Body condition and evolution of maturation of Atlantic cod in Newfoundland

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Atlantic cod (Gadus morhua, L.) stocks off Newfoundland and Labrador underwent severe depletions that started in the late 1980s and led to moratoria in the early 1990s. Fisheries closures are still applied in most of the areas where cod is found. A very low stock level, probably resulting from the combined effects of overfishing and unfavorable environmental conditions, has been accompanied with modifications of life history traits of the fish. Among reproductive traits, a decrease in both age and size at first reproduction has been observed. A partial genetical determinism of these shifts is supported by earlier analyses of probabilistic maturation reaction norms, revealing a consistent trend towards earlier maturation but also strong short-term fluctuations. In this study, we elucidate the effect of changes in individual body condition on short and long-term changes in maturation of cod. Laboratory studies have demonstrated that condition of individuals can influence the number and quality of offspring in cod. Here we use probabilistic maturation reaction norms with three explanatory dimensions (age, size and condition) to examine to what extent changes in age- and size-dependent maturation probabilities are linked with changes in condition, as measured by the hepato-somatic index.

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Introduction

Fishing, particularly when selective, does not only affect fish populations demographically, but can also impact them genetically (Heino and Godø, 2002). For a long time, it was difficult to isolate genetic changes in life history traits from the effects of the environment through phenotypic plasticity. Indeed, changes in some life history traits can appear as consequences of modifications in the environment experienced by fish (temperature, food availability, density-dependence) as well as being driven by evolution. The disentangling of these effects is even made more intricate when several traits are linked. Thus, a change in growth rates due to an increase in prey abundance or temperature will lead to a reduced age at maturation, since maturation is often related to the size of individuals. But the emergence of the method of probabilistic reaction norms (PRN), first appearing in Heino *et al.* (2002) and already applied to maturation in numerous fish stocks (Grift *et al.*, 2003; Engelhard and Heino 2004; Olsen *et al.*, 2004, 2005;**,** Barot *et al.* 2004a, 2005; Dunlop *et al.* 2005) to assess the evolution of size at maturation at a given age, provides a way to isolate the consequences of certain plastic effects. The fact that these reaction norms are probabilistic enables a more realistic representation for it appears to be a way to cope with the stochasticity of the described process (*e.g.* maturation, metamorphosis), taken explicitly into account in the reaction norm representation (Heino *et al.,* 2002). When applied to the maturation process, this technique aims at describing the probability of an individual to become mature during a given time span as a function of its characteristics (*e.g.* age, size). This method is not sensitive to variations in growth rates or in mortality rates, unlike the method traditionally in use (Stearns and Koella, 1986) and consisting in the description of the value of those characteristics at which the maturation is meant to occur. The former method assumes a variability in the values of individuals' characteristics at which maturation occurs due to the influence of other

factors not taken into account in the reaction norm, which distinguishes it from the latter that considers maturation a deterministic process.

Here, we applied the method of maturation reaction norms to cod stocks off Newfoundland-Labrador. These stocks underwent a strong fishing pressure for several centuries (Hutchings and Myers, 1995) that ended in a collapse of fisheries in the late 1980's, after a severe decline in the previous fifteen years. This collapse lead the Canadian government to adopt moratoria in 1992, 1993 and 1994 in the concerned NAFO (Northwest Atlantic Fisheries Organization) divisions and subdivisions. Except in subdivision 3Ps (St. Pierre Bank) since 1997 and from 1998 to 2002 in some coastal areas of 2J3KL subdivisions, cod fisheries off Newfoundland-Labrador have remained closed. Despite this relaxation of fishing pressure, Northern cod (NAFO subdivisions 2J3KL) and Southern Grand Bank cod (3NO) have remained at very low abundance ever since then.

The method of probabilistic maturation reaction norm has already been applied by Olsen *et al.* (2004, 2005) to the same data set. Two explanatory dimensions (age and body length) were used to describe maturation probabilities. Among other things, these authors highlighted a decreasing trend in the length at which cod of a given age reach a certain probability of maturating, starting from the first available years (mid-1970's) and extending to the early 1990's. This trend is obvious for both males and females. However, after the implementation of moratoria, a slight increase in these lengths at maturation seems to have come about, although the shortness of the moratorium period renders this conclusion uncertain. This supposed recovery appears more obvious for females than for males. The observed decrease in age-specific length at maturation is in accordance with life-history theory: if cod have to face a high size-selective fishing pressure (trawl is the most used gear to fish cod), the trade-off between reproduction and growth (larger cod producing higher numbers of eggs) will be affected and fish expressing earlier maturation at a smaller length will increase their probability to reproduce and beget offspring before being caught and therefore will have a higher fitness.

Olsen et al. raised the point that changes in body condition of fish may have an influence on their results, although they stated that the observed trend in average condition of cod was downwards and therefore would have been likely to induce an increase in the size at maturation (assuming a positive influence of condition on maturation probability as is well established (Bernardo 1993, Marteinsdottir and Begg, 2002). While apparently ruling out the possible influence of an environment-driven change in physiological condition as the cause of the observed decline in age at maturation, this study does not dismiss the consequences of condition at maturation. Thus, beside increasing the accuracy of maturation reaction norms by adding a third explanative factor to age and length, the present study aims at discerning the confounding effects of length and condition on maturation probabilities.

A similar study has already been carried out about plaice (*Pleuronectes platessa,* L.) by Grift *et al. (submitted)*. The authors concluded in a trend toward a reduced length at maturation with an good physiological condition, and in a progressive decrease in the importance of condition as a cue for triggering the maturation process. These changes are considered likely to be consequences of the fishing pressure . Grift *et al. (submitted)* used the Fulton's condition factor K (weight x length^{-3}) as a proxy for physiological condition. The data we have at our disposal allow us to approximate physiological condition through the hepato-somatic index (HSI), which is defined as the ratio between liver weight and gutted weight multiplied by 100. Whereas Fulton's condition factor is strongly related to the energy content of muscles (mainly constituted of proteins), HSI, associated with the energy content of liver, is more linked to the lipid content of cod. While muscle energy content reaches a ceiling as somatic energy content grows high, energy storage in liver and therefore HSI still increases (Lambert and Dutil, 1997a). Most of the sampling being made prior to spawning at a period when cod have stored a lot of energy, variability of the hepato-somatic index seems to be more suitable to describe differences in physiological condition between individuals here.

Material and methods

The data used for this study come from trawl surveys carried out by the Department of Fisheries and Oceans, Canada (DFO) in NAFO divisions 2J, 3K, 3L, 3N, 3O and subdivision 3Ps (Fig. 1) from the early seventies onwards.

Analyses are based on data from surveys realized up to the year 2002. Measured variables include sex, age, maturity status (binary variable), total length, round weight, gutted weight and liver weight of cod. However, liver weights were not taken before the late seventies (1977 or 1978 depending on the area considered). The main part of the sampling was done in the second half of the year, that is to say between July and early January, before reproduction takes place. During this period, the maximum value of HSI is observed (Lambert and Dutil, 1997b), cod storing energy in their liver prior to spawning. However, a few surveys were completed in the period February-June. For convenience, the

first period will be referred to as "autumn" and the second one as "spring". These "spring" surveys were carried out in NAFO subdivision 3Ps from 1972 onwards and in division 3L in 1971 and subsequent years. More details about the sampling procedure are given by Lilly et al. (2001). Table 1 summarized the data.

Data from division 3L were used to assess existing correlation between variations in physiological condition and other measured variables, given it is the only area where data linked to condition of fish are available before and after reproduction. These data have been collected in years 1981–1982 and from 1985 onwards. Generalized linear models (GLMs) with a Gaussian error distribution and an identity or a logarithm link function were tested in this purpose.

Maturation reaction norms were analyzed separately by sex and NAFO group of divisions or subdivision. Owing to the data scarceness in some divisions, samples from contiguous divisions had to be pooled in order to obtain more robust results. Thus, data from NAFO divisions 2J, 3K and 3L (so-called Northern cod) collected in autumn were pooled while data from divisions 3N and 3O (Southern Grand Bank cod stock) collected in spring were analyzed jointly.

The method of probabilistic reaction norms devised by Heino et al. *(2002) was used to calculate maturation reaction norms. This method was adapted by Barot* et al. *(2004) to data with unknown age at first reproduction, as it is the case here. It has already been applied by Olsen* et al (2004, 2005) to the same data set for two-dimensional maturation reaction norms (age and length). The calculation includes three steps :
- Choice of a model to describe the maturation ogive for each sex and area. This model must among others incorporate the variables as a function of which the probability of maturing is described, namely length, age and HSI. Model choice was guided by the value of the Akaike Information Criterion (AIC), which is a measure of goodness-of-fit penalized by the complexity of the model. The lower its value, the more credible the model. In order to make comparisons between areas and sexes easier, the same GLM was chosen to describe all maturity ogives. The selected model was the one with the lowest average AIC value and with variables that are all significantly correlated with the variability of HSI in each data subset.

Unlike Olsen *et al.* (2005), we did not choose fixed age ranges (either 3-6 years or 4-8 years of age). Instead, we selected for each combination of sex and area the age range encompassing the central 90% of mature individuals in a given area. The advantage of a restricted age-range to describe maturity ogives is a better description of the proportion of mature individuals for ages at which fish actually mature.

- Calculation of the probability for an individual to mature between age a-1 and a, considering that its length increased by δL and its condition changed by δHSI in this time span. This probability is given by the following equation, which is direct extension of the equation by Barot *et al.* (2004) for two-dimensional maturation reaction norms :

$$p(a, L, HSI) = \frac{o(a, L, HSI) - o(a-1, L-\delta L, HSI - \delta HSI)}{1 - o(a-1, L-\delta L, HSI - \delta HSI)} \tag{1}$$

where p(a,L,HSI) is the probability for an individual of age a, length L and condition HSI of having matured during the preceding year. Increments used here are differences from one year to the next in measured averages calculated independently by sex, cohort and age. Due to the fact that liver weight is not always reported, HSI increments calculation was based on a slightly lower number of individuals than the calculation of growth increments.

- Derivation of length or HSI at a probability of maturating of interest, chosen to summarize maturation reaction norms, such as p=0.50 (PMRN midpoint).

For this step, linear models describing p as a function of L and HSI are used. Given that interaction between length and condition was not always significant, the model used here was :

$$p(a, L, HSI) \sim L_a + HSI_a + \varepsilon \tag{2}$$

Two approaches were used for this last step:
- At given age and length, calculation of the value of HSI corresponding to a maturation probability of 0.50.
- At a given age and energetic status, calculation of the value of length corresponding to a maturation probability of 0.50.

This latter method enables the assessment of the existence of a trend in the length at maturation after the influence of condition has been filtered out.

In order to limit the variance of data, a lower threshold of five individuals per subdivision, sex, cohort and age was used as filter preliminary to analyses.

A correction to HSI values of fish sampled in spring (+23.6 g. liver/hg. gutted weight) was applied on the basis of the average difference observed in division 3L between the two sampling seasons.
Along analyses, it appeared that the significance of the hepato-somatic index was relatively low in the explanation of maturity ogives. As a consequence, it was thought that a trend in the condition at maturation could also reflect a change in the average condition of fish sampled. Thus, the significance of a linear trend of HSI was tested for each area, sex, and age for mature individuals and its slope was noted in order to evaluate in which cases the second explanation could be plausible or dismissed.
Trends in condition at maturation were assessed through observed changes in the reaction norms midpoints at a given age, for a given NAFO group of divisions or subdivision and by sex. In order to improve the quality of reading of graphics representing changes in maturation reaction norm midpoint over time, a smoothing of plot was applied. But trends were only tested statistically for subdivision 3Ps. The methodology used here does not allow the direct calculation of confidence intervals around probabilities of maturing. So, simple a bootstrap method (Manly, 1997) was applied to calculate confidence intervals around reaction norms midpoints. 500 bootstrap resampling were performed. 2.5 and 97.5 percent quantiles were set as lower and upper limits of confidence intervals. A linear trend was tested with reaction norms midpoints weighted by the inverse of the variance obtained by bootstrap resampling.

Results
Fluctuations in condition
First, the results of linear models testing the correlation between hepatosomatic index of mature individuals and time (years) for each sex and age indicate no common pattern of change of HSI over time, even if in the majority of cases with a significant trend, a linear decrease of HSI is put in evidence (Tab. 2). Besides, when the correlation happens to be significant, the slope remains fairly low, since it stays within the interval [–0.282; 0.244 g. liver/hg. gutted weight/year]. The lower limit being obtained for females of age 4 in division 3N whilst the upper one is reached for females of age 8 in division 3L sampled during autumn surveys. It is thus very unlikely that a trend in condition at maturation is imputable to a global change in HSI, if the absolute value of the slope of plots over time of HSI at a probability of maturing of 0.5 is beyond 0.3 g. liver/hg. gutted weight.
As far as correlations between the variability of HSI of cod sampled within NAFO division 3L and other variables are concerned, only results of models with an identity link function are displayed here (Tab. 3), the use of GLMs with logarithm link function always leading to weaker correlations and equally or less balanced residuals.
The variable "month of sampling" appears to be the first explanatory variable of HSI variability in division 3L, far before other tested variables. Indeed, when tested as a factor, this variable explains 21.4% of the total deviance of data, whereas year, the second explanatory variable, only explains 5.7% of the same deviance. These fluctuations of HSI as a function of months reflects a strong drop in hepatosomatic index during the spawning period. When months are aggregated in a two-modality variable "season", within which months April to June and October to December are pooled, 20.4% of the total variability are still explained. A variable summarizing the influence of years on HSI values was also tested. "year type", a two-modality factor classifies years as a function of an arbitrary criterion: years are qualified "good" if the mean HSI of sampled fish is above 6 g. liver/hg gutted weight, they are qualified "bad" otherwise. It turned out that this new variable describes a small proportion of the observed variability of the energetic condition of fish, with 2.0% of the deviance of data explained. On average, cod in spring have a HSI of almost 2.4 g. liver/hg. gutted fish less than those sampled in autumn. As a whole, it appears that individuals' characteristics such as age, maturity status, length or sex have a lower explanatory power than variables linked to time: month and year of sampling.

Maturation reaction norms
In every combination area-sex, the variable length is the first variable describing maturity ogives. In the "average model" comes then the year of sampling, the age of fish and the HSI. Both year and age are used as factors in the GLM describing maturity ogives. The factor cohort is always significant, but in most cases to a lesser extent than the year. It always becomes non-significant when used as a third factor or variate after the year of sampling. It has to be mentioned that the variable month was not tested in this study, provided that the timing of sampling is not the same from one year to the next. The hepatosomatic index turns out to be the best explanatory variable to add only at the fourth position. No interactions were retained in this model, given that every possible interaction between

$$\text{logit}(maturity) = a \cdot length + b_{year} + c_{age} + d \cdot HSI \qquad (3)$$

tested variables was proven non-significant in at least one of the combinations sex-subdivision. Therefore, the model selected to describe maturity ogives is the following:
Length and HSI are used as continuous variables, whereas year and age are considered as factors here.

Three-dimensional plots of midpoints of probabilistic maturation reaction norms for males and females belonging to cohort 1985 in subdivision 3Ps are represented in figure 2. As expected, the influence of condition on maturation probability is such that at a given age, the better the condition, the lower the size at a probability of maturation p equal to 0.5. So, energetic condition has a positive effect on the probability of maturing.

When HSI at p=0.50 is calculated at given age and length for each cohort, a decreasing trend is obvious for both sexes in every area, even though graphics (Fig. 3) show some differences between patterns of evolution in the distinct groups of divisions or subdivision considered. Thus, whereas this trend seems to be present from at least cohort 1975 for both sexes in NAFO divisions 2J3KL and at least for females in divisions 3NO, it clearly appears only from cohort 1984 (females) or 1982 (males) in subdivision 3Ps. But it can be pointed out that the minimum value of HSI at p=0.5 is always observed for cohorts from the early nineties, both for females and males.

The reduction of the energetic condition necessary to reach to become mature is fairly impressive, as illustrate slopes of reaction norms midpoints calculated for subdivision 3Ps (Tab. 4), values of slopes calculated over the whole data set getting up to –0.7 g. liver/hg. gutted weight/year. Therefore, there is no ambiguity left on the existence of a decreasing trend in the HSI at maturation, at least as far as St.-Pierre Bank cod is concerned.

Moreover, a trend in length at maturation still stands after influence of hepatosomatic index has been filtered out (Fig. 4). This decrease in length at maturity at a given age is observed in every data subset as well.

After that steep decrease in HSI at maturation, a slight rise of this energetic condition seems to occur, spreading of the remaining cohort of the data set. This trend reversal is most visible when females of northern cod and St.-Pierre Bank cod are considered.

Discussion
The influence of energetic condition on the probability of maturing is evident in the case of cod off Newfoundland-Labrador, for both males and females. This influence is such that at a given age and a given length, a fish has higher chances to mature when it is in good condition, as indicated by a high hepato-somatic index (HSI). Energetic status however appears to be less influential than length on the maturation propensity of cod. Moreover, downward trends in the length at maturation still exist after the effect of energetic condition of fish has been controlled for.

Differences in the values of HSI at given age and length occur between the considered areas. Notwithstanding changes in cod distribution, lags between sampling periods in these areas make them intricate to interpret. Even though HSI remains relatively stable during autumn (Lambert and Dutil, 1997b), significant differences exist between seasons. In this paper, seasonal differences have only been partially compensated for by the use of a rough correction to adjust values observed in spring to those measured in autumn.

Even if this study seems to solve the question of the influence of the energetic condition of cod on the maturation process, several factors such as water temperature or food availability at the time when maturation decision is made may have contributed to changes in the maturation propensity of cod. But, as cited in Olsen *et al.* (2005), the decrease in average water temperature (Drinkwater, 2002) would have been more likely to induce a shift of maturation towards older ages, larger size and better condition of maturing fish.

Although a trend in average HSI was noticed in some areas for certain categories of individuals, it is never strong enough to explain the magnitude of observed trends in condition at maturation. It seems that evolution in the condition at maturation of these cod stocks may have occurred. Even though we can not date the start of the trend from the data we have at our disposal, it is very likely that this trend has been driven by a high fishing pressure. This trend is reflected in the requirement of a lower condition to induce the maturation process: cod tend to engage in maturation even though their energetic reserves are low. It might have consequences in terms of natural mortality rates and the occurrence of suppressed reproduction. However, Rideout *et al.* (*submitted*) did not report any trend in the percentage of cod experiencing skipped spawning. So, a trade-off between reproduction and mortality risk, either of spawners or offspring which would not have enough lipid reserves to overcome

severe environmental conditions after reproduction or hatching is likely to exist, even if not proven here.

Trend in condition at maturation has already been reported for plaice by Grift *et al.* (*submitted*), but in their study an ambiguity persists because of the potential influences of the methodology used. Grift *et al.* (*submitted*) measured condition through Fulton's condition factor (total body weight divided by length cubed). Total body weight has been shown to be strongly influenced by the repletion of individuals, as well as by food condition or diseases (Grift *et al.*, *submitted*). In that study, it was also necessary to apply corrections to account for seasonal changes in body weight, and thus uncertainty to the estimated condition factor, because plaice of distinct maturity stages were sampled during the spawning season. Another point, raised in the same paper, is that the decision of maturing is already taken when cod are sampled in autumn (vitellogenesis starts in summer). Therefore, the increased energy storage in the liver is potentially only a consequence of the maturation decision, because fish that had "decided" to mature would store more energy in anticipation of reproduction. Yet, GLMs applied here to describe the variability of HSI in NAFO subdivision 3L have shown that maturity status only explains a small proportion of the total deviance of HSI data (3.4% of total deviance explained, mature individuals having an average HSI 0.97 g. liver/hg. gutted weight higher than immature ones). This current study thus alleviates some doubts about the possible influence of the choice of the index summing up the energetic status of fish on results to support the existence of a trend in the condition at maturation.

However, several remarks about the methodology used here and possible implications in terms of results have to be brought up.

First, as far as the representation of trends is concerned, it would certainly have been more relevant to apply two distinct linear models to describe the evolution of maturation reaction norms midpoints, as done in Olsen *et al.* (2005), to account for the apparent increase noticed after the implementation of moratoria. Indeed, after an indisputable downward trend in the value of the hepato-somatic index at maturation reaction norms midpoints, an apparent "recovery" seems to occur. It happens after the relaxation of the fishing pressure imposed by moratoria.

The slopes of this recent upward trend appear to be steeper for females than for males. Life history theory would not predict such a prompt trend reversal, unless maybe considered fish populations underwent a tremendous fishing mortality and that condition at maturation is a highly heritable trait. Alternatively, this observation may be attributable to the small number of older cod sampled as time is going on, giving therefore a high weight to a low number of individuals in the fit of the models used to calculate maturation probabilities. It has also to be kept in mind that this trend stretches over a short period and might only reflect a punctual influence of factors not taken into account in the calculation of maturation probabilities. It would be interesting to see whether the data from sampling after 2002 supports the existence of this upward trend.

Then, it would have certainly been better to use an other probability than 0.5 to summarize maturation reaction norms at higher ages when most of the fish are mature. Although midpoints of reaction norms are maybe the most intuitive, their calculation leads to extrapolation in model (2) when older individuals are considered. Thus, the use of a maturation probability like 0.75 would be more appropriate to sum up maturation reaction norms in these case. A perhaps more elegant way would be to track over time the fluctuation of maturation probability of cod of fixed length and condition.

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TABLES AND FIGURES

Table 1: Summary of characteristics of the data set used in for this study

Area and season	Sex	Years	Number of weighted livers	Ages used in maturity ogive
2J+3KL autumn	Females	1977 - 2002	10690	4 - 8
2J+3KL autumn	Males	1977 - 2002	9540	3 – 7
3L spring	Females	1978, 1980-82, 1984-1987, 1989-2002	2747	
3L spring	Males	1978, 1980-82, 1984-1987, 1989-2002	2669	
3Ps spring	Females	1978 – 2002	4652	4 – 8
3Ps spring	Males	1978 – 2002	4036	3 – 8
3NO spring	Females	1978 – 1982, 1984-1987, 1989-2002	4465	3 – 8
3NO spring	Males	1978 – 1982, 1984-1987, 1989-2002	4495	3 - 7

Table 2: Significant trends in HSI of mature individuals from age 3 to 8 as a function of time for each combinaison sex-NAFO area. Only slopes significantly (at a 0.05 significance threshold) different from 0 are reported.

Area and Season	Sex	3 years	4 years	5 years	6 years	7 years	8 years
2J – Aut.	Females			-0.119	-0.195	-0.170	
2J – Aut.	Males		-0.152	-0.133	0.120		
3K – Aut.	Females			-0.114	-0.081		
3K – Aut.	Males			-0.063			
3L – Aut.	Females			-0.220			0.215
3L – Aut.	Males					0.119	0.244
3L – Spr.	Females			-0.098	-0.097		-0.140
3L – Spr.	Males			-0.048	-0.054	-0.083	-0.144
3Ps – Spr.	Females			-0.100	-0.074	-0.048	
3Ps – Spr.	Males		-0.11	-0.094	-0.083	-0.062	-0.061
3N – Spr.	Females		-0.282				
3N – Spr.	Males						
3O – Spr.	Females						
3O – Spr.	Males						

Table 3: Proportion of the total variability of HSI values measured in division 3L explained by variables tested individually

Variable	Type of variable	Percentage of total deviance explained
Month	Factor (6 modalities)	21.4
Season	Factor (2 modalities)	20.4
Year	Factor (20 modalities)	5.7
Age	Factor (17 modalities)	5.1
Age	Variate	3.9
Maturity status	Factor (2 modalities)	3.4
Body length	Variate	3.4
Cohort	Factor (33 modalities)	2.1
Year type	Factor (2 modalities)	2.0
Sex	Factor (2 modalities)	1.4
Year	Variate	0.0

Table 4.: Slopes of regressions of HSI at p=0.5 over the whole studied period, and probabilities of having slopes not significantly different from 0 (p.values given by Student-tests)

Sex	Age	Slope (g. liver/hg. gutted weight/year)	p.value of Student test
Females	5 years	-0.370	1.32e-06
Females	6 years	-0.326	3.45e-05
Females	7 years	-0.698	1.11e-06
Males	4 years	-0.588	7.38e-09
Males	5 years	-0.546	4.02e-07
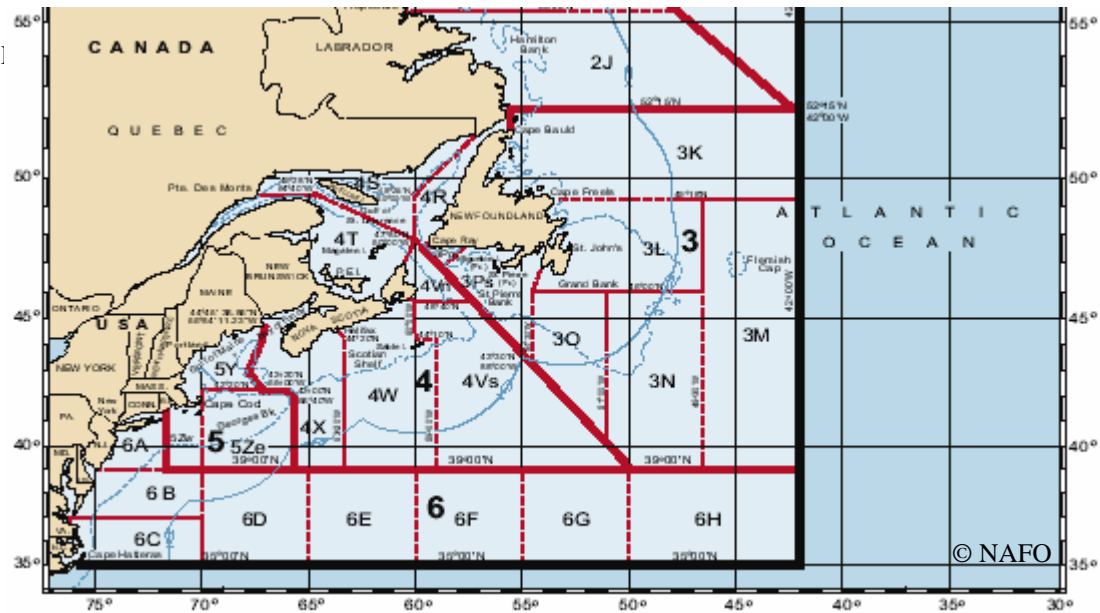
Figure 1: Map of the southern part of the NAFO Convention area
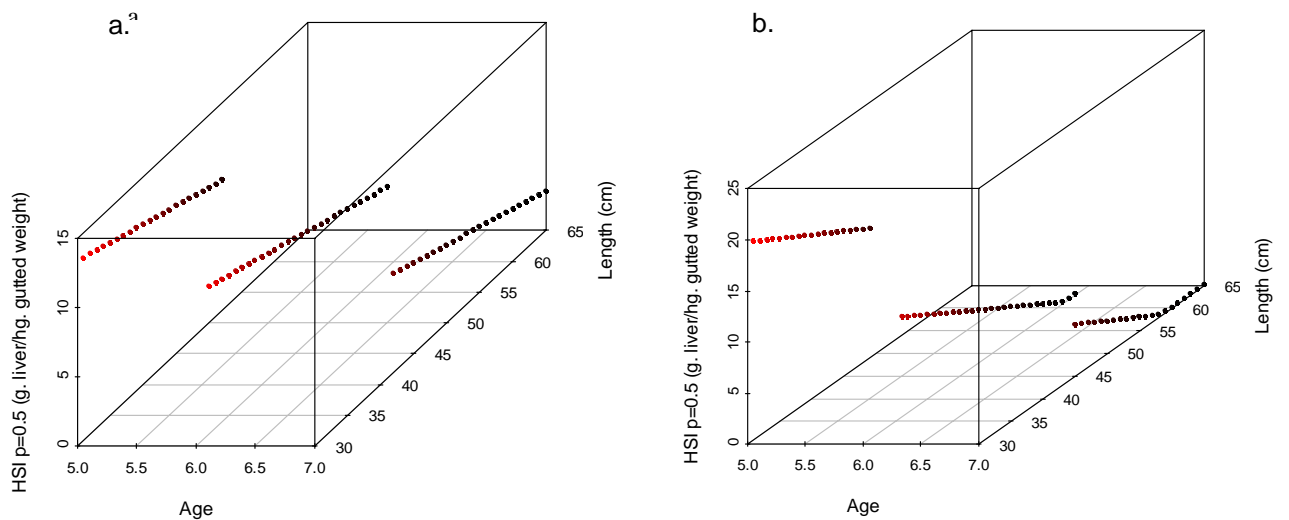
Figure 2: Plots of three-dimensional maturation reaction norms midpoints for cohort 1985 in NAFO subdivision 3Ps *a. Females ; b. Males.*

FEMALES   MALES
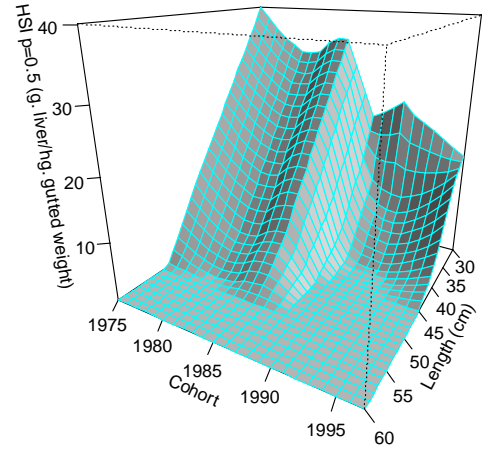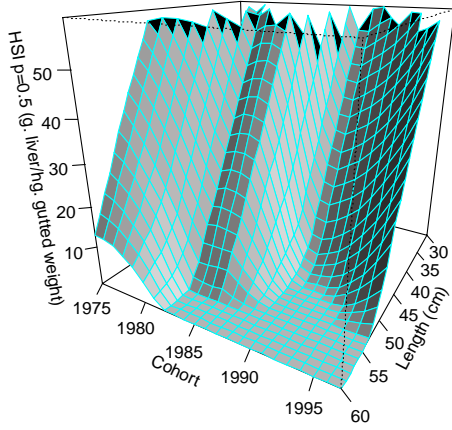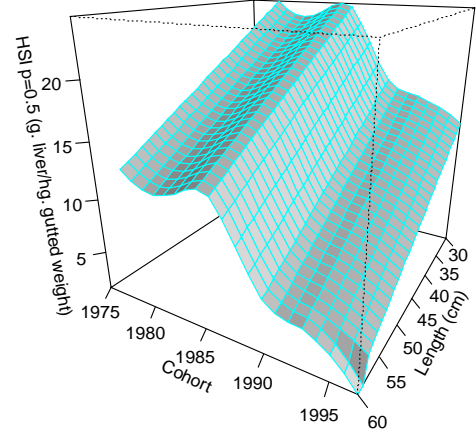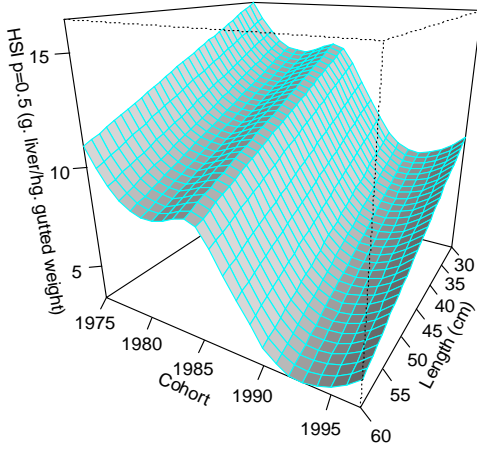
Figure 3: Changes in the HSI at a probability of maturing of 0.5. *Values of HSI at p=0.5 are calculated at age 5 for females (left column) and age 4 for males (right column), for body length between 30 and 60 cm.*
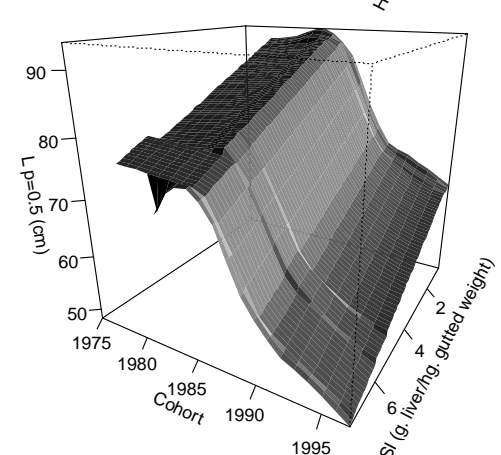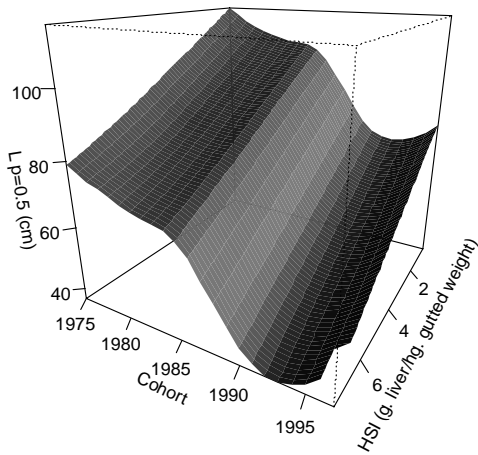
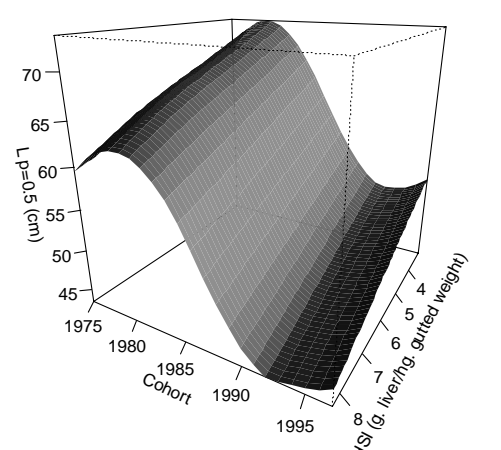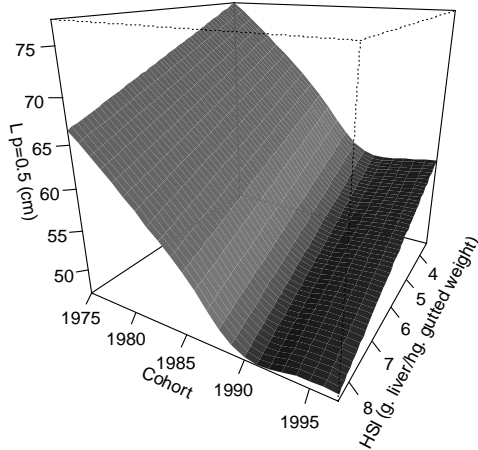FEMALES   MALES

2J3KL
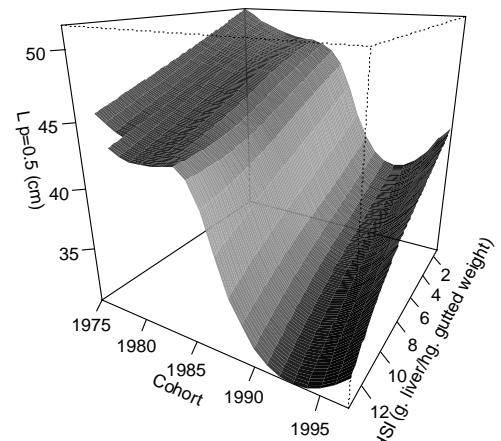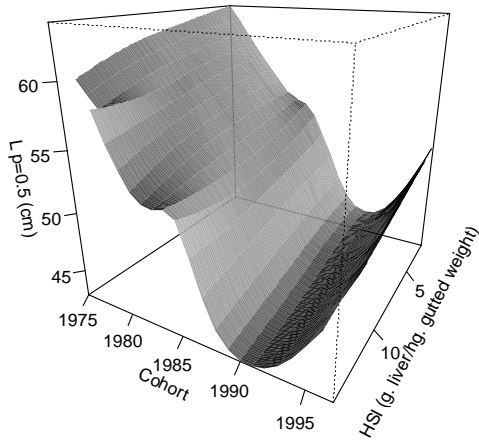
3Ps

3NO

Figure 4: Changes in the body length at a probability of maturing of 0.5. *Values of body length at p=0.5 are calculated at age 5 for females (left column) and age 4 for males (right column), for the range of HSI values observed in each data subset.*