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

by

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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 it is reviewed the effect of this apparent reduction in the stock abundance in two main groups of biological parameters, namely growth and reproductive parameters, since late-1980s.

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. About the reproductive parameters, two aspects are considered: the interannual variations in length-at-maturity and in the potential fecundity.

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.

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/URSS surveys, a pronounced decrease in the stock biomass occurred since late-1980s, specially among the older ages (Bowering *et al.*, 1995; Brodie *et al.*, 1998), while above average recruitments appeared since 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 in two groups of biological parameters, namely the reproductive parameters and growth related parameters. Among the first ones, we will analyse the trends in the females length at maturity and in the potential fecundity and among the second, the first year growth and the condition factor, assuming that density - dependence, in case of been an important regulatory factor in this species, would be stronger at early ages.

Female length and age at maturity in other fish stocks in NAFO area, has 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 for a certain 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 *et al.*, 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 linked with density dependence (Agnalt, 1989). In this paper, we analyse whether there exist a difference 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 1993-1994 (area B in Fig.1). A total of 1 236 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 x 12, which gave a equivalence of 13 epu/mm. Only the left otolith was used. Otolith L_1 variability was examined in three ways: by sex, by area and by year-class, using a test-t and an ANOVA, respectively.

- 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 obtained 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 respective 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 3). 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, weighted, assigned to one of the four macroscopic stages in Table 1 and fixed immediately in 10% buffered formalin (Hunter, 1985). For histological analysis, sections of the ovaries were dehydrated, embedded in paraffin and 5 m-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). 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 summarised 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 3, where also are described the equivalencies between the macroscopic and the macroscopic 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 considered immature if they had ovaries in stage 1 and mature in either Stages 2, 3 or 4. In case of discrepancies, the macroscopic assignment have 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 tranformation:

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

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 of the L_{50} estimates was calculated from the variances and covariance of the maturity curve coefficients by the expression:

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

(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. Then the incidence of pre-spawning atresia in this advanced group to be spawned must be evaluated.
- Females used to estimate the potential fecundity have not yet spawned during the current reproductive cycle, as in this 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). 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 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 weighted sample of ovarian tissue. Subsamples (n) of 100-00 mg have been taken from different parts of the ovaries, weighted to the nearest 0.001 g (wi) and the number of oocytes larger than 1 000 µm counted (o_i). The size of 1 000 µm was assumed after examination of the length distribution of the oocytes as the threshold that separate the oocyte group that are going to be spawned (Fig. 3). The total potential fecundity (F_r) is obtained with the expression:

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

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 5 and a total of 9 cohorts (1988 to 1996). Their respective means and standard deviations are presented in Table 2. Neither significant differences in the first annual growth between sexes ($t = 2.06$; d.f. = 786; $P < 0.001$), nor between the three areas analysed ($F = 0.86$; d.f = 2, 1006; $P < 0.46$) have been observed. The ANCOVA between first annual growth and cohort (all areas and sexes combined), using the age as covariant, either gave significant differences over the period analysed ($F = 1.24$; d.f. = 3, 26; $P < 0.315$).

- *Condition*

In table 4 is presented 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; $P < 0.50$) nor the factor year ($F = 0.13$; d.f. = 6, 72; $P < 0.50$) presents significant differences.

- *Maturity*

The accuracy of the observers in the macroscopic diagnosis of the stage of maturity is presented in Table 5. Accuracy varied among observers, but discrepancies were mainly related with spent females classified as resting – maturing (21%) followed by a 10% of maturing females classified as immatures (juveniles) and 7% of immatures classified as maturing females.

(A) Length at maturity analysis

The female length at 50 % maturity obtained from macroscopic (1990) and combined microscopic and macroscopic criteria (1991 to 1997) appears in Table 6. 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 fig. 3 the length distribution of the oocytes at the successive stages of development is presented. Cortical alveoli and vitellogenic oocytes only coexists at the initial stage of growth. Since vitellogenesis progress, only one kind of oocytes is present in the ovaries and this supports our assumption that in this species the fecundity is determinate, and the spawning of the 'group synchronous' type.

The incidence of atresia in the growth stages prior to spawning is presented in Fig.4. 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. However the numbers of this kind of oocytes that are left behind in the ovary after the spawning varied a lot.

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 7). 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 90 000 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 8. Fecundity increase significantly with female age ($F = 16.25$; d.f. = 9, 255 ; $P < 0.000$), but the variations of the mean fecundity at age were not significant neither between the sampling years ($F = 0.07$; d.f.= 4, 36; $P < 0.50$) nor between cohorts ($F = 1.2$; d.f. = 13, 35; $P < 0.50$).

Discussion

In this paper we review a series of biological parameters of this species that could be expected to show variability as a response to this apparent reduction in stock abundance.

Differences in the first year growth has been associated with differences in the peak spawning time, environmental conditions and population size (Hopkins, 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. This is an interesting aspect, if we consider that spawning of this species here do not have a clear seasonality (Junquera and Zamarro, 1994, Junquera and Saborido-Rey, 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.*, 1998). The only way of interpreting this is if the first year growth could be also year round constant, that is, the early stages could grow at the same rate

either they are born in summer or in winter. However in this case, how could we interpret the ring structure of the otoliths?

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 . 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), 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. Besides, they reported a 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. Much of the inconsistencies in determining the mature proportions are lessened by using complementary histological techniques to check the macroscopic diagnosis. 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 it must 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 regulations, 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, but the number of mature oocytes of this kind that are left behind in the ovary after the end of the spawning to be subsequently resorbed vary a lot and sometimes is quite high. In such occasions the actual annual fecundity would be substantially overestimated by a factor very difficult to quantify. As also was found by Walsh and Bowering (1981), atresia is absent on immature ovaries.

The values of the potential fecundity obtained in the present study is within the range of the ones reported by Serebryakov *et al.* (1992) in Davis Strait area and Bowering (1980) in Southern Labrador and St. Lawrence. The same as happened in the other biological parameters analysed 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. Besides, it is the Pleuronectidae which spawn the largest eggs (Miller *et al.*, 1991), and based on the balance between the growth and the reproductive parameters can be considered to be a k-selected species. Thus Greenland halibut reproductive strategy would consist in producing an 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 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.*, 1998)), and though the hatching depth is unknown, there are indications that it occurs at depths beyond 500 m. 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 is either no need of having a fixed mass population spawning season in order to match the planktonic blooms, as is the common feature in species from shallower waters which exploit the upper planktonic layers at their early stages.

Another aspect that could contribute to reduce much further the potential fecundity of this species is that, though according to our results and Morgan and Bowering (1997) females age at maturity is between ages 9 and 15, 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 ready to spawn by the first time not before age 15. It could be an indication that the time required to go from cortical alveoli (stage from where females are computed as mature in our case) to fully yolked stage takes longer than one year. Then if vitellogenesis takes longer than one year, likely individual spawning cannot occur on a yearly basis, as it was suspected time ago. 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 general picture we got from our results about the biological parameters in this stock over this period is a situation of stability. Two conclusions could be drawn from it: one is that probably the mentioned reduction of the stock size was as large as it was thought and the other is that probably Greenland halibut biological parameters are resilient to change so quickly due to external factors and that longer time periods are required to produce it. Indeed, the assessment of the Greenland halibut biomass and abundance variation is extremely difficult just because a substantial part of the adult population is distributed beyond 1 500 m (de Cárdenas *et al.*, 1996) and those depths are poorly covered by the surveys, and further, we ignore the distribution and abundance over the non-trawlable areas.

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

	MATURITY							
	MACROSCOPIC				MICROSCOPIC			
YEAR	Data type	Period	Length range	Number	Data type	Period	Length range	Number
1990	C	Jul. - Dec.	13 - 103	33581				
1991	C	Jan. - Dec.	16 - 120	107227	C	Dec.	60 - 90	150
1992	C	Jan. - Dec.	14 - 120	164818	C	Jan. - Mar. / Oct. - Nov.	36 - 104	250
1993	C	Jan. - Dec.	21 - 103	40136	C	Jan. - Mar.	58 - 90	130
1994	C	Jan. - Dec.	16 - 103	42558	C . R	Jul. / Sept. - Dec.	40 - 106	433
1995	-	-	-	-	R	Feb.	46 - 95	90
1996	C	Jan. - Dec.	23 - 94	5497	C . R	Feb. – Apr. / Jul.	29 - 100	526
1997	C	Jan. - Dec.	21 - 101	3164	C	Feb. - Mar.	35 - 102	175

	CONDITION FACTOR			
YEAR	Data type	Period	Length range	Number
1991	R	July	14 - 77	410
1992	R	July	12 - 76	903
1993	R	July	10 - 79	1061
1994	R	July	13 - 69	1250
1995	R	July	13 - 70	728
1996	R	July	10 - 82	908
1997	R	July	13 - 81	1337
	OTOLITH L_1 DIAMETER			
YEAR	Data type	Period	Length range	Number
1992	R	Jul.	12 - 25	67
1993	R . C	Jul. / Feb. - Nov.	10 - 25	315
1994	R . C	Jul. / Set. - Oct.	13 - 25	161
1995	R	Jul.	13 - 25	104
1996	R	Jul. / May	10 - 25	225
1997	R	Jul. / May	13 - 25	364

Table 2.- L_1 (first annual ring diameter in mm) mean, 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	-	-	-
1991	2.158	0.19	127	2.201	0.28	103	-	-	-
1992	2.232	0.27	62	2.230	0.35	117	-	-	-
1993	2.122	0.11	5	2.171	0.35	115	-	-	-
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

Table 3.- 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 FP	425 - 2300 µm
3	Spawning	Presence of NM or H	2 - 4 mm
4	Postspawning	Presence of FPO and AT. without either CA or new VIT	-

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 - 1997).

	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

Table 6.- Greenland halibut mean number of eggs per gram 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 ($F = a \cdot length^b$)		($F = a \cdot weight^b$)	
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
Present study	Flemish Pass	0.0052	3.7	7.3	1.03

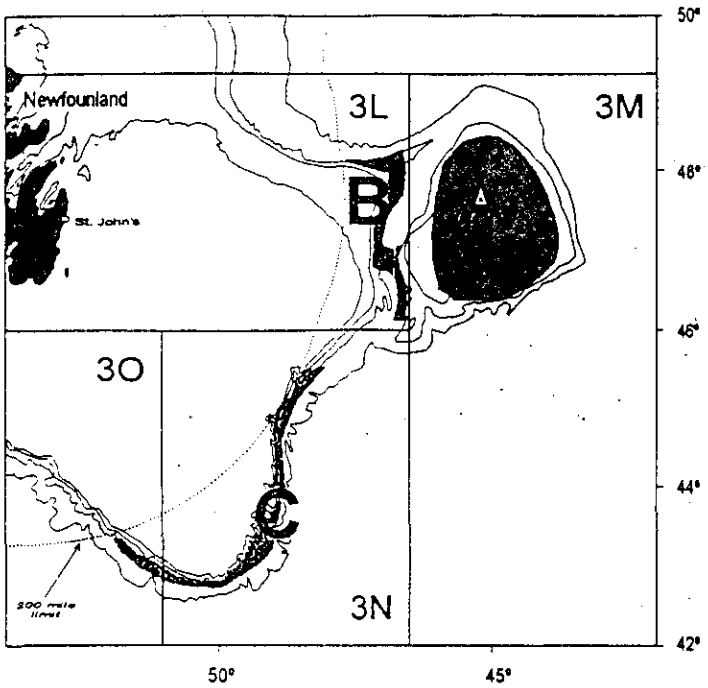

Fig. 1 - Sampling areas. A = Flemish Cap; B = Flemish Pass; C = Southern Grand Bank.

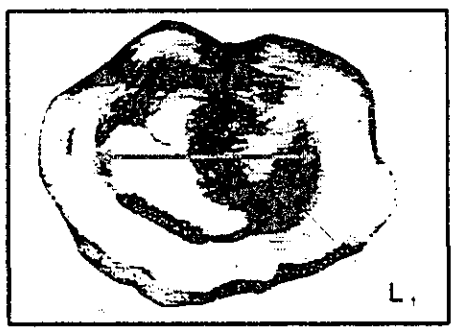

Fig. 2 - Representation of the Greenland halibut otolith first annual ring diameter (L_1)

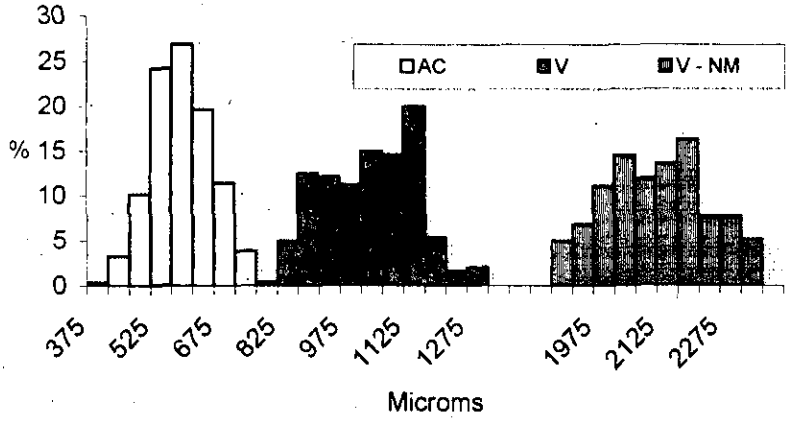

Fig. 3 – Length distribution (diameter in microms) of Greenland halibut oocytes at successive growth stages: cortical alveoli (CA), vitellogenesis (V) and fully yolked-nuclear migration (V-NM).

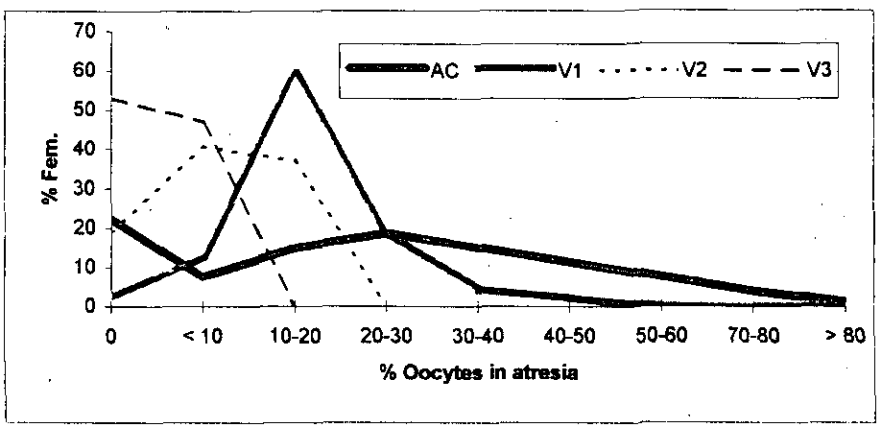

Fig.4 – Proportion of females that have a certain proportion of oocytes in alpha-atresia (X axis) expressed here as intervals, at the successive stages of oocyte growth (AC = cortical alveoli stage; V1, V2 and V3 = primary, secondary and final vitellogenesis respectively).

ANNEX I.- Comparison between the terminology used by Fedorov (1968) in the firts description of the Greenland halibut oogenesis and the one used in the present study.

Fedorov (1968)	*Present study*
I- Period of trophoplasmic growth	**I- Primary growth**
1. Initial protoplasmic growth. .	1. Chromatin nucleolar stage
2. RNA accumulation in the ooplasm.	2. Perinucleolar stage.
3. Monolayer follicle phase.	
	II- Cortical alveoli stage
II- Period of trophoplasmic growth	**III- Vitellogenesis**
1. Vacuolation of the peripheral ooplasm and primary yolk accumulation	1. Primary vitellogenesis
2. Intensive yolk accumulation	2. Secondary vitellogenesis
3. Fully yolked oocytes	3. Fully yolked, advanced or tertiary vitellogenesis
III- Maturation	**IV- Maturation**
1. Nuclear migration	1. Nuclear migration
2. Yolk fusion.	2. Yolk fusion.
3. Hydration.	3. Hydration.