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Trends in Growth Parameters Analysed in the Light of Selection Responses to the Exploitation of Greenland Halibut

by

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Abstract

The possibility that fishing pressure has an effect on the evolution of life histories and yields of fish is of great importance for management purposes. Nevertheless, this possibility has been widely ignored because of the difficulty of finding direct evidence for it. It has been proposed that observed reductions in the growth rate and yield of the North sea cod (*Gadus morhua*) is an effect of life history changes, initiated by removing the largest individuals within the selection range of the trawls in a heavy fishery for cod. This study analyses growth as a measure of selection responses in Greenland halibut (*Reinhardtius hippoglossoides*). Greenland halibut in North East Atlantic have been heavily exploited since the 1970s and the fishery for this species was strictly regulated in 1992. Both trawls, longline and gillnets have been used in the fishery that has led to a collapse of the stock. The selective properties of these gears could lead to repeated selection of the largest individuals in a year class before reproduction. We have analysed growth in a nine-year perspective and discuss the results in the light of evolution and gear selection parameters. No conclusive evidence of significant selection differentials was found.

Keywords: Greenland halibut, Selection differentials, Exploitation.

Introduction

Fisheries biologists have a long tradition of studying the effects of selective harvesting of commercial stocks (Beverton and Holt 1957, Ricker 1931). However, this research has usually focused on the effects on the stock yield per recruit, its spawning stock biomass and maximum yield. The question of how selective harvesting influences the genetic constitution, and thereby the evolution, of fish stocks, has been less frequently addressed. Fisheries scientists using genetic tools have focused on how to differentiate between stocks and species (Allendorf *et al.* 1987), and few studies deal with the genetic consequences of exploiting stocks.

In the exploitation of living resources, it is usually the case that some individuals are more valuable to the harvester than others, and exploitation methods are developed to remove preferentially those of high commercial value. The exploitation of such self-renewing resources is likely to be selective, and fisheries often selectively cull the largest individuals. This may result in an evolutionary decrease in adult size. The selection produced by harvesting is also capable of genetically altering the life histories of other traits, leading to further decreases in the economic value of the populations involved.

Selective harvesting can change the genetic composition of a population, as has been shown in small-scale experiments on *Daphnia* (Edely and Law 1988), and some observations indicate that similar effects can be seen in harvested fish populations (e.g. Law and Rowell 1993, Rijnsdorp 1993, Policansky 1993 and references therein). Law and Rowell (1993) described a method whereby the quantitative genetics of correlated characters with age-specific

expressions can be embedded in an age-structured model of population dynamics so that certain evolutionary effects of exploitation may be investigated. They illustrated this method using data on directional selection for reduced body length in North Sea cod (*Gadus morhua*) arising from exploitation over the period 1984-1990. The method suggested that there was a reduction in length of 1 cm of one-year-old individuals over a period of 40 years. This effect ought to be examined in populations recently subjected to selective fishing, and Kirkpatrick (1993) has shown that changes can occur within a few generations. The selective forces can be observed as changes in phenotypic differences between catches and stock. In principle, these differences can be detected as long as the selection process continues.

Rapidly declining stocks in an expanding fishery are influenced by severely selective processes. A commercially important species that has been exposed to such an expanding fishery is the Greenland halibut (*Reinhardtius hippoglossoides*) in the North East Atlantic. Landings of this species have fallen from 350,000 tons in 1970 to 10,000 tons in 1998. In the period from 1970 to 1995 the estimated total spawning stock biomass has declined from 240 441 to 48 690 tons (Anon 1997).

Until the 1960s the harvesting of Greenland halibut in Norwegian waters was restricted to a coastal longline fishery with annual yield of about 3,000 tons. In the mid-60s an expanding trawler fleet started to exploit this resource and annual landings rose to some 80,000 tons in the early 1970's, subsequently falling to about 20,000 tons a year, which remained stable until 1991. In 1991 the catch rose sharply to 30,000 tons. Since 1992 the fishery has been strictly regulated and only longliners and gillnetters below 27.5 m have been allowed to target the species. Other vessels were only allowed to catch Greenland halibut in by-catch quotas of 10 %, which were reduced to 5% in 1995. This management regime lead to total landings of about 10,000 tons (Anon 1997). Since the regulation of the fishery was established in 1992, a controlled scientific fishery has been conducted by chartered commercial boats every year, with one survey taking place in spring and one in autumn. These surveys conduct extensive sampling of the catches. This history of recent over-exploitation makes the Greenland halibut a tempting species on which to carry out investigations of selective differentials.

The aim of this paper is to employ the model presented by Law and Rowell (1993) to look for changes in growth of Greenland halibut caused by selective fishing. It is possible that a repeated selective pressure for different age groups can make the selection effect more easily detectable for older individuals. For example: the trawl may select the largest four- and five-year-old specimens, while the largest six- and seven-year-old fish will be selectively taken by longline via competition for bait, while finally the fastest growing eight-year-olds are large enough to be gilled in gillnets. If both trawl and longline can be regarded as having a constant selectivity for fish larger than L_{100} (the length at which all specimens are retained) then this could lead to a profound selection differential. Greenland halibut recruit to the trawl fishery at about five years of age. The recruit age for gillnet and longline fisheries is believed to be higher (Nedreaas et al. 1996).

Materials and Methods

Data from the Norwegian scientific surveys in the period 1989 to 1997 were used. The mean length at age from the winter surveys with small-meshed liners in the codends was taken as a representative measure of the "true" mean length, and is referred to here as length at age before fishing. The length-dependent selection pattern of commercial gears was estimated from the controlled fishing with commercial boats that has been carried out every year since 1992. The mean length at age was estimated separately for each type of gear. The gear-specific mean length at age in catches was weighted according to size of landings. Length at age after fishing was then found for the new length distribution. The selection differential is the difference of the mean phenotypic values of the trait before and after selection.

Lengths were weighted for the length-stratified sampling procedure, but pooled for all areas and depths. The lengths at age observed in the commercial gears were weighted by the proportion of the total catch landed by that type of gear (Table 1). For the mathematical analyses we used the IML and STAT procedures in SAS (1985).

Since there were few observations for the years 1989-1991, we could not use a complete data matrix for length at age for gillnet, trawl and longline. Although this may have led us to underestimate the variance in the matrix, we used the mean length for each gear and age over all years when this was necessary to fill in for missing observations.

Results

We estimated the length-dependent fishing pattern for each gear in each year from the controlled scientific fishing using commercial gears (1992-1997). The gear selection pattern from 1992 was used for 1989-1991 (Fig. 1).

Estimated mean lengths for each gear and for each year class are shown in Table 2. The estimated values of selection differential vary with both age and year, with approximately as many positive as negative values. Instantaneous fishing mortality (F) at age is given in Table 3. The selection differentials (last row, Table 2) appear to be random and there are few distinct patterns in our results.

For age 4, the effect of fishing is small, and almost absent after 1992, in accordance with the small F-values for this age (Table 3). For age 5, five out of nine selection differentials are positive, and three of these are greater than 0.25. Six-year-olds also shows five out of nine selection differentials as positive; two of these (1990 and 1991) are larger than 0.5 cm. The seven-year-olds have six occurrences of positive selection differentials, and here the first observation of a negative value greater than -0.25 is found. At the same age, half of the positive differentials are greater than +0.25. For eight-year-olds the patterns of the selection differentials are much the same: positive values for the first seven years and a large negative value for 1997. The nine-year-olds have four positive values at the beginning of the period, and a large negative value in 1997. At age ten, there are no negative selection differentials at all.

The age group 'twelve plus' shows the largest and most highly variable selection differentials. It does not appear to be significant even for the age groups 10-14, where F exceeds 0.5 in several years (Table 3). For the 12- plus group the selection differential is large and variable; this is probably influenced by the fact that the 12- plus group used in this analysis was different from the 14- plus group used in the F-table.

In 1990 and 1991 all selection differentials are positive in all age groups. This appears to be contradicted by the F-table (Table 3), which shows large mortalities for almost all year-classes. If the gears used are size-selective for different length-groups, we would expect the opposite result, with negative selection differentials in those years.

Weighting the magnitude of fishing pressure is not done by the F-table, as this is age-structured. Instead, the selection pattern of the commercial gears used in the scientific fishery is found, and the number caught in each length group is weighted to take into account the number of fish (landings divided by mean weight in each gear) fished by this kind of gear. For this reason, the agreement between the selection differentials and the F at any given age does not need to be consistent.

Discussion

Greenland halibut may have passed through a severe 'bottleneck' in the seventies and it may therefore be impossible to track possible genetic changes within the time-span of our data. Bottlenecks are not necessarily a cause of differential selection, but they may increase the likelihood of occurrence of arbitrary changes. Selective fisheries may change the genetic composition of stocks regardless of their size, but the probability of such changes occurring is higher when the population size is at a minimum. However, the limited fishing in the period examined here could have produced a new bottleneck effect, as the estimated Fs in this period are almost as high as those estimated for 1977 and 1978 by Anon. (1988). We will limit our discussion to the observed selection differentials and the selection caused by the fishery for this species.

The calculated selection differentials in this study show little consistency and clarity, since both magnitude and absolute values vary both within and between ages and between years (Table 2). The pitfalls are, however, numerous. The typical problem is large variation and missing values, with the smallest fish occasionally missing from the catches of the commercial gears, and the oldest Greenland halibut not caught in the scientific surveys. A typical example is the length of four-year-olds in the gillnet catches. However, the number caught in gillnets of this sizes is small, and the error introduced by the estimated mean value is probably negligible.

Even under high fishing pressure the selection differentials when using several gears simultaneously need not be negative in absolute value. If a combination of gears leads to a prolonged selection range, within which individuals

chronologically recruit to a new gear, the direction of the selection pressure from different gears can act differently for a given trait, and will probably reduce the risk of genetic selection responses for any given trait. Mesh selection in trawls and gillnets is dependent on the girth of the fish, and this may select for specimens in a year-class that has a high GSI (Gonadosomatic Index). Linear growth often decreases after the age of first maturity (Wotton 1990), and if mature specimens are selected for in gillnets the selection differential for the ages at which Greenland halibut recruit to the gillnet fishery can be the opposite to when they recruit to the trawl fishery. The longline is probably not very selective for any traits regarding Greenland halibut, and the bait size (width: 25-27 mm of mackerel, squid or herring) and hooks (Mustad EZ 12) normally used in the high-seas fishery are not likely to give selective effect, in contrast to circle hooks and baits of twice that size, which select larger Greenland halibut (Woll *et al.* 1998). This is in accordance with the finding of size-related prey selection shown for Greenland halibut by Yang and Livingston (1988).

Both the positive selection differentials for the 12+ group (Table 2) and the comparisons of selectivity between gears (Fig. 1) suggest that the largest Greenland halibut can avoid the trawl, but there are no direct observations of this. The mesh size in codends in the scientific fishery has gradually been decreased from 135 mm to 60 mm between 1992 and 1996. This could lead to clearer selection differentials for the youngest specimens in the later years. This does not emerge clearly in Table 2. However, specimens around the selection range of 135 mm trawl (43 cm total length), are often weakly represented in the catches of any of the gears in the area and at depths where fishing is taking place (Nedreaas 1994).

Huse *et al.* (1997) have demonstrated effects of fishing gear selectivity on the life-history parameters calculated from the catch, with significant lower growth rates and higher L_{∞} in females caught in gillnets than by other types of gear. Variations in phenotypic traits in the catches reflect the selective properties of the gear and the effects of the fishing on the stock being harvested. Individual variations in gene markers (Vis *et al.* 1997 and references therein) in Greenland halibut are large, although no significant differences were found between stocks in the North Atlantic. The vast distribution area of this species and the wide range of environmental conditions around the main spawning and feeding areas in the western, central and eastern North Atlantic, suggest that variation in phenotypic traits may also be large. However, fishing pressure has varied within the central area of distribution. Bowering (1983) found differences in growth rates among seven banks in the Canadian Northwest Atlantic, while Nizovtsev (1991) showed that Greenland halibut from Icelandic waters have a higher mean growth rate than specimens from the Barents Sea. Morgan and Bowering (1997) conclude that due to large temporal and spatial variation in growth and maturation at length, the most correct way to obtain an accurate reflection of these life history parameters of the population of Greenland halibut in Canadian waters is to conduct a synoptic survey. A comparison between the main distribution areas in selection pressure and phenotypic traits would be capable of revealing selection responses, even if there is some migration between the areas and the stocks are not totally isolated in a genetic sense.

Sex differences in the growth rates of Greenland halibut older than five years of age have been demonstrated by Nizovtsev (1991). These differences are presumed to be connected to differences in natural mortality rates between males and females older than five to seven years. Such analyses should preferably also be conducted for the two sexes separately, but due to lack of data, we have pooled the sexes in our analysis. The survey strategy in these scientific fisheries using commercial gears has been modified since 1996, and all length-measured fish are now sexed. This will provide valuable data for later analyses. The highest fishing pressure has been due to trawling, and in this gear the female:male ratio is about 40 %, whereas with gillnets it is approximately 95 % and in longlining about 70 % (Huse *et al.* 1997). A shift in selection pressure when the stock is very low will produce important effects with the parameters that are normally used as references in population management (SSB and Y/R).

Tagging studies have shown that there is some migration between western and eastern stocks of Greenland halibut (Boje 1993, Bowering 1984). Stocks in the North-west Canadian Atlantic have also been severely overexploited during the past few decades, and migration patterns and spawning area have changed since stocks of Greenland halibut have fallen in size (Anon 1995). In Icelandic waters, the stock appears to be in a better state, and so far no overfishing has been reported (Bowering and Brodie 1995). Migration between stocks exposed to different fishing pressure could add variance to the observed selection differentials, but the magnitude and variance of any such migrations are not known.

Part of the negative selection differential we observed could be due to growth of the fish between the time of the survey, which provide the "true" length, and the time of the scientific fishing with commercial gears (May and September-October). The error introduced by growth is probably larger for older individuals, and this may result in larger calculated than actual negative selection differentials. This is in accordance with the results for the 12 plus group in the six latest years, but not for 1989-1991. However, the mean selection differential in our analysis is positive for all age groups except the four year-olds and the 12 plus group.

In order to understand the genetic consequences of harvesting natural populations, we need a predictive theory of how growth trajectories and related traits evolve in response to harvesting. A basic requirement of such analysis is a covariance matrix of inherited traits, for example a measure of growth. The closest source of such information would be a study of the otoliths collected. This approach has been used in a study of the growth of Greenland halibut by Bowering (1983).

In order to isolate the effects of genetic changes in growth from those of changes in environmental factors, knowledge of the distribution of food or of density-dependent food availability is essential. However, as these factors are likely to vary over time in all time perspectives, estimates are difficult to obtain. One approach might be to consider the sum of "disturbances" from changing environments as null, as was done by Law and Rowell (1993). The problem is partly that genotypic changes are likely to be masked by other such factors, and the selection response may be very small in comparison with other effects. Even so, the effects that originate from selection pressure are probably difficult to reverse, and may accumulate over longer periods.

The selection pressure (Table 3) is different from that for cod in the North Sea, where F is as high as 1 for all the recruited year classes in area RFA 4 (see Law and Rowell 1993). Selection in the codend and thereby the selection differential for four- to six-year-old Greenland halibut might be limited because the nursing area is in areas north and east of the areas in which commercial fishery is concentrated (Gundersen *et al.* 1997). The size at which the species recruits to the gillnet fishery is rarely observed in the standard scientific surveys, and the results should be interpreted with care. The total fishing pressure during the time-span covered by this study (Table 3) is less than observed for cod in the example of Law and Rowell. Huse *et al.* (1997) suggest that the largest Greenland halibut may be able to avoid the trawl. If this is the case, the result of such a selection window would probably result in a selection response in favour of larger and faster-growing females and smaller males. Our data did not distinguish between male and female, but sex should be taken into account when using the model in later analyses.

Fishing mortality is often very high and selective with respect to several life-history traits that are supposed to be partly heritable. At any rate, it seems likely that fishing causes changes in the gene pool of the species. The degree to which growth is affected is difficult to measure because of the large environmental component of food availability, temperature, etc. Other life-history traits may also be affected, either directly or because of covariation with growth rate. However, very little is known about phenotypic and genetic correlation or about genetic and environmental interactions in marine fishes. Alm (1959) used 80 years of fishery statistics and more than 20 years of experimentation in an attempt to understand the relationship between size at age and maturation in fishes, but he could not separate the effects of genetic factors from environmental ones. This difficulty is probably the reason for the general lack of attention paid by fishery managers to the genetic effects of selective fishing, despite the existence of a considerable discussion in the scientific literature (Beverton *et al.* 1984, Policansky 1993). Fish are quite plastic in their response to environmental conditions (e.g. McKenzie *et al.* 1983) and genetic responses could easily be masked by plastic responses to improved environmental conditions, as suggested by many authors for cod (see Borisov 1979, Policansky 1993). This plasticity may well be an expression of genetic/environmental interaction. Another factor that might mask possible effects is the definition of stocks in fishery management. Stocks in fishery management are mainly related to geographical areas rather than genetically isolated gene pools, mainly because of lack of knowledge and different interpretations of the genetic variation that have been observed, but partly also because of a lack of 'good' genetic markers. Managers have tended to look at phenotypically similar fish instead of genetically distinct stocks. In looking for genetic changes in these fish stocks, genetic markers such as proteins or DNA fingerprint markers should be used to describe the stock and its structure. Other genetic markers that are related to different life history parameters such as growth, fecundity or disease resistance have been identified, (Ferguson 1998, Gauldie 1984, Gauldie 1991, Nevo *et al.* 1984) and such markers could be used to explore variation and temporal changes in life history traits.

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Table 1. Landings (thousand tonnes) of Greenland halibut in the North East Atlantic (ICES areas I, IIa ,b) by fishing gear.

Year	Landing by gear (tons).			Total
	Gillnet	Longline	Trawl	
1980	1189	336	11759	13284
1981	730	459	13829	15018
1982	748	679	15362	16789
1983	1648	1388	19111	22147
1984	1200	1453	19230	21883
1985	1668	750	17527	19945
1986	1677	497	20701	22875
1987	2239	588	16285	19112
1988	2815	838	15934	19587
1989	1342	197	18599	20138
1990	1372	1491	20325	23188
1991	1904	4552	26864	33320
1992	1679	1787	5787	9253
1993	1497	2493	7889	11879
1994	1403	2392	5353	9148
1995	1500	4034	5494	11028
1996	1480	4616	7977	14073
1997	1044	3421	4799	9264

Table 2. Mean length at age of Greenland halibut from survey and controlled scientific fishing with commercial gear.

Age 4	1989	1990	1991	1992	1993	1994	1995	1996	1997
Gillnet	36.00	36.00	36.00	36.00	36.00	36.00	36.00	36.00	36.00
Trawl	38.84	38.84	38.84	39.09	38.80	38.92	38.59	38.80	38.84
Longline	39.36	39.36	39.36	39.3	39.42	39.36	39.36	39.36	39.36
Stock before	37.61	37.64	38.11	37.70	37.80	37.50	38.00	38.50	37.86
Stock after	37.44	37.66	38.27	37.68	37.80	37.50	38.00	38.50	37.85
Selection diff.	-0.17	0.02	0.16	-0.02	0.00	0.00	0.00	0.00	-0.01

Table 2 continued

Age 5	1989	1990	1991	1992	1993	1994	1995	1996	1997
Gillnet	43.42	43.42	43.42	43.42	42.93	43.67	43.66	43.42	43.42
Trawl	43.89	43.48	43.48	43.17	43.55	43.45	43.39	43.43	43.48
Longline	43.62	43.62	43.62	43.83	43.64	43.37	43.62	43.62	43.62
Stock before	41.92	42.16	41.22	42.05	44.02	43.05	42.67	42.89	40.50
Stock after	41.68	42.57	41.75	42.07	44.33	42.92	42.39	42.82	40.54
Selection diff.	-0.24	0.41	0.53	0.02	0.31	-0.13	-0.28	-0.07	0.04

Table 2 continued.

Age 6	1989	1990	1991	1992	1993	1994	1995	1996	1997
Gillnet	47.79	47.79	47.79	48.14	47.71	48.14	47.18	47.79	47.79
Trawl	48.23	47.32	47.32	47.4	47.11	47.34	46.95	46.88	47.32
Longline	47.37	47.37	47.37	47.68	47.46	48.14	46.74	46.84	47.37
Stock before	46.62	48.26	46.83	47.58	47.00	47.19	46.31	46.98	46.36
Stock after	46.58	48.87	47.74	47.72	47.00	47.23	46.08	46.98	46.43
Selection diff.	-0.04	0.61	0.91	0.14	0.00	0.04	-0.23	0.00	0.07

Table 2 continued.

Age 7	1989	1990	1991	1992	1993	1994	1995	1996	1997
Gillnet	53.66	53.66	59.31	52.52	52.48	52.71	51.52	53.39	53.66
Trawl	52.61	51.60	51.60	51.73	51.54	51.50	51.23	50.96	51.60
Longline	51.51	51.51	51.51	52.02	51.64	51.57	51.17	51.15	51.51
Stock before	52.18	52.83	52.00	51.50	51.67	51.29	50.54	51.82	50.69
Stock after	52.47	53.15	52.26	51.60	51.67	51.42	50.62	51.79	50.43
Selection diff.	0.29	0.32	0.26	0.10	0.00	0.13	0.08	-0.03	-0.26

Table 2 continued.

Age 8	1989	1990	1991	1992	1993	1994	1995	1996	1997
Gillnet	57.95	57.95	62.93	57.52	56.86	57.07	55.89	57.41	57.95
Trawl	57.49	56.54	56.54	56.61	56.46	56.74	56.55	55.40	56.54
Longline	56.48	56.48	56.48	56.76	56.76	56.72	56.72	55.46	56.48
Stock before	54.73	55.48	54.68	55.29	56.40	56.92	55.39	55.89	54.79
Stock after	55.33	55.61	54.74	55.53	56.40	56.92	55.62	55.83	53.79
Selection diff.	0.60	0.13	0.06	0.24	0.00	0.00	0.23	-0.06	-1.00

Table 2 continued.

Age 9	1989	1990	1991	1992	1993	1994	1995	1996	1997
Gillnet	60.50	60.50	65.61	59.00	59.16	59.09	59.14	60.99	60.50
Trawl	61.71	59.91	59.91	59.16	59.70	59.87	59.54	59.47	59.91
Longline	59.71	59.71	59.71	59.00	60.00	60.25	59.18	60.14	59.71
Stock before	57.11	61.20	58.38	58.31	59.08	59.08	58.94	59.78	59.83
Stock after	58.00	61.40	59.08	58.25	59.08	59.08	58.90	59.86	59.33

Selection diff.	0.89	0.20	0.70	-0.06	0.00	0.00	-0.04	0.08	-0.50
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Table 2 continued.

Age 10	1989	1990	1991	1992	1993	1994	1995	1996	1997
Gillnet	64.25	64.25	67.12	63.56	63.11	63.41	64.07	64.21	64.25
Trawl	65.22	63.55	63.55	62.15	63.30	63.47	63.48	63.69	63.55
Longline	63.52	63.52	63.52	62.84	63.18	63.34	63.96	64.26	63.52
Stock before	63.00	62.71	62.01	62.01	61.00	63.07	63.38	64.08	66.01
Stock after	63.00	62.80	62.38	62.32	61.00	63.57	63.43	64.39	66.08
Selection diff.	0.00	0.09	0.37	0.31	0.00	0.50	0.05	0.31	0.07

Table 2 continued.

Age 11	1989	1990	1991	1992	1993	1994	1995	1996	1997
Gillnet	68.60	68.60	68.35	68.05	68.13	69.04	68.29	69.73	68.60
Trawl	65.95	67.93	67.93	67.23	68.03	68.90	68.88	68.58	67.93
Longline	68.59	68.59	68.59	68.15	68.73	68.55	68.32	69.22	68.59
Stock before	66.29	63.10	59.93	67.42	68.65	66.00	66.00	69.08	70.13
Stock after	65.00	63.50	60.00	67.50	69.50	66.00	66.00	69.10	70.29
Selection diff.	-1.29	0.40	0.07	0.08	0.85	0.00	0.00	0.02	0.16

Table 2 continued.

Age 12+	1989	1990	1991	1992	1993	1994	1995	1996	1997
Gillnet	72.90	72.90	70.08	74.56	73.27	73.05	72.64	73.80	72.90
Trawl	68.71	71.87	71.87	73.38	72.94	73.47	72.68	70.03	71.87
Longline	73.08	73.08	73.08	73.53	72.38	73.10	72.63	73.76	73.08
Stock before	67.44	70.80	70.71	70.50	71.09	72.00	71.49	74.12	71.62
Stock after	70.50	71.50	71.00	68.00	68.50	69.80	69.80	72.82	69.50
Selection diff.	3.06	0.70	0.29	-2.50	-2.59	-2.20	-1.69	-1.30	-2.12

Table 3. Instantaneous fishing mortality (F): from ICES working group report 1998.

Age	1989	1990	1991	1992	1993	1994	1995	1996
4	0.044	0.037	0.116	0.030	0.026	0.019	0.055	0.055
5	0.101	0.128	0.201	0.079	0.098	0.089	0.288	0.288
6	0.279	0.366	0.342	0.098	0.099	0.076	0.176	0.176
7	0.439	0.493	0.632	0.139	0.175	0.147	0.242	0.242
8	0.338	0.414	0.472	0.185	0.201	0.118	0.151	0.151
9	0.320	0.421	0.383	0.113	0.043	0.073	0.071	0.071
10	0.199	0.318	1.023	0.378	0.474	0.264	0.220	0.220
11	0.251	0.239	1.124	0.361	0.503	0.349	0.281	0.281
12	0.059	0.610	1.605	0.631	0.489	0.809	0.526	0.526
13	0.107	0.024	0.801	0.782	0.281	0.585	1.006	1.006
14	0.188	0.110	0.196	1.261	0.429	0.508	0.828	0.828

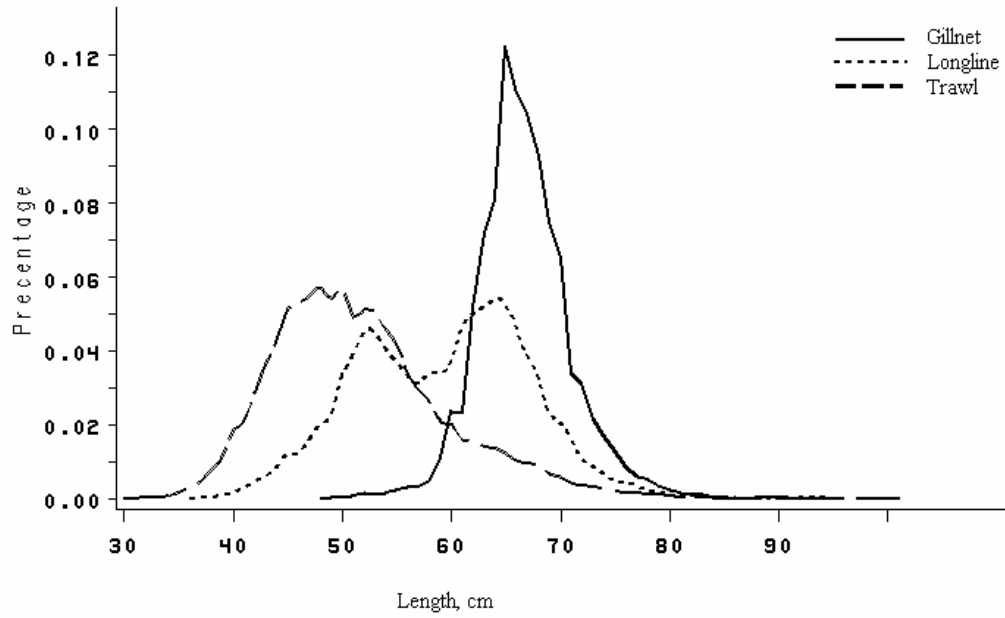


Fig. 1. Catch selection pattern for trawl, gillnet and longline in 1992. This pattern was also used as selection pattern in 1989-1991.