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Report

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Growth and maturity of North Sea plaice and sole

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Samenvatting

Een van de drie werkpakketten van het F-project, werkpakket “F1”, richt zich op de verbetering van de toestandsbeoordeling. Dit rapport “A6” vormt onderdeel van dit werkpakket F1 en onderzoekt biologische karakteristieken. Dit rapport richt zich op veranderingen in groei en geslachtsrijpheid van Noordzee schol en tong. Verandering in groei kan van invloed zijn op toestandsbeoordelingen en heeft daarnaast een grote invloed op de productiviteit van een visbestand, en daarmee op de hoeveelheid die duurzaam aan het bestand kan worden onttrokken. Groeiveranderingen kunnen worden weergegeven als verandering van de gemiddelde lengte van vissen op een leeftijd of van de conditie van vissen, weergegeven als ratio van gewicht en lengte tot de derde macht. Verandering van groei, bijvoorbeeld lagere gemiddelde lengte van vissen op een leeftijd of een lagere conditie, kan de perceptie van de biomassa van het visbestand en het paaibestand en de hoeveelheid vis die kan worden geoogst, negatief beïnvloeden als geen rekening wordt gehouden met deze lagere groei. Geslachtsrijpheid wordt gebruikt bij het schatten van het paaibestand en daarmee ook voor de bepaling van de biologische referentiepunten. Geslachtsrijpheid wordt per leeftijd constant aangenomen over de jaren, terwijl deze in werkelijkheid niet constant is. De mate waarin dit varieert wordt onderzocht in dit rapport

Verandering in groei van Noordzee schol en tong werd onderzocht aan de hand van verschillende gegevens: gemiddelde lengte per leeftijd en conditie berekend uit marktmonsters en surveygegevens (gegevens verzameld met onderzoeksvaartuigen) en gegevens van lengtetoename berekend uit de terugberekening van otolieten (gehoorsteentjes). Op deze structuren worden elk jaar ringen aangemaakt die overeen komen met de jaarringen van een boom, waarmee de leeftijd van vissen kan worden bepaald. De drie gegevensbronnen lieten zien dat voor zowel schol als tong een duidelijke verandering in productiviteit is opgetreden gedurende de laatste 45 jaar, met een relatieve hoge groei in de jaren ’70. Voor de jaarklassen die geboren zijn tussen 1960 en 1970 is er sprake van een groeiversnelling gemeten in gemiddelde lengte per leeftijd. Voor de jaarklassen die geboren zijn tussen 1970-77 is er sprake van een stabiele groei, terwijl de jaarklassen die geboren zijn tussen 1978 en het midden van de jaren ’80 een afnemende groei laten zien. De jaarklassen die geboren zijn in de jaren ’90 laten weer een stabiele maar lagere groei laten zien. De daling in groei van schol rond 1980 was sneller dan de daling in de groei van tong. Alleen 0-jarige vissen laten een ander patroon zien, met een lichte stijging van de groei vanaf het midden van de jaren ’80 tot heden. Voor schol werd een lagere groei gevonden voor een aantal jaarklassen, namelijk uit 1963, 1972, 1985, 1986, 1987, 1996 en 1997. Veranderingen in de conditie van schol en tong per leeftijd kwamen overeen met de veranderingen in gemiddelde lengte per leeftijd. De verandering in conditie verliep echter minder drastisch dan de verandering in gemiddelde lengte.

De verandering in groei van jonge schol en tong kwam voor beide soorten overeen en hangt waarschijnlijk samen met een verandering in de productiviteit van het zuidoostelijke deel van de Noordzee. De oorzaak van deze veranderde productiviteit van de zuidoostelijke Noordzee is niet opgehelderd. De waargenomen verandering in groei van schol en tong kwam niet overeen met de verandering in de inspanning van de boomkorvloot, maar kwam wel sterk overeen met de verandering in de hoeveelheid voedingsstoffen in de Noordzee, zoals fosfaten en stikstof. Omdat er in de literatuur duidelijke aanwijzingen zijn voor de effecten van klimaatsveranderingen op de toestand van het Noordzee ecosysteem, en omdat de afname van de gemiddelde lengte per leeftijd in verschillende scholpopulaties in het noordoostelijk Atlantisch gebied is waargenomen, is het waarschijnlijk dat de veranderingen in groei gerelateerd zijn aan grootschalige klimaatsveranderingen, in combinatie met locale effecten van eutrofiering en mogelijk met de bodemomwoeling door de boomkorvisserij.

Geslachtsrijpheid werd onderzocht voor schol en tong vrouwtjes aan de hand van gegevens van percentage geslachtsrijpheid per leeftijd en de lengte van vissen waarbij 50% van de vissen van een bepaalde leeftijd geslachtsrijp is. Voor deze analyse werden gegevens gebruikt van de Nederlandse (schol en tong) en Engelse (alleen schol) marktbemonstering. Analyse van de Nederlandse vangsten liet zien dat over de laatste 45 jaar vrouwtjes op jongere leeftijd en op kleinere lengte geslachtsrijp worden. In 1960 was bijvoorbeeld 25-50% van de 4-jarige schol geslachtsrijp, in de jaren ’70 en ’80 was dit 50%-75% terwijl in de recente periode dit zelfs boven de 75% uitkwam. De verandering in de percentages volwassen dieren is deels gekoppeld aan de veranderingen in de groeisnelheid. Bij een hoge groeisnelheid neemt het percentage geslachtsrijpheid toe. Anderzijds is er sprake van een geleidelijke afname van de lengte waarop 50% van de vissen geslachtsrijp worden. Jaarlijkse variatie in groeisnelheid en temperatuur tijdens de juveniele fase beïnvloedt het percentage geslachtrijpe vissen uit een jaarklasse. Daarnaast is het voor schol aannemelijk dat de waargenomen verandering in het percentage geslachtsrijpe vissen een gevolg is van de selectieve effecten van de visserij die tot genetische veranderingen in de populatiesamenstelling heeft geleid. Deze bevindingen impliceren dat de SSB tegenwoordig groter is dan geschat wordt in de toestandsbeoordeling. Echter, de gevolgen voor het beheer zijn niet duidelijk, omdat de studie ook impliceert dat de huidige referentiepunten niet meer geldig zijn. Deze kwestie zal behandeld worden in rapport A16/17 (over de huidige en alternatieve referentiepunten).

Een werkdocument met aanvullende analyses van geslachtrijpheid is gepresenteerd op de WGNSSK in 2004 (werkgroep die jaarlijks de toestand van de demersale visbestanden in de Noordzee en Skagerrak berekent). Het werkdocument is opgenomen als Appendix II. Deze analyse bevestigde dat de geslachtsrijpheid van schol toegenomen is. Opgemerkt dient te worden dat het voor de bepaling van de productiviteit van een bestand ook van belang is naar de geslachtsverhoudingen te kijken.

De waargenomen veranderingen in groei en geslachtsrijpwording hebben belangrijke implicaties voor de bepaling van de biologische referentie punten die in het visserijbeheer worden toegepast. Deze implicaties zullen worden behandeld in rapport A16/A17 van het F-project.

Summary

This report A6 of the F-project deals with biological parameters: changes in growth and maturity of North Sea plaice and sole. Changes in fish growth have effects on stock biomass, spawning stock biomass and yield, either through changes in mean length-at-age or through changes in condition (ratio of the fresh weight over the cube of the length). In the stock assessments and projections the maturity at age has been assumed to be constant over time. Violation of this assumption may lead to a bias in the perception of the status of the stock.

Changes in growth patterns were investigated through changes in mean length-at-age, length increments, and condition of North Sea plaice and sole, by using market samples, otolith back-calculation and survey data. The market sampling and research vessel surveys and back-calculation showed the overall pattern with an increase in growth in length of the year classes born between 1960 and 1970, a stable growth for the year classes born between 1970 and 1977, a decrease for the year classes born between 1978 and the mid 1980s, and a rather stable growth for the year classes born in the 1990s for both plaice and sole. In plaice, the abrupt decrease around 1980 contrasts to the rather gradual decline in sole. The trend in length at age 0 is somewhat different suggesting an increase between 1980 and 2003. Particularly low growth indices were observed for plaice for the year classes 1963, 1972, 1985, 1986, 1987, 1996 and 1997, coinciding with above average year class strength. Changes in condition reflected changes in length-at-age in both plaice and sole, although the amplitude of the changes in condition was smaller than in length-at-age.

The synchronous changes in growth of juvenile plaice and sole suggest changes in the benthic productivity of the southeastern North Sea. The temporal trends in growth do not match the trends in beam trawling effort, but closely match the trend in nutrient enrichment. However, the evidence that changes in ocean climate on a time scale of decades can affect changes in productivity and the observation that the declining trends in length-at-age in plaice occurred in several populations in the northeastern Atlantic suggest that the growth signal may be related to large-scale changes in ocean climate in conjunction with the local effect of eutrophication and perhaps beam trawling.

Analysis of the Dutch commercial catches of North Sea plaice and sole reveals that over the past 45 years fish have become more likely to be mature at younger age and smaller length. These findings correspond with the results of an earlier study of 41 cohorts of plaice using the Dutch market samples, where it was concluded that females have become more likely to mature at a younger age, partly because they grow faster, but also due to a fisheries-induced genetic shift in the fish' propensity to mature. Although these findings imply that SSB is probably higher than currently estimated, the management implications are not clear, since the study also implies that the current reference points are not valid anymore. This issue will be dealt with in report A16/17 (on the current and alternative reference points).

A working document with additional analyses on maturity was presented during the meeting of the WGNSSK (Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak) in 2004. This working document is presented in Appendix II. This analysis confirmed that maturity of plaice has increased. It should be noted that when considering the productivity of a stock the sex ratios should be taken into account as well.

1. Introduction

The F-project is a 4-year research project with the objective to improve the mutual understanding between fishermen, scientists and fisheries managers, by stimulating communication and collaboration between fishermen, fisheries scientists and fisheries managers. One of the three working packages of the F-project is concerned with the improvement of stock assessment of plaice and sole. The results of the annual stock assessments of plaice and sole by ICES have raised serious criticism on the transparency of the methodology, the quality of the input data and the quality of the stock assessment models used. The objectives of the F-project are to prepare for comprehensive fisheries evaluations of North Sea flatfish by analyzing and seeking improvements of the following points:

- Representativity of the input data
- Uncertainty and bias in the stock assessment
- Uncertainty and bias in the short-term prognosis
- Biological reference points
- Produce a manual on quality assurance
- Explore alternative methods

These issues will be investigated in several smaller studies of which a total of 13 separate reports and 4 other products will be produced, which, taken together, represent an extensive analysis of the problem. Product A6 within working package F1 investigates the representative nature of the input data and deals with biological parameters. This product investigates changes in growth and maturity of North Sea plaice and sole.

Changes in biological parameters such as fish growth and maturity influence the stock assessment and stock projections and may have important implications for the derivation of the biological references points (B_{lim}, B_{pa}, F_{lim}, F_{pa}) used in the management advice. Changes in fish growth have an effect on stock biomass, spawning stock biomass and yield, either through changes in mean length-at-age or through changes in condition. Trends in growth can bias the stock projections if they are not accounted for. More important is the effect of changes in growth on the productivity of a stock, and hence on the proportion that can be harvested sustainable. At a higher growth rate, the effort that can be applied as well as the maximum sustainable yield will be higher. Therefore, we did not restrict our study to a simple update of the time series of growth, but attempted to interpret the observed changes as a reflection of changes in the productivity of the North Sea ecosystem.

In the stock assessments, maturity at age is used to estimate the size of the spawning stock, and is assumed to be constant over time for North Sea plaice and sole. The historic time series of SSB and recruitment are important for the determination of biological reference points such as B_{lim} and B_{pa}. Maturity at age, however, is not constant over time and assuming it is fixed may bias the assessment and projections leading to incorrect conclusions as regards to reference points.

This study investigates:
1) patterns in growth
2) patterns in maturity.

Growth patterns (chapter 2) are investigated through mean length-at-age, length increments, and condition. Estimates of mean length-at-age were derived from market samples, otolith back-calculations and survey samples, while estimates of condition were derived from market and survey samples only, and estimates of length increments were derived from otolith back-calculations. The temporal patterns in these estimates were investigated in relation to temperature, eutrophication and beam trawl disturbance.

The assumption of constant maturity (chapter 3) was investigated through maturity at age and length at 50% maturity per age group. Estimates of maturity at age were derived from Dutch and English market samples. Estimates of maturity at age were available for plaice and sole from Dutch market samples and for plaice from English market samples. Estimates of length at 50% maturity were derived from Dutch market samples.

Both chapters include an introduction and a discussion that focuses on biological effects of these two parameters. An overall discussion is given in chapter 4 and conclusions are presented in chapter 5.

2. Growth

2.1. Introduction

Growth of fish may be affected by external environmental conditions such as temperature, food availability, oxygen, as well as intrinsic conditions such as physiology of reproduction and growth. Environmental conditions may determine the availability of suitable food and the rate of the metabolic processes. Improved feeding conditions will result in increasing growth rates until the physiological maximum growth rate is reached. Food can be limiting growth if there is not sufficient food available either due to variations in the productivity of the ecosystem, or to variations in the abundance of intra- or inter-specific competitors. If food is not limited, growth rates will increase with temperature up to a maximum beyond which growth rate will decrease sharply. Also, growth rate may be reduced at low oxygen concentrations. The growth of fish may also be affected by the intrinsic process of energy allocation over somatic growth and reproduction. Hence, a change in somatic growth may be linked to a change in the onset of maturation or a change in the energy investment into reproduction.

Changes in growth are generally studied from the changes in the mean size at age attained by the population, but also by the condition of fish. As the size attained at a certain age reflects the cumulative growth rate during the previous ages, it is impossible to determine in which year(s) and at which age(s) a change in growth occurred. A large fish at age 6 may have grown faster throughout its life but may also have experienced a fast growth only during one particular year. Another complicating factor is that age groups may differ in their spatial distribution. Hence, changes in local environmental conditions may have an effect on specific age groups only. Previous investigations suggest that for plaice, growth changes occurred in the juvenile size classes, whereas in sole, all size classes appeared to have increased in growth (Rijnsdorp and van Beek, 1991). Finally, it should be realized that growth, expressed as the annual increment in length, is itself a function of the size of the fish. A small fish will show a larger length increment than a larger fish. A study of changes in growth therefore should estimate length increments in relation the size of the fish at the start of the year.

Changes in the environment can also affect the growth of fish in weight. High food availability can result in heavier fish at the same length than fish from areas with lo food availability. The condition factor of a fish is often used to investigate changes in weight, and is estimated as the ratio of the fresh weight over the cube of the length. It has been shown that the condition factor was positively related with the length increment in both plaice (Rijnsdorp et al., in prep) and sole (Van Beek, 1988; Millner & Whiting, 1996).

One of the important factors determining the productivity of a fish stock is its growth rate. Changes in growth rate in North Sea plaice and sole have been reported previously (de Veen, 1976; Bannister, 1978; Van Beek, 1988; Rijnsdorp and Van Beek, 1991; Rijnsdorp and Van Leeuwen, 1992; 1996; Millner and Whiting, 1996; Millner et al, 1996). The general picture that emerged from these studies is that growth in both species accelerated during the 1960s and 1970s and decreased in the late 1980s. Superimposed on these long-term changes, a short-term pattern was observed with a reduced growth of strong year classes in plaice, but not so in sole.

In this chapter, we will

1) update the time series of the mean length-at-age of plaice and sole as observed in the commercial samples taken in the fish auctions since 1957, and in the various research vessel surveys conducted by RIVO since 1970;
2) update the time series of growth estimates for various size classes of female plaice as obtained by back-calculation of the growth patterns from the otoliths;
3) present a time series of condition factors;

4) analyze the observed changes in the context of changes in environmental conditions and population abundance. In particular, we focus on the question whether the changes in growth may be related to changes in temperature, eutrophication, or beam trawl disturbance.

2.2. Methods

Mean length-at-age and condition factors were used to examine changes in growth of North Sea plaice and sole. Estimates of mean length-at-age and condition were derived from regular market samples of plaice and sole and from three different surveys. Also otolith back-calculations from female plaice were used to estimate mean length-at-age.

2.2.1. Mean length-at-age

2.2.1.1. Market samples

Regular samples of the commercial landings of plaice and sole have been collected since 1957 by market category for each quarter. As such the market samples are length-stratified. Mean length-at-age (LAA) was calculated from market samples, taking account of the length distribution of the population. As such the LAA is an estimate of the mean length of each age group in the population. LAA in the market samples were determined for the spawning season when all age groups are accessible for the fishery.

2.2.1.2. Otolith back-calculation

Otolith samples of female plaice were collected in the southern North Sea (around 53°N) during the spawning months (January-March) to back-calculate the size at each annual ring. Rijnsdorp et al. (1990) presented a description as well as a validation of the method. For the F-project, additional samples were processed for the years since 1999. Most otolith samples were length stratified with up to 4 females sampled by each cm-group in a year.

The mean back-calculated length at each age was calculated taking account of the length distribution of the female population during the spawning period. Females younger than 5 years old have not yet recruited fully to the population of marketable fish ($>=27$ cm) and were therefore excluded from the analysis. Growth rates were estimated for 10, 20 and 30 cm fish by fitting the following model for the size ranges: $5<L<14.9$ cm; $15<L<24.9$ cm; $25<L<34.9$ cm, respectively:

$$dL = L + Y + \varepsilon$$

where dL is the length increment between the back calculated lengths of two successive annuli (i and i+1), L is the back-calculated length at the start of the growing period (i), and Y is the year of growth.

2.2.2. Survey data

Three surveys were used to investigate changes in growth. For each survey the numbers at length and age by haul were derived from the numbers at length, by applying age-length keys (proportion of each age within a length-class) to the data. These age-length keys differed between areas within each survey and will be described for each survey in the paragraphs below. The numbers at length were summed for each age to obtain the numbers at age by haul. From the numbers at age by haul, the numbers at age by area were calculated for the different surveys. Mean length-at-age was calculated for each area and over all areas combined, using the numbers at age per area as a weighting factor. This means that if in one area many fish were caught and in another area only a few, the area with the few fish contribute less to the calculation of the mean length-at-age than the other area. The correction of the numbers at age per area differed for each survey and will be described in the paragraphs below.

2.2.2.1. Beam Trawl Survey

The Beam Trawl Survey (BTS) is directed at obtaining fisheries-independent indices of abundance for North Sea plaice and sole up to age 10. The survey is conducted in the North Sea and waters around the United Kingdom in cooperation with institutes from England, Germany and Belgium, and is coordinated by the ICES Working Group on Beam Trawl Surveys (WGBEAM). The Dutch contribution to the survey was initiated in 1985 with research vessel “ISIS”, covering the southeastern part of the North Sea (Figure 2.1, left). From 1995 the survey is also conducted with research vessel “TRIDENS”, covering the southwestern, western and central part of the North Sea (Figure 2.1, right). The BTS is conducted each year in August/September using an 8 m beam trawl with 40 mm mesh cod-end. The haul duration is 30 minutes. The research vessel “ISIS” executes 1-3 hauls per ICES rectangle, while “TRIDENS” only executes 1 haul per rectangle.

The numbers at age used in the calculation of mean length-at-age were corrected for the number of hauls in a rectangle. In some rectangles three hauls were executed, while in other rectangles only one haul was executed. If no correction was applied, the rectangle with three hauls would have more contribution to the calculation of mean length because of the longer sampling period than the rectangle with only one haul.

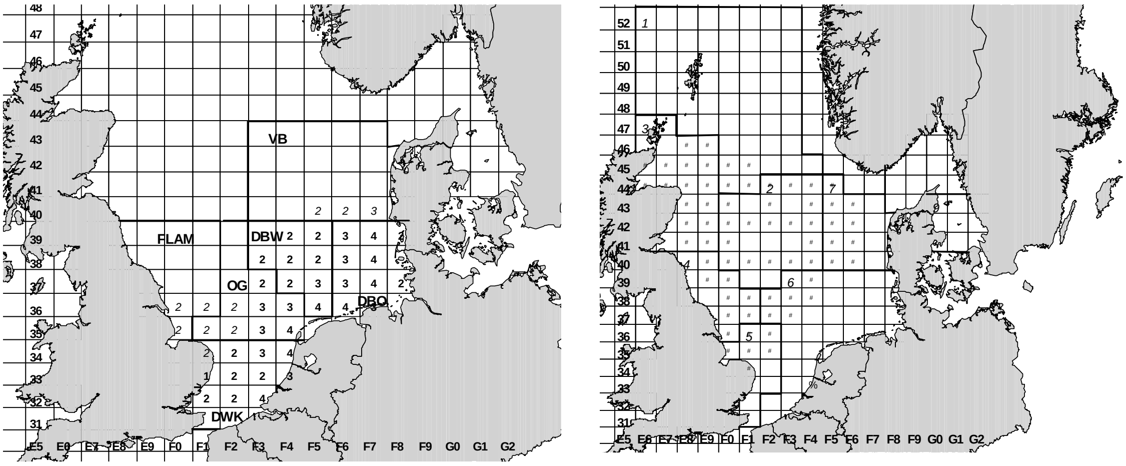

Figure 2.1. BTS. Sampling coverage of research vessel ISIS (left) and Tridens (right).

2.2.2.2. Sole Net Survey

The Sole Net Survey (SNS) is directed at obtaining fisheries-independent indices of abundance for age 1-4 North Sea plaice and sole. The survey was initiated in 1969 and is based on 10 fixed transects (parallel or perpendicular to the coastline) along the Dutch, German and Danish coast (Figure 2.2). The position of stations within a transect is chosen such that the entire depth-range of the transect is covered. During 1969-1989 the survey was conducted in spring and in autumn, while during 1990-2002 the survey was conducted in the autumn. From 2003 the survey is conducted in the spring. The SNS is using a 6 m beam trawl with 40 mm mesh cod end. The haul duration is 15 minutes.

The 10 transects presented in Figure 2.2 were selected as age-length keys areas for the SNS survey. After applying the age-length keys, mean length-at-age was calculated over all areas combined. The numbers at age used in the calculation of mean length-at-age were corrected for the total duration of all hauls in a transect, since some transects had more hauls than other transects.

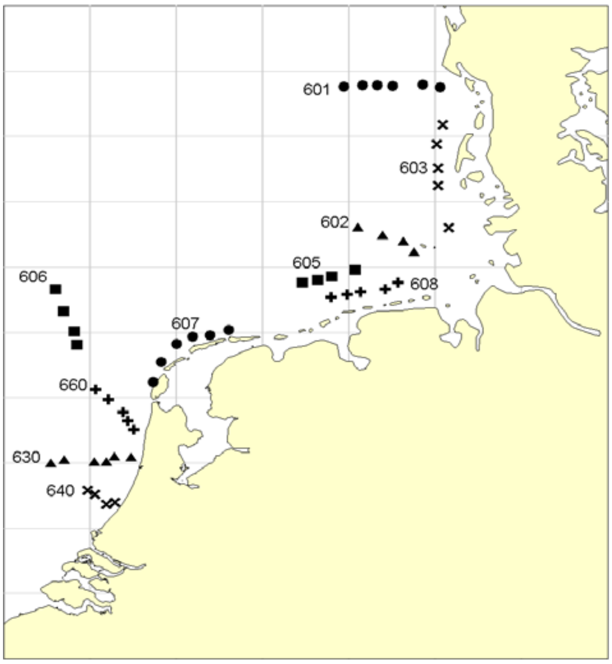

Figure 2.2. SNS. Sampling coverage of the 10 transects.

2.2.2.3. Demersal Fish Survey

The Demersal fish Survey (DFS) is directed at monitoring juvenile plaice and sole, shrimps and non-commercial demersal fish species. The survey was initiated in 1969 and covers the Wadden Sea, the Westerschelde, the Oosterschelde and the coastal zone (Figure 2.3). During 1969-1986 the survey was conducted in spring and autumn, but from 1987 onwards the survey is only conducted in the autumn. A 6 m beam trawl is used by research vessel “ISIS” in the coastal zone, while a 3 m trawl is used by research vessel “Stern” in the Wadden Sea and by “Schollevaar” in the Westerschelde and Oosterschelde. All trawls use a 20 mm mesh cod end, and the haul duration is 15 minutes. Other “young fish surveys” are executed by institutes from England, Germany and Belgium, and are combined to form international indices.

The numbers at age used in the calculation of mean length-at-age were corrected for the total duration of all hauls in the different areas, since some areas had more hauls than other areas. The numbers at age were also corrected for differences in the distribution of the fish over water depths. Four categories of water depths were selected as used in the index calculation, and the proportion of the surface area of each of these water depth categories to the total surface area of the entire area was used to correct the numbers at age.

Figure 2.3. DFS. Sampling coverage along the coast.

2.2.3. Effect of environmental variables

The inter-annual variation in length was studied in relation to environmental variables that may affect growth of fish (Figure 2.4). We used 2nd and 3rd quarter mean of the monthly sea surface temperatures recorded at Den Helder as an index of the temperature conditions during the growing period in the distribution area of plaice and sole in the southeastern North Sea. The number of horsepower days of the Dutch beam trawl fleet was used as an index of the seabed disturbance. Horsepower days were available since 1972. For the period 1957-1971, the horsepower days were estimated from the significant relationship between horsepower days and the fishing mortality rate of sole. The concentration of dissolved inorganic phosphate (μmol.s^{-1}) and nitrogen (kmol.s^{-1}) in the river Rhine at Lobith (Raaphorst & de Jonge, 2004) were used as an index of the nutrient input in the coastal waters. The NAO-winter index was used as an index of the atmospheric influence on the ocean climate (http://www.cru.uea.ac.uk/~timo/projpages/nao_update.htm). There is growing evidence that decadal variability in North Atlantic ecosystem properties is related to this index although the causal links have rarely been elucidated. To explore the effects of population density on growth, we used year class strength and spawning stock biomass estimates (ICES, 2003) as well as an index of mean crowding. The mean crowding index estimates the number of conspecifics that share the same unit of habitat (ICES rectangle) and may potentially compete for food. The index was calculated from the population numbers at age from VPA and an index for the overlap in distribution of the age groups (Rijnsdorp and van Beek, 1991).

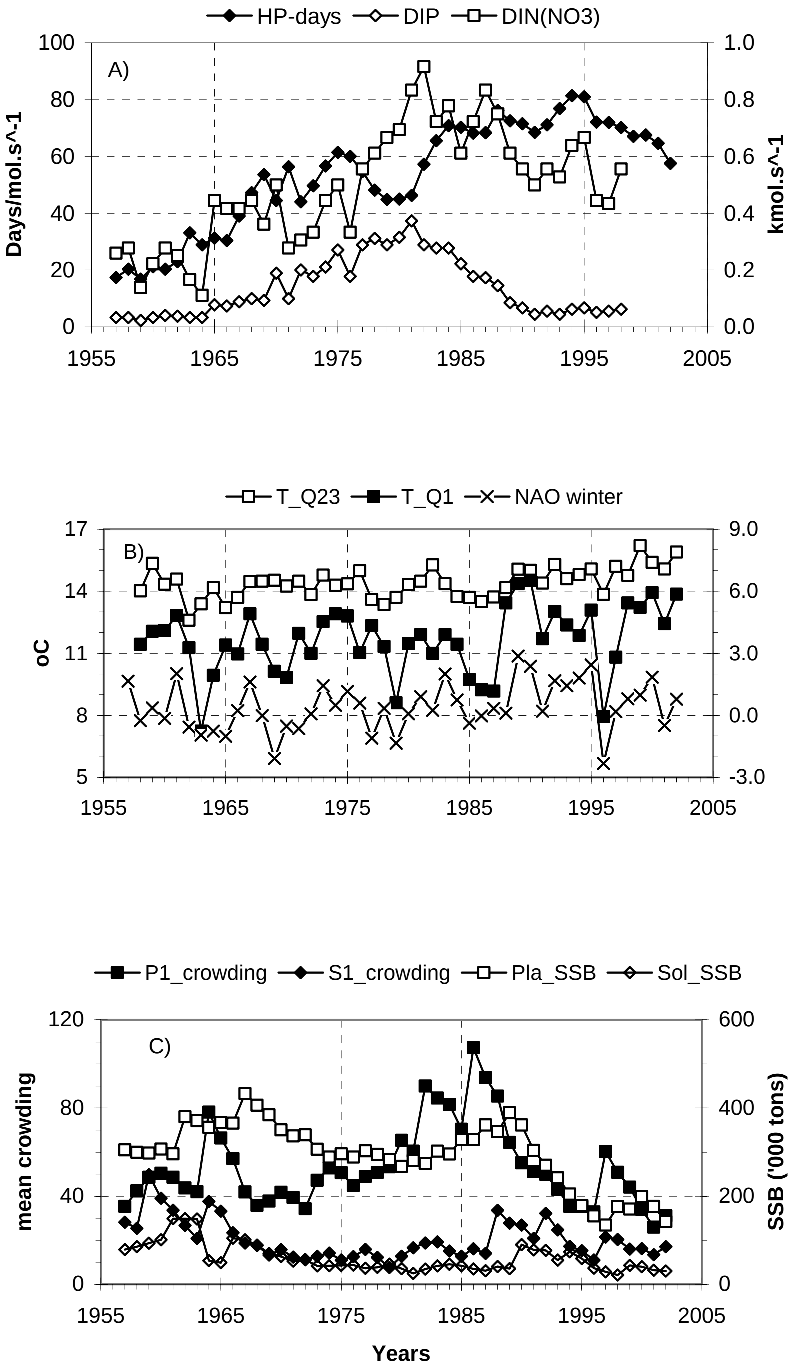

Figure 2.4. Time trends in environmental variables that may affect growth of plaice and sole. A) eutrophication (DIP - dissolved inorganic phosphate; DIN - dissolved inorganic nitrogen concentrations in the Rhine at Lobith) and sea bed disturbance (horse power days of the Dutch beam trawl fleet); B) mean daily sea surface temperature during the 1st (T_Q1) and the 2nd and 3rd quarter (T_Q23) at a coastal station (Den Helder) and the winter index of the North Atlantic Oscillation; C) index of mean crowding on age group 1 (plaice: P1_crowding; sole: S1_crowding) and the spawning stock biomass (plaice: Pla_SSB; sole: Sol_SSB)

2.2.2. Condition factors

To evaluate the changes in the relative weight, the condition factor (cf) was calculated from the weight (W in g) and length (L in cm):

$$cf = 100 * W * L^{-3}$$

As the condition factor varies seasonally in relation to the periodicity in spawning and feeding, the annual condition factor was estimated with the following model:

$$cf = year + year*sex + month*sex + \varepsilon$$

where year, sex and month are class variables with respectively 1958-2002, 1-2 and 1-12 levels and ε is a normally distributed error term. The interactions between year*sex and between month*sex allow for a difference in the seasonal pattern in condition factor between males and females, as well as a difference in the condition factor of males and females between years.

2.3. Results

2.3.1 Mean length-at-age

2.3.1.1. Market samples

The change in length-at-age and in condition factor has been expressed as the difference from the means for age 4 and 8 between 1958 and 2002. Length-at-age in plaice and sole showed a considerable change in the late 1950s (Figure 2.5a-d). Both males and females showed similar changes. In plaice, the length-at-age of 4-year-olds increased from about –5% of the average in the late 1950s to about +5% in the mid 1970s (Figure 2.5a). Length-at-age of 8-year-old plaice did not show such an increase and varied in that period between 0% and 5% of the average (Figure 2.5c). Around 1985, length-at-age started to decrease in both 4- and 8-year-olds to about –5% of the average for 4-year-old and -8% for 8-year-old. Low values of length-at-age were observed for the strong cohorts born in 1963, 1972, 1985 and 1996, but not for that of 1981.

In sole, the length-at-age was stable at –5% of the average until the mid 1960s and then increased rapidly to +5% of the average in the 1970s and early 1980s (Figure 2.5b,d). In the second half of the 1980s, length-at-age decreased to –5% of the average in the late 1990s. Both 4 and 8 year old soles showed a similar temporal changes in length-at-age, although the increase in 8-year-olds occurred somewhat later than in 4-year-olds. No particularly low length-at-age was observed for the strong cohorts born in 1963, 1987 and 1996.

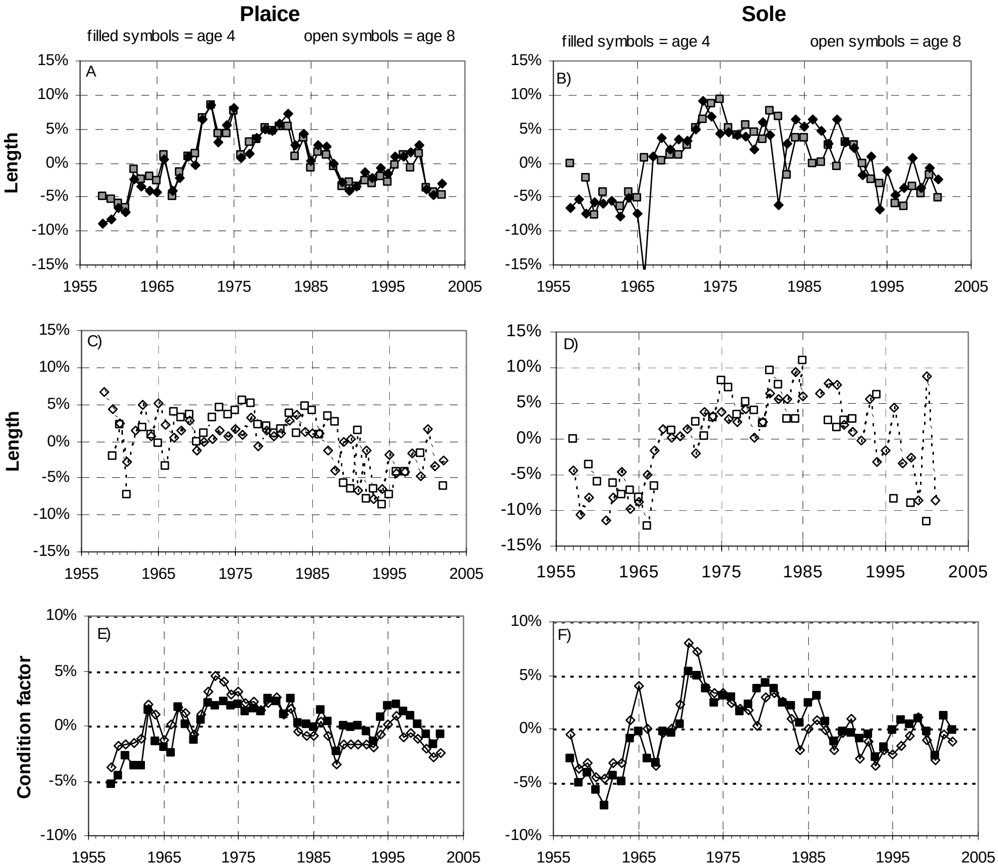

Figure 2.5. Time trends in mean length-at-age and condition factor of male (diamonds) and female (squares) plaice and sole in the Dutch market sampling data. The data are expressed as the difference (%) of the overall mean.

a) deviance in length of 4-year-old plaice during the 1st quarter spawning period (mean length of female age 4 = 31.8, male age 4 = 30.9)

b) deviance in length of 4-year-old sole in the 2nd quarter spawning period (mean length of female age 4 = 31.0, male age 4 = 27.8)

c) deviance in length of 8-year-old plaice during the 1st quarter spawning period (mean length of female age 8 = 38.5, male age 8= 35.5)

d) deviance in length of 8-year-old sole in the 2nd quarter spawning period (mean length of female age 8 = 37.7, male age 8 = 32.0)

e) deviance in condition factor of plaice (mean condition of female = 1.034, male = 0.945)

f) deviance in condition factor of sole (mean condition of female = 0.959, male = 0.863)

2.3.1.2. Back-calculated growth

The data set of length back-calculations of female plaice was analyzed in two ways. First, the annual length increment was estimated for fish between 5-15 cm, 15-25 cm and 25-35 cm. The trends in length increments and the 95% confidence limits are shown in Figure 2.6a. The length increment varied between 8–12 cm for 5-14 cm plaice, between 6–10 cm for 15-24 cm plaice and between 4-6 cm for 25-34 cm plaice. For the 5-14 and 15-24 cm plaice, a clear increase in growth occurred in the 1970s. Closer inspection of Figure 2.6 shows that the increase occurred quite suddenly in 1967-1968 for 5-14 cm plaice, in 1969-1970 for 15-24 cm plaice and in 1971 for 25-34 cm plaice, after the strong 1963 year class has passed through the particular size class. For the juvenile plaice, the fastest growth was observed in the second half of the 1970s and the first half of the 1980s. In the second half of the 1980s, growth rate appeared to have decreased. In the first half of the 1990s, growth rate recovered to slightly below the maximum rates of the 1970s. For 25-34 cm plaice, growth rates tended to show an increasing trend throughout the time period ($r2=0.12$, $n=44$, $p<0.10$ two-sided).

In the second analysis the mean length for age groups 1– 4 was estimated (Figure 2.6b). In the figure, we can clearly see the slower growth of the strong year classes that were born in 1963, 1972, 1985 and 1996. No reduced growth was apparent for the strong year class of 1981, as was the case with the analysis of length-at-age from the market samples.

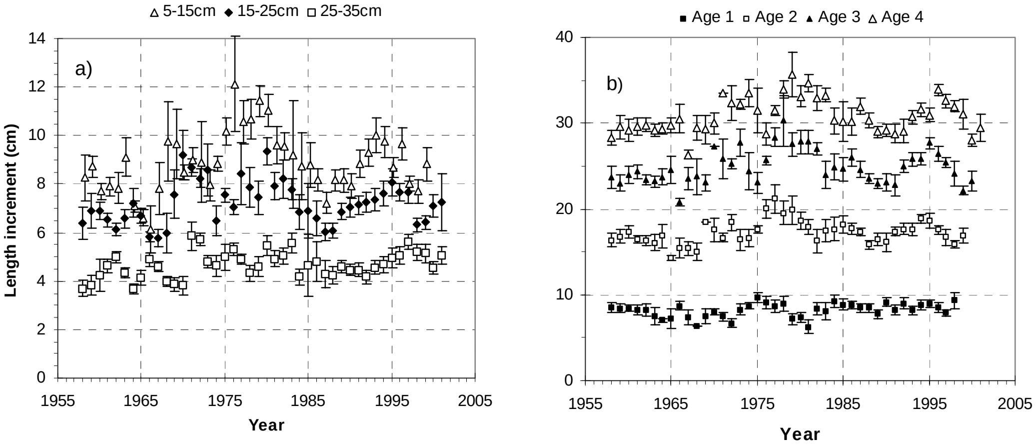

Figure 2.6. Growth estimates of female plaice between 1958 and 2001 as estimated by back-calculation of the annual rings in the otoliths. a) annual growth increment (cm) of three size classes of female plaice (5-15 cm, 15-25 cm, 25-35 cm) ; b) mean length-at-age 1 to 4.

2.3.1.3. Surveys

The mean length-at-age of plaice and sole as observed in the surveys is shown in Figure 2.7 and refer to males and females together. The consistency of the inter-annual variation in mean length-at-age for the various surveys and for market and otolith back-calculations was analysed using a statistical model that described the mean length-at-age as a function of the data source (survey) and year. The result of the analysis showed that the inter-annual variation in length-at-age was consistent across the surveys for all age groups except age group 3 in plaice and age group 4 in sole (Table 2.1).

The statistical analysis further revealed that the differences in mean length between the surveys for age groups 1-3 (plaice) and 1-2 (sole) were significant (Table 2.1). The DFS estimates were generally lower than the estimates of the SNS of the same age group, whereas the BTS-Tridens estimates were generally higher than those of the BTS-Isis or SNS. This difference can be explained by the differences in spatial coverage and by the difference in the timing of the surveys – BTS in August-September, DFS and SNS in September-October. The DFS covers the shallow waters along the coast and in the estuaries, the SNS covers slightly deeper coastal waters, whereas the BTS surveys covers both coastal and offshore waters in the southern (BTS-Isis) and central North Sea (BTS-Tridens).

Table 2.1. Percentage of the variance in length-at-age explained by year and data source (survey).

	Plaice				Sole			
	Surveys		Surveys market sampling back-calculation		Surveys		Surveys market sampling	
	year	survey	year	survey	year	survey	Year	survey
age 0			68.0%*	20.0%**				
age 1	51.1%*	8.7%**	50.2%*	10.3%**	54.1%*	12.3%**	54.1%*	12.3%**
age 2	80.7%**	11.2%**	66.5%**	20.2%**	71.0%*	11.0%**	34.4%**	58.5%**
age 3	58.1%	11.2%**	39.1%**	46.3%**	84.3%**	0.4%	43.6%**	45.9%**
age 4	76.5%*	0.8%	53.9%**	29.1%**	70.4%	1.4%	40.8%**	41.0%**

** = highly significant ($P<0.01$)
* = significant ($0.05>=P>0.01$)

For plaice, inspection of the overall patterns in Figure 2.7 suggests two cycles of an increase and subsequent decrease in length with peaks in the second half of the 1970s and the first half of the 1990s, and dips in the late 1980s and the late 1990s. This pattern is also shown in the back-calculated length of female plaice. The peaks and dips in length tended to shift to later years with increasing age of the fish. In sole, the time series of length-at-age-1 showed relatively low values in the late 1980s. In the other years since 1970, the length varied around about 20 cm. For 2- and 3-group sole, the surveys showed a decline in length to a low in the mid 1990s and a slight increase since then.

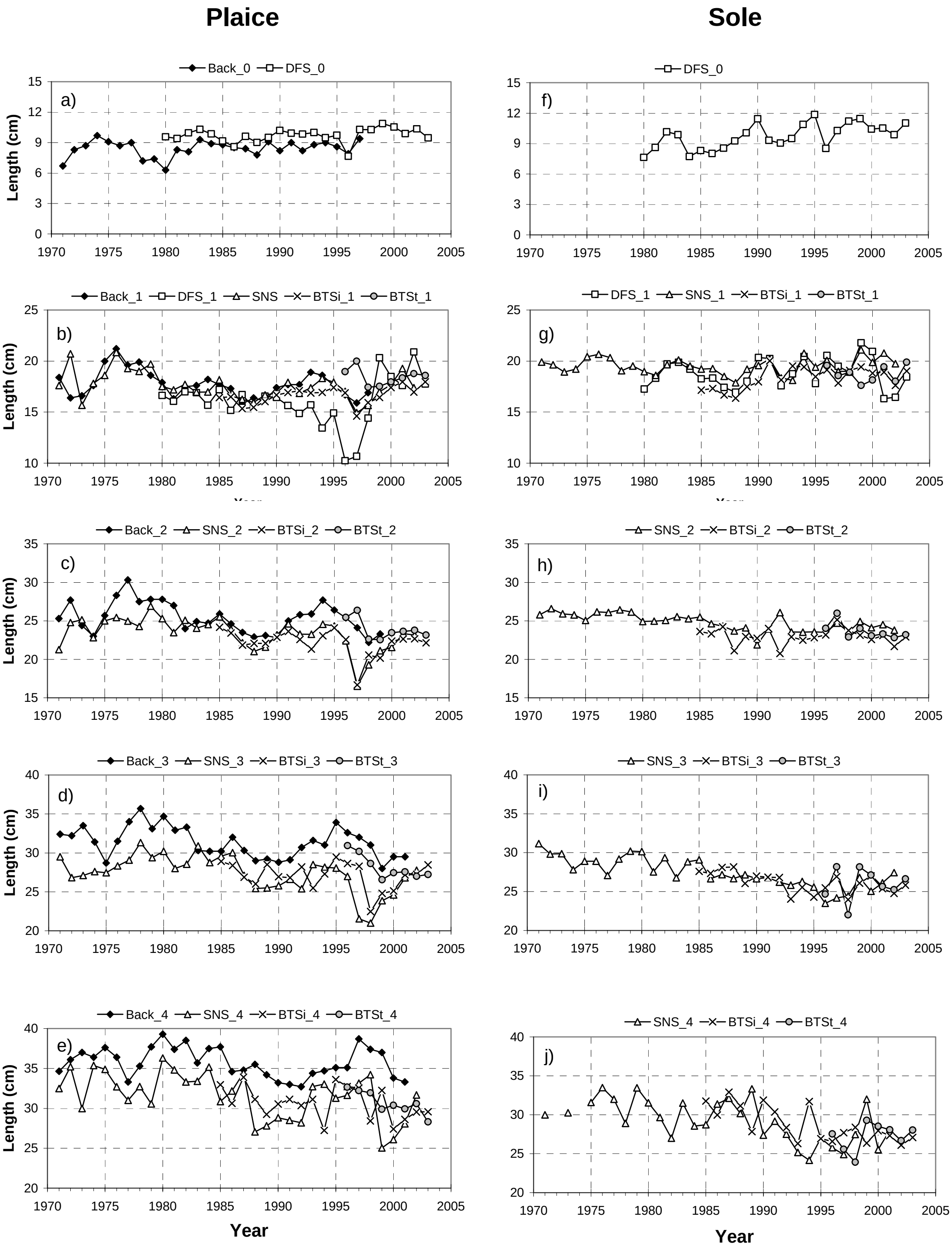

Figure 2.7. Time trends in the length-at-age of plaice and sole in the summer/autumn demersal fish surveys. For plaice, the time series of back-calculated length-at-age is shown for comparison. The back-calculated length is shown as length-at-age i-1 in year-1 to correct for the difference in the timing of the annulus formation in the otolith (start of the next year) and the timing of the survey (autumn).

2.3.1.4. Integration

The market sampling, research vessel surveys and back-calculation showed significant inter-annual variation in the length-at-age. Within age groups, the pattern was generally consistent among surveys, market sampling and back-calculation (Table 2.1). We then tested whether the observed inter-annual variation in mean length-at-age was consistent across cohorts. Table 2.2 shows that the cohort effect (YCLS) in the model: L = YCLS + A + S, where L = length in the various sampling programs, A= age and S= sampling program, was significant. Hence, a difference in length early in life translates to a difference in length later in life. The year class effects of the model are indices for growth and are plotted in Figure 2.8. The full lines, showing the 10 year moving averages, illustrate the overall pattern with an increase in growth of the year classes born between 1960 and 1970, a stable growth for the year classes born between 1970 and 1977, a decrease for the year classes born between 1978 and the mid 1980s, and a rather stable growth for the year classes born in the 1990s. In plaice, the abrupt decrease around 1980 contrasts to the rather gradual decline in sole. In plaice, the growth indices for individual year classes showed a larger inter-annual variation than in sole. Particularly low growth indices were observed for the year classes 1963, 1972, 1985, 1986, 1987, 1996 and 1997. Comparison of the overall pattern in Figure 2.8 and the trends of its components in Figures 2.5, 2.6 and 2.7 show that the overall pattern is mainly apparent in the age groups 1 to 4. The trend in length at age 0 is somewhat different suggesting an increase between 1980 and 2003.

Table 2.2. Analysis of covariance of the length-at-age 0–4 in relation to age (A), year class (YCLS) and sampling program (S: surveys DFS, SNS, BTSi, BTSt; back calculations and market sampling). Data range analysed: 1958-2003.

	Plaice					**Sole**				
	SS	**df**	**MS**	**F**	**P**	**SS**	**df**	**MS**	**F**	**P**
A	1876.87	4	469.22	7731.30	<0.001	620.19	4	155.05	2679.51	<0.001
S	26.95	6	4.49	74.01	<0.001	51.89	5	10.38	179.36	<0.001
A*S	17.14	12	1.43	23.54	<0.001	4.21	10	0.42	7.28	<0.001
YCLS	34.30	50	0.69	11.30	<0.001	19.17	50	0.38	6.63	<0.001
error	35.87	591	0.0607			27.83	481	0.0579		
total	1991.14	663				723.29	550			

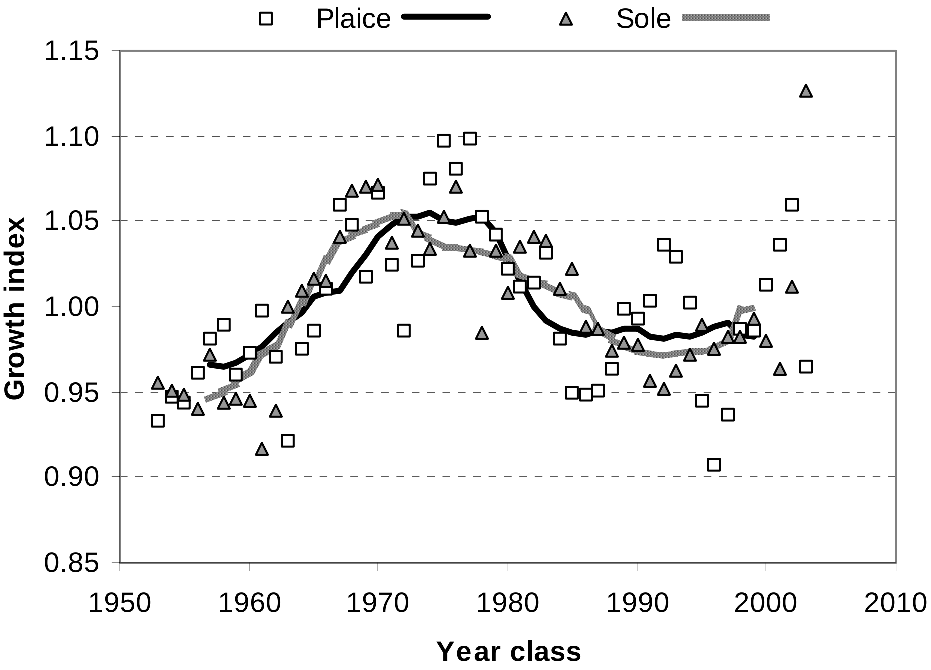

Figure 2.8. Growth index of year classes according to the analysis of the length-at-age 0-4 from surveys and market sampling in Table 2.3. The continuous lines show the 10 year moving averages.

Table 2.3. Results of the analysis of covariance of length-at-age in relation to age (A), sampling program (S: surveys DFS, SNS, BTSi, BTSt; back-calculation; market sampling), crowding (C), eutrophication (DIP) and seabed disturbance (TBB). The contribution of the covariables was tested against the full model (type3). A substantial part of the explained variance (colinearity) could not be ascribed to a single covariate.

	Plaice					Sole				
	SS	**Df**	**MS**	**F**	**P**	**SS**	**df**	**MS**	**F**	**P**
A+S+A*S	1695.5	22	77.1	1036.56	<0.001	494.4	19	26.0	370.3	<0.001
C	9.3	1	9.3	125.14	<0.001	0.7	1	0.7	10.5	<0.01
DIP	14.9	1	14.9	200.97	<0.001	3.5	1	3.5	49.2	<0.001
TBB	0.3	1	0.3	3.47	0.063	0.02	1	0.02	0.2	0.636
colinearity	30.7					45.0				
error	41.1	553	0.07			31.1	442	0.07		
total	1791.8	578				574.7	474			

Table 2.3 shows the results of the analysis of variance of the length-at-age data from the different sampling programs in relation to the environmental variables. After taking account of the effects of the sampling program and age (A+S+A*S), both the number of competitors (C) as well as the index of eutrophication (DIP) explained a significant proportion of the variability in length. Replacing the eutrophication index for phosphorus with the index for nitrogen, did not alter the result. No statistical significant effect of trawling disturbance (TBB) could be detected. However, as the environmental variables are mutually correlated, a substantial proportion of the explained variance could not be ascribed to a single variable. This proportion, indicated by the colinearity, is substantially larger than the estimated effects of the individual covariables.

2.3.2. Condition factors

The condition factors (weight-cubic length ratio) of individual fish from the market sampling program were analyzed in relation to year, month and sex. The full model explained 27% (plaice) and 31% (sole) of the variation in condition (Table 2.4). The major proportion of the variance, 24.5% in plaice and 26.9% in sole, was explained by the interaction of sex*month, reflecting the seasonal patterns in condition of males and females (Figure 2.9). Condition reached a seasonal low at the end of the spawning period (March-April in plaice and June-July in sole) and increased to a high value at the end of the feeding season in autumn. Adding the variable year explained another 2.2% (plaice) and 3.6% (sole) of the variance, indicating that the condition factor varied significantly across years (Figure 2.5e,f). The year effect differed significantly between males and females. However, the interaction only explained a minor proportion of the variance, so the difference in the trends in condition factor across years was negligible.

Figure 2.5 showed that the changes in condition reflected changes in length-at-age in both plaice and sole, although the amplitude of the changes in condition was smaller than in length-at-age. In sole, the changes in length-at-age and condition were slightly larger than in plaice.

The condition factor of 1- and 2-group plaice and sole measured during some of the SNS-surveys suggested a decrease between the early 1970s and the 1990s (Figure 2.10), but this change needs to be interpreted with caution because of the less accurate scale in the 1970s. In the 1990s a decrease in condition of 1- and 2-group plaice is apparent in all three areas along the continental coast, in contrast to sole where no such trend seems occur. This decrease does not correspond to the changes observed in the condition factor of the older plaice in the market samples (Figure 2.5e).

Table 2.4. Results of the analysis of variance in condition of plaice (A) and sole (B).

	deviance	%explained	df	MS	F	P
A) Plaice						
month*sex	793,8	24,5%	23	34,510	3835,14	<<0.001
Year	70,9	2,2%	45	1,575	175,04	<<0.001
Year*sex	7,9	0,2%	45	0,175	19,53	<<0.001
error	2364,8	73,0%	262794	0,0089		
total	3237,4		262907			
B) Sole						
month*sex	604,08	26,9%	23	26,2642	2882,5	<<0.001
Year	81,23	3,6%	45	1,8052	198,1	<<0.001
Year*sex	6,96	0,3%	45	0,1547	17,0	<<0.001
error	1552,23	69,2%	170360	0,0091		
total	2244,50		170473			

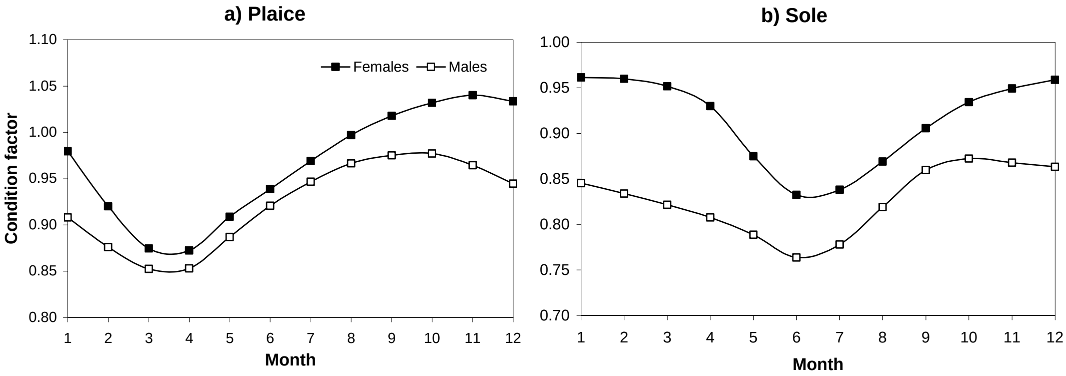

Figure 2.9. Seasonal pattern in the condition factor of male and female plaice (A) and sole (B). The seasonal pattern was estimated from the model: cf = sex*month + year +year*sex.

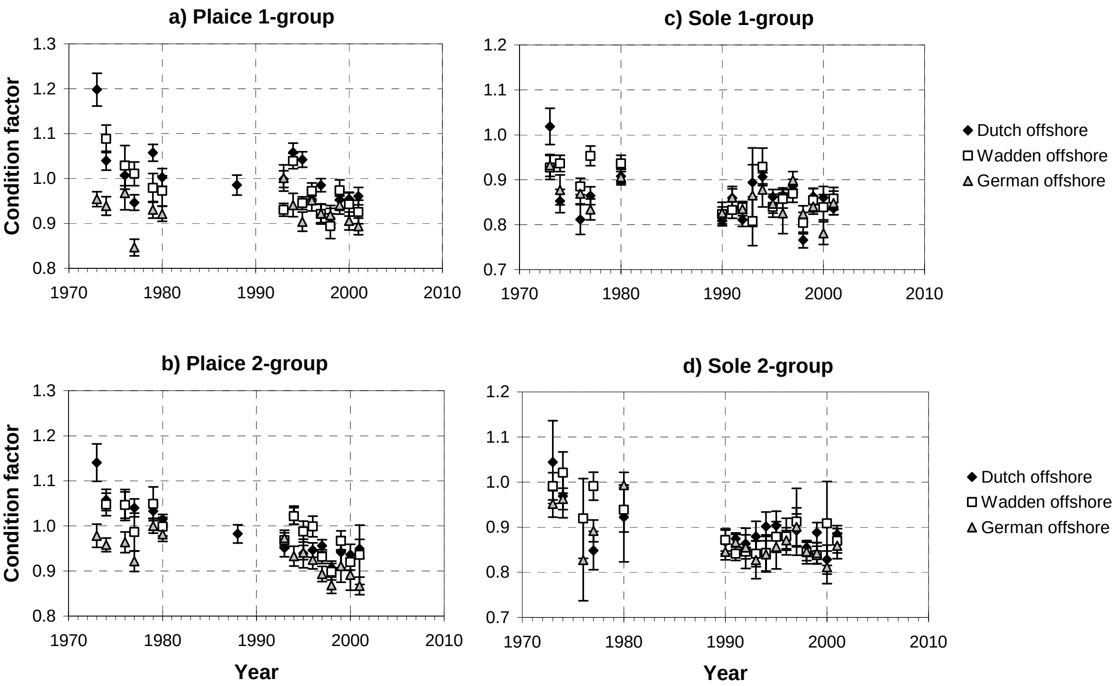

Figure 2.10. Mean condition factor of 1- and 2-year-old plaice and sole as observed in the SNS survey.

2.4. Discussion

The overall time trends in length-at-age show a common pattern for age groups up to age 4 for plaice and sole (Fig 2.8). The decrease in growth of plaice in the 1980's was however more abrupt and inter-annual variations were larger. For older plaice and sole the time trends in growth differed during the 1960s. In older sole the length-at-age of older fish increased, whereas in plaice no such increase occurred. Length-at-age of older fish decreased in the 1980s in both species. The difference between the species is likely to be related to the differences in distribution. The older age groups of sole share their habitat with the younger age groups, whereas a large proportion of the older age groups of plaice leave the southeastern North Sea during their summer feeding period (Rijnsdorp and van Beek, 1991).

The length of age groups up to age 4 started to increase from the 1965 year class onwards and reached a peak around the 1970 year class. In plaice, the peak was maintained until the end of the 1970s after which it decreased in the 1990s. In sole, length decreased steadily after the peak in the year classes born in the early 1970s. The length of age group 0 (L0) showed a different pattern of an increase in recent years in both species. The difference in the L0 as compared to the length at older age groups may be due to the differences in the length of the growing season in the first year of life, as the L0 showed a significant positive correlation with the winter temperature, which is known to affect the timing of spawning (van der Land, 1991; Rijnsdorp and Witthames, in press), as well as with the mean temperature during the 2nd and 3rd quarter. Hence the increase in L0 in recent years may be due to a combined effect of a longer growing season and an increased growth rate.

The common signal in the length-at-age across the surveys, market sampling program and back-calculations shows a striking correspondence between plaice and sole, as well as with the changes in condition factor of both species. Both growth indices must reflect changes in growth conditions in the coastal waters of the southeastern North Sea, the main distribution area of the age groups analyzed (Rijnsdorp and van Beek, 1991).

The condition factor will reflect the actual conditions for growth, whereas year class signals extracted from the mean lengths at ages 0-4 reflect the conditions integrated over a period of four years.

The southeastern North Sea has been subjected to anthropogenic influences, such as increased nutrients (DIN and DIP) and an increase in seabed disturbance through bottom trawling. Eutrophication is mainly due to the runoff of dissolved inorganic phosphate (DIP) and nitrogen (DIN) of the rivers (Hickel et al., 1993; Bot and Colijn, 1996; Laane et al., 1996; Van Raaphorts and De Jonge, 2004) and to a lesser extend to the atmospheric deposition (De Leeuw et al., 2003). Nutrient concentrations started to rise around 1965, reached a peak in the early 1980s and decreased in the 1990s (Figure 2.4a). Trends in phosphorous reflect a proportional and immediate response to decreasing riverine outputs (De Vries et al., 1998). The decrease in growth of plaice and sole is in agreement with the hypothesis of Boddeke and Hagel (1995) that the reduced input of nutrients into the coastal waters of the southeastern North Sea would result in a reduction in the productivity of the area. It is well established that an increase in nutrients results in an increase in primary production (Richardson and Heilmann, 1995; Colijn et al., 2002) and that there is an empirical relationship between primary production and fish production (Nielsen and Richardson, 1996). However, the existence of different type of food webs in which energy is transferred to higher trophic levels with varying degrees of efficiency makes it clear that the relationship between primary production and fish production is not a simple one (Richardson and Bo Pedersen, 1998). The available evidence on the transfer of nutrients into primary production and the subsequent transfers to higher trophic levels and the timing of the observed changes is summarized in Appendix 1. Although the evidence does not support the view of a simple and proportional transfer of nutrients to primary production to fish production, the lack of evidence of a decline in productivity in response to the decrease in nutrient concentrations, is not sufficient to reject the hypothesis when the paucity of empirical data is taken into account.

The increase in beam trawling since the 1960s may have caused an increase in food availability for flatfish due to the ‘production’ of damaged organisms (de Veen, 1976) or because of a shift in the benthic communities from low productivity large animals to high productivity small animals (ICES, 1988; Rijnsdorp and van Beek, 1991). In line with this hypothesis, it has been suggested that the decrease in yield of plaice since the introduction of the plaice box, a protected area in the southeastern North Sea that was established to reduce discarding of undersized plaice, was related to the reduction of the benthic productivity which could be due to the reduction in bottom trawling in the box (Pastoors et al., 2000). Considering the available evidence, this hypothesis seems unlikely to play a dominant role in explaining the observed changes in growth in plaice and sole. First, the timing of the decrease in the growth indices does not match the timing of the decrease in beam trawl fishing effort. The growth index of plaice already started to decrease around 1980, whereas the beam trawl effort remained high throughout the 1980s and 1990s. Within the plaice box, beam trawl effort decreased in two steps to 40% of the pre-closure effort, after the box was closed during the 2nd and 3rd quarter starting in 1989 and to 15% of the pre-closure effort from 1995 onwards after the box was closed year round. Beam trawl effort remained high in the areas just outside the box (Pastoors et al., 2000). Secondly, Jennings et al (2001) showed, in a first large-scale study on the trawling effects on benthic production, that in the Silver Pit area the infaunal production rose with increased trawling disturbance due to the dominance of smaller animals in disturbed communities. This increase, however, did not compensate for the loss of total production that resulted from the depletion of large individuals. They concluded that the increase in biomass and production of small infaunal invertebrates in the North Sea are attributable largely to recent increases in primary production that were driven by climate change. With only one field study available, no final conclusion of the effects of trawling on the benthic productivity can be made. The trawling effects may differ between areas in relation to seabed characteristics, natural disturbances and the availability of organic food for the benthos.

The changes in growth observed in our study may reflect changes in productivity of the southeastern North Sea that are related to large scale decadal variations in the ocean climate. There is an accumulating body of evidence that shows the importance of ocean climate for the marine ecosystems. Reid et al. (1998) suggested that the changes in phytoplankton color were related to changes in ocean climate on a timescale of decades. A stepwise change occurred circa 1987/88 that could be related to changes in the atmospheric forcing (NAO-index). Other step-wise changes in both environmental parameters and biotic parameters were reported to have occurred around 1979, 1988 and (perhaps) 1998 (Weijerman and Lindeboom, in press), although the causal pathway of these changes remains unclear. Changes in macro-benthos in coastal water of the German Bight were related to changes in ocean climate (Kroncke et al., 1998).

In conclusion, the clear and synchronous changes in growth of plaice and sole as documented in this paper, suggest changes in the benthic productivity of the southeastern North Sea. The temporal trends in growth do not match the trends in beam trawling effort, but closely match the trend in nutrient enrichment (Table 2.4) and are in broad agreement with the predictions of the ERSEM ecosystem model. However, the evidence that changes in ocean climate on a time scale of decades can affect changes in productivity and the observation that the declining trends in length-at-age in plaice occurred in several populations in the northeastern Atlantic (North Sea, English Channel, Irish Sea: Millner et al., 1996) suggests that the growth signal may be related to large-scale changes in ocean climate in conjunction with the local effect of eutrophication and perhaps beam trawling.

3. Maturity

3.1. Introduction

Environmental factors that influence growth or condition will influence the probability to mature at a certain age. While in the age-structured stock assessment models the proportion of fish that are mature is considered to be a function of age, the timing of maturation is dependent on both age and length (Rijnsdorp, 1993b; Grift et al. 2003). In North Sea plaice, females of a given age are more likely to mature with increasing lengths, while the length at which a female has a 50% probability to mature slightly decreases with increasing age (Grift et al. 2003). Factors like food availability may influence condition and thereby the probability of becoming mature. In an experiment on turbot it was found that the feeding regime influenced the probability of becoming mature in females of given age, length and condition (Bromley et al. 2000). Therefore it is to be expected that maturity at age will not be temporally and spatially constant.

The resulting variation in maturity is phenotypic: fish with a given genetic maturation schedule will mature at different ages depending on the environment the individuals experience. Hence, we say that maturity at age is a phenotypically plastic trait. The genetic program itself that determines the tendency to mature at a certain age and length (and at a certain condition and feeding regime, for that matter) may also vary spatially and temporally. The combinations of length and age with a certain probability to mature that are favoured by natural selection depend, among other things, on the mortality schedule that is experienced. In general, when adults experience relatively low mortality, late maturation is favoured. By contrast, when adult mortality is high, early maturation is favoured. Populations exploited by fisheries experience high adult mortality. The increase of fishing mortality on many stocks over the last century may have induced a genetic change in their tendency to mature (Law 2000). Indeed, analysis of the Dutch market sampling data on North Sea plaice provides evidence that the length and age at maturation have decreased over the last half of the century (Rijnsdorp, 1989) and suggests that this change is at least partly genetic (Rijnsdorp, 1993a; Grift et al. 2003). Females that tend to mature at an early age and a small length are more likely to reproduce before being fished, and pass on their genes at a higher rate than late-maturing females which may well end up in the catch before having reproduced.

Although maturity of North Sea plaice has already been extensively studied (Rijnsdorp, 1989; 1993a, 1993b; Grift et al. 2003), we present here analyses of maturity in plaice as well as sole. For plaice we explore the English market sampling data in addition to the Dutch market sampling data.

3.2. Methods

3.2.1. Dutch market-sampling program

The maturity stage (I-VII for plaice and I-VIII for sole, in the spawning period only) of the sampled fish was recorded (Table 3.1). In sole, the distinction between the maturation stages is less clear than in plaice. In particular it is uncertain whether stage 3 females could spawn (De Veen, 1970, 1976; van Beek, 1985). In line with the earlier analysis of Van Beek (1985) we considered stages >=3 to represent mature fish.

Table 3.1. Maturity stages for plaice and sole.

Stage	Plaice	Sole
I	immature: *lumen transparent, colour grey*	immature: *Ovary transparent, eggs visible under microscoop*
II	ripening: *colour orange, oocytes visible*	immature: *ovary dull and transparent, eggs visible with a pocket lens*
III	spawning: *as 2 but with a few hyaline eggs*	immature: *ovary untransparent, some eggs visible with naked eye*
IV	spawning: *ovary completely filled with hyaline eggs*	ripening: *ovary untransparent, lumen still visible*
V	spawning: *eggs partly shed*	spawning: *eggs as in IV, only completely round, lumen compressed*
VI	spent: *ovary contains a small amount of hyaline eggs*	spawning: *eggs ripe, lumen filled with ripe transparent eggs*
VII	spent: *ovary small and flabby and bloodshot, back to stage 2*	half spent: *lumen very big, filled with some eggs and fluid*
VIII		spent: *lumen big with much fluid,* *back to stage II*

In the Dutch market-sampling program samples are taken by market category. In calculating the proportion mature by age group, we took account of the length-stratified nature of our basic data. For each size-class the ratio of the number sampled over the number in the catch was calculated as a weight vector. The analysis is performed for females only, because males are often already mature before appearing in the catch. Maturity was examined during the spawning season, for plaice in the first quarter, and for sole in the second quarter.

Maturity probabilities were studied using logit analysis. Generalized linear models were fitted, employing a binominal error distribution and a logit link function. The logit link function is analogous to a logit transformation of proportions maturity. From the GLM model, the length at 50% maturity was estimated including its 95% confidence limits.

3.2.2. English market-sampling program

The English market-sampling program for plaice has been carried out since 1983 and data became available to us from CEFAS, Lowestoft (Kell and Reckham) for the years 1990-2001. The maturity stage (1-7, but defined differently than in the Dutch classification) of the sampled fish was recorded. As with the plaice in the Dutch sampling program, fish with stage 1 are considered immature and fish with maturity stage 2 or beyond are considered to be mature

In the English market-sampling program samples are not taken by market category, but by length class. Within each quarter, year, sex, length class, and age group, raising factors were calculated. The numbers of sampled fish are multiplied by the raising factors to arrive at the estimated numbers of fish caught of each sex and age and length group (within quarter and year). Subsequently, these numbers are summed over the length classes to arrive at total estimated numbers of fish caught of each sex and age group (within quarter and year). The mature and immature fish within a sex and age group are raised separately, and the estimated proportion of fish that is mature is calculated by sex and age group. Maturity in the first quarter is analyzed for females caught in the years 1990 to 2001.

3.3. Results

3.3.1. Dutch market sampling program

3.3.1.1. Female plaice

The percentage of mature female plaice in the Dutch sampling fluctuated but overall it increased over time (Figure 3.1). This increase was significant for ages 3, 4 and 5. For example, around 1960 only about 25-50% of 4-year-old females were mature. This percentage increased to 50-75% in the 1970s and 1980s. In the most recent period the percentage of 4 years olds that are mature even increased to >75%.

Female plaice are also mature at a smaller length in recent times than in the past. Figure 3.2 shows the length at which 50% of plaice of each age group is mature. This length fluctuated over time, but decreased over the whole time series, implying that females are mature at smaller lengths. For example, at the beginning of the time series the length at which 50% of 5-year-old females were mature was around 32 cm, whereas in recent times 50% of 5-year-old female plaice are mature at around 27 cm.

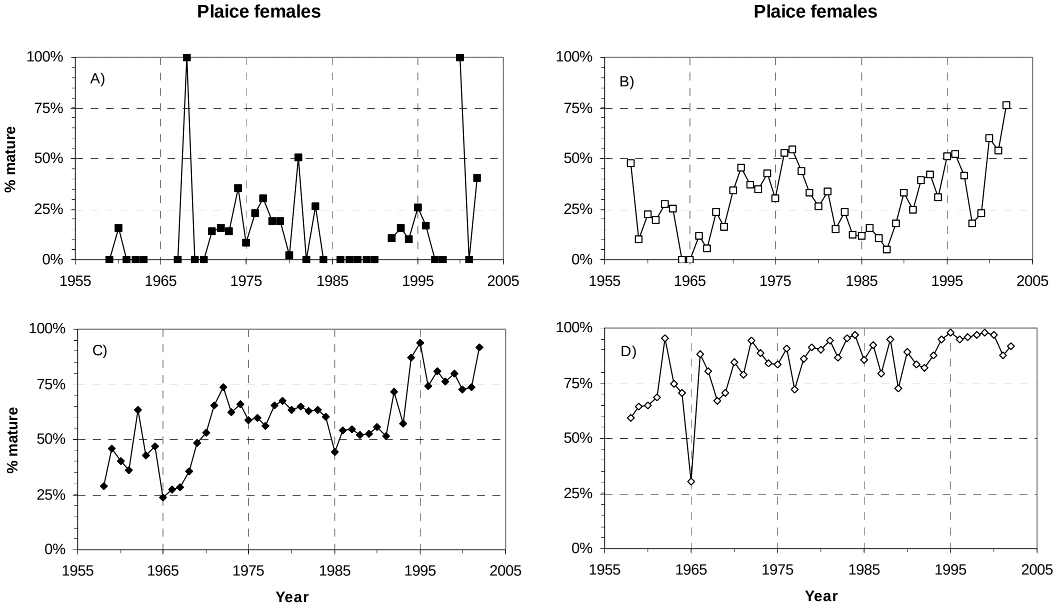

Figure 3.1. Female plaice in the Dutch sampling. Percentage mature in the first quarter versus time. A) 2-year-old females (P >0.10); B) 3-year-old females (P<0.01) ; C) 4-year-old females (P<0.01); D) 5-year-old females (P<0.01). The P-values indicate the significance level of the regression of the % maturity against year.

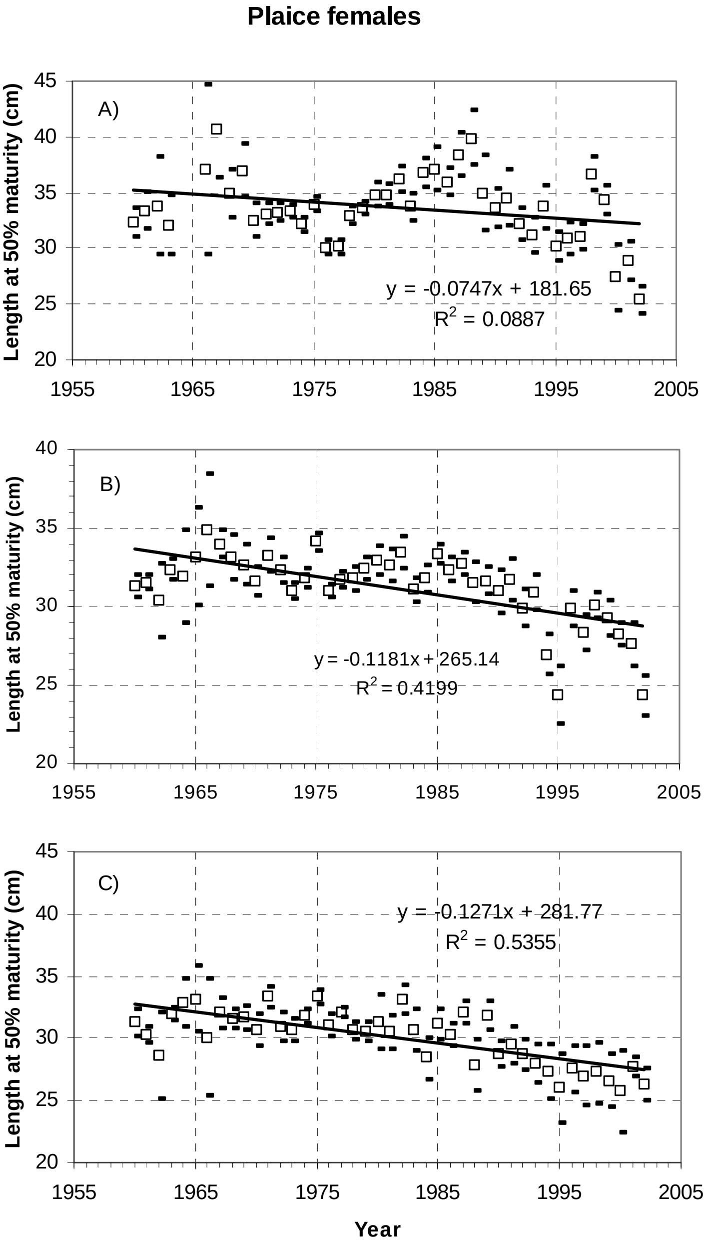

Figure 3.2. Female plaice in the Dutch sampling. The length at which 50% are mature in the first quarter versus time. A) 3-year-old females; B) 4-year-old females; C) 5-year-old females. Squares are means; dashes are 95% confidence limits.

3.3.1.2. Female sole

Female sole maturity increased over time except for age 5, where for all years more than 75% of the sole were mature (Figure 3.3) For ages 2, 3 and 4 there was a significant increase in percentage mature over time. For example, at the beginning of the time series the percentage of 3-year-old female sole that were mature was usually below 50%, whereas in recent times this is above 50% (Figure 3.3). Similar to plaice, also in female sole the length at which 50% of each age group is mature fluctuated over time and decreased over the whole time series (Figure 3.4).

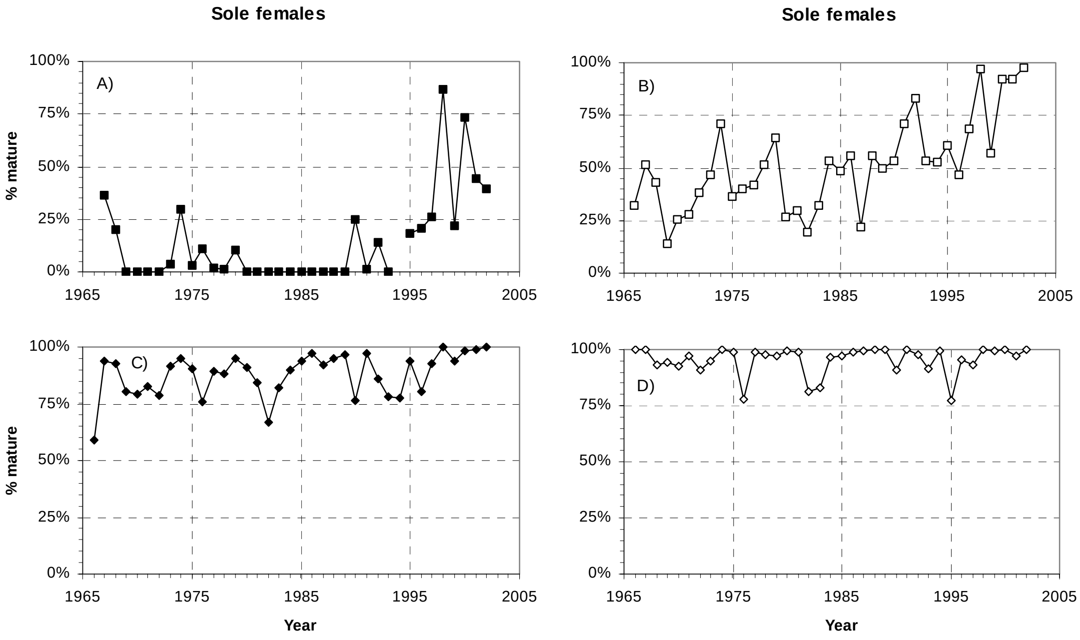

Figure 3.3. Female sole in the Dutch sampling. Percentage mature in the first quarter in the course of time. A) 2-year-old females (P<0.01); B) 3-year-old females (P<0.01); C) 4-year-old females (P<0.05); D) 5-year-old females(P>0.10). The P-values indicate the significancy level of the regression of the %maturity against year.

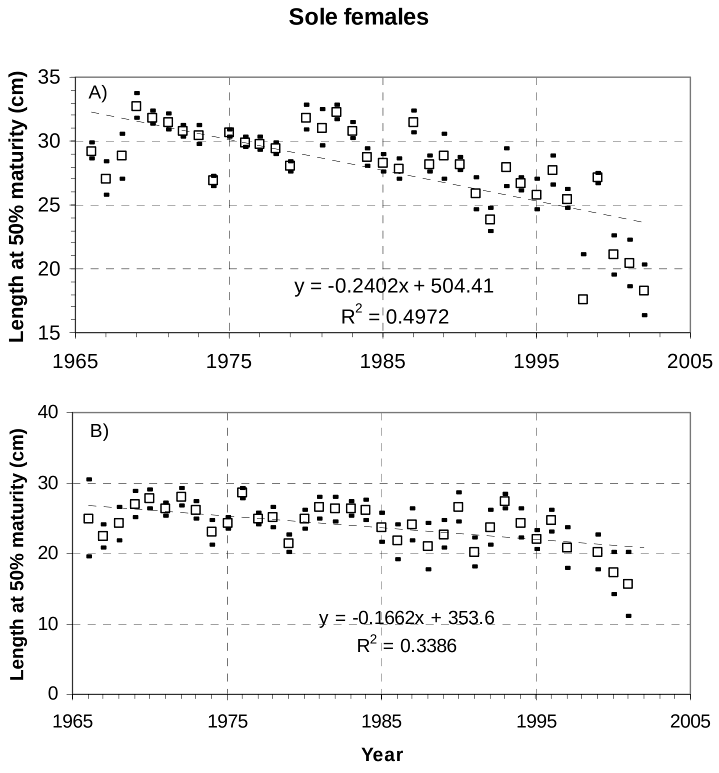

Figure 3.4. Female sole in the Dutch sampling. The length at which 50% are mature in the first quarter versus time. A) 3-year-old females; B) 4-year-old females. Squares are means; dashes are 95% confidence limits.

3.3.3. English market program

3.3.3.1. Female plaice

The time series for female plaice in the English sampling is much shorter than the Dutch time series, and no trends are seen (Figure 3.5). The percentage of female plaice that are mature was higher in the English landings than in the Dutch landings for 3 years olds as well as for 4-year-olds: at 4 years old almost all female plaice in the English sampling were mature.

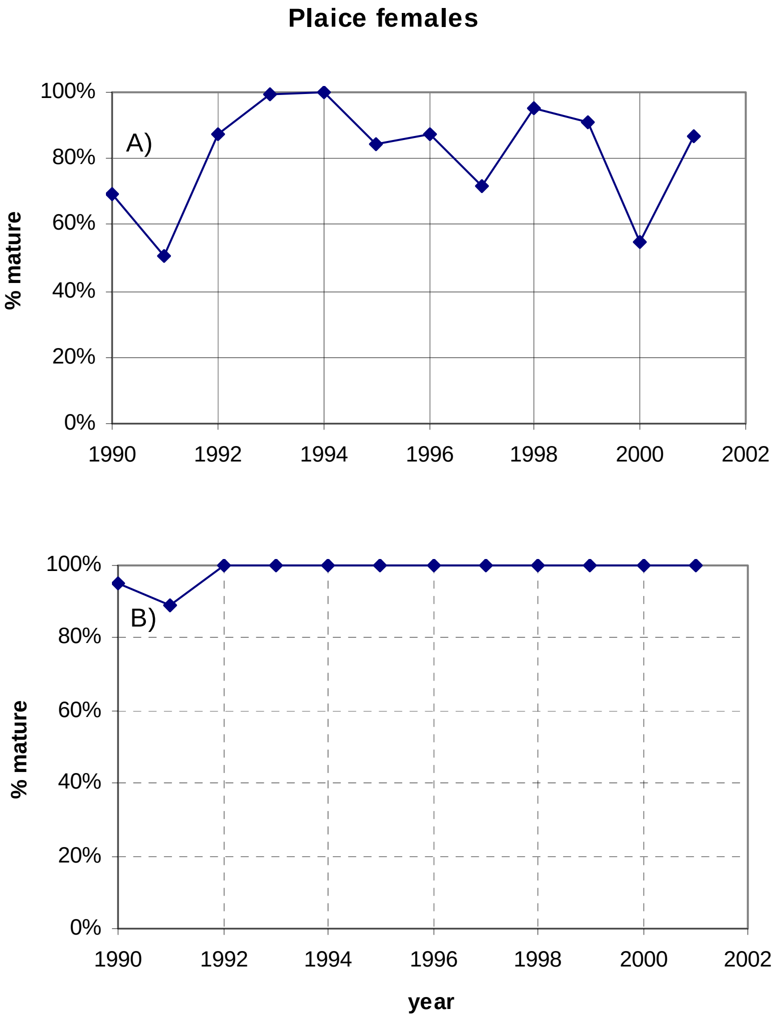

Figure 3.5. Female plaice in the English sampling. Percentage mature in the first quarter versus time. A) 3-year-old females; B) 4-year-old females.

3.4. Discussion

3.4.1. Comparison of Dutch and English results

Comparison of Figures 3.1 and 3.5 would suggest that plaice of a certain age caught by the English are more likely to be mature than those caught by the Dutch. If the difference was real, it could be caused by spatial differences in maturity, each fleet exploiting different geographic areas. However, the difference may also be an artifact caused by the maturity being defined differently by the Dutch and the English, as noted by Bromley (Bromley, in press).

Systematic differences between the Dutch and the English data, should be examined carefully before concluding that such differences found are biologically meaningful; because they may simply be the result of different sampling and measuring practices. The comprehensive study on time trends and spatial patterns in North Sea plaice maturity that we are carrying out in collaboration with our English colleagues addresses these problems. However, progress of this study has been hampered by difficulties in combining Dutch and English data due to different data formats and the differences in sampling practices.

3.4.2. Possible causes of increased maturity at age

It has been shown that maturation of plaice and sole is influenced by the growth rate during the juvenile phase (Rijnsdorp et al., 1991; Rijnsdorp, 1993a), and by temperature conditions for plaice (Rijnsdorp et al., in press). The inter-annual variations in the proportion mature fish at a specific age will reflect variations in growth rate and temperature conditions of the cohorts during the juvenile phase. Whether temperature affects the maturation in sole is not known.

Another process that may play a role is fisheries-induced adaptive (genetic) change: the high fishing mortality exerts a selection pressure through which individuals with a genetic propensity to mature at an early age and a small length are favoured and are more likely to pass on their genes to the next generation. It is well established that fishing may act as a selection force on life history traits in fish (Law, 1998; Heino and Godø, 2002). Length and age at first maturation decreased in plaice most likely as a genetic response to fishing (Rijnsdorp 1993a; Grift et al., 2003). It is expected that a decrease in the size at maturation will lead to a decrease in the growth rate of the adult fish since energy will not be allocated into somatic growth but into reproduction. Fishing can also select directly for a higher or lower growth rate as shown for cod by Sinclair et al. (2002a, 2002b). The potential effect of genetic changes in growth and reproductive parameters on the productivity of the fish stock is large (Conover, 2000; Conover and Munch, 2002).

Through a statistical method that considers the probability to mature at a given length and a given age ("probabilistic reaction norms for maturation"), Grift et al. (2003) provided strong evidence that besides the phenotypic plasticity effect of increased growth rate, a genetic shift has taken place towards smaller length and younger age at maturation. The study corroborated conclusions from earlier work on North Sea plaice (Rijnsdorp 1993) that fishing has induced adaptive change in the genetic program that directs the onset of maturation. For sole, the trend in proportion maturity at age has not yet been subjected to such a detailed analysis.

4. General discussion

The observed lower mean length-at-age and condition of North Sea plaice and sole will affect the stock assessment by a decrease in the weight per fish resulting in a lower spawning stock biomass, yield and reproducing capacity. As the growth of the fish decreased both in length and in condition, the weight of an individual decreased therefore resulting in a lower total biomass and spawning stock biomass and yield. The reduction in growth may further negatively affect the reproductive potential of the stock through interaction of size and egg production.

Although the observed decrease in growth results, as argued above, in a lower spawning stock biomass, the increased maturity compensates for that to a certain extent. Although fish remain smaller, more of them are mature. We do not know the extent of this compensation, because we did not calculate SSB on the basis of the newly perceived maturity at age. The increased maturity may have partly been caused by faster growth in the juvenile stage, whereby juveniles have reached the length at which they have a high probability to mature at an earlier age, and partly by a downward genetic shift in the length-at-age with a certain probability to mature, whereby juveniles have reached this smaller length at an earlier age.

A lower growth will extend the period that fish are discarded. Discard practices by the Dutch beam trawl fleet were described in product A3 (Van Keeken et al. 2004). In recent years a higher discard rate of plaice was observed compared to the 1970s and ‘80s, which was partly caused by a change in the spatial distribution of juvenile plaice moving to offshore areas, making the fish more available to the fishery. Slower growth rates will also affect the discard rates, since slower growing fish will experience an extended period in which they are available to the fishing gear, since they have not yet reached minimum landing size.

The inter-annual variations in the proportion mature females imply that the assumption of a constant maturation proportion is not appropriate. Variable maturities at age should be used instead to allow for an improved time series of SSB estimates. The overall increasing trend in the maturity proportions indicates that the current SSB are underestimated as compared to the historic ones.

Fishing may not only affect the quantity of eggs produced, but also the quality of eggs, as it has been convincingly shown that the probability of survival of larvae originating from eggs of first-time spawning females is lower than that of larvae originating from repeat spawners (Chambers and Trippel, 1997).

The biological reference points used in the formulation of management advice for plaice and sole are based on the relationship between the recruitment and the spawning stock biomass. The changes in growth and maturity reported are some of the necessary ingredients for a revision of the biological reference points. The variations in the proportions maturity affect the estimated SSB, whereas the changes in juvenile growth will influence the time period during which fish will be exposed to discarding. Once an updated time series of recruitment is available, that takes account of the changes in discard mortality across cohorts due to e.g. changes in juvenile growth, new values for the biological reference points can be derived. Another important question is over which time period the stock-recruitment relationship should be determined. The results of our study provides strong evidence for a decrease in the productivity of plaice and sole since the late 1980s, which would imply that the biological reference points should be based upon the stock-recruitment relationship for this recent period and not on the relationship for the full period between 1957-2002.

5. Conclusions

- Growth of juvenile plaice and sole (age group 1-4) increased for the year classes born between 1960 and 1970, growth was stable for the year classes born between 1970 and 1977, it decreased for the year classes born between 1978 and the mid 1980s, and it remained relatively stable for the year classes born in the 1990s.

- Changes in condition of plaice and sole showed the same pattern as changes in mean length-at-age.

- Age 0 plaice and sole showed a gradual increase in mean length-at-age from the 1980s onwards.

- Changes in growth of plaice and sole suggest changes in the benthic productivity of the southeast North Sea. The cause of the productivity change remains unclear. The temporal trend in growth does not match the trend in beam trawling effort, but closely match the trend in nutrient enrichment. However, changes in ocean climate may play a role as well as the decrease in growth was observed in several Atlantic stocks.

- The age and size at first maturity of plaice and sole decreased over the last four decades. These changes were at least in part related to changes in growth and probably to changes in the genetic composition of the population.

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Appendix I. Transfer of nutrients to higher trophic levels

There is an empirical positive relationship between fish production and primary production (Nielsen and Richardson, 1996). However, the existence of different type of food webs in which energy is transferred to higher trophic levels with varying efficiency makes it clear that the relationship between primary production and fish production is not a simple one (Richardson and Bo Pedersen, 1998). An increase in primary production is clearly indicated by the continuous plankton recorder survey[1] (CPR) time series that shows an increase in phytoplankton color since 1948. The main increase occurred in the mid 1980s, but in the 1960s there is no evidence for an increasing trend (Reid et al., 1998). Although it is claimed that the CPR phytoplankton color index is a proxy for primary production, it will miss the summer production in the subsurface areas that account for up to 70% of the primary production during summer (Richardson and Bo Pedersen, 1998). The time series of phytoplankton biomass near Helgoland shows changes in the phytoplankton community in 1979 and suggest that an increase occurred already in the 1960s (Figure 6c and 7 in Hickel, 1998). However, as the monitoring station is situated in a hydrodynamic variable site at the boundary of the continental coastal and North Sea water masses, Hickel concluded that “the expected effect of increasing nutrient concentrations on long-term changes of phytoplankton stocks could not be determined definitively”. The time series of phytoplankton monitoring in the Marsdiep area, the entrance of the western Wadden Sea, did not start before the 1970s and reported a doubling of the primary production between 1976 and 1978 (Cadee and Hegeman 1993, 2001; de Jonge, 1997). The production in the early 1970s corresponded to that measured in 1964 (Cadee and Hegeman, 1993). Phillipart et al (2000) showed that the phytoplankton community structure responded to the changes in TN:TP ratio from a phosphorous-controlled community between 1974-1976, to a nitrogen-controlled community between 1978-1987 and back to a phosphorous-controlled community between 1988-1994. The available empirical evidence does not clearly support the expected synchrony in timing of the increase in nutrients, starting around 1965, and the timing of the increase in primary production (at the end of the 1970s). Despite the lack of empirical data, ecosystem models, such as the ERSEM model, indicate that the primary production started to increase in the coastal waters as early as the mid 1960s (Patsch and Radach, 1998). These state of the art ecosystem models integrate the detailed knowledge on the growth physiology of plankton organisms and can be used to evaluate the impact of anthropogenic driven changes in nutrient concentrations on the primary production.

Whether the decrease in nutrients in the 1990s has resulted in a decrease in primary production has been debated heatedly. The ERSEM ecosystem model predicts that the recent decrease in nutrients will lead to a reduction in the primary production (Lenhart, 2001). Cadee et al. (2002) stated the despite the substantial decrease in phosphorous, the primary production in the Marsdiep remained at its high level (Cadee et al., 2002). This conclusion was revised when additional data became available. Philippart et al. (in prep) concluded that the primary production in the Marsdiep has decreased between 1994 and 2003 from a peak of about 1200 to 600 $mgCm^{-2}d^{-1}$. Because the primary production is also affected by the light attenuation, changes in the turbidity in the coastal waters may play an important role in the changes in primary production. Bot and Colijn (1996) showed that the suspended matter concentration in the Wadden Sea water doubled between 1980 and 1985 and then decreased to 25% of the peak level in the late 1980s, whereas the coastal North Sea water in summer showed a gradual increase in turbidity (Cadee and Hegeman, 2002). Hence, variations in time and space in the turbidity may have affected the observed changes in primary production. It is therefore questionable whether the time series of Cadee and Hegeman is representative for the productivity in the coastal waters of the southeastern North Sea.

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[1] The CPR surveys samples the phyto- and zooplankton in the surface layers of the North Atlantic by towing a continuous recording plankton sampler from merchant ships.

The relationship between the primary production and the secondary production is even more difficult to evaluate. A number of studies showed that macro benthos biomass has increased and species composition has changed towards opportunistic species (e.g. polychaetes) (Reise, 1982; Beukema and Cadee, 1988; Rachor, 1990). These changes are consistent with the expected effects of eutrophication, but may also be caused by other factors such as pollution or bottom disturbance. Beukema et al. (2002) are among the few who have been able to substantiate convincingly the relationship between primary production and biomass and production of macrobenthos. They showed that the macro benthos biomass on the Balgzand, a tidal flat in the western Wadden Sea, doubled in 1981, two years after the doubling in primary production. The biomass remained high until present with biomass in the early 2000 even the highest of the time series.

Appendix II. Addition maturity analysis

Calculation of annual spawning stock biomass (SSB) in the North Sea plaice stock assessment: taking annual variation in maturity into account.

By Sarah B. M. Kraak, Adriaan D. Rijnsdorp, Loes Bolle.

Introduction

The ICES working group WGNSSK, which is responsible for the stock assessment of North Sea plaice, is used to calculate yearly SSB as the sum of the estimated numbers at age multiplied by the estimated stock weights at age multiplied by a fixed maturity ogive (proportion mature at age). However, several studies have shown that in North Sea plaice female maturity at age is not constant over time. Maturity at age not only fluctuates, but it has increased over the past half century, meaning that in recent times females mature at younger ages than in the past (Grift *et al.*). In the present Working Document we derive an annually varying maturity ogive, which can be used to calculate SSB while taking this change into account.

The approach taken is that, for each year, female maturity at age and male maturity at age are estimated, as well as the sex ratio at age. The new yearly maturity ogive is taken to be female maturity at age times the proportion of females at that age plus male maturity at age times the proportion of males at that age. Hence, the new yearly maturity ogive is the average of female and male maturity at age weighted by the proportions females and males at age respectively.

Ideally, male and female stock weights at age of the mature component should be used in the calculation of a more realistic SSB as well, instead of a combined weight at age. However, we did not estimate these.

Methods

Male maturity
Male maturity at age was assumed to be constant over time at a level observed in a dedicated maturity survey conducted during the spawning period in 1985 and 1986 (Rijnsdorp 1989) (see text table below).

Age	1	2	3	4	5+
Male maturity	0.005	0.51	0.72	0.95	1

Female maturity
In principle, yearly female maturity at age was calculated by raising the Dutch market samples (note that over the past years the Dutch landings contributed about 45% of the total international landings of North Sea plaice). However, this will introduce a bias because at the younger ages, only the larger individuals, which are more likely to be mature, are recruited to the fishery. Therefore, the estimates of female maturity at age were corrected for variations in the size distribution by age and variations in the maturity-length relationship.

The size distribution by age was estimated from the time series of otolith back-calculation of otoliths of female plaice collected in the southern North Sea (around 53°N) during the spawning months (Rijnsdorp & Van Leeuwen, 1992; 1996). Additional samples were processed for the years since 1999. In general, otolith samples were length stratified with up to 4 females sampled of each cm-group in a year. The mean back-calculated length at each age was calculated taking account of the length distribution of the female population during the spawning period.

The maturity-length relationship was then estimated using the model:

P = Length + Length*Age + Year*Age

P is a binomial variable that indicates whether a female was immature (0) or mature (1). A logit link function and binomial error was used to model a sigmoid relationship. The slope of the maturity ogive was allowed to differ between age groups, whereas the intercept of the ogive was allowed to differ between years and ages. With the model, the proportions mature females were fitted by cm-size class and applied to the length distributions by age and year to derive the proportion mature females for each age group.

In order to smooth out yearly variation due to measurement error, for each year the average maturity at age (arcsine square root transformed) was taken from 5 years, *i.e.* the 2 years before, the year itself, and the 2 years after (Figure II.1).

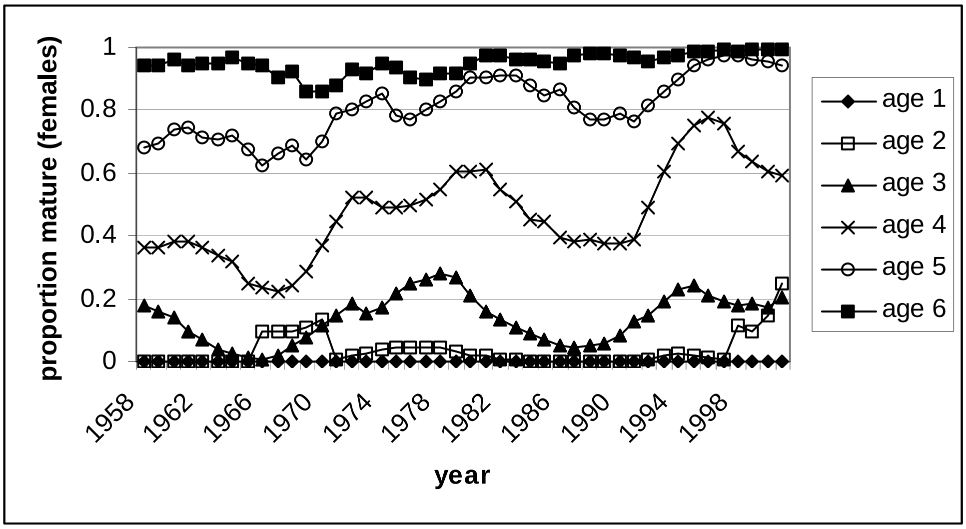

Figure II.1. Smoothed female maturity by age versus time. Smoothing was done by taking the 5-year running average.

Sex ratios

In general, fishing mortality is stronger on males than on females. Therefore, the proportion of females in the population increases with age. Fishing mortality has increased over the past half century, resulting in a higher proportion of females at older ages in recent years compared to earlier years. In this study, both these effects (the age effect and the year effect) should be accounted for.

For the older ages (>4) that are fully recruited to the fishery, the raised Dutch market sampling data were used to estimate the proportions of females at age for each year. In order to smooth out measurement error, for each year the average proportion (arcsine square root transformed) was taken from 5 years, *i.e.* the 2 years before, the year itself, and the 2 years after.

For the younger ages (<4) that are not fully recruited to the fishery, survey data were used to arrive at estimates for the proportion of females at age. The survey data were raised as usual for the tuning indices, but for the sexes separate. The three surveys are (1) SNS from 1970 onwards, (2) BTS Tridens from 1996 onwards, (3) BTS Isis from 1985 onwards. For the younger ages no year effect was assumed. For each of the younger ages, in order to smooth out measurement error, the average proportion (arcsine square root transformed) was taken from all survey-year observations.

For age 4, the proportion of females in each year was estimated as the average (arcsine square root transformed) of the estimates for age 3 and age 5.

Figure II.2 shows the resulting proportions female for the years 1960, 1970, 1980, 1990 and 2000. The Figure shows clearly that in more recent years the proportion of females in the population was higher than in the more distant past.

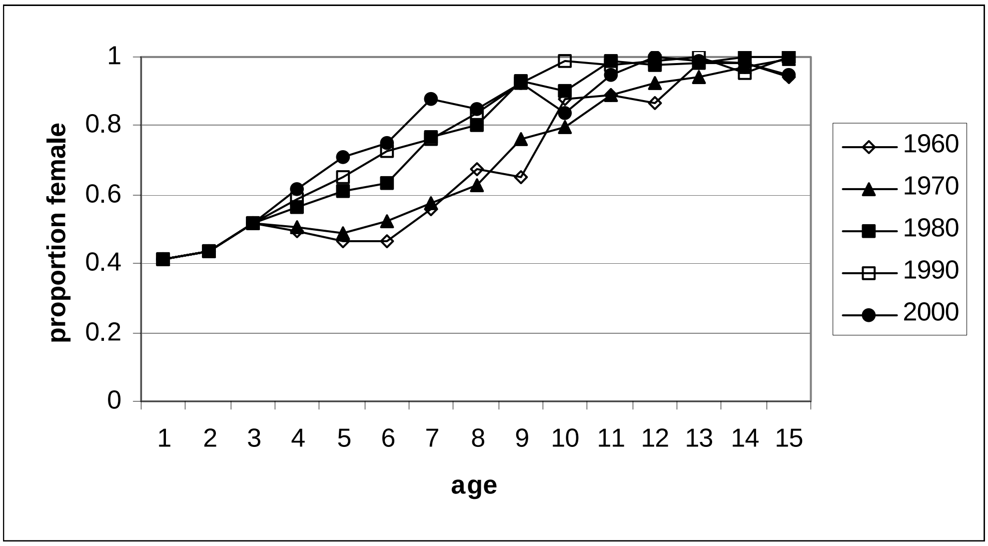

Figure II.2. Smoothed proportions female versus age in different years. For the procedure of smoothing see main text.

Results

Following the procedure outlined in the introduction, the new yearly maturity ogive is calculated as female maturity at age times the proportion of females at that age plus male maturity at age times the proportion of males at that age. The resulting combined maturity at varying over time is displayed in Figure II.3.

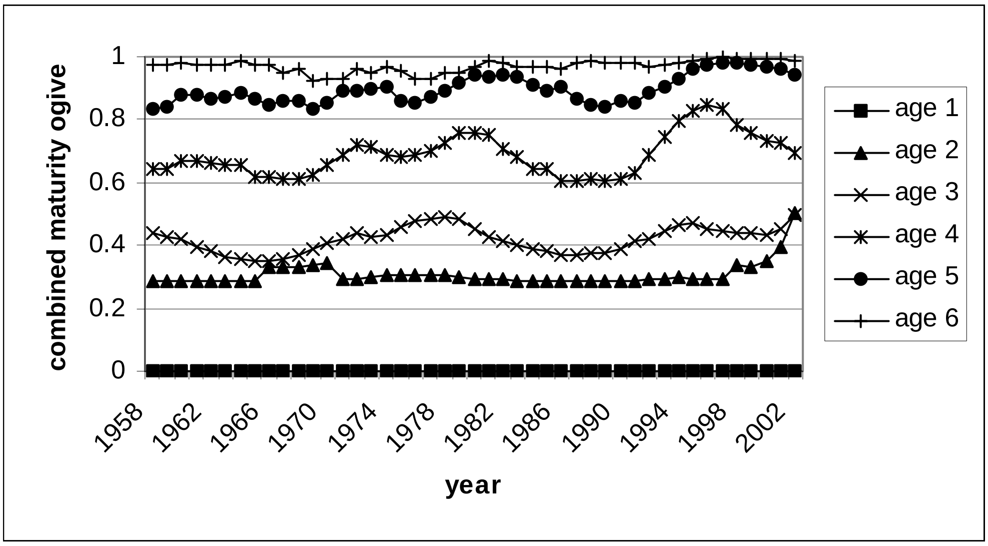

Figure II.3. Combined maturity at age versus time. For each year, maturity at age equals female maturity at age times the proportion of females at that age plus male maturity at age times the proportion of males at that age.

Discussion

When comparing Figure II.1 with Figure II.3, it can be seen that the increase in female maturity over time is partly cancelled out by the decrease in the proportion of males (Figure II.2), which have a higher maturity than females. Overall, maturity has fluctuated and slightly increased over the past half century.

Using this annually varying maturity ogive for multiplication with the estimated numbers at age and estimated stock weights at age will give more biologically realistic estimates of SSB.

However, it can be argued that, since SSB is used as a proxy for the productivity of the stock, it would be better to calculate separate female and male SSBs. This way, trends in male and female SSB can be appreciated. This is important, because the adult sex ratio, via its influence on the mating system, can have important implications for the productivity of the stock.

Separate values of SSB of the sexes could be estimated by applying the proportions of males and females as estimated in this study to the estimated numbers at age (followed by multiplication with their respective maturities at age and stock weights at age). Better still would be to conduct separate VPAs for each sex, to account for the differing fishing mortality on the sexes, and arrive at separate estimates of numbers at age by sex (followed by multiplication with their respective maturities at age and stock weights at age). This approach was taken by Kell and Bromley (2004).

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