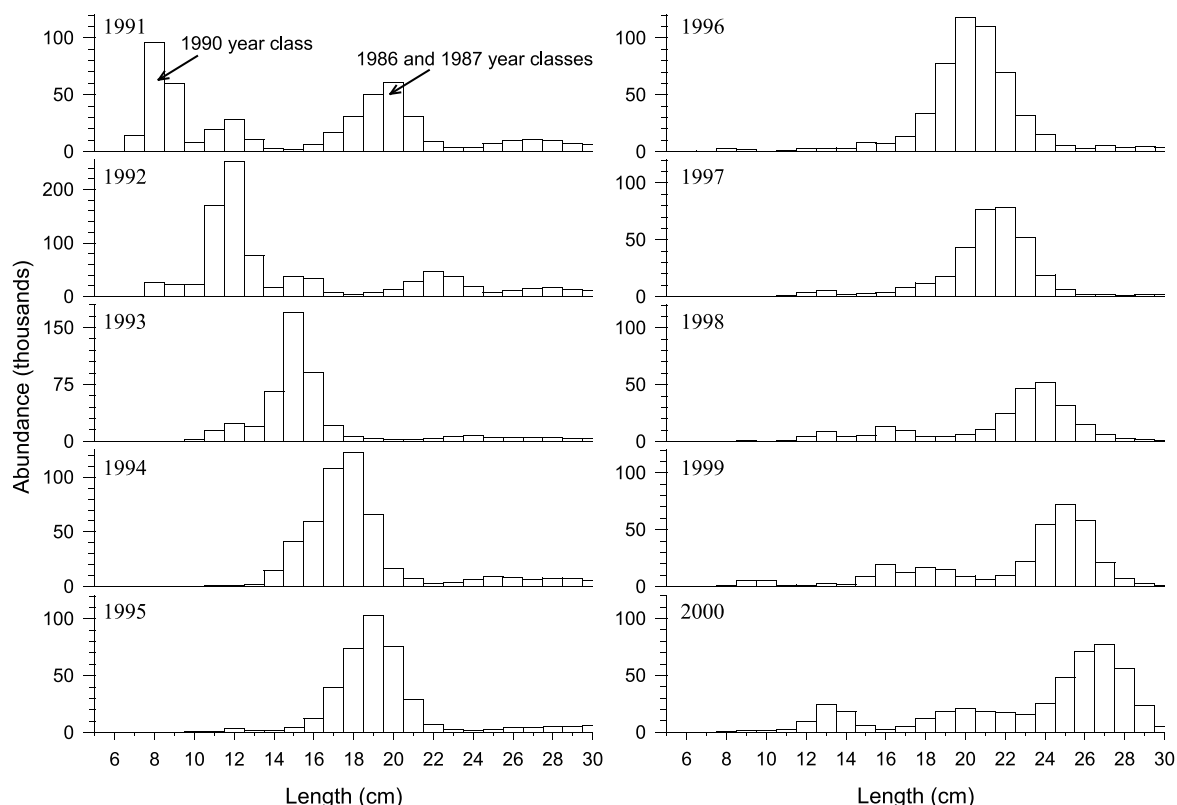


Figure 1. Population abundance at length (up to 30 cm) of *S. mentella* on the Flemish Cap in the period 1991–2000 estimated from EU research vessel bottom-trawl surveys. Note the different scales on the y-axis for 1992 and 1993.

test (Table 3) reveals differences already at an age of 4 years, but noticeably different mean lengths at ages 6–10. In general, cohorts earlier than 1990 (in this analysis, those of 1985–1989) had larger mean lengths at all ages considered, but especially for ages older than 6 years, where such cohorts were well represented (data on the age of *S. mentella* are available from the 1991 survey onwards). However, for cohorts later than 1990, there is no clear common pattern of growth (Figure 3). Thus, the 1992 cohort had one of the highest mean lengths at ages 1–3, but the lowest at ages 4 and 5, and the mean length of the 1994 cohort was the lowest at age 3, but about average at older ages. Generally, the mean lengths of cohorts during the 1990s were smaller than those in the 1980s, but larger than that of the 1990 cohort.

The growth trajectories of the 1990 cohort and adjacent year classes are depicted in Figure 4. For most cohorts there are two stanzas with different growth rates, but the decline in growth rate is more pronounced for the 1990 cohort. For this cohort, the change in growth rate was between ages 5 and 6, whereas the change in growth rate for the 1986–1989 and 1991 cohorts was between ages 6 and 7, producing a considerable difference in mean length between cohorts from that age on, because those cohorts were

growing faster for one year more. The two cohorts that do not appear to follow this trend are those of 1992 and 1994, for each of which the growth trajectory appears to be constant over the whole period, with no distinct stanzas.

Comparison of growth among sexes and species

The von Bertalanffy growth curves for each species and sex are shown in Figure 5, and their respective growth curve parameters are listed in Table 4. The maximum ages recorded were 38, 34, and 16 years for male *S. marinus*, *S. mentella*, and *S. fasciatus*, respectively, and 42, 31, and 32 years for females of the same species; only in *S. mentella* was a greater age observed for a male than for a female. However, only 8 of the 2559 female *S. fasciatus* subject to age determination were older than 18 years, so conclusions on female age and growth rate at older ages of that species have to be viewed with caution.

Results of the Chow test comparing growth curves among sexes and species reveal that growth profiles were significantly different between sexes ($p < 0.001$) of each species (Table 5). The greatest difference was in *S. marinus* ($F = 62.2$), and the lowest in *S. fasciatus* ($F = 8.9$). Females grow faster in all three species, though more

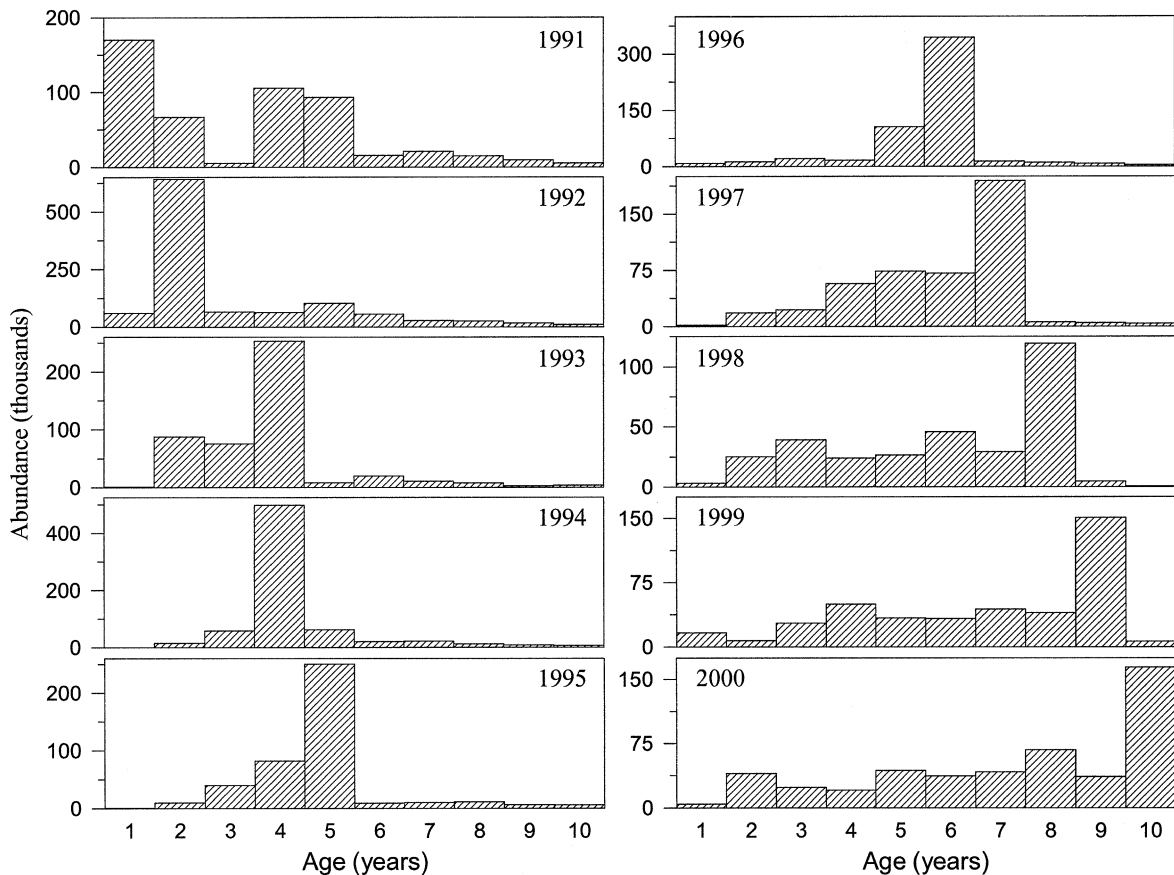


Figure 2. Population abundance at age (up to age 10) of *S. mentella* on the Flemish Cap in the period 1991–2000 estimated from EU research vessel bottom-trawl surveys. Note the different scales on the y-axis.

conspicuously so in *S. marinus* (though the small sample of large *S. fasciatus* again makes this conclusion tenuous for that species). Differences in L_{∞} are related to differences in length between the sexes (Table 6). Females seem to grow longer than males, i.e. the larger the fish, the greater the proportion of females for all three species (Table 6). Samples were dominated by fish aged 3–15 (Tables 7 and 8), except for *S. fasciatus*, for which the age spectrum was narrower (Table 9).

The Chow test compares growth curves but does not permit evaluation of the ages where mean length differs. To evaluate such differences in mean length between sexes at each age, t-tests were employed. Results are shown for *S. mentella*, *S. marinus*, and *S. fasciatus* in Tables 7, 8, and 9, respectively. For *S. mentella*, differences were significant ($p < 0.01$) at age 2 and from age 14 years (Table 7), and for *S. marinus*, differences were significant from an age of 12 years (Table 8). Using the same value of $p < 0.01$, there were no significant differences in mean length at age between sexes for *S. fasciatus*, although at a level of $p < 0.05$, differences would be regarded as significant from an age of 6 years (Table 9). The scarcity of older fish in the

samples makes this statement less rigorous for older fish, but older females were always larger than males of the same age. For *S. fasciatus*, the number of males older than 12 years was very small, and no males exceeded 16 years, the onset of the asymptotic region of the growth curve.

Growth between species was compared separately for each sex (Table 5). Growth of females of the three species was significantly different, particularly between *S. marinus* and *S. mentella* ($F = 213.1$); the least (but still significant) difference was between females of *S. mentella* and *S. fasciatus* ($F = 6.1$). Male growth of the three species was also significantly different, although the male growth curves for each species were more similar than were the growth curves of females (Figure 5).

Discussion

S. mentella is the most abundant of the three species of redfish on the Flemish Cap, representing between 80% and 90% of the total number of redfish younger than 10 years caught on every survey. For management purposes,

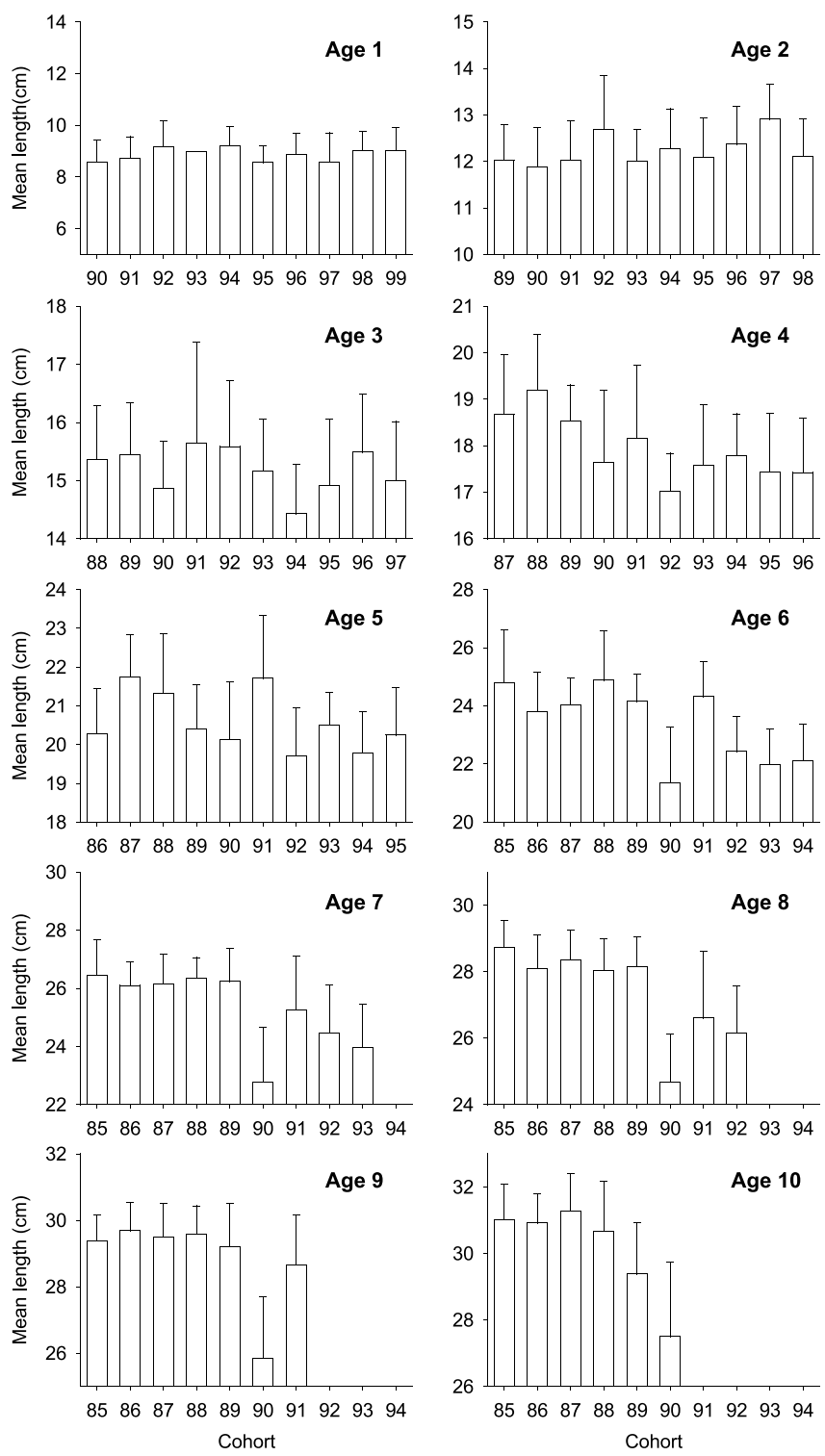


Figure 3. Mean length histograms and standard deviations at age by cohort (1985–1999) of *S. mentella* from summer bottom-trawl surveys on the Flemish Cap, 1991–2000.

Table 3. Results of the Tukey HSD *post hoc* comparison to test the differences in *S. mentella* mean length at age between the 1990 cohort and other cohorts. Italicized values are significant at $p < 0.05$; emboldened values are significant at $p < 0.01$.

Cohort	Age									
	1	2	3	4	5	6	7	8	9	10
1985						<0.001	<0.001	<0.001	<0.001	<0.001
1986					0.999	<0.001	<0.001	<0.001	<0.001	<0.001
1987				0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
1988			0.976	0.006	0.023	<0.001	<0.001	<0.001	<0.001	0.018
1989		0.998	0.699	0.034	0.976	<0.001	<0.001	<0.001	<0.001	<0.001
1990	—	—	—	—	—	—	—	—	—	—
1991	0.999	0.997	0.273	0.540	<0.001	<0.001	<0.001	<0.001	<0.001	—
1992	0.203	0.073	0.018	0.212	0.959	0.020	<0.001	<0.001	—	—
1993	1.000	0.999	0.531	1.000	0.974	0.328	0.009	—	—	—
1994	0.012	0.504	0.375	1.000	0.744	0.325	—	—	—	—
1995	0.999	0.978	0.999	0.970	0.999	—	—	—	—	—
1996	0.838	0.177	0.001	0.999	—	—	—	—	—	—
1997	0.999	<0.001	0.999	—	—	—	—	—	—	—
1998	0.487	0.950	—	—	—	—	—	—	—	—

therefore, age validation is crucial. Although routine assignment of <15 cm redfish to species on surveys is not possible, it is likely that most of the young redfish caught are *S. mentella*. Taking this to be the case, the length data on young redfish can be used to observe the progression of discrete length modes through the length frequency profiles, an approach generally considered to be reasonably reliable for validating the interpretation of annuli in young fish (Campana, 2001). The same method has been proved to be useful for other redfish populations (Mayo *et al.*, 1981; Nedreaas, 1990).

On the Flemish Cap, bottom-trawl surveys were conducted by Canada in winter of the years 1978–1985 (Lilly, 1987), by the USSR/Russia during spring/summer 1983–1993 (Bulatova *et al.*, 1997), and by the EU in summer since 1988 (Alpoim *et al.*, 2002). In addition, ichthyoplankton surveys were conducted by the USSR in spring of the years 1978–1983 (Serebryakov *et al.*, 1984), and by Canada in summer 1978–1982 (Anderson, 1984). The lengths of redfish caught during the ichthyoplankton surveys ranged from 0.7 to 1 cm in spring and early summer to 2.8 cm in August (Anderson, 1984; Serebryakov

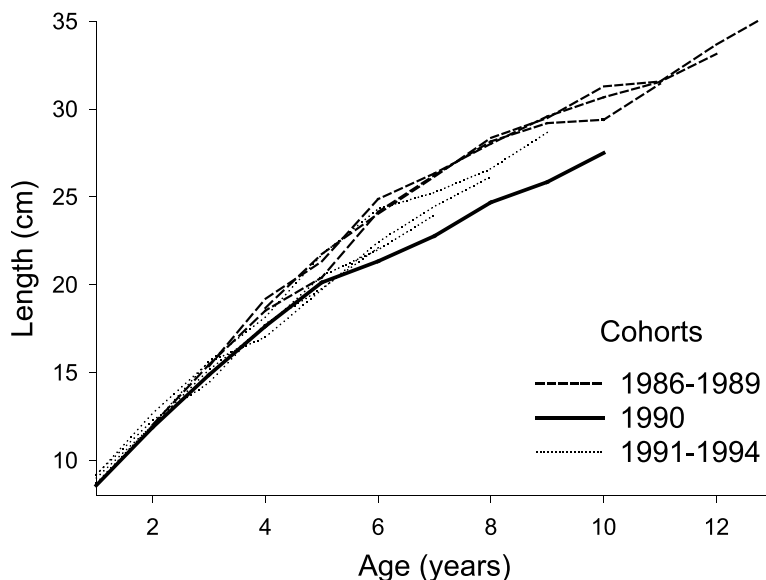


Figure 4. Growth trajectory for 1986–1999 cohorts of *S. mentella* on the Flemish Cap (growth is represented as mean length at age from summer bottom-trawl surveys).

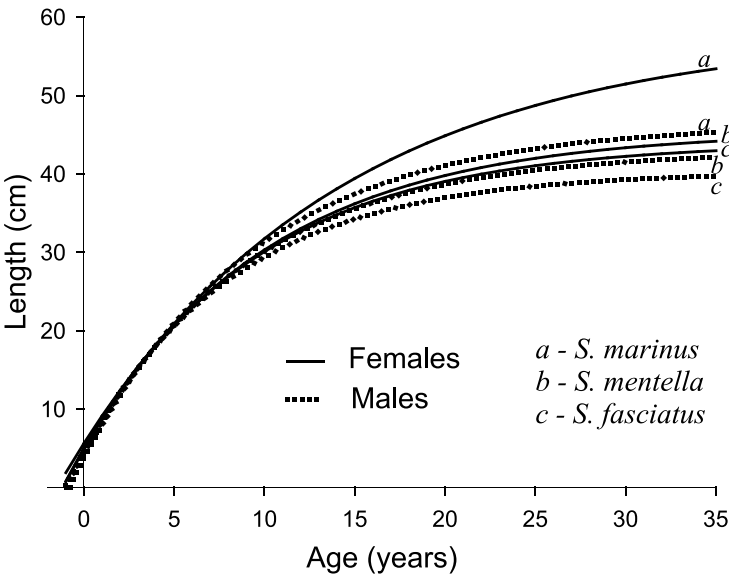


Figure 5. Von Bertalanffy growth curves for males and females of the three redfish species on the Flemish Cap from research vessel bottom-trawl surveys carried out during summer 1990–2000 for *S. marinus* and 1991–2000 for *S. mentella* and *S. fasciatus*.

et al., 1984). The smallest juvenile redfish in the trawl survey catches ranged from 6–7 cm in January (Lilly and Gavaris, 1982) to 8–9 cm in summer (Saborido-Rey, 1994). In other areas of the Atlantic, the 0-group surveys reveal that juvenile redfish attain 4–5 cm by autumn (Gulf of Maine – Kelly and Barker, 1961; Labrador Sea – Bainbridge and Cooper, 1971; Svalbard – Nedreaas, 1990; Greenland – Wieland, 1992). Therefore, the published growth rate of larvae and juveniles is consistent with the assumption that the earliest length mode found during this study corresponds to 1-year-old fish.

Since 1988, when the current survey series started, several relatively strong year classes of *S. mentella* have been detected (Saborido Rey, 1995), those of 1980, 1981, 1986, 1987, and 1990. The 1980 and 1981 year classes were already too old to be followed successfully through the survey series, but during the surveys of 1988, 1989, and

1990, there was a clear mode at a length of 24–30 cm, depending on the year (Saborido Rey, 1995); the age of these fish was determined to be 9 and 10 years. Power and Atkinson (1986) reported two strong modes during the 1982 Canadian survey on the Flemish Cap, at some 12 and 8 cm (1980 and 1981 year classes, respectively). No other strong modes appeared either just before or just after those years, so it is assumed that those two modes correspond to those identified during the EU surveys. The ages assigned to those modes are therefore considered to be accurate. Strong 1986 and 1987 year classes were also identified during the current EU survey series, but their abundance dropped suddenly in 1993, making it difficult to follow them further. However, the 1990 year class (about 8 cm long in 1991) was present throughout the whole survey series, partially

Table 4. Von Bertalanffy growth parameters and maximum age recorded for the three species of *Sebastes* on the Flemish Cap.

Parameter	Value					
	<i>S. marinus</i>		<i>S. mentella</i>		<i>S. fasciatus</i>	
	Males	Females	Males	Females	Males	Females
L_{∞} (cm)	46.40	58.15	43.24	45.82	40.31	44.04
K	0.104	0.069	0.107	0.096	0.119	0.103
t_0 (years)	−0.79	−1.49	−1.07	−1.28	−1.05	−1.19
Maximum age recorded (years)	38	42	34	31	16	32

Table 5. Results of the Chow test comparing von Bertalanffy growth curves for the three species of redfish on the Flemish Cap by sex.

Comparison		F*	d.f.†
<i>S. marinus</i>	Females vs. males	62.2	6 026
	<i>S. mentella</i>	14.7	7 030
	<i>S. fasciatus</i>	8.9	5 175
Females	<i>S. marinus</i> vs. <i>S. mentella</i>	213.1	6 265
	<i>S. marinus</i> vs. <i>S. fasciatus</i>	86.4	5 370
	<i>S. mentella</i> vs. <i>S. fasciatus</i>	6.1	6 001
Males	<i>S. marinus</i> vs. <i>S. mentella</i>	90.5	6 791
	<i>S. marinus</i> vs. <i>S. fasciatus</i>	73.0	5 837
	<i>S. mentella</i> vs. <i>S. fasciatus</i>	7.5	6 204

*Critical F = 5.42 ($\alpha = 0.001$) for all tests.
†Denominator d.f. (numerator d.f. = 3 for all comparisons).

Table 6. Proportion of each sex by length for the three redfish species (combined data for the years 1991–2000).

Length (cm)	Proportion (%)					
	<i>S. marinus</i>		<i>S. mentella</i>		<i>S. fasciatus</i>	
	Female	Male	Female	Male	Female	Male
12–14	47.06	52.94	36.94	63.06	48.50	51.50
15–17	47.20	52.80	52.07	47.93	46.34	53.66
18–20	49.23	50.77	43.08	56.92	47.96	52.04
21–23	46.57	53.43	45.95	54.05	48.18	51.82
24–26	47.84	52.16	52.60	47.40	48.84	51.16
27–29	46.04	53.96	45.60	54.40	50.60	49.40
30–32	45.68	54.32	44.50	55.50	56.90	43.10
33–35	37.39	62.61	45.81	54.19	82.72	17.28
36–38	37.02	62.98	52.95	47.05	90.00	10.00
39–41	51.14	48.86	79.31	20.69	90.91	9.09
42–44	59.52	40.48	81.16	18.84	100.00	0.00
45–47	60.00	40.00	88.89	11.11		
48–50	100.00	0.00				
51–53	94.12	5.88				
54–57	100.00	0.00				
Total	46.67	53.33	49.27	50.73	49.96	50.04

because of its strength and partly because of the reduction in fishing mortality of redfish on the Flemish Cap in the 1990s. From 1991 to 2000, one strong mode was present every year in the surveys. Redfish migration is not pronounced off or onto the Flemish Cap, there are no other strong modes during the series, and the strength of the year class is consistent. Therefore, we assume that we tracked the same cohort throughout the series.

Results presented here support the criteria used for our age determination of *S. mentella*, our validation supporting age determinations up to at least age 10, though not necessarily for older fish, in which the annuli are not always continuous in some parts of the otolith. For older fish, therefore, other techniques of validation should be used. Taking into account the ecology of the system in which redfish live, the most suitable technique would likely be marginal increment analysis. This technique requires seasonal sampling in year (monthly, quarterly...), which has not been possible on the Flemish Cap because commercial catches do not distinguish between *S. mentella* and *S. fasciatus*, and there is confusion regarding even *S. marinus*. Only during the annual summer research surveys carried out on the Flemish Cap since 1991 are species identified. Species identification of redfish (especially between *S. mentella* and *S. fasciatus*) is difficult in the Northwest Atlantic, so a robust analysis of the comparative growth rates of *S. mentella* and *S. fasciatus* across the whole area has not been possible to date.

The growth rate of the 1990 cohort has been revealed here to have been slower than for other cohorts, the mean lengths at ages 7–9 of the 1990 cohort being 4 cm less than that of others. Since 1988, when the EU survey com-

Table 7. Results of the t-test to evaluate the differences in mean length between sexes for each age of *S. mentella* on the Flemish Cap.

Age (years)	Males		Females		t
	Mean length (cm)	n	Mean length (cm)	n	
2	12.7	80	13.1	51	−3.17**
3	15.6	176	15.5	154	0.95
4	18.2	351	18.1	296	1.02
5	20.9	476	20.9	434	0.00
6	23.4	352	23.6	391	−1.31
7	25.8	423	25.8	401	−0.51
8	27.0	508	27.1	438	−0.67
9	28.1	430	28.1	375	−0.18
10	29.9	327	29.9	290	0.23
11	31.7	255	31.9	193	−1.05
12	33.1	226	33.4	222	−1.36
13	34.1	208	34.3	204	−0.87
14	34.8	190	35.4	173	−2.66**
15	35.5	159	36.2	155	−3.74**
16	36.3	106	37.4	126	−4.00**
17	36.9	82	37.9	102	−3.54**
18	36.8	68	38.1	97	−3.67**
19	37.9	47	39.1	80	−3.33**
20	38.9	21	40.3	58	−2.37*
21	38.7	16	40.3	46	−2.19*
22	40.0	9	40.6	27	−0.71
23	39.8	13	41.3	35	−2.31*
24	39.0	9	41.6	25	−3.81**
25	40.1	7	41.6	18	−1.50

*Significant at $p < 0.05$.

**Significant at $p < 0.01$.

menced, the 1990 cohort has regularly been the strongest year class. We therefore conclude that density-dependence has impacted the growth rate of this cohort. Population density is one of the main factors influencing the individual growth rate of fish populations (Wootton, 1990). Several authors have studied density-dependent growth in exploited fish populations in Newfoundland waters, including Flemish Cap cod, for which an inverse relationship between growth rate and cohort abundance has been documented (Templeman and Bishop, 1979; Wells, 1983; Pérez-Gándaras and Zamarro, 1990). Density-dependence in young stages occurs as a response to intracohort competition for a limited food resource (Shepherd and Cushing, 1980). A slower than normal growth rate in earlier years can affect the growth trajectory throughout a fish's life (Marshall and Frank, 1999; Lorenzen and Enberg, 2002). Different growth rates have, however, been observed in other cohorts of redfish than that of 1990. Except for the 1991 cohort, the growth rates of all year classes were slower than those of the 1980s. It is possible, therefore, that an environmental change such as a reduction in food availability or temperature may have affected growth rate. However, the 1991 cohort grew at the same rate as those of the late 1980s, and during the 2000 survey, the average

Table 8. Results of the t-test to evaluate the differences in mean length between sexes for each age of *S. marinus* on the Flemish Cap.

Age (years)	Males		Females		t
	Mean length (cm)	n	Mean length (cm)	n	
2	13.0	47	13.0	63	-0.10
3	15.3	169	15.3	229	0.44
4	17.8	359	17.6	391	1.90
5	20.9	499	20.9	464	0.95
6	23.6	409	23.9	372	-2.46*
7	26.2	376	26.1	298	0.76
8	28.1	259	27.9	238	0.99
9	30.0	195	30.1	193	-0.47
10	31.5	168	31.9	157	-2.16*
11	32.7	130	32.9	119	-0.65
12	33.9	122	35.1	94	-3.92**
13	35.1	110	36.1	75	-2.88**
14	35.8	63	37.5	58	-3.62**
15	37.2	73	38.6	38	-2.80**
16	38.2	38	40.8	24	-3.49**
17	39.0	32	41.3	26	-4.11**
18	39.5	13	42.9	18	-4.05**
19	42.0	9	43.5	16	-1.26
20	41.1	15	44.3	10	-2.84**
21	43.3	6	46.7	7	-2.43*
22	43.0	1	47.1	8	-1.05
23	41.5	2	49.3	3	-6.54**
24	46.0	3	49.1	11	-1.59
25	46.0	2	52.0	4	-2.31

*Significant at $p < 0.05$.**Significant at $p < 0.01$.

length of 9-year-old fish (i.e. the 1991 cohort) was already larger than that of 10-year-old fish (the 1990 cohort).

In some fish populations, when growth over the lifetime is measured, stanzas are observed, with sudden changes in growth rate between the stanzas. The most commonly reported growth rate stanzas are those related to larval metamorphosis, with different growth patterns, pre- and post-metamorphosis. Other well-described stanzas are related to physiological change (e.g. when salmon migrate from salt-water to freshwater), or to maturation. In redfish, the growth rate stanzas precede and follow an age of 5 or 6 years, and it is difficult to explain the change. However, we know that the change is not related to maturation, because age at maturity of *S. mentella* is some 10 years (Saborido-Rey, 1994). Redfish in the North Atlantic are known to adopt a pelagic existence sometime during their life. On the Flemish Cap, pelagic behaviour is mainly when the fish are young (Saborido-Rey, 1994). In fact, during the EU surveys, the relative abundance of a given cohort increases with age, which means they are not totally recruited, first to the gear but also possibly later to the demersal habitat, where they are liable to be captured by trawl gear. Therefore, it is likely that *S. mentella* progressively shift from a more pelagic to a more demersal habitat with age, becoming demersal at

Table 9. Results of the t-test to evaluate the differences in mean length between sexes for each age of *S. fasciatus* on the Flemish Cap.

Age (years)	Males		Females		t
	Mean length (cm)	n	Mean length (cm)	n	
2	12.7	92	12.7	81	0.42
3	15.3	191	15.4	201	-1.49
4	18.0	449	18.1	374	-1.54
5	20.5	739	20.6	657	-1.65
6	23.0	515	23.2	419	-2.08*
7	25.2	269	25.6	259	-2.43*
8	26.1	161	26.7	199	-2.10*
9	27.7	115	28.3	116	-1.97*
10	29.6	35	30.2	65	-1.77
11	31.1	26	31.7	49	-1.09
12	31.4	19	32.6	48	-2.19*
13	31.8	10	32.9	32	-1.72
14	33.3	3	35.8	25	-1.77
15	32.8	4	34.7	11	-1.01
16	33.5	2	35.6	8	-0.78

*Significant at $p < 0.05$.

age 5 or 6. This would also imply a change in feeding behaviour. It would be anticipated that growth of the demersal population of redfish would be more influenced by population density than would the pelagic population, and certainly the growth rate of the 1990 cohort declined more rapidly after age 6 than did that of other cohorts.

In many fish species, the onset of maturity is size-dependent. In cohorts with an accelerated growth rate, the age at maturity decreases, i.e. the fish mature younger (Saborido-Rey and Junquera, 1998), which may have an important impact on stock dynamics (Saborido-Rey and Junquera, 1999). In contrast, a slower growth rate will produce a delay in maturation (Wootton, 1990). On the Flemish Cap, the length at maturity of *S. mentella* has not changed during the study period (unpublished data), but because growth of the 1990 cohort has been slower, the age at maturity for that cohort would be expected to increase. Histological observation of *S. mentella* ovaries has revealed that most of the 1990 cohort are still immature (unpublished data), so the decelerated growth seems to have prevented this cohort from maturing at the normal age. In 2000, the 1990 cohort (age 10) constituted 44% of the total biomass and 84% of the 10+ biomass, i.e. the expected spawning biomass (Ávila de Melo et al., 2003). Therefore, the reduction in the age at maturity of this cohort has had a profound effect on spawning stock biomass (Ávila de Melo et al., 2000).

The growth rate of each sex of the three species of redfish on the Flemish Cap is significantly different. In other areas of the North Atlantic, male and female redfish growth follows a similar profile, but the females live longer (Sandeman, 1961; Surkova, 1961). Sandeman (1969) also

reported different growth rates for male and female redfish on the Flemish Cap, but he did not differentiate between *S. mentella* and *S. fasciatus*, so his results cannot be taken to be conclusive for either species. In the areas where *S. mentella* and *S. fasciatus* co-exist, it is difficult to compare growth rates because of the problem in identifying to species. The skill we acquired during our surveys now allows us to identify both species routinely, and our analysis reveals significant differences in growth rate between all three species of redfish on the Flemish Cap. Apparently, *S. marinus* lives longer and *S. fasciatus* has a shorter lifespan. However, this difference could be simply the result of *S. fasciatus* living where the directed effort and by-catch of redfish is higher (Saborido-Rey, 1993), resulting in larger, older individuals being removed.

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