http://journal.nafo.int

J. Northw. Atl. Fish. Sci., Vol. 25: 17–28

Changes in Greenland Halibut Growth, Condition and Fecundity in the Northwest Atlantic (Flemish Pass, Flemish Cap and Southern Grand Bank)

S. Junquera, E. Román , X. Paz and G. Ramilo
Instituto Español de Oceanografía
Vigo, Spain

Abstract

The Greenland halibut fishable stock has been declining substantially since late-1980s, according to both surveys and commercial fishery indices, particularly among the ages 10+, which corresponds to the females age at 50% maturity. In this paper the effect of this apparent reduction in the stock abundance on growth and reproductive parameters is examined.

Among growth parameters, the analysis of the first year growth is undertaken both by cohort and by geographic areas, assuming that density dependence might be the most severe at younger age classes. This is made using records of the respective first annual ring otolith diameters. Other growth related index such as the condition factor is also analysed. Neither significant differences in the first year growth have been observed between areas analysed, nor between cohorts, during the period 1988 to 1996. Mean condition factor-at-age for ages 1 to 13 were stable during this same period. About the reproductive parameters, two aspects are considered: the interannual variations in length-at-maturity and in the potential fecundity. Female length at maturity varied between 64.5 and 69.5 cm. Female potential annual fecundity ranged between 15 000 and 158 000. It increases with female age, but the mean fecundity-at-age variations were not significant either between years of sampling or between cohorts.

A common feature observed is the relative stability of those characteristic through the period analysed, which could support a certain resiliency of the life history traits in this species.

Key words: fecundity, Flemish Cap, Greenland halibut, Grand Bank, growth

Introduction

The Greenland halibut stock in NAFO Subarea 2 and Divisions 3 KLMNO is considered to be part of a stock complex, which includes also Subareas 0 and 1 (Anon., 1997). According to the Canadian and Russian/USSR surveys, a pronounced decrease in the stock biomass occurred since late-1980s, especially among the older ages (Bowering *et al.*, MS 1995; Brodie *et al.*, MS 1998), while recruitment has been above average since the mid-1990s.

The objective of this study is to analyse whether this apparent decline in the adult stock followed by an increase in juvenile abundance in recent years could have some compensatory effect on the reproductive parameters and growth related parameters. The reproductive parameters we analysed were trends in the female length at maturity and in the potential fecundity, and the growth parameters were the first year growth and the condition factor, assuming that density – dependence would be stronger at early ages.

Female length and age at maturity in other fish stocks in NAFO area, have shown a decrease in recent years as a response to population decline (Pitt, 1975; Bowering, 1989; Rinjsdorp, 1993; Saborido-Rey and Junquera, 1998), and it has been described as an index of population stress (Trippel, 1995). In contrast, the fecundity component of the compensatory response in fish populations is far less documented. It could be expected that an

accelerated growth under low population densities would result in larger fish at age, and this in turn would increase the reproductive potential of fish at that age. Trippel (1995) reports some examples of such increases in reproductive output under fast growing conditions in exploited populations.

Otolith morphology is genetically determined and reflects phylogenetic relationships (Lombarte and Castellón, 1991), but there is also a strong intraspecific variability related to environmental factors (Aldrich, 1989). The amount of growth in the first year can be measured from the otolith first annual ring diameter (L_1). Differences in the first year growth has been associated with differences in the spawning time (Dawson, 1991), and it has also been shown to vary between year classes, and to be linked with density dependence (Agnault, 1989). In this paper, we analyse whether a difference exists between cohorts in the first annual growth that could be density related and whether geographic patterns in this variable exists.

Material and Methods

The areas involved in this study are located in NAFO Regulatory Area of Div. 3LM (Flemish Pass), Flemish Cap (Div. 3M) and southern Grand Bank (Div. 3NO) (Fig. 1). The two later ones (areas A and C in Fig. 1) are areas of juvenile concentrations, whereas Flemish Pass (area B) is an area of adult concentration.

First year growth

In order to analyse the variations in the first year growth, a sample of fish smaller than 25 cm total length have been selected from the July EU Flemish Cap survey series (area A in Fig. 1), from the Spanish Div. 3NO surveys (area C in Fig. 1) and from the commercial catches in 1993–94 (area B in Fig. 1). A total of 1 262 individuals have been examined, with ages ranging from 1 to 4 (Table 1). Age 0 otoliths have been excluded.

The otolith L_1 diameter is defined as the longitudinal axis to the outer edge of the hyaline ring of the first year growth (Fig. 2). Measurements were taken using a binocular microscope with reflected light and recorded in micrometer eyepiece units (epu), with a magnification of × 12, which gave a equivalence of 13 epu/mm. Only the left otolith was used. Otolith L_1 variability was examined by area and by year-class using two ANOVA.

Condition

Fish from the EU summer survey series in Flemish Cap (area A, Fig.1) have been analysed for this purpose (Table 1). The condition factor was

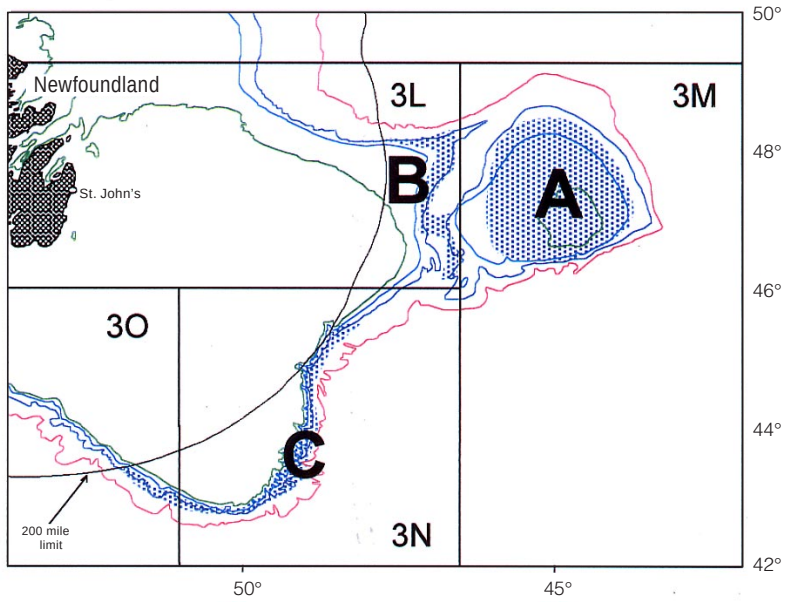

Fig. 1. Sampling areas. **A** = Flemish Cap; **B** = Flemish Cap, and **C** = Southern Grand Bank.

TABLE 1. Greenland halibut sampling summary. Data type: C = commercial (observers), R = research survey, Length range = total length (cm) of the sampled fish.

	Macroscopic				Microscopic			
Year	Data type	Period	Length range	Number	Data type	Period	Length range	Number
				Maturity				
1990	C	Jul–Dec	13–103	33 581				
1991	C	Jan–Dec	16–120	107 227	C	Dec	60–90	150
1992	C	Jan–Dec	14–120	164 818	C	Jan–Mar/Oct–Nov	36–104	250
1993	C	Jan–Dec	21–103	40 136	C	Jan–Mar	58–90	130
1994	C	Jan–Dec	16–103	42 558	C.R	Jul/Sep–Dec	40–106	433
1995	–	–	–	–	R	Feb	46–95	90
1996	C	Jan–Dec	23–94	5 497	C.R	Feb–Apr/Jul	29–100	526
1997	C	Jan–Dec	21–101	3 164	C	Feb–Mar	35–102	175

Year	Data type	Period	Length range	Number
		Condition Factor		
1991	R	Jul	14–77	410
1992	R	Jul	12–76	903
1993	R	Jul	10–79	1 061
1994	R	Jul	13–69	1 250
1995	R	Jul	13–70	728
1996	R	Jul	10–82	908
1997	R	Jul	13–81	1 337
		Otolith L_1 Diameter		
1992	R	Jul	12–25	193
1993	R.C	Jul/Feb–Nov	10–25	315
1994	R.C	Jul/Sep–Oct	13–25	161
1995	R	Jul	13–25	104
1996	R	Jul/May	10–25	225
1997	R	Jul/May	13–25	264

calculated as the percentage ratio between the gutted weight and the cube of the total length. The analyses of the condition factor between years and between cohorts have been performed by means of ANOVA.

Maturity

Variations in maturity are analysed from two points of view: (A) female length at maturity and (B) potential fecundity. Data from area B of Fig. 1 have been used (Table 1). Total length and weight of fish were recorded on board and otoliths removed for age determination. A maturity stage was assigned, according to a four-point macroscopic scale (Table 2). In research surveys, samples included all the Greenland halibut caught per tow, while in the commercial ones, the sampling is a length-stratified proportion of the haul catch. Subsamples of those were taken for further histological analysis (Table 1). The ovaries were dissected out, weighed, assigned to one of the four macroscopic stages in Table 2 and fixed immediately in 10% buffered formalin. For histological analysis, sections of the ovaries were dehydrated, embedded in paraffin and 5µm-thick sections were stained with Harris' haematoxylin and eosin.

The characteristics of the different stages of oocyte development and maturation during the reproductive cycle, have been described in the Barents Sea Greenland halibut by Fedorov (1968). However, in this study an updated terminology is used, and Fedorov's oocyte classification has been partly modified according to more recent literature

on teleost oogenesis. The fish oogenesis is divided into oocyte growth (development), maturation and ovulation (Guraya 1986). The presence/absence of oocytes in circumnuclear ring, cortical alveoli, vitellogenesis, nuclear migration, hydration, atresia, and postovulatory follicles have been recorded in each of the ovary sections, following the classification of Wallace and Selman (1981) and West (1990), and the photographic description of these stages given by Fedorov (1968) and Walsh and Bowering (1981). Atresia is the degeneration of the oocyte to its complete resorption. The nomenclature and general characteristics of this process have been defined by Hunter and Macewicz (1985) for the northern anchovy (*Engraulis mordax*), who divided it into four sequential stages. In this study, only the first stage of degeneration (alpha-atresia) have been recorded. Levels of atresia are computed as the proportion of the total developing oocytes that are in alpha-atresia in every ovary section.

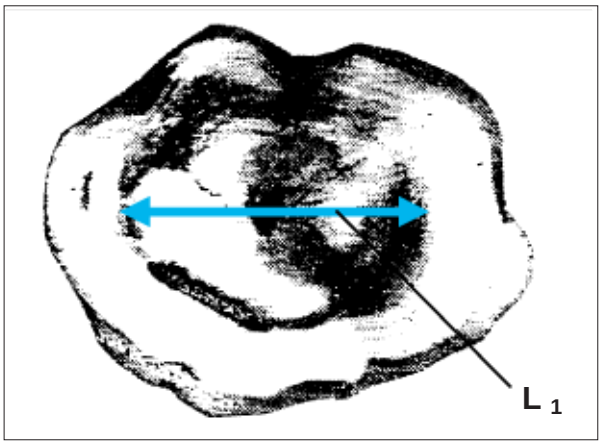

Fig. 2. Representation of the Greenland halibut otolith first annual ring diameter (L_1).

The equivalencies between the terminology used in this study and the one used by Fedorov (1968) in his first description of oogenesis in Greenland halibut are summarized in Annex 1. The main difference is that we do not include the cortical alveoli within the vitellogenic stage (the equivalent to the trophoplasmic growth stage in Fedorov's classification), as according to Wallace and Selman (1981) and West (1990) the cortical alveoli do not contain yolk in a strict sense and do not have a trophic function, although their appearance indicates the onset of ovary maturation.

An initial objective of the histological analysis is to establish a link between the oocyte development process and the macroscopic maturity scale that we use, to determine the level of agreement achieved with the macroscopic staging of the ovaries. To assess the ovarian stage of development, the frequency in the samples of each one of the different types of oocytes postovulatory follicles and atresic oocytes was recorded. Microscopic maturity stages were assigned according to the criteria described in Table 2, where also are described the equivalencies between the macroscopic and the microscopic stages used in this study, and their corresponding oocyte diameter range. The length frequency distribution of the oocytes at the successive stages was obtained by measuring all the previtellogenic (cortical alveoli) and the vitellogenic oocytes in the sections. The diameter of the oocytes, according to Foucher and Beamish (1980), was calculated as the mean between the largest and the shortest diameter recorded in those oocytes cut through the nuclei. The results were grouped in 50 µm classes and presented as percentages.

a) ***Length at maturity analysis***

Data from 1990 to 1997 (Table 1) were used to generate maturity curves by year. Fish were

TABLE 2. Description of the macroscopic and microscopic maturity stages and the corresponding oocyte diameter range. CA = oocytes in cortical alveoli stage; VIT = vitellogenic oocytes; NM = nuclear migration; H = hydration; AT = oocytes in atresia; PF = postovulatory follicles.

Stage	Macroscopic	Microscopic	Diameter Range
1	Immature	All oocytes in primary growth	<425 µm
2	Maturing	Presence of either CA. VIT. AT or PF	425–2 300 µm
3	Spawning	Presence of NM or H	2–4 mm
4	Postspawning	Presence of PF and AT. without either CA or new VIT	–

considered immature if they had ovaries in Stage 1 and mature in either Stage 2, 3 or 4. In case of discrepancies, the macroscopic assignment had been corrected using the microscopic diagnosis. The proportion of mature female by length were adjusted to a logistic equation as described by Ashton (1972):

$$\hat{P} = \frac{e^{a+bl}}{1+e^{a+bl}}$$

and the logit transformation:

$$\ln \frac{\hat{P}}{1-\hat{P}} = a + bL$$

where $\hat{P}$ is the predicted mature proportion, a and b the coefficients estimated of the logistic equation and L the length. The length-at-maturity can be estimated as the minus ratio of the coefficients (- a/b) by substituting $\hat{P}$ = 0.5 in the second equation. The variance (V) of the L_{50} estimates was calculated from the variances and covariance of the maturity curve coefficients by the expression (Ashton, 1972):

$$V(L_{50}) = \frac{1}{b^2}\left[V(a) + \frac{a^2}{b^2}V(b) - \frac{2a}{b}\mathrm{cov}(a,b)\right]$$

b) ***Potential fecundity determination***

Fecundity estimates have been made assuming that Greenland halibut is a determinate, group synchronous spawning species. This means that a single group of oocytes develops through vitellogenesis and matures to be spawned, without recruitment of any new group of vitellogenic oocytes. In species with determinate fecundity, potential annual fecundity, which is the total number of advanced yolked oocytes per female matured every year, uncorrected for atretic losses, is considered to be equivalent to the total fecundity, before spawning starts. A key problem in those species is to establish that potential annual fecundity is an unbiased estimate of the annual fecundity (Horwood and Greer Walker, 1990; Hunter *et al.*, 1992). For this to be true, four assumptions are required:

- Fecundity becomes fixed before the spawning begins, without addition of new vitellogenic oocytes.
- Potential annual fecundity is equivalent to annual fecundity, and it would be equal to the standing stock of vitellogenic advanced oocytes. The incidence of pre-spawning atresia in this advanced group to be spawned must be evaluated.
- Females used to estimate the potential fecundity must not have spawned during the current reproductive cycle. If that is the case the fecundity would be underestimated.
- The oocytes that constitute the potential annual fecundity are clearly recognisable. If the ovary is not sufficiently developed it will not be possible to distinguish the oocytes destined to be spawned.

The gravimetric method was used to estimate the total potential fecundity by year (Hunter *et al.*, 1989) in ovaries having oocytes 1 000 µm and larger. The ovaries in the most advanced vitellogenic stage were previously screened to verify the absence of recent postovulatory follicles. In this method, fecundity is the product of the gonad weight (W_{ovary}) and the oocyte density. Oocyte density is the number of oocytes per gram of ovarian tissue and it is obtained by counting the number of oocytes (o_i) in a weighed sample of ovarian tissue. Three subsamples (n), one from the middle and two from both sides, were taken in the ovaries, and weighed to the nearest 0.001 g (w_i). Subsamples weight ranged from 150 mg to 750 mg. The number of oocytes larger than 1 000 µm were counted (o_i). The size of 1 000 µm was assumed after examination of the length distribution of the oocytes as a threshold from where the oocyte group that are going to be spawned is clearly recognizable. This value is in agreement with the length distribution range for vitellogenic oocytes of 0.9–1.65 mm, reported by Ronneberg *et al.* (1998), and 1–2 mm reported by Albert *et al.* (MS 1998). The total potential fecundity (F_r) is obtained with the expression:

$$F_r = \frac{\left(\Sigma \frac{o_i}{w_i}\right)}{n} \cdot W_{ovary}$$

The mean potential fecundity per gram of gutted female-at-age was calculated from 1992 to 1997 and this value was compared between ages and years by respective ANOVA, and between cohorts by an ANCOVA using age as covariant.

All the statistical analysis included in this paper have been performed using the Statistica package (StatSoft, Inc., 1995).

Results

First year growth

The sample of L_1 records included ages 1 to 4 and a total of 9 cohorts (1988 to 1996). Their respective means and standard deviations are presented in Table 3. No significant differences in the first annual growth between the three areas analysed have been observed (F = 0.86; $d.f.$ = 2, 1006; P >0.05). The ANCOVA between first annual growth and cohort (all areas combined), using the age as covariant, did not gave significant differences over the period analysed (F = 1.24; $d.f.$ = 3, 26; P >0.05).

Condition

Table 4 presents the mean condition factor at age, for ages 1 to 13, in Flemish Cap (Fig. 1 area A). The values obtained are very homogeneous during the seven years analysed and the two-way ANOVA performed with those data indicate that neither the factor age (F = 0.33; $d.f.$ = 12, 72; P >0.05) nor the factor year (F = 0.13; $d.f.$ = 6, 72; P >0.05) presents significant differences.

Maturity

a) ***Length at maturity analysis***

The female length at 50% maturity obtained from macroscopic (1990) and combined microscopic and macroscopic criteria (1991 to 1997) is shown in Table 5. It can be observed that this parameter is quite constant over this period of time, ranging from 69.5 cm in 1991 to 64.5 cm in 1994. Differences between years are not significant.

b) ***Potential fecundity determination***

In Greenland halibut the advanced vitellogenic stage is achieved by a single cohort of oocytes. When the vitellogenic stage is achieved in the ovaries, only oocytes in primary stage, whose developing time takes longer than one year, coexist with the vitellogenic group. Cortical alveoli and vitellogenic oocytes only coexist at the initial stage of oocyte growth. As vitellogenesis progresses, only one kind of oocytes is present in the ovaries and this supports our assumption that in this species the fecundity is determinate, and that the spawning is of the 'group synchronous' type.

The incidence of atresia in the different growth stages prior to spawning is presented in Fig. 3. No atresia is observed in immature females, and it starts to appear in first maturing females, with the onset of the cortical alveoli stage. The highest frequency have been observed at the initial stage of vitellogenesis. Once the oocytes achieve the fully yolked stage, the incidence of the atresia becomes negligible.

The potential annual fecundity has been determined in a total of 256 females ranging in length between 63 and 104 cm and of ages between 11 and 20+ years (Table 6). The number of eggs per gram of gutted female ranged from 4.7 and 19.9, what gives a total potential fecundity range between 15 000 and 158 000 eggs per female. The parameters of the relationship between weight and fecundity along with results obtained in previous studies and in other areas are presented in Table 7. Fecundity

TABLE 3. Mean L_1 (first annual ring diameter in mm), standard deviations and numbers in the samples by cohort and by NAFO Divisions.

	Division 3L			Division 3M			Division 3NO		
Cohort	Mean	SD	Number	Mean	SD	Number	Mean	SD	Number
1988	–	–	–	1.923	–	1	–	–	–
1989	–	–	–	2.200	0.19	5	–	–	–
1990	2.089	0.17	22	2.079	0.29	34	2.088	0.17	13
1991	2.158	0.19	127	2.201	0.28	103	2.159	0.19	65
1992	2.232	0.27	62	2.230	0.35	117	2.232	0.27	36
1993	2.122	0.11	5	2.171	0.35	115	2.179	0.16	7
1994	–	–	–	2.195	0.41	111	2.164	0.20	50
1995	–	–	–	2.100	0.37	197	2.208	0.23	59
1996	–	–	–	2.269	0.42	112	2.090	0.12	22
Total			216			794			252

TABLE 4. Greenland halibut condition factor at age (mean, standard deviation and number) in Flemish Cap (NAFO Div. 3M) during the EU summer bottom trawl survey (1991–97).

	1991			1992			1993			1994			1995			1996			1997		
Age	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N
1	0.82	–	1	0.85	0.14	47	0.78	0.13	102	0.87	0.18	46	0.81	0.13	86	0.87	0.22	113	0.76	0.09	172
2	0.80	–	1	0.85	0.13	42	0.80	0.08	104	0.83	0.09	57	0.78	0.13	62	0.79	0.07	124	0.77	0.09	161
3	0.82	0.04	7	0.82	0.06	21	0.79	0.06	68	0.83	0.06	88	0.81	0.06	64	0.83	0.07	67	0.80	0.07	165
4	0.79	0.23	21	0.81	0.11	77	0.82	0.06	59	0.86	0.07	96	0.82	0.05	46	0.81	0.06	77	0.81	0.06	133
5	0.80	0.06	45	0.83	0.07	143	0.85	0.08	88	0.87	0.09	106	0.85	0.07	48	0.83	0.07	102	0.80	0.06	131
6	0.82	0.04	31	0.85	0.08	179	0.85	0.08	139	0.86	0.08	166	0.84	0.06	87	0.84	0.07	158	0.82	0.07	186
7	0.85	0.06	65	0.85	0.07	159	0.86	0.08	156	0.88	0.08	151	0.85	0.06	76	0.85	0.06	89	0.83	0.06	162
8	0.85	0.05	16	0.85	0.08	90	0.87	0.08	131	0.87	0.08	91	0.84	0.04	61	0.85	0.11	96	0.85	0.07	113
9	0.86	0.05	14	0.87	0.09	41	0.88	0.08	88	0.89	0.08	57	0.87	0.05	63	0.87	0.07	40	0.88	0.06	62
10	0.83	0.07	11	0.86	0.10	24	0.90	0.08	25	0.90	0.1	23	0.88	0.05	22	0.93	0.09	10	0.89	0.07	25
11	0.81	0.03	4	0.90	0.05	13	0.88	0.07	13	0.91	0.08	8	0.87	0.08	8	1.11	0.19	4	0.97	0.15	4
12	0.93	–	1	0.89	0.09	7	0.99	0.08	5	0.88	0.07	4	0.97	0.04	4	0.98	0.09	5	0.88	0.03	5
13	0.91	–	1	0.88	0.18	4	1.00	0.00	3	0.89	0.07	2	0.91	–	1	0.91	0.06	2	0.88	0.01	4

TABLE 5. Female Greenland halibut length at 50% maturity (L_{50}), from 1990 to 1997 in Flemish Pass area (NAFO Div. 3LM). E (b) = error of the slope (b) of the maturity curve; V (L_{50}) = variance of the L_{50} estimate.

	1990	1991	1992	1993	1994	1996	1997
E (b)	0.002	0.008	0.006	0.001	0.001	0.012	0.007
V (L_{50})	1.39	1.28	1.62	2.17	2.19	1.29	2.50
L_{50}	**67.5**	**69.5**	**65.2**	**65.5**	**64.5**	**65.8**	**66.7**
Length range	13–103	16–120	14–120	21–103	16–103	23–94	21–101

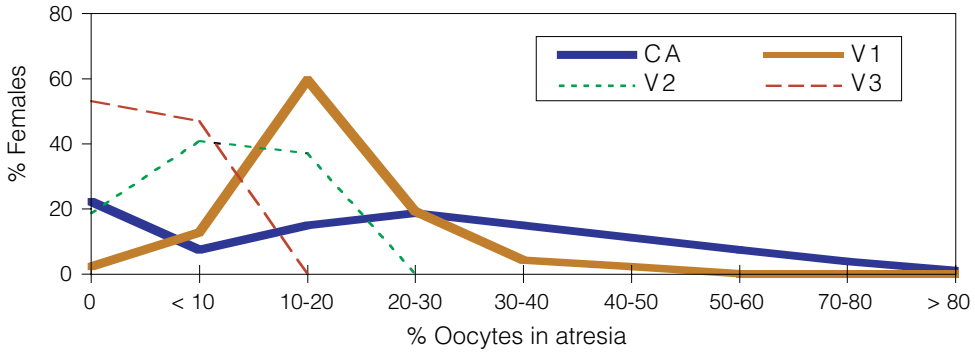

Fig. 3. Proportion of females that have a certain proportion of oocytes in alpha-atresia (X axis) expressed here as intervals, at successive stages of oocyte growth (CA – cortical alveoli stage; VI, V2 and V3 = primary, secondary and final vitellogenesis respectively).

increased significantly with female age (F = 16.25; $d.f.$ = 9, 255; P <0.001) but the variations of the mean fecundity at age were not significant neither between the sampling years (F = 0.07; $d.f.$ = 4, 36; P >0.05) nor between cohorts (F = 1.2; $d.f.$ = 13, 35; P >0.05).

Discussion

In this paper we examine a series of biological parameters of this species that could be expected to show variability as a response to the apparent reduction in stock abundance of Greenland halibut in NAFO Div. 3LMN.

Differences in the first year growth has been associated with differences in the peak spawning time, environmental conditions and population size (Hopkins, MS 1986; Agnault, 1989; Dawson, 1991; Lombarte and Lleonart, 1993). Our results however indicate that this character is very stable in the Greenland halibut from Flemish Pass – Flemish Cap – Div. 3NO area during this study. This is an interesting finding, considering that spawning of this species in this area does not have a clear seasonality (Junquera and Zamarro, 1994; Junquera and Saborido-Rey, MS 1995; Morgan and Bowering, 1997), as peak spawning time varies a lot from year to year. Further, some amount of year round spawning activity is frequently observed (Albert *et al.*, MS 1998). This may mean that the early stages could grow at the same rate whether they are born in summer or in winter.

The Greenland halibut condition factor also remained fairly stable during the period analysed and this is in agreement with results from the Canadian catches, where no trends were seen in the mean weight-at-age over the period 1988–97 (Anon., 1998).

The length/age at 50% maturity (L_{50}) is a character that shows a high degree of density dependent variability in fish stocks (Adams, 1980; Beacham, 1983). However Greenland halibut female L_{50} in Flemish Pass area did not show significant differences about a mean value of 66.5 cm over a period of seven years (1990 to 1997),

TABLE 6. Greenland halibut mean number of eggs per g of gutted female, range of variation and numbers at age in Flemish Pass area (area A in Fig.1).

	1992			1993			1994			1996			1997		
Age	Mean	Range	N	Mean	Range	N	Mean	Range	N	Mean	Range	N	Mean	Range	N
11	4.7	–	1	5.7	–	1	6.0	–	1	5.4	–	1	5.7	–	1
12	5.5	–	1	5.3	–	1	8.5	5.7–13.2	3	5.7	–	1	6.6	5.7–7.6	2
13	9.4	–	1	5.6	–	1	8.5	5.2–12.5	8	6.0	5.3–6.6	2	9.1	7.6–10.8	6
14	9.0	–	1	7.7	–	1	10.1	5.4–13.3	5	6.7	6.4–7.0	2	10.6	9.9–11.1	3
15	8.1	7.8–8.5	2	9.8	9.4–10.4	2	9.5	5.2–13.3	9	7.9	5.6–9.4	7	10.8	9.6–12.5	4
16	11.5	9.1–13.8	6	10.7	–	1	9.5	5.2–13.5	10	10.1	6.5–14.9	25	10.8	9.6–11.9	4
17	12.2	8.7–13.9	6	10.7	–	1	11.5	5.9–17.0	13	10.5	7.5–14.7	12	12.9	11.5–14.6	4
18	11.8	8.2–13.4	4	13.4	–	1	12.2	10.1–15.3	13	12.8	9.7–16.9	10	13	12.1–14.9	5
19	12.8	7.3–15.7	4	14.9	12.9–17.5	4	15.6	7.4–19.8	11	12.8	7.3–19.1	16	14.8	12.2–18.2	3
20+	12.5	7.0–18.2	7	15.0	–	1	16.9	8.3–19.9	13	15.7	7.3–19.9	8	14.8	11.4–18.2	7
Total			33			14			86			84			39

TABLE 7. Greenland halibut fecundity parameters obtained by different authors and in the present study.

		Fecundity parameters			
		($F = a \times length^b$)		($F = a \times weight^b$)	
Source	Area	*a*	*b*	*a*	*b*
Lear, 1970	Eastern Newfoundland	0.00006	4.66	–	–
Bowering, 1980	Southern Labrador	0.0623	3.082	–	–
Bowering, 1980	St. Lawrence	0.0007	4.26	–	–
Dayakov, 1982	Bering Sea	0.00074	2.58	0.071	1.15
Serebryakov *et al.*, 1992	Davis Strait	6.3×10^{-6}	3.62	7.6	1.07
Gundersen *et al.*, 1999	Barents Sea	1.155×10^{-7}	4.598	2.539×10^{-4}	1.439
Present study	Flemish Pass	0.0052	3.7	7.3	1.03

where the reduction of the stock was observed. Morgan and Bowering (1997) found a somewhat larger L_{50} (71.5 cm) over the last 17 years, for a broader area, which also includes the one, analysed in this study. They also reported large spatial and temporal variations in this parameter not related with the variations in the abundance of the stock that they attribute to the peculiarities of the spawning behaviour of this species. This variability is not confirmed by our results. The use of complementary histological techniques to check the macroscopic diagnosis can improve the accuracy of the results (Junquera and Saborido-Rey, MS 1995), as it is difficult to distinguish visually between certain maturity stages. In particular the resting adult stage and an immature (juvenile) can be easily confused (11% of misclassification in the present study data). Also frequently confused macroscopically are the postspawning and maturing stages (7% of misclassification in the present study data). Besides, a year round sampling scheme seems to us essential to avoid the seasonal effect in the estimates.

The most important assumption made in the fecundity determination is that potential annual fecundity becomes fixed before the spawning, in which case it would be equal to the standing stock of advanced oocytes (total fecundity). In Greenland halibut this seems to be the case, as it has been shown that the advanced vitellogenic stage is achieved by a single cohort of oocytes, and in those ovaries only oocytes in primary stage, whose developing time takes longer than one year, coexist with them. In this study, the potential annual fecundity has been assumed to be equivalent to the annual fecundity. Hunter *et al.* (1992) however point out that it is probably never true, as a certain number of advanced oocytes are usually resorbed by atresia in all fish species. In Greenland halibut, according to our results, atresia as a mechanism of fecundity regulation occurs mainly in the transition from cortical alveoli to primary vitellogenesis that is in the early stage of the oocyte growth. In the fully yolked stage it is negligible, and is absent on immature ovaries, as also was found by Walsh and Bowering (1981).

The values of the potential fecundity obtained in the present study are within the range of the ones reported by Serebryakov *et al.* (1992) in Davis Strait area and Bowering (1980) in Southern Labrador and Gulf of St. Lawrence. As with the other biological parameters analysed in this study, fecundity remained rather constant between years and between cohorts. Compared to other fish species, Greenland halibut fecundity is among the lowest reported in the literature. Also, it is the Pleuronectidae with largest eggs (Miller *et al.*, 1991), and based on the balance between the growth and the reproductive parameters it can be considered as a *k*-selected species. Thus Greenland halibut reproductive strategy would consist in producing small, though highly protected quantity of descendants: large eggs, long lasting hatching time and large larvae. Large larvae are able to feed on large long living plankton (i.e. the plankton found in the deeper pelagic layers), which do not only appear in seasonal blooms. This hypothesis is supported by the fact that Greenland halibut larvae have been found very rarely (Jensen, 1935; Haug *et al.*, 1989, Albert *et al.*, MS 1998), and though

the hatching depth is unknown, there are indications that it occurs at depths beyond 500 m (Jensen, 1935; Haug *et al.*, 1989; Stene *et al.*, 1999). Accordingly, if the risk of competition, predation and starvation in the planktonic stage is reduced, there is no need to have either a large or highly variable fecundity. There may also be no need of having a fixed mass population spawning season in order to match the planktonic blooms.

Another aspect that could contribute to the low potential fecundity of this species is that only 2% of the females analysed over a period of eight years achieved the fully yolked stage at age 11, and only 5% at age 12. Most of the females were not ready to spawn for the first time before age 15. The age at which Greenland halibut first produce cortical alveoli (i.e. are first considered to be mature) is between 9 and 15 (Morgan and Bowering, 1997; and present results). This may be an indication that the time required to go from cortical alveoli to the fully yolked stage is longer than one year. This would mean that it would be likely that individuals would not spawn on a yearly basis, as has been hypothesized previously (e.g. Fedorov, 1971). This fact can explain the high geographic and temporal variability in maturity reported by Morgan and Bowering (1997) in this stock.

Despite the reported decrease in the Greenland halibut stock since the early-1990s, the biological parameters examined in this study appear to have been stable. Two conclusions could be drawn from it: one is that the reduction in stock size was not as large as it was thought and the other is that Greenland halibut biological parameters are resilient to change in such a short time and that longer time periods of low stock size would be required before changes was observed.

Acknowledgements

This study was made with the financial support of the DG XIV of the European Commission.

References

ADAMS, P. B. 1980. Life history patterns in marine fishes and their consequences for fisheries management. *Fish. Bull.*, **78**: 1–12.

AGNAULT, A. L. 1989. Long-term changes in growth and age at maturity of mackerel *Scomber scombrus* L. from the North Sea. *J. Fish. Biol. (Supplement A)*, **35**: 305–311.

ALBERT, O. T., E. M. NILSSEN, A. STENE, A. C. GUNDERSEN, and K. H. NEDREAAS. MS 1998. Spawning of the Barents Sea/Norwegian Sea Greenland halibut (*Reinhardtius hippoglossoides*). *ICES C.M Doc.*, No. 0: **22**: 19 p.

ALDRICH, J. C. 1989. The world beyond species, an argument for greater definition in experimental work. *In*: Phenotypic responses and individuality in aquatic ectotherms. J. C. Aldrich (Ed.). Japaga. Ashford. p. 3–8.

ANON. 1997. Scientific Council Report 1996. *NAFO Sci. Coun. Rep.*, 1996. 226 p.

1998. Scientific Council Report 1997. *NAFO Sci. Coun. Rep.*, 1997. 274 p.

ASHTON, W. D. 1972. The logit transformation with special reference to its uses in bioassay. Hafner Publishing Co., Inc., New York, 88 p.

BEACHAM, T. D. 1983. Variability in median size and age at sexual maturity of Atlantic cod (*Gadus morhua*) on the Scotian shelf in the Northwest Atlantic Ocean. *Fish. Bull.*, **181**(2): 303–321.

BRODIE, W., W. R. BOWERING, D. POWER, and D. ORR. MS 1998. An assessment of Greenland halibut in NAFO Subarea 2 and Divisions 3KLMNO. *NAFO SCR Doc.*, No. 47, Serial No. N3038, 37 p.

BOWERING, W. R. 1980. Fecundity of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), from Southern Labrador and Southern Gulf of St. Lawrence. *J. Northw. Atl. Fish. Sci.*, **1**: 39–43.

1989. Witch flounder distribution off southern Newfoundland, and changes in age, growth and sexual maturity patterns with commercial exploitation. *Trans. Amer. Fish. Soc.*, **118**: 659–669.

BOWERING, W.R., W. BRODIE, D. POWER, and M. J. MORGAN. MS 1995. An assessment of the Greenland halibut resource in NAFO Subarea 2 and Divisions 3KLMN. *NAFO SCR Doc.*, No. 64, Serial No. N2579, 19 p.

DAYAKOV, Y. P. 1982. The fecundity of the Greenland halibut, *Reinhardtius hippoglossoides* (Pleuronectidae), from the Bering Sea. *J. Ichthyol.*, **22**(5): 59–64.

DAWSON, W. A. 1991. Otolith measurement as a method of identifying factors affecting first year growth and stock separation of mackerel (*Scomber scombrus* L.). *ICES J. Cons.*, **47**: 303–317.

FEDOROV, K. Ye. 1968. Oogenesis and the sexual cycle of the Greenland halibut. *Tr. Polyarn. N.-i. inst. Morsk. Rybn. Khoz. I okeanogr.*, **23**.

1971. The state of the gonads of the Barents Sea Greenland halibut (*Reinhardtius hippoglossoides* Walb.) in connection with failure to spawn. *J. Ichthyol*. **11**: 673–682.

FOUCHER, R. P., and R. J. BEAMISH. 1980. Production of nonviable oocytes by Pacific hake (*Merluccius productus*). *Can. J. Fish. Aquat. Sci.*, **37**: 41–88.

GUNDERSEN, A. C., O. S. KJESBU, A. STENE, and K. H. NEDREAAS. 1999. Fecundity of the Northeast

Arctic Greenland halibut (*Reinhardtius hippoglossoides*). *J. Northw. Atl. Fish. Sci.*, **25**: 29–36 (this volume).

GURAYA, S. S. 1986. The cell and molecular biology of fish oogenesis. *Monographs of Developmental Biology*, **18**: 223 p.

HAUG, T., H. BJORKE, and I. B. FALK-PETERSEN. 1989. The distribution, size composition and feeding of larval Greenland halibut (*Reinhardtius hippoglossoides* Walbaum) in the eastern Norwegian and Barents Sea. *ICES Rapp.*, **191**: 226–232.

HOPKINS, P. J. MS 1986. Mackerel stock discrimination using otolith morphometrics. *ICES C.M. Doc.*, No. H:**7**.

HORWOOD, J. W., and M. GREER WALKER. 1990. Determinacy of fecundity in sole (*Solea solea*) from the Bristol channel *J. Mar. Biol. Assoc. U. K.*, **70**: 803–813.

HUNTER, J. R., and B. J. MACEWICZ. 1985. Measurement of spawning frequency in multiple spawning fishes. *NOAA Tech. Rep., NMFS*, **36**: 79–94.

HUNTER, J. R., B. J. MACEWICZ, and C. A. KRIMBELL. 1989. Fecundity and other aspects of the reproduction of the sable-fish, *Anaplopoma fimbria*, in Central California waters. *CalCoFi Rep.*, **30**: 61–72.

HUNTER, J. R., B. J. MACEWICZ, N. C. LO, C., and A. KIMBRELL. 1992. Fecundity, spawning and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. *Fish. Bull. U. S.*, **90**: 101–128.

JENSEN, A. S. 1935. The Greenland halibut (*Reinhardtius hippoglossoides*) its development and migrations. *K. Dan. Viden. Sels. Skr.*, **6**: 32 p.

JUNQUERA, S., and J. ZAMARRO. 1994. Sexual maturity and spawning of Greenland halibut (*Reinhardtius hippoglossoides*) from Flemish Pass Area. *NAFO Sci. Coun. Studies*, **20**: 47–522.

JUNQUERA, S., and F. SABORIDO-REY. MS 1995. Histological assessment of sexual maturity in Greenland halibut in Div. 3LM and 3N. *NAFO SCR Doc.*, No. 28, Serial No. N2537, 9 p.

LEAR, W. H. 1970. Fecundity of Greenland halibut (*Reinhardtius hippoglossoides*) in the Newfoundland–Labrador Sea. *J. Fish. Res. Board Can.*, **27**: 1880–1882.

LOMBARTE, A., and A. CASTELLÓN. 1991. Inter and intraspecific otolith variability in the genus *Merluccius* as determined by image analysis. *Can. J. Zool.*, **69**: 2442–2449.

LOMBARTE, A., and J. LLEONART. 1993. Otolith size changes related to body growth, habitat depth and temperature. *Environ. Biol. of Fish.*, **37**: 297–306.

MILLER, J. M., J. S. BURKE, and G. R. FITZHUGH. 1991. Early life history patterns of Atlantic North American flatfish: likely and unlikely factors controlling recruitment. *Neth. J. Sea Res.*, **27**(3/4): 261–275.

MORGAN, M. J., and W. R. BOWERING. 1997. Temporal and geographic variation in maturity at length and age of Greenland halibut (*Reinhardtius hippoglossoides*) from the Canadian Northwest Atlantic with implications for fisheries management. *ICES J. Mar. Sci.*, **54**: 875–885.

PITT, T. K. 1975. Changes in abundance and certain biological characteristics of Grand Bank American plaice, *Hippoglossoides platessoides. J. Fish. Res. Board Can.*, **32**: 1383–1398.

RIIJNSDORP, A. D. 1993. Fisheries as a large scale experiment on life-history evolution: disentangling phenothypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. *Oecologia*, **96**: 391–401.

RONNEBERG, J. E., A. C. GUNDERSEN, and J. BOJE. MS 1998. Fecundity of Greenland halibut (*Reinhardtius hippoglossoides* Walbaum) in East Greenlandic waters. *ICES C.M. Doc.*, No. 0:26, 12 p.

SABORIDO-REY, F., and S. JUNQUERA. 1998. Histological assessment of variation in the sexual maturity of cod (*Gadus morhua* L.) at the Flemish Cap (Northwest Atlantic). *ICES J. Mar. Sci.*, **55**: 515–521.

SEREBRYAKOV, V. P., A. K. CHUMAKOV, and I. I. TEVS. 1992. Spawning stock, population fecundity and year-class strength of Greenland halibut (*Reinhardtius hippoglossoides*) in the Northwest Atlantic, 1969–88. *J. Northw. Atl. Fish. Sci.*, **14**: 107–113.

STATSOFT, INC. 1995. STATISTICA for Windows [Computer program manual]. Tulsa, OK, USA.

STENE, A., A. GUNDERSEN, P. SOLEMDAL, K. J. NEDREAAS, and T. ALBERT. 1999. Early development of Northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides*). *J. Northw. Atl. Fish. Sci.*, **25**: (171–177) this volume.

TRIPPEL, E. A. 1995. Age at maturity as a stress indicator in fisheries. *BioScience*, **41**(11): 759–771.

WALSH, S. J., and W. R. BOWERING. 1981. Histological and visual observations on Oogenesis and sexual maturity in Greenland halibut off Northern Labrador. *NAFO Sci. Coun. Studies*, **1**: 71–75.

WALLACE, R. A., and K. SELMAN. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. *Amer. Zool.*, **21**: 325–343.

WEST, G. 1990. Methods of assessing ovarian development in fishes: a review. *Austr. J. Mar. Fresh. Res.*, **41**(2): 199–222.