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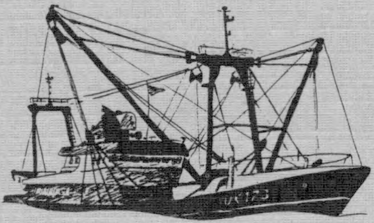
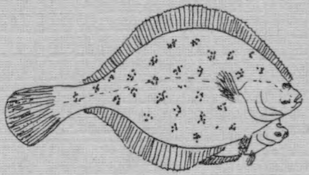
Long-term effects of fishing in North Sea plaice

Disentangling genetic and phenotypic plasticity in growth, maturation and fecundity





A.D. Rijnsdorp

R.D.

Long-term effects of fishing in North Sea plaice

Disentangling genetic and phenotypic plasticity
in growth, maturation and fecundity

(Lange-termijn effecten van de visserij op schol:
het ontwarren van genetische en fenotypische plasticiteit
in groei, het geslachtsrijp worden en eiproductie)

Academisch proefschrift

ter verkrijging van de graad van doctor
aan de Universiteit van Amsterdam
op gezag van Rector Magnificus
Prof. dr P.W.M. de Meijer
in het openbaar te verdedigen in de Aula der Universiteit
(Oude Lutherse Kerk, ingang Singel 411, hoek Spui)
op vrijdag 11 december 1992 te 12:00 uur

door

Adrianus Dirk Rijnsdorp
geboren te Rotterdam

Promotor:	Prof. dr N. Daan
Promotion committee:	Prof. dr R.J.H. Beverton Prof. dr O. Diekmann Prof. dr R.H. Drent Prof. dr H.J.Th. Goos Prof. dr M.W. Sabelis

This study was carried out at the Netherlands Institute for Fisheries Research (RIVO-DLO)

Gedrukt door: Drukkerij Haveka B.V., Alblasserdam

voor mijn ouders

CONTENTS / INHOUD

OVERVIEW

BACKGROUND

The exploitation of marine living resources by man has been a component of the predation mortality in the system since the dawn of human history. Due to the exponential growth of the human population and to the development of a variety of powerful tools, the relative importance of this component of the predation pressure has increased considerably during the last few centuries. The industrial revolution of the 19th century triggered a substantial growth of the fishing intensity expressed both in the number of vessels and in their fishing power and the increase in the level of exploitation has caused a great concern (Cushing 1988). Already at the start of the 20th century, the catch rates of for instance plaice had dropped and questions were raised about the causes of this decline and the necessary management measures to be taken (Garstang 1909; Heincke 1913; Masterman 1914; Wimpenny 1953). These questions have dominated fisheries science ever since. In order to solve these questions, it was acknowledged that first of all a sound knowledge of the biology of the different exploited species was required and as a consequence, a huge body of knowledge on the ecology of commercial fish species has accumulated, particularly since the 1950s. Mathematical models of the population dynamics of exploited populations were developed that have become the common tools to assess the status of the stocks and to provide the biological basis of management advice (Beverton & Holt 1957; Pitcher & Hart 1982; Gulland 1983). In general, management issues focus on short term objectives and most fisheries biologist are biased towards evaluation of the short term effects of exploitation.

Long term effects, however, can easily be envisaged, not only through changes in the ecosystem in response to fishing, but also within the biological characteristics of individual species, such as somatic growth, maturation and reproduction. The latter, indeed, is well documented for a variety of exploited fish species (e.g. Hempel 1978; Bowering & Brodie 1991). Most studies documented the observed changes in biological parameters, but did not attempt to evaluate quantitatively which factors were involved in the causation of the observed changes. Three types of explanations have been postulated; changes in biological parameters are due to: 1 - a change in food availability, which may be related to the relaxation of density-dependence due to a reduction in population biomass by fishing (Nikolskii 1969; Rothschild 1986; Weatherley & Gill 1987), or to other anthropogenic influences such as eutrophication, pollution or disturbance of the sea bed by fishing gear (de Veen 1976, 1978; Rijnsdorp & van Beek 1991) ; 2 - a change in abiotic conditions (temperature); 3 - a genetical selection by the fisheries (Ricker 1981; Nelson & Soulé 1987).

A major difficulty in the interpretation of changes in biological parameters is that somatic growth, maturation and reproduction are interdependent (see below). A change in growth rate will influence maturation and reproduction and vice versa. A study of changes in growth should address the question of density-dependence by taking account of the variability in abundance but also of the distribution patterns of different age- or size groups (Rijnsdorp & van Beek 1991). Only those age groups that live in the same area can potentially compete over common food resources. Finally, the evaluation of observed changes is hampered by the fact that no information on the changes in food availability are available.

The possible genetical effects of long term exploitation had already been raised in the 1950s (see review in Nelson & Soulé 1987), but has only recently got full attention after Ricker and coworkers showed in the late 1970s that this was an important factor in Pacific salmon fisheries. The prerequisite that life history parameters have a genetical basis was shown in various studies (see Roff 1991). Further steps ahead were made in the USA by Ryman & Utter (1987) who tried to bridge the fields of population genetics and fisheries management. In Europe, Law & Grey (1989), intrigued by the reduction in age at first maturity in Arcto-Norwegian cod, showed that this change could be explained by genetical selection through age-selected harvesting. They further showed that genetical selection for early maturation resulted in a reduction in the long-term equilibrium yield and that harvesting strategies could be envisaged that maximized the long term yield, taking account of genetical selection. In the case of Arcto-Norwegian cod, however, it is not yet clear whether the change in maturation is due to genetical selection, since it may equally be a compensatory response to the reduced stock size (Jørgensen 1990). In the summer of 1991 Law and Stokes organised a Symposium on the Exploitation of Evolving Populations in order to bring together the various scientific disciplines dealing with this kind of problems, and to review the present state of the art.

The genetical selection of growth and reproductive parameters due to exploitation is related to the notion that reproductive parameters are adapted to the environment through natural selection. This general concept offers a very fruitful approach to interpret the variability in ecological characteristics both between species as well as between individuals of the same species and nowadays dominates ecological theory (Lack 1966; Krebs & Davies 1982; Sober 1984). Comparative studies on reproductive strategies in fish have for instance shown that inter-specific differences in the onset of maturation can be related to differences between the mortality rates in the juvenile and the adult phase (Roff 1982; Stearns & Crandall 1984; Stearns & Koella 1986).

Plaice is one of the North Sea fish species that has been exploited for several centuries. Thanks to its major economic importance it has also been one of the target species of fisheries research (Wimpenny 1953; Bannister 1978). Because the rate of growth and maturation and the level of reproductive investment influence the productivity of a fish stock, data on these parameters have been collected since the late 19th century. Therefore, this species is a good candidate for studies of the potential effects of long term exploitation on reproductive characteristics. However, despite the wealth of information available on changes in these parameters, the interpretation is not easy and before genetic questions can be addressed their interactions in the processes that govern growth and reproduction must be resolved

SURPLUS PRODUCTION AND THE ENERGETICS OF GROWTH AND REPRODUCTION

Somatic growth, maturation and reproduction are intricately linked within the energy budget of an animal (Nikolskii 1969; Jones 1977; Tytler & Calow 1985). In annually reproducing species such as plaice, somatic growth and reproduction will be interdependent since the energy allocated into reproduction is no longer available for somatic growth. Similarly, somatic growth affects the amount of energy that is available for reproduction. The total amount of energy available for somatic growth and reproduction will be called surplus production (Ware 1980; Roff 1983) and the basic concept is adopted here that environmental conditions (particularly food availability and temperature) will affect the annual surplus production of a fish and consequently also the somatic growth and the process of maturation and reproduction. The definition of surplus production used here should not be confused with a similar term used for the increase in population biomass discounting mortality in stock production models.

PHENOTYPIC VERSUS GENOTYPIC PLASTICITY

In studying changes in growth and reproductive characteristics one is faced with the major problem of how to disentangle phenotypic and genetic effects. The phenotype is the result of the interaction between the genotype and the environment during the ontogeny of the individual. Life history parameters generally show a large phenotypic variability, but heritability estimates are rather low (Roff 1991). Therefore, observed phenotypic variability must be largely due to environmental variability. Interpretation of changes in growth and reproduction is further complicated because environmental factors may themselves have changed over time.

The relation between genotype and phenotype under various environments is given by the norm of reaction. This norm of reaction is a function that translates the genotype into a phenotype given certain environmental conditions (Stearns 1982; Stearns & Koella 1986). In order to disentangle phenotypic and genetical effects, the phenotypic response of reproduction parameters to variability in growth rate should be established. The obvious approach to answer this question would be to determine experimentally the onset of sexual maturity and reproductive investment at different levels of food availability and temperature. However, apart from the fact that the relatively large size and high age at first maturity (33 cm and 4-5 years) makes this species less suitable for experimental work, food availability as well as activity levels as they apply to the fish in the sea, can hardly be mimicked in aquaria. Therefore, an alternative approach has been adopted in which the observed variability in reproductive parameters and growth, both at the level of individual fish and on the population level, is used to derive hypotheses about the norms of reaction for maturation and reproductive investment in relation to differences in growth.

The observed changes in the onset of maturation and reproductive investment at the population level are compared to the expected changes given the estimated individual phenotypic plasticity in response to different growth rates. If the observed changes in maturation and reproduction corresponds to the derived reaction norm, they are likely related to the observed changes in growth, whereas a discrepancy between the observed changes and the reaction norm would support the hypothesis for a genetical change.

This thesis is organised in four parts. Part I presents the basic concepts of the allocation of surplus production over reproduction and somatic growth and examines the potential selective effects of fishing at the current level. Part II describes the changes in somatic growth, maturation and fecundity that have occurred since the beginning of this century. Part III studies the phenotypic plasticity in maturation and in fecundity, and derives the norm of reaction in maturation and reproduction in relation to growth rate. Part IV provides a synthesis.

PART - I: CONCEPTS

CHAPTER 1. Male and female plaice show distinct surplus production allocation patterns In the juvenile phase the two sexes are characterized by similar rates of surplus production. However, beyond a length of about 30 cm the rate of surplus production levels off in males, whereas a steady increase is apparent in females. During the spawning period males and females loose on average about 44% and 25% of their body energy reserves, respectively. Somatic growth of males is smaller than that of females firstly because they become mature 1-2 years earlier and secondly because their surplus production does not increase any further once they have reached a size of about 30 cm at the age of IV years.

CHAPTER 2 presents an analysis of the selective effects of fishing on length at first maturity and reproductive investment. Due to fishing, the mortality rate of plaice increases from about 10% to about 40% per year, once they have reach a size of 18 cm. Males suffer a higher mortality than females due to behavioural differences during the spawning period. The level of fishing mortality during the first half of this century is not certain, but based on the stable yield it is argued that the fisheries probably were quite stable and that the plaice stock was in equilibrium at a mortality between 30 and 50% per year. The mortality due to fishing is not evenly distributed over age. The younger age groups are distributed over the shallow inshore waters and are characterized by a low fishing mortality. With increasing size and age the plaice disperse over the deeper offshore grounds and experience a higher fishing mortality. The fishing mortality on the oldest age groups is again slightly lower, because these fish are distributed outside the main fishing area during at least part of the year. In a simulation model the fitness of various reproductive strategies, in terms of combinations of length at first maturity and reproductive investment, was estimated for the present level of exploitation by employing a simple allocation model of surplus energy over reproduction and somatic growth. This model describes the cost of reproduction in terms of a decelerated somatic growth and reduced future reproduction. It is shown that the present rate of exploitation acts as a selection pressure for a decrease in length at first maturity and an increase in reproductive investment.

PART II: CHANGES IN SOMATIC GROWTH, MATURATION AND REPRODUCTION SINCE 1900

CHAPTER 3 deals with changes in somatic growth that have occurred since 1930 as deduced from the growth patterns in otoliths. It is shown that both density-dependent and density-independent factors are responsible for the observed changes. During the second world war, when fishing activities were substantially reduced, the stock biomass tripled and concurrently somatic growth decreased. This was particularly pronounced in the larger size-classes, whereas the smaller size classes were hardly affected. Additional support for density-dependent growth is provided by the reduction in growth of the strong year class born in 1963, which was about three times more abundant than an average year class and led to a temporary increase in stock biomass. In addition, there have been changes in growth which could not be related to changes in density. After the second world war there is a generally increasing trend in growth rate. The increase is first seen within the smaller size classes in the 1950s followed by a similar increase in the intermediate size classes up to 30 cm in the 1960s. No change in growth is apparent in size classes > 30 cm compared to the pre-war situation. The post-war increase in growth rate cannot be explained by density effects, temperature or by a genetical selection for fast growing plaice and is likely to be related to anthropogenic effects such as eutrophication, pollution or the effects of bottom trawling, although the true cause remains uncertain.

CHAPTER 4 examines the onset of sexual maturity based on samples from commercial catches as well as research vessel programmes. Two surveys were carried out in January - February 1985 and 1986 to investigate whether mature and immature plaice showed differences in spatial distribution that could bias estimates of the onset of sexual maturity based on market samples. The estimated maturity - length and maturity - age relations from survey data and from market-sampling data were rather small for female plaice. However, male plaice mature at a length that is well below the minimum landing size and therefore surveys are required to obtain information that is representative for the total population. At present 50% of the males in the southern North Sea are sexually mature at 20 cm and age II; the females at 33 cm and age IV. The length and age at first maturity is slightly higher in the western and eastern North Sea. Since the beginning of this century, the length and age at first maturity have decreased in both males and females by about 35% and 13% (length) and 50% and 35% (age), respectively. This chapter further presents estimates of the average spawning duration of male and female and shows that plaice do not feed during spawning.

CHAPTER 5 summarizes information on changes in fecundity and ovary weight since the beginning of the century. There are data available for three periods: 1900-1910, 1947-1949 and 1979-1985. The interpretation, however, is complicated because significant differences in fecundity - size relationships were observed between areas and years in the most recent period. Nevertheless, fecundity appears to have changed since the first half of this century. Present fecundity of a standardized 30-cm plaice was about 30-100% higher compared to the earlier periods depending on the area. Fecundity of larger fish (50 cm) in recent years was similar to that in the beginning of this century, but values just after the second world war were 30-60% lower. In contrast to the substantial reduction in fecundity in the period 1947-1949, the ovary weights showed a much smaller decrease, which suggests that there has not been a major change in total energy allocated to reproduction, but rather a change in egg sizes.

PART III: PHENOTYPIC PLASTICITY IN MATURATION AND REPRODUCTION

CHAPTER 6 explores the relation between juvenile growth and the onset of sexual maturity in females based on maturity - length relations for individual year classes sampled between 1958-1990 in three areas in the North Sea and on the analysis of individual growth curves back-calculated from otoliths of both mature and immature fish. Whether a female becomes mature depends on the length reached within a certain year, but also on the growth rate in the three preceding years. A high growth rate in the penultimate year (year -1) will positively affect the length at which 50% of the females become mature. A high growth rate in the two earlier years has a negative effect on the length at maturation, in particular the growth rate three years before sampling (year -3). These effects were supported by the differences in length at first maturity of individual cohorts and by latitudinal differences in the length at first maturity. The latitudinal differences, however, could not be fully explained by differences in growth and it is suggested that these may also be related to the differences in the temperature conditions on the nursery grounds. A model of the juvenile-adult transition process is proposed that provides a consistent interpretation of the observations. The model postulates a maturation envelope in the length-age space that encompasses the maturation points of individual females. The length at first maturity increases with increasing growth rate, although the length is also affected by the actual curvature of the juvenile growth curve.

CHAPTER 7 describes the annual somatic growth and reproduction cycle and explores the phenotypic plasticity in reproductive investment in relation to somatic growth in the penultimate year. In the annual cycle, the periods of somatic growth and reproduction are quite distinct. Somatic growth peaks between March and October, main ovary growth takes place between October and January and the fish spawn between January and March. About 50% of the ovary growth is estimated to be subsidized from body reserves accumulated during the growing period. Size-specific fecundity is highly variable but was not or only weakly correlated with growth in the preceding growing season. The only indication that there is a growth effect on reproductive investment is given by the significant correlation between somatic growth and pre-spawning condition factor, which can be considered a proxy for the available resources for reproduction. Somatic growth estimated from the width of the last full annulus laid down in the otolith of individual fish was not significantly correlated with size-specific fecundity, nor with ovary weight or pre-spawning condition factor. The results are summarized in a 'physiological' model of the energy allocation over reproduction and somatic growth. In this model, the incoming surplus energy is channelled into somatic growth if body condition exceeds a threshold value and into body reserves if the body condition is below the threshold value. The threshold value increases from a post-spawning low to a pre-spawning high during the growing period. Implications of this model are that improving conditions for surplus production will primarily enhance somatic growth. Although the net result will be a higher total fecundity because of the larger body size attained, size-specific reproductive investment will remain constant.

PART IV: SYNTHESIS

CHAPTER 8 attempts to synthesize the observed changes in maturation and reproductive output in the light of a possible genetical selection by the fisheries and given the results of the study of phenotypic plasticity in reproductive parameters. Current exploitation acts as a selection pressure for a decrease in the length at first maturity and an increase in reproductive investment. Reproductive investment has apparently been stable since the beginning of this century and it is concluded that an increase in reproductive investment may have been restricted by some morphological constraint or a mortality constraint related to reproduction. The observed decrease in L_{mat} was 4 cm in age group V and VI. Of this decrease 1 cm could be ascribed to the observed increase in growth rate and about 1 cm to the difference in temperature, suggesting that 2 cm could be due to genetical selection of fishing. However, the observed decrease in L_{mat}, corrected for the effect of growth and temperature, is higher than predicted from the selection differential exerted by the present fisheries. This discrepancy may be due to the rather crude quantitative analysis of the selective effects of fishing and the temperature effect on maturation. These uncertainties prevents a final conclusion on the genetical effect. Nevertheless, the qualitative agreement between the observed and predicted change indicates that genetical selection may be exerted. Exploration of the potential genetical effects of a continuation of the current exploitation on the evolution of the equilibrium yield and spawning stock biomass per recruit suggests that the current exploitation pattern only marginally affect the long term equilibrium yield.

Part I

CONCEPTS

Stellingen behorend bij het proefschrift Long-term effects of fishing in North Sea plaice
van A.D. Rijnsdorp, Universiteit van Amsterdam, 11 december 1992

1 - Het maximale niveau van energie acquisitie van schol is de uitkomst van een evolutionair optimalisatie proces waarbij de voordelen van een verhoogde voortplantings-inspanning zijn afgewogen tegen de nadelen van een verhoogde sterfte.

2 - De waarneming dat bij toenemende populatiedichtheid scholvrouwtjes minder maar grotere eieren produceren, kan worden verklaard uit een aanpassing aan de afweging tussen de kans voor de larven in open zee de schaars voorkomende rijke voedselgebieden te treffen, en de kans dat de post-larvale stadia zich succesvol in de kinderkamers kunnen vestigen.

3 - De groei van jonge schol in de Noordzee is voedsel gelimiteerd. *contra van der Veer, Pihl and Bergman 1990. Mar. Ecol. Prog. Ser. 64: 1-12.*

4 - Een reductie in de visserij-inspanning leidt niet noodzakelijk tot een evenredige vermindering van de visserijsterfte.

5 - Het Nederlandse visserij-onderzoek is onvoldoende ingebed in de academische wereld.

6 - De tendens naar een meer marktgericht visserij-onderzoek vormt een bedreiging voor lange-termijn onderzoek naar de oorzaken van veranderingen in het mariene oecosysteem.

7 - De discussie over het terugdringen van de milieueffecten van de boomkorvisserij richt zich op een beperking van de bodemverstoring en gaat voorbij aan de vervuiling ten gevolge van het hoge verbruik van fossiele brandstoffen. Het terugdringen van beide kan beter gerealiseerd worden door een vermindering van de visserij-inspanning dan door de nu voorgestelde instelling van een gesloten gebied.

8 - Het concept van natuurreservaten verbonden door verbindingszones zoals gehanteerd in het natuurbeleidsplan is niet van toepassing op het mariene oecosysteem.

9 - Vogelaars die zeldzame dwaalgasten met eigen ogen willen zien vervuilen het milieu.

Chapter 1

Sexual dimorphism in the energetics of reproduction and growth of North Sea plaice, *Pleuronectes platessa* L.

Rijnsdorp, A.D. & B. Ibelings. 1989. Sexual dimorphism in the energetics of reproduction and growth of North Sea plaice, *Pleuronectes platessa* L. - J. Fish Biol.35: 401-415

ABSTRACT. The chemical composition and energy content of North Sea plaice during the spawning period were examined in mature males and females and in immature fish, to study differences in the allocation of energy over reproduction and somatic growth between the sexes.

At the beginning of the spawning period mature males and females had equal dry weights of lipid that were 70% higher than in immatures. Protein content in mature males was equal to that in immatures but was 23% higher in mature females. Immature males and females did not differ in chemical composition. At the end of the spawning period, spent and immature fish had equal lipid contents, but protein content in spent females was 10% lower than in spent males, and 17% lower than in immatures. Gross energy content of the body decreased by 44% (65.2 to 36.3 $J.cm^{-3}$) in mature females, by 27% (55.0 to 40.0 $J.cm^{-3}$) in mature males and 9% (48.7 to 44.2 $J.cm^{-3}$) in immatures. Energy content of plaice eggs was estimated at 6.60 kJ per 1000 eggs.

Reproductive investment was estimated from the energy loss during the spawning period and included the energy of sex products and spawning metabolism. Somatic growth comprised the annual increase in energy content of fish. The pattern of energy allocation over reproduction and somatic growth differed between males and females. Males started their reproduction at a smaller length and a younger age and allocated a higher proportion of the available energy into reproduction than females. Available energy resources for somatic growth and reproduction (surplus production) were equal between the sexes up to a length of about 30 cm. Beyond this length male surplus production levelled off whereas female surplus production continued to increase. The differences in surplus production and the allocation patterns are discussed.

For female plaice the energy allocated into egg production was estimated as between 48 and 64% of the total amount of energy lost during spawning. The remaining energy is used for metabolism during the spawning period, yielding an estimate of the metabolic rate of mature females of between 6.4 and 9.1 kJ day^{-1}. A maximum estimate of the metabolic rate of mature males was 7.4 kJ day^{-1}.

INTRODUCTION

Male and female flatfish often show differences in both growth and the onset of reproductive activity. Males start reproducing at a younger age and ultimately reach a smaller length than females. Although differences in growth between sexes of flatfish have been explained by differences in reproductive strategy (the earlier maturation of males causes a drain of resources from body growth into reproduction; Roff 1982), a quantitative comparison of the allocation of resources over reproduction and growth of male and female flatfish is lacking. Comparison of the allocation of resources over reproduction and growth of several other fish species shows that the sexes differ not only in the pattern of allocation but also in the amount of energy accumulated during the year (Craig 1977; Diana & McKay 1979; Foltz & Norden 1977).

Energy allocation patterns have been viewed as adaptive traits moulded by natural selection (Calow 1985). The allocation pattern influences the amount of resources invested into reproduction and therefore affects the fitness of a particular trait. Mortality on the one hand, and the available resources on the other hand, are the crucial environmental parameters with which the animal has to cope. A high mortality risk is supposed to reduce the age at first maturity and to increase the relative amount of energy channelled into reproduction. Abundant resources leading to high surplus energy, defined as the sum of the energy available for reproduction and somatic growth (Ware 1982), will favour a strategy with delayed maturation or a reduced investment in reproduction or both (Roff 1982; Stearns & Crandall 1984; Calow 1985). Maximization of surplus energy is expected to occur, if no penalty in the form of increased mortality risk is imposed (Ware 1982; Calow 1985).

This paper presents a quantitative analysis of the allocation of energy over reproduction and growth of both male and female North Sea plaice on an annual basis. North Sea plaice spawns from the end of December to the beginning of April (Harding *et al.* 1978). The average time during which individual plaice are in spawning condition is at least 11 weeks for males and 5 weeks for females, and during the spawning period feeding is reduced in immatures and almost stops in mature fish (Chapter 4). Therefore, the energy required for metabolism and production of eggs and milt is drawn from the energy reserves stored in the body tissues (Dawson & Grimm 1979), which are built up during the growing period from April to November (Chapter 7). The annual cycle is thus characterized by separate growing and spawning periods. This provides the opportunity to estimate the reproductive investment from the energy loss over the reproductive period in both sexes. Such an approach has been applied previously to estimate the reproductive investment of female North Sea plaice (Rijnsdorp *et al.* 1983).

MATERIALS AND METHODS

Growth in length and weight

The growth in length and weight was studied in market samples taken between 1981 and 1985 from plaice landings of Dutch beam trawlers fishing in the southern and central North Sea (Chapter 4), which give us, quarterly, the length frequency distribution and age composition of the landings as well as the mean length-at-age, weight-at-age and condition factor (K).

The annual length increment was estimated from the mean length-at-age in the first quarter. The total number of fish sampled in the first quarter between 1981 and 1985 was 9309. Because plaice recruit to the fishery at an age of 2 - 4 years and considerable numbers of the youngest age-groups are discarded at sea, the mean length-at-age of these age-groups will be overestimated by the market samples. Therefore, the mean length-at-age for the not yet fully recruited age-groups was studied from research vessel surveys (Chapter 4). The condition factor was calculated as

$$K = W\ L^{-3} * 100$$

where W is whole fresh weight in grammes and L is length in centimetres. As the majority of the plaice landed were gutted but still contained the gonads, gutted weight was converted to whole fresh weight by multiplying by 1.07.

Energy measurements

The energy content was measured by bomb calorimetry and by chemical analysis. Special samples of ungutted plaice were obtained from commercial beam trawlers during the spawning seasons in 1982/1983, 1983/1984 and 1985/1986 from the different spawning grounds in the southern North Sea (Fig.1). On board, the fish were stored on ice and landed within 1 week. At the laboratory, length (mm below) and weight (g) were determined and the body cavity was opened to determine sex and maturity stage. In a few instances the fish sampled had been feeding and contained sand or shell particles in their guts. In order to avoid bias the gut was removed. After sorting the plaice according to sex, stage of maturation and length group, between three and 25 plaice, depending on availability, were pooled in a mixed sample. The mixed samples were packed in polythene bags and deep frozen at -20° C until further analysis. In 1983 and 1984 energy values were also obtained for a number of individual plaice.

Before further analysis, the samples were thawed and completely minced (including gonads, liver and bones). A subsample of between 20 - 30 g was oven dried at 70° C to constant weight and then homogenized in a Warren blender.

Pellets of 0.15 - 0.20 g were combusted in a Parr microbomb calorimeter. In order to test the homogeneity of the minced fish, 36 samples were oven-dried and combusted separately. The mean difference was 2.06% with a range of 0.0 - 4.6%. Further tests showed that calorific measurements of the same sample were all within 1% of the mean. Therefore, only one measurement was taken for individual fish, but for the mixed samples at least two measurements were taken.

In the chemical analysis, lipid content was measured by the method of Blight & Dyer (1959) and ash content was determined by heating a sample for 12 h at 550° C (Paine 1964). Protein content was not measured directly but estimated as the difference between the dry weight and the sum of the ash and lipid content. The amount of carbohydrates in fish is generally very small and can be neglected (Craig 1977; Dawson & Grimm 1980). The gross energy value was calculated using specific energy values for lipid 39.5 kJ g^{-1} dry wt and protein 23.6 kJ g^{-1} dry wt and because fish cannot use all the energy, the following physiologically useful energy values were employed: lipids - 36 kJ g^{-1} and proteins - 19.7 kJ g^{-1} (Brett & Groves 1979). In this paper the physiological useful energy is denoted as kJf.

Bomb calorimetry and chemical analysis were calibrated by determining the energy values of three mixed samples of stage 2 females. The bomb calorimetric determination gave an energy value of 22.25 ± 0.36 kJ.g^{-1} dry wt, the chemical method 23.18 ± 0.09 kJ.g^{-1} dry wt. The discrepancy of 4% is about the same as observed by Beukema & de Bruin (1979) analysing the tissue of the bivalve *Macoma balthica*:. they suggested that chemical methods tend to produce overestimates because the commonly used conversion factor for lipids may be too high. On the other hand, bomb calorimetry can cause underestimates through incomplete drying of the pellets or through incomplete combustion (Brafield & Llewellyn 1982).

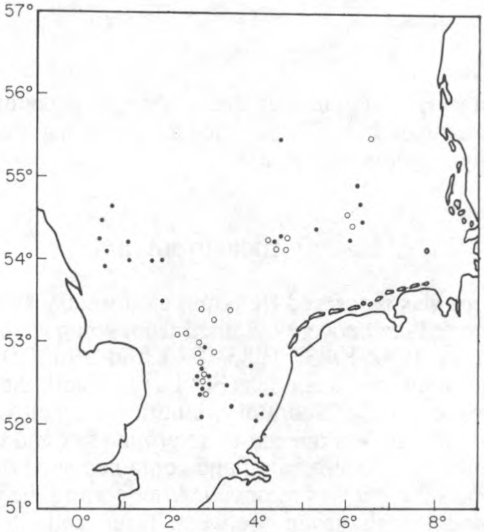


Figure 1. Plaice sampling positions for energy content and chemical composition of whole fish (●) and dry weight and energy content of ripe eggs (O).

Energy content of ripe eggs

Ripe eggs were stripped from stage 3, 4 and 5 females from market samples and preserved in 4% formaldehyde in sea water. After washing the eggs in demineralized water a sample of about 750 eggs was counted by eye and weighed after drying to constant weight in an oven at 60° C. A second sample, which was deepfrozen before analysis (-20° C.), was oven dried and the energy value was determined by bomb calorimetry. In egg samples from stage 3 females variable amounts of unhydrated eggs were included.

RESULTS

Composition of the total body

Body composition (Table 1) does not differ significantly between the sexes within the same month in immature plaice, except for a lower ash content in immature females in February-March; nor did it (g^{-1} dry wt) change significantly in immatures between December and February-March. Only the condition factor and the percentage dry weight decreased significantly (t test, $P<0.05$). In mature males and females, percentages dry weight and lipid peaked in December at the end of the growing season. In the course of the spawning period lipid stores were depleted and reached minimum values in February-March, the difference being significant (t test, $P<0.01$). Protein content, however, did not change significantly in female plaice, whereas it increased significantly in male plaice (t test, $P<0.01$).

Table 1. Body composition of male and female North Sea plaice in percentage per gram dry weight and the energy per gram dry weight (E.gd^{-1}) as estimated from chemical analysis and measured with bomb calorimetry. N = number of mixed samples; The total number of fish in the samples is given between parenthesis.

	Male immature, stage 1				Female immature, stage 1			
	Dec		Febr-March		Dec		Febr-March	
Chemical analysis:								
%dry	21.8	(0.36)	21.1	(0.24)	21.4	(0.34)	21.1	(0.30)
%lipid	11.5	(0.78)	10.2	(0.59)	11.2	(0.64)	11.2	(0.39)
%protein	72.3	(1.46)	71.7	(0.32)	74.4	(0.61)	72.8	(0.37)
%ash	16.2	(0.80)	18.1	(0.71)	14.5	(1.04)	15.8	(0.45)
E.gd-1	21.6	(0.13)	21.0	(0.26)	22.0	(0.33)	21.6	(0.15)
N	6 [82]		6 [55]		3 [52]		7 [63]	
Bomb calorimetry:								
%dry	-	-	-	-	23.6	-	21.4	(0.27)
E.gd-1	-	-	-	-	21.5	-	20.4	(0.05)
N	-		-		1 [6]		4 [16]	

	Male ripe, stage 2-4				Female ripe, stage 2			
	Dec		Febr-March		Dec		Febr-March	
Chemical analysis:								
%dry	23.8	(0.10)	21.2	(0.18)	24.1	(0.28)	-	-
%lipid	17.4	(1.00)	12.3	(0.93)	15.9	(0.33)	-	-
%protein	67.5	(1.20)	69.8	(0.77)	71.5	(0.33)	-	-
%ash	15.2	(0.31)	21.4	(0.26)	23.2	(0.04)	-	-
E.gd-1	22.8	(0.13)	21.4	(0.26)	23.2	(0.04)	-	-
N	4 [140]	6 [149]		3 [57]	-			
Bomb calorimetry:								
%dry	24.4	(1.03)	-	-	24.3	(0.41)	22.4	(0.81)
E.gd-1	21.7	(0.77)	-	-	22.2	(0.17)	21.8	(0.21)
N	2 [5]		-		4 [97]		5 [29]	

	Male spent, stage 6-7				Female spent, stage 6-7			
	Dec		Febr-March		Dec		Febr-March	
Chemical analysis:								
%dry	-	-	21.0	(0.20)	-	-	19.6	(0.55)
%lipid	-	-	9.8	(0.42)	-	-	10.9	(0.94)
%protein	-	-	72.7	(0.65)	-	-	70.2	(1.09)
%ash	-	-	17.5	(0.41)	-	-	18.9	(0.33)
E.gd-1	-	-	21.1	(0.11)	-	-	20.9	(0.07)
N	-		9 [121]		-		3 [56]	
Bomb calorimetry:								
%dry	-	-	20.9	(0.26)	-	-	20.4	(0.47)
E.gd-1	-	-	19.8	(0.11)	-	-	19.4	(0.05)
N	-		3 [18]		-		4 [33]	

Such changes in body composition expressed as percentage of dry weight may confound real differences in the biochemical composition if the length-weight relation (condition factor) is not taken into account. In order to trace possible differences, the body composition was calculated for a standard plaice of length 35 cm at the beginning and at the end of the spawning period, December and February-March, respectively. The results are given in Table 2. The percentages dry weight, lipid, protein and ash used in the calculation were taken from Table 1, and the condition factors from Table 3.

In December, dry weight, lipid and protein content were considerably lower in immature than in mature fish, with the reservation that protein content was not significantly different from that in mature males. In February-March dry weight, lipid and protein content in immatures were significantly higher than in mature fish, with the reservation that lipid content was not significantly different from that in spent females.

In December, mature females had accumulated 15% more dry weight and 22% more protein weight than mature males, whereas the lipid and ash weights did not differ significantly. In March, the spent females have 11% lower protein weight than males. The lipid content of spent plaice did not differ significantly between the sexes. The ash content, dominated by the skeleton, did not differ between sexes or maturity stages, or between months, except in mature males between December and February-March.

During the spawning season 35-cm mature males and females lost nearly equal amounts of lipids (10.2 and 11.0 g, respectively) but females lost nearly three times as much proteins as males (33.8 and 11.4 g, respectively). Immatures only lost 1.3 g lipids and 5.4 g protein. A striking feature of the body composition is that the depleted body of the spent fish after several months of starvation showed only relatively small differences from immatures, compared with the differences found at the beginning of the spawning period.

Table 2. Body composition (g dry weight) of a standard plaice of 35 cm body length in December just before spawning and in February-March just after spawning.

	A		B		C	
	Immature male and female		Mature male		Mature female	
	Dec	Feb-Mar	Dec	Feb-Mar	Dec	Feb-Mar
Wfresh	437.7	418.5	436.9	387.2	498.2	378.6
Wdry	94.8	88.3	104.0	80.9	120.1	74.2
Lipid	10.8	9.5	18.1	7.9	19.1	8.1
Protein	69.2	63.8	70.2	58.8	85.9	52.1
Ash	14.9	14.9	15.8	14.2	15.1	14.0

t-test	December			Feb-March			A	B	C
	A B	A C	B C	A B	A C	B C	Dec F-M	Dec F-M	Dec F-M
Wdry	**	**	**	**	**	**	**	**	**
lipid	**	**	n.s.	*	n.s.	n.s.	n.s.	**	**
protein	n.s.	**	**	**	**	**	**	**	**
ash	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.

n.s. not significant
* P<0.05
** P<0.01

Table 3. Condition factor (K), % dry wt, and energy contents (kJ) per g dry wt (E.g^{-1} dry wt), per g fresh wt (E.gf^{-1} fresh wt) and cm^{-3} x 10^{-2} of the whole body of North Sea plaice: means with S.E. in parentheses; n number of mixed samples, except where asterisk denotes the number of individual samples.

	December		*n*	February- March		*n*
	Male and female immature (stage 1)					
K	1.021	(0.0041)	338 *	.976	(0.0031)	1140*
%dry	21.9	(0.298)	10	21.2	(0.158)	17
E.g^{-1} dry wt	21.8	(0.146)	10	21.3	(0.134)	17
E.gf^{-1} fresh wt	4.77	(0.084)	10	4.53	(0.047)	17
E.cm^{-3} x 10^{-2}	4.87	(0.089)	10	4.42	(0 048)	17
	Male ripe (stage 2-4)			Male spent (stage 6-7)		
K	1.019	(0.0029)	620*	.913	(0.0031)	935*
%dry	24.0	(0.295)	6	20.9	(0.155)	12
E.g^{-1} dry wt	22.5	(0.3070	6	20.9	(0.141)	12
E.gf^{-1} fresh wt	5.40	(0.042)	6	4.38	(0.039)	12
E.cm^{-3} x 10^{-2}	5.50	(0.046)	6	4.00	(0.038)	12
	Female ripe (stage 2)			Female spent (stage 6-7)		
K	1.162	(0.0037)	834 *	.881	(0.0027)	1643 *
%dry	24.2	(0.245)	7	20.1	(0.340)	7
E.g^{-1} dry wt	23.2	(0.085)	7	20.5	(0.189)	7
E.gf^{-1} fresh wt	5.60	(0.073)	7	4.12	(0.082)	7
E.cm^{-3} x 10^{-2}	6.52	(0.086)	7	3.63	(0.073)	7

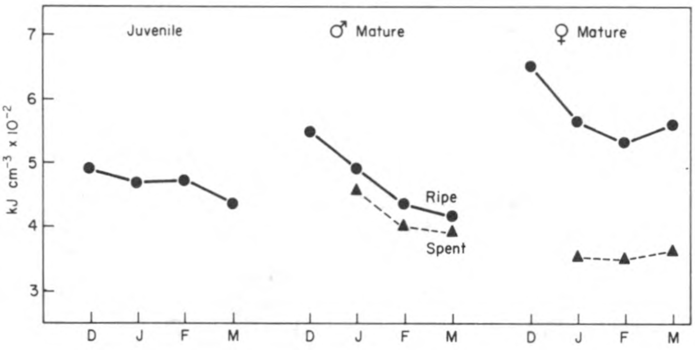


Figure 2. Change in energy content (kJ cm^{-3} x 10^{-2}) of immature, mature male and mature female North Sea plaice.

Energy content of the body.

The energy value of the total body was calculated from the chemical composition and measured directly by bomb- calorimetry (Table 1). In table 3 the energy values obtained from chemical and bomb calorimetric measurements were pooled after converting the bomb-calorimetric measurements by 1.04 (see methods). In order to follow the changes in the total energy content the energy factor was calculated E/L^3, which gives the energy value per cubic centimetre. In the course of the spawning period energy stores were clearly depleted (Fig.2). During the spawning season the energy factor of mature females decreased from 65.2 $J.cm^{-3}$ in December to 36.3 $J.cm^{-3}$ in February- March. The energy factor of mature males decreased from 55.0 to 40.0 $J.cm^{-3}$. Mature females thus used up 44% of their total energy content during the spawning period while males used up only 27%. In immatures the energy factor decreased by 9% from 48.7 to 44.2 $J.cm^{-3}$.

Energy content of ripe eggs

Although the dry weight of ripe eggs did not differ between the years, the energy values (Table 4) in 1983 and 1984 were significantly different (t test; $P<0.01$). This difference might have been related to differences between geographical areas: the 1983 samples were taken mainly in March in the German Bight, whereas the 1984 samples were taken mainly in March on more southern spawning grounds. Dry weight and energy value of ripe eggs decreased in the course of the spawning of an individual plaice as shown by the differences between the maturity stages (Table 5). Energy values per gramme dry

Table 4. Dry wt and energy values of ripe North Sea plaice eggs in mixed samples

Year	Dry weight (g per 1000 eggs) Mean	S.D.	n	Energy value ($kJ.g^{-1}$ dry wt) Mean	S.D.	n
1983	0.231	0.023	7	24.56	0.238	4
1984	0.234	0.016	4	23.44	0.508	72*
1985	0.231		1			
1987	0.235	0.015	3			

*individual fish

Table 5. Dry weight (mixed samples) and energy values (individual samples) of ripe eggs of different maturity stages.

Maturity stage	dry weight (g per 1000 eggs) Mean	S.D.	n	energy value ($kJ.gd^{-1}$) Mean	S.D.	n	energy value kJ per 1000 eggs Mean
3	0.274	0.012	2	24.10	0.350	8	6.60
4	0.235	0.015	3	23.44	0.508	72	5.51
5	0.218	0.002	3	23.06	0.568	48	5.03

weight at the beginning of spawning (stage 3) were 3 - 5 % higher than at the end of spawning. The 14 - 20% decrease in dry weight of eggs was even steeper. Overall energy content of ripe eggs decreased by 17 - 24%. Because the eggs in the gonad at maturity stage 4 and 5 represent only a minor fraction of the total amount of eggs spawned, the average energy value should correspond broadly to the mean value measured in stage 3 females of 6.6 kJ per 1000 eggs.

Energy allocation over reproduction and somatic growth.

The pattern of energy allocation over reproduction and somatic growth can be calculated from the energy factors of immature and mature plaice (Table 3) and the length-at-age in the spawning season (Table 6). The somatic growth of age-group 1 - 4 and the maturity percentages were obtained from the two research vessel surveys conducted in 1985 and 1986, covering both spawning areas and nursery grounds (Chapter 4). For the older age-groups, which are fully recruited to the fishery, the mean length-at-age was determined from the first quarter market sampling data of 1981 - 1985.

Immature plaice are smaller and have lower energy content than mature plaice of the same age-group. Therefore, the mean energy content for each age-group was calculated as the average energy content of immature and mature plaice weighted according to the maturity percentage (Table 6). Somatic growth has been calculated as the increase in energy content in February-March of spent fish between successive age-groups. The reproductive investment can be approximated by the energy loss over the spawning period between December and February- March. This energy loss comprises of the energy of sex products, spawning metabolism and some migration to the spawning areas. The sum of somatic growth and reproductive investment is the surplus production realized during the growing season preceding the spawning period.

Figure 3 summarizes the patterns of energy allocation in males and females. Somatic growth increased in both sexes up to the age of 5 years and decreased thereafter. Both reproductive investment and surplus production increased steadily in females but levelled off in males. As a percentage of surplus production male plaice showed a higher reproductive investment than female plaice (Fig.4). Plotted against body size, the surplus production of males and females were the same up to a body weight of 300 g (corresponding with a body length of about 30 cm) but larger females showed an increasingly higher surplus production (Fig.7).

DISCUSSION

Body composition

The biochemical composition of mature female North Sea plaice, as observed in this study, can be compared with values reported for Irish Sea plaice by Dawson & Grimm (1980). Ripening females in December and January are closely similar in protein, lipid and ash contents expressed as percentage dry weight, but North Sea spent females have 8% lower protein content. Dry weight percentages reported in the Irish Sea were somewhat higher than those observed in our study.

The body shows differences in composition in relation to sex and reproductive state. Since plaice do not feed during the spawning period (Chapter 4) they have to draw upon body stores of proteins and lipids for their metabolic requirements and the formation of spawning products. Body composition prior to the spawning period reflects the different functions of mature males and females. Proteins are relatively more important for egg production whereas lipids are relatively more important in male spawning behaviour (Love 1970, 1980). Immature fish continue to feed throughout the winter, although at a low level (Chapter 4), and do not build up energy reserves as high as mature plaice.

A standard female of 35-cm will have a gonad weight of 70 g (16% of gutted body weight: Chapter 7). With the chemical composition of ripe gonads taken from Dawson & Grimm (1980), i.e. dry weight 33%, protein 86%, lipid 10% and ash 4%, the loss of proteins and lipids through egg production can be calculated. Thus, our standard female

Table 6. Growth in length (*L*, in cm) and energy content (*E*, in kJ) of the body and the maturity percentage at age (%mat) of male and female North Sea plaice. E_d ,energy content in December at the beginning of the spawning period. $E_{f\text{-}m}$, energy content in February-March of spent fish at the end of the spawning period.

MALE PLAICE

	Immature			Adult			Immature + Adult		
Age (years)	*L*	E_d	$E_{f\text{-}m}$	*L*	E_d	$E_{f\text{-}m}$	%mat	E_d	$E_{f\text{-}m}$
1	9.7	44	40	16.2	234	183	0.5	45	41
2	19.0	339	308	20.9	502	392	51	422	351
3	25.1	770	699	26.4	1012	791	72	944	765
4	28.1	1081	981	30.9	1622	1268	95	1596	1254
5				34.1	2181	1705	100	2181	1705
6				36.1	2588	2022	100	2588	2022
7				37.3	2854	2231	100	2854	2231
8				37.7	2947	2304	100	2947	2304
9				38.0	3018	2359	100	3018	2359
10				39.4	3364	2630	100	3364	2630

FEMALE PLAICE

	Immature			Adult			Immature + Adult		
Age (years)	*L*	E_d	$E_{f\text{-}m}$	*L*	E_d	$E_{f\text{-}m}$	%mat	E_d	$E_{f\text{-}m}$
1	9.7	44	40				0	44	40
2	19.8	378	343	23.4	835	465	1	383	344
3	27.3	991	899	28.1	1446	805	6	1018	893
4	31.3	1493	1355	33.3	2407	1340	29	1759	1351
5	33.1	1766	1602	37.3	3383	1883	80	3060	1828
6	36.5	2368	2149	40.1	4204	2340	99	4180	2338
7				41.2	4559	2538	100	4559	2538
8				42.3	4934	2747	100	4934	2747
9				43.8	5478	3050	100	5478	3050
10				45.2	6020	3352	100	6020	3352
11				46.4	6513	3626	100	6513	3526
12				47.5	6987	3890	100	6987	3890
13				49.1	7717	4296	100	7717	4296
14				50.9	8598	4786	100	8598	4786
15				52.1	9220	5133	100	9220	5133

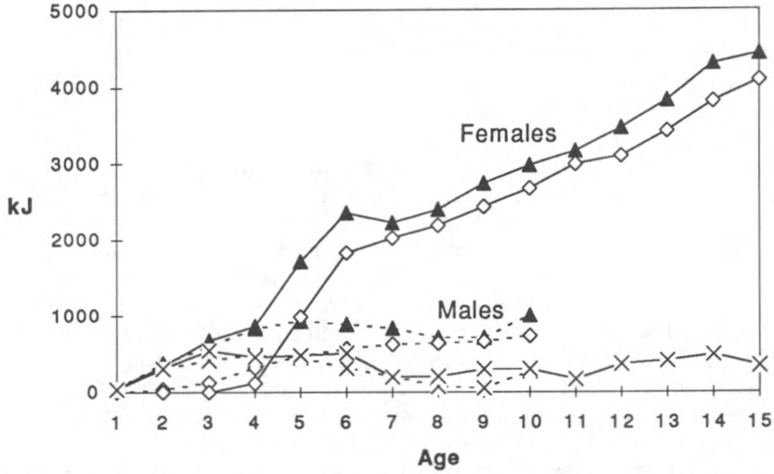


Figure 3. Allocation of energy over reproduction and somatic growth in relation to age in male (hatched lines) and female (full lines) North Sea plaice. ▲ = surplus production; ◇ = reproduction; X =somatic growth.

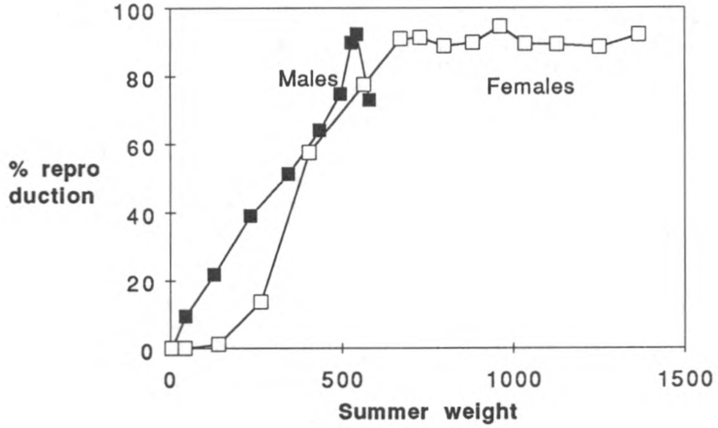


Figure 4. Percentage of surplus production allocated into reproduction in relation to the third-quarter (summer) body weight of male (full symbols) and female (open symbols) North Sea plaice.

has a gonad dry weight of 23 gram, comprising 19.9 g proteins, 2.3 g lipid and 0.9 g ash. The total loss during spawning between December and February- March was estimated in this study at 33 g protein and 8 g lipids (Table 2). The difference between total loss and gonad loss (13.1 g protein and 5.7 g lipids) should equal the amount used as fuel for metabolism. Given the physiological energy values of protein and lipid, it can then be estimated that lipids supplied about 55% of the energy for spawning metabolism, which compares with 75% in Irish sea plaice (Dawson & Grimm 1980). The use of an equal share of lipid and protein in metabolism during starvation was also found in experimental studies of starving plaice (Fonds, pers comm).

Rijnsdorp *et al.* (1983) showed that a 35-cm female produces on average 90 thousand eggs. The energy loss through egg production can thus be calculated at 594 kJ. By subtracting the energy loss through egg production from the total energy loss during the spawning season the rate of metabolism of mature female plaice can be estimated. Based on values in Table 3, the energy loss between December and February - March for a standard female can be calculated as 1239 kJ; of this, 594 kJ would have been used for egg production and thus 645 kJ remained for spawning metabolism. Only 85% of the gross energy is physiologically useful, thus 548 kJf was left for metabolism. Because the energy content of spent females does not differ between February and March (Fig.2), the period over which the females use up this energy will be approximately 60 days. Metabolic rate during the spawning season thus amounts up to 9.1 kJf.day-1.

Hislop & Bell (1987) showed that dry weight measurements of ripe eggs of plaice preserved in 4% formaldehyde were underestimated by *c* 25%. Although it is not known which materials are lost during preservation, the underestimation of dry weight will seriously affect the estimated energy loss in egg production and the estimated spawning metabolism. Assuming that the materials which are lost from the eggs have an energy value equal to that of the total egg, the energy loss due to egg production will be 790 kJ and the corresponding loss due to spawning metabolism 449 kJ (382 kJf) or 6.4 kJf day^{-1}.

A standard 35-cm male loses 643 kJ between December and February - March (approximately 75 days), which is equal to 7.3 kJf day^{-1}. The loss of spawning products in male fish is not well known (Wootton 1985) but the low testis weight of male plaice (< 2.5% of the body weight; Deniel 1981) suggests that this loss will be very small in comparison with the total energy loss of 28%. The daily energy loss in male plaice thus gives a maximum estimate of the metabolic rate of spawning males. The energy loss of a standard immature plaice (35 cm) between December and February-March (approximately 75 days) amounts up to 193 kJ or 2.2 kJf day^{-1}.

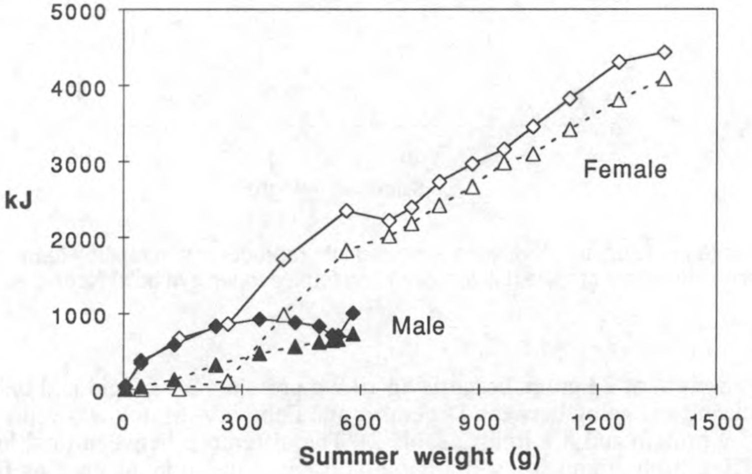


Figure 5. Relation of surplus production (◆) and (◇) and reproduction (▲) and (△) to the third-quarter (summer) body weight of male and female North Sea plaice, respectively.

Using experimental data on metabolic rates given in Priede & Holliday (1980) and Fonds *et al.* (1985), and the average bottom temperature in the spawning areas in the southern North Sea (6.8 °C; Doggerbank area; Tomczak & Goedecke 1962) a theoretical estimate can be derived of the average daily metabolic rate of a standard plaice (35 cm) in the period between mid December and mid February. After correcting the results of Priede and Holliday (1980) to the fish weight of a standard 35 cm plaice by the formula:

$R = a\,W^{0.78}$ (Fonds *et al.* 1985),

the resting metabolic rate (R) of a standard mature plaice can be estimated at 3 kJ.day $^{-1}$ and maximum metabolic rates at 15 kJ.day $^{-1}$. Fonds *et al.* (1985) estimated the resting metabolic rate at 4 kJ.day $^{-1}$ and the feeding metabolic rate at 8 kJ.day $^{-1}$.

Although our estimates may be rather crude they nevertheless indicate a high level of metabolism in spawning plaice. Aerobic activities of a fish are restricted by the maximum level of metabolism (metabolic scope: Priede 1985). If spawning and related activities in plaice fill a substantial part of the metabolic scope, as suggested by our estimates, the oxygen supply for other activities might be restricted. This could explain why mature plaice cease feeding during the spawning season while immatures and spent fish do show some feeding activity (Chapter 4). A spawning fast is reported in a wide variety of fish species (Winters 1970; Diana & MacKay 1977; Folz & Norden 1977; Roff 1982; McEvoy 1984), although it certainly is not a general rule. This feature will be most prominent in sluggish fish species characterised by a small metabolic scope, e.g.flatfish.

Fitness aspects of energy allocation patterns

From an evolutionary point of view, it might be expected that surplus production is maximised (Ware 1982) because it results in, on one hand a reduced time between birth and onset of sexual maturity and, on the other hand, in a larger body-size which implies a larger reproductive output and lower predation risk. However, counteracting selection forces may operate and the rate of surplus production is expected to be a compromise between the two counteracting forces (Calow 1985).

In the nursery areas along the continental coast young plaice show growth rates that equal the maximum growth rates in the laboratory under optimum food conditions (Fonds 1979; Zijlstra *et al.* 1982), suggesting that young plaice maximize their surplus production. In this study we observed that males and females showed similar surplus production up to the body size of about 300 g and a length of about 30 cm, but that male surplus production levelled off beyond this size whereas female surplus production continued to increase. Male plaice thus appear to switch from maximal growth rate to reduced growth rate at a length of about 30 cm, which is well above the length at first maturity (about 20-25 cm: Chapter 4). In Chapter 4 it is shown that male plaice of age-group 4 onwards, corresponding to a length of about 30 cm, are capable of taking part in spawning for at least 11 weeks during almost the complete spawning season, whereas younger males below this size are in spawning condition for a shorter time (about 9 - 10 weeks). This suggests that the reproductive output of male plaice does not further increase after they have reached a critical size at which they can take part in spawning throughout the spawning season. The question remains as to which evolutionary constraint limits growth rate in males, or, in other words, which penalties may be connected with maximum surplus production (Calow 1985). Maximum surplus production will result from maximum food intake and a high level of foraging activity. Food intake as well as foraging activities may increase the encounter rate of the fish with predators and diseases and thus pose a mortality risk (Roff 1983). In female plaice the reproductive output continues to increase with body size, which may compensate for the higher mortality risk. Beverton (1964) estimated the annual natural mortality rates of mature males and females at 13% and 8% respectively. These mortality rates seem to be in contradiction with the above hypothesis, but it may well be that differences in mortality rates between the sexes during the growing period are confounded by differences in mortality during the spawning period. Without empirical data on the mortality rate of plaice in the growing period in relation to size, age and sex it will not be possible to test the above hypothesis.

In the calculation of the allocation pattern, we assumed that the energy content of plaice did not change with age or size and that the energy loss during spawning was a fixed percentage of the total energy content. The condition factor of ripe female plaice was almost constant between 30 and 55 cm, but decreased by nearly 10% in bigger females (Chapter 7). Because the energy values of individual plaice as obtained in this study were positively correlated with the gutted condition factor ($r=0.53$, $n=202$, $P<0.01$) a 10% lower condition factor corresponds to a 10% reduction in energy content of the body and thus will have a relatively small effect on the calculated allocation pattern. The data of individual fish did not allow for an analysis of the effect of age and size on the allocation pattern because the number of energy measurements were too limited with regard to larger size and older age-groups and did not cover well enough the different maturity stages of both sexes. The assumption of a constant reproductive effort in relation to age or body size will not lead to serious bias in the estimated allocation pattern, because the January gonad index is constant for age-groups 6 and older at 17.6% of the gutted weight and is only slightly lower in age-group 3 to 5 at respectively 13.5%, 14.1% and 15.4%.

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Chapter 2

Selection differentials of male and female North Sea plaice *Pleuronectes platessa* L. and changes in maturation and fecundity

Rijnsdorp, A.D. Selection differentials of male and female North Sea plaice *Pleuronectes platessa* L. and changes in maturation and fecundity. - *In* R.Law, T.K.A. Stokes & J. McGlade (eds.). The exploitation of evolving populations. Springer Verlag. in press.

ABSTRACT. This paper presents an analysis of the selective effects of fishing on reproductive parameters of North Sea plaice. This species has been exploited intensively since the late 19th century, and the fishing mortality substantially exceeded the level of natural mortality. Since the start of biological research in the early 1900's, life history parameters such as growth, onset of sexual maturity and fecundity have changed. In order to evaluate possible genetical effects of exploitation, the mortality imposed by fishing is estimated for males and females separately and factors determining the relationship between fishing mortality and age are analysed. Fitness profiles of various reproductive traits are studied under the present regime of exploitation, employing a simple allocation model of surplus production over somatic growth and reproduction. This model describes the cost of reproduction in terms of decelerated somatic growth and reduced future reproduction. Selection differentials are estimated from the fitness profiles and are compared to the selection differentials estimated from the observed changes in reproductive parameters. It is concluded that the direction of the observed changes is in agreement with the expected change due to selective fishing.

INTRODUCTION

The additional mortality induced by fishing may act as an artificial selection pressure on life history parameters, such as growth rate, length and age at first sexual maturity and reproductive investment (Nelson & Soulé 1987). The way in which these parameters may change will depend on their heritability and the fishing intensity and pattern of exploitation. In this paper a method is presented to estimate the selection pressure exerted by the fisheries. The relationship between fishing mortality and age, i.c. the exploitation pattern, is studied and factors that determine the exploitation pattern are analysed. The fitness of various reproductive traits, taken here as combinations of length at first maturity and reproductive investment, are studied under the present regime of exploitation, employing a simple allocation model of surplus production over somatic growth and reproduction that describes the cost of reproduction in terms of decelerated somatic growth and reduced future reproduction.

The method is explored using data on North Sea plaice distinguishing between males and females. This species has been exploited for several centuries and has shown changes in reproductive parameters and somatic growth. Selection differentials are calculated from the observed changes in reproductive parameters and compared with those estimated from the exploitation pattern of the fisheries.

DEVELOPMENTS IN THE FISHERIES

Cushing (1988) gives the following account on the major developments in the demersal fisheries in the North Sea. In the 18th and 19th century, the fishery was mainly conducted with sailing vessels deploying small beam trawls. With the introduction of steam trawlers in the late 19th century the traditional beam trawl was replaced by the otter trawl and the number of vessels expanded substantially. In conjunction the area fished greatly expanded and covered all of the North Sea by the end of the 19th century. In the first half of the 20th century the steam trawlers were gradually replaced by motor trawlers, although the principal gear, the otter trawl, remained largely the same. Finally in the early 1960s, heavy beam trawlers quickly outcompeted the otter trawlers. According to Thursby-Pelham (quoted in Wimpenny 1953), plaice landings from the North Sea were already at a level of 47,000 tonnes in 1892. Landing statistics collected by the International Council for the Exploration of the Sea (ICES) since 1906 show that the plaice landings varied around 50,000 tonnes annually until the mid 1950s (Bannister 1978). Since then they increased to a level of around 150,000 tonnes in the 1980's (ICES 1991).

GENERAL BIOLOGY OF PLAICE

Plaice is a flatfish species living in temperate waters down to a depth of about 100 m. The distribution range extends from the Bay of Biscay in the south to the Barents Sea and the waters around Iceland in the north. The areas and intensity of spawning in the North Sea and adjacent waters indicate that plaice abundance is highest in the southern and southeastern North Sea (Wimpenny 1953; Harding *et al.*1978a). Tagging studies have shown that the population in the North Sea is composed of various sub-groups that partially mix on the summer feeding grounds but separate on their spawning grounds in winter (de Veen 1978).

The different life history stages are spatially segregated (Wimpenny 1953; Rijnsdorp & van Beek 1991). After spawning, the pelagic eggs and larvae drift with the residual current in open sea. At the end of the larval stage, plaice settle in very shallow nursery areas on sandy beaches with a marked preference for estuarine areas. In the following years they leave the inshore areas and disperse over the southern and central North Sea. Beverton & Holt (1957) showed that the off-shore movement of juvenile plaice could be described by a process of diffusion. After maturation plaice show distinct migrations between their feeding areas in summer and spawning grounds in winter (de Veen 1978).

Natural mortality (M) of adult age groups was estimated at 0.08 for female plaice and 0.14 for male plaice (Beverton 1964), although in general a value of 0.1 is accepted for both sexes. A recent review of 0-group mortality rates indicated an annual mortality rate from eggs to juveniles of M_0=10.38 (Beverton & Iles 1992a).

The annual cycle of plaice is composed of a distinct spawning period between December and March during which plaice stop feeding, and a growing period between March and November. During the spawning period adult male and female plaice lose respectively 27% and 44% of their total energy content, while juvenile plaice lose only 9%

(Chapter 1). During the growing period energy is mainly accumulated in the soma. Ovary growth does not start before October and 50% of the energy for ovary growth is reallocated from the soma (Dawson & Grimm 1980; Chapter 7). Total energy accumulated during the growing period, here defined as surplus production, is a continuous increasing function of body size, but in male plaice surplus production levels off at a body size above 30 cm (Chapter 1).

CHANGES IN POPULATION PARAMETERS

Growth

Changes in growth of North Sea plaice have been reported by Bannister (1978) and Rijnsdorp & van Beek (1991). At present, the juvenile growth, reflected in the length attained at the end of their 1st and 2nd year of life, is higher than those observed between 1900-1950. Changes in growth in the adult stage are less well documented. Comparison of the mean weight-at-age in the 1st quarter between the 1930's and the 1980's indicates that the rate of growth was higher in the 1930's from about 8 years onwards. The weight of younger age groups in the 1930's however, were lower than at present, reflecting the then lower growth rate of juveniles. The above data have to be interpreted with caution, because they do not take account of growth differences between the sexes. Market sampling data collected for males and females separately showed an increase in the length-at-age of the younger age groups in both sexes, and a decrease in the older age groups of female plaice in the period 1950 - 1970 (Bannister 1978). Rijnsdorp & van Beek (1991) observed a similar increase in the length-at-age of 4-year old plaice in the 1960s and concluded that this was probably related to an increase in the availability of benthic food.

Changes in growth rate may (in part) be related to density effects. Beverton & Holt (1957) showed that growth rate of plaice in the southern North Sea was substantially reduced during the second world war coinciding with a threefold increase in the stock size. An analysis of density-dependent aspects in changes in growth between 1958 and 1989, however, did not give unequivocal evidence for density-dependent effects. Only the decrease in the length of I- and II-group plaice in the 1980's might be related to the above average level of year class strength in that period (Rijnsdorp & van Beek 1991).

Maturity

Changes in the onset of sexual maturity, given in Chapter 4, indicate that in the early 1900's, depending on the area within the North Sea, females became sexually mature at a length of 31 - 43 cm, and an age of V-VII years. In 1985-1986 the length at 50% maturity (L_{mat}) had decreased to 30 - 35 cm (10-16%) and the age at 50% maturity (A_{mat}) to IV-V years (30-35%). In the early 1900's males became sexually mature at 30 - 37 cm and V-VI years, whereas in 1985-1986 L_{mat} had decreased to 20-24 cm (35%) and A_{mat} to II-III years (50-60%). The observed change in L_{mat} and A_{mat} in females was larger than the between year variability as observed in the period 1958-1989 (Rijnsdorp *et al.* 1991). A regression of L_{mat} of 4-year old females against time for the time period 1963-1988 indicated a decrease of 0.026 cm per year, although the decrease did not differ significantly from zero (r^2=0.024, n=22).

Fecundity

Changes in fecundity between three time periods (I - 1900-1910, II - 1948-1949 and III -1977-1985) were reviewed by Chapter 5. Fecundity of 30 cm females increased between periods II and III by 30 -100%, but not between period I and II. Fecundity of 50 cm females did not change substantially between period I and III, but was drastically reduced in period II by 30-60%. The reduction in fecundity in period II of the larger females coincided with the reduced growth in the preceding years and a threefold increase in stock size during the second world war. However, since no substantial change was observed in size-specific ovary weights, it was concluded that the energy allocation over reproduction and growth did not change in response of a increased stock size, but the trade-off between egg number and egg size. The observed change in fecundity suggests that the reproductive investment may have increased in smaller, but not in larger females.

SURPLUS ENERGY ALLOCATION

Somatic growth, maturation and reproduction are interacting processes that are related to the allocation of surplus energy (Ware 1980; Roff 1983). Surplus production (SP_x), defined as the energy available in excess of maintenance requirements that is available for somatic growth and reproduction, can be described as a continuously increasing function of body weight W_x (Reiss 1989).

$$SP_x = \alpha W_x{}^{\beta} \qquad (1)$$

Figure 1 shows that this model gives a reasonable, though not a perfect, description of the observed relationship between *SP* and *W* for both male and female plaice.

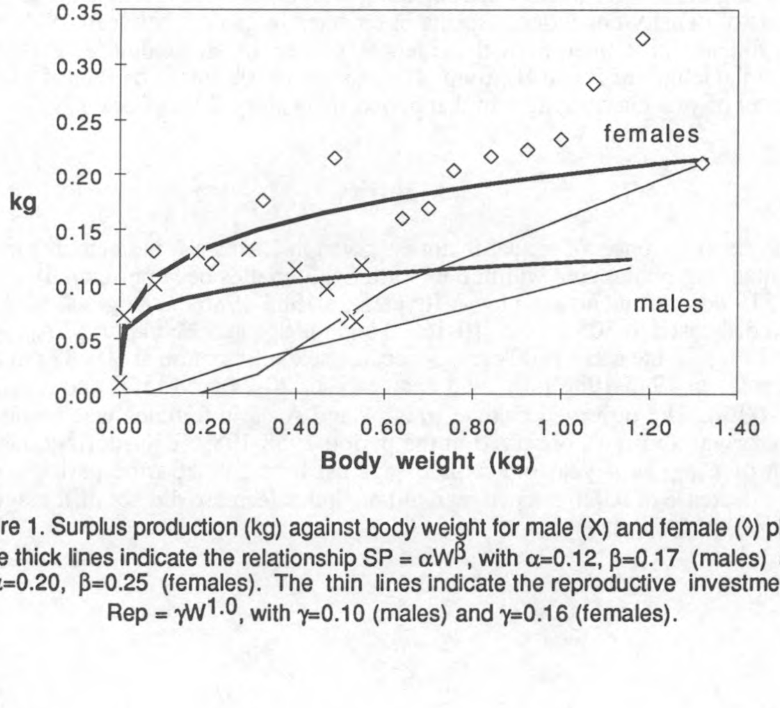


Figure 1. Surplus production (kg) against body weight for male (X) and female (◊) plaice. The thick lines indicate the relationship SP = αW^{β}, with α=0.12, β=0.17 (males) and α=0.20, β=0.25 (females). The thin lines indicate the reproductive investment Rep = $\gamma W^{1.0}$, with γ=0.10 (males) and γ=0.16 (females).

The reproductive investment at age x (m_x) can be described as

$$m_x = 0 \qquad for\ W_x < W_{mat} \tag{2a}$$

$$m_x = \gamma W_x{}^{\delta} \qquad for\ W_x >= W_{mat} \tag{2b}$$

In the present paper m_x is expressed in grammes which has the advantage that males and females can be treated in equal terms. Furthermore, it is assumed that $\delta = 1.0$ based on the fact that fecundity shows an almost proportional relationship with body weight (Rijnsdorp *et al.* 1983; Chapter 5). For females γ=0.16, corresponding to the observed gonadosomatic index (Chapter 4). For males a comparable index was calculated from the ratio of the male over female energy loss during the spawning season times the female gonadosomatic index: γ= (0.27/0.44) x 0.16 = 0.10.

The somatic growth can then be described by

$$W_{x+1} - W_x = SP_x - m_x \tag{3}$$

With this model, where reproduction clearly causes a reduction in somatic growth, the interaction of surplus production, maturation and reproduction can be modelled to study the effects of changes in maturation or reproduction on somatic growth.

FISHING MORTALITY

The decline of population numbers of a cohort of fish over time period t will be a function of the natural mortality (M) and the fishing mortality (F) according to:

$$N_t = N_0\, e^{-(F+M)t} \tag{4}$$

Fishing mortality is age specific and related to fishing effort (*E*) according to:

$$F_x = q_x\ E \tag{5}$$

where q_x is the catchability coefficient at age x (Beverton & Holt 1957; Gulland 1983).

The catchability coefficient q is a function of the probability that a fish in the path of a trawl will be captured (catch efficiency), the mesh selection, and the spatial overlap between fishing effort and fish. The array of F by age is called the exploitation pattern.

Exploitation pattern.

The exploitation pattern is estimated from the annual age compositions of the commercial landings, that are based on market samples for length distributions and otolith samples as reported in ICES (1991). The sampling programme covers all of the main fleets and about 90% of the total international landings. The catch-at-age matrix was analysed by two methods.

Firstly, the separable VPA (Pope & Shepherd 1982) was applied, which gives a least square solution of the exploitation pattern that fits best to the catch-at-age matrix under the assumption of a level of natural mortality (*M*), fishing mortality on some reference age in the last year and the exploitation factor on the oldest age. Figure 2 shows the exploitation pattern for the period 1974-1977. The exploitation factor on the oldest age was chosen at

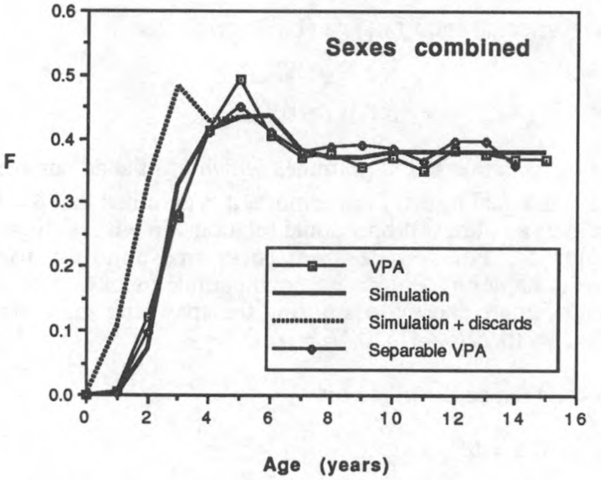


Figure 2. Comparison of the exploitation pattern in the period 1974-1977 as determined by VPA, separable VPA and as calculated from the quarterly distributions of effort and age groups including and excluding discards (respectively simulation + discards and simulation).

0.8 x F_5 because for this value the F 's of the older age groups are constant, which is in line with the high overlap in spatial distributions between these age groups (Rijnsdorp & van Beek 1991).

Secondly, a standard VPA (Gulland 1983) was applied, where the level of F in the last year was 'tuned' on fishing effort, assuming that catchability-at-age is constant over the years and that there is a positive relation between the trend in fishing mortality and effort (Laurec & Shepherd 1983; Pope & Shepherd 1985). It was further assumed that the fishing mortality on the oldest age group XV was equal to the mean of the previous five age groups. Effort data used were the number of fishing hours of the Dutch beam trawl fleet (fh) corrected for horsepower (HP) by $E = fh \times HP$. The exploitation patterns obtained by both methods show a close correspondence (Fig.2).

The fishing mortality in plaice thus characteristically increases with age to a maximum value at age V and decreases slightly thereafter (Fig.2). This pattern corresponds to the observed spatial distribution of the various age groups as described in Rijnsdorp & van Beek (1991). Age group I to IV were shown to have rather distinct spatial distribution patterns with coefficients of overlap between 0.1 - 0.6, whereas age groups V and older showed almost similar spatial patterns with coefficients of overlap between 0.8 and 1.0.

ICES (1987) provides estimates of the exploitation pattern for the period 1974 - 1977 based on spatially disaggregated data on the distribution of age groups and fishing effort under the assumption that the catch efficiency was constant over seasons and age groups. The result is plotted in Figure 2 as 'simulation'. The close agreement with the earlier results indicates that the exploitation pattern is indeed largely determined by the relative distribution of age groups and effort, and that the catch efficiency is approximately constant over the recruited age-groups.

The gradual increase in F for age groups I - IV is related to recruitment to the offshore fishing grounds. In the southeastern North Sea, the age at which plaice leave the nursery areas increases with latitude, from about age group II - III in the eastern part of the

Southern Bight to age group II - IV along the Danish coast (ICES 1987). There is some evidence that fast growing fish of a cohort leave the shallow nursery areas at a younger age than slow growing fish (Wimpenny 1953; Beverton & Holt 1957; Chapter 4).

Mesh selection.

At present the major fisheries for flatfish use a cod-end mesh size of 80 mm or less, which corresponds to a 50% retention length of about 18 cm. Since the minimum landing size of plaice is 27 cm, large quantities of undersized plaice are discarded at sea (van Beek 1990). The length range of discards is between 10 and 33 cm, representing age groups I - IV. The survival chances of these discards is virtually zero (van Beek *et al.* 1990a). The level of fishing mortality on undersized plaice was estimated by ICES (1987) from the quarterly distribution of fish and effort and is shown together with the *F* on the landed fish in Fig.2. Exploitation rate is apparently high from age II onwards. Fishing mortality on 0-group and I-group may in fact be somewhat higher since discards made by small vessels fishing in the nursery areas were not included. However, at present this fleet is smaller than in the past and the vessels also use special devices to prevent the by-catch of undersized fish (separating panel) or to increase their survival (rotary sieves). Their contribution to the discard mortality will probably be small compared to that of the flatfish fisheries itself. In the past they may have contributed substantially to the fishing mortality of I- and II-group plaice (Boddeke 1989).

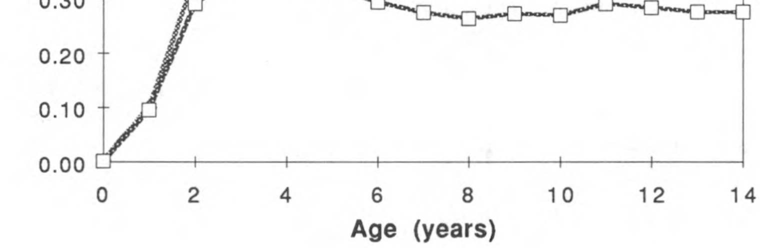


Figure 3 Exploitation pattern of male and female in the period 1958-1986 from VPA excluding discards.

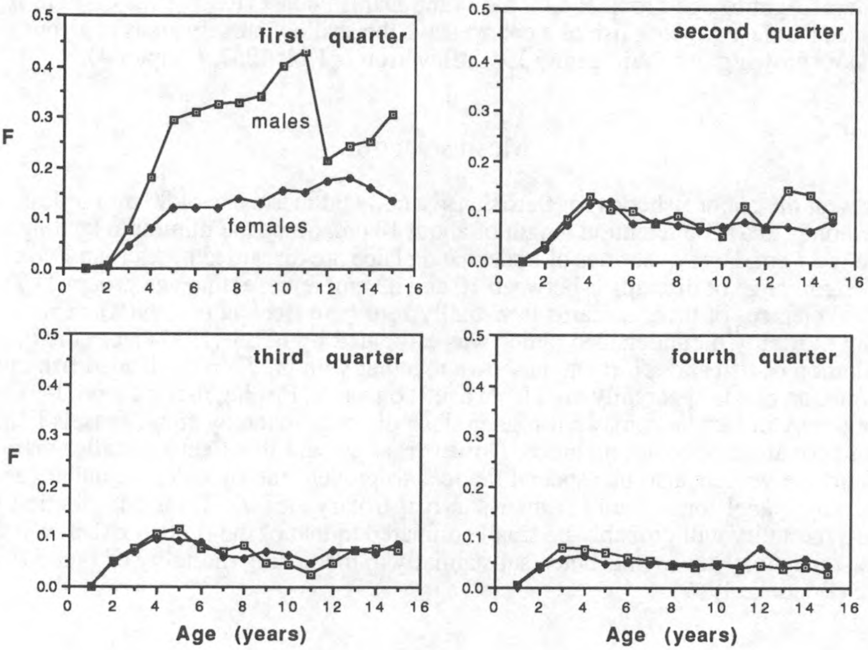


Figure 4. Quarterly exploitation patterns of males and females in the period 1974-1977 excluding discards.

Differences in catchability of male and female

Beverton (1964) showed that males have a higher catchability than females. Figure 3 shows that fishing mortalities on males are indeed higher. In order to trace the origin of this difference, the annual F-values were partitioned over the quarters in proportion to the quarterly landings of the various age-groups by sex. Figure 4 shows that the differences in *F* are restricted to the first quarter when plaice spawns. This suggests that behavioural differences during spawning affect their vulnerability to fishing gear, which may be related to the fact that males stay for a much longer period on the spawning grounds than females (Wimpenny 1953; Beverton 1964; Chapter 4), as well as to differences in vertical migrations during spawning time (Arnold *et al.* in prep).

Conclusion

Fishing mortality is mainly determined by the overlap of spatial distributions of the various age groups on the one hand and that of fishing effort on the other, although the increase in vulnerability of males during the spawning period suggests that also a behavioural component is involved.

HISTORIC LEVEL OF FISHING MORTALITY

Although no estimates of the level and pattern of exploitation are available for the late 19th and early 20th century, it may be inferred from the high landings that it probably did not differ much from the 1930 level. The estimated F-values for the latter period range from 0.3 (Bannister 1978) to 0.7 (Beverton & Holt 1957). Obviously these values are not very precise and it seems likely that the average fishing mortality has been in the same order of magnitude (0.5) as in recent years (ICES 1991).

Some inferences on the exploitation pattern for the historic period can be made from the distribution of effort. In the first half of the century, the United Kingdom (UK) was responsible for 35-60% of the total international landings. The distribution maps of the UK effort given by Bannister (1978) indicate that effort was distributed all over the southern and central North Sea. Fishing effort of the other countries e.g. Netherlands, Germany and Denmark, taking account of 40-60% of the international landings, was concentrated in the southern and southeastern parts (Wimpenny 1953). During the 20th century the fishing grounds of the trawler fleets have not changed very much, although the fishing effort in the coastal nursery grounds, which also employed smaller mesh size, may have been higher in the past. The main changes that occurred are in the types of gear used and the power of the fishing vessels. Data on the relationships of catch efficiency and fish size of commercial gears used in the past are not available, but it is likely that catch efficiency may have declined with fish size in the historic period as a result of lower towing speeds and lower weight of the gear. The historic exploitation pattern thus might have shown a more distinct peak on the youngest age-groups. However, without more detailed information, it seems justified to assume that the exploitation pattern as observed in the last 30 years also applied to the previous period.

Table 1. Parameter values used in the simulation of growth and reproductive investment in male and female plaice.

	Males	Females
Bertallanfy growth parameters: $L_t = L_{inf} (1-e^{-Kt})$		
L_{inf}	39.7	51.3
K	0.41	0.24
t_0	0.31	0.005
Surplus production (kg): $SP = \alpha W^{\beta}$		
α	0.12	0.20
β	0.17	0.25
L(cm)		
1985	22	33
1910	32	38
Reproductive investment (kg): $m_t=\gamma W_t^{\delta}$		
γ	0.10	0.16
δ	1.0	1.0
Fecundity (eggs.g^{-1}):	-	265

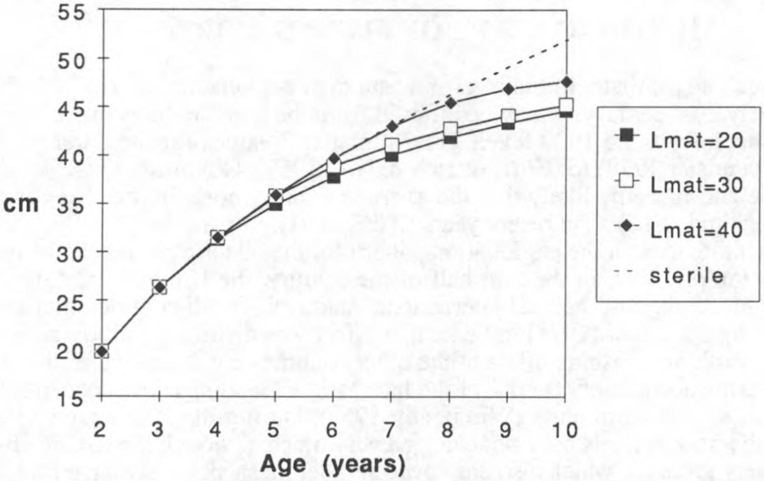


Figure 5. Simulated somatic growth curves of female plaice varying in the length at first maturity (L_{mat}) with a surplus production - body weight relationship according to Table 1. The dashed line indicate the somatic growth of females that do not become sexually mature.

SELECTION DIFFERENTIALS

With the above information we now can evaluate the effect of exploitation on the fitness of various reproductive traits. The first step is to model the interaction between somatic growth, reproductive investment and maturation using equation (3) and parameter values from Table 1. The onset of sexual maturity was simulated by specifying a length at 50% maturity and a range of 10 cm over which the maturity linearly increased from 0% to 100%. Figure 5 shows the effects of the L_{mat} on somatic growth. The dashed line indicates the expected somatic growth without maturation. The somatic growth of a female that matures at a small size lags behind that of a female maturing at a larger size, but the reduction in somatic growth becomes smaller when L_{mat} decreases (Fig.5). For instance, a L_{mat} =20 (A_{mat} = II) does not decrease somatic growth substantially until age V. Obviously the reproductive investment at age III and IV, which is a fixed proportion of the body weight, is still insignificant compared to the total available surplus production.

The second step is the calculation of the fitness using Fisher's reproductive value:

$$V_0 = \Sigma \lambda^{-x} l_x b_x \qquad (6)$$

where λ is the intrinsic rate of population increase, l_x is the survival to age x and b_x is the number of females born at age x. The fitness of a reproductive trait will depend on the population growth parameter λ. Therefore, the present value of λ was estimated for the total population of female plaice from the life table given in Table 2, using empirical estimates for all relevant parameters. The l_x was estimated according to equation (4) using

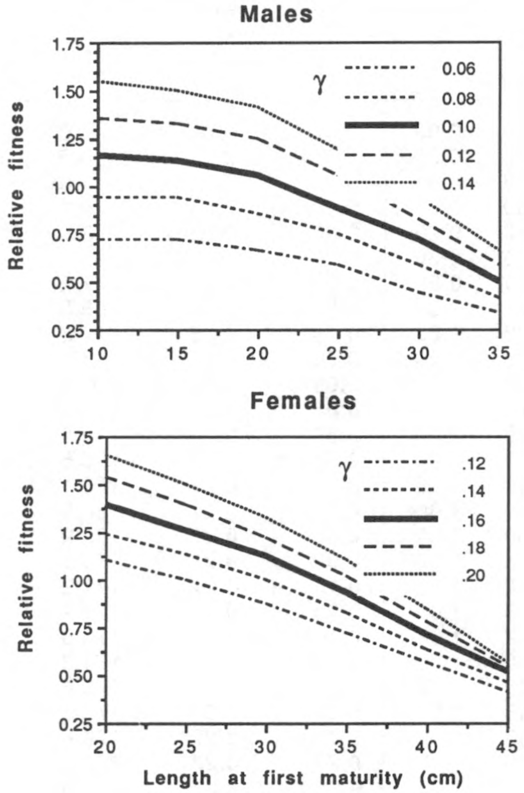


Figure 6. Fitness profiles for length at first maturity (L_{mat}) for various levels of reproductive investment (g) with $\lambda = 1.0$. The fitness is expressed relative to that at the average observed length at first maturity and the observed reproductive investment. males: L_{mat}= 22 cm, $\gamma = 0.10$; females: $L_{mat} = 33$ cm, γ=0.16.

estimates for M_x and the average F_x from sexes separated VPA for the period 1958-1986, after correction for discarding. Natural mortality was assumed to increase geometrically with age from a low of 0.08 (females) and 0.14 (males) at age II to reduce the adult life span to a realistic value of 30 years. $M_0 = 10.38$ and M_1 was taken at 0.20. The calculations gave an estimate of $\lambda = 1.056$.

Fitness profiles for L_{mat} and reproductive investment, assuming $\lambda = 1.00$, are given in Fig.6. Fitness values are expressed relative to the fitness values of the present reproductive tactic (male: L_{mat} =22 cm, γ=0.10; female: L_{mat} =33 cm, γ=0.16). In both males and females fitness decreases with increasing L_{mat}. The fitness of the L_{mat} in the early 1900's compared to the present L_{mat} is 0.42 (males) and 0.80 (females). Assuming

Table 2. Life table of female North Sea plaice giving an estimate of λ = 1.056. Length is given by the von Bertalannfy growth equation from Table1. Weight (W_x)=10^{-5} x Length^3; P_x is the proportion maturity (Chapter 1); M_x is the natural mortality; F_x is the average fishing mortality from VPA for 1958-1986 including discards;. b_x=W_x x P_x x 265 x 0.5, represents the number of female eggs produced; l_x represents the survival of one female offspring.

Age (x)	Length (cm)	W_x (kg)	P_x	M_x	F_x	b_x x10^3	l_x x10^{-6}	$\lambda^{-x} l_x b_x$
0	0.0	0.000	0.00	10.38	0.00	0.0	10^6	0.000
1	10.8	0.013	0.00	0.20	0.14	0.0	30.99	0.000
2	19.4	0.073	0.01	0.08	0.39	0.0	22.06	0.000
3	26.2	0.180	0.06	0.08	0.41	0.1	13.74	0.001
4	31.5	0.313	0.29	0.08	0.35	3.5	8.45	0.024
5	35.7	0.456	0.80	0.08	0.32	38.6	5.49	0.162
6	39.0	0.594	0.99	0.08	0.29	77.2	3.68	0.205
7	41.6	0.721	1.00	0.08	0.27	95.5	2.53	0.165
8	43.7	0.833	1.00	0.08	0.26	110.3	1.78	0.127
9	45.3	0.928	1.00	0.08	0.27	123.0	1.26	0.095
10	46.5	1.009	1.00	0.08	0.27	133.6	0.89	0.069
11	47.5	1.075	1.00	0.08	0.29	142.4	0.62	0.049
12	48.3	1.129	1.00	0.08	0.28	149.6	0.43	0.033
13	49.0	1.173	1.00	0.08	0.27	155.5	0.30	0.023
14	49.4	1.209	1.00	0.09	0.27	160.1	0.21	0.016
15	49.8	1.237	1.00	0.09	0.27	163.9	0.14	0.010
16	50.1	1.260	1.00	0.09	0.27	166.9	0.10	0.007
17	50.4	1.278	1.00	0.09	0.27	169.3	0.07	0.005
18	50.6	1.292	1.00	0.10	0.27	171.2	0.05	0.003
19	50.7	1.303	1.00	0.10	0.27	172.7	0.03	0.002
20	50.8	1.312	1.00	0.11	0.27	173.9	0.02	0.001
21	50.9	1.320	1.00	0.13	0.27	174.8	0.02	0.001
22	51.0	1.325	1.00	0.14	0.27	175.6	0.01	0.001
23	51.0	1.330	1.00	0.17	0.27	176.2	0.01	0.000
24	51.1	1.333	1.00	0.21	0.27	176.6	0.00	0.000
25	51.1	1.336	1.00	0.27	0.27	177.0	0.00	0.000
26	51.1	1.338	1.00	0.38	0.27	177.3	0.00	0.000
27	51.2	1.340	1.00	0.60	0.27	177.5	0.00	0.000
28	51.2	1.341	1.00	1.06	0.27	177.7	0.00	0.000
29	51.2	1.342	1.00	2.21	0.27	177.8	0.00	0.000
30	51.2	1.343	1.00	4.42	0.27	177.9	0.00	0.000

λ= 1.056, these ratios become 0.37 (males) and 0.76 (females). Figure 6 also shows that fitness has not yet reached the maximum level at the current level of exploitation, suggesting that there is still selection for a reduction in the L_{mat}. With regard to reproductive investment, the simulations indicate that there is selection for an increase in reproductive investment.

The selection differential that corresponds to the estimated fitness profile for L_{mat} at λ=1.00 can be approximated by calculating the average L_{mat} weighted over the fitness profile. The calculation is illustrated in Figure 7. With an average L_{mat} = 35 cm, halfway between the present and historic value, and with a S.D = 2.5 cm (Chapter 4), the weighted average L_{mat} was calculated as 34.73 cm, giving a selection differential of 0.27 cm. At

λ=1.056 the selection differentials becomes 0.33 cm. For males (L_{mat} = 27 cm, S.D. = 5 cm) the selection differential was calculated as 1.89 and 2.09 cm for λ=1.00 and λ=1.056 respectively.

DISCUSSION

The accuracy of the estimated fitness values depends on the relationship between surplus production and body weight, the measure of reproduction, the mortality estimates and the innate rate of population increase (λ). The two former parameters are likely to be less certain. The fit between the observed values and the assumed surplus production - body weight relationship is far from perfect (Fig.1), making the fitness estimates necessarily crude. Also the use of reproductive energy as a measure of gene propagation is a rather crude simplification. In females this assumption neglects the possibility of differences in the viability of eggs produced at different ages or maternal body sizes. In males, gene propagation is an even more difficult question, and it may be speculated that in addition to the available reproductive energy, also the competitive power in relation to other males will play an important role. The latter may be a function of body size. If true this would reduce the fitness of precocious males. It was also assumed that there is no mortality cost of reproduction, although the opposite can be expected (e.g. Roff 1983, 1991). Comparison of the fitness ratio for λ= 1.0 and λ = 1.056 indicated only a small influence on the estimated difference in fitness ratio. Although a value close to unity will be

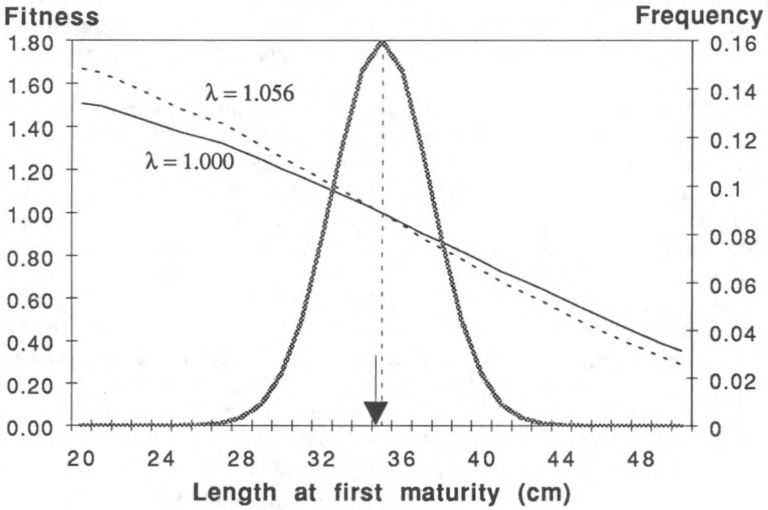


Figure 7. Estimation of the selection differential from the fitness profiles of female plaice with a L_{mat} that is normally distributed with μ=35 cm and σ=2.5 cm. The arrow indicates the average length at first maturity (L'_{mat}=34.73 cm), weighted over the fitness profile at λ=1.00. The selection differential is the difference between μ and L'_{mat} (S = 0.27 cm). The fitness profile for λ=1.056 is shown by the dashed line.

likely, the true value during the period 1900 - 1990 will probably have varied around unity. The mortality estimates will be reasonably accurate since they are dominated by the fishing mortality that is well estimated for the recent period. Backwards extrapolation to the historic period however remains speculative. Given the above considerations, the fitness profiles should be taken as crude estimates indicating the likely level and direction of selection.

Between 1910 and 1985 the L_{mat} decreased by 10-13 cm in males and 3-7 cm in females. In order to estimate the change per generation, the age at which an individual has produced 50% of its offspring was estimated as an approximation of the generation time. At the present level and pattern of exploitation, the generation time was 4.8 and 7.7 years, corresponding to 15.6 and 9.7 generations, of males and females, respectively. The change in L_{mat} per generation is then 11.5/15.6=0.74 cm in males and 5/9.7=0.52 cm in females. Within the period 1963-1988 female L_{mat} decreased by 0.026 cm.year^{-1}, or with 7.7x0.026=0.20 cm per generation. Although this value did not differ significantly from zero, it suggests that the change may have been smaller in the recent period.

An estimate of the 'observed' selection differential (S) can be obtained from $R = h^2 S$, where R is the change in a quantitative trait per generation and h^2 is the heritability coefficient (Falconer 1989). Taking a mean heritability for life history traits of $h^2 = 0.24$ (Roff 1991), S can be calculated as 0.74/0.24 = 3.1 cm in males and 0.52/0.24 = 2.1 cm for females. The 'predicted' selection differentials, estimated from the fitness profiles for λ=1.00, were 1.89 and 0.27 cm for males and females respectively. Averaged over males and females the selection differential is 1.08 cm. For λ=1.056 the selection differentials are 2.09 (males), 0.33 (females) and 1.21 cm (male and female).

The 'observed' selection differential is higher than the 'predicted' value, especially in females. Whether the averaged selection differential for males and females is a correct measure depends on the genetic coding of the onset of sexual maturity. If autosomal genes affect L_{mat}, selection on one sex will influence the other sex as well and different selection pressures on the sexes may result in an average effect. In this case it is essential to study the selection differential of both males and females. However, if maturation is primarily coded by genes on the sex chromosome, the selective effects on male and female will be independent.

The 'observed' and 'predicted' selection differentials were at least qualitatively in agreement. This agreement however, does not necessarily indicates that the observed decrease in L_{mat} is due to a genetical change, it can also be a phenotypic response to improved conditions for growth. Although a discussion of the phenotypic versus genetic changes is beyond the scope of the present paper, a genetic change in L_{mat} is not unlikely since the observed decrease in L_{mat} is in the opposite direction of the expected change due to phenotypic plasticity. Present day variation in L_{mat} suggests that at a higher growth rate in the juvenile phase, as actually observed in North Sea, L_{mat} should increase rather than decrease (Chapter 4). The question is even more complicated if we realise that there exists a cline in L_{mat} and A_{mat} within the North Sea,which could be related to differences in growth rate several years before the actual onset of sexual maturity.

The simulations predict that fitness should increase with increasing reproductive investment. The increase in fecundity since the late 1940's of the smaller females (30 cm) is unlikely to be due to phenotypic plasticity, because Chapter 7 and Millner *et al.*(1991) obtained evidence that improved conditions for growth will mainly result in a higher somatic growth, but not in a higher size-specific fecundity. It may therefore be tentatively concluded that the increase in fecundity of small fish might be related to a genetical change. In contrast to the prediction however, the fecundity of larger females did not increase, suggesting that the fitness calculation may be deficient in some respect. The model assumed that the cost of reproduction was restricted to a reduced future fecundity, although an additional mortality cost may also occur because body reserves become severely depleted during spawning (Roff 1991). Also a further increase in reproductive investment may be impossible due to morphological constraints.

It is obvious that our ignorance with regard to many of the factors influencing the fitness of reproductive traits in plaice make any conclusion speculative. The best we can achieve is a consistent and concise description of the empirical data in terms of a basic model describing the interaction of growth and reproduction. The at least qualitative agreement between the predicted and expected change in L_{mat} give some support for a genetical change.

In the present study only age-based methods were used to study the mortality imposed by fishing in relation to sex, reproductive status and age. Analysis of the effects of this additional mortality on the fitness of slower and faster growing fish is therefore not possible. Such an influence is not unlikely since it is known that recruitment to the fishing grounds and the onset of sexual maturity is influenced by both size and age. If the catch efficiency of the commercial trawl declines with fish size we further can expect a size-selective component additional to the age-dependent component. These size differentials will mainly affect the fitness of fast- and slow growing genotypes. If the additional mortality is high at an intermediate size groups of plaice we can expect that fast growing genotypes will have an advantage over slower growing genotype because they have a reduced time period of highest vulnerability. If the additional mortality is high beyond the size at first maturity the slow growing genotypes will have an advantage. Future studies of the size-selective aspects of fishing mortality may reveal whether the observed changes in growth rate of juveniles may be in line with the changes which can be expected due to the selective effects of fishing.

Part II

CHANGES IN POPULATION PARAMETERS SINCE 1900

Chapter 3

Density-dependent and independent changes in somatic growth of female North Sea plaice (*Pleuronectes platessa* L.) between 1930-1985 as revealed by back-calculation of otoliths

Rijnsdorp, A.D. and Leeuwen, P.I. van. Density-dependent and independent changes in somatic growth of female North Sea plaice (*Pleuronectes platessa* L.) between 1930-1985 as revealed by back-calculation of otoliths. - Mar. Ecol. Prog. Ser. in press

ABSTRACT. Changes in the somatic growth of female plaice between 1930 and 1985 is studied by back-calculation of otoliths. It is shown that in the period 1940-1949 growth rate was reduced, which coincided with a threefold increase in the plaice stock due to the closure of the fishery during the second world war. The growth reduction was largest in large fish (>45 cm) as compared to medium sized fish (30-40 cm), but could not be detected in the size classes below 20 cm. In large plaice the growth reduction occurred later in time as compared to the medium sized fish. Growth in the immediate pre- and post-war years appeared to be similar. At some time in the 1950's and 1960's a growth acceleration started in the size classes up to 30 cm, which levelled off in the 1970's. This growth acceleration was largest in the smallest size classes. Within the period of growth acceleration, the 1963 year class, which was about three times the average year class strength, showed a slight but significant reduction in growth. The reduction in growth was restricted to size classes < 30 cm and was largest in smaller fish. It is concluded that growth rate in plaice is reduced at high density both in the juvenile phase (pre-war period and year class 1963) and in the adult phase (period 1940-1949). The increase in growth of juvenile plaice starting in the 1950's appears to be related to an increase in the availability of food in the coastal waters of the southern North Sea.

INTRODUCTION

Growth rate of fish is a characteristic that may show considerable changes in response to food availability, population density and temperature (Weatherley & Gill 1987). In addition, growth rate may be under selective pressure by the fishery (Ricker 1981; Nelson & Soulé 1987). In order to evaluate the influence of each of these factors, long time series of growth data are required which are collected in a consistent way.

North Sea plaice is a suitable candidate for such an analysis, because this well studied species has shown substantial changes in growth and remarkable fluctuations in population density due to the reduced fishing during two war-time periods. The older literature, reviewed by Wimpenny (1953) and Bannister (1978), suggests density-dependent growth effects, based on smaller length at age of strong year-classes and on a reduced length or weight at age during war time periods (Borley 1923; Bückmann 1944; Beverton & Holt 1957). More recent studies have been unable to provide convincing evidence for density-dependent growth, although a considerable increase in growth rate of small plaice has been observed in the 1960's and 1970's (Bannister 1978). Rijnsdorp & van Beek (1991) suggested that this increase in growth is related to an increased availability of food.

Long term growth studies have a number of inherent difficulties. Firstly, it is always questionable whether age determinations carried out over a long time period by different people have been consistent. In plaice, age determinations have traditionally been carried out using untreated otoliths. This methodology is suitable for ageing the younger, fast growing fish up to about 8 years old, but may seriously underestimate the age of older, slow growing plaice (Heincke 1907; van Leeuwen & Groeneveld 1988). In addition, a different assumption about the date of birth as the reference to age determinations have been made in the past (January 1, April 1 or variable depending on the appearance of a new growth zone; compare Wallace 1907, 1914). A study of growth in plaice is further complicated because the size and age-groups are distributed differently (Heincke's law: Wimpenny 1953). Small plaice are concentrated in the shallow coastal and estuarine nursery grounds from where they disperse over the deeper off-shore grounds. Since this dispersion is size- and age-dependent (Beverton & Holt 1957; Chapter 4), it is necessary to take account of the differences in spatial distribution of slow and fast growing fish. This problem can be circumvented for adult fish if sampling is restricted to the spawning period, when the mature plaice gather on the spawning grounds (de Veen 1964).

One possible way to overcome sampling and age reading problems is to reconstruct the changes in growth from the pattern of otolith growth employing a back-calculation technique (Southward 1962). The back-calculation technique has been validated for plaice using tagging experiments in combination with tetracycline labeling of otoliths (Rijnsdorp *et al.* 1990). This paper presents the results of a back-calculation study of female North Sea plaice using otoliths collected between 1948 and 1985. The older fish included in these samples allowed us to look back as far as the late 1920's. We will focus on changes in growth during the period of the second world war (1940-1945) as compared to that in the immediate pre- and post-war years, and to the growth acceleration in the 1960's and 1970's. Special attention is further given to the question of which size classes of plaice have been particularly affected. The observed changes will be discussed in relation to trends in population abundance.

MATERIAL AND METHODS

Otolith samples

The somatic growth of female plaice in the period 1930 - 1985 was studied by back-calculation of growth patterns in otoliths. Otolith samples collected in the southern North Sea, roughly between 52° and 54°N and 1° and 4°E, and in the spawning period between January and March were considered, except for a few otoliths collected in summer in 1955. The study was constrained by the availability of otolith samples, since prior to 1958 when intensive sampling started in among others the Netherlands, only limited numbers were available. From the period 1948-1955 two sets of otolith samples (set 2 and 3) were made available by the Fisheries Laboratory Lowestoft (courtesy of Drs R.S. Millner and J.D.

Riley). These otolith sets represent a length stratified random selection of plaice >25 cm of age-groups IV-XV, with a few older females up to age-group XXVIII. In the period 1958-1985 otoliths were selected from Dutch market samples belonging to individual year classes sampled at age-IV, V, VI, VIII, X-XVI (sets 4-7) or from a range of fish sizes in individual years (set 8-10). Although not sampled at the appropriate time and place, additional otoliths collected during summer on coastal grounds just north of Terschelling in 1932 and 1933 (otoliths set 1), were analysed to compare estimates of juvenile growth rate from otolith of old fish and of young fish. In total 1421 otoliths of individual females between age II and XXVIII were studied. A summary of the age composition of the available otolith sets is given in Table 1.

Back-calculation method

Preparation of otoliths and back-calculation procedure followed Rijnsdorp *et al.* (1990), of which a short summary follows. One otolith per fish was cut along the lateral plane through the nucleus, polished and burned on a brass plate above a Bunsen gas flame to clarify the pattern of white and dark bands. The burned otoliths were mounted in plasticine and read with a binocular microscope under reflected light. The outer tips of the hyaline bands were drawn on paper using a drawing mirror at a magnification of 24x and the maximum diameter of each annulus was measured from the drawing with a ruler in units of 0.5 mm. The measurements were all taken using the main axis of growth of the otolith.The length at the time of annulus formation (L_i) was calculated according to

$$L_i/L_t = \alpha\,(O_i/O_t)^{\beta} \qquad (1)$$

Table 1. Summary of the available otoliths samples used. Sampling type indicates whether the otoliths were sampled from a size-range of plaice (S) or from a particular year-class (Y).

	Otolith set									
	1	2	3	4	5	6	7	8	9	10
Type	S	S	S	Y	Y	Y	Y	S	S	S
Year/	1932	1948	1955	1955	1963	1969	1972	1982	1960	1974
Year class	1933	1951		1961			1974	1985		
Age										
II	1	0	0	0	0	0	0	0	0	0
III	10	0	0	2	0	0	4	8	0	12
IV	5	1	2	51	39	40	50	35	6	6
V	32	4	2	23	43	43	50	28	7	7
VI	17	8	4	35	33	41	47	28	10	9
VII	8	3	5	48	0	0	9	22	11	3
VIII	6	0	6	43	36	39	15	9	9	5
IX	6	5	0	41	0	0	20	9	2	1
X	5	4	1	26	33	28	14	8	7	2
XI-XV	6	13	6	23	0	0	6	5	24	24
XVI-XX	2	22	0	0	18	0	0	0	5	15
XX-XXX	0	7	3	0	0	0	0	0	5	5
Total	98	67	29	292	202	191	215	152	86	89

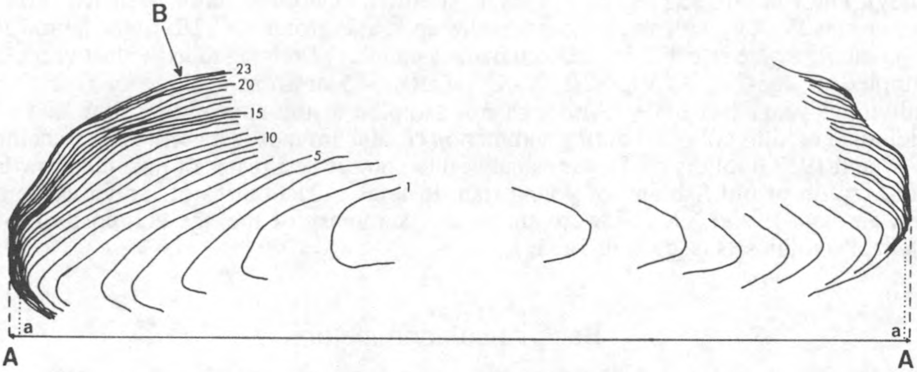


Figure 1. Drawing of a transversal section of an otolith of a female plaice caught on 18 June 1955 (#18, set 3). The age was estimated at 23 years. Otolith measurements for back-calculation were made along the main axis of growth A-A. Age determination employed the axis B-B, which facilitated the determination of the annuli. Around age X the direction of otolith growth gradually changed and new growth zones were increasingly laid down in the ventral-dorsal direction. The zone between the dashed and the full line shows the zone where otolith measurements were interpolated because annuli could no longer be recognised individually along the main axis of growth A-A.

where L_t is the length at capture; O_i is the otolith diameter of the ith annulus in the otolith; O_t is the diameter of the total otolith; α is the proportionality coefficient and β is the back-calculation coefficient estimated from the relationship between fish length and otolith width ($\beta = 1.364$). Rijnsdorp *et al.* (1990) presented evidence for the validity and accuracy of the back-calculation method and further showed that the time of annulus formation corresponds to April 1.

Since it was our purpose to reconstruct growth rate of plaice as far back in time as possible, we have used otoliths of very old females, which need special treatment. Fig.1 shows a drawing of a transversal section of a burned otolith of a 23-years old female plaice. The pattern of light and dark zones can be recognized easily in the central parts of the otolith, but at the periphery the annuli become densely packed. The age can be estimated most easily by counting the annuli from the centre to the arrow B. Drawing the outer tips of the annuli, projected on the major growth axis A-A, however, becomes difficult in the peripheral zone. The dense packing of annuli along the major axis is due to a change in the direction of growth of the otolith, which occurred around age X. Up to this age, the annuli were laid down in the posterior-anterior direction, whereas beyond this age the direction of growth shifted more and more to the dorso-ventral axis. This change in the axis of growth occurs gradually. When the packing of annuli along the major growth axis became so dense that the individual annuli could no longer be distinguished, the diameter was interpolated between the ultimate otolith size and the size of the last annuli which could be effectively distinguished. This is indicated by the dashed lines in Fig.1. Interpolation of otolith measurements implies that within the year range that corresponds to the interpolated annuli, no differences in growth could be distinguished between individual years. Interpolation occurred in about 30% of the females beyond age group XII or size >45 cm.

The back-calculation method assumes that the curvilinear relationship between otolith width and body size as estimated for the population also applies to individual females, or in other words that the back-calculation coefficient β in equation (1) applies to individual female. It is likely, however, that individual females will differ in the body size at which the change in direction of growth of the otolith starts, as well as in the extent to which this occurs. Deviations of the individual back-calculation coefficient from the population estimate will introduce a bias in the estimated growth curve of that individual. If $\beta_{individual} > \beta_{population}$ the growth at early ages will be overestimating and the growth at older ages will be underestimated. Since the otolith width - body size relationship was determined over a range of body sizes from 8-60 cm, only otoliths of fish <60 cm were included in the analysis. Although individual growth curves may be biased to some degree, the average growth estimates should be unbiassed.

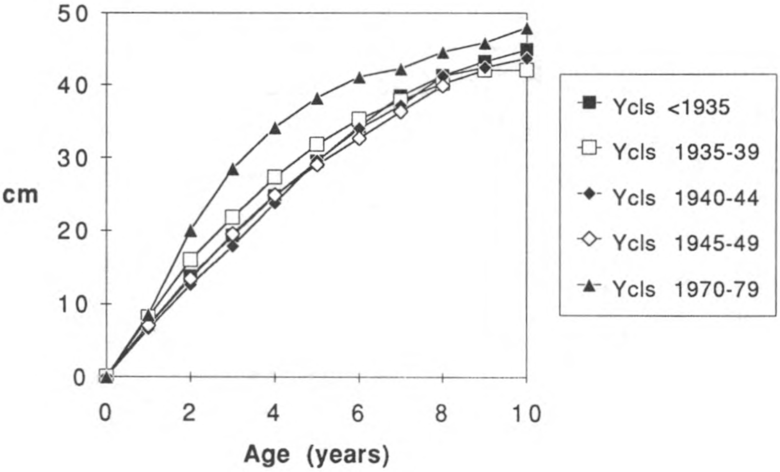


Figure 2. Average back-calculated length at age I-X of year classes born in various time periods since 1925.

RESULTS

The average back-calculated lengths for females born in various periods since 1925, omitting females sampled at an age <6 years (see below), show that the present growth rate (year classes 1970-1979) is substantially higher (t-test, $P<0.05$) than in year classes born before 1950 (Fig.2). The length of the year classes born between 1935-1939 is higher than those born between 1940-1949 up to age group VI but then becomes smaller, the difference being significant for age groups II - V (t-test, $P<0.05$). The length of plaice born during the war (1940-44) is smaller than any other group of year classes for age group II - IV, but varies around a similar value for older age groups. The difference is significant with year class 1970-79 and 1935-39 ($P<0.05$) and almost significant with year classes 1945-49 (t-test, $0.05<P<0.10$). It is difficult to interpret the changes in the average cumulative length shown in Fig.2 in terms of changes in the rate of growth in certain periods. Because the

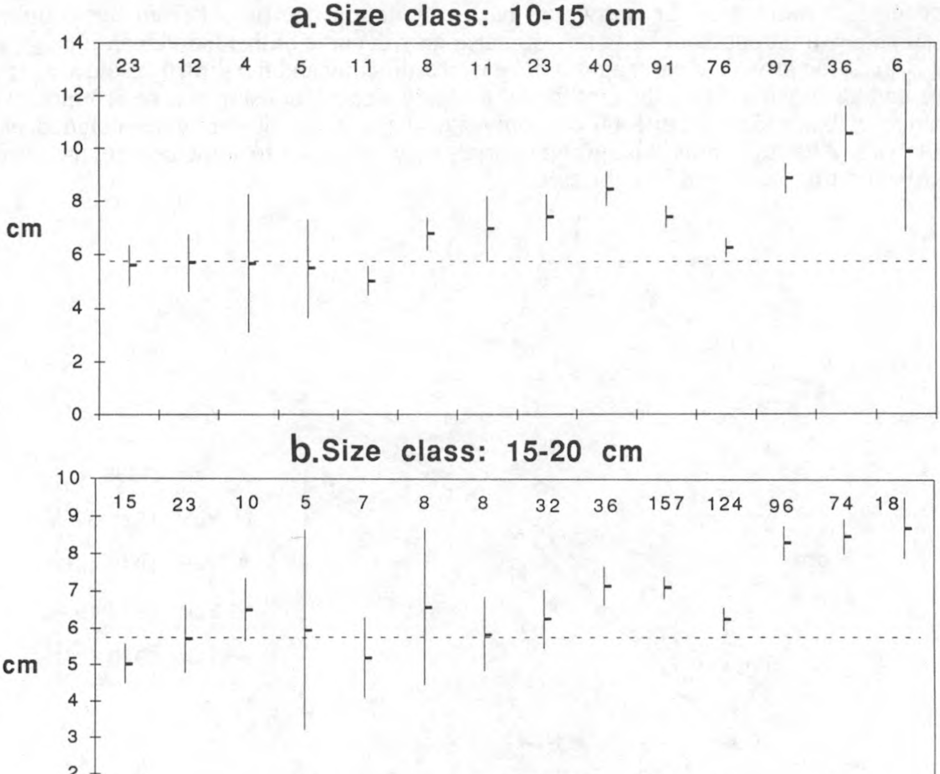


Figure 3 Back-calculated annual length increments in the period 1930-1984 for different size classes of female plaice. The vertical bars indicate 2 x S.E. The dashed line shows the pre-war length increment. The numbers in top indicate the number of observations.

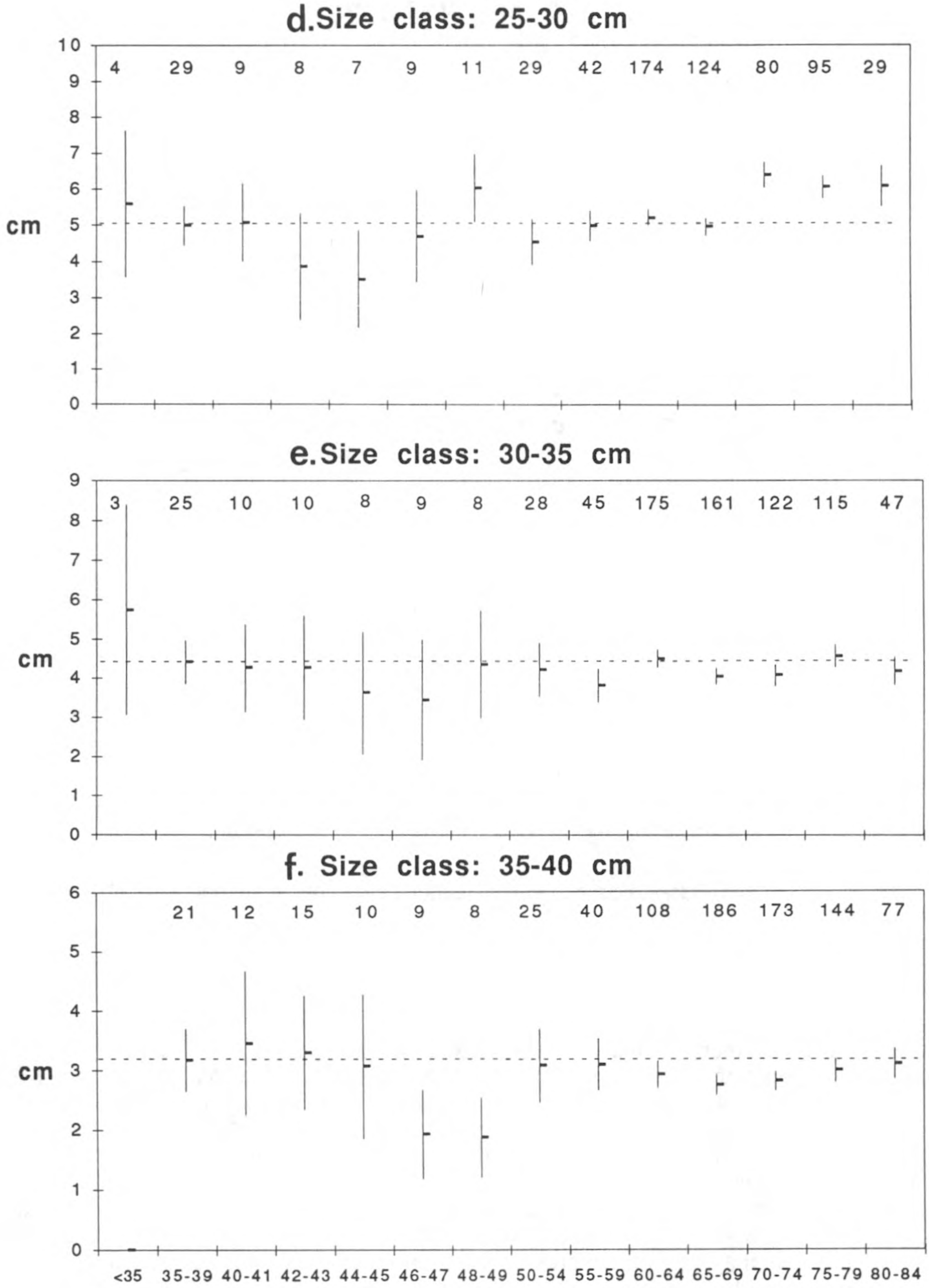
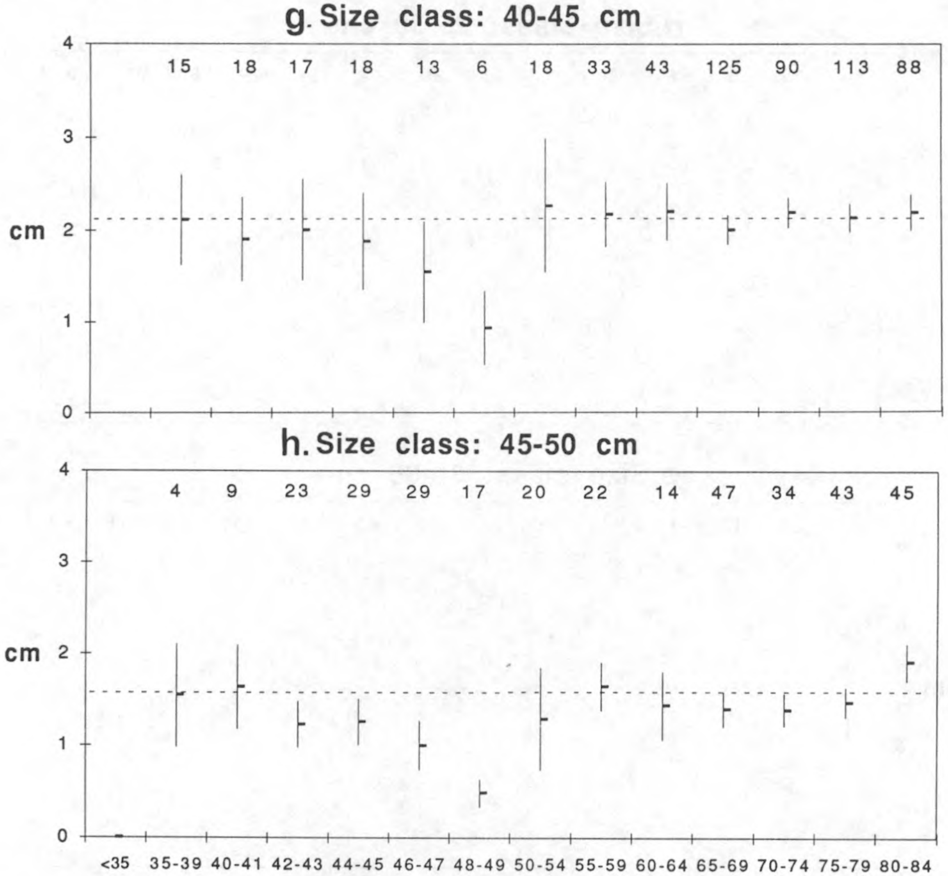


Figure 3 continued. Back-calculated annual length increments in the period 1930-1984


g. Size class: 40-45 cm

h. Size class: 45-50 cm

Figure 3 continued. Back-calculated annual length increments in the period 1930-1984.

annual length increment decreases with fish size, the analysis of the changes in growth should take account of the size of the fish. We therefore estimated the length increments for 5-cm size classes in various time periods of 5-years. The time period between 1940 and 1949 was divided into five 2-year periods, because if there is an effect of density due to lack of exploitation, then this effect will gradually build up and shorter time periods might show the development in the density-dependent effect more clearly.

The annual length increments, estimated from the pooled data of otolith sets 2-10, are shown in Fig.3a-h together with the approximate 95% confidence limits. Since an individual female may provide several estimates of length increment in a particular size-class or time-period, the mean length increment was calculated for each female before calculating the population average. The number of observations in the legend thus refers to the number of individual females in a particular cell. In general, the confidence limits are much wider in the earlier periods due to lower sampling levels.

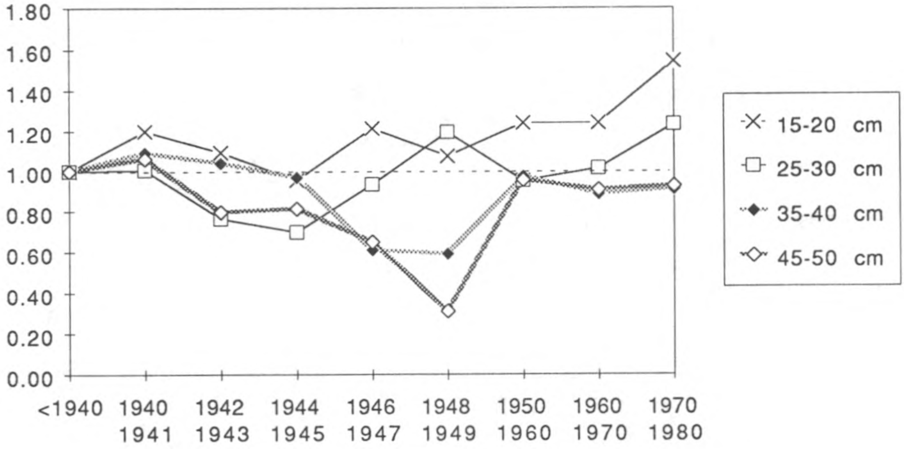


Figure 4. Growth rates, standardized to the growth rate in the pre-war period, of a selection of size-classes illustrating the difference in the timing and the level of the reduction in growth in the period 1940-1949.

The growth estimates of size-class 10-15 cm indicate an almost twofold increase after 1950 compared to the 1930's. The growth acceleration is also shown by larger size-classes up to 25-30 cm, but is absent in the larger ones. A growth reduction during the war is only apparent in the size-classes 20-25 and larger. The magnitude of the growth reduction appears to increase with size, and the timing shifts from actual war-time period (1940-1945) in size classes 20-30 cm to the immediate post-war years in the larger plaice (Fig.4). Finally, the present growth rate of size classes >=30 cm is markedly similar to the one in the pre-war period.

The back-calculated growth rates for the pre-war period based on otolith samples collected on the spawning grounds between 1948-1951 showed a close agreement with the growth rate back-calculated from the 1932-1933 samples collected on the nursery grounds in size classes <10 cm and 10-15 cm (Table 2). However, for the size classes 15-19 cm and 20-25 cm the estimates from the nursery samples were slightly lower. From the 1932-1933 samples only age groups II-VI were selected because these are typically representative for the coastal grounds. The growth rate of the females between VI-XII years old was somewhat lower, about 0.6-1.3 cm less than the females of age groups II-VI of size class up to 24.9 cm. For size classes between 25 and 35 cm the average annual growth was 2.7 cm. However, these older females are considered to be not representative since they have been sampled on the shallow nursery grounds and not in the more deeper offshore waters.

Fig. 3 shows that in the period 1965-1969 a dip in growth rate occurs in the three smallest size classes, which is related to the 1963 year class. This year class was about three times the average size and strongly dominated the data set for this period. In order to analyse whether this year class differed in growth rate it's growth is compared to that of year classes born between 1955-1960 (set 4) and between 1969-1974 (pooled data set 6 and 7). Fig.5 clearly shows that the annual length increment of the 1963 year class was reduced in the size classes up to 30 cm. Compared to the 1955-1960 year classes the largest reduction in growth occurred in the smallest size classes. The data for the 1969-1974 year classes again illustrate the increase in the growth during the 1970's.

Table 2. Back-calculated length increments in the period 1920-1939 from A: otoliths of 2-6 year old female plaice collected in June on the nursery grounds north of Terschelling (set 1) and B: otoliths of adult females collected on the spawning grounds in 1948-1951 (set 2)

	A: Set 1 samples 1932-33			B: Set 2 samples 1948-1951		
Size-class (cm)	Growth (cm)	S.D. (cm)	n	Growth (cm)	S.D. (cm)	n
<10	6.3	1.5	59	6.8	1.8	44
10-14	5.7	1.4	47	5.7	1.9	26
15-19	4.8	0.8	38	5.2	1.5	30
20-24	4.5	1.2	20	5.6	1.8	33
25-29	-	-	-	5.0	1.5	32
30-34	-	-	-	4.8	1.9	28
35-39	-	-	-	3.2	1.4	24
40-44	-	-	-	2.6	1.8	18
45-50	-	-	-	1.3	0.5	5
>50	-	-	-	1.9	-	1

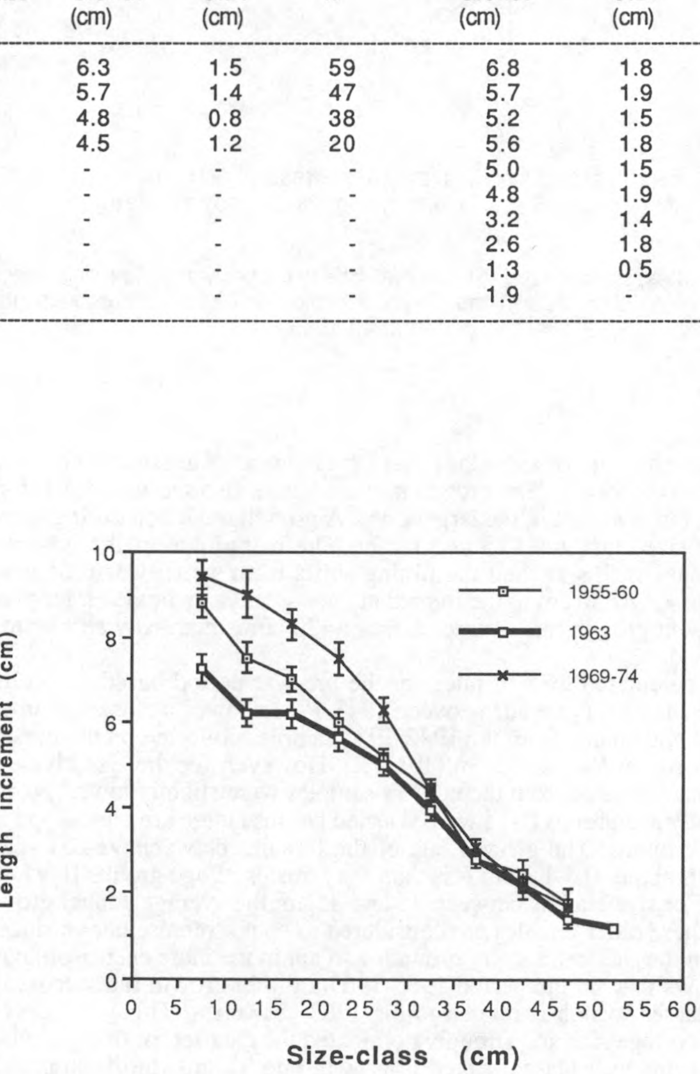


Figure 5. Back-calculated annual length increments in relation to body size for year class born in 1963, which was about three times the average size, compared to those born earlier (1955-1960) and later (1969-1974). The vertical bars indicate 2 x S.E.

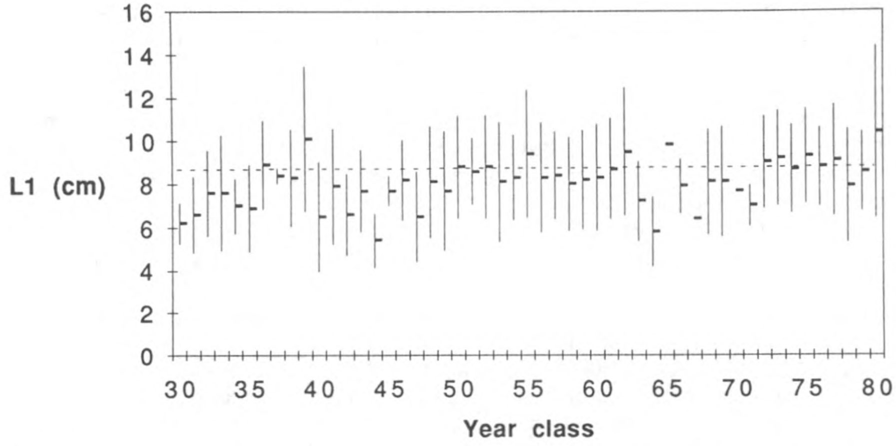


Figure 6. Variations in the back-calculated length at the end of the first year (L1 in cm) for the year classes born between 1930 and 1980.

The length at the end of the first year (L1) and the approximate 95% confidence limits for year classes born between 1930 and 1980 is plotted in Fig.6. For the year classes born in the late 1920's two estimates are available: those based on otolith samples collected since 1948 on the spawning ground; and those based on otolith samples collected in 1932 and 1933 on the nursery grounds north of Terschelling (Table 2). The results of both samples were close. The number of observations varies substantially between individual year classes and the results can therefore be used only to inspect changes in overall level between periods. The L1 of year classes 1930 - 1950 varies around 7 cm, with slightly higher values for year classes 1936-1939. Year classes born between 1950 and 1980 vary around 8 - 9 cm. The higher value of the L1 since the 1950's corresponds to the higher growth rate of 10-15 cm plaice observed in this period (Fig.3a). The L1 of the 1940-1944 year classes is slightly lower than the average pre-war level.

DISCUSSION

Methodology

A number of factors may bias growth estimates obtained by back-calculation of otoliths: incorrect back-calculation procedure, sampling bias, size-selective mortality (Casselman 1987; Francis 1990). The back-calculation procedure applied here has been verified by tagging experiments in which otoliths were labelled with tetracycline at tagging (Rijnsdorp *et al.* 1990). Strictly, this validation only applies to growth estimates of medium sized fish, because no large plaice were included in the experiment. Therefore, back-calculated growth rates of large plaice (>40 cm) have been compared with estimates obtained from tagging experiments. In Table 3 the growth rate of female plaice tagged with Peterson discs and recaptured after 11-13 months in the 1970's, is compared with growth rates estimated by back-calculation. Growth rate of tagged fish was corrected for shrinking according to Rijnsdorp *et al.*(1990). The correspondence between the two data sets is rather good, although the number of observations in the larger size groups is small. Back-calculated growth in older fish may be underestimated because underestimation of age is likely to occur in large fish that grow very slowly. In the otoliths of these fish the annuli become densely packed at the outer edge and are sometimes difficult to count. This problem does not occur in younger fish which still show a reasonable somatic growth. An indication for such bias might be that the number of females assigned to the outstanding year class 1928, was smaller than to the rather poor year classes 1930 and 1931 (Bannister 1978).

Sampling bias may lead to overestimation of the back-calculated length of younger age-groups if the otolith samples are taken from market samples which include partially recruited age-groups. Fig.7 shows the relationship between growth increment and body size estimated from samples taken at selected ages for the two largest data sets (5 and 6) of individual year classes (1963 and 1969). In both data sets the estimated growth rate is highest when the females are sampled at a young age: age IV, V and VI in year class 1963, and age IV in year class 1969. Inspection of the back-calculated size distributions of these year classes revealed that at these younger ages part of the cohort was indeed below the minimum landing size. In order to reduce this source of bias, only females of 6 years and older have been included in the present analysis.

A further bias may be caused by size-selective mortality (Ricker 1969). This type of mortality due to either natural causes or to fishing may be directly or indirectly related to growth rate. Although very little is known about growth related mortality in natural populations, we may speculate that slower growing fish suffer from a higher predation mortality, because of their smaller size. On the other hand, fast growing plaice may be expected to experience a higher mortality due to fishing, since they will leave the shallow coastal nursery areas and enter the main fishing grounds at a younger age than slow growing fish. Given the high level of fishing mortality of 40% per year as compared to the level of natural mortality (10% per year: Beverton 1964), size-selective fishing mortality will probably dominate over other type of size-selective mortality, leading to a proportional increase of slow growing fish among the survivors up to the age of full recruitment. This type of bias may also have contributed to the higher growth estimates obtained from otolith samples of young females in Fig.7.

Table 3. Comparison of annual length increments of female plaice as obtained by tagging experiments and back-calculation of otoliths. The tagging data refer to the Southern North Sea in the period 1970-1980 (Rijnsdorp *et al.* 1990). The back-calculations refer to the pooled data of otolith set 6 and 7 (year classes 1969-1974).

	Tagging data			Back-calculation		
Size-class (cm)	Growth increment (cm)	S.D. (cm)	Number	Growth increment (cm)	S.D. (cm)	Number
<10	-	-	-	9.4	2.6	145
10-14	-	-	-	9.0	2.8	98
15-19	-	-	-	8.3	2.1	130
20-24	7.3	2.4	124	7.5	2.0	112
25-29	5.9	2.0	9	6.3	1.6	125
30-34	4.4	2.1	26	4.4	1.5	149
35-39	2.8	1.4	40	3.1	1.1	143
40-44	1.9	1.0	31	2.2	0.8	65
45-50	1.5	1.2	8	1.7	0.3	10
>50	1.3	0.9	12	-	-	-

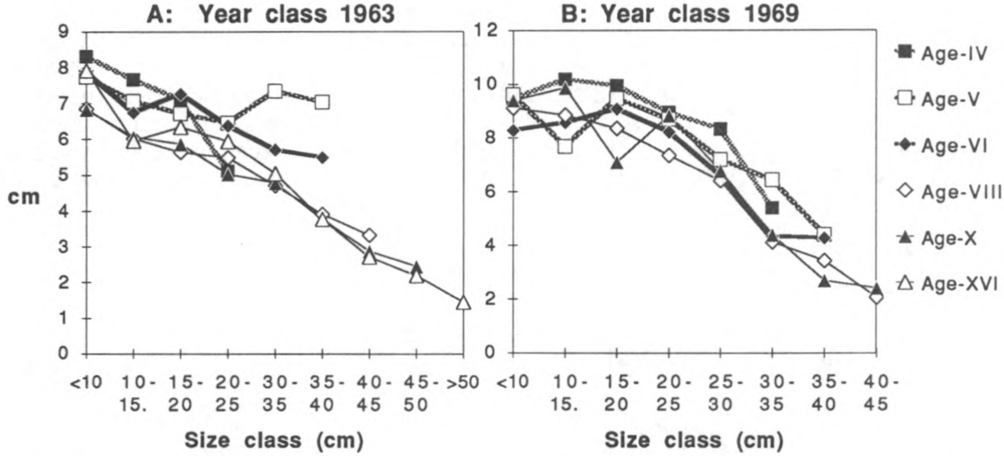


Figure 7. Back-calculated annual length increments in relation with the size for different sampling ages. A - year class 1963; B - year class 1969.

Spatial differences in growth rate

Table 4 presents estimates of annual length increments for different areas in the North Sea as obtained from tagging experiments carried out in the period 1905-1911 (Borley 1916). The growth rates are similar to the results of tagging studies carried out between 1920 and 1940 (Carruthers 1924; Hickling 1938). These data provide interesting information on differences in growth rate between various parts of the southern North Sea. On the main nursery grounds, represented by Southern Bight East (area SB), the growth rate appears to be poor, while on the Doggerbank growth rates are much higher. The fish recaptured on the Doggerbank and adjacent areas were transplanted from the coastal nursery grounds along the Dutch coast and in the German Bight to the Doggerbank and therefore do not reflect their 'natural' growth rate. Because the female used in our back-calculation study will have largely originated from the nursery areas in the Wadden Sea and adjacent shallow coastal waters (Hickling 1938), the back-calculated growth rate should be compared to the growth rate observed on the nursery grounds in the Southern Bight East.

The back-calculated growth of 4.5 - 5.6 cm in size classes 20-24 cm and 25-29 cm (Table 2), corresponds reasonably well with the estimated growth of 3.9 - 4.6 cm from the tagging experiments (Table 4). This correspondence again indicates that the changes in back-calculated growth reflect real changes in growth rate, despite the sources of bias discussed above.

The high growth rate of the Dogger recaptures in Table 4, serves as an indication of the growth potential of plaice. Maximum growth at unlimited food will be dependent on temperature conditions. Fonds *et al.* (1992) observed in tank experiments that at unlimited food the maximum growth rate of 20 cm plaice increased with temperature from about 0.2 mm.day^{-1} at 6°C to 0.7 mm.day^{-1} at 14°C, reached a peak of 0.75 mm.day^{-1} at 18°C and decreased to 0.35 mm.day^{-1} at 22°C. Given these growth rates and the annual temperature cycle (Fig.8), we can calculate the expected cumulative length increments for both the coastal nursery area Southern Bight east (SB pred) and the Doggerbank (Dogger pred). Fig. 9 shows that the expected growth increment at unlimited food is somewhat higher on the coastal nursery grounds than on the Dogger due to the higher water temperatures in the coastal shallows in summer. In autumn when water cools down, the growth rate decreases but remains substantial throughout the winter. This may not be realistic, since food intake decreases in autumn and almost stops in winter (Todd 1916; Chapter 4; Fonds *et al* 1992).

Fig.9 also provides the observed cumulative length increments on the coastal nursery ground and Doggerbank as observed in historic (Borley 1916) and recent tagging experiments. In the historic experiment, which is similar to the one given in Table 4, plaice were released in March-April between 1905 - 1911 on the nursery grounds in the eastern

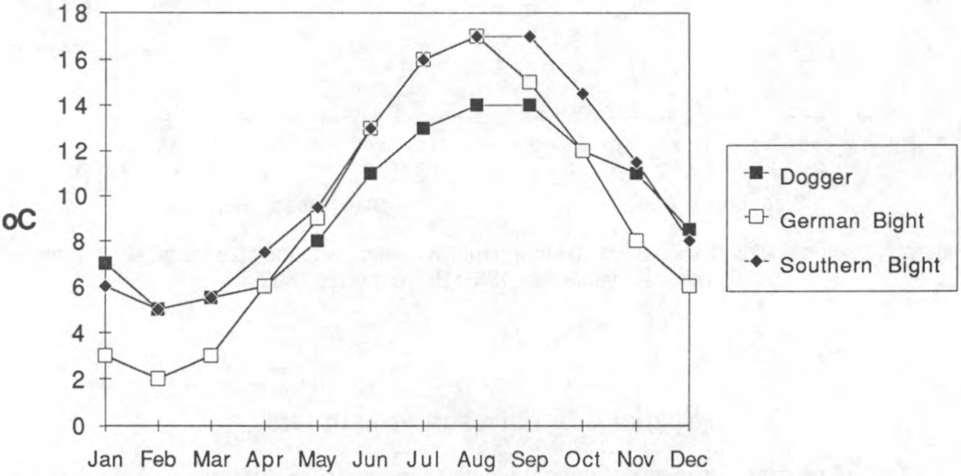


Figure 8. Annual cycle in water temperature at the bottom in the coastal nursery areas along the Dutch coast and in the German Bight (east Frisian and Danish coast) and on the Doggerbank. (Tomsczak & Goedecke 1964).

Table 4. Annual length increment between 1905-1911 of tagged plaice. The length increment was calculated as the difference between the length at liberation and recapture 11-13 month later for various time periods, size-classes and areas. The recaptures made on the Doggerbank refer to plaice transplanted from the crowded nursery grounds in the German Bight and along the Dutch coast to the Doggerbank. From Borley (1916).

Size-class (cm)	Area	Annual growth increment (cm)	Number
15-19	Doggerbank	13.3	33
	Southern Bight East	4.4	8
20-24	Doggerbank	13.6	75
	West of Dogger	7.3	5
	East of Dogger	5.8	4
	Southern Bight East	3.9	33
25-29	Doggerbank	12.3	17
	West of Dogger	6.5	4
	East of Dogger	7.7	4
	Off Wash	5.3	5
	Southern Bight West	6.5	10
	Southern Bight East	4.6	15

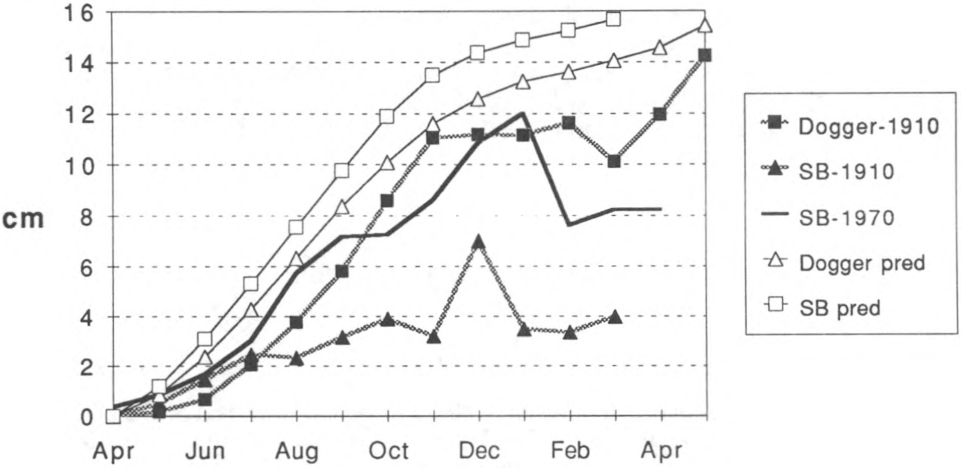


Figure 9. Cumulative length increments of 20-25 cm plaice of plaice tagged and released in March-April on the nursery grounds (SB-1910 and SB-1970) and those transplanted to the Doggerbank (Dogger-1910) compared with the predicted growth rates with unrestricted food an the average bottom temperature shown in Fig.8 according to Fonds *et al.* (1992) for the Doggerbank (Dogger pred) and the coastal nursery ground (SB pred).

Southern Bight (SB-1910) and in the region of the Doggerbank (Dogger-1910). In the recent experiment plaice were tagged and released in the western Wadden Sea in March 1970 - 1975 of which 156 were recaptured within fourteen months after release (SB-1970).

The cumulative length increment in 1910 gradually increased during the year to reach a maximum in the period between October and March of about 4 cm in fish recaptured close to the coastal nursery area, and a maximum of about 11 cm in the transplanted plaice. In the early 1970's the cumulative growth shows a similar seasonal pattern with a maximum level of about 8 cm. The high values in December and January are based on only two observations and are considered atypical.

Comparison of the observed and predicted growth from observed temperatures and unlimited food shows that on the coastal nursery grounds growth is well below the expected level in both 1910 and 1970. The slopes of the observed growth curve in 1910 is less steep than expected throughout the year, but in 1970 the slope is less steep in spring and autumn but similar between July and September. A smaller slope suggests that growth is restricted by food. On the coastal nursery grounds in 1910, growth thus seems to be restricted by food throughout the year whereas in 1970 growth seems to be restricted in spring and autumn but not in summer. The observed growth of plaice transplanted to the Dogger is only slightly below the predicted maximum possible growth in those temperature conditions. In April and May, just following tagging, the growth increments still lags behind the expected growth, but between June and November the observed growth curve run almost parallel to the expected one, suggesting that growth on the Dogger is not restricted by food. The observation that in the first month after release growth rate is smaller than expected in all tagging experiments may be artificial due to tagging

Analysis of the monthly growth increments of the recaptures stored in the files of several of the fisheries laboratories may be used to study the periods during the year in which growth might be restricted by food in more detail. This should be done against the back ground of the circannual rhythm in appetite and the possible effects of tagging. Further, it should be realised that differences between the observed and expected growth rate may be due to temperature when during extremely warm summers the sea temperature exceed the temperature at which plaice show maximum growth. Fonds *et al.* (1992) showed that this upper temperature decreased with fish size, from 22°C in 5 cm plaice to 18°C in 25 cm plaice. This temperature effect is most likely to occur in shallow coastal areas but is likely to be restricted in time.

Density-dependent growth

Variations in plaice abundance

Variations in the abundance of juvenile plaice is indicated by data of Bannister (1978) and Rijnsdorp *et al.* (1991) derived from cohort analysis which are reproduced in Table 5. The data indicate that the number of plaice recruiting to the fisheries has increased substantially since the second world war. However, the year class strength estimates should be treated with caution for two reasons. Firstly, the cohort analysis did not take account for variations in the catch of undersized plaice (discards) which may substantially affect the number recruiting to the fisheries (van Beek *et al.* 1990). Secondly, there appears to be a discrepancy in the estimate of the pre-war fishing mortality by Bannister (1978) and by Beverton and Holt (1957) and Gulland (1968). Nevertheless, the conclusion seems justified that recruitment has increased considerably since the 1950's.

Variations in the abundance of adult plaice are illustrated by the catch per unit of fishing effort (CPUE) of English first class steam trawlers (Fig.10). Before the war the CPUE varied around a low level. During the war fishing was substantially reduced in the southern North Sea and the CPUE increased by a factor of 4 - 5 in 1946. When the fisheries were resumed in 1946 the CPUE fell quickly to a low in 1950 which was slightly above the pre-war level Although the CPUE is not corrected for trends in the fishing power of the vessels (Simpson 1959) and may give an overestimate due to differences in the pattern of fish distribution (Gulland 1964), it is generally accepted that the immediate

Table 5. Estimates of the number of 2-year old plaice (millions) recruiting to the fisheries as obtained by cohort analysis. The original data from Rijnsdorp *et al.* (1991) refered to 1-year old recruits and were converted into 2-year olds by assuming an annual total mortality of 10%

Period	Bannister (1978)	Rijnsdorp *et al.* (1991)
1929-1938	260	-
1947-1949	466	-
1950-1954	268	-
1955-1959	307	-
1960-1964	409	460
1965-1969	473	282
1970-1974	-	330
1975-1979	-	417
1980-1985	-	578

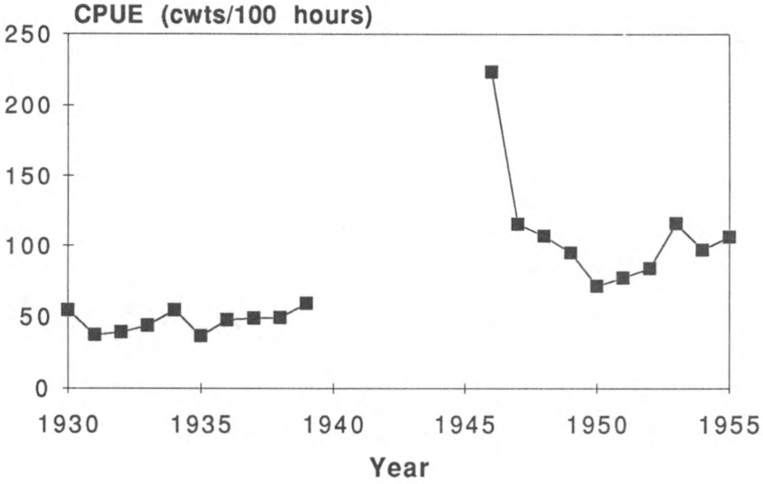


Figure 10. Time series of the catch per unit of fishing effort (cwt per 100 hours' fishing) of 1st class steam trawlers in the Southern Bight in January and February (from Simpson 1959).

post-war increase in CPUE reflect the increase in the plaice stock by a factor of three (Baerends 1947; Margetts & Holt 1947; Jenssen 1947; Beverton & Holt 1957; Simpson 1959). Changes in the adult plaice stock since 1958 are given by Rijnsdorp *et al.* (1991) who showed that the spawning stock biomass increased from about 300 thousand tonnes in 1958 to a peak of 500 thousand tonnes in 1967 and decreased to a level of 300 thousand tonnes between 1974 and 1982.

Density-dependent growth can only occur through competition between fish sharing the same food and space. The variations in plaice abundance presented above, therefore, may not reflect variations in competitive biomass since they did not consider the distributional aspects. The CPUE on the spawning grounds does not necessarily reflect quantitatively the density on the feeding grounds. Also variations in spawning stock biomass do not necessarily reflect variations in density if the area of distribution changes. In plaice, the latter has actually occurred. Egg surveys have shown that the egg production increased substantially in the German Bight between the 1930's and 1955 (Bückmann 1961; Harding *et al.*1978), in the eastern English Channel and the Flamborough area between 1948 and the 1970's (Heessen and Rijnsdorp 1989). The increase in adult biomass indicated by trends in CPUE and SSB biomass may therefore overestimate the actual increase in competitive biomass.

In a first attempt to tackle the effect of spatial overlap, Rijnsdorp & van Beek (1991) estimated the potential competitive biomass experienced by each age group from the spatial distribution of individual age groups and information on their number and weight. The distribution of the juvenile age groups (I-IV) were distinct and therefore competition will be mainly restricted to individuals within a cohort. Adult plaice (age group V and older) exhibit a considerable overlap in distribution and therefore competition among adults will occur across cohorts.

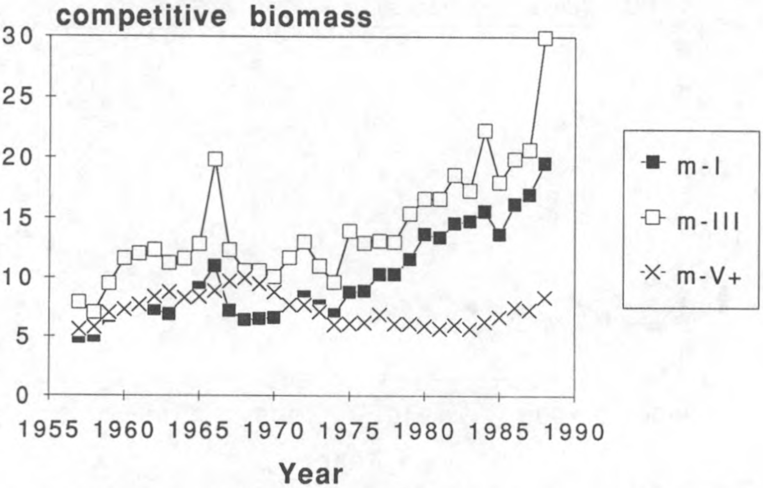


Figure 11. Time series estimates of intra-specific competitive biomass for juvenile age groups I (m-I) and III (m-III), and adult age groups V and older (m-V+). From Rijnsdorp & van Beek (1991).

Figure 11 reproduces the timeseries information on the estimates of competitive biomass experienced by 1-group (m-1), 3-group (m-3) and 5-group and older plaice (m-5+). A distinct feature in Fig.11 is that the variations in the competitive biomass of 1-group and 3-group are almost identical and are driven by the variations in year class strength, as illustrated by the peak in the mid sixties due to the very strong 1963 year class.

Density-dependent growth in juveniles

Evidence for density-dependent growth in juveniles (<30 cm) was already given in the comparison of the growth rates on the crowded nursery grounds and the less crowded Doggerbank area (Fig.9) and the reduced growth rate of the 1963 year class which was about three times the average size (Fig.5).

The growth acceleration of plaice <30 cm in the 1960's and 1970's was restricted to those age groups that are mainly distributed in the southern North Sea and coincided with an increase in the competitive biomass (Fig.11) which was due to an increase in the level of recruitment (Table 5). Variations in the temperature on the coastal nursery grounds of the Southern Bight east, given in Fig.12 for the main growing period in the second and third quarter, does not show a clear relation with the increase in growth of juvenile size classes since 1950. Since a similar growth acceleration was observed in the sole *Solea solea* (L.), which occupies the same areas, food availability must have increased (de Veen 1978; Rijnsdorp & van Beek 1991).

The present growth rate, although much higher than in the 1930's, is still substantially lower than the potential growth rate indicated by the transplanted fish, suggesting that density-dependent growth still occurs.

Although there is evidence that the present level of recruitment is higher than in the 1930's, this does not necessarily imply that competition has increased. In a situation of a low food availability causing a reduction in growth rate, the density-dependent effects may be higher because of the accumulation of slow growing plaice belonging to several cohorts on the coastal nursery areas, as indicated by the occurrence of relatively old fish of up to 12 years in the otolith samples taken in 1932-1933 on the coastal nursery ground (Table 1). At higher levels of food availability and consequently higher growth rates, plaice will stay in the shallow coastal nursery grounds for a shorter period, which may lead to a decrease in the density-dependent effects. From the growth curves shown in Fig.2 we can infer that it took a plaice on average 3 - 3.5 years to reach 20 cm in the 1930's and 2 years in the 1970's. In the nursery areas we will therefore find an accumulation of about 3-3.5 age groups in the 1930's compared to 2 age groups in the 1970's, which roughly compensates for the lower level of recruitment.

The absence of a reduction in juvenile growth during the war period suggests that the cessation of fishing has not led to an increase in the abundance of small plaice in the coastal nurseries. However, the cessation of fishing was far from complete, especially in the coastal waters of the eastern North Sea where a limited amount of fishing was continued (Baerends 1947; Jenssen 1947).

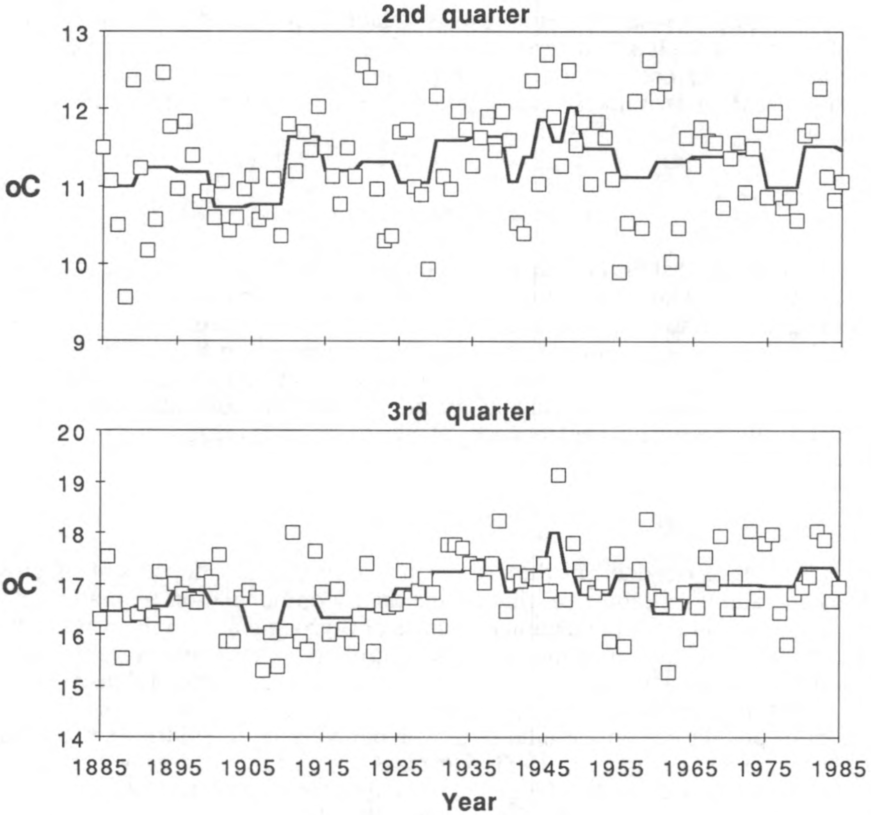


Figure 12. Time series of the average surface water temperature on the coastal nursery ground in the Southern Bight of the North Sea in the second and third quarter. The thick line indicates the 5-year average (2-year average in the period 1940-1949).

Density-dependent growth in adults

Rijnsdorp & van Beek (1991) were not able to identify density-dependent growth effects in adult plaice over the time period 1958-1988. Over this time span adult biomass fluctuated by a factor of two (m-5+ in Fig.11). However, the growth depression of large plaice as observed between 1940-1949 suggests that growth may also be density-dependent in the adult population.

A growth depression was first seen in medium sized plaice and later on also in the larger size groups. This might be explained by the longer time necessary to build up the competitive biomass of large plaice. However, this can not explain why the largest growth depression occurred in 1948-1949 when the cpue had already dropped. The observation that the absolute growth depression increased with body size may be tentatively related to the relative increase in reproductive investment with body size compared to investment in somatic growth. Small fish allocate only a small proportion of their annual surplus production to reproduction and a large proportion to somatic growth, while large fish invest almost all in reproduction. A reduction in surplus production will therefore result in a relatively larger reduction in somatic growth in large fish than in small fish (Chapter 1, Chapter 7).

No time series of sea temperatures is available for the central North Sea, the main distribution area of adult plaice during the growing period. Since this area is characterized by a stratified water column and relatively stable temperature conditions (Tomsczak & Goedecke 1964), it is unlikely that adult plaice have experienced major changes in temperature.

Genetical changes in growth rate

The possibility that the growth changes in small plaice reflect a change in the genetical make up of the population due to size-selective exploitation seems unlikely since the increased growth rate was restricted to a relatively short period of about 20 years, compared to a generation time of about 5 years in males and 8 years in female plaice (Chapter 2). In addition, the transplantation experiments carried out in the early 20th century (Borley 1916) indicated potential growth rates that corresponded reasonably well to the growth rates observed in the laboratory at unrestricted food ration (Fig.9).

Population regulation

The evidence obtained in the present paper for density-dependent of growth in juveniles and adults has some bearing on the theory on population regulation in plaice. Intensive research into the population dynamics of 0-group plaice in the western Wadden Sea has shown that growth at this stage is controlled by the ambient temperature and corresponds to the growth rate in the laboratory at unlimited food conditions (Zijlstra *et al.* 1982). Density-dependent mortality is restricted to a short time period directly following the settlement of post-larvae on the tidal flats (van der Veer *et al.* 1990). The fact that very strong year classes, such as the 1963 year class, exhibit reduced growth rates and the continuous slow growth in the 1930's, may imply increased vulnerability for predation, resulting in an increased mortality. Reanalysis of the abundance indices of 0- and 1-group plaice in the continental nursery areas indeed showed a density-dependent mortality component (Beverton & Iles 1992). The substantial reduction in somatic growth of adult plaice during the war implies an indirect effect on the number of eggs produced. Fecundity estimates carried out in the spawning seasons of 1948 and 1949, the period of the largest growth depression (Fig.3), showed a substantial reduction in the size-specific fecundity.

However, the size-specific ovary weight was only marginally reduced suggesting a density-dependent trade-off between egg numbers and egg-size (Chapter 5).

ACKNOWLEDGEMENTS.

The analysis of the pre-war growth rates would not have been possible without the support of Drs R.S. Millner and J.D. Riley (Fisheries Laboratory Lowestoft, U.K.), who supplied the otolith material from the late 1940's and early 1950's. Dr M Fonds provided data on laboratory growth of plaice. The paper improved considerably from the critical comments of Dr N Daan and an anonymous referee.

Chapter 4

Maturation of male and female North Sea plaice (*Pleuronectes platessa* L.)

Rijnsdorp, A.D. 1989. Maturation of male and female North Sea plaice (*Pleuronectes platessa* L.).- J. Cons. int. Explor. Mer, 46: 35-51.

ABSTRACT: The maturation of North Sea plaice is studied on the basis of two research vessel surveys and market sampling data from the commercial fisheries. In female plaice the juvenile - adult transition occurred between May and September. Development of the female gonad took place between July and December, although the gonad did not gain weight before October. Gonad weight reached a maximum of circa 17% of the gutted body weight between January and March. The average female plaice was in spawning condition for about five weeks from late January to early March. Male plaice were in spawning condition for at least 11 weeks from the second half of December to the second half of March. In females the start of spawning was earlier in older fish, but the end of spawning did not differ between age groups. In males spawning ended later in older fish. The time that mature plaice were in spawning condition increased with the age of the fish in males and females. During the spawning season mature plaice hardly fed. Spent fish resumed feeding in January. The cessation of feeding in mature plaice was not related to the absence of food.

Male plaice became sexually mature as II - and III-group, females as IV - and V-group. Length at 50% maturity (L_{mat}) was 22 cm and 34 cm respectively. L_{mat} and age at 50% maturity (A_{mat}) differed between geographical areas, increasing from south to north. Annual differences were observed in L_{mat} and A_{mat} which were related to annual differences in growth rate. Slower-growing plaice reached maturity at a smaller length but higher age than faster-growing plaice. Comparison with published data shows that at present both male and female plaice mature at a younger age and at a smaller size than in the beginning of this century.

INTRODUCTION

North Sea plaice have attracted the interest of both fishermen and fishery biologists for almost a century. Reviews of much of the earlier research are given by Wimpenny (1953), Simpson (1959) and Bannister (1978). The main spawning occurs in the southern and southeastern North Sea between late December and early April (Simpson 1959; Harding *et al.* 1978a). Males predominate on the spawning grounds and are thought to spend several months there - in contrast to female plaice which remain for a few weeks Hefford 1916), although a precise estimate of the duration of spawning is not available. During the spawning period plaice almost cease feeding (Todd 1914; Lande 1973), but it is not known whether this is caused by the absence of food or by behavioural changes associated with spawning. Data on the annual maturity cycle, which could yield information on the time of the year when maturation starts and on the duration of the spawning process, are not available for North Sea plaice, although LaHaye (1972) and Deniel (1981) present qualitative data for plaice along the coast of Brittany.

Data on the length and age at first maturity in North Sea plaice are given by Kyle (1900), Wallace (1914; 1916) and Hefford (1916). These studies showed that males became mature at a smaller length (30 - 37 cm) and a younger age (V - VI years) than females (32 -43 cm; V - VII years) and that the onset of sexual maturity differed between the southern and south eastern North Sea. Simpson (1959) concluded that female plaice of the 1943 and 1944 year class became mature as IV-, V- and VI-group. More recent information is lacking.

This paper is the first of a series of papers dealing with the changes in biological parameters such as growth, onset of maturity and fecundity (Bannister 1978; Rijnsdorp *et al.* 1983; Horwood *et al.* 1985) and will focus on the following aspects of the reproductive biology of plaice: 1) annual maturity cycle; 2) duration of the spawning process; 3) relation between the reproductive state and the level of feeding; 4) spatial distribution of immature and mature plaice; 5) the length and age at first maturity in different parts of the southern North Sea; 6) changes in the length and age at first maturity since 1900.

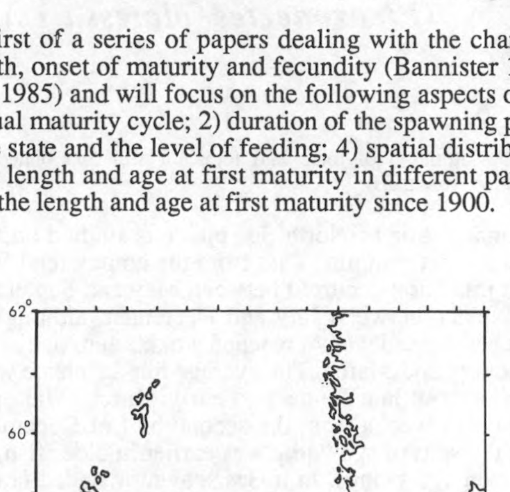


Figure 1. Map of lines A to E of sampling stations of the maturity survey in 1985 and 1986. The total spawning area (light shaded) and the main centers of egg-production (dark shaded) are indicated according to Harding et al. (1978).

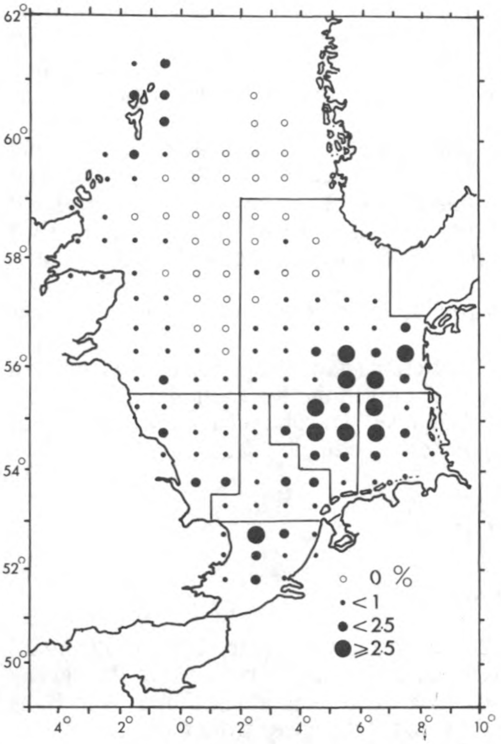


Figure 2. Distribution of plaice (>= 27 cm) in the International Young Fish survey in February (data 1983 - 1985) as indicated by the percentage of the total population present in each rectangle (from ICES 1987).

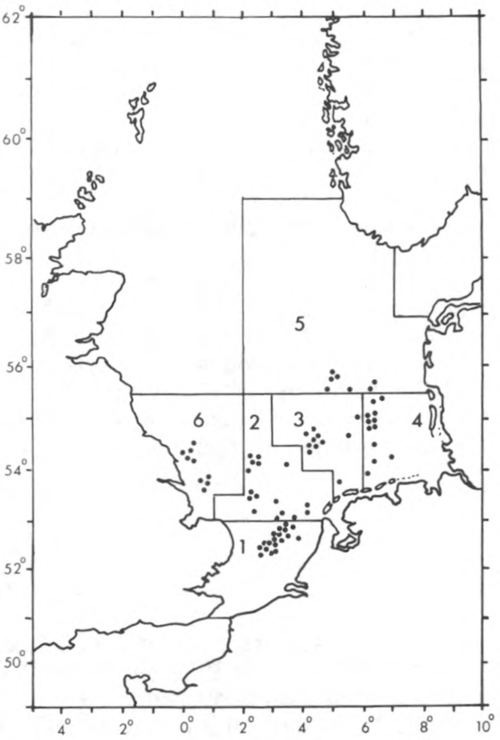


Figure 3. Distribution of market samples in the 1st quarter of 1985 and 1986 and the geographical areas used in the market sampling program: area 1 = DWK, 2 = OG, 3 = DBW, 4 = DBO, 5 = VB and 6 = FLAM.

NORTH SEA PLAICE

Tagging experiments with spawning plaice have shown the existence of four main spawning groups in the southern North Sea: Southern Bight, Transition area, German Bight and Flamborough (de Veen 1962, 1978). From the distribution map of egg-production (Fig.1) the existence of several smaller spawning groups can be inferred along the east coast of England and Scotland (Lockwood & Lucassen 1984) and in the Fisher bank area.

The structure of the North Sea plaice population may therefore be visualized as a series of distinct spawning groups that partially mix on the summer feeding grounds (de Veen 1962). Differences between the spawning groups in the southern North Sea have been shown in otolith and meristic characters (de Veen & Boerema 1959) and in frequencies of abnormal pigmentation (de Veen 1969), but not in serological or biochemical characteristics (de Ligny 1967, 1969; Purdom *et al.* 1976).

It is not fully understood from which nursery areas the adult fish of the different spawning groups originate. The results of tagging experiments with juvenile plaice reported by Hickling (1938), suggest that the Southern Bight spawners mainly recruit from the nursery grounds in the Dutch Wadden Sea and along the Frisian coast, whereas the

German Bight spawners recruit from the nursery areas in the German Bight. Juvenile plaice along the English east coast mainly recruit to the Flamborough spawning population (Lockwood & Lucassen 1984). However, the reported tagging experiments indicate that juveniles can recruit to other spawning populations than the main ones listed above. It is not established to which spawning group the juvenile plaice from the nursery area along the Jutland coast recruit.

The relative importance of the different spawning groups is indicated by their total egg-production. In the 1960s the total production of fertilised eggs in the North Sea and English Channel was estimated at 25 10^{12}: of this total 65% occurred in the central and eastern North Sea; 20% in the Southern Bight; less than 5% in the western English Channel, and 10% in the eastern English Channel. Spawning along the English and Scottish east coast was insignificant in relation to the total North Sea egg-production (Harding *et al* 1978a), although in 1976 egg-production in the Flamborough area was estimated at 3.10^{12} (Harding *et al.* 1978b).

Another indication of the importance of the different spawning populations is given in Fig.2 by the relative catch per hour of plaice (>=27 cm) in the International Young Fish Surveys of 1983, 1984 and 1985 (ICES 1987). This result corroborates the importance of the German Bight subpopulation as indicated by the egg-production data.

SOURCES OF DATA

Maturity survey

Maturity surveys were carried out from 28 January to 6 February 1985 and from 27 January to 6 February 1986 by RV TRIDENS and RV ISIS. In both years the survey encompassed a total of 49 stations. The stations were distributed along 5 lines A to E, as shown in Fig.1, more or less perpendicular to the coast at distances from the coast of 3, 6, 12, 18, 24, 36, 48, 60, 72, 84 and 96 miles. In 1986 the first 4 stations in line E had to be omitted due to bad weather.

Table 1. Maturity stages of male and female North sea plaice. * milting males or running females

		Males
1	immature	testis very small
2	ripening	testis bigger, grey coloured
3*	ripe	testis big and white, milt can be expelled under pressure
4*	spawning	as 3, milt freely running or can be expelled under slight pressure
5*	nearly spent	milt brownish, can be expelled under strong pressure
6	spent	small, form of half moon, colour brown
7	spent	shrunken, often going back to stage 1
		Females
1	immature	lumen transparent, colour grey
2	ripening	colour orange, oocytes visible, vitellogenesis in progress
3*	spawning	as 2 but with few ripe hyaline eggs
4*	spawning	ovary completely filled with hyaline eggs
5*	spawning	eggs partly shed
6	nearly spent	ovary contains only a small amount of hyaline eggs
7	spent	ovary small, flabbish and bloodshot, back to stage 2

Catches were made with a 6-metre heavy beam trawl with four tickler chains as used by RV TRIDENS in the Demersal Young Fish Survey (meshsize: 40 mm; haul duration: 30 minutes; fishing speed: 4 knots). For each haul the length-frequency distribution of plaice was recorded to the cm below and an otolith sample was taken. From each cm-group, four plaice, taken at random, were sampled for age, sex, maturity stage and feeding condition, giving a total over both years of 2772 male and 2270 female plaice

Market sampling

The landings of plaice by commercial vessels in the Netherlands were sampled monthly on a routine basis for age, length, weight, sex and maturity. The market samples (80 fish) were stratified according to geographical area and to the four market size categories in use in the Netherlands: 27-34 cm; 34-38 cm; 38- 41cm; >41 cm. Each market category consisted of 20 plaice taken at random. Comparison of the geographical distribution of market samples in the first quarter of 1985 and 1986 (Fig.3) shows that they covered the whole North Sea plaice population except the smaller spawning groups along British east coast north of Flamborough Head (Fig.1).

METHODS

Maturity staging

The maturity stages were recorded using the scale given in Table 1 (modified from Wimpenny 1953). In female plaice staging was quite straightforward but in male plaice problems arose in distinguishing spent males from immature males. Macroscopically no reliable diagnosis appeared to be possible. A preliminary attempt to facilitate the diagnosis by histological examination of the testis suggested that some of the bigger males recorded as stage 7 (spent) in January might have been immatures.

Duration of spawning

The annual maturity cycle was analysed on a monthly basis for the period 1981 - 1985 (n=12180) from the relative frequencies of maturity stages in the samples. The mean duration of the individual spawning activity was estimated following the method used by Iles (1964) for herring. In this method the duration of spawning is calculated as the time elapsed between the time when 50% of the adult population has reached maturity stage 3 or higher and the time when 50% of the adult population has become spent (stage >=6). Market sampling data from the most intensively sampled period 1974 - 1976 (n=18200) were analysed with a time unit of half a month. As spawning periods and spawning stock sizes differed between geographical areas the relative frequency of each maturity stage in each market category and area were weighted by the monthly catch per unit of effort of the corresponding market category and geographical area to arrive at an estimate for the total North Sea population. This estimate for the total North Sea population is the most representative as it is based on all available data and is not affected by bias due to immigration or emigration of adult fish

Maturity-length and maturity-age relationships

From the market sampling data the maturity-age relationship was determined for each market category separately and then summed over the categories after weighting them by the proportion of each market category in the total Dutch landings.

The maturity data from the surveys were analysed by taking account of the distribution of mature and immature plaice. First the proportion of mature plaice was determined for each station by length or age group. Then the average proportion of mature plaice was calculated for each line by weighting over the station abundance and the surface area of the zone sampled, approximated by the inter-station distance. So for the first two stations at 3 and 6 miles from the coast the weighting factor was 1, for the next three stations at 12, 18 and 24 miles the factor was 2 and for the remaining stations at 36, 48 etc miles the factor was 4.

The length at which 50% of the population reached maturity (L_{mat}) was determined by a functional regression of the logit transformed maturity proportions (P) against length.

$$\text{Logit } P = 0.5 \log_n(P/1-P)$$

In age reading, 1 January was taken as birthday.

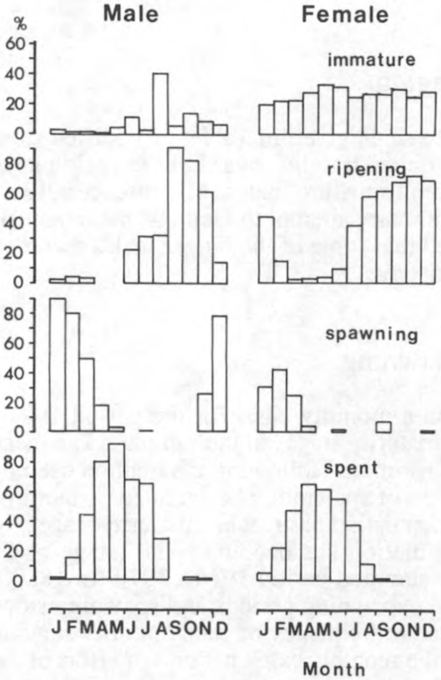


Figure 4. Monthly percentages of immature (stage 1), ripening (stage 2), spawning (stage 3, 4 and 5) and spent (stage 6 and 7) male and female plaice in the market samples of 1981 - 1985.

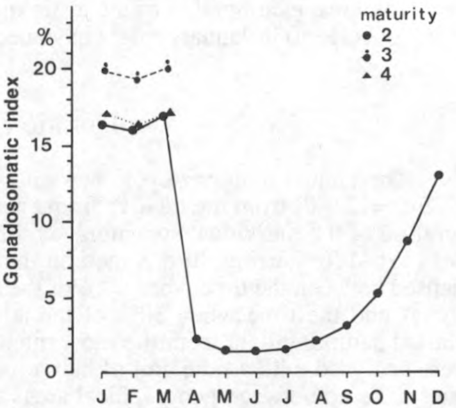


Figure 5. Gonad weight of female plaice as percentage of the gutted body weight (including gonads) by month for maturity stages 2, 3 and 4 in the market samples of 1981-1985.

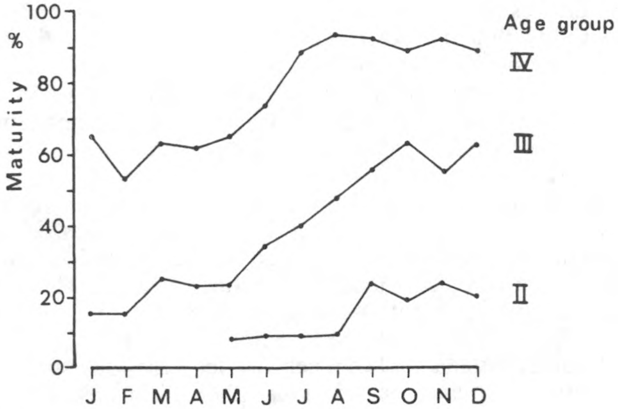


Figure 6. Time of the juvenile - adult transition in female plaice as indicated by the increase in the percentage of mature fish (stage >=2) in age groups II, III, and IV in the market samples of 1981-1985.

Feeding condition

From the presence or absence of visible food remains in the gut, fish were classified as either 'feeding' or 'non-feeding'. Information to test whether there was a relation between stage of maturity and feeding condition was available from the maturity surveys and from part of the market samples between 1983 and 1985. In total 1356 plaice were investigated for feeding condition in these market samples and 5042 in the maturity survey samples.

Statistical analysis of feeding incidence in relation to maturity stage and distance from the coast was carried out with an ANOVA technique fitting a GLM model (Baker & Nelder 1978) with a binominal error distribution.

RESULTS

Annual maturity cycle

In both sexes the resting (stage 7) and ripening stage (stage 2) dominated during the growing season between April and November (Fig.4). In females visual inspection of the ovaries indicated that vitellogenesis started in July and continued until the spawning period. Substantial growth of the female gonad did not, however, occur before October (Fig.5). The transition from juvenile to adult female plaice took place between May and September and appeared to be slightly earlier in the older age groups. The percentage adult increased between May and August in age group IV, between May and September-October in age group III and between August and September in age group II (Fig.6).

Duration of spawning

Spawning females (stages 3, 4 and 5) were observed from January until April with a peak in February, but their proportion never exceeded 50% (Fig.4). Spawning males (stages 3, 4 to 5) were observed from November until May and predominated in the total population between December and March. Male plaice thus started their spawning activity at an earlier date and continued for a longer time. The few male and female plaice that were recorded as being in spawning condition outside the main spawning period were probably due to errors in the maturity staging.

In Fig.7 the cumulative proportions of maturity stages within the adult population (maturity stages 2 - 7) are shown. The decending lines, which connect the cumulative proportions of the successive maturity stages (2, 2+3, 2+3+4, etc) demonstrate the transition of adult fish through successive maturity stages. The shaded area in Fig.7 indicates the proportion of fish within the adult population that were in a spawning stage (stage 3 - 5). The distance between the two lines encompassing the shaded area at the points where 50% of the population had reached at least maturity stage 3 and 6 indicates the duration of spawning of an average individual plaice. Thus estimated, the average male plaice was in a spawning stage (maturity stage 3 - 5) for a minimum of 11 weeks ending in mid March. The start of the spawning in December could not be determined precisely. The average female was in a spawning stage (maturity stage 3 - 5) for about five weeks from late January to the beginning of March. The time that plaice were engaged in the spawning process increased with the age of the fish (Fig.8 left and right). In females that increase coincides with an earlier start of spawning in older fish and a longer duration of maturity stage 3. The end of the spawning in females is remarkably similar between age groups. In males the end of spawning is later in older age groups.

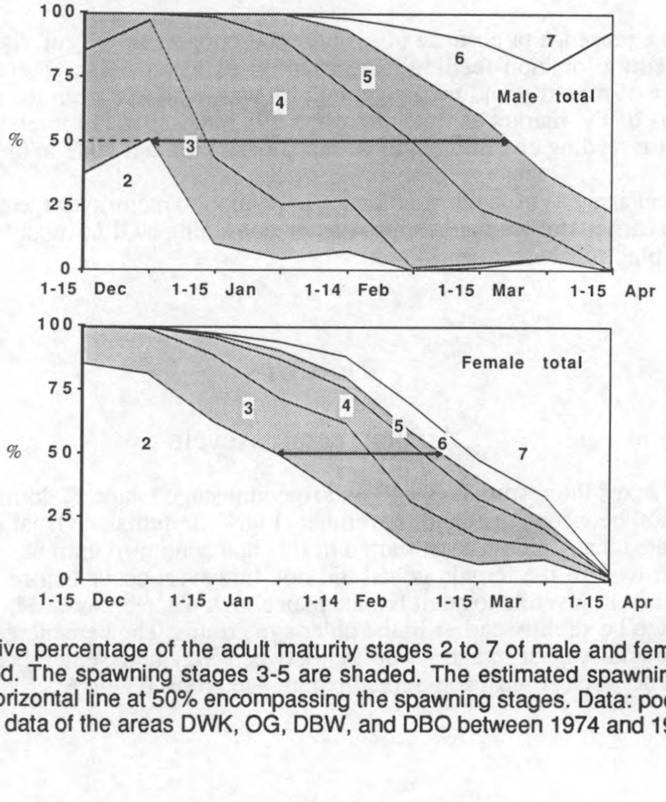


Figure 7. Cumulative percentage of the adult maturity stages 2 to 7 of male and female plaice by half-monthly period. The spawning stages 3-5 are shaded. The estimated spawning duration is indicated by the horizontal line at 50% encompassing the spawning stages. Data: pooled market sampling data of the areas DWK, OG, DBW, and DBO between 1974 and 1976.

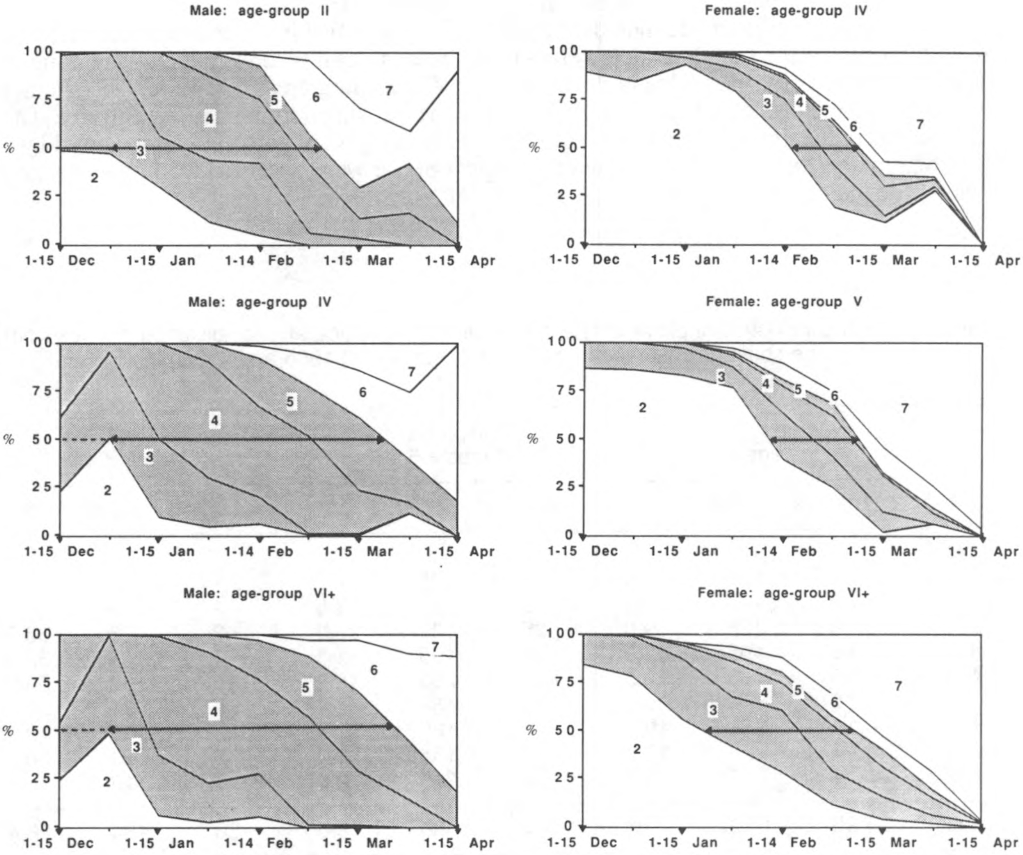


Figure 8. Cumulative percentage of the adult maturity stages 2 to 7 by half-monthly period for (left) males: age groups II, IV, and VI+; and (right) females: age groups IV, V, and VI+. The spawning stages 3-5 are shaded. The estimated spawning duration is indicated by the horizontal line at 50% encompassing the spawning stages. Data: pooled market samplingdata of the areas DWK, OG, DBW, and DBO between 1974 and 1976.

Feeding condition and reproductive state

The lower incidence of feeding during the spawning period was apparent in both immature and mature fish, but was most pronounced in fish of maturity stages 2 - 5, that is, fish that are (nearly) engaged in spawning (Fig. 9). After spawning the spent fish resumed feeding as early as January.

Because the distribution of mature and immature plaice differed it is possible that this might be the cause of differences in feeding condition. Therefore, the relation between maturity and feeding condition was studied in more detail during the maturity surveys in 1985 and 1986 with reference to the distance from the coast (Table 2). ANOVA showed that both maturity stage (males: F=22.6; d.f. = 2,14; P<0.01; females: F= 48.2; d.f. = 2,16; P<0.01) and distance from the coast (males: F=5.88; d.f. = 8,14; P<0.01; females:

F= 6.89; d.f. = 8,16; P<0.01) were significantly related to the feeding incidence. Overall feeding incidence was highest between 6 and 18 miles from the coast. Spawning fish showed a lower feeding incidence than immature or spent fish irrespective of the distance from the coast. Ripe female plaice were hardly feeding at all wherever they were caught. The same applies to ripe males in the centre of the spawning areas. However, the smaller ripe male plaice at the edges of the spawning areas did show some feeding activity. The differences in feeding incidence between the maturity stages are apparently not caused by a lack of suitable food, because immature and spent plaice were observed feeding at stations where ripe plaice did not feed.

Table 2. Feeding incidence of plaice in relation to the maturity stage and the distance in miles from the coast as observed in the maturity surveys in 1985 and 1986.

	Male plaice								
	stage 1			stages 2-5			stage 6-7		
	feeding	total	%	feeding	total	%	feeding	total	%
Distance									
3	59	229	25.9	2	26	7.7	-	-	-
6	64	175	36.6	9	72	12.5	-	-	-
12	48	123	39.0	25	105	23.8	2	6	33.3
18	45	105	42.9	23	195	11.8	1	3	33.3
24	36	160	22.5	41	253	16.2	16	32	50.0
36	15	74	20.3	32	432	7.4	7	31	22.6
48	10	51	19.6	5	180	2.8	3	16	18.8
60	4	39	10.3	2	154	1.3	6	29	20.7
>=72	4	17	23.5	5	249	2.0	2	16	12.5
Total	285	972	29.3	144	1666	8.6	38	134	28.4

	Female plaice								
	stage 1			stages 2-5			stage 6-7		
	feeding	total	%	feeding	total	%	feeding	total	%
Distance									
3	83	244	34.0	1	3	33.3	1	1	100.0
6	90	209	43.1	0	1	0.0	1	1	100.0
12	91	161	56.5	1	15	6.7	3	3	100.0
18	85	182	46.7	1	33	3.0	1	1	100.0
24	120	319	37.6	2	75	2.7	5	9	55.6
36	39	233	16.7	1	130	0.8	4	5	80.0
48	35	134	25.9	0	48	0.0	2	5	40.0
60	32	117	27.4	2	40	5.0	3	11	27.3
>=72	71	200	35.5	1	74	1.4	1	16	6.3
Total	646	1799	35.9	9	419	2.1	21	52	40.4

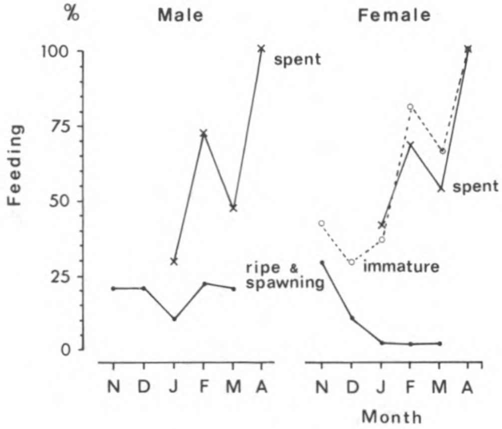


Figure 9. Percentage of feeding fish of immature (stage 1), ripe (stages 2-5), and spent (stages 6 and 7) male and female plaice by month as observed in market samples and the maturity surveys.

Spatial distribution of plaice in the spawning period

In Fig.10 the catch per hour of age groups I to V and the percentage of immature plaice are shown in relation to the distance from the coast. Data for lines C+ D only are shown. The distribution patterns on the other lines were essentially the same. The location of spawning grounds, as indicated by the presence of 'running' females, is shown by black bars at the top of Fig.10. 'Running' females (maturity stages 3-5) were first observed at 18 miles from the coast. From 24 miles onwards on average 34% of the mature females were in 'running' condition (range 24-47%). The distribution of plaice eggs indicated that around line C+D the main spawning occurred in an area between 40 - 100 miles from the coast (Fig.1).

The I-group male and females showed a strictly coastal distribution, and the centres of distribution of older age groups moved farther offshore. Mature males of age groups II and III (length range 15-30 cm) were concentrated on the edges of the main spawning grounds (18 - 36 miles from the coast) and occured farther offshore than the immature fish of the same age. Older males (>30 cm) predominated in the central parts of the spawning grounds (>36 miles). II-group females, though still mainly immature, had already started to spread out from the coastal nursery grounds towards the offshore spawning grounds. In the older age groups the proportion of mature females increased, while the dispersion of the immatures over the offshore grounds was further advanced. The proportion of mature female plaice, mainly ripening females (maturity stage 2), was highest at the edges but decreased towards the centre of the spawning grounds. With the other lines (A, B, E) the proportion of mature females was also highest at the edges of the spawning areas. Although female plaice matured at an older age than male plaice the dispersion from the nursery areas towards the spawning grounds was similar.

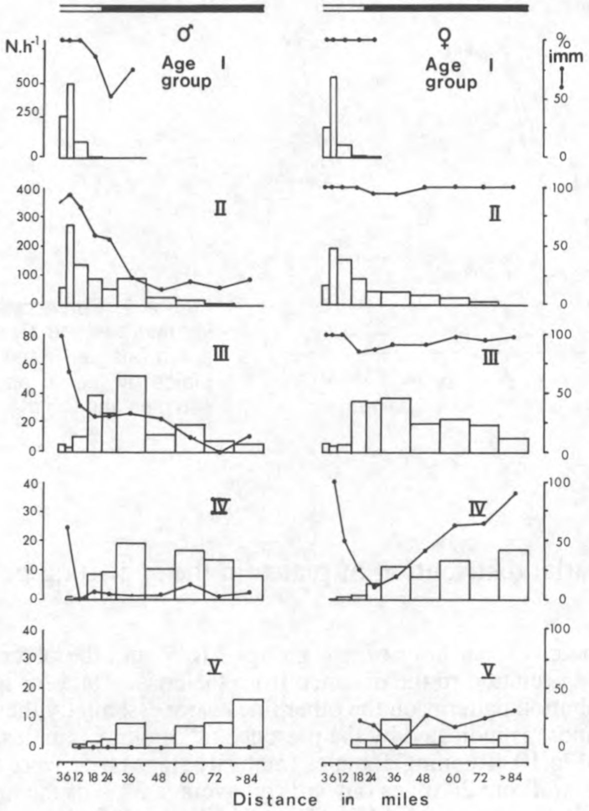


Figure 10. Density (c.p.u.e) of plaice (histograms) and the percentage of immatures (dots) by age group in relation to the distance to the coast in lines C + D (survey data for 1985 and 1986). The bars at the top of the figure show the spawning areas as indicated by the presence of 'running' females.

Length and age at first maturity

In Fig.11 the length-frequency distribution of mature and immature plaice from the maturity survey is shown. From Fig.12 it can be seen that males reached sexual maturity over a range of length between 15 and 30 cm, while 50% reaching maturity at a length of 21.9 cm (L_{mat}) (Table 3). Females attained maturity between 24 and 37 cm with 50% reaching maturity at a length of 33.9 cm. In male plaice the maturity percentage did not increase continuously with fish length but levelled off between 20 and 27 cm before increasing again (Fig.12). This levelling off was observed in males on all lines but not for females.

The maturity-length relationships differed between areas and years (Table 3). Going from south to north the L_{mat} increased in males from 20 cm on line A+B to 22 on line C+D and to 24 cm on line E; and in females from 33 cm on line C+D to 36 cm on line E. The market sampling data also indicated an increase in the L_{mat} in females from 30 cm in area DWK to 34-35 cm in area VB and FLAM. The L_{mat} in males was 23 cm in the 1985 survey but only 20 cm in the 1986 survey: respectively. In females the L_{mat} did not differ between these two years.

In general the maturity-length relations obtained from the maturity survey were in agreement with these obtained from the market sampling, even though the market sampling areas did not exactly coincide with the lines of the maturity survey. The maturity-length relation for line C+D corresponded to that for areas OG, DBW and DBO. The maturity-length relation for line A+B was based on a relatively small number of females, which were mainly taken at line B, and differed markedly from the relation for area DWK but only slightly from the relationship for area OG. The maturity-length relation in line E was close to that of area VB.

The maturity-age relation based on the survey data is given in Table 4. The mean over all lines was calculated by weighting by the abundance per line. The majority of the male plaice became mature as II- and III-group. A very small proportion of males already mature as I-group . As explained in the methods section some of the males recorded as spent (stage 7) could have been immature. To indicate the possible bias from this misinterpretation two values for the proportion mature males are included in Table 4, one including and one excluding stage 7. The majority of female plaice became sexually mature as IV- and V-group. The youngest sexually mature females observed were of age group II.

Differences were observed in the age at which plaice became sexually mature between year classes and between areas. Year class 1983, as II-group fish, contained a much higher percentage of mature fish than did year class 1984 at the same age. Females of the 1983 year class also showed a slightly higher proportion of mature fish, particularly in the southern lines (A to C). These differences persisted when the 1983 year class was III-group. The percentage of mature fish declined from south (line A+B) to northeast (line E). Especially in line E both male and female plaice appeared to become sexually mature one year later than in the southern area.

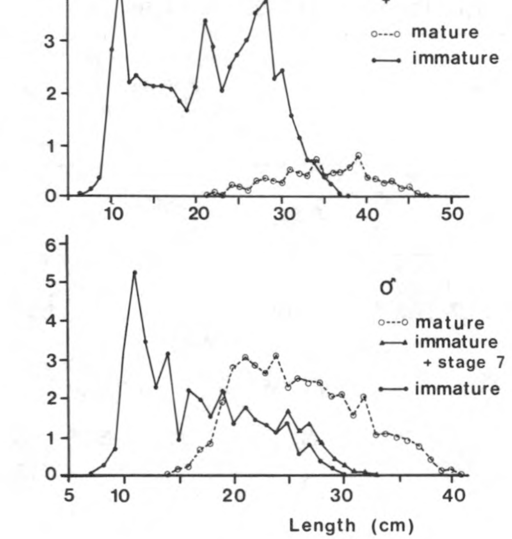


Figure 11. Length-frequency distribution of mature and immature plaice in the maturity surveys of 1985 and 1986. For male plaice the occurrence of stage 7 males is indicated.

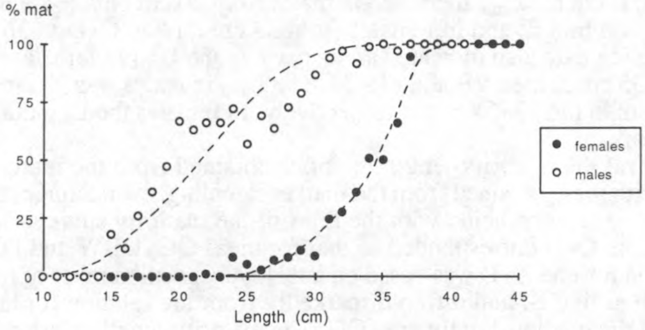


Figure 12. Percentage of mature fish in relation to length in male and female plaice in the maturity surveys of 1985 and 1986. The lines are drawn by eye.

For comparison, the maturity-age relationship derived from market sampling in the first quarter of 1985 and 1986 is given in Table 5. The average maturity percentage was calculated over the areas that included the lines of the survey. Because plaice abundance differed between these areas, the maturity percentage at age was weighted over the abundance on the lines of the maturity survey by age group. Market sampling results for males are not tabulated because the minimum landing size in use prevents the landings of plaice below 27 cm. In female plaice the market sampling estimate was only slightly higher in age group III (9% against 6%) and IV (36% and 29%), but not in age groups II, V and

Table 3. Length (cm) at which 50% of the plaice are mature (L_{mat}) as estimated from geometric mean regression of logit P = a + b length. Pooled data of 1985 and 1986.

	Maturity Survey					Market sampling	
	Male		Female			Female	
	L_{mat}	95%CL	L_{mat}	95%CL		L_{mat}	95%CL
Line					Area		
A+B	19.8	18.9-20.7	34.0	32.5-35.5	DWK	30.1	29.5-30.7
C+D	21.6	20.0-22.2	32.8	31.9-33.7	OG	32.5	31.2-33.3
E	24.2	23.1-25.3	35.9	34.7-37.2	DBW	32.9	32.5-33.3
					DBO	33.2	32.4-34.0
					VB	34.6	33.7-35.5
					FLAM	33.8	32.9-34.7
total	21.9	21.1-22.7	33.9	32.6-35.2	total*	32.9	32.3-33.5

*excluding FLAM

older. Comparison within market sampling areas shows higher discrepancies, the market sampling data generally yielding higher estimates, especially in areas DWK + OG compared with the line A+B and area VB compared with line E. Areas DBW and DBO showed good correspondence with lines C+D.

For the partially mature age groups the maturity-length relationships were studied by age group in the survey data and market sampling data (Figs.13a-c). In both male and female plaice the maturity percentage at a certain length generally increased with age. Consequently the L_{mat} decreased with age.

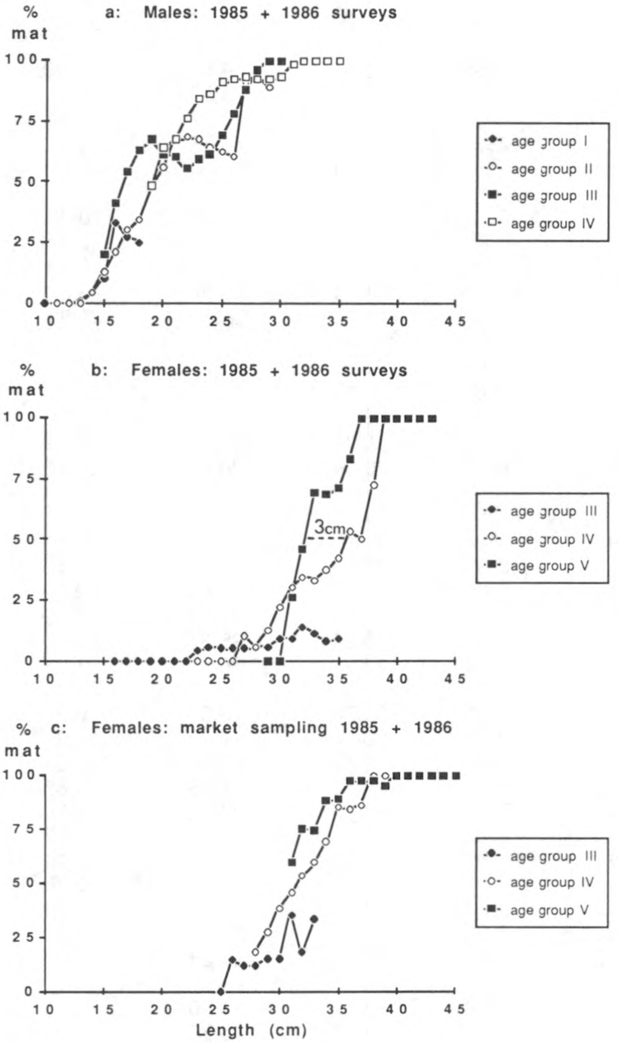


Figure 13. Maturity-length relation by age group for (a) male and (b) female plaice in the maturity surveys of 1985 and 1986 and (c) female plaice in the first quarter market samples of 1985 and 1986.

Table 4. Number of plaice caught per hour fishing (N/h), proportion of mature plaice by age group (mat), and mean length (L in cm) of immature and mature plaice for line A+B, line C+D and line E. In the mat* stage 7 males were considered to be immature. **) In 1986 the first 4 stations of line E were not fished

				Males: 1985 survey			
age group :		I	II	III	IV	V	VI
Line							
A+B	N/h	0.65	27.34	13.57	5.45	0.86	0.18
	mat	0.06	0.78	0.67	0.94	1.00	1.00
	mat*	0.06	0.76	0.57	0.94	1.00	1.00
	Limm	12.40	21.27	24.74	24.50	-	-
	Ladult	16.50	21.66	27.05	31.57	33.33	36.08
C+D	N/h	0.85	40.50	14.00	12.00	4.87	1.28
	mat	0.00	0.57	0.57	0.91	1.00	1.00
	mat*	0.00	0.57	0.57	0.91	1.00	1.00
	Limm	12.87	19.96	24.55	28.35	-	-
	Ladult	-	20.18	26.80	31.13	34.82	37.31
E	N/h	2.13	7.40	17.02	20.99	3.53	2.03
	mat.	0.00	0.37.	0.84	0.96	1.00	1.00
	mat*	0.00	0.37	0.42	0.79	1.00	1.00
	Limm	11.61	18.64	26.50	29.30	-	-
	Ladult	-	19.05	26.50	29.91	34.33	36.60
Tot.	N/h	1.03	28.61	14.43	11.18	2.99	0.99
	mat	0.002	0.64	0.67	0.94	1.00	1.00
	mat*	0.002	0.63	0.53	0.87	1.00	1.00
	Limm	12.22	20.15	24.85	27.92	-	-
	Ladult	16.50	20.84	26.81	30.75	34.58	36.85
				Males: 1986 survey			
A+B	N/h	29.30	13.47	19.90	3.43	1.25	0.00
	mat	0.01	0.52	0.88	0.99	1.00	-
	mat*	0.01	0.50	0.83	0.99	1.00	-
	Limm	10.47	20.90	25.57	28.50	-	-
	Ladult	15.66	21.70	26.17	31.51	32.20	-
C+D	N/h	79.81	66.08	26.56	9.90	8.87	3.37
	mat	0.01	0.34	0.78	0.94	1.00	1.00
	mat*	0.01	0.33	0.71	0.93	1.00	1.00
	Limm	10.61	17.42	24.85	26.68	-	-
	Ladult	15.87	20.75	25.56	30.76	34.36	36.61
E**	N/h	11.67	6.60	27.58	8.08	12.17	2.25
	mat	0.00	0.29	0.53	0.95	1.00	1.00
	mat*	0.00	0.29	0.21	0.72	1.00	0.88
	Limm	13.52	19.24	25.70	32.50	-	-
	Ladult	-	21.18	27.28	30.92	32.93	35.53
Tot	N/h	45.98	33.14	24.10	6.95	6.48	1.80
	mat	0.007	0.37	0.76	0.95	1.00	1.00
	mat*	0.007	0.35	0.63	0.90	1.00	0.97
	Limm	10.73	17.94	25.35	28.30	-	-
	Ladult	15.80	20.98	26.07	30.95	33.66	36.30

Table 4 continued. Number of plaice caught per hour fishing (N/h), proportion of mature plaice by age group (mat), and mean length (L in cm) of immature and mature plaice for line A+B, line C+D and line E. **) In 1986 the first 4 stations of line E were not fished

Females: 1985 survey

age group :		I	II	III	IV	V	VI
Line							
A+B	N/h	0.36	7.90	12.93	2.10	1.58	0.65
	mat	0.00	0.004	0.05	0.32	0.98	1.00
	Limm	11.75	21.81	26.57	32.38	32.50	-
	Ladult	-	22.48	27.89	33.79	39.61	41.24
C+D	N/h	0.97	30.53	17.56	10.05	2.27	3.20
	mat	0.00	0.02	0.07	0.46	0.94	1.00
	Limm	12.54	20.95	26.29	31.73	32.20	-
	Ladult	-	23.36	27.60	33.59	36.65	39.26
E	N/h	2.03	8.15	25.06	19.59	1.94	1.03
	mat	0.00	0.00	0.02	0.07	0.64	1.00
	Limm	11.61	18.68	28.69	32.01	34.05	-
	Ladult		-	- 29.92	32.84	39.41	38.40
Tot	N/h	.94	17.00	17.21	8.78	2.13	1.74
	mat	.00	.02	.05	.27	.90	1.00
	Limm	11.94	20.89	27.09	31.95	33.38	-
	Ladult	-	23.43	28.00	33.53	37.97	38.96

Females: 1986 survey

A+B	N/h	24.62	6.94	12.41	1.21	.54	.29
	mat	0.00	0.00	0.23	0.49	1.00	1.00
	Limm	10.49	21.31	27.51	30.94	-	-
	Ladult	-	-	28.09	33.71	37.93	41.93
C+D	N/h	72.06	52.01	27.52	4.14	3.44	2.28
	mat	0.00	0.00	0.06	0.48	0.92	0.96
	Limm	11.07	18.17	27.19	31.73	33.35	36.50
	Ladult	-	23.41	27.71	33.39	37.17	41.17
E	N/h	11.00	5.83	47.18	11.07	4.80	2.60
	mat	0.00	0.00	0.01	0.14	0.34	1.00
	Limm	13.65	21.74	27.60	30.09	32.59	-
	Ladult	-	23.41	28.14	33.10	36.69	41.17
Tot	N/h	40.87	24.74	25.40	4.35	2.55	1.55
	mat	0.00	0.004	0.07	0.31	0.70	0.97
	Limm	10.76	19.06	25.89	30.81	33.66	36.30
	Ladult	-	23.41	28.54	33.33	37.08	41.20

DISCUSSION

Annual maturity cycle

Gametogenesis in plaice extends over the major part of the reproductive cycle in accordance with the general pattern in teleosts (Scott 1979). The cycle of vitellogenesis, gonad growth and spawning of North Sea plaice is similar to that of plaice caught in the English Channel although the timing is slightly different (LaHaye 1972; Deniel 1981; Houghton & Harding 1976).

At the end of the growing season nearly all females have started to develop their gonads, as can be seen from the very small proportion of spent fish in November and December (Fig.4). This indicates that in North Sea plaice almost all adult females will take part in spawning in each succesive spawning season.

Table 5. Proportions maturity at age derived from the market sampling data in comparison with the average proportions as obtained from the survey. The market sampling total was obtained by weighting over the female abundance by age group in the maturity survey excluding market sampling area FLAM.

	Age groups					
	I	II	III	IV	V	VI
	Female plaice; market sampling data 1985-1986					
area:						
DWK	-	0.00	0.26	0.86	1.00	1.00
OG	-	0.00	0.13	0.62	0.93	0.98
DBW	-	-	0.11	0.40	0.92	0.98
DBO	-	-	0.06	0.44	0.81	0.99
VB	-	-	0.00	0.19	0.68	1.00
FLAM	-	0.00	0.13	0.30	0.94	0.98
Total*	-	0.00	0.09	0.36	0.82	0.99
	Female plaice; survey data 1985-1986					
Lines:						
A+B	0.00	0.00	0.14	0.41	0.99	1.00
C+D	0.00	0.01	0.07	0.47	0.93	0.98
E	0.00	0.00	0.02	0.11	0.49	1.00
Total	0.00	0.01	0.06	0.29	0.80	0.99
	Male plaice; survey data 1985-1986					
Lines:						
A+B	0.03	0.65	0.78	0.97	1.00	1.00
C+D	0.01	0.46	0.68	0.93	1.00	1.00
E	0.00	0.33	0.69	0.96	1.00	1.00
Total	0.005	0.51	0.72	0.95	1.00	1.00

* excluding FLAM

Duration of spawning

The duration of spawning was estimated using the pooled data over three years. This could lead to an overestimation if the timing of spawning and the level of sampling differed between the three years. Harding *et al.* (1978a) showed that the timing of spawning in plaice was fairly constant so we can accept the estimated spawning times as a first approximation.

In this paper females of maturity stage 3 were considered as taking part in spawning. During the final stage of maturation, the oocytes hydrate and greatly increase in volume. Egg diameter in plaice ranges between 1.66 and 2.17 mm, egg volume between 2.4 and 5.4 mm^3 (Russell 1976). Given a relative fecundity of 220 eggs per g body weight (Rijnsdorp *et al.* 1983), and assuming an equal specific weight of eggs and body of 1.0, the volume of eggs to be shed will be 0.86 cm^3 as compared to a gonad size of 0.17 cm^3 (gonado-somatic index = 17%; Fig.5), a fivefold increase. The mean gonado-somatic index of stage-4 females with a gonad completely filled with hydrated eggs is about equal to that of stage-2 females with ripening gonads. Thus at stage 4 only 20% of the total volume of eggs can be accounted for, the other 80% must already have been shed by stage-3 females, although it cannot be ruled out that a small part of the hyaline eggs were expelled during fishing or handling the fish on board. This also implies that female plaice will produce several batches of eggs during the spawning period.

The average male is in spawning condition for at least 11 weeks between the second half of December and mid March, the average female for only five weeks between the end of January and the beginning of March. From this it can be inferred that an average male can fertilize eggs from early- as well as late-spawning females over nearly the complete spawning period.

Feeding condition

The incidence of feeding in plaice decreased in winter. Feeding incidence was already low by December when the water temperature was still relatively high and increased again in March when temperatures reached their seasonal low. In the laboratory also, food intake in plaice has been found to decrease in autumn under natural daylight (Fonds pers. comm.). The decrease was therefore not related to the water temperature as suggested by Lande (1973). The difference in feeding condition between reproductive states suggests that spawning and feeding are mutually exclusive. Such mutual exclusion of feeding and spawning might stem from the limited metabolic scope of plaice that does not allow for both oxygen demands for spawning and related activities and feeding metabolism (Chapter 2).

Distribution

As juvenile plaice grow they gradually disperse from the nursery areas in the estuaries and shallow coastal zone. The correspondence of the spatial distributions of male and female plaice (age groups I, II and III), as observed in this study, corroborates the conclusion of Beverton & Holt (1957) that the offshore movement of plaice mainly results from a process of random diffusion. However, the difference in distribution between mature and immature females in age group III and IV indicates that active behaviour must also be involved. Mature females of age- group III and IV were found to be distributed in a band 18 - 36 miles from the coast. Immature females of these age groups were, however, distributed over a wider area farther offshore. As the area of main egg-production extends between 40 and 100 miles from the coast (Fig.1), it can be inferred that the mature females of these age groups have to migrate to the actual spawning areas farther offshore to shed their eggs. Arnold *et al.* (in prep) showed that in the spawning period especially, females of maturity stage 2 and 3 were caught in midwater on the spawning grounds. This suggests that the ripening females may migrate to the spawning areas to shed their eggs and that they avoid the spawning areas during the final stages of ripening just prior to spawning.

Length and age at first maturity

The maturity percentages of III- and IV-group females in the market-sample data were somewhat higher than in the survey data. The market samples were obtained from the beam-trawl fishery that mainly operates on offshore spawning concentrations of plaice (Fig.3). The observed differences between survey and market sampling results will be mainly due to the discarding of plaice smaller than the minimum landing size of 27 cm. In the survey nearly 100% of the females of age groups I and II, 40% of age group III and 4% of age group IV were smaller than 27 cm. Because of differences in growth between areas these percentages will be lower in the south and higher in the northern areas.

From the distribution of mature and immature females in relation to the distance from the coast it can be deduced that sampling of the edges of the spawning areas will give lower values of the maturity percentage than in the centre. However, this will only slightly affect the maturity percentage in age group II, III and V, but will be more pronounced in age group IV, because this age group shows the biggest change in maturity percentage with distance from the coast. The error in the estimation of the maturity percentage from market samples due to differences in distribution of mature and immature fish will be relatively small if the market samples are taken over a wide area comprising both the edges as well as the centre of the spawning grounds. The ripening females concentrated at the edge of the main spawning area will also migrate into the main spawning area to shed their eggs.

However, the maturity survey will not be free of bias. A survey in the first half of the spawning period, which does not take into account changes in the distribution during the spawning period and comprises only 49 stations may not give an unbiased picture of the maturation of the plaice population in the southern North Sea. In particular, line A +B is assumed not to have given an unbiased sample of the Southern Bight spawning population to judge from the low catches of female plaice (Table 4) in comparison with the amount of eggs produced in this area (Harding *et al.* 1978a; Arnold *et al.* in prep). This can also be a part of the explanation for the difference in maturity percentage in age group IV between line A+B and area DWK.

Furthermore, the survey did not encompass the estuarine area of the Waddensea, a major nursery area for 0- and I-group plaice (Zijlstra 1972). Although some juveniles leave the estuaries in winter a considerable part will be distributed outside the survey area within the three-mile zone and the estuary (Fonds 1978). Therefore, the maturity percentage and also the mean length will be overestimated for I-group plaice. From Demersal Young Fish Surveys in 1983, 1984 and 1985 the average length of 0-group plaice is estimated at 9.7 cm in September-October (unpublished RIVO data).

From the relatively small differences in the estimated maturity-length and maturity-age relations from the survey and market sampling data it can be concluded that the market sampling data will give a reliable estimate of the length and age at first maturity in female plaice, but for male plaice special surveys are needed to obtain representative data.

It is generally assumed that the onset of sexual maturity is determined by a constant threshold length (Roff 1982), which can be affected by the growth rate of the fish (Alm 1958; Nikolski 1969). In this study the L_{mat} decreased with age (Fig.13a-c). Before we can conclude that the length at first maturity in plaice is affected by the growth rate we have to examine the possibility that differences in L_{mat} between age groups were caused by the time interval between the onset of maturation and the spawning time. This could allow the younger and faster-growing plaice, after passing a threshold length for maturation out of season, to reach a greater length in the next spawning season than the older and slower-growing plaice.

This study showed that the juvenile - adult transition took place between May and September. In females the difference in the L_{mat} between age group IV and V was about 2 - 3 cm (Fig.13b and c), whereas the difference in annual length increment between the age group IV (increment = 5.4 cm) and age group V (increment = 4.8 cm) is only 0.6 cm (Table 4). Therefore, differences in length increment after passing the assumed 'maturity threshold' can only partly explain the decrease in L_{mat} with age; we may therefore tentatively conclude that the maturity threshold length is not constant but decreases with the growth rate. Stearns & Crandall (1984) interpreted the variability in length and age at first maturity as a reflection of the plasticity of the reproductive strategy of fish in response to environmental stress. Annual differences in growth can affect both the length and age at first maturity as shown by the difference in L_{mat} in male plaice in 1985 and 1986 and the differences in maturity percentage of year classes 1982, 1983 and 1984 in both males and females.

In male plaice the maturity-length relation levelled off between 20 and 27 cm. This phenomenon can be partly explained by a year class effect, the 1983 year class having a higher L_{mat}. However, because it was also apparent in the maturity-length relations of individual year classes, it is possible that the male population consisted of two groups returning atdifferent length thresholds.

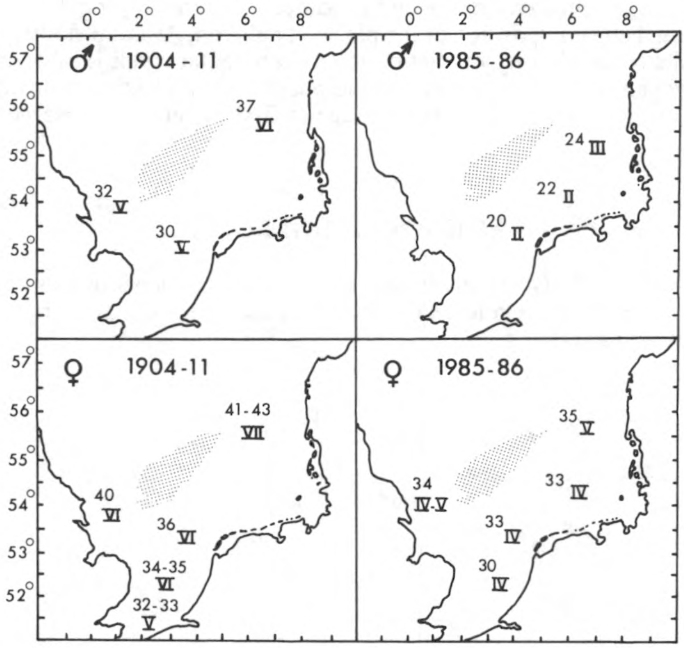


Figure 14. Comparison of the present length (L_{mat}) and age (A_{mat}) at 50% maturity with those at the beginning of the century (from Wallace 1914) in male and female plaice. The A_{mat} in 1904-1911 have not been corrected for the different method of age determination (see text).

Historic changes in the onset of sexual maturity

In Fig.14, the L_{mat} and A_{mat} obtained in the present study are compared with data from the beginning of this century as summarized by Wallace (1914). At the beginning of this century female plaice became mature as V- and VI-group at a length of 32-35 cm in the Southern Bight; and as VI- and VII-group at 40-42 cm in the region of the Dogger. Male plaice became mature as V- and VI-group at a length of 32-37 cm in the Dogger region. The onset of sexual maturity in males in the Southern Bight was unclear. However, some males were already mature as II-group and at a length of 18 cm. Because our method of age determination (birthday at 1 January) differed from that of Wallace (variable birthday between January and April depending on the formation of a new growth zone in the otolith) the A_{mat} as determined by Wallace's method will be on average 0.5 years too low compared to our method (see Appendix Table VI in Wallace 1914). The data of Wallace given in Fig.14 have not been converted. Simpson (1959) estimated female plaice of 1943 and 1944 year classes became mature as IV- and V-group in the Southern Bight .

Compared to these historic data it is obvious that North Sea plaice now reaches maturity about 2 to 3 years younger and also at a smaller size than in the beginning of this century. However, Rijnsdorp & van Leeuwen (1985) showed that the L_{mat} of female plaice could vary by 2 - 3 cm between successive years, so the observed difference in L_{mat} in the Southern Bight may not be real. It remains an intriguing question as to whether the change in length at first maturity is in any way related to the recent extension of the area inhabited by plaice in the northeastern North Sea (Bannister 1978; Harding *et al.* 1978a; Cushing 1982) and whether the observed change in L_{mat} is a reflection of the phenotypic plasticity in response to changes in the environmental conditions (Stearns & Crandall 1984) or reflects changes in the genetic composition of the plaice population. A future study of the variability in the onset of sexual maturity in relation to environmental conditions during the juvenile phase may give an indication of whether the phenotypic plasticity is sufficiently large to take account of the changes in length and age at first maturity as observed in North Sea plaice

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Chapter 5

Changes in fecundity of female North Sea plaice (*Pleuronectes platessa* L.) between three periods since 1900

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ABSTRACT. Variations in size-specific fecundity were studied over a period of seven years between 1977 and 1985 and fecundity - body length relationships were compared between three periods: 1900-1910, 1947-1949 and 1977-1985. Significant differences were observed between years and areas. The average fecundity for a 40 cm female was 12% less in the German Bight than in the southern North Sea, but the annual variability was higher, respectively 15% and 7%. Length-specific fecundity showed a significant positive correlation with pre-spawning condition factor, but not with the somatic growth in the preceding year. Fecundity appears to have changed since the early 1900's and 1947-1949. In 30-cm females the present fecundity was about 30-100% higher compared to the first two periods depending on the area. Fecundity of larger females (50-cm) was similar to that in 1900, but was 30-60% higher than in 1947-49. The substantial reduction in fecundity in the period 1947-1949 contrasted with the much smaller change in ovary weight, suggesting not a change in the energy allocation over reproduction and somatic growth, but in the energy allocation over a small number of large eggs versus a large number of small eggs. Both length- and weight-specific fecundity decreased with age. The effect was largest in young fish. Weight-specific fecundity decreased by 3.9 % when age increased from 4 to 5 years, by 1.7% when age increased from 10 to 11 years and by 0.8% when age increased from 20 to 21 years. Significant differences in length-specific ovary weight were also observed between years and geographical areas, but the variability between years was less than in fecundity. Ovary growth was not synchronous between age groups, the younger age groups lagging behind by about one month. Egg weight calculated from ovary weight and fecundity was lower than egg weight measured from ripe running females, suggesting that ovary growth continues after the start of spawning in an individual plaice. The differences in fecundity and ovary weight between the three time periods are discussed in relation to the question whether these are a phenotypic response due to changes in the conditions for growth or to a change in the genetical composition of the population.

INTRODUCTION

Fecundity is defined as the number of eggs spawned by an individual female and can be estimated by counting the number of developing oocytes in the ovary. For comparative purposes, fecundity is often reported as relative fecundity, defined as the number of eggs per gram body weight (Bagenal 1973). In applying relative fecundity it is assumed that fecundity is proportional to body weight, which is not always the case. In the present paper therefore, fecundity is given for females of a standard length, weight, or age in order to compare fecundity between areas and years. This will be referred to as length-, weight-, or age-specific fecundity.

Fecundity of female plaice has been studied by Fulton (1891), Reibisch (1899), Franz (1910a,b), Simpson (1951), Kändler & Pirwitz (1957), Kändler (1959), Bagenal (1966), Rijnsdorp *et al.* (1983), and Horwood *et al.* (1986). Bagenal (1966) showed a geographical pattern in length-specific fecundity increasing from a relatively low value in populations in the centre of the species distribution area to higher values in populations at the edge. He suggested that these differences "were related to the amount of food available, which in turn is related to population density". Rijnsdorp *et al* (1983) and Horwood *et al.* (1986) reported higher fecundity values in the late 1970's and early 1980's in the North Sea than those Simpson (1951) reported for the late 1940's, and Reibisch (1899) and Franz (1910a,b) for the beginning of the century.

The reported change in fecundity of North Sea plaice since the late 1940's was questioned by Horwood *et al.* (1986), because of doubts about the comparability of the methods used. However, they concluded that the reported increase in fecundity must reflect a real change because ovary weights showed a corresponding increase. Although a comparison of ovary weights between the two periods offers the possibility for an independent test, such a comparison should take account of the fast growth in ovary weight in the months prior to spawning (Chapter 7). Since Simpson (1951) collected ovary samples between October and February, and Horwood *et al* (1986) between December and February, the lower ovary weights in the 1940's might be related to the earlier sampling dates.

Changes in fecundity and ovary weight do not have to be proportional or to occur simultaneously, since concurrent changes in egg weight may occur. The question whether the fecundity, or more generally, the reproductive investment of plaice has increased therefore remains unanswered. This question is an important one, because it bears directly on two fundamental problems: 1) is the total number of eggs produced annually by a population proportional to the biomass of female fish (Rothschild 1986)?; 2) does a continued high level of fishing mortality cause changes in the genetic composition of the population with respect to reproductive parameters (Horn & Rubenstein 1984; Allendorf *et al.* 1986; Nelson & Soulé 1986)?

Plaice has been exploited in the North Sea since the late 19th century at a level of fishing mortality that exceeds the natural mortality and, as a consequence, the age structure of the adult population must have changed towards younger age groups compared to the unexploited population. Certain biological parameters have been shown to have changed correspondingly: thus length-at-age of juvenile plaice has increased, while that of adult fish appears to have decreased (Bannister 1978). And present maturity occurs at a younger age and a smaller length than at the beginning of this century (Chapter 4).

This paper analyses the changes in fecundity of female North Sea plaice between three periods: 1900 - 1910, 1947-1949 and 1977 - 1985, based on literature data and new data. Changes in ovary weight between 1947-1949 and 1982-1988 are analysed. Egg weight, which links fecundity and ovary weight, is compared from estimates obtained both indirectly from ovary weight and fecundity and directly from running females.

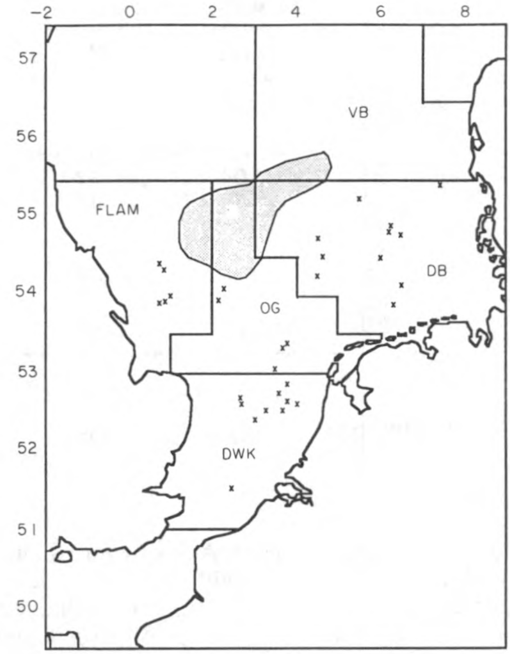

Figure 1. Sampling positions for fecundity (x) in 1982-1985 and the geographical areas distinguished in the present study. The shaded area shows the Doggerbank.

Table 1. Number of ripening females (maturity stage 2) sampled for fecundity and ovary weight. Data sources: (1) Reibisch (1899), Franz (1910a,b); (2) Simpson (1951); (3) Horwood *et al.* 1986; (4) this study.

	Areacode:					
	DWK	OG	DB	FLAM	Total	Source
FECUNDITY						
1900-1910	-	-	108	-	108	1
1947/49	221	-	-	33	254	2
1976/77	29	37	65	-	131	3
1978/79	46	64	37	-	147	3
1979/80	68	49	137	88	342	3
1981/82	31	24	26	21	102	4
1982/83	17	33	65	38	153	4
1983/84	45	8	34	42	129	4
1984/85	38	14	52	0	104	4

Table 1 continued. Number of females sampled for ovary weight.

	Areacode:					
	DWK	OG	DB	FLAM	Total	Source
OVARY weight (first quarter only)						
1947/49	47	-	-	33	80	2
1982	44	92	104	82	322	4
1983	80	116	154	92	442	4
1984	111	98	171	14	394	4
1985	86	55	154	40	335	4
1986	88	49	174	49	360	4
1987	10	42	48	2	102	4
1988	27	28	63	29	147	4

MATERIAL AND METHODS.

Notation

In this paper the following notation is used: A - age with 1 January as birthdate; DEW - dry egg weight (mg); %DEW - dry egg weight (%); EW - wet egg weight (mg); E - fecundity in thousands of eggs; G - ovary weight (g); RG - relative ovary weight = 100 x G x L^{-3}; L - length in cm; W_t - total weight (g) including viscera and ovaries; W_g - gutted weight (g) excluding viscera; SW - somatic weight (g) = W_g - G; K - condition factor = 100 x W_t x L^{-3}; SC - somatic condition = 100 x SW x L^{-3}; %dry - percentage dry weight;

Gutted weight in plaice is related to total weight according to $W_t = 1.07 \times W_g$ (Chapter 1).

Ovary samples

Ovary samples were taken from market samples of the landings of commercial beam trawlers at fish auctions as described in Chapter 4. On board, the fish are stored on ice for less than one week before being sold, but some of the samples were deepfrozen at -20°C for some weeks before analysis. Market samples were taken randomly from various geographical areas (Fig.1) and consists of four length strata. From each length stratum, ripening females, which had not yet started to spawn (maturity stage 2: Chapter 4), were randomly selected and total length (mm), gutted weight (g), ovary weight (g) were recorded. Otoliths were collected for age-determination with 1 January assigned as the birthdate. Table 1 summarizes the sampling for fecundity and ovary weight and includes the new data as well as the data taken from literature.

Fecundity estimates

Female plaice in maturity stage 2 were selected randomly from all size classes in the market samples taken between December and February. Sampling information is summarized in Table 2 and the sampling positions are shown in Figure 1. The spatial distribution of the samples covers the main spawning areas of plaice in the North Sea except the southward extension in the eastern English Channel (Harding *et al* 1978; Heessen & Rijnsdorp 1989; Chapter 4).

Ovary samples were stored in methanol (50-70%) for a period between 2 and 12 weeks. The oocytes were separated from the connective tissue by washing in coarse- and small-meshed sieves under a gentle flow of water. The developing oocytes were finally cleaned of small fragments of connective tissue and small primary oocytes by decanting. This method is a further development of the one described in Reibisch (1899) and van Leeuwen (1972) and serves as a suitable alternative for the traditional technique using Gilson's fluid (Simpson 1951), which produces substantial amounts of toxic mercury waste products. Finally, the number of oocytes was counted using a wet counting device.

Table 2. Dates and positions of the fecundity samples

Sample #	Date	Position	Number	Areacode
SPAWNING SEASON: 1981/1982				
82-1	21 December	5300 N 330 E	14	DWK
82-2	21 December	5130 N 230 E	5	DWK
82-3	7 January	5250 N 340 E	12	DWK
82-4	11 January	5400 N 200 E	11	OG
82-5	11 January	5445 N 630 E	8	DB
82-6	18 January	5403 N 215 E	13	OG
82-7	25 January	5420 N 100 E	10	FLAM
82-8	1 February	5445 N 530 E	12	DB
82-9	8 February	5425 N 050 E	11	FLAM
82-10	22 February	5410 N 630 E	6	DB
SPAWNING SEASON: 1982/1983				
83-1	13 December	5415 N 415 E	20	DB
83-2	13 December	5320 N 230 E	33	OG
83-3	10 January	5355 N 050 E	38	FLAM
83-4	14 January	5430 N 420 E	20	DB
83-5	14 January	5450 N 610 E	25	DB
83-6	21 January	5245 N 345 E	17	DWK
SPAWNING SEASON: 1983/1984				
84-1	9 December	5240 N 240 E	19	DWK
84-2	16 December	5240 N 240 E	20	DWK
84-3	22 December	5355 N 055 E	41	FLAM
84-4	20 January	5430 N 600 E	25	DB
84-5	13 February	5320 N 350 E	8	OG
84-6	27 February	5355 N 620 E	9	DB
84-7	9 March	5240 N 353 E	6	DWK
84-8	12 March	5400 N 100 E	1	FLAM
SPAWNING SEASON: 1984/1985				
85-1	14 December	5230 N 355 E	4	DWK
85-2	14 December	5530 N 730 E	25	DB
85-3	18 January	5240 N 400 E	15	DWK
85-4	18 January	5225 N 300 E	14	DWK
85-5	20 January	5455 N 610 E	13	DB
85-6	25 January	5320 N 350 E	14	OG
85-7	28 January	5515 N 530 E	14	DB
85-8	8 February	5230 N 320 E	5	DWK

Fecundity was estimated by counting the number of oocytes from a subsample of the ovary tissue of known weight and raising this number to the total weight of the ovary. Weights were determined to the nearest 0.01 g. Ovary subsamples were taken from the middle region and had a weight of 1-4 g (about 2 - 10% of the ovary weight). Pilot counts showed that the egg densities of the two ovaries of an individual female did not differ significantly, neither did the egg densities of the various sections of one ovary. The variance of repeated estimates of relative egg density between ovaries was 9% (n=186) and of repeated estimates of the various sections from the same ovary was 5% (n=320). The precision of the fecundity estimate of an individual female using two subsamples was estimated at $1.96 \times 9\% / \sqrt{2} = 12\%$, indicating that 95% of the measurements were within ± 12% of the true egg density. Two ovary subsamples were taken per female in 1982, 1983 and 1984 and one subsample in 1985.

The number of oocytes was determined using a wet counting device (Philips PW4232) according to Parrish *et al.* (1960). The accuracy of this equipment was regularly tested by comparing the results with eye counts of test samples of 500 - 1000 oocytes. In a pilot experiment the deviation between the wet counting device and the eye count was observed to be + 0.5% with a standard deviation of 2% (n= 10).

Table 3a. ANCOVA results of the fecundity data 1982 - 1985 according to the GLM model: $\log_n E = \alpha + \alpha_{year} + \alpha_{area} + \beta.\log_n L + \gamma \log_n SC + \delta.\log_n A$; with E = fecundity; L = length; A = age; SC = somatic condition .

	SS	d.f.	MS	F	P
$\log_n A^1$	0.010	1	0.010	0.22	n.s.
$\log_n SC^1$	16.26	1	16.26	359.0	<0.01
$\log_n L^1$	29.84	1	29.84	658.8	<0.01
Area^1	0.693	3	0.231	5.10	<0.01
Year^1	0.870	3	0.290	6.40	<0.01
error	21.56	476	0.045		
total	170.2	485			

^{1} after adjusting for main effects.

Table 3b. Parameter estimates of the significant parameters of the GLM model of table 3a: $\log_n E = \alpha + \alpha_{year} + \alpha_{area} + \beta.\log_n L + \gamma \log_n SC + \delta.\log_n A$; with E = fecundity; L = length; A = age; SC = somatic condition .

Parameter estimate	
α	-6.872
β	3.220
γ	1.882
α1982	0.000
α1983	-0.0172
α1984	-0.0738
α1985	-0.1167
αDWK	0.000
αOG	-0.0954
αDB	-0.0407
αFLAM	-0.1041

Egg dry weight

Sampling of ripe eggs for determining dry weights of eggs was carried out in area DWK in the second half of January 1990 on board a commercial beam trawl vessel. Ripe eggs were stripped from running females (maturity stages 3 to 6) directly on capture. Length, weight, age, ovary weight after the ripe eggs had been stripped, and percentage dry weight of the ovary were determined for each fish. Eggs were stored in 4% formaldehyde in sea water and the hydrated eggs separated from the non-hydrated eggs by sieving over a plankton gauge with a mesh size of 240 µm. After storing for 1-4 weeks the samples were washed with demineralized water; a subsample of about 400 eggs was counted and dried at 60°C and the dry weight determined to the nearest 0.1 mg. Replicates of weight estimates indicated that with 95% probability the measured weight per egg deviated less than 0.006 mg of the real value.

Statistical methods

Analyses of covariance (ANCOVA) and backwards stepwise regression analyses were carried out with the NAG statistical package GLIM (Baker & Nelder 1978). The basic general linearized (GLM) model (McCullagh & Nelder 1983) to study the dependent variable (Y: fecundity, ovary weight), in relation to covariables (X: length, weight, somatic condition), and factors (F: age, geographical area, spawning season) was:

$$\log_n Y = \alpha + \beta \log_n X1 + \gamma \log_n X2 + F_i + F_j + \varepsilon$$

The assumption of the ANCOVA that the error term (ε) is normally distributed was tested by making a probability plot of the residuals. Parameter values were estimated: α for intercept, β and γ for the slopes of the main covariables and α_i, α_j for the factorial effects of F_i and F_j. The multiplicative effect of a factor F was calculated as the antilog of the parameter estimate $\exp(\alpha_i)$.

RESULTS

Fecundity

New data 1982-1985.

The results of the ANCOVA for fecundity length relation with covariables, age and somatic condition, and factors, area and year (i.e. spawning season), are given in Table 3a. Variance in fecundity was explained by length of the fish (18%) and somatic condition (10%). The other factors, though statistically significant, contributed much less (area - 0.4% and year - 0.5%). Age was not significant. A substantial part of the variance in fecundity (59%) could not be ascribed to a single factor. A test of the interaction of the significant covariables length and somatic condition, with area and year showed that the secondary and tertiary interactions were all non-significant, just as the interaction between the factors geographic area and spawning season.

Table 4a. ANCOVA results of the fecundity data 1982 - 1985 according to the GLM model: $\log_n E = \alpha + \alpha_{year} + \alpha_{area} + \beta.\log_n W + \delta.\log_n A$; with E = fecundity; W = weight; A = age.

	SS	d.f.	MS	F	P
$\log_n A$[1]	0.728	1	0.728	14.6	<0.01
$\log_n W$[1]	52.43	1	52.43	1054	<0.01
Area1	0.613	3	0.204	4.11	<0.01
Year1	1.086	3	0.362	7.28	<0.01
error	23.71	477	0.0497		
total	170.2	485			

[1] after adjusting for main effects.

Table 4b. Parameter estimates of the significant parameters of the GLM model of Table 4a: $\log_n E = \alpha + \alpha_{year} + \alpha_{area} + \beta.\log_n W + \delta.\log_n A$; with E = fecundity; W = weight; A = age.

Parameter estimates	
α	-2.658
β	1.241
δ	-0.172
α1982	0.000
α1983	-0.0523
α1984	-0.1114
α1985	-0.1314
αDWK	0.000
αOG	-0.0820
αDB	-0.0510
αFLAM	-0.1028

Table 5. ANCOVA results of the fecundity data 1977 - 1985 according to the GLM model: $\log_n E = \alpha + \alpha_{year} + \alpha_{area} + \beta.\log_n L + \delta.\log_n A$; with E = fecundity; L = length; A = age;

	SS	d.f.	MS	F	P
$\log_n A$[1]	5.21	1	5.21	57.2	<0.01
$\log_n L$[1]	112.3	1	112.3	1233.0	<0.01
Area[1]	2.59	3	0.863	9.48	<0.01
Year[1]	7.52	6	1.254	13.77	<0.01
error	99.64	1094	0.0911		
Area.Year	2.209	15	0.147	1.70	<0.05
$\log_n$L.Area	1.671	3	0.557	6.43	<0.01
$\log_n$L.Year	0.265	6	0.044	0.51	n.s.
$\log_n$A.Area	0.941	3	0.314	3.62	<0.05
$\log_n$A.Year	0.583	6	0.097	1.12	n.s.
error	91.84	1061	0.0866		
total	374.3	1105			

[1] after adjusting for main effects.

Table 5b. Parameter estimates of the ANOVA of table 5a according to the GLM model: $\log_n E = \alpha + \alpha_{year} + \alpha_{area} + \beta.\log_n L + \delta.\log_n A$; with E = fecundity; L = length; A = age; $\alpha_{area \cdot year} = \alpha_{common} + \alpha_{year} + \alpha_{area}$

	DWK	OG	DB	FLAM
β	3.593	3.343	3.016	4.425
γ	-0.313	-0.267	-0.070	-0.425
$\alpha_{area \cdot year}$:				
1977	-7.650	-6.813	-6.062	-
1979	-7.705	-6.921	-6.308	-
1980	-7.550	-6.834	-5.904	-10.496
1982	-7.534	-6.783	-5.916	-10.494
1983	-7.699	-6.771	-6.054	-10.653
1984	-7.669	-7.049	-6.199	-10.707
1985	-7.679	-7.081	-6.118	-

The parameter estimates for the covariables length and somatic condition and for the factors area and year are given in Table 3b. The slope of the fecundity - length relation $\beta = 3.22$ is slightly but significantly larger than 3 ($p<0.01$). The somatic condition of the females prior to spawning positively influenced fecundity ($\gamma = 1.882$), indicating that a 10% increase in somatic condition results in an approximately 10% increase in fecundity. The multiplicative effect of area and year, calculated as the antilog of the parameter estimates, indicated that fecundity decreased between area DWK in the south and the more northern areas OG (-9%), DB (-4%) and FLAM (-10%) and also by 11% between 1982 and 1985.

Distribution of the error term showed a slight skewness and kurtosis with parameters of -0.336 and 0.554, respectively (n=486). Outliers were checked but there was no reason to suspect these observations; all were subsequently included in the analysis.

The relationship between fecundity and body weight was studied and the result of the ANCOVA is given in Table 4a. Only the primary factors are included since secondary and tertiary interaction terms were not statistically significant. The slope of the fecundity - weight relationship ($\beta = 1.241$) is significantly larger than one ($P<0.01$). Overall, the results of this ANOVA are very similar to those of the fecundity-length relationship, except that the covariable age is also significant. The parameter estimates in Table 4b indicate that

Table 6. Mean, standard deviation and coefficient of variation of predicted fecundities according to the parameter estimates of Table 5 for three size classes and age groups of plaice.

	30 cm age-IV		40 cm age-VI		50 cm age-X		
	mean	s.d.	mean	s.d.	mean	s.d.	C.V.
Area							
DWK	63	4.5	157	11.2	298	21.4	7.3
OG	61	7.5	144	17.6	264	32.4	12.3
DB	60	8.5	138	19.8	259	37.4	14.3
FLAM	48	5.2	145	15.7	310	33.9	10.8

weight-specific fecundity decreases with increasing age. An increase in age from 4 to 5 years old reduces fecundity by 3.9%, from 10 to 11 years old by 1.7%, and from 20 to 21 years old by 0.8%. The age effect is thus particularly pronounced in the younger age groups.

Data 1977-1985.

A similar ANCOVA to that of Table 3 applied to the data of Horwood *et al.* (1986) for the areas DWK, OG, DB and FLAM is shown in Table 5, except that the covariable somatic condition could not be included because the information required is not available for the years 1977-1980.

ANCOVA of the combined data set of 1106 female plaice showed again the significant effect of length, year and area, but in this case also age contributed significantly to the variance in fecundity (Table 5). A study of the secondary interaction terms showed a significant interaction of Area.Year, $\log_n$L.Area and of $\log_n$A.Area. None of the tertiary interaction terms was found to be significant. The parameter estimates of the model including all significant terms indicate that the slope of the fecundity - length relationship is steeper in area FLAM (Table 5). The estimated age effect was lowest in area DB and highest in area FLAM. In area DB an increase in age from 4 to 5 years old reduces fecundity by 1.5%, whereas in area FLAM this was 9.0 %.

The fecundities for three size classes (30, 40 and 50 cm) and four geographical areas (DWK, OG, DB, FLAM), predicted from the parameter estimates in Table 5, fluctuated in concert with relatively low values in 1979, 1984 and 1985 and relatively high values in 1980 and 1982 in all areas (Fig.2). No differences appear in the level of or the variability in fecundity between the data sets for 1977-1980 (Horwood *et al* 1986) and for 1982-1985 (present study). Table 6 shows that the between-year variability, expressed as the coefficient of variation (C.V.) of predicted fecundity, appears to be lowest in area DWK (C.V. = 7%) and highest in area DB (C.V. = 14%), the other areas being intermediate (FLAM: C.V. = 11%; OG: C.V. = 12%).

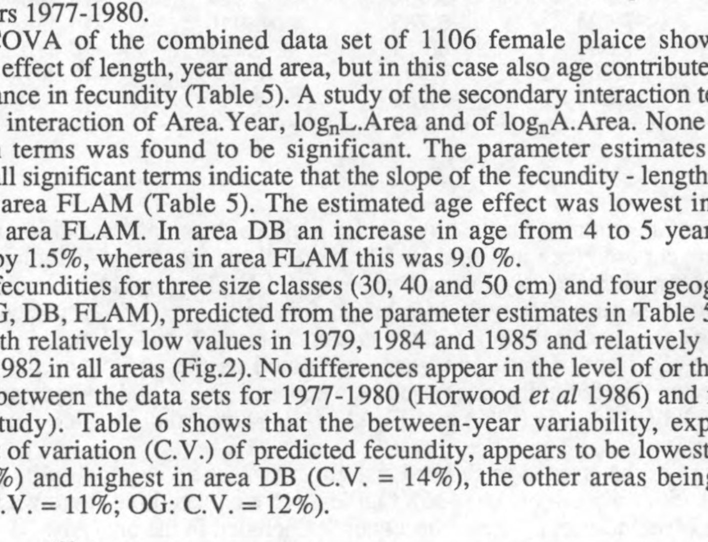

Figure 2. Annual variability in predicted fecundities for three size classes (30, 40 and 50 cm) by geographical area from parameter estimates in Table 5.

—□— = DWK, —●— = OG, —■— = DB, —△— = FLAM.

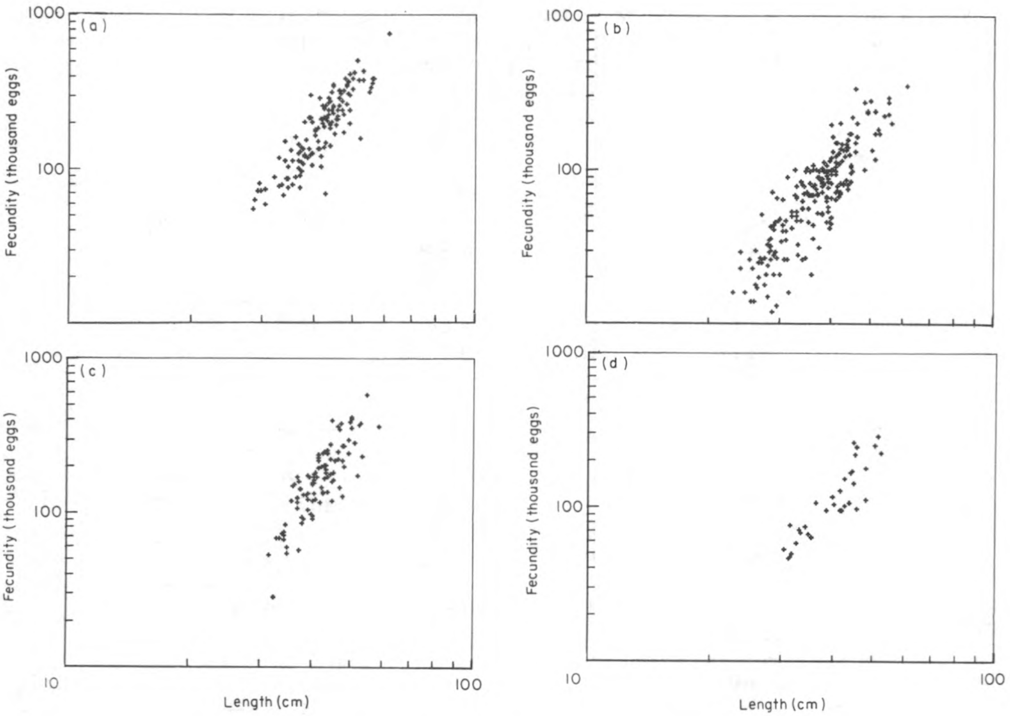

Figure 3. Scatter plots of fecundity (thousand eggs) against fish size (cm) in the period 1947 - 1949 and 1982 - 1985 for areas DWK (a) and FLAM (b). Data from Simpson (1951) and present study.

Comparison of 1947-1949 data with data for 1977-1985.

Simpson (1951) studied fecundity in area DWK in 1947/48 and 1948/49 and in area FLAM in 1948/49. The $\log_n$-$\log_n$ scatter plots of fecundity against fish length are shown in Fig 3a-d. ANCOVA of the data for both areas separately showed that the slopes of the regressions were significantly different between both periods in area DWK, but not in area FLAM (Table 7). Comparison of the predicted fecundities for three size classes from the parameter estimates of Table 7 showed that fecundity increased by 26% in area FLAM. In area DWK the increase in fecundity was between 62 and 103% depending on fish size (Table 8).

Comparison of 1900-1910 data with data for 1977-1985.

From the fecundity data collected around 1900 by Reibisch (1899) and Franz (1910a,b), plaice with hyaline eggs were excluded from the analysis, leaving a total number of fecundity estimates of 108 for these years. The samples originated mainly from the German Bight and were therefore compared with the data for this area (DB) from the period 1977-1985. The $\log_n$-$\log_n$ scatter plots of fecundity against fish length are shown in Figure 4. The regression slopes differed significantly between both periods (Table 7). At a fish length of 50 cm, present fecundity was 4% higher than in 1900 - 1910, but the difference increased to 35% at 40 cm and 90% at 30 cm (Table 8). Comparison of the 1900-1910 data with the individual years between 1977-1985 showed significant differences between slopes for all years except for 1979.

Table 7a. ANCOVA results of the fecundity data for three periods: 1900-1910 (Reibisch 1899; Franz 1910a,b); 1947-1949 (Simpson 1951) and 1977 - 1985 (Horwood *et al.* 1986; present study). for areas DB, DWK and Flam separately according to the GLM model: $\log_n E = \alpha + \beta.\log_n L$; with E = fecundity; L = length.

	SS	d.f.	MS	F	P
Area: DB					
$\log_n L^1$	158.1	1	158.1	1290	<0.01
Year^1	4.236	1	4.236	34.6	<0.01
error	63.90	521	0.1226		
$\log_n L$.Year	4.86	1	4.86	42.8	<0.01
error	59.04	520	0.1135		
total	228.2	523			
Area: DWK					
$\log_n L^1$	150.4	1	150.4	1307	<0.01
Year^1	43.63	1	43.63	379.1	<0.01
error	56.29	489	0.115		
logL.Year	0.829	1	0.829	7.29	<0.01
error	55.46	488	0.114		
total	284.6	491			
Area: FLAM.					
$\log_n L^1$	58.87	1	58.87	581	<0.01
Year^1	1.532	1	1.532	15.1	<0.01
error	21.99	217	0.101		
$\log_n L$.Year	0.316	1	0.316	3.15	n.s.
error	21.67	216	0.100		
total	82.84	219			

[1] after adjusting for main effects.

Table 7b. Parameter estimates of the fecundity data for three periods: 1900-1910 (Reibisch 1899; Franz, 1910a,b); 1947-1949 (Simpson, 1951); 1977 - 1985 (Horwood *et al.* 1986; present study). for areas DB, DWK and Flam separately according to the GLM model of Table 7a: $\log_n E = \alpha + \beta.\log_n L$; with E = fecundity; L = length.

period	parameter	Area		
		DB	DWK	FLAM
1900-1910	α	-9.908	-	-
	β	3.947	-	-
1947-1949	α	-	-7.198	-7.852
	β	-	3.169	3.400
1977-1985	α	-5.241	-5.004	-7.618
	β	2.763	2.732	3.400

Table 8. Predicted fecundity in thousand eggs, for three size classes of plaice and three time periods according to the parameter estimates of Table 7. The percentages at the bottom of the table indicate the percentage change from the historic period to the present period.

	30 cm		40 cm		50 cm	
Period: 1900-1910						
DB	33.6		104.8		252.8	
Period: 1947-1949						
DWK	35.9		89.3		181.1	
FLAM	40.9		108.9		232.5	
Period: 1977-1985						
DB	63.8	+90%	141.4	+35%	261.9	+4%
DWK	72.8	+103%	159.8	+79%	294.0	+62%
FLAM	51.7	+26%	137.6	+26%	293.8	+26%

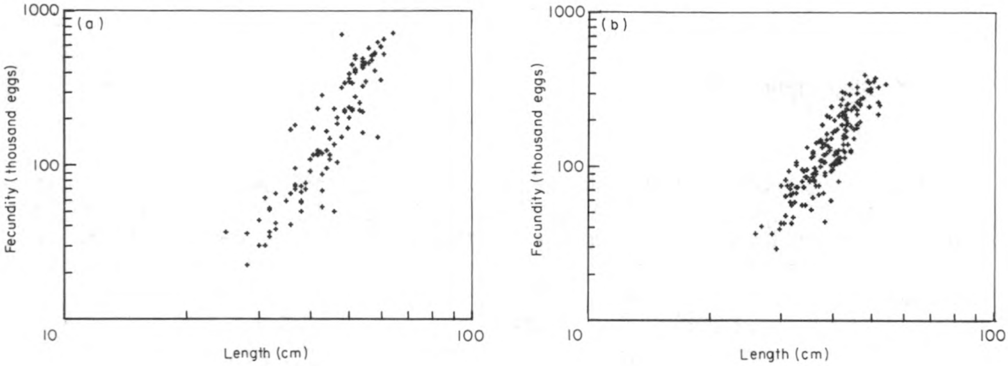

Figure 4.Scatter plots of fecundity (thousand eggs) against fish size (cm) for area DB in the period 1900 - 1910 and the period 1982 - 1985. Data from Reibisch (1899); Franz (1910a,b) and present study.

Ovary weight

New data for 1982-1988.

The relationships between ovary weight and the covariables length and somatic condition, and the factors age, spawning season, and geographical area, were studied in first-quarter samples of pre-spawning females (maturity stage 2). Table 9 shows that length was the main covariable explaining 75% of the variance in ovary weight. Somatic condition explained 0.3%, area - 1.4% and year - 0.2%. Age was not found to be significant. The analysis was complicated because there was a significant heterogeneity in the slopes of the regressions of ovary weight with length and somatic condition between areas and between years. However, this heterogeneity explained only 1% of the variance in ovary weight. The significant interaction $\log_n L$.Area indicates that the slopes of ovary weight on length were slightly steeper in the more northern areas.

Table 9a. ANCOVA results of ovary weights in the period 1982-1988 according to the GLM model: $\log_n G = \alpha_{area \cdot year} + (\beta + \beta_{year} + \beta_{area}) \log_n L + \gamma_{area} \log_n SC + \delta \log_n A + Area + Year$; with G = ovary weight; L = length; A = age; SC = somatic condition. Data FLAM in 1987 excluded.

	SS	d.f.	MS	F	P
$\log_n A$[1]	0.149	1	0.149	1.81	n.s
$\log_n SC$[1]	2.570	1	2.570	31.20	<0.01
$\log_n L$[1]	570.8	1	570.8	6930	<0.01
Area[1]	10.29	3	3.43	41.64	<0.01
Year[1]	1.793	6	0.299	3.63	<0.01
error	171.9	2087	0.0824		
Area.Year	2.789	17	0.164	2.05	<0.01
$\log_n L$.Area	0.799	3	0.266	3.32	<0.01
$\log_n L$.Year	1.694	6	0.282	3.52	<0.01
$\log_n SC$.Area	1.062	3	0.354	4.41	<0.01
$\log_n SC$.Year	0.959	6	0.160	1.99	n.s.
error	164.7	2053	0.0802		
total	760.5	2099			

[1] after adjusting for main effects.

Table 9b. Parameter estimates according to the GLM model of Table 9a with all significant interaction terms: $\log_n G = \alpha_{area \cdot year} + (\beta + \beta_{year} + \beta_{area}) \log_n L + \gamma_{area} \log_n SC + \delta \log_n A + Area + Year$; with G = ovary weight; L = length; A = age; SC = somatic condition. Data FLAM in 1987 excluded.

$\alpha_{area\ year}$

Area:	DWK	OG	DB	FLAM
Year:				
1982	-7.048	-8.470	-7.710	-8.659
1983	-8.603	-9.964	-9.184	-10.319
1984	-8.687	-9.983	-9.186	-10.318
1985	-8.620	-9.973	-9.219	-10.392
1986	-9.383	-10.791	-9.969	-10.980
1987	-9.816	-11.225	-10.353	-
1988	-10.447	-11.711	-11.066	-12.091

Year:	β	β_{year}	Area:	β_{area}	γ_{area}
1982	3.213	0.000	DWK	0.0000	0.3201
1983	3.213	0.433	OG	0.3613	0.8986
1984	3.213	0.436	DB	0.1109	0.1673
1985	3.213	0.422	FLAM	0.3887	0.4747
1986	3.213	0.627			
1987	3.213	0.752			
1988	3.213	0.921			

The annual variability in ovary weight was studied by comparing the predicted ovary weight of female plaice of 30, 40 and 50 cm in area DWK and DB (Fig.5). The C.V. was generally below 10% (Table 10). The variability in ovary weight was less in area DWK and increased in more northern areas. For the size class of 40 cm, which is close to the average length in the sample, the C.V. was 2% in DWK and 6% in areas OG, DB and FLAM. These values are substantially lower than those for fecundity.

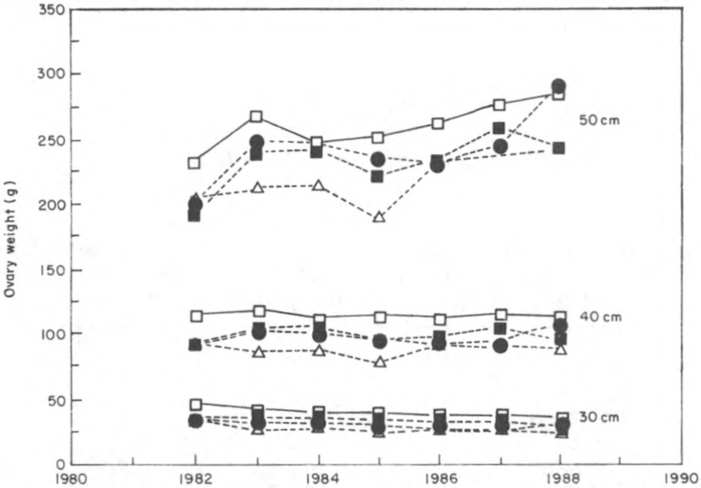

Figure 5. Annual variability in predicted ovary weights for three size classes of plaice (30, 40 and 50 cm)
—□— = DWK, —●— = OG, —■— = DB, —△— = FLAM.

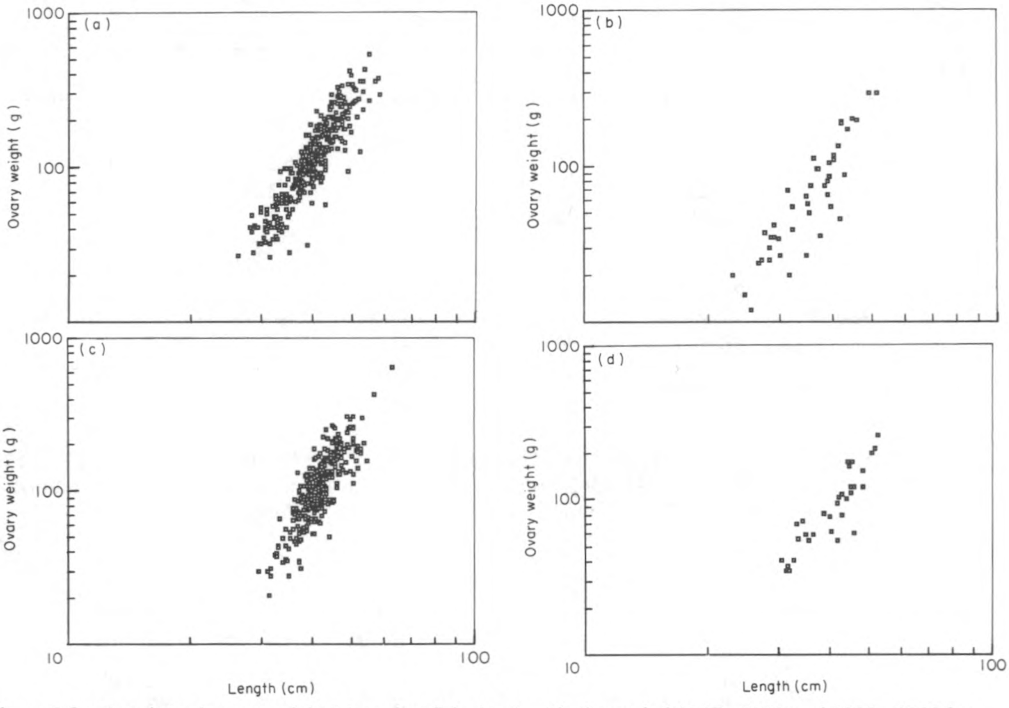

Figure 6.Scatter plots of ovary weight (g) against fish size (cm) in the period 1947 - 1949 and 1982 - 1988 for areas DWK (a) and FLAM (b). Data from Simpson (1951) and present study.

Table 10. Means, standard deviations and coefficients of variation of predicted ovary weights according the parameter estimates of Table 9 for three size classes of plaice and with a somatic condition of 0.800.

	30 cm			40 cm			50 cm		
	mean	s.d.	C.V.	mean	s.d.	C.V.	mean	s.d.	C.V.
Area									
DWK	39	3.5	8.9	113	2.7	2.4	261	17.7	6.9
OG	30	2.4	7.8	97	5.9	6.2	243	26.2	11.2
DB	33	2.7	8.0	99	5.2	5.2	233	21.3	9.2
FLAM	27	3.1	11.1	87	5.4	6.2	217	19.7	9.3

Table 11a. ANCOVA results of the ovary weight data 1982 - 1988 (present study) and those of 1947-1949 (Simpson 1951) for areas DWK and FLAM separately according to the GLM model: $\log_n G = \alpha + \beta . \log_n L$; G = ovary weight; L = length.

	SS	d.f.	MS	F	P
Area: DWK (January data only)					
$\log_n L^1$	128.5	1	128.5	1718	<0.01
Year^1	0.588	1	0.588	7.86	<0.01
error	30.75	411	0.0748		
$\log_n L$.Year	0.0181	1	0.0181	0.24	n.s.
error	30.73	410	0.0750		
total	174.1	413			
Area: Flam (January and February data)					
$\log_n L^1$	66.30	1	66.30	752.0	<0.01
Year^1	0.290	1	0.290	3.28	n.s.
error	28.39	322	0.0882		
$\log_n L$.Year	0.3934	1	0.393	4.51	<0.05
error	26.00	309	0.087		
total	96.43	324			

[1] after adjusting for main effects.

Table 11b. Parameter estimates of the GLM model of Table 11b of ovary weight data 1982 - 1988 (present study) and those of 1947-1949 (Simpson 1951) for areas DWK and FLAM separately: $\log_n G = \alpha + \beta . \log_n L$; G = ovary weight; L = length.

period	parameter	DWK	FLAM
1947-1949	α	-9.007	-7.081
	β	3.691	3.118
1977-1985	α	-8.884	-9.720
	β	3.691	3.859

Comparison of 1947-1949 data with data for 1982-1988.

Simpson (1951) reported ovary weights of ripening females from areas DWK and FLAM between October and February in 1947-1949. Since ovary weight increases rapidly in the month prior to spawning a comparison was made between ovary weights for January and February only. Figure 6(a and b) shows the $\log_n$-$\log_n$ scatter plots of the ovary weight against fish length for area DWK (January) and area FLAM (January-February), respectively. ANCOVA of the data for both areas separately showed that about 70% of the variance in ovary weight was explained by $\log_n L$ (Table 11). The factor Year, coding for the two periods of 1947-1949 and 1982-1988 respectively, explained only a minor proportion of the variance (<1%). The difference in ovary weight between the two periods was significant in area DWK but not in area FLAM. At present the length-specific ovary weight in area DWK is 13% higher than in 1947-49 (Table 12). However, the analysis for area FLAM was complicated by the significant interaction of $\log_n L$.Year, indicating that the slopes of the ovary weight - fish length relationship differed between the two periods. Comparison of the predicted ovary weights between the two periods, accepting the difference in slope, showed that at present the ovary weight was 11% lower at a fish size of 30 cm, and 10% and 30% higher at a fish size of 40 cm and 50 cm, respectively, than in 1947-1949 (Table 12).

Table 12. Predicted ovary weight (g), for three size classes of plaice and two time periods according the parameter estimates of Table 11. The percentages at the bottom of the table indicate the percentage change from the historic to the present period.

	30 cm		40 cm		50 cm	
Period: 1947-1949						
DWK	34.7		100.3		228.7	
FLAM	33.9		83.2		166.8	
Period: 1977-1985						
DWK	39.1	+13%	113.5	+13%	258.6	+13%
FLAM	30.1	-11%	91.4	+10%	216.3	+30%

Table.13. Coefficients of the predictive regression of ovary weight (g) against body size (cm) in stage 2 plaice according to the GLM model: $\log_n G = \alpha + \beta \log_n L$; where G = ovary weight and L = length. Pooled market sampling data 1981-1985.

	α	S.E.	β	S.E.	r^2	N
October	-14.5	0.455	4.89	0.124	0.692	699
November	-12.2	0.353	4.39	0.095	0.706	885
December	-11.3	0.363	4.26	0.098	0.753	623
January	-9.56	0.205	3.85	0.055	0.773	1411
February	-7.86	0.382	3.38	0.104	0.687	487
March	-6.93	1.458	3.14	0.394	0.523	60

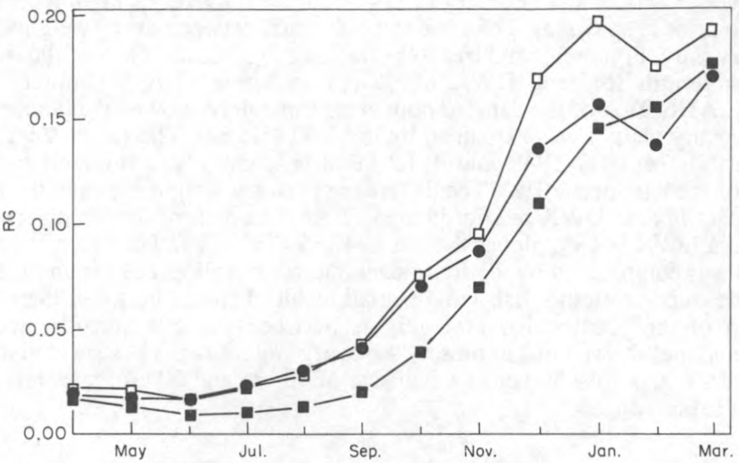

Figure 7. Increase in relative ovary weight (RG = G x L^{-3}) for various age groups of female plaice. Data 1982-1988. —■— age 3-4, —□— age 5-14, —●— age 15+.

Seasonal pattern in ovary weight.

In order to interpret the observed changes in fecundity and ovary weight, the seasonal growth in the female ovary was studied from data collected between 1982 and 1988. Body length, body weight, and ovary weight show a characteristic annual cycle that is related to the periodicity in feeding and spawning (Chapter 7). By expressing ovary weight relative to the length of the fish (GxL^{-3}), the seasonal cycle can be studied independently of the change in body weight. Size-specific ovary weight increased from June-July onwards to a maximum in January-February (Fig.7). Ovary growth in younger age groups lags behind by about one month compared to older age groups. In December, just before the spawning season, the ovary weight in age group-III females is still increasing, but has levelled off in older fish. The highest size-specific ovary weights occur in medium-aged females (age groups VI - XIV). The difference in timing of ovary growth between age groups is also reflected in the decrease in slope of the regression between ovary weight and length from October onwards (Table 13).

Within the actual spawning season (January-March) the ovary weights of the mature females which have not yet started to spawn show minor changes (Fig.8). In February and March the ovary weight of the smaller females (<35 cm) is still increasing but in bigger fish it is decreasing. The increase in ovary weight in smaller females may be related to the observed difference in timing of the spawning activity. Figure 9 indicates that the larger females start spawning earlier than the smaller females. In December only a few of the larger females have started spawning and in January the proportion of pre-spawning females (stage 2) decreases with the length of the females. Since almost all females have started spawning by February the decline in ovary weight of the larger pre-spawning females (>45 cm) in February - March, as shown in Fig.8, thus relates to a small part of the total population.

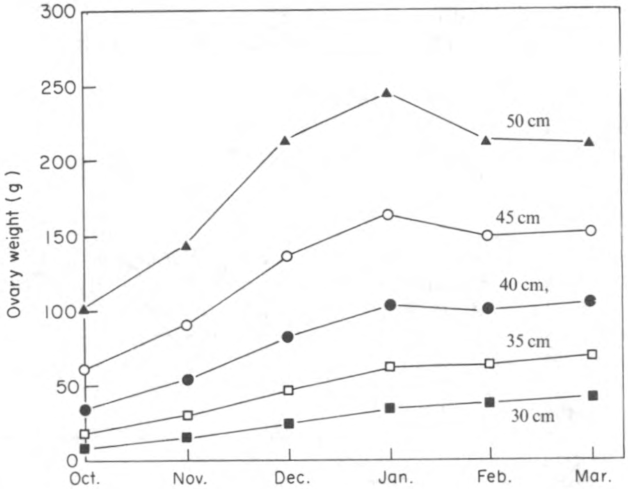

Figure 8. Increase in ovary weight (g) within the spawning period. Data 1982-1988.

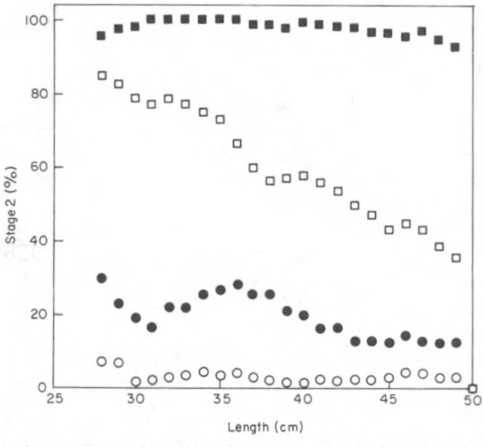

Figure 9. The proportion of pre-spawning female plaice (maturity stage 2: ripening ovaries) within the adult population between December and March. Data 1982-1988.
■ = December, □ = January, ● = February, ○ = March.

Egg weight

The dry weight of eggs stripped from ripe running females decreases with the progress through spawning (Table 14). This decrease in egg weight coincides with a decrease in size-specific ovary weight and a decrease in percentage ovary dry weight as the successive batches of eggs are released (Table 15). To estimate the average weight of the total number of eggs spawned during the spawning period, this decrease in egg weight during the spawning period of individual females must therefore be accounted for. A weighted average egg dry weight can be calculated from the observed stage-specific egg weight (DEW_i) if the proportion of eggs (P_i) spawned at the various maturity stages i is available:

DEW = Σ P_ix DEW_i. Estimates of maturity stage duration (D_i), available from Chapter 4, can be taken as crude approximation of the number of eggs spawned at each stage, assuming constant batch size and inter-batch spawning interval. The result of this calculation is given in Table 14 and yields an estimate of the average egg dry weight of 0.264 mg.

No clear relationship was evident between egg weight and age of female plaice, although the samples were confined to age groups-V and older (Table 16). Figure 10 shows the relationship between egg size (ES) and dry egg weight (DEW). The predictive regression is: ES = 1.288 + 2.151 DEW (r=0.801, n=42, P<0.01).

Table 14. Mean and standard deviation of dry weight per egg after fixation in 4% formaldehyde in seawater in relation with maturity stage. N denotes the number of observations. The overall mean was weighted over the stage durations of each stage

Maturity stage *i*	Dry weight (mg)	s.d.	n	Proportion of total spawning time P_i
3	0.274	0.025	73	0.49
4	0.266	0.024	14	0.28
5	0.241	0.020	16	0.10
6/7	0.240	0.020	23	0.13
Overall mean	0.264	0.025		

Table 15. Average percentage and standard deviation of dry weight of ovary samples and relative ovary weight (RG = $G.L^{-3}$) in relation to maturity stage. N denotes the number of observations.

Maturity stage	%dry	s.d.	RG.	s.d.	%dry RG.	s.d.	n
2	33.3	0.7	0.165	0.057	0.055	0.019	43
3	26.2	3.4	0.194	0.057	0.052	0.019	73
4	19.4	3.2	0.133	0.036	0.026	0.009	14
5	18.8	4.4	0.049	0.026	0.014	0.007	16
6/7	14.4	1.6	0.034	0.017	0.005	0.003	23

Table 16. Average and standard deviation of dry weight per egg after fixation in 4% formaldehyde in seawater for maturity stage 3 females. N denotes the number of observations.

Age	egg dry weight (mg)	s.d.	n
III	0.286		1
IV	-	-	-
V	0.278	0.031	10
VI	0.267	0.024	17
VII	0.267	0.028	12
VIII	0.281	0.023	16
IX	0.279	0.025	9
X+	0.274	0.023	9

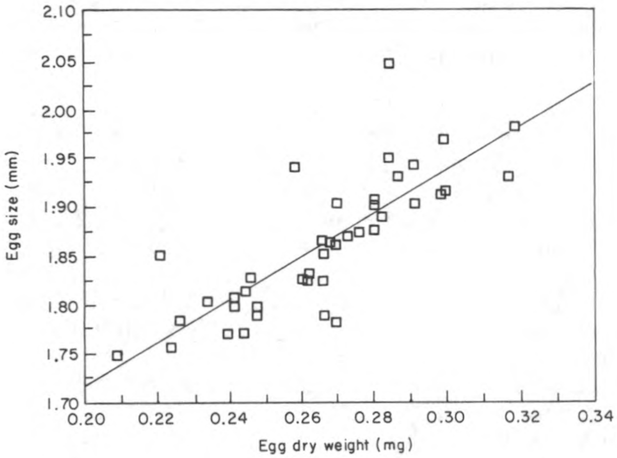

Figure 10.Relationship between the egg size and dry weight of formaldehyde preserved eggs. The predictive regression is given by Y= 1.288 + 2.151 X (r^2=0.642, n=42; P<0.01).

DISCUSSION

Methodology

In comparing the results of various fecundity studies carried out at different times and by different methods, care has to be taken that the methods are comparable (Schmitt & Skud 1978). In the various fecundity studies of plaice which have been carried out over the last century, different methods have been applied to: (a) isolate the oocytes from the ovaries; and (b) subsample and count the oocytes. These differences could affect the comparability of the results and will now be discussed.

Franz (1910a,b), Simpson (1951) and Horwood *et al.* (1986) preserved the ovaries in Gilson's fluid. Reibisch (1899) boiled the ovaries for 15 minutes to harden and isolate the oocytes. A small number of oocytes was isolated from the ovary wall using a spatula and brush. In the present study the oocytes were hardened in methanol and isolated from the connective tissue by gently washing above a fine meshed sieve. Because the oocytes hardened sufficiently, it is unlikely that the method of preparation of oocytes could have significantly affected the fecundity estimation.

In all studies the oocytes were separated from the debris of connective tissue by decanting. This step could have resulted in some loss of the smallest developing oocytes especially in the samples of the smaller females taken early in the season, as ovary development in these fish lags behind. This probably did not affect the results for the period 1977 - 1985 as the sampling did not start before December, but could have affected Simpson's (1951) results which included samples collected in October and November. However, comparison of the fecundity - length relationships for Simpson's October - November and December - February samples did not indicate a significant difference in slopes or intercepts. This effect cannot be tested for Franz's (1910a,b) data as sampling dates were not specified.

Oocytes were generally subsampled before being counted. In the present study subsampling was done by counting all the eggs from a subsample of the ovary from the middle region. Total fecundity was calculated by raising the weight of the sample to the total ovary weight. Replicate samples from the individual fish showed no systematic difference in egg density between various parts of the ovary, nor between the left and the right ovary. Equal egg densities in both ovaries were also reported for Pacific halibut (*Hippoglossus stenolepis*) (Schmitt & Skud 1978) and pike (*Esox lucius*) (Kipling & Frost 1969).

Franz (1910a,b) and Simpson (1951) suspended the oocytes and used a stemple pipette to obtain a volumetric subsample. This method was criticized by Kändler and Pirwitz (1957) and Bagenal & Braum (1978) because the oocytes quickly sink to the bottom and might result in undercounting. Witthames & Greer Walker (1987) compared the volumetric method of fecundity determination as used by Franz and Simpson with fecundity estimates counting all oocytes with an automatic particle counter; they found that the volumetric method underestimated the fecundity by about 6%. The actual fecundity - body size relation might therefore be underestimated by the volumetric subsampling method over the entire size range of fish, but this bias is probably small in comparison with the observed difference in fecundity between the time periods.

Horwood (1990), studying plaice fecundity in the Irish Sea, could not find a significant difference compared with the results of a similar study of Simpson (1957) in the 1950's. This suggests that the methodological differences between Simpson's and Horwood's studies cannot have played a major role in explaining the fecundity increase in the North Sea. Finally, the agreement between the results of the present study and those of Horwood *et al.* (1986) with regard to both the general level of fecundity and the residual variance is further support of the conclusion that methodological differences have not seriously distorted the fecundity - body size relationships reported here.

Long term changes in fecundity

In these circumstances, it is concluded that the observed differences in size-specific fecundity between the three time periods are so large that they must reflect real changes between 1900 and present.

The historic changes in fecundity - length relationship can be summarized as follows. Fecundity in 1947-1949, as compared to 1900-1910, had not changed in females up to about 40 cm, but was substantially lower in larger females, especially in area DWK (Fig.11a). By 1977-1985 fecundity had increased substantially in females of 30-40 cm, but not in larger sized females (50cm). The substantial change in the fecundity - length relationship between 1947-1949 and present was not reflected in the ovary weight - length relationships, which showed no change (area FLAM) or at most a marginal increase only (area DWK; Fig.11b).

Changes in ovary weight

A puzzling result is the discrepancy between the changes in fecundities and ovary weights between 1947-49 and 1977-85 (Figure 11a and b). For area DWK, fecundity increased by 70 - 100%, whereas the ovary weights increased by only 13%. For area FLAM, fecundity increased by 26% whereas ovary weight did not change.

If these discrepancies between changes in fecundity and ovary weight are real and the proportion of connective tissue in the ovaries is constant, they imply that the egg weights between both periods were different. The average dry egg weight of a 40-cm female in area DWK can be estimated from the predicted fecundity (159800) in Table 8, ovary weight (113.5 g) in Table 12, and ovary dry weight (33.3%) in Table 15 as 0.333 x (113.5 / 159.8) = 0.237 mg. The average dry weight of eggs stripped from spawning females was estimated at 0.264 mg after fixation, corresponding to 0.352 mg after correction for the loss in dry weight by 25% due to fixation (Hislop & Bell 1987).

The substantial discrepancy between observed and calculated egg weight indicates that the reallocation of matter continues after the start of spawning (Dawson & Grimm 1980; Chapter 1 and 7).

As the reallocation from soma to ovary continues into the spawning season an accelerated ovary growth in 1948-1949 could in theory explain the discrepancy between the changes in fecundity and ovary weights between 1947-1949 and the present. However, the seasonal egg production curves given by Simpson (1959) and Harding *et al.* (1978) showed that the peak of spawning in 1948 was only two weeks later than in an average year. The low between-year variability in first-quarter ovary weights between 1982 and 1988 is a further indication that difference in timing of ovary development between years is small.

Assuming that the substantial increase in fecundity and the only marginal increase in ovary weight between 1947-1949 and the present is real, the corresponding change in egg weight can be predicted from the ratio of ovary weight and fecundity. For a 40-cm female in area DWK this difference is - 1947-49: 100.3/89.3 = 1.12; 1977-85: 113.5/159.8=0.71. Thus, egg weight should have declined by 37% (0.71/1.12). Similarly for a 40-cm female in area FLAM, the predicted decrease in egg weight is 13%. From the positive relationship between egg size and egg weight (Fig.10) it can be calculated that a 13% and 37% decreases in weight of an average egg of 0.28 mg (1.89 mm) correspond to decreases in egg size of 4% (1.81 mm) and 12% (1.67 mm), respectively. The latter decrease seems fairly large compared with the coefficient of variation in egg size of 5% as observed in the sea (mean = 1.87; s.d. = 0.09), but falls within the range of egg sizes observed (Rijnsdorp & Jaworski 1990).

Fecundity and growth

We now consider how the changes in fecundity between the three time-periods are related to changes in growth. Wallace (1914) and Heincke (1908) give data on growth of plaice for the beginning of the 20th century for the same area as the fecundity data. Wallace (1914) has reported the average length-at-age of plaice from commercial samples taken in the eastern North Sea (our areas DB and VB) in the period 1906-1909. Heincke (1908) gives similar data for the youngest age groups in the area DB. Length-at-age data for the

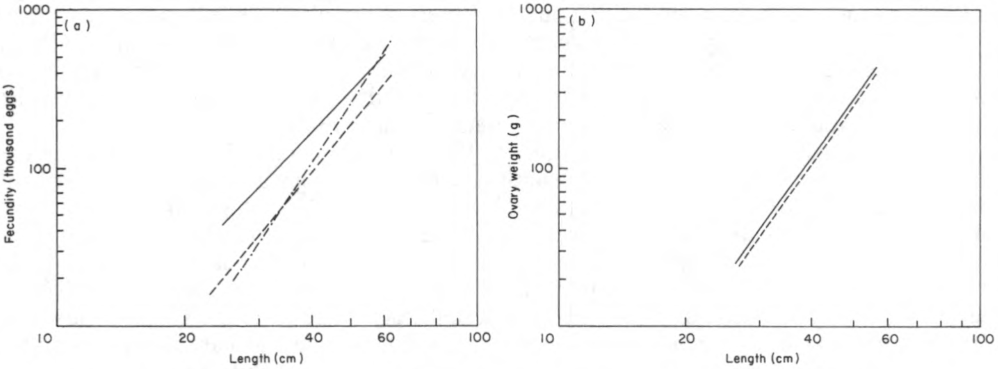

Figure 11. (a) Fecundity - size relationships for 1900 (area DB), 1947-1949 (area DWK) and 1977-1985 (area DWK) - · - = 1900, --- = 1947-1949, ——— = 1977-1985. (b) ovary weight - size relationships for 1947-1949 (area DWK) and 1982-1988 (area DWK). - - - = 1947-1949, ——— = 1982-1988. The regression parameters are given in Table 7 and 11.

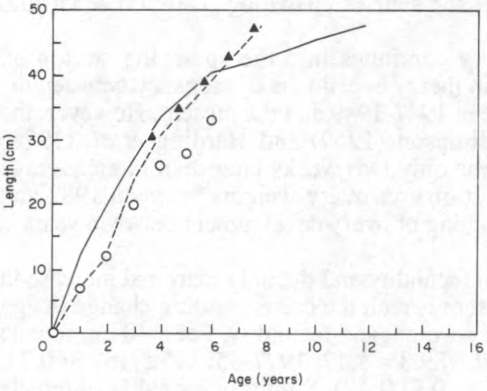

Figure 12. Comparison of the length-at-age relations of female plaice in 1900-1910 and 1980-1986 in the southeastern North Sea. The dotted line shows the estimated growth in 1900-1910 from data of Heincke (1908) - coastal areas around Heligoland - and Wallace (1914) - mainly offshore grounds in area DB and VB. The full line refers to the area DB in the period 1980-1986 O = Heincke (1908), ▲ = Wallace (1914), --- = 1900-1910, — = 1980-1986.

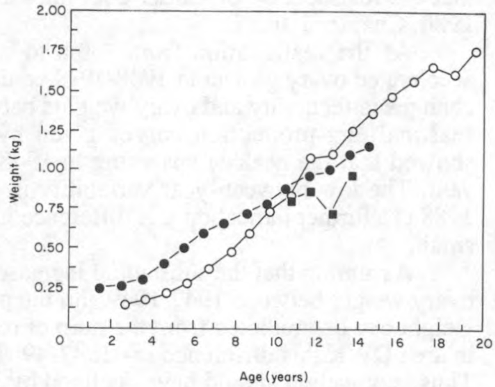

Figure 13. Comparison of the body weight-at-age relations of plaice (sexes combined) in 1928-1939 and 1946 from commercial samples of U.K. fleet (Beverton & Holt, 1957) and 1980-1985 from commercial samples (ICES 1990). -O- =1929-1938,–■–=1946,-●-1980-1985.

period 1985-1986 (Chapter 4) are compared to the historic data in Figure 12. In Figure 13 the weight-at-age of plaice (sexes combined) in the late 1940's, given by Beverton & Holt (1957), are compared to similar data for the period 1980-1985 (ICES 1990).

A study of the growth of plaice is complicated because the mean length of a particular age group increases with increasing distance from the coast, i.e. Heincke's law (Wimpenny 1953). Another factor which might influence the estimated growth is the accuracy and precision of age determinations. Van Leeuwen & Groeneveld (1988) showed that the age determination in plaice, when carried out from untreated otoliths, is less precise and may even be biased for age groups older than VIII-years (see also page 96 in Heincke 1908). Finally, the mean length or weight of the younger age groups may be overestimated due to partial recruitment or discarding of undersized fish. All these factors may have affected the comparison of the growth data presented in Figures 12 and 13.

Comparison of growth data of Heincke (1908) and Wallace (1914) suggests that the former may have underestimated the length of the older age groups due to the restricted sampling area in the German part of the North Sea, while Wallace may have overestimated the length of the youngest age groups sampled due to the extension of the sampling area over the offshore grounds of the Doggerbank and the central North Sea. The dotted line in Figure 12 subjectively connects the most likely values of Heincke and Wallace and may be taken tentatively as an indication of the growth in the period 1900-1910. This line now can be compared to the full line representing present growth, which was based on first-quarter samples and took account of the relationship between length-at-age and distance from the coast (Chapter 4). Comparison of the growth between both periods in the eastern North Sea suggests that the growth rate of the youngest age groups (up to age III or IV) has increased between 1900 and 1985, but growth in older plaice has not changed.

Growth data of plaice for the late 1940's are restricted to weight-at-age of sexes combined from commercial samples taken from the English fleet and showed that growth

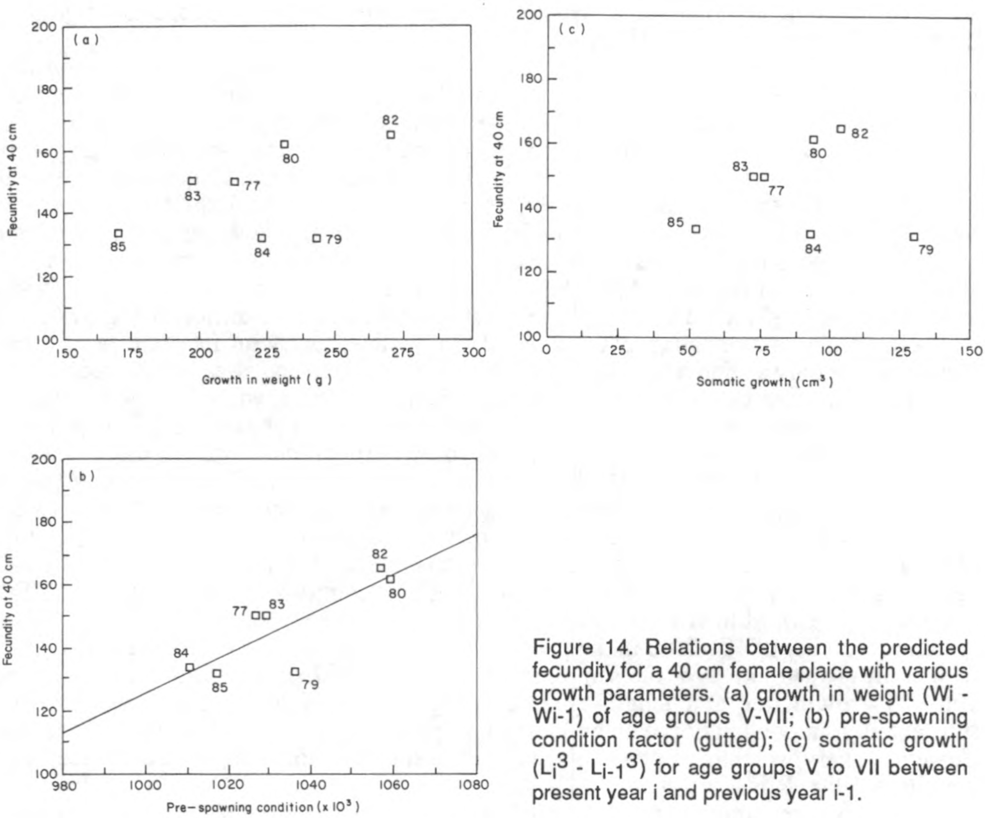

Figure 14. Relations between the predicted fecundity for a 40 cm female plaice with various growth parameters. (a) growth in weight (Wi - Wi-1) of age groups V-VII; (b) pre-spawning condition factor (gutted); (c) somatic growth (L_i^3 - L_{i-1}^3) for age groups V to VII between present year i and previous year i-1.

was substantially reduced between 1939 and 1945 when stock size increased at least threefold due to the almost complete closure of the fishery during the Second World War (Beverton & Holt 1957). Figure 13 shows the decrease in mean weight-at-age of age groups XI - XIV that lived through this period and were sampled in 1946 as compared to the average weight-at-age of similar age groups in the period 1929-1938. This figure also compared the average weight-at-age from the market samples taken from the fishery and indicates that the growth of the youngest age groups may have increased, whereas that of the older age groups remained the same or has decreased. The differences in weight-at-age of the older plaice between the two periods may have been influenced to some extend by inaccuracies in age determination and should be treated with caution. However, the age groups XI - XIV in 1946 would have had to be overestimated by 2-4 years to explain the differences. This is not in the direction in which errors are likely.

The observed increase in fecundity of smaller size groups of plaice since 1947-1949 (Table 8) seems to correspond to the inferred increase in growth of the youngest age groups (up to age III or IV). For the moment it remains unresolved in which way these changes in fecundity are related to the reported advance in the onset of sexual maturation (Chapter 4). The decrease in fecundity for the larger females in 1947-1949 corresponds to the substantial decrease in growth during the Second World War. The decrease in fecundity was restricted to the DWK spawning group suggesting that the increase in plaice density was particularly pronounced on the feeding grounds of this spawning group, but less on that of the FLAM group. De Veen (1978) showed that the DWK plaice are distributed in the southern and southeastern North Sea during the feeding period whereas the FLAM group is distributed in the western North Sea.

Further indications that the conditions for growth might affect size-specific fecundity were obtained when analysing the annual variability between 1977 and 1985. The predicted fecundities of a 40 cm female appeared to be correlated with some growth parameters of age groups V to VIII estimated from first quarter market sampling data. These age groups dominate the mature population, are well sampled, and their average length ranges between 35 - 40 cm (Rijnsdorp *et al.* 1991). Figure 14a indicates that fecundity is associated positively with the increase in weight in the preceding year, although the correlation is not significant. The positive relation was mainly due to the positive correlation with pre-spawning condition factor ($p<0.05$; Fig.14b) and not with the preceding increase in the cube of length (Fig.14c). These results suggest that favourable conditions for growth will result in an above-average growth in length and consequently an increase in absolute fecundity, but only a slight increase in pre-spawning condition and size-specific fecundity.

The literature on the relation between fecundity and growth rate, food ration or population density is not unequivocal. Increased food ration has been shown to enhance fecundity in a number of experimental studies (brown trout (*Salmo trutta*), Bagenal 1969; cod (*Gadus morhua*), Waiwood 1982; *Cichlasoma nigrofasciatum*, Townshend & Wootton 1984; rainbow trout (*Salmo gairdneri*), Springate *et al.* 1985; plaice, Horwood *et al.* 1989).

However, field studies on the relation between fecundity and growth or population density have not usually shown a clear interdependence (haddock (*Melanogrammus aeglefinus*), Hislop & Shanks 1977; Pacific halibut, Schmitt & Skud 1978: ; North Sea sole (*Solea solea*), Millner *et al.* 1991). Kipling & Frost (1969) found an increase in size-specific fecundity of 10 - 20% in the pike (*Esox lucius*), but could not find a clear relation with adult growth rate over the same period. De Veen (1976) showed that in the period 1960-75 growth rate and length-specific ovary weight of North Sea sole increased substantially, in conjunction with an increase in pre- and post-spawning condition factor. However, ovary weight as a percentage of body weight did not change during these years (van Beek 1988; Rijnsdorp *et al.* 1991).

The observed annual and geographical differences in slope of the relationships of fecundity and fish size and of ovary weight and fish size suggest that environmental conditions for growth (e.g. temperature, availability, and quality of food) of small and large plaice were different both within and between geographical areas, as well as within and between years. This is reasonable, since there are considerable differences in spatial distribution between size groups of plaice, small fish concentrated close to the coast, and larger fish dispersed over deeper water (Heincke 1908; Wimpenny 1953; Rijnsdorp & van Beek 1991). The reproduction of the smaller fish, mainly recruit spawners, would largely be determined by the feeding conditions on the nursery grounds, whereas reproduction of larger size groups, mainly repeat spawners, would be determined by the conditions on the feeding grounds of the adult fish.

Tagging experiments suggest that the population in the nursery areas inside the west Frisian Islands recruits mainly to area DWK and OG, whereas juveniles from the nursery areas along the German and Danish coast mainly recruit to area DB (Hickling 1938; unreported results of tagging data RIVO). The spawning fish in area FLAM derive from a local nursery area along the English east coast (Lockwood & Lucassen 1984). The summer feeding grounds are widespread in the southern and central North Sea, including both stratified waters where bottom temperature is about 7 °C, and non-stratified waters where the maximum summer temperature reaches 14 - 17 °C (Tomczak & Goedecke 1964).

Since extensive migrations of adult fish occur during the months prior to spawning (de Veen, 1978; Arnold et al., in prep), the time and place of sampling can affect the observed geographical differences in reproduction - body size relationships. Samples could include both fish that will spawn locally and fish that are still migrating, particularly when samples are taken just before or early in the spawning season. This should include mainly data for repeat spawners.

Egg weight

Horwood *et al.* (1986) showed that length-specific fecundity decreased with age. A similar result was obtained in this paper (Table 4 and 5), although this effect disappeared when the covariable somatic condition was included in the analysis (Table 3). The decline in fecundity with increasing age leads immediately to the question whether it is compensated for by an increase in egg weight. The absence of an age effect on ovary weights (Table 9) suggests that egg weight indeed increases with age. The egg dry weights collected in this study, however, did not reveal a significant relation with age (Table 16), but this might be due to the restricted sampling period in the first half of the spawning season and the fact that hardly any 3- and 4-year old females were sampled. In haddock, Hislop (1988) observed that egg size in the youngest age groups, mainly recruit spawners, was significantly lower than in older age groups.

The fecundity of individual plaice of a given size varies considerably, and the question arises as to whether also the level of fecundity in individual fish is in some way related to egg weight, i.e. do females with a relatively high fecundity produce smaller eggs and those with a low fecundity produce larger eggs?

This question was tackled by examining the relation between the egg weight and size-specific fecundity. Only first quarter samples were analysed to reduce the influence of the continuous ovary growth. Egg weight was estimated by the quotient of ovary weight and fecundity. Size-specific fecundity was calculated by analysis of covariance (Table 3). Egg weight and size-specific fecundity showed a significant negative correlation ($r = - 0.36$; $n = 308$; $P<0.01$; first-quarter samples only), suggesting that females with relative high fecundity produce on average smaller eggs. However, this result could be an artefact if the timing of ovary development of females with a relative high size-specific fecundity is delayed. On the population level an inverse relationship between egg number and egg size was observed in herring (*Clupea harengus*) (Parrish & Saville 1965), rainbow trout, (*Oncorhynchus mykiss*) (Bromage *et al.* 1990) and Pacific salmon, (*O. kisutch*) (Fleming & Gross 1990).

A complicated picture emerges from the few experimental studies that deal with the relationship between egg numbers and egg sizes with respect to food intake. Experimental restriction of food before the spawning period resulted in a reduction in size-specific fecundity and lower egg weight (haddock: Hislop *et al.* 1978; rainbow trout: Springate *et al.* 1985; Knox *et al.* 1988), a reduction in size-specific fecundity and constant egg weight (rainbow trout: Scott 1962; stickleback (*Gasterosteus aculeatus*), Wootton, 1973, 1977), a reduction in fecundity and increase in egg weight (brown trout, Bagenal 1969). The duration and timing of starvation prior to spawning can explain part of the difference in experimental results (rainbow trout: Ridelman *et al.* 1984). Again, factors other than food can influence the trade off between egg size and egg number. Tanasichuk & Ware (1987) showed for Pacific herring (*Clupea harengus pallassi*) that ovary weight did not change with temperature, but in a year with high water temperature the size-specific fecundity was higher and the egg weight lower. The interaction between the growth and the allocation of the available reproductive resources in relation to egg size therefore remains an intriguing but rather unexplored territory.

In this context, Rijnsdorp (1990) (Chapter 7) proposed a hypothetical allocation model of energy over reproduction and somatic growth, that was inspired by the observation that the body condition was fairly constant between years and was not related

Table 17. Condition factors (K) of adult plaice at the start of the spawning period. Values were converted from gutted (including ovaries) to whole weight by multiplying with 1.07. For the period 1970-1988 the mean , standard deviation (s.d.) and coefficient of variation (C.V.) of the annual condition factors of pre-spawning female plaice (maturity stage 2; length range 30-55 cm) are given for different areas in the North Sea. n denotes the number of observations, except for 1970-1988 where it denotes the number of years.

Period		size group	K	n	source
1900	female	40-55	1.07	5	Reibisch (1899)
	male and female	30-55	1.07	-	Borley (1909) [1]
1948	female	25-55	1.11	82	Simpson (1951)

[1] areas B1, B2, B4, C1, C2, C3, D2

Area	K	s.d.	C.V.	n
DWK	1.114	0.023	2.1	19
OG	1.084	0.028	2.6	19
DB	1.068	0.029	2.7	19
FLAM	1.099	0.028	2.5	19

to the rate of somatic growth. According to this model an individual fish allocates the incoming energy to somatic growth and energy reserves for reproduction during the growing season in such a way as to maintain its body condition at a threshold level, which increases during the season. In the few month prior to spawning the body reserves are reallocated from the soma to the ovary (Dawson & Grimm 1980; Chapter 7). Poor conditions for growth in the main growing period result in a reduced somatic growth but not necessarily in a reduced energy reserve for reproduction. Only if conditions for growth deteriorate in the later part of the growing period will a fish be prevented from allocating sufficient energy to its body reserves for reproduction, hence resulting in a lower pre-spawning body condition. Larger fish are more vulnerable in this respect since they allocate a relative large proportion of their total surplus production to restoring their depleted energy reserves after the previous spawning period and only a small proportion to somatic growth (Chapters 1 and 7). According to this hypothesis, the timing of energy intake therefore plays a significant role in determining the variability of pre-spawning energy reserves and size-specific fecundity.

The present study revealed that substantial changes in fecundity but much smaller changes in ovary weight had occurred between three historic periods. Further, comparison of condition factors of pre-spawning females in two periods, which gives a rough approximation of the energy reserves available for spawning (Chapters 1 and 7), does not suggest major changes (Table 17). Finally, the comparison of the weight - length relationship between 1947-1949 and the present period for the pooled data of area DWK and FLAM did not show significant change in the slope ($F_{1,422} = 2.45$) or intercept ($F_{1,424} = 1.83$) between both periods. This suggests that the energy allocation to reproduction versus somatic growth has not changed, but rather that the reproductive energy has been allocated to a larger number of small eggs compared with a smaller number of larger eggs.

Effect of fishing on changes in fecundity

In the North Sea the total annual mortality in the adult population is about 40% ($F=0.4$: Rijnsdorp *et al.* 1991); this compares with a natural mortality of about 10% ($M=0.10$: Beverton & Holt 1957). The plaice population is now dominated by younger age groups and concurrently the growth rate of juveniles has increased. At present, plaice of a given length will on average be younger than at the beginning of the century. Since the length-specific fecundity decreases with age, it may be asked whether the age effect alone can explain the observed change in fecundity?

The present fecundity of a 4-years-old female of 30-cm is 63 thousand (Table 6). Fecundity of a 30 cm female in 1947-1949 was 36 thousand. If lower fecundity in 1947-1949 was due to the age effect on fecundity and the present fecundity-length relation applies to the period 1947-1949, we can predict the age of a 30-cm female in 1947-1949 with a fecundity of 36 thousand from the equation:

$$\log_n E = \alpha + \beta \log_n L + \delta \log_n A.$$

The parameter estimates for area DWK are given in Table 5: $\alpha = -7.640$ (average over years 1977-1985); $\beta = 3.593$; $\delta = -0.313$. Thus $\log_n 36 = -7.640 + 3.593 \log_n 30 - 0.313 \log_n A$. Giving an age of 24 years. Obviously the observed decrease in size-specific fecundity with age is much too small to account for the observed change in fecundity.

The basic question raised in the Introduction was whether the differences in fecundity of plaice or, more generally, reproductive energy, between years or areas are due to differences in the environmental conditions for growth or to changes in the population genetics due to fishing. As plaice is an iteroparous species which matures at an age of 3 - 6 years (Chapter 4), and which has a maximum life span of at least 25 years (Wimpenny 1953; Beverton 1964), the spawning population will be largely composed of the same individual fish for a number of successive years. If the intensive exploitation of the adult stock has resulted in a change in the genetics of the population we can expect a gradual increase in size-specific fecundity or size-specific reproductive investment over a number of years. The observed changes do not seem to be consistent with a gradual change of this kind, except perhaps with the increase in fecundity of the smaller size groups (about 30 cm). It is therefore concluded that they are most likely due to differences in the environmental conditions for growth.

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Part III

THE ANALYSIS OF PHENOTYPIC VARIABILITY

Chapter 6

The relation between juvenile growth and the onset of sexual maturity of female North Sea plaice, *Pleuronectes platessa* L.

Rijnsdorp, A.D. The relation between juvenile growth and the onset of sexual maturity of female North Sea plaice, *Pleuronectes platessa* L. - submitted.

ABSTRACT. The relation between juvenile growth and the onset of sexual maturation of female plaice is explored by analysing individual growth curves back-calculated from otoliths of immature and mature fish, and by analysing maturity-length ogives for individual year classes sampled between 1958-1990 in three areas in the North Sea. Growth rate of females sampled as mature fish was higher than that of immature females up to three years prior to sampling and the maximum growth superiority occurred at age-I. Analysis of the process of maturation showed a significant effect of the length reached as well as of growth rate in previous years. The length at which 50% of the females matured (L_{mat}) increased with growth rate in the penultimate year, but seems to decrease with growth rate three years before. Maturity-length relationships from market samples showed significant differences in slopes and intercepts between age groups, geographical areas and between individual year classes. L_{mat} decreased with age and increased from south to north. The geographical differences in L_{mat} and the variation in the L_{mat} of individual year classes corresponded to the differences in the growth rate during early life. A model of the juvenile-adult transition process is proposed that provides a consistent interpretation of the observations.

INTRODUCTION

North Sea plaice has been exploited intensively for more than a century (Masterman 1914; Wimpenny 1953; Bannister 1978). In a previous paper on maturation of plaice it was shown that the length (L_{mat}) and age (A_{mat}) at sexual maturity changed since the early 20th century. At present, the fish become mature at a younger age and at a smaller size (Chapter 4). This raises the question as to whether the change in sexual maturation reflects a change in the genetical composition of the population, or reflects phenotypic plasticity in response to changes in environmental conditions.

Genetical changes in intensively exploited fish populations are not unlikely because fisheries may act as a strong selective force for earlier and higher rate of reproduction as shown by simulation studies of Rowell (1992) and in Chapter 2. The possibility of genetical changes has already been recognized for several decades, but few studies have so far yielded conclusive evidence (Allendorf *et al.* 1987; Nelsen & Soulé 1987). The prerequisite that maturation is under genetic control has been proved for a number teleost species (Kallman & Borkosky 1978; Purdom 1979; Mork *et al.* 1984; Roff 1991).

Changes in length and age at maturation are not necessarily linked to changes in the genetical composition as it is a well established fact that these represent plastic characters that respond to environmental conditions (Alm 1959; Stearns & Crandall 1984; Stearns & Koella 1986). Maturation is a developmental process comparable to other life history transitions such as hatching and metamorphosis (Policansky 1983; Chambers & Leggett 1987; 1992). As such, maturation is coupled to the physiology of energy acquisition and hormone kinetics. Ample evidence exists that maturation is linked to the rate of growth during the juvenile phase and it is generally assumed that a fish matures when it has passed some size or age threshold (Nikolskii 1969; Roff 1983, 1991; Thorpe 1986; Rijnsdorp & van Leeuwen 1986). Stearns & Crandall (1984) argued that the maturation threshold would be neither length nor age-specific, but would follow a trajectory in the length-age space, as has already been shown for other life-history transitions (MacKenzie *et al.* 1983; Policansky 1982, 1983). This trajectory is called a 'reaction norm' according to the conventions of the developmental physiology and represents the function that translates the genotype into the phenotype given certain environmental conditions. The trajectory can be viewed as adaptative with mortality in the juvenile and adult phase and the growth potential as critical factors (Stearns & Crandall 1984; Stearns & Koella 1986; Kozlowski 1992).

A factor complicating the analysis of changes in length at first sexual maturity is that maturation of the ovary already starts well before the actual spawning season (Barr 1963; Lahaye 1972; Deniel 1981). Chapter 4 showed that transition from juvenile to adult female plaice took place during the main period of somatic growth between May and September. Since it is generally assumed that reproduction reduces the somatic growth because of the additional investment required (Nikolskii 1969; Roff 1982, 1983), the length at first sexual maturity may be influenced by the maturation process itself. Various authors even have suggested that the process of ovarian ripening spans more than one year (Yamamoto 1956; Dunn & Tyler 1969; Hilge 1976; Burton & Idler 1984). This would imply that growth in early years could also influence maturation later in life.

In the present paper, an attempt is made to derive the reaction norm for maturation in female plaice from the variability in the onset of sexual maturity. Firstly, the juvenile growth of immature and mature female plaice is studied by back-calculation of otoliths. Secondly, the variability in the onset of sexual maturity is analysed between year classes and between geographical areas in comparison to differences in juvenile growth as observed by back-calculation of otoliths and direct observations from pre-recruit surveys.

MATERIAL AND METHODS.

Data

The growth history of individual female plaice was studied by back-calculation of the length at age from the pattern of annuli in the otoliths. The evidence for the validity of the method and an analysis of its accuracy and precision is provided by Rijnsdorp *et al.* (1990). Four sets of otoliths were used to estimate individual growth curves. Set A, B and C are used to compare growth rates of immature and mature females during different years of life. Set D is used to compare early growth in various areas in the North Sea. Only set A was typically established to compare individual growth curves between immature and mature females. The other sets were prepared for other reasons, but contained relevant information for investigating the present problem. The geographical areas distinguished in the present study are the Southern Bight (SB), German Bight (GB) and Flamborough area

(FLAM), which correspond to the areas DWK and OG, DB and VB and FLAM as defined in Chapter 4.

Set A comprised otoliths of females of age groups III, IV, V and VI sampled in January of 1985 and 1986 during two maturity surveys. For each age group, up to 30 otoliths of both immature and mature females were selected from the samples taken at each station of the lines C, D and E in the German Bight (see Chapter 4). These samples are not fully representative for the population since the tails of the size-distribution within each age group are relatively over-represented.

Set B and set C comprised otoliths of year classes 1963 and 1969 respectively, which were sampled at age IV, V, VI, VIII and X during the spawning period in the southern North Sea (around 53° N 3° E; area SB) from market samples. For the present purpose only the data for age groups IV, V and VI were used, because these contained both immature and mature females. Year class 1963 and 1969 have been selected, because they had shown substantial differences in juvenile growth and maturation (Table 1).

Set D comprised otoliths of mature females sampled for fecundity estimates in the spawning period between December and March between 1982 and 1985 in the Southern Bight, German Bight and Flamborough area (Chapter 5).

Table 1. Growth and maturation characteristics of female plaice of year classes 1963 (otolith set B), 1969 (otolith set C) in area SB, and of year classes 1980 - 1983 (otolith set A) in area GB. The number of immature (imm) and mature (mat) female were recorded in the 1st quarter market samples. The lengths refer to the mean back-calculated lengths.

Age-group	Length (cm)	imm	mat	%mat	Length (cm)	imm	mat	%mat
	year class 1963				year class 1969			
I	7.3	-	-	-	8.0	-	-	-
II	14.9	-	-	-	17.1	62	8	11
III	21.7	8	1	11	25.9	134	87	39
IV	27.7	56	41	42	32.9	35	180	84
V	32.5	44	133	75	37.0	18	234	93
VI	35.7	29	313	92	39.7	3	239	99
	year class 1980				year class 1981			
I	7.0	0	0	-	8.5	0	0	-
II	17.4	2	0	0	18.0	0	0	-
III	25.5	88	11	11	25.7	128	10	7
IV	31.6	53	44	45	32.0	159	80	34
V	36.1	10	70	81	35.7	18	138	89
VI	35.4	1	52	98	-	2	106	98
	year class 1982				year class 1983			
I	8.8	0	0	-	8.1	0	0	-
II	18.1	1	0	0	18.5	0	0	-
III	26.4	53	5	9	27.1	100	7	7
IV	31.9	43	33	43	-	58	53	48
V	-	21	55	72	-	4	64	94
VI	-	1	62	98	-	0	52	100

Maturation of individual cohorts was studied by means of market sampling data collected routinely during the spawning period (January - March) between 1958 and 1990 (year classes 1956-1985). This market sampling programme is described in Chapter 4.

In the present paper, growth in the penultimate year is used to denote the growth in the year prior to sampling. For instance, for a 4-year old plaice sampled in the spawning period, the growth in the penultimate year refers to the length increment between L_{III} and L_{IV}, representing the growth at age III. Growth in the ultimate year, corresponding to age IV, is still insignificant since plaice were sampled during the first quarter of the year.

Statistical methods

Statistical analyses of the number of mature females were carried out with analyses of covariance technique (ANCOVA) fitting a GLM model (Baker & Nelder 1978; McCullagh & Nelder 1983) with a binominal error distribution and a logit link function:

$$logit\ Y = X + F1 + F2 + F3 + \varepsilon$$

where Y = the number of mature females; X is the covariable length; $F1, F2, F3$ are factors coding for age group, area and year class. ε is an error term with a binominal distribution. The logit link function is analogous to a logit transformation of proportions maturity.

In the analysis of market sampling data the number of mature females was analysed per 2-cm size classes. A logit analysis of the probability of becoming mature in relation with the back-calculated growth history of individual females was carried out according to a GLM model similar to the one above. In this case, the Y-variable took values of 0 or 1 for immature and mature females respectively.

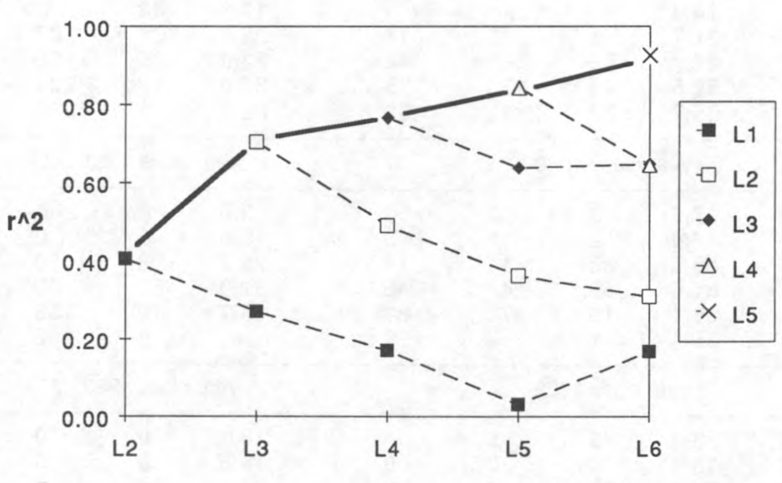

Figure 1. Correlation of the length attained at different ages by individual female plaice. Data: otolith set A.

RESULTS.

Back-calculated growth of immature and mature females

Back-calculated individual growth patterns indicate that a relationship exists between the length attained at successive ages by an individual fish. Fig.1 shows the correlation matrix of back-calculated length at different ages for otolith set A as an example. Results for otolith set B and C were similar. The correlation between the length at consecutive ages improves when the fish become older, as shown by the heavy line in Fig.1, but the correlation decreases when length at a young age is compared with the length later in life.

The length at the end of the first year (L_I) still has some predictive value for the L_{II}, but less so beyond L_{III}, as shown by the dashed lines in Fig.1. Length at older ages appears to be better correlated. For instance, the length attained at age-II is still significantly correlated with the length reached at age-VI. Thus, the size of an individual fish after the first year influences the length attained at subsequent ages, although the effect decreases gradually.

The slopes of the linear regressions of L_{i+1} against L_i decrease with i, although the curves differ between the three otolith sets. In set A the slope (β) is greater than 1 up to age III, whereas in set B the slope is only greater than 1 up to age-II and in set C the slope is smaller than 1 for all ages. $\beta>1$ implies that the annual length increment increases with size of the fish at the start of the growing period. At $\beta=1$, the growth increment is not affected, whereas for $\beta<1$ the growth increment decreases with the size. Because the slopes in most correlations differ significantly from unity, individual growth rates can only be compared after correction for starting length (L_i). Individual growth rates (R_i) were therefore calculated as the residuals between the observed length (L_{i+1}) and the length predicted by the regression ($\hat{}L_{i+1}$). The growth rates for age group I-VI were standardized with one

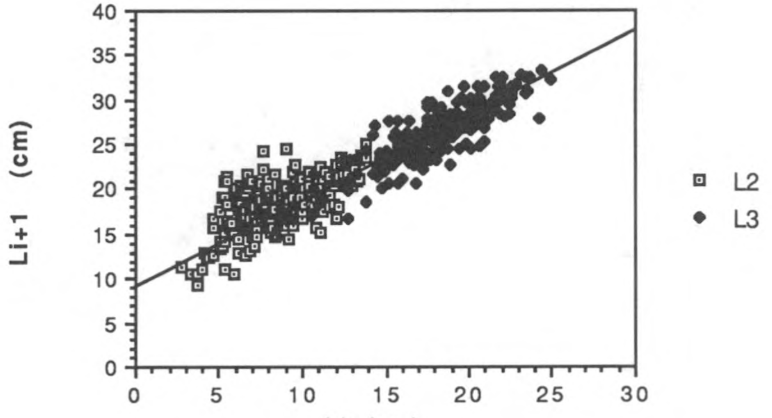

Figure 2. Scatter plot of the lengths attained by individual females at age II and age III in relation with the length attained in the previous year. The individual growth rate (annual increment) was estimated from the deviance between the observed L_i and the $\hat{}L_i$ predicted from the linear regression line $L_i = \alpha + \beta L_{i-1}$. Data: otolith set A.

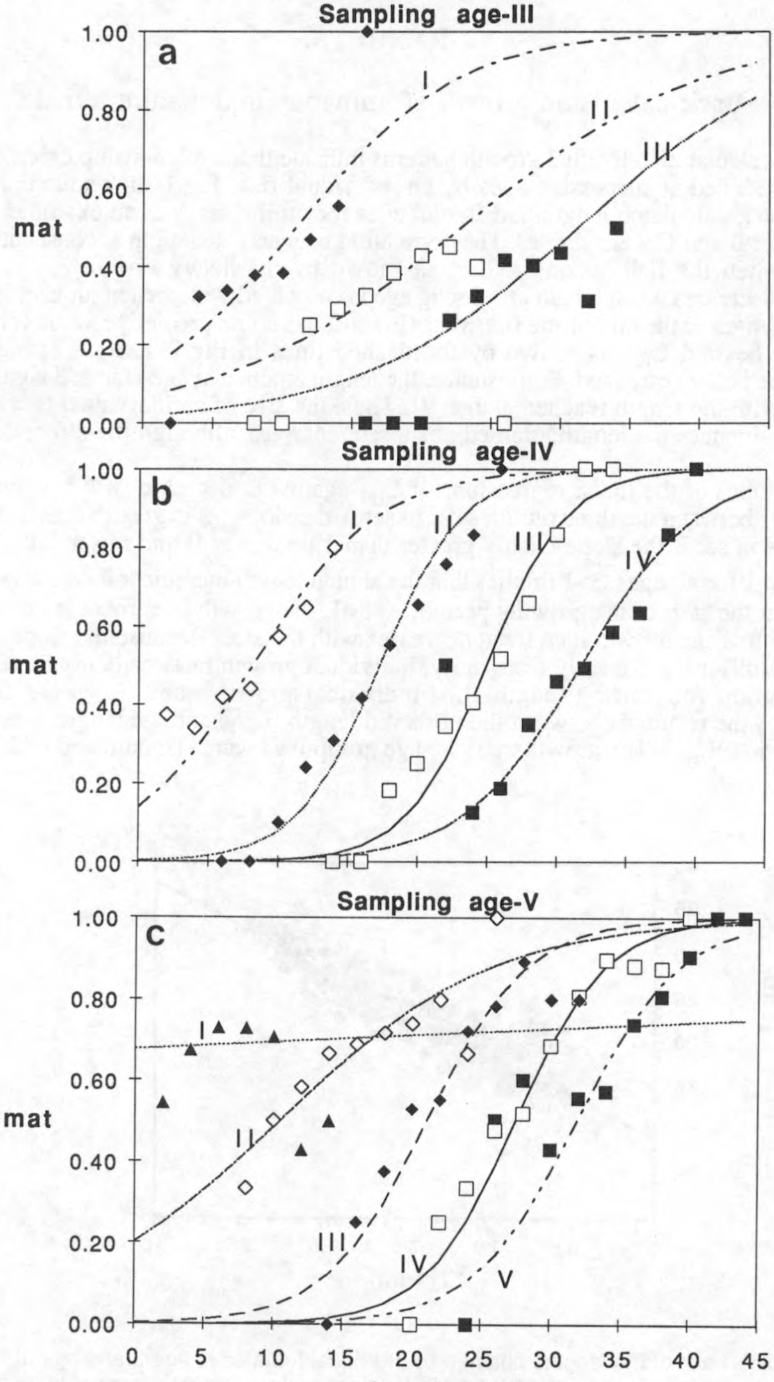

Figure 3. Maturity proportions in relation to the ultimate length and to the back-calculated lengths at previous ages for the females sampled at age III (a), age IV (b) and age V (c).

Table 2. Correlation coefficients (r^2) of growth rate at various ages of the juvenile phase. The growth rate was calculated as the annual length increment (cm) corrected for the length at the start of the growing period. * $P<0.05$; ** $P<0.01$

		Ages			
Otolith set		0-I	I-II	II-III	III-IV
A	r^2	0.009	0.021^*	0.014	0.046^*
	n	262	262	182	81
B	r^2	0.000	0.009	0.022^*	0.065^{**}
	n	201	201	201	162
C	r^2	0.000	0.034^*	0.007	0.060^{**}
	n	191	191	191	151

regression $L_{i+1} = \alpha + \beta L_i$ calculated for i=1 and 2 for each otolith set separately. Growth rate at age 0 was calculated as the difference between the L_I and the mean L_I. Individual growth rates can vary substantially, as illustrated by the wide scatter around the regression line in Fig.2. Individual growth rates at successive ages 0, I and II appeared to be hardly correlated in all three data sets (Table 2), suggesting that the environmental conditions for growth between consecutive years are variable and unpredictable.

Table 3 presents the differences in previous growth history between females sampled as immature and mature fish during the spawning period for all three otolith sets, showing that immature females are smaller than mature females. This difference is not only apparent in the year of sampling, but also in previous years. In all but one case, the length attained after the first growing period is smaller in immatures. Table 3 also shows that the mean length at age of both matures and immatures appears to decline with increasing age at time of sampling.

Following the proportions mature females by length class backwards from the age of sampling to age-I, shows that the maturity-ogives generally run parallel for the different age groups (Fig.3). Pairwise comparison revealed that none of the slopes differed significantly at the 5% level, except for those at age-I and age-II for sampling age-V, which were significantly flatter than the common slope of age-III to age-V (F test, $P<0.05$).

Since the length of immature females was shown to be smaller than the length of mature females during their early life (Table 3), the data of Fig.3 do not reveal during which part of the juvenile phase differences in growth rate are related to maturation. Therefore, the growth rate at all ages was compared between females sampled later as immatures and matures. As before, the individual growth rate was calculated by linear regression of L_{i+1} against L_i for i=1,2 and for each otolith set separately. Since the three otolith sets yielded similar results, the data of the three otolith sets were pooled (Fig.4). For the females sampled at age-IV and V, the differences were statistically significant at age 0, I and age I, II respectively (two-tailed t-test, $P<0.05$). The age at which the largest difference in previous growth between mature and immature females occurred appeared to shift with sampling age: from age-0 for sampling age-III, to age-I for sampling age-IV, and to age-I and II for sampling age-V. These results suggest that differences in growth rate early in the juvenile phase are correlated with the probability of sexual maturity three years later. Fig.4 further shows that the growth rate of mature females in the penultimate year is significantly lower than that of immature females for the cohorts sampled at age-IV and V (two-tailed t-test, $P<0.05$), indicating that reproduction is associated with a reduction in somatic growth in the penultimate year.

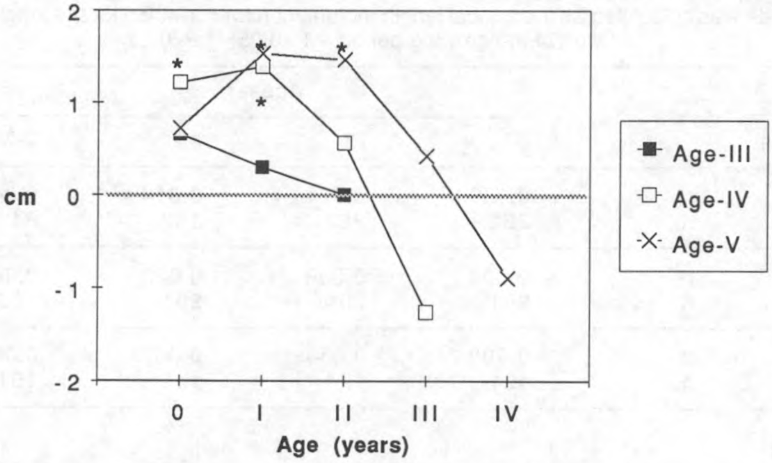

Figure 4. Difference in length increment (cm) of mature and immature females at previous ages. The three lines represent samples taken of 3, 4 and 5-year old females. A positive difference means that the mature females showed a higher growth increment. The asterisk shows a significant difference at $P<0.05$ (two-tailed t-test). Pooled data from otolith set A, B and C.

Table 3. Back-calculated length and standard deviation at age I - VI (L_I - L_{VI} in cm) of immature and mature females sampled at spawning time at different ages.

Otolith set A.

		L_I	L_{II}	L_{III}	L_{IV}	L_V	number
Year class 1980, Sampling age V							
immature	mean	6.6	15.1	22.1	28.2	33.3	6
	s.d.	1.7	3.7	4.2	3.8	4.1	
mature	mean	7.4	18.7	27.3	34.0	38.4	18
	s.d.	2.0	2.8	2.4	2.3	2.1	
Year class 1981, Sampling age V							
immature	mean	8.0	17.3	23.8	29.9	34.8	14
	s.d.	2.4	2.6	3.4	3.1	2.5	
mature	mean	7.7	17.6	25.3	31.7	36.2	24
	s.d.	1.8	2.4	2.5	3.3	3.7	
Year class 1981, Sampling age IV							
immature	mean	8.3	16.9	24.8	31.8	-	24
	s.d.	2.2	2.5	2.7	2.9	-	
mature	mean	9.7	19.8	28.0	33.7	-	26
	s.d.	2.8	2.8	3.1	3.1	-	
Year class 1982, Sampling age IV							
immature	mean	7.8	16.4	24.0	31.1	-	27
	s.d.	2.8	3.3	2.8	2.4	-	
mature	mean	9.4	18.8	26.5	33.0	-	22
	s.d.	2.3	2.3	2.9	2.2	-	

Table 3. cntd.

Otolith set A.							
		L_I	L_{II}	L_{III}	L_{IV}	L_V	number
Year class 1982, Sampling age III							
immature	mean	8.8	18.6	27.5	-	-	23
	s.d.	2.4	2.8	3.2	-	-	
mature	mean	9.7	19.5	28.9	-	-	16
	s.d.	3.0	2.8	2.2	-	-	
Year class 1983, Sampling age III							
immature	mean	8.0	18.3	27.0	-	-	29
	s.d.	1.8	2.6	2.8	-	-	
mature	mean	8.4	19.1	27.3	-	-	14
	s.d.	1.5	2.0	2.0	-	-	

Otolith set B (Year class 1963)								
Year class		L_I	L_{II}	L_{III}	L_{IV}	L_V	L_{VI}	number
Sampling age IV								
immature	mean	7.9	16.1	23.2	30.0	-	-	28
	s.d.	1.4	1.8	1.6	1.7	-	-	
mature	mean	8.9	17.2	24.5	30.3	-	-	11
	s.d.	1.6	2.0	1.4	1.7	-	-	
Sampling age V								
immature	mean	6.8	13.9	20.2	26.0	31.7	-	13
	s.d.	1.8	2.0	1.9	1.9	2.3	-	
mature	mean	7.6	16.0	23.2	29.8	35.5	-	29
	s.d.	2.5	4.1	4.8	5.4	5.2	-	
Sampling age VI								
immature	mean	6.9	14.2	20.5	27.0	31.5	35.6	2
	s.d.	0.6	1.7	0.1	0.8	1.4	1.3	
mature	mean	7.3	14.9	22.4	28.5	34.1	38.5	31
	s.d.	1.8	2.3	3.2	3.6	3.6	3.5	
Otolith set C (year class 1969)								
Sampling age IV								
immature	mean	7.5	15.3	24.6	31.9	-	-	6
	s.d.	1.4	1.5	3.3	2.3	-	-	
mature	mean	9.2	19.2	28.8	35.1	-	-	34
	s.d.	3.1	4.4	3.9	2.7	-	-	
Sampling age V								
immature	mean	4.6	12.2	20.9	28.6	34.0	-	4
	s.d.	1.3	1.9	3.4	2.4	3.1	-	
mature	mean	8.1	17.5	26.8	34.0	38.4	-	39
	s.d.	2.4	3.4	4.5	3.7	3.0	-	

In order to investigate how the growth rate in early life affects the maturity-length relationship, the individual data from otolith sets A, B and C were analysed by logit analysis in which the dependent variable reproductive status - immature (0) or mature (1) - was related to the actual length and growth rate during previous years. The growth rate in previous years was standardized according to $L_{i+1} = 10.8 + 0.82\ L_i$. This regression equation was estimated from the pooled data of otolith sets A, B and C for age groups I to VI. The mean and standard deviation of the standardized growth rate for the various age groups of the individual year classes present in the otolith sets are given in Table 4. For the pooled data set the average growth rate is close to zero for all ages groups, but differs for the individual year classes. Year-class 1963 represents a below average growth rate, whereas the growth rates of year classes 1981 and 1982 are in general above average.

Table 4. Mean standardized growth (in cm), standard deviation (s.d.) and number of observations (n), at age 0 to V or in 1 to 3 years prior to sampling of the year classes studied in otolith sets A (year class 1979-1983), B (year class 1963) and C (year class 1969).

Year-class		Age						Previous Years		
		0	I	II	III	IV	V	-3	-2	-1
1963	mean	-0.4	-1.4	-0.9	-0.4	-0.1	-0.4	-1.0	-0.5	-0.2
	s.d.	2.0	2.0	1.6	1.7	1.5	1.3	1.7	1.5	1.4
	n	114	114	114	114	75	33	114	114	114
1969	mean	0.1	-0.2	1.4	0.9	-0.5	-1.1	0.9	0.8	-0.3
	s.d.	2.6	3.8	4.4	3.5	3.0	2.2	2.3	1.9	1.6
	n	121	121	121	121	81	38	121	121	121
1979	mean	0.2	-0.1	0.7	0.5	-1.3	-2.0	0.5	-1.3	-2.0
	s.d.	1.4	1.8	1.8	1.7	0.9	1.4	1.6	1.5	1.0
	n	12	12	12	12	12	12	12	12	12
1980	mean	-1.3	0.9	0.4	-0.1	-0.7	-2.2	0.0	-0.1	-0.9
	s.d.	2.0	2.5	2.3	1.8	1.5	1.7	2.3	1.9	1.5
	n	31	31	31	31	31	8	31	31	31
1981	mean	0.2	0.2	0.1	0.1	-0.6	-	-0.1	0.3	-0.1
	s.d.	2.4	2.2	1.8	1.5	1.3	-	2.1	1.7	1.4
	n	87	87	87	87	38	-	87	87	87
1982	mean	0.6	0.1	0.7	0.5	-	-	0.2	0.2	1.0
	s.d.	2.7	2.1	1.8	1.4	-	-	2.4	1.8	1.6
	n	89	89	89	50			89	89	89
1983	mean	-0.1	1.0	1.1	-	-	-	-0.1	1.0	1.1
	s.d.	1.7	2.2	1.3	-	-	-	1.7	2.2	1.3
	n	43	43	43	-	-	-	43	43	43
Total	mean	0.0	-0.2	0.4	0.2	-0.5	-1.1	0.0	0.2	0.0
	s.d.	2.4	2.4	2.1	1.7	1.4	1.3	2.2	1.9	1.6
	n	500	500	500	418	240	94	500	500	500

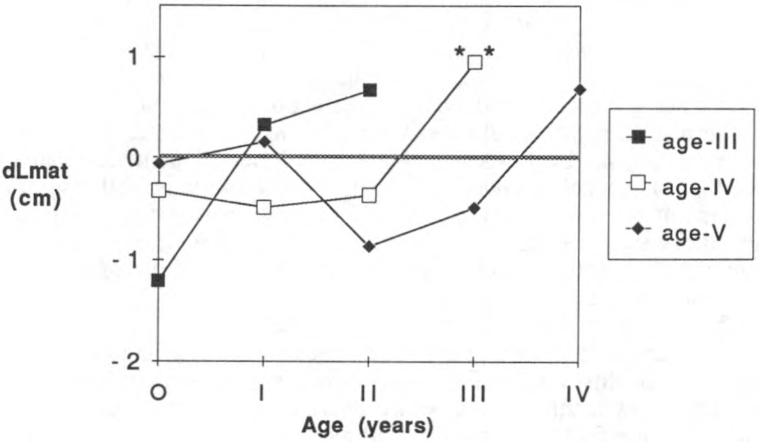

Figure 5. The change in the length at 50% maturity (dL_{mat} in cm) of female plaice in relation with a 1-cm increase in growth rate at previous ages for females sampled at age-III, age-IV and age-V. The asterisk shows a significant difference at $P<0.01$ (two-tailed t-test).

Table 5. ANCOVA of maturity in individual females (Y) as a function of body size (L in cm), standardized growth rate (G-i in cm) in three previous years and the factors year class (YC) and age (A). The analysis follows a stepwise backwards elimination procedure and employs a binominal error and a logit link function.

	SS	df	MS	F	P
Run 1: logit Y= $\alpha + \beta L$ + G-1 + G-2 + G-3					
L					
G-1	11.83	1	11.83	12.22	<0.01
G-2	0.338	1	0.338	0.35	n.s.
G-3	4.321	1	4.321	4.46	<0.05
error	479.3	495	0.968		
total	648.7	499			
Run 2: logit Y= $\alpha + \beta L$ + YCLS + A + G-1 + G-2 + G-3					
L	15.48	1	15.48	16.83	<0.001
YC	17.19	6	2.86	3.12	<0.001
A	12.61	3	4.20	4.57	<0.001
G-1	9.31	1	9.31	10.12	<0.01
G-2	0.979	1	0.979	1.06	n.s.
G-3	0.060	1	0.060	0.07	n.s.
error	447.0	486	0.920		
total	648.7	499			

Two analyses were carried out. In the first analysis, the effect of previous growth on the probability of maturation was analysed separately for three sampling age groups III, IV and V. In the second analysis, the sampling age groups were combined.

The result of the first analysis is given as the difference in the L_{mat} in females showing a 1-cm higher growth rate at a particular age (Fig.5). A 2-cm difference in growth rate will double the difference in L_{mat}, and a change in sign will change the sign of the effect. In all three age groups sampled the largest effect of growth rate seems to occur in the penultimate year and three years before sampling. A fast growth rate three years prior to sampling tend to reduce the L_{mat}, whereas a fast growth rate in the penultimate year tends to increase the L_{mat}. The results, however, were in general not statistically significant.

The second analysis explored the effect of previous growth rate (G) irrespective of sampling age. Backwards stepwise analysis, showed that beside actual length both growth rate in the penultimate year (G-1) and three years earlier (G-3) were statistically significant (Table 5). The parameter estimates of the GLM model, given in Table 6, can be used to calculate the effect of the previous growth history on the L_{mat}. The effect of a 1-cm growth superiority 1 to 3 years prior to sampling on L_{mat}, keeping the growth rate of the other ages at the standard rate, is illustrated in Fig.6. Fast growth in the penultimate year increases L_{mat}, whereas fast growth three years before decreases the L_{mat}. Extending the model further by including the factors year class and age group, shows a significant effect of length, year class, age group and G-1 (Table 5), but removed the significant effect of the G-3. This may be explained by the differences in G-3 between year classes or age groups (Table 4).

The analysis of the probability of maturation in relation with previous growth thus clearly indicates that the L_{mat} increases with growth rate in the penultimate year. The effect of the growth rate 3-years prior to sampling suggests that the L_{mat} decreases in fast growing females, although this effect might also be ascribed to a year class or age effect.

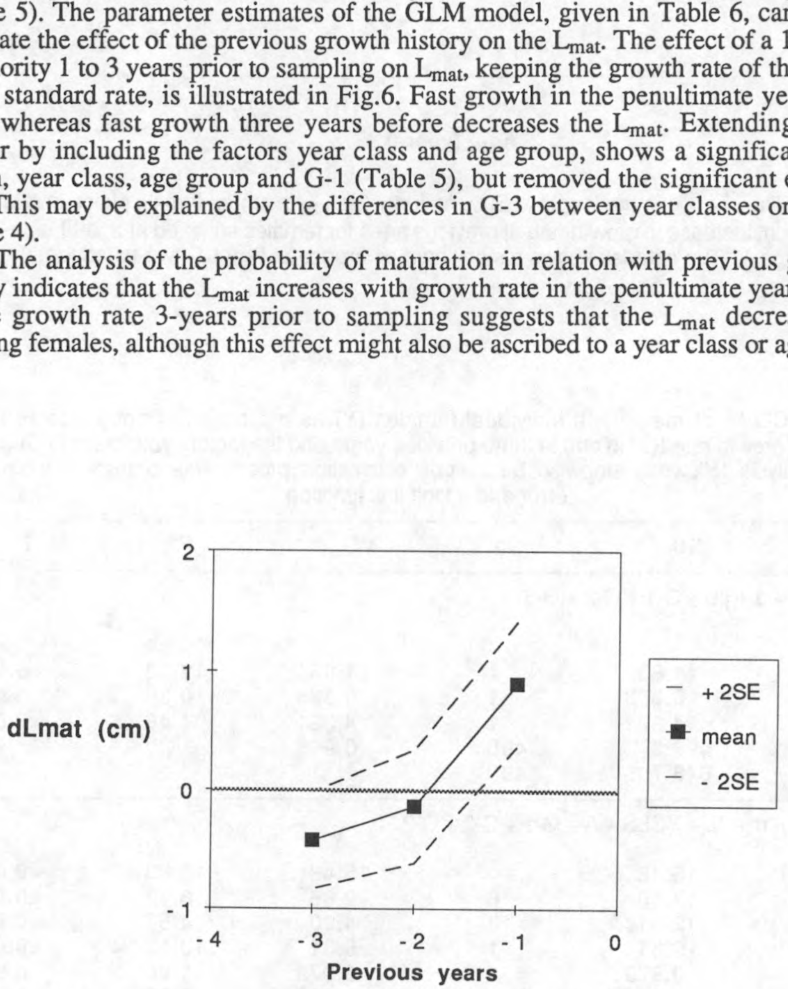

Figure 6. The change in L_{mat} (± 2 SE) of female plaice in relation with an increase in growth rate 1-3 years before sampling as estimated from the logit analysis of Table 6.

Table 6. Parameter estimates of the GLM model of individual maturity data: logit Y= a + bL + G-1 + G-2 + G-3

	parameter	S.E.
a	-8.244	0.9924
b	0.2698	0.03038
G-1	-0.2406	0.07066
G-2	0.0374	0.06438
G-3	0.1141	0.05535

Annual variability in the onset of maturation between 1958-1990

Regression of the maturation data from the market samples showed that the maturity - length relations differed significantly between year classes, areas and age groups (Table 7). The full model: logit Y = L + A + AR+ YC + L.A + L.YC + L.AR + A.AR + YC.AR, including the biologically relevant interaction terms, explained 91% of the variance. The significant contribution of the covariables age, area and year class indicates that the intercept differs between these covariables. The significant interaction terms indicates that both age-effect and year class effect differ between the areas and that the slope of the maturity ogive differs significantly between respectively age groups, year classes and areas.

The significant differences in maturity-length ogives between age groups, both in slope and intercept, indicate that at a particular length the proportion mature females increases with age and that the predicted L_{mat} decreases with age (Fig.7). The decrease in L_{mat} with age is illustrated for the three areas from a reduced model including length, age, area and their interactions, but omiting the factor year class (Fig.8). The decrease in L_{mat} with age implies that faster growing females will mature at a larger size and a younger age, whereas slower growing ones mature at a smaller length and an older age.

Table 7. ANCOVA results of the proportion mature females (Y) according the GLM model: logit Y = L + A + AR+ YC + L.A + L.YC + L.AR + A.AR + YC.AR with L = length (2 cm size classes); A = age (3,4,5,6,7); AR = area (1,2,3); YC = year class. L.A, L.YC, L.AR, A.AR and YC.AR are the interactions between the main variables. The model employs a binominal error and a logit link function.

	SS	df	MS	F	P
L	2695	1	2695	1710	<0.01
A	830.0	4	207.5	131.6	<0.01
AR	772.3	2	386.2	245	<0.01
YC	489.2	29	16.87	10.7	<0.01
error	2322	1473	1.576		
L.A	137.1	4	34.28	27.1	<0.01
L.AR	31.25	2	15.63	12.4	<0.01
L.YC	227.5	29	7.85	6.21	<0.01
A.AR	84.8	8	10.60	8.39	<0.01
YC.AR	82.9	40	2.073	1.64	<0.01
error	1757	1390	1.264		
total	20440	1509			

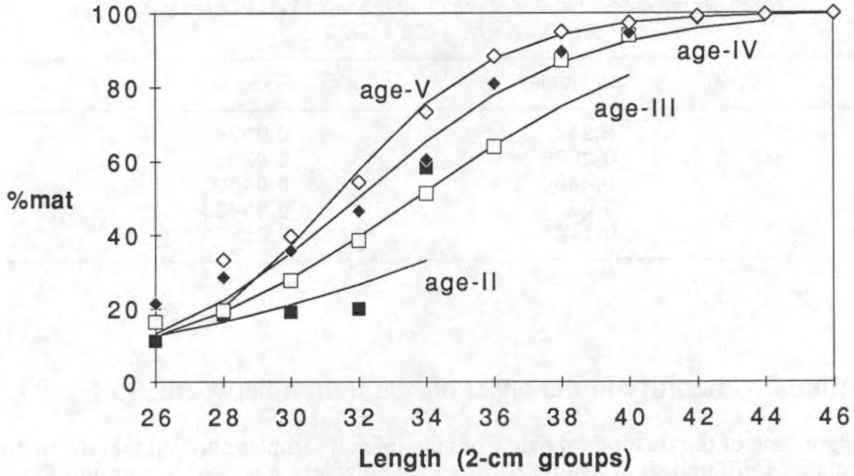

Figure 7. Maturity - length ogives for females of age group III, IV, V and VI. The observed proportions maturity are indicated by age-II, age-III, age-IV, age-V and age VI. Data: pooled market sampling data for areas SB, GB and FLAM for the years 1958-1990.

The position of the maturity ogive is determined by its slope and intercept. In order to simplify the presentation of variations in maturity ogives between year classes and areas, the L_{mat} is used to illustrate the variations. The L_{mat} is calculated for age group IV from the parameter estimates of the full model. This age group was selected because it is the overall mean A_{mat}. The range of year classes included in the analysis was reduced in areas GB and FLAM, due to the low sampling level in a number of years. Fig.9 shows that the L_{mat} show substantial variations between year classes in all three areas. The coefficient of variation of the fitted L_{mat} was between 5% - 9%.

In order to test whether the difference in the L_{mat} between year classes is related to the growth rate at an early age, the L_{mat} is correlated with the length attained at age IV (L_{IV}), as an approximation of the cumulative growth in the early life. The L_{mat} showed a significant negative correlation with L_{IV} in the Southern Bight and German Bight ($P<0.05$), but not in the Flamborough area (Fig.10).

In order to test whether the geographical difference in the L_{mat} between between areas SB, GB and Flam is related to the growth rate at an early age, the growth rate in these areas is compared. Pre-recruit surveys indicate that the growth rate at age-I in the German Bight is significantly lower than in the Southern Bight (Table 8). No survey data are available for the Flamborough area. Back-calculation of otoliths of mature females of age group VI and older of otolith set D revealed that the standardized growth rate differed between the geographical areas (Fig.11). Compared to the Southern Bight, the growth rate was significantly lower at age-I and age-II in the German Bight ($P<0.05$) and at age-I in the Flamborough area ($P<0.10$). For the other age groups the growth rate did not differ significantly.

DISCUSSION.

In the present paper cohorts were sampled at successive ages to study their maturation in relation to differences in back-calculated growth. This approach implicitly assumes that there is no selective mortality between successive sampling ages. This assumption is not

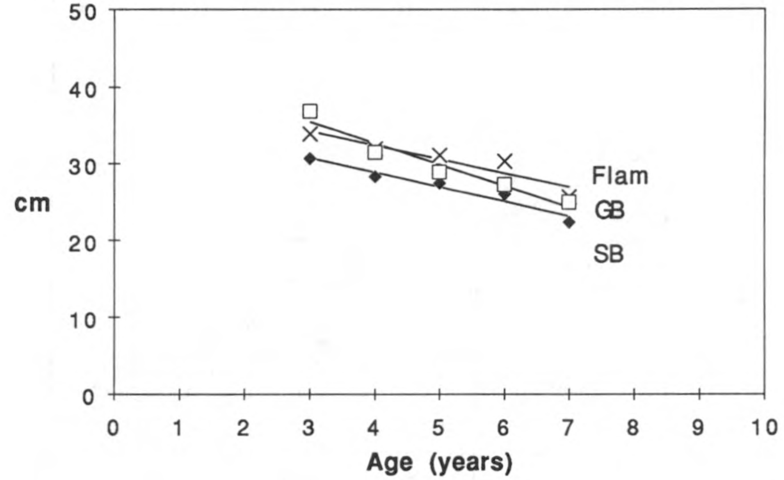

Figure 8. Relationship between the predicted L_{mat} for different age groups in area SB, GB and FLAM. The lines show the linear regressions of L_{mat} against age. Data: market sampling data 1958-1990.

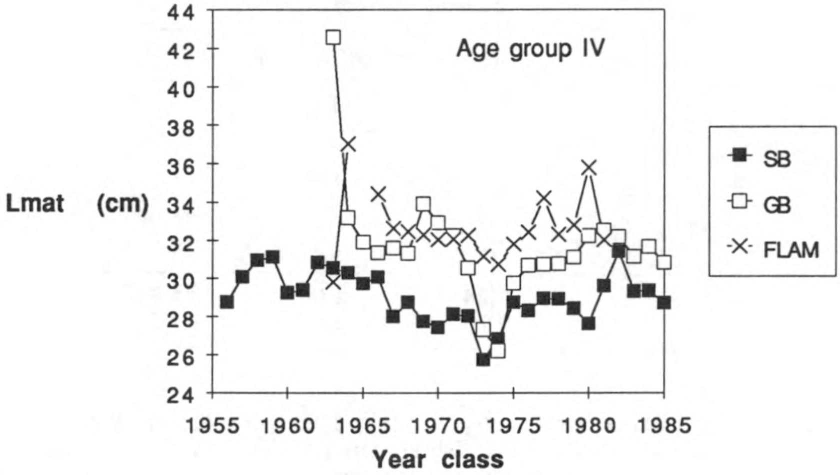

Figure 9. Variability in the L_{mat} of 4-year old females of year class 1956-1985 in area SB, GB and FLAM.

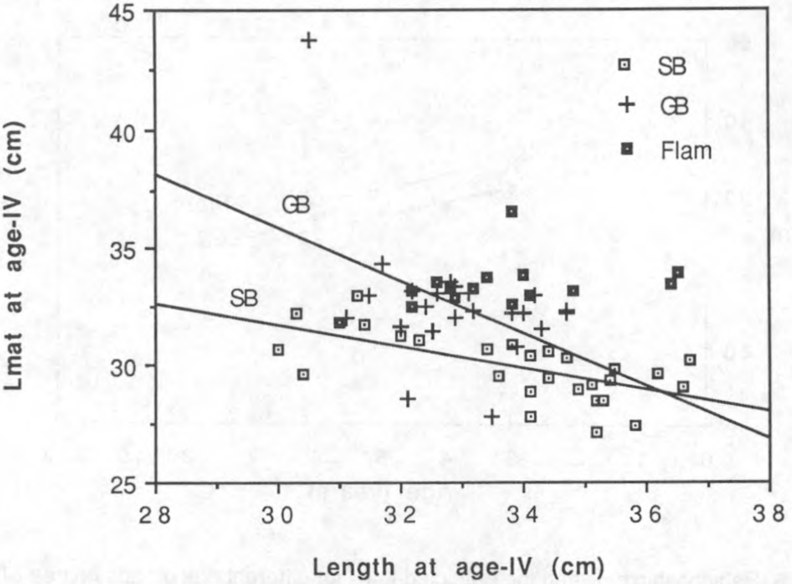

Figure 10. Relationship between the predicted L_{mat} (cm) at age-IV for different year classes and the length attained by that year class at age IV (L_{IV}) for area SB, GB and Flam. Significant regression lines are shown for area SB and GB. Data: market sampling data 1958-1990.

Table 8. Average length of age group 0, I and II of year classes 1978-1986 as observed in the autumn pre-recruit surveys carried out in the Southern Bight and German Bight (van Beek *et al.* 1989).

		Age group		
Area		0	I	II
SB	mean	10.1	18.3	25.3
	s.d.	0.6	0.9	1.3
GB	mean	9.8	16.2	24.0
	s.d.	0.7	1.3	2.1
difference	mean	0.24	2.06	1.26
t-value		0.78	3.99*	1.52

necessarily correct. It has been often observed (Lee's phenomenon) that length of the same age group back-calculated from older fish are smaller than those back-calculated from younger fish and a similar phenomenon can be observed in Table 2. This phenomenon may be due to an incorrect back-calculation procedure, sampling bias or size-selective mortality (Jones 1958; Ricker 1971; Casselman 1986). A full discussion of the Lee's phenomenon is beyond the scope of this paper, but since the back-calculation method has been validated for plaice (Rijnsdorp *et al.* 1990), sampling bias and size-selective mortality are the most likely factors involved. In the present case, sampling bias might well apply to the results for otolith set B and C. These samples were drawn from market samples and comprised of fish above the minimum landing size only. In set A, otoliths were collected from up to 4 fish per cm-group irrespective of sex or maturity. From these samples, otoliths were selected at random from the immature and mature fractions within the age groups of interest. Although stratified sampling by cm-group will lead to a relatively over-representation of the tails of the length distribution, this is not likely to have substantially affected the mean of the back-calculated lengths. Lee's phenomenon in otolith set A might therefore be due to increased mortality with size. Such size-selective mortality due to fishing is not unlikely, since recruitment to the fishing grounds is a function of body size. Fast growing plaice will leave the shallow coastal nursery grounds at an earlier age than slow growing ones (Beverton & Holt 1957; Chapter 4).

Within the present context, an important question is as to whether the samples were biased with respect to immature and mature females. Rijnsdorp (1989) (Chapter 4) compared the maturity-age relationships as obtained from market samples with those estimated directly from survey results. He concluded that the proportion mature fish was slightly overestimated in not fully recruited age groups, since the non-recruited fraction comprised of undersized, mainly immature, fish. The maturity-length relationships are less likely to be biased if recruitment to the fishery is size-dependent, which is generally assumed for this species (Beverton & Holt 1957). However, the higher fishing mortality experienced by fast growing and early maturing females implies that these will be selectively removed from a cohort compared to the slow growing and later maturing females. Since, somatic growth of mature females was less than of immature ones (Fig.4), it can be inferred that size-selective mortality may have influenced the observed maturity-length relationship. The number of mature females should be reduced compared to the number of immature ones, leading to an increase in the L_{mat}. However, the analysis of the maturity-length relationships showed a decrease in the L_{mat} with age (Fig.8), which is opposite to the expected effect from size-selective mortality.

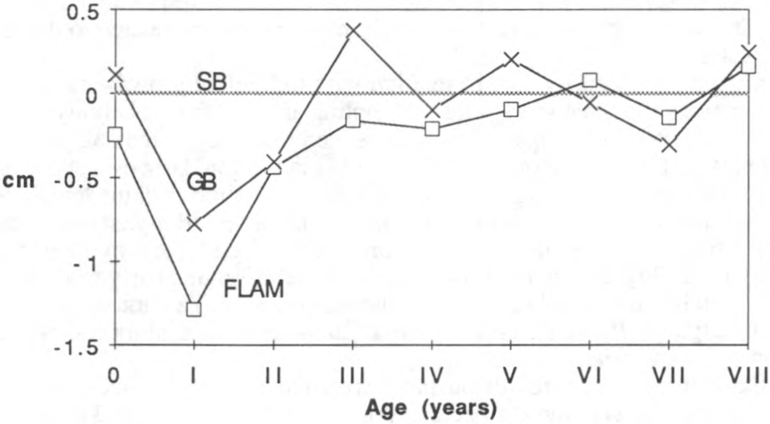

Figure 11. Differences in growth rate at age 0 - VIII of area GB and FLAM relative to the growth rate in area SB. The growth rate in area SB is shown as the dotted line. The asterisk indicates the age groups for which the growth rate differed significantly from area SB (P<0.05). Data: otolith set D.

The central problem in the present paper is to derive a hypothesis on the effects of growth in the juvenile phase on the onset of sexual maturity. The approach adopted has been to analyse the phenotypic plasticity in maturation by interpreting the variability between individual fish, years and geographic areas, in order to try to derive a consistent interpretation of the observed patterns. A basic assumption is that the observed variability in maturity patterns is largely driven by environmental variation. Studies of the heritability of maturation as well as other life history parameters have shown heritabilities around h^2=0.24, suggesting that the observed variability in the phenotype is 76% due to environmental variation and 24% to genetical variation (Roff 1991).

The observation that growth in the penultimate year was lower in mature females than in immature females (Fig.4) supports the general concept that growth and reproduction are activities that compete for limited resources. That no such effect was observed in females sampled at age III might be related to the fact that the mature III-year old females were all reproducing for the first time (Table 1). Recruit spawners have to build up energy reserves for reproduction, but do not have to recover from a depleted body condition following the previous spawning season (Chapter 1). Reproduction will thus only have its maximum effect on somatic growth after the first reproductive season.

It was shown that fast growth in the penultimate year increases the L_{mat}. This might be explained by the time interval between the onset of maturation and spawning time. Faster growing females may reach a larger size at spawning time after passing some threshold size earlier during the growing period compared to slower growing fish. Rijnsdorp (1989) (Chapter 4) showed that the juvenile-adult transition took place between May and September, well within the period of somatic growth (Chapter 7).

Females, sampled as mature fish at some later age, appeared to be characterised by faster growth at age 0-II compared to fish of the same age which were still immature (Fig.4). The age at which this early growth was enhanced shifted with the age of the fish at the time of sampling. The estimated age of growth superiority of mature fish relative to immature fish might be biased by the fact that part of the mature fish will already have been mature for some years. The first mature females of the year classes studied belonged to age III and must therefore be considered first time spawners (Table 1). Hence this bias will only affect the older age groups. Therefore, we can expect that the estimated growth superiority of mature females may have been underestimated from age-IV onwards, which may explain part of the decline in growth superiority with age. Despite this bias, the results indicate that differences in growth rate in an early phase of life are related to the maturation several years later.

Logit analysis of maturity data in relation with individual growth history suggested that the growth rate up to three years prior to sampling affected the probability to be mature. This effect was removed when age and year class were included in the analysis. It remains therefore, unresolved which factor actually affected maturation. However, the observation that the L_{mat} of individual year classes showed a negative relation with the length attained at age IV in two of the three areas studied (Fig.10), and the observation that the differences in the maturity ogives between areas in the North Sea (Fig.8) corresponded to a lower growth rate at age I (Fig.11), gives support for the conclusion that early growth rate affect maturation later in life and corroborates the inferences made by Yamamoto (1956), Dunn & Tyler (1969), Hilge (1976) and Burton & Idler (1984) that the maturation process could span a period of several years.

The effect of previous growth on the differences in L_{mat} between areas may be quantified using the results of the logit analysis of maturation in individual females. Table 6 present the parameter estimates of the effect of the relative growth in three years prior to sampling. The growth standard is given by the linear regression of L_{i+1} against L_i with an intercept of 10.8 and a slope of 0.82. Given the average length at age in the three areas, as obtained by back-calculation of otolith set D (only sampling ages >=6), the differences in

Table 9. Differences in standardized growth of female plaice in three areas. The observed length at age (L_{obs}) were back-caculated from otolith set D (sampling age >=6 years). The predicted length at age (L_{pred}) were obtained from the regression $L_{i+1} = 10.8 + 0.82 L_i$. The standardized growth rate (G) was calculated as $G = L_{obs} - L_{pred}$

	SB			GB			FLAM		
Age	L_{obs}	L_{pred}	G	L_{obs}	L_{pred}	G	L_{obs}	L_{pred}	G
I	8.5	8.3	0.2	8.3	8.3	0.0	8.1	8.3	-0.2
II	20.0	17.8	2.2	17.7	17.6	0.1	17.6	17.4	0.2
III	28.4	27.2	1.2	25.4	25.3	0.1	25.1	25.2	-0.1
IV	34.1	34.1	0.0	31.6	31.6	0.0	31.9	31.4	0.5
V	38.1	38.8	-0.7	35.7	36.7	-1.0	36.4	37.0	-0.6

Table 10. Predicted and observed L_{mat} in three areas with the corresponding standard errors. The predicted L_{mat} was estimated according to the GLM model of Table 6 and standardized growth rates of Table 9. The observed L_{mat} were estimated from the GLM model: logit Y= L + A + AR + L.A + L.AR. (market sampling data 1958-1990).

		Predicted		Observed
	Area	L_{mat}	95% C.L.	L_{mat}
Age IV				
	SB	29.4	29.1-29.7	29.7
	GB	29.6	29.4-29.8	32.0
	Flam	30.0	29.8-30.2	33.0
Age V				
	SB	29.5	29.0-29.8	29.6
	GB	30.5	30.4-30.6	29.9
	FLAM	30.9	30.8-31.1	32.1

L_{mat} due to differences in early growth can be estimated. Since the majority of females become mature at age IV and V, the growth effect was calculated for these two ages. Table 9 shows the length at age of females in areas SB, GB and FLAM and the standardized growth rates relative to the standard regression of L_{i+1} against L_i. With the values for the standardized growth in the three years prior to sampling and the parameter estimates from Table 6, the L_{mat} and its approximate 95% confidence interval can be estimated. The result of this calculation, given in Table 10, shows that the predicted L_{mat} in area SB is close to the observed value, but is lower in areas GB and FLAM. Nevertheless, the predicted L_{mat} in area GB and FLAM are higher than in area SB, corresponding to the observed differences.

The lack of a quantitative agreement between the predicted and observed L_{mat} implies that other environmental factors may affect L_{mat}, or that the model provides a poor representation of reality. Both may be true. The model describing the effect of previous growth on the probability of maturation is a crude one. On the other hand, the geographical trend in L_{mat} appears to be correlated with the maximum and cumulative sea temperature during the main growing period. In the western North Sea (Flamborough area) the summer temperature does reach a maximum in September of about 14-16°C compared to 17°C in the southeastern North Sea. In the eastern North Sea north of 55°30'N the temperature cycle is more steep with a delayed increase to a maximum of about 16-17°C in September (Tomczak & Goedecke 1962). This tentatively suggests that temperature might be one of the factors involved. This inference is in line with the observed negative correlation between the average temperature in the third quarter and the L_{mat} of 4-year olds in the following spawning season (slope = 0.7, r^2=0.146, n=30, P<0.05). The correlations with average temperatures in the other quarters were all highly insignificant.

In theory, genetical differences could explain differences in L_{mat} within the North Sea. A genetical explanation however, seems less likely since various studies of the enzyme polymorphism did not provide evidence for genetical differences between the various sub-groups of plaice (de Ligny 1969). Moreover, tagging experiments have shown an exchange of individual fish between sub-groups (de Veen 1978; ICES 1992).

Thorpe (1986) postulated a model of maturation in salmonids in which a fish will mature only if the rate of acquisition of surplus energy during a critical period exceeds a genetically determined threshold. Experimental tests yielded general support for the model (Thorpe 1989), but could not explain all observations (Svedang 1991). We may hypothesize, that in juvenile plaice the maturation will be determined by both the length attained and by the accumulation of some factor. This factor is related to the growth rate in a critical period of the annual cycle and may fine-tune the maturation threshold: slow growth early in the juvenile phase will increase the threshold size, whereas fast growth will decrease the threshold size. In salmonids, the rate of acquisition appeared to work through the accumulation of lipids in the body. If the lipid level surpasses a threshold level during a critical period in the annual cycle, individual fish starts maturation (Row *et al.* 1991). Lipid level could be a candidate in plaice, since lipid levels clearly differ between immature and mature fish (Chapter 1).

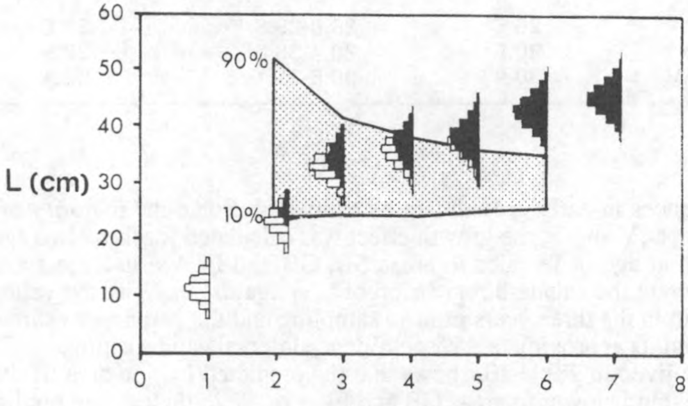

Figure 12. Maturation envelope (shaded) that encompasses the individual juvenile-adult transitions of female North Sea plaice, representing the population of reaction norms for maturation of female North Sea plaice. The envelope connects the lengths at which 10% and 90% of the different age groups become mature. The observed length distributions of immature (light histogram) and mature females (dark histogram) are also indicated. Pooled market sampling data 1958-1990 for area SB, GB and FLAM.

The simplest description of the juvenile-adult transition is given by the trajectory connecting the L_{mat} for the various ages. Such a trajectory could be interpreted as the average reaction norm for maturation in a population of female plaice. However, there are two observations that suggest that a single trajectory is too much of a simplification: 1 - these trajectories differed between geographical areas (Fig.8); 2 - the maturity-length ogives are affected by the growth rate between one to three years before (Fig.6). Therefore, we chose to visualise the juvenile-adult transition by an envelope encompassing the individual maturation points in the length-age space (Fig.12). The maturation envelope in Fig.12 was constructed by connecting the estimated length at which 10% (L10) and 90% (L90) of the females had matured for age groups II-VIII. It should be noted that the age at the x-axis is in discrete steps of one year, since reproduction occurs annually. The L10 and L90 values were estimated by a reduced GLM model including only length, age and their interaction as independent variables, thus pooling the data for the areas SB, GB and FLAM and the years 1960-1990. This GLM model explained 99.4% of the total variance.

The maturation envelope encompasses the juvenile-adult transition points of individual females in the two-dimensional length-age space. The suggestion that the probability of maturation is affected by the previous growth history of up to three years however may imply that the envelope change its shape in response of the growth trajectories of the individual fish. The envelope shown in Fig.12, therefore refers to the growth trajectories observed during the present period, which are indicated by the the length distributions at different ages and the proportion mature and immature fish. The part of the maturation envelope outside the observed length distributions was extrapolated from the fitted maturity ogives for each age group.

From the decrease in L_{mat} with age it was inferred that the maturity threshold increases with increasing growth rate. Fast growing fish maturing at an early age show a larger L_{mat} than slow growing fish maturing at a later age. This interpretation seems contradictory to the conclusion from the logit analysis of maturation in individual females, that the L_{mat} increased for females growing slow three years prior to sampling. This paradox however, is apparent and not real, because the probability of maturation is not only influenced by previous growth rates, but also by the ultimate length reached. Moreover, the observed growth trajectories are only a part of the potential phenotypic plasticity. If we follow a cohort during the process of maturation, we can see that the largest individuals at age III will mature. At age-VI, when almost all individuals have become mature, only some of the smallest individuals are still immature. The L_{mat} estimated from the maturity-length relationships of the youngest and oldest age groups represent thus extrapolations and not actual observations. They nevertheless predict what might be expected if females were growing much faster or much slower than at present.

The present analysis has clearly shown that growth rate affects the process of sexual maturation. Although indirect descriptive studies like the present one, will probably never allow one to unravel the intricate interactions between growth rate, fish size and maturation, which will only become known through ingenious experiments, they may provide a consistent interpretation of various observations and yield testable hypothesis about the critical part of the juvenile phase during which growth may influence the juvenile-adult transition.

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Chapter 7

The mechanism of energy allocation over reproduction and somatic growth in female North Sea plaice, *Pleuronectes platessa* L.

Rijnsdorp, A.D.1990. The mechanism of energy allocation over reproduction and somatic growth in female North Sea plaice, *Pleuronectes platessa* L. - Neth. J. Sea Res. 25: 279-290.

ABSTRACT. The mechanism of surplus production allocation over reproduction and somatic growth was studied in female plaice using market sampling data, tagging data and a tank experiment. Somatic growth peaked between March and October and main gonad growth occurred between October and January. However, an estimated 50% of the gonad growth was subsidized from body reserves built up during the growing period. Therefore, processes of somatic growth and the building up of energy reserves for gonad growth take place simultaneously.

Market sampling data and a tank experiment showed that pre-spawning energy reserves were positively correlated with somatic growth but also indicated that a twofold increase in somatic growth only results in an increase in energy reserves of less than 10%. Analysis of the relation between back-calculated somatic growth and reproductive investment in individual females did not reveal a significant effect of somatic growth on size-specific fecundity, gonad weight and pre-spawning body weight. It is concluded that size-specific reproductive investment is not, or only slightly, enhanced by an increase in surplus production. In the tank experiment females, which did not grow by more than 20% of the initial body weight, did not develop their gonads, but this phenomenon of skipping a spawning season does not seem to occur in the North Sea population.

The results of this study are summarized in a hypothetical model of the mechanism of surplus production allocation that is based on physiology and can be tested with tank experiments. The model postulates that surplus production is used to maintain body energy reserves at a threshold level that increases from a post-spawning low to a pre-spawning high. Surplus production exceeding the demands for maintaining body energy reserves at the threshold level is channelled into somatic growth. Implications of the mechanism for the changes in biological parameters in relation to reproductive strategies are discussed.

INTRODUCTION

In a number of exploited fish species changes in biological parameters including growth, fecundity and the length and age of first sexual maturity have been observed (Burd 1962; de Veen 1976; Daan 1978). As fish are characterized by a great phenotypic plasticity for growth (Purdom 1979), age and length at first maturity (Stearns & Crandall 1984) and fecundity (Bagenal 1973; Wootton 1977), these changes have been related to an increase in food supply through a reduction in population abundance. Since egg production per unit of biomass tend to increase in numerically depressed populations and to be reduced at high population abundance (Rothschild 1986), the pattern of energy allocation may have an important impact on the relation between stock and recruitment.

For North Sea plaice changes in all these parameters have been reported. Growth rate increased during the last century especially among juvenile plaice (Bannister 1978). Fecundity appears to be higher in recent years than at the beginning of this century and in 1947-1949 (Rijnsdorp *et al.* 1983; Horwood *et al.* 1986) and sexual maturity is attained at a smaller size and a younger age then around 1900 (Chapter 4).

The causal mechanisms behind the observed changes in biological parameters are still obscure. They do not necessarily reflect the phenotypic plasticity of fish, because from an evolutionary point of view changes in fecundity and onset of sexual maturity may be expected as fisheries do substantially increase the annual mortality among exploited fish species and therefore may cause a genetical selection for early maturation and increased fecundity (Horn & Rubenstein 1984).

Before the role of phenotypic and genetic plasticity in the causation of the observed changes in biological parameters can be assessed, a theoretical framework is required to study the inter-relations between processes of growth, fecundity and sexual maturation. The study of the allocation of resources over reproduction and somatic growth offers such a framework (Ware 1982; Roff 1983). Once the physiological mechanism of resource allocation is understood the theoretical response of fish to changes in the environmental conditions and exploitation can be compared to the observed response in natural populations.

This paper, which explores this approach and extends the earlier analyses by Rijnsdorp (1986), will focus on the allocation of surplus production over reproduction and somatic growth in female plaice. Firstly, the seasonal pattern in energy allocation is analysed to see whether processes of somatic growth and gonad growth are confined to different times of the year. Secondly, the relation between somatic growth and reproductive investment in terms of fecundity, gonad weight, and pre-spawning body reserves is studied in a) the population according to market sampling data collected during 1965 - 1986, b) individuals sampled for fecundity and back-calculated somatic growth and c) in a tank experiment.

MATERIAL AND METHODS

Definitions

In this paper the following definitions will be used. The condition factor (*K*) is calculated from the weight of the fish (*W* in g) and the length of the fish (*L* in cm):

$$K = 100\, W L^{-3}$$

The beginning of the growing period will be taken as starting point in the calculations of somatic growth and growth of body reserves. This starting point coincides with the end of the spawning period. Therefore, somatic growth at time i (SG_i) is calculated as the increase in body size relative to the condition of spent fish at the end of the spawning period (K_{spent}) :

$$SG_i = (L_i^3 - L_{i-3}^3)\, K_{spent}$$

Reproductive investment (R_i) in year i is calculated as the weight (g) or energy equivalent (kJ) of the gonad of ripening females (maturity stage 2) .

The surplus production in year i (SP_i) is the sum of somatic growth (SG_i) and reproductive investment (R_i) and can be expressed in units of weight (g) or energy (kJ). In a few cases the surplus production also includes the energy reserves for metabolism in the spawning period. (M_i)

$$SP_i = SG_i + R_i + [M_i]$$

The body reserves at time i (BR_i) will be expressed as the increase in condition factor (K_i) relative to the condition of spent fish (K_{spent}):

$$BR_i = L_i^3\ (K_i - K_{spent})$$

Seasonal allocation pattern

The monthly pattern in energy allocation was calculated from the length increment of tagged females, the condition factors and gonad weight percentages from the market sampling programme, gonad energy values given by Dawson & Grimm (1980), and an empirical relation between energy factor in kJ.cm^{-3} (E) and condition factor g.cm^{-3} (K) (Rijnsdorp, unpublished data)

$$E = 5.76\,K - 0.433$$

Tagging experiments have been carried out in the period 1960 - 1970 by the late J.F. de Veen and recaptured females which had been between 30 - 35 cm at release were selected from the data base. The average monthly length increment was obtained by combining tagging experiments conducted in different months. Somatic growth was calculated from the monthly volume increase and the post- spawning energy value. The relation between annual surplus production, reproductive investment and body size was determined from the length increment of tagged females, which were recaptured after 11 - 13 months in sea, and from somatic and gonad condition factors from market sampling data. Length at recapture was corrected for shrinkage (S in cm) according to the empirical relation: $S = -\,0.176 - 0.009\,L$. This relation was obtained from the predictive regression of the apparent negative growth of tagged plaice which were recaptured less than a month after release.

Somatic growth and reproductive investment

The relation between somatic growth and reproductive investment was studied following three approaches. The first approach was to establish the relation between the average annual somatic growth of adult females and the pre-spawning condition in January using market sampling data for the period 1965 - 1986. Somatic growth (cm^3) was estimated from successive first quarter lengths. Only females of 5 - 8 year old were selected because these age-groups are fully recruited to the fishery and dominate the landings. The market sampling programme has been set up to obtain representative samples from the plaice in the southern and central North Sea which form the major component of the total North Sea population (Chapter 4).

The second approach was to relate the back-calculated somatic growth of individual females with data on fecundity, pre-spawning gonad weight and condition factor. Samples were obtained from the commercial beam trawl fishery on the spawning grounds in the southern and central North Sea between December and February of 1981/1982, 1982/1983, 1983/1984 and 1984/1985. On board the fish were stored on ice and brought to the laboratory within one week after catching. Gonads were removed for fecundity estimates (see Rijnsdorp *et al.* 1983) and otoliths were taken for age determination. From a subsample of 269 fish, collected between December 1981 and February 1984, the somatic growth was estimated from the width of the last annulus of the otolith as described by van Leeuwen & Rijnsdorp (1986) and Lucio (1986).

The third approach was a tank experiment conducted in 1984 to study the influence of food ration on the allocation of energy over somatic growth and gonad growth. Female plaice of about 35 cm were collected by RV TRIDENS between 7-11 May at 56°N 3° E and kept together in a circular tank (diameter 3 m, height 1 m) to acclimatise at 12 - 14 °C and were fed with lugworm and cockle three times per week. At the start of the experiment

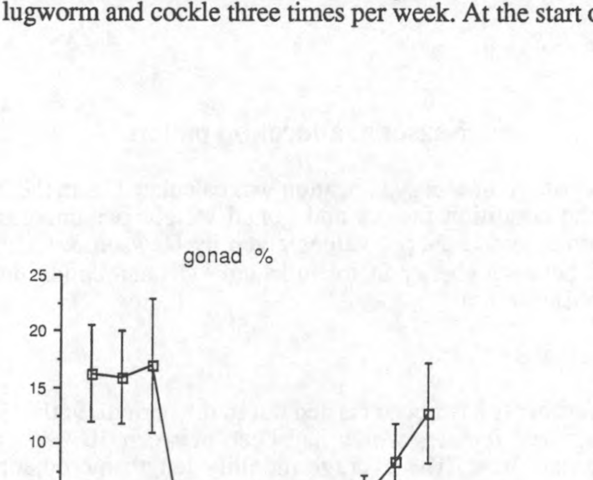

Fig 1 Monthly variation in the percentage gonad weight of gutted body weight of ripening females (upper panel) and in gutted condition factors of adult females and of ripening and spent females (lower panel). The vertical bars indicate the standard deviations.

on 31 June four circular tanks (diameter 1.45 m, height 1.10 m) were stocked with 5 female plaice each. Temperature and daylight regime were adjusted every fortnight to mirror the conditions in the central North Sea. Temperature increased from 12 °C at the start of the experiment to 14 °C in August and decreased to 9 °C in December. Number of hours daylight decreased from 17 h to 9 h over the same period. The fish were fed mainly with lugworms although occasionally mussels or cockles were given. The fish in the tanks were fed ad libitum during daytime once (2 tanks) or three times per week (2 tanks). Remaining food was removed the next morning. At the start of the experiment length (mm) and weight (g) were measured and the pattern of red spots was photographed for individual recognition. At the end of the experiment on 7 January 1985, the fish were killed and length, weight, gonad weight, fecundity and gonad stage were recorded for each individual.

Statistical methods.

Analyses of Variance (ANOVA) were carried out with the NAG statistical package GLIM (Baker & Nelder 1978), which allows for non-normal error distributions and non-linear relationships of dependent and independent variables. A nonorthogonal ANOVA model

$$Y = \alpha X1 + \beta X2 + Z + \varepsilon$$

was used in which Y is the dependent variable (fecundity or somatic growth); $X1$ and $X1$ are covariables such as length or age; Z is a discrete variable as month; α, β are parameters and ε is an error term. In practice only linear mappings of the independent to the dependent variable were used; error distributions were chosen minimizing the correlation of residuals and fitted values. Standardized somatic growth and fecundity were calculated as the observed somatic growth and fecundity, adjusted for primary effects of age and length as estimated from these ANOVA's.

RESULTS

Seasonal allocation pattern

During the growing period plaice ingest food in excess of the maintenance requirements. The excess is used for somatic growth and for building up energy reserves for reproduction and winter metabolism. The lower panel of Fig.1 shows the body condition of mature females and of ripening and spent females separately. Condition steadily increased during the growing period and reached a maximum in November-December. During the growing period the spent females start to develop their gonad and become ripening fish. Within the adult population the percentage of spent females steadily decreased from 96% in March to 2% in October and November and 0% in December. The condition factors of spent females which had not started gonad development at the end of the growing period were more variable and lower. The coefficient of variation of the condition factor varied around 9% during the year but increased to 15% in spent females in autumn. Substantial gonad growth did not start before October (Fig 1; upper panel).

The seasonal pattern of surplus production allocation over somatic growth, body reserves and gonad growth of a 35 cm mature female is shown in Fig.2. In this analyses surplus production comprises of somatic growth and energy reserves for reproduction and winter metabolism. Surplus production was low in late autumn and winter and peaked between April and September. Somatic growth as well as the increase in body reserves occurred throughout the growing period. The percentage surplus production allocated to somatic growth varied around 25%. The remaining surplus production was mainly channelled into the body reserves until August and in both body reserves and gonad growth thereafter. From November onwards gonad growth exceeded surplus production and was subsidized from body reserves. Overall, about 50% of the gonad energy was reallocated from body reserves build up during the growing period. Hence there is no evidence that periods of somatic growth and of building up body reserves for gonad growth and winter metabolism are separated in time, but the two processes occur simultaneously.

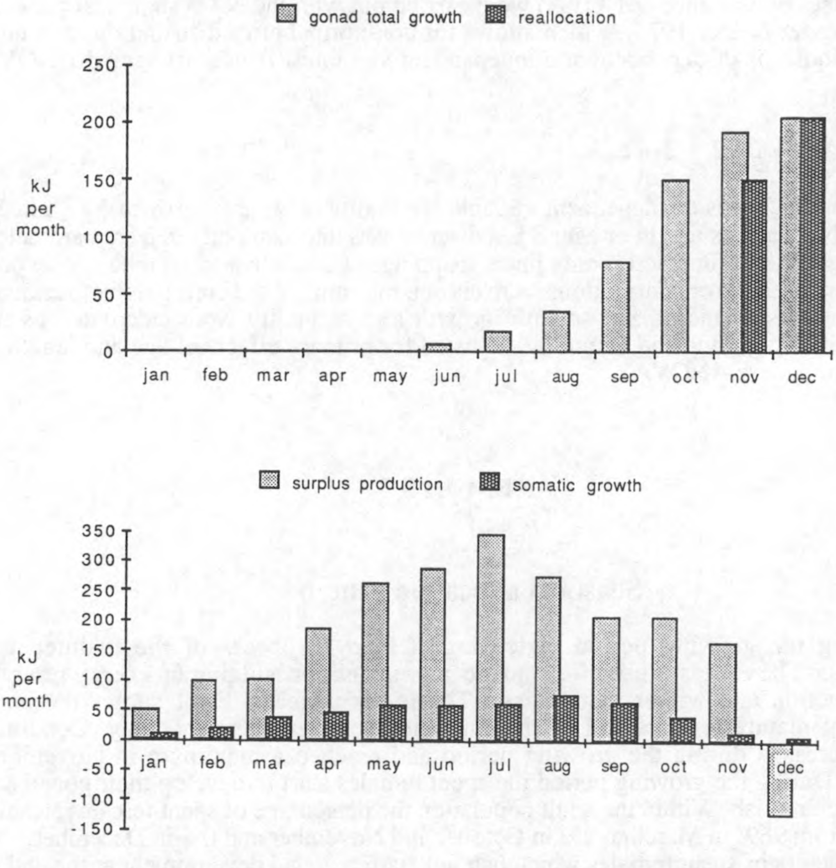

Fig 2. Monthly pattern in net gonad growth and the part reallocated from body tissues (upper panel) and in surplus production and somatic growth of an adult female growing from 35 cm at 1 January to 38 cm at 31 December.

Surplus production and allocation pattern

Fig.3 shows the mean annual length increment of tagged females in relation to the length at tagging. Growth in length decreased in larger fish and showed an increasing coefficient of variation from about 40% in females of 20-25 cm to well over 100% in females above 40 cm. Fig.4 shows the relation of the total and somatic condition factor of pre-spawning fish in January and the somatic condition of spent females during the 1st quarter with body size. Total condition including the gonads increased slightly with body size up to a length of about 50 cm. Somatic condition excluding gonads appeared to be constant or decrease slightly over a wide range of fish sizes, whereas the gonad condition factor increased with fish size up to a length between 45 - 50 cm (Fig.6). In the largest females (>50 cm) both body and gonad condition factors appeared to decrease

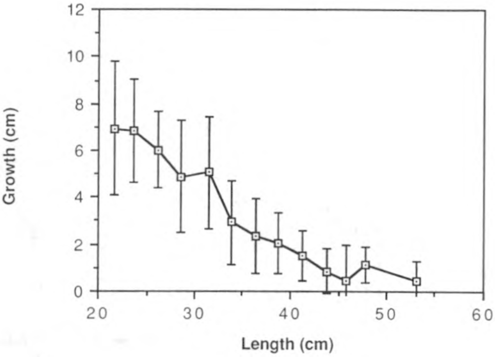

Fig 3.Length increment of tagged female plaice after 11 - 13 month in sea in relation with length at tagging. The vertical bars indicate one standard deviations.

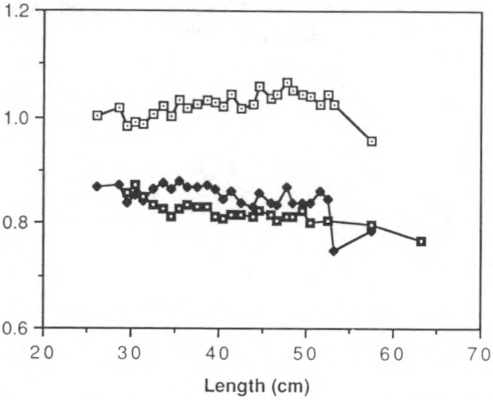

Fig 4. Total gutted (□) and somatic condition (◆) factor (excluding gonads) of ripening female in January and of spent (-■-) females in the 1st quarter in relation to length.

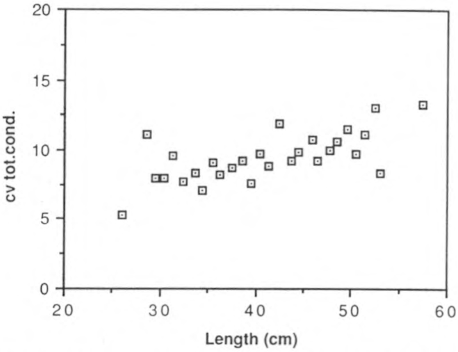

Fig 5. Relation between the coefficient of variation of total somatic condition factor and length of ripening female plaice in January.

The coefficient of variation in the pre-spawning condition varied around 9% with a slight positive trend (Fig 5). The coefficient of variation of the gonad condition factor varied around the 30% without a trend (Fig 6).

With the data from Fig 4 - 6 and the maturity-length relation (Chapter 4) the surplus production and gonad weight were calculated in relation with body size. Surplus production increased with body size (Fig.7). Reproductive effort expressed as the ratio of gonad weight over surplus production showed an increase from 0% in females up to 25 cm to about 90% in females of 50 cm. Assuming somatic and gonad growth to be independent the approximate 95% confidence limits of surplus production were calculated as 2*SE. Thus measured, variability increased with body size and the confidence limits of surplus production included the reproductive investment of larger females. This may implicate that surplus production in some of the larger females may not be sufficient for the normal size-specific reproductive investment.

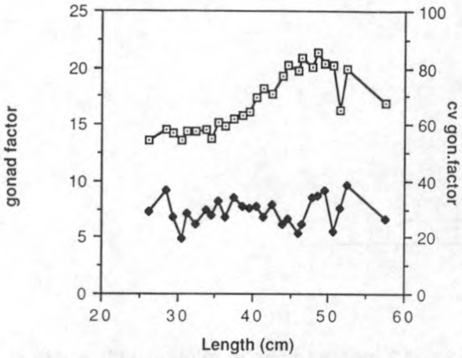

Fig 6. Relation between gonad condition factor (-□-), coefficient of variation (◆) and length of ripening female plaice in January.

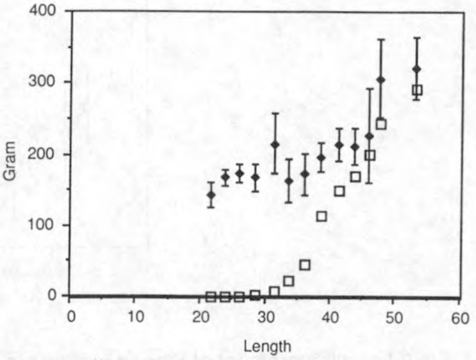

Fig 7. Relation between the annual surplus production (◆) and gonad weight (□) of female plaice. The vertical bars indicate 2*SE of surplus production.

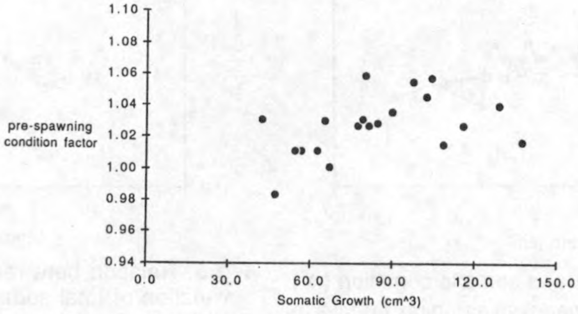

Fig 8. Relation between the annual somatic growth (cm^3) of 5-8 year old female plaice and the subsequent pre-spawning condition factor in January. Data for the period 1965 - 1985.

Table 1. Results of the nonorthogonal ANOVA of somatic growth (SG in cm^3) in the last year according the model: SG = L + L2 + L3 + ln(A) + Fec + L * ln(A).L = back-calculated length at the last spawning period; A = age; Standardized somatic growth was calculated as observed minus fitted values.

source of variation	SS	d.f.	MS	F	P	remarks
L	0.85	1	0.85	4.57	<0.05	excluding
ln(A)	12.12	1	12.12	65.2	<0.01	interaction
L2	0.80	1	0.80	4.35	<0.05	
L3	1.27	1	1.27	6.91	<0.01	
L*ln(A) interaction	0.73	1	0.73	3.97	<0.05	
error	48.17	263	0.183			
total	68.15	268				

Table 2. Results of the nonorthogonal ANOVA of fecundity (FEC) according the model: ln(Fec) = ln(L) + ln(A) + SG Fec = fecundity; L = length at present spawning period; A = age; SG = standardized somatic growth.

source of variation	SS	d.f.	MS	F	P
ln(L)	22.72	1	22.72	259.7	<<0.01
ln(A)	0.63	1	0.63	7.2	<0.01
SG	0.00	1	0.00	0.0	n.s.
error	23.18	266	0.087		
total	87.81	268			

The variability in individual surplus production raises the question as to how the allocation pattern over reproduction and somatic growth is influenced by the amount of surplus production. The first approach was to compare the annual somatic growth of female plaice according to market sampling data with the average pre-spawning condition factor. In Fig.8 the relation is shown for age group 5-8 in the period 1965 - 1986. Both somatic growth and pre-spawning condition showed a weak positive correlation (r= 0.42, P<0.05, n=20) The predictive regression indicates that a twofold increase in somatic growth will give a 2% increase in the pre-spawning condition.

The second approach was to study the relation between reproductive investment and back-calculated somatic growth in individual females. Reproductive investment was measured as fecundity, pre-spawning body weight and pre-spawning gonad weight. Some standardization was necessary using ANOVA procedures, because both fecundity and somatic growth were found to be functions of body size and age. Standardization of somatic growth for the covariables size and age was carried out with gamma errors to remove the observed correlation between residuals and fitted values (Table 1). A plot of the residuals against the fitted values showed that the residuals were skewed to the right. Standardization of ln fecundity for ln length and ln age gave residuals with an approximately normal distribution and with constant variance. The next step was to carry out an ANOVA of ln fecundity against ln length, ln age and standardized somatic growth. This analysis did not show a significant effect of standardized somatic growth on fecundity (Table 2).

Table 3. Results of the nonorthogonal ANOVA of pre-spawning body weight according the model: ln(W) = ln(L) + ln(A) + SG + TW = gutted body weight; L = length at present spawning period; A = age; SG = standardized somatic growth and T = factor time in 7 half monthly periods between December and the first half of March.

source of variation	SS	d.f.	MS	F	P
ln(L)	15.40	1	15.40	1394.6	<<0.01
ln(A)	0.112	1	0.112	12.8	<0.01
SG	0.013	1	0.013	1.2	n.s.
T	0.141	6	0.024	2.128	~0.05
error	2.86	259	0.011		
total	57.97	268			

Table 4. Results of the nonorthogonal ANOVA of gonad weight according the model: ln(G) = ln(L) + ln(A) + SG + T. G = gonad weight; L = length at present spawning period; A = age; SG = standardized somatic growth and T = factor time in 7 half monthly periods between December and the first half of March.

source of variation	SS	d.f.	MS	F	P
ln(L)	24.16	1	24.16	304.9	<<0.01
ln(A)	0.00	1	0.00	0.00	n.s.
SG	0.00	1	0.00	0.00	n.s.
T	2.08	6	0.347	4.37	<0.01
error	20.60	259	0.0795		
total	114.9	268			

In the ANOVA of pre-spawning body and gonad weight an extra covariable time (T) was included because body and gonad weights change between December and March. Time was entered as a discrete level factor coding for seven halfmonthly periods. The results of the analyses indicated that the standardized somatic growth did not significantly affect pre-spawning body weight and gonad weight (Table 3 and 4).

The results of the third approach, the tank experiment, are shown in Table 5. Individual growth was rather variable for all feeding regimes, but the number of good growing females was higher in the high ration tanks. In the fish that showed poor or even negative growth no gonad development was observed and the gonads were recorded as immature (stage 1) or spent (stage 7). Most females with a weight increase of more than ±20% of the initial weight did develop gonads (stage 2) except female #2.3, which showed a 58% weight increase but did not ripen. Somatic growth, calculated as the product of the volume increase and the condition factor at the start of the experiment, showed wide variations also. The final condition factors of the ripening females that did develop a gonad showed a significant positive correlation with somatic growth ($r=0.79$, $n=8$, $P<0.05$). A twofold increase in somatic growth from 75 to 150 g resulted in a 5% increase in total condition. The condition factors of these ripening females were close to the values observed in the sea (1.05) but the gonad weights were much lower than would be expected (16%). Because the observed fecundities were also much lower it seems likely that the experimental conditions have negatively affected the normal development of the gonad.

Table 5. Results of the tank experiment from 31-06-1984 to 7-01-1985 on the effect of ration level on the allocation of energy over somatic growth and reproduction. Length (cm) , weight (g), age (years) and condition factor (K) is given at the start and end of the experiment (columns A to G). Fecundity (Fec) is shown in column I, somatic growth in column J and total growth (somatic plus ovary weight) in column K. Column L gives the developmental stage of the ovary according to description in Chapter 4. The ratio of somatic over total growth is given in column M

Fish	Length		Weight		Age	Condition		Gonad weight	Fec 10^3	Growth		Mat	Ratio
Nr	start A	end B	start C	end D	 E	start F	end G	(g) H	eggs I	som J	total K	 L	 M
Tank 1: 3 rations per week													
1.1	34.0	37.7	373	546	5	0.95	1.02	24.4	55	135	174	2	0.78
1.2	34.0	33.6	336	279	4	0.85	0.73	1.5	-	-12	-57	1	-
1.3	35.5	37.9	329	557	3	0.74	1.02	49.4	90	72	228	2	0.32
1.4	34.1	35.8	365	435	4	0.92	0.95	1.9	-	57	70	1	-
1.5	34.5	43.0	346	946	4	0.84	1.19	51.2	108	324	600	2	0.54
Tank 2: 3 rations per week													
2.2	37.1	39.6	413	642	5	0.81	1.03	75.4	90	89	229	2	0.39
2.3	38.8	42.6	469	739	5	0.80	0.96	6.4	-	152	271	7	-
2.4	39.5	40.6	528	613	4	0.86	0.92	4.2	-	45	85	7	-
2.5	38.8	38.4	492	427	3	0.84	0.76	6.1	-	-15	-65	7	-
Tank 3: 1 ration per week													
3.1	36.1	37.6	423	537	4	0.90	1.01	43.9	88	55	113	2	0.48
3.2	32.2	32.8	298	321	5	0.89	0.91	3.7	-	17	23	7	-
3.3	36.5	36.7	463	490	4	0.95	0.99	5.3	-	8	27	7	-
3.4	35.2	35.7	390	460	4	0.89	1.01	36.9	80	17	70	2	0.24
3.5	36.2	36.2	413	367	5	0.87	0.77	3.6	-	0	-46	7	-
Tank 4: 1 ration per week													
4.2	37.6	39.8	467	698	5	0.88	1.11	55.9	109	87	231	2	0.38
4.4	39.5	39.1	495	435	5	0.80	0.73	4.5	-	-15	-60	7	-
4.5	36.5	38.1	429	511	4	0.88	0.93	22.2	51	59	82	2	0.72

DISCUSSION

The main response of individual females to a low surplus production in the tank experiment was to skip the spawning season, corroborating the results of Horwood *et al.* (1989). In the North Sea this situation appeared to be very rare as can be inferred from the low proportion of the mature females in spent condition at the end of the growing period (Chapter 4).

In order to give a sensible interpretation of the observed lack of relation between reproductive investment and back-calculated somatic growth in individual females, it is important to have some idea of the magnitude of measurement error, since these may have been confounding a real relation. Duplicates of fecundity determinations are characterized by a coefficient of variation of about 5% (Rijnsdorp *et al.* 1983). The back-calculation technique has been validated by Rijnsdorp & Visser (1987) by using tetracycline labelled otoliths in tagged plaice. Independent back-calculations of length in the previous year by two individuals showed an average absolute deviation of 0.5 cm. These errors are relatively small in comparison with the differences in individual fecundity (cv = 30%) and somatic growth (cv = 50%) for a 40 cm female. Therefore, variability due to measurement error can only have confounded a weak, but not a strong relation between somatic growth and fecundity.

The lack of relation between reproductive investment and back-calculated somatic growth in individual females contrasted with the results of the tank experiment and the market sampling analysis. In the latter two, a weak but significant positive correlation was observed between somatic growth and pre-spawning condition, suggesting that high surplus production will lead to high energy reserves for reproduction. The biological relevance however is low because a twofold increase in somatic growth gave only an increase in condition of less than 10%. The results lead to the general conclusion that surplus production in female plaice do not or only marginally affect size-specific fecundity or reproductive investment in general.

The analysis of individual females showed that fecundity and pre-spawning body weight were negatively correlated with the age of the fish. Thus in a comparison of two similar sized fishes of different ages the younger fish which by definition had grown faster also had a higher fecundity and a higher pre-spawning condition. Nevertheless the ANOVA of individual fecundity and pre-spawning condition did not indicate a significant effect of standardized somatic growth. Therefore, it is concluded that the growth history at earlier ages and not the relative somatic growth in the last growing period affects fecundity and pre-spawning condition. Further analysis including the possible relation between the age at first maturation and reproductive investment is required.

The relation between somatic growth and reproduction observed in this study can be summarized in the following hypothetical mechanism of energy allocation. We start with the life-history assumption that the allocation mechanism is moulded by natural selection to give an optimum body condition at the end of the growing period. This optimum body condition reflects the sum of two different components: 1) a minimum condition required to survive after spawning and 2) an optimum amount of energy available for reproduction

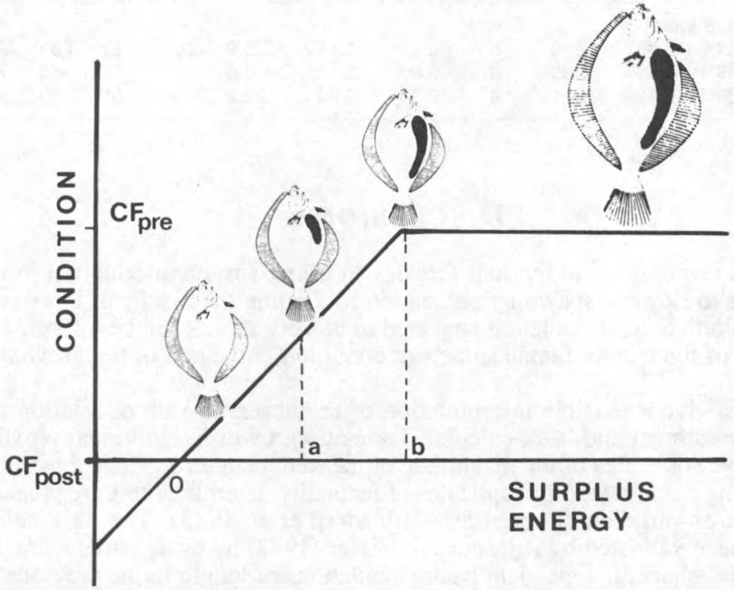

Fig 9. Hypothetical relation of pre-spawning condition, gonad growth and somatic growth of adult female plaice with surplus production (for explanation see text).

(egg-production and behaviour related to spawning). In evolutionary terms a trade-off is expected between the minimum post-spawning condition and the amount of energy available for reproduction. This will have resulted in different reproductive strategies depending on the available surplus production and the juvenile and adult mortality risks (Stearns & Crandall 1984; Ware 1982). The two reproductive strategies of a) priority to body maintenance over reproductive investment and b) priority to reproduction over body maintenance proposed by Tyler & Dunn (1976) might be viewed as the two extremes of a continuum.

If the physiological mechanism of a fish aims at this optimum body condition at the end of the growing period then surplus production will first be used for the building up of energy reserves. When surplus production is below some minimum level ($SP<\mathrm{a}$ in Fig.9) the fish may not reproduce at all and skip the spawning season. This energy reserve is necessary for metabolism during the winter period during which also immature plaice shows a reduced food intake (Chapter 1). When surplus production is insufficient to build up the body reserves necessary for normal reproduction ($\mathrm{a}<SP<\mathrm{b}$), reproductive output will be reduced to prevent post spawning condition falling below the minimum level required. When $\mathrm{SP}>\mathrm{b}$ the fish will be able to build up the necessary body reserves and will produce an amount of eggs proportional to its body size. Somatic growth will only occur when surplus production is above b. The corresponding relation of surplus production and the proportion allocated into reproduction (R) and somatic growth (G) is then: $R=0$ and $G=0$ when $SP<=\mathrm{a}$, $R=1$ and $G=0$ when $\mathrm{a}<SP<\mathrm{b}$, and R will decrease from 1 to the asymptote GSI (gonado-somatic index = gonad weight/body weight) and G will increase from 0 to the asymptote $1\text{-}GSI$ when $SP>\mathrm{b}$.

A simple physiological mechanism that can produce this response is illustrated in Fig.10. During the growing period a condition threshold indicates the state of the energy reserves and determines the partitioning of incoming surplus production. If the energy reserves are below the threshold the fish will allocate surplus energy into body reserves. If energy reserves exceed the threshold surplus energy will be allocated into somatic growth.

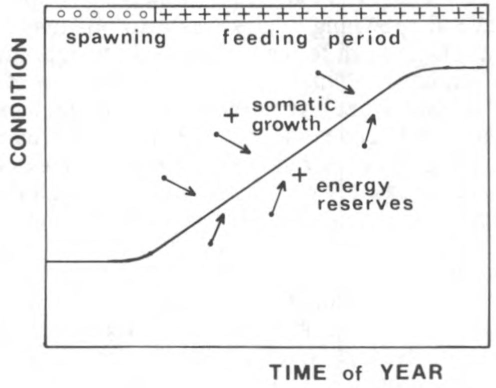

Fig 10. Hypothetical mechanism of energy allocation during the year. Incoming surplus production is channelled into somatic growth if body energy reserves are above the condition threshold and channelled into energy reserves if below the condition threshold.

This hypothetical mechanism may be a crude simplification. The wide variation observed in the present study suggests that the mechanism of energy allocation is rather imprecise. An important source of variation may be found in the variability in environmental conditions within the growing period of about 8 months. Poor conditions may be expected to result in a body condition below the threshold level. If this occurs early during the production period the fish might recover when conditions improve. A fish that has already spent energy on growth during the early part of the season when conditions were good may, if faced with poor conditions at the end of the growing period, show a lower reproductive investment and a lower size-specific fecundity. Hislop *et al.* (1978) showed that in haddock low rations at the end of the growing period substantially reduced fecundity.

The assumption of the present model that building up condition is given priority over somatic growth is supported by the observation in the tank experiment that the coefficient of variation in somatic growth (91%) was higher than in the increase in body condition (61%) of maturing females (maturity stage 2). Also, the annual somatic growth in recaptured fish showed a substantially larger coefficient of variation (40->100%) among individuals than gonad condition factor (30%)

Food ration has been shown to enhance fecundity in a number of experimental studies (Bagenal 1969; Wootton 1973; Waiwood 1982; Townshend & Wootton 1984; Springate *et al.* 1985; Horwood *et al.* 1989). Since these studies did not specifically address the question of energy allocation over reproduction and somatic growth the results can not be used as independent tests of the proposed mechanism still, they contain valuable indirect information indicating that although reproductive investment increased at high food rations, somatic growth was much stronger affected and was therefore more variable than fecundity or reproductive investment.

Horwood *et al.* (1989), studying the effects of ration level on fecundity in female plaice, found that size-specific fecundity was not or only slightly reduced in females upto a body size of 45 cm, but clearly reduced in two larger females (their Fig.3) and that gonad weight was 17% of total body weight at the high ration level and 10% at the low ration level. This suggest that poor feeding conditions can negatively affect reproductive investment mainly through a change in egg-weight.

Wootton (1977) in a nice experiment showed that female sticklebacks balanced somatic growth and reproduction to prevent serious depletion of body reserves. Fecundity per spawning was determined by female body size, but total egg-production during the spawning season increased with ration size due to increasing spawning frequency. The somatic growth over several spawning cycles was also positively correlated with food ration. If food ration was not enough to maintain a body weight after spawning at about 70% of the initial body weight, spawning ceased. Body condition of spawning stickleback females was not related to ration size. As in the proposed hypothesis, body condition of female sticklebacks thus varied between a post-spawning minimum and a pre-spawning maximum, neither of which is related to ration size. Although sticklebacks do not normally survive for a second breeding season, they may be viewed as iteroparous fish with several cycles of feeding and spawning within one year. The only difference compared with an iteroparous fish such as plaice is that the period of the spawning cycles varies and is adjusted to the food conditions, whereas in plaice the period is constant.

An important inference drawn from the hypothetical mechanism is that unfavourable conditions for surplus production will primarily affect somatic growth but will not, or only slightly, affect size-specific fecundity. Only the bigger females might represent an exception to this rule, because not only the proportion of surplus production allocated into reproduction increases with fish size, but also the annual variability of surplus production. Therefore, the chance for a fish not being capable of building up the necessary body reserves during the growing period will increase with fish size. This might explain the apparent decrease in the pre-spawning body and gonad condition factor in large plaice and might also offer an explanation for the "jellied" condition of flatfish in the west Atlantic, which increases with fish size (Templeman & Andrews 1959). In these waters sea temperatures are much lower than in the North Sea, where "jellied" plaice are not observed. These lower temperatures may result in a more variable surplus production among individuals. Roff (1983) explained this "jellying" from the assumption that energy expense for reproduction exceeded the incoming surplus energy. The hypothetical mechanism of energy allocation proposed in the present paper is complementary to the model of Roff (1983), who aimed at a simple model to explore the effect of the pattern of allocation on the fitness.

The present thesis would imply that density dependent fecundity is mainly to be expected in populations dominated by relatively large and old fish. In exploited populations with a high mortality rate intra-specific competition is more likely to result in density dependent growth and only secondarily in density dependent fecundity.

With regard to the question of environmental and genetical factors governing changes in size-specific fecundity, we expect that a change in the genetical basis of reproductive investment will give an increasing trend in fecundity in time. Annual variations in fecundity that do not show a trend in time are likely to reflect annual variations in surplus production. Only a substantial increase in fecundity that exceeds the undirected annual variability may indicate genetical changes. The plaice fecundity studies of Bagenal (1973), Rijnsdorp *et al.* (1983) and Horwood *et al.* (1986) showed that the coefficient of variation of adjusted fecundity did not exceed 15%, although individual years could differ by about 40%. The substantial increase of 60% in adjusted fecundity, which was reported by Rijnsdorp *et al.* (1983) and Horwood *et al.* (1986), thus can be interpret as an indication of a genetical change. However, because doubts were raised about the comparability of the methods used in the fecundity determinations, a final conclusion has to await a critical test of the methods used in the fecundity studies.

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Part IV - SYNTHESIS

Chapter 8

Intensive exploitation and changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. : disentangling phenotypic and genetic effects

Rijnsdorp, A.D. Intensive exploitation and changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. : disentangling phenotypic and genetic effects. - Submitted.

ABSTRACT. This paper attempts to interpret the observed changes in reproductive strategy of North Sea plaice since 1900 in the light of a possible genetical selection exerted by the fisheries. The approach adopted is to study the effects of variations in growth rate on the variability in maturation and reproduction in order to disentangle phenotypic plasticity and genetic effects. Simulation of the genetical selection by the fisheries predicts a decrease in the length at first maturity and an increase in the reproductive investment. No convincing evidence for a change in the latter was observed, but the changes in fecundity that occurred since 1900 indicate a trade-off between numbers and size of eggs in relation to the density-dependent growth of adult females. The length of first sexual maturity (L_{mat}) decreased in both male and female plaice since 1900. Analysis of the variability in the onset of maturation in relation to juvenile growth rate and temperature suggested that the decrease in L_{mat} could be partly explained (<25%) by phenotypic plasticity in response to the increase in growth rate during the juvenile phase and partly by a difference in water temperature (<18%). The observed decrease in L_{mat} supports the hypothesis that fishing has caused a genetical change in the L_{mat}, although an unequivocal interpretation is not possible since there remain a number of uncertainties in the quantitative analysis of 1) the selection differentials exerted by the fisheries, and 2) the phenotypic plasticity in maturation. Implications for fisheries management of genetical selection for a reduced L_{mat} are explored. It is shown that continuation of the current level of exploitation may result in a 5% decrease in the equilibrium yield and a 15% increase in spawning stock biomass.

INTRODUCTION

Plaice has been a commercially important fish species in the North Sea for more than a century and its biology has been studied intensively since the late 19th century (Heincke 1913; Masterman 1914; Wimpenny 1953; Bannister 1978). Reproductive and growth parameters of North Sea plaice have changed considerably since 1900 and the question was raised as to whether these changes could be related to the selective effects of exploitation, or to phenotypic plasticity in response to environmental changes, in particular in the conditions for growth (Rijnsdorp *et al.*1983).

Teleosts are well known for their large phenotypic plasticity (Purdom 1974, 1979; Stearns & Crandall 1984). Exploitation may lead to an increase in growth rate due to the reduction of population size. Reproductive parameters, such as length and age at first sexual maturity and reproductive investment, may be expected to change in response to changes in the conditions for growth, since reproduction is intimately linked to the process of acquisition and allocation of energy (Jones 1976; Roff 1983; Rothschild 1986; Stearns & Koella 1986; Chapter 1). On the other hand one might expect that exploitation cause genetical selection, because it reduces the life span and thus the total life-time reproductive output of individual fish. Genotypes coding for an increased reproductive investment due to high fecundity or to early maturation, will have a selective advantage over genotypes coding for low fecundity or delayed maturation (Nelson & Soulé 1987; Law & Rowell in prep; Rowell in prep; Chapter 2).

Direct avenues to the study of genetical changes, that may have occurred in the plaice population over a century of exploitation, are not available. An indirect approach, however, may be envisaged. The indirect approach adopted in this study is to focus on the phenotypic variability in reproductive parameters in response to variations in growth rate. Once the phenotypic plasticity is known, the phenotypic response can be predicted from the observed changes in growth and compared to the observed changes in reproductive parameters. This indirect approach explicitly assumes that the observed changes in reproductive parameters are due to changes in growth conditions. If the observed changes do not correspond with the predicted response given the observed change in growth a genetical explanation is likely. A final proof is not possible since changes in other environmental factors may always be suggested to have caused the observed changes in reproductive parameters. A prerequisite of this approach is that the observed variability in reproductive parameters is mainly due to variability in environmental conditions. Although no estimates of the heritability of reproductive parameters of plaice are available, comparative work in teleosts has shown that about 24% of the phenotypic variability in life history parameters is due to genetical and 76% to environmental variability, thus fulfilling our prerequisite (Roff 1991).

Reproductive parameters studied are the onset of sexual maturity, characterised by length (L_{mat}) and age at first maturity (A_{mat}), and reproductive investment. In females, reproductive investment can be estimated as the number of eggs (fecundity) or ovary weight, but the estimation of reproductive investment in males is more difficult. The study has therefore mainly focused on females.

Various aspects of this central theme have been dealt with in separate papers (Rijnsdorp *et al.* 1983; Chapters 1 to 7). The present paper is aimed at a synthesis of the detailed results. Firstly, it considers the theoretical framework within which phenotypic plasticity in reproductive parameters was studied in relation to changes in somatic growth. Secondly, the available information on changes in growth, maturation and reproductive investment is reviewed in the light of phenotypic plasticity. Thirdly, the selection imposed by the fisheries will be discussed and the predicted changes are compared to the observed ones. Finally, some implications for fisheries management will be discussed.

CONCEPT

Surplus energy allocation

Somatic growth and reproduction of an organism are intimately linked to the process of energy acquisition and allocation. During the growing period, the energy ingested will be partly metabolized and partly accumulated in the body as protein and lipids. Part of the accumulated energy will be used for metabolism particularly during the spawning period when plaice do not feed. On an annual basis the accumulated energy, corrected for metabolic losses, determines the available energy for somatic growth and reproduction. This energy is further called 'surplus production' (Ware 1982; Roff 1983). The surplus production (SP_x), will be determined by physiological characteristics of the fish (growth capacity) and by environmental factors, such as food availability and temperature conditions. A simple representation of surplus production is given by a continuously increasing function of body size which gives a reasonable, though not a perfect, fit to the observations (Chapter 2):

$$SP_x = \alpha W_x{}^{\beta} \tag{1}$$

The reproductive investment at age x (m_x) can be described by

$$m_x = 0 \qquad \text{for } W_x < W_{mat} \tag{2a}$$

$$m_x = \gamma W_x{}^{\delta} \qquad \text{for } W_x >= W_{mat} \tag{2b}$$

with W_{mat} indicating the body size at first maturity. The change in weight between age x and age $x+1$ can be expressed as

$$W_{x+1} - W_x = SP_x - m_x \tag{3}$$

This model describes an inverse relationship between reproduction and somatic growth. The interaction of surplus production, maturation and fecundity can be simulated to show the expected effects of changes in reproductive investment on somatic growth. Parameter estimates of this model are given in Chapter 2. Here it suffice to illustrate the qualitative behaviour of the model. Fig.1 illustrates the surplus production curve of female plaice and the line determining the allocation over somatic growth and reproduction. Reproduction commences at size W_{mat}. The slope of the reproduction line that determines the relationship between reproductive investment and body size is taken as a fixed proportion of body

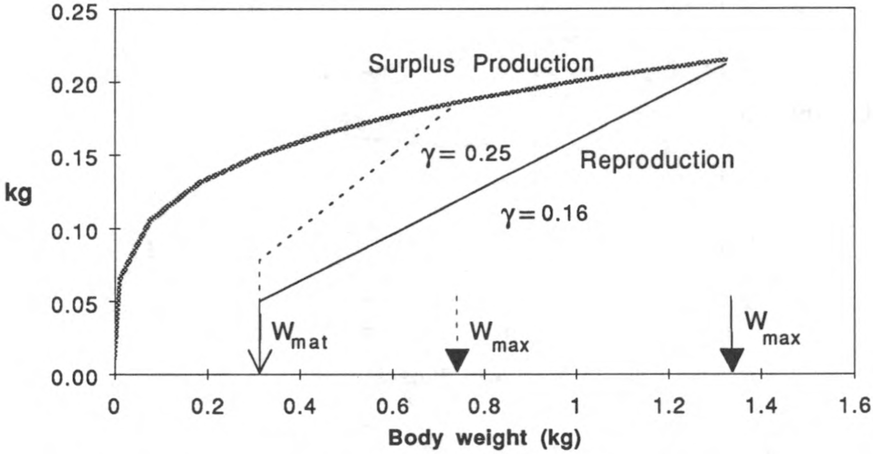


Figure 1. Relationships between surplus production, reproductive investment and body size. Maximum body size is determined by the level of surplus production and the reproductive investment (γ).

weight (γ=0.16; δ=1). The point where reproductive investment equals surplus production determines the maximum body size (W_{max}). Fig.1 also shows that if reproductive investment is increased (γ=0.25) the surplus production line will be cut off at a smaller ultimate body size W_{max} and lead to a decrease in somatic growth. A decrease in the size at first maturity will reduce the energy available for somatic growth, but the effect is restricted to the size range between the original and the new length at first maturity. Therefore, W_{max} would not be affected by a change in the size at first maturity. A change in the surplus production will affect somatic growth and W_{max} but not the size-specific reproductive investment.

Phenotypic plasticity

A phenotype is the result of the interaction between the genotype and the environment during the ontogeny of the individual. Given one genotype, a range of different phenotypes can develop under a range of different environmental conditions. A large scope for phenotypic plasticity may itself be adaptive, since it offers the genotype an optimal response over a wide range of environmental conditions (Stearns 1982; Stearns & Koella 1986). The relation between the genotype and the phenotype is given by the norm of reaction. This reaction norm represents the function that translates the genotype into a phenotype given certain environmental conditions. Surplus production is determined by environmental conditions and physiological characteristics of the organism and may itself be under selection by the fisheries (Ricker 1981; Nelson & Soulé 1987).

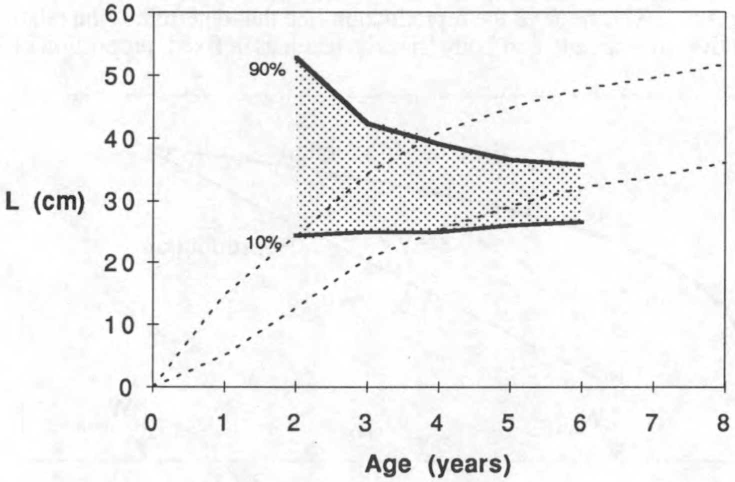


Figure.2. Maturation envelope of female plaice that encompasses the lengths-at-age at which 10% (lower limit) and 90% (upper limit) of the females have become mature. The dashed lines indicate the upper and lower limits of the somatic growth presently observed. The maturation envelope encompasses the population of reaction norms for maturation of the present female population under thepresent environmental conditions.

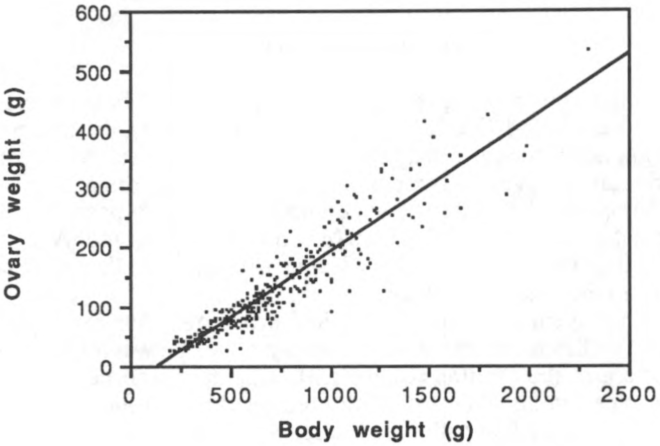


Figure 3. Scatter plot of ovary weights against body weight indicating and the average reaction norm for reproductive investment (linear regression).

The onset of sexual maturity in Fig.1 was characterised by a particular threshold size. However, sexual maturation is a developmental process and both length and age at first maturity may be influenced by environmental conditions. Therefore, the juvenile-adult transition, like any other developmental process, can be described by an envelope in the length-age space, encompassing the sizes of first maturation of individuals of a single genotype raised at different environmental conditions (MacKenzie *et al.* 1983; Policansky 1982, 1983; Chambers & Leggett 1987, 1992). For annually reproducing species like plaice, the X-axis is in discrete units of one year. For a population of different genotypes, the envelope will represent the population of individual reaction norms. Fig.2 shows the maturation envelope of female plaice, representing the phenotypic expression of the genotypes in the present population as they developed under the present environmental conditions (Chapter 6). The maturation envelope (heavy lines) was constructed by estimating the length at which 10%, respectively 90% of a particular age group had become mature. The dashed lines in Fig.2 show the upper (90%) and lower (10%) limit of growth that have been observed in recent years. Parts of the envelope outside the limits of growth were extrapolated from the age-specific maturity ogives.

Reproductive investment can be expressed either as ovary weight, number of eggs (fecundity) or energy loss during spawning. Fig.3 shows the scatter plot of ovary weight against body size as observed in the southern North Sea between 1982 and 1988. The data encompass the population of individual reaction norms realized within the population of female plaice in recent years. The shape of individual reaction norms for reproductive investment are unknown, since only single observations of individual fish can be made. However, the average reaction norm of the population can be estimated by the regression of ovary weight against body size shown in Fig.3.

PHENOTYPIC PLASTICITY AND OBSERVED CHANGES IN GROWTH, MATURATION AND REPRODUCTIVE INVESTMENT

Somatic Growth

Although changes in somatic growth of female plaice have been reported by various authors (reviews in Bannister 1978; Rijnsdorp & van Beek 1991), the interpretation of the data remains complicated. Samples may not always be representative because the mean length of a particular age group increases with increasing distance from the coast (Heincke's law; Wimpenny 1953). Other uncertainties are due to possible inconsistencies in the age determinations of different authors over a long time period. Also, the estimated mean length-at-age may be affected by size-selective mortality and thus the true growth rate may be different from the observed values.

In order to circumvent such methodological problems, changes in somatic growth were reconstructed for different size classes of female plaice between 1930 and 1985 based on the growth pattern in the otoliths (Chapter 3). This approach has the advantage that representative samples can be taken from fully recruited age groups collected during the reproduction period when the fish gather on the spawning grounds.

Fig. 4, that summarizes the results, shows a decrease in growth of the larger size classes between 1940-1949 and an increase in growth of the smaller size-classes starting in the 1950s. The growth potential of fish is generally related to the ambient sea temperature during the main growing period which for plaice runs from April to October (second and third quarter). Fig. 5 shows the average sea water temperature during the second and third quarter by year at a coastal station in the southern North Sea near Texel (van der Hoeven 1982), which may be considered representative for the temperature conditions experienced by juvenile plaice in the southern North Sea. Five year average values are shown by the heavy line, except for the period 1940-1949 for which two year averages are given to facilitate the comparison with the growth data of Fig.4.

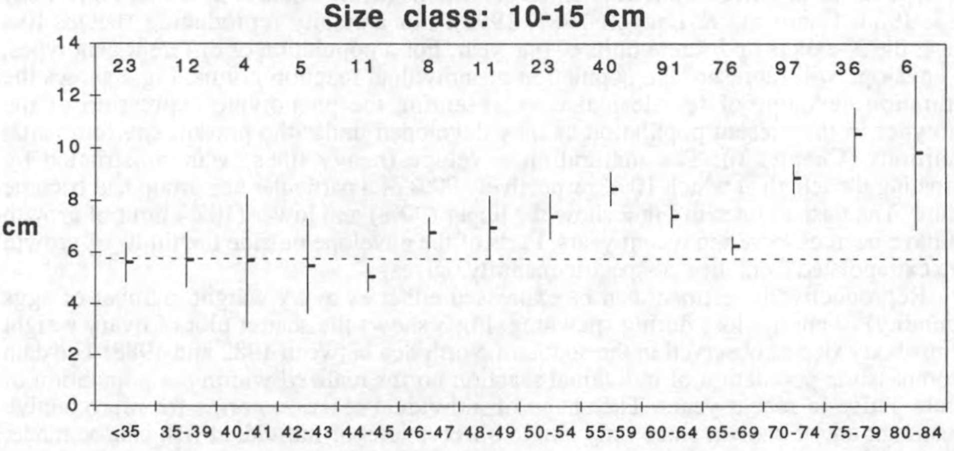


Fig.4. Changes in somatic growth of different size classes of female plaice between 1930 and 1985 as obtained by back-calculation of otoliths. The dashed line indicates the average growth before 1940. The period 1940-1949 is divided in 2-year sub-periods. The bars indicate 2xSE The numbers in top indicate the number of observations (from Chapter 3).

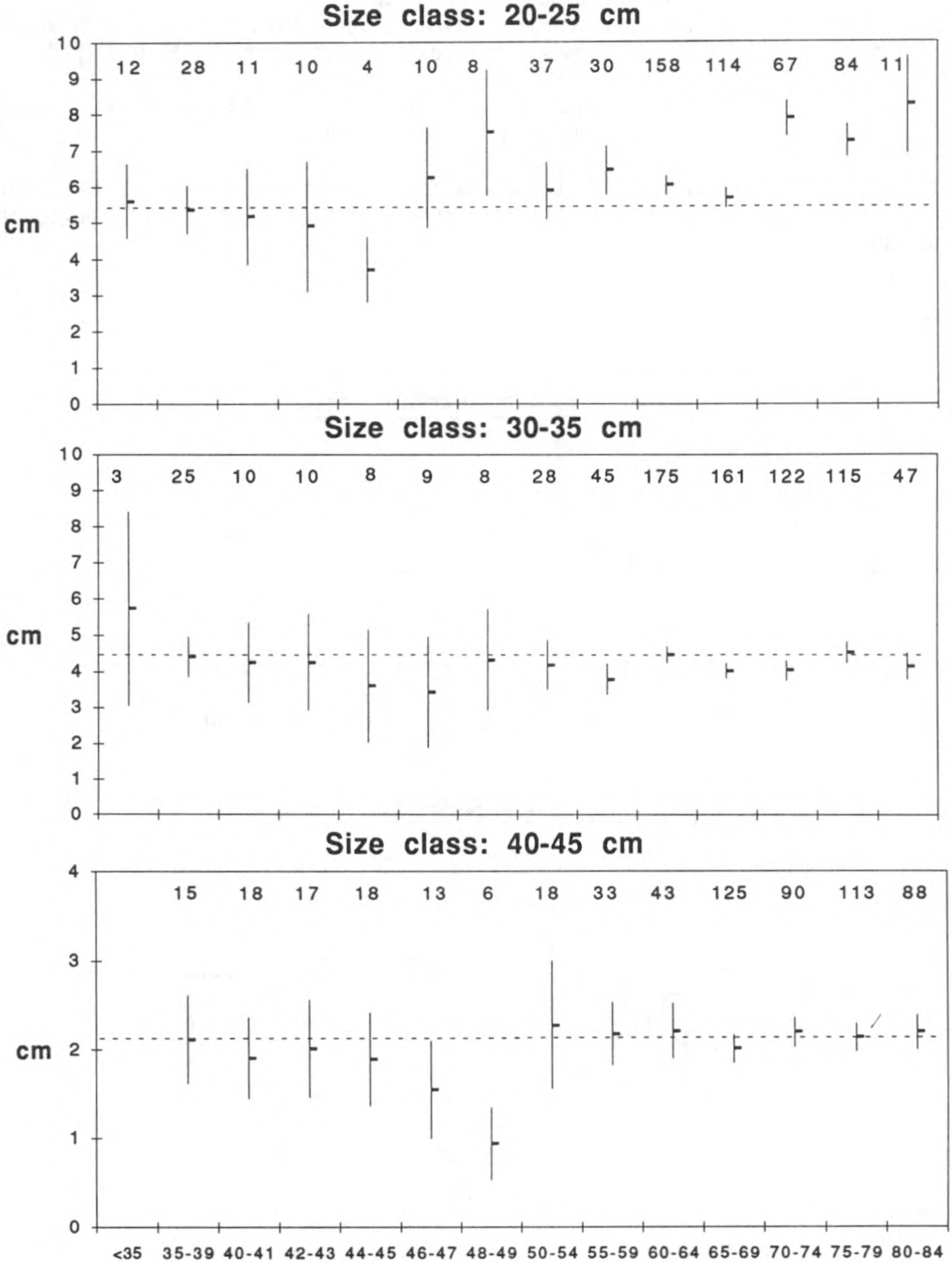
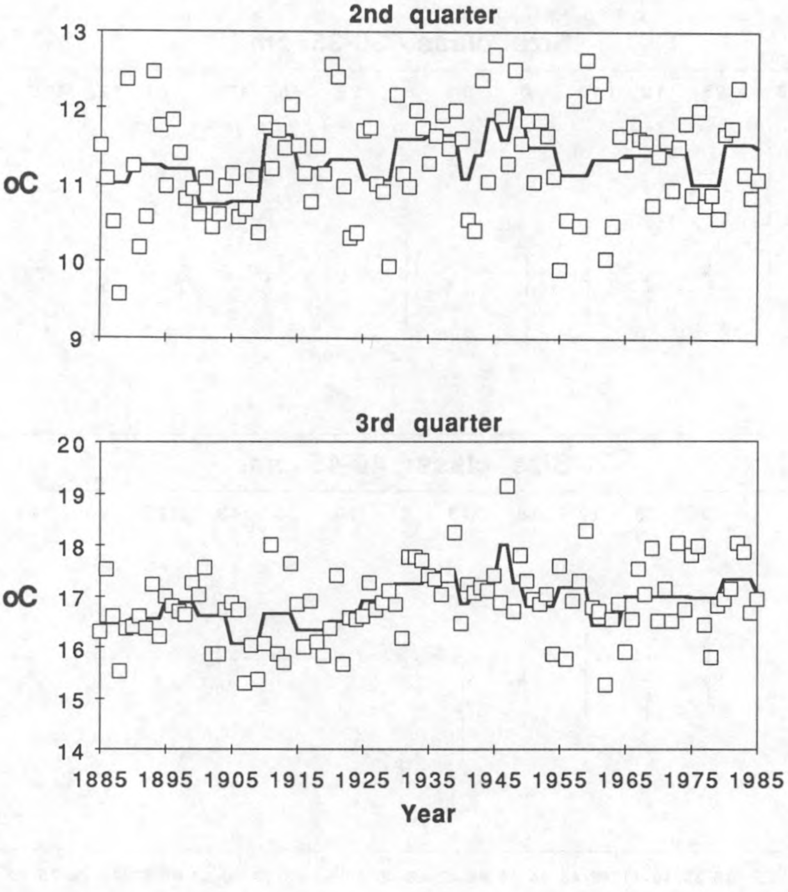


Fig.4 continued. Changes in somatic growth between 1930 and 1985 as obtained by back-calculation of otoliths The dashed line indicates the average growth before 1940. The period 1940-1949 is divided in 2-year sub-periods. The bars indicate 2xSE. The numbers in top indicate the number of observations (from Chapter 3)..

Although there is a clear indication of a relatively cold period between 1900 - 1910 and a warm period between 1935-1950, especially in the third quarter, it is quite obvious that between 1930 and the present water temperatures have fluctuated without a clear trend and cannot be related to the observed growth changes (Chapter 3; see also Rijnsdorp & van Beek 1991).

No time series of sea temperatures is available for the area in which the adult plaice are distributed. Adult plaice are distributed in the central North Sea during the major part of the feeding period (Rijnsdorp & van Beek 1991). Since this area is characterized by a stratified water column and relatively stable temperature conditions (Tomczak & Goedecke 1962, 1964), it is unlikely that adult plaice will have experienced major changes in temperature.


2nd quarter

3rd quarter

Figure 5. Time series of the average surface water temperature on the coastal nursery ground in the Southern Bight of the North Sea in the second and third quarter. The thick line indicates the 5-year average (2-year average in the period 1940-1949).

The observed changes in both adults and juveniles appear to be related to density-dependent effects. Adults (size classes >=30 cm) showed a reduced growth during the period 1940-1949, concurrently with a threefold increase in stock abundance due to the reduced fishing effort in the southern North Sea (Baerends 1947; Jenssen 1947; Margetts & Holt 1947; Beverton & Holt 1957; Simpson 1959), while juvenile growth was reduced between 1965 and 1969, when the strong year class 1963 entered the population and competitive biomass tripled (Rijnsdorp & van Beek 1991). Throughout the study period, juvenile growth rate, back-calculated at 3-8 cm for size class 20-30 cm, was lower than might be expected from the growth of tagged plaice. Tagged females of 20-30 cm, which had been transplanted from the coastal nursery areas to the shallow Doggerbank in the central North Sea where small plaice are absent, showed growth rates of about 12-14 cm per year, compared to the 4-5 cm observed on the coastal nursery grounds during the same period (Borley 1916). The cumulative growth of the transplanted plaice (12-14 cm) corresponds closely to the maximum growth rates observed in laboratory experiments (Fonds *et al.* 1992; Chapter 3). The growth on the coastal nursery grounds indicated by the tagging experiments (4-5 cm) comes close to the growth rate prior to 1940 (5 cm) estimated by back-calculation of otoliths (Fig.4).

Fig.4 further indicates that the growth rate of the smaller size classes (<30 cm) increased since the 1950s, whereas growth rates of the larger size classes remained the same. However, the timing is different between size classes. An increase is first observed in size classes <20 cm since 1955 followed by an increase in the 20-30 cm plaice since 1970. The increased growth of juvenile plaice since the 1950s, which was also reflected in the mean length of 4-year old females during the spawning period, was not related to sea temperature nor to the density of juvenile plaice, but coincided with an increase in anthropogenic influences such as eutrophication, pollution and disturbance of the sea-bed by beam trawling (Rijnsdorp & van Beek 1991). These anthropogenic influences were most pronounced in the coastal areas of the southern and southeastern North Sea which represent the main area of distribution of the size classes that showed increased growth rates. A similar increase in growth was observed in the sole, *Solea solea* (L.), a flatfish species that also inhabits the shallow waters in the southern North Sea. These observations led Rijnsdorp & van Beek (1991) to the conclusion that the increase in growth rate is most probably related to an increased food availability. However, the possibility of genetical selection on growth rate should not be a priori rejected.

If we assume that genetical selection will primarily seize upon surplus production, somatic growth would only be affected indirectly. Although direct estimates of changes in surplus production since 1930 are not available, inferences have to be made from the observed changes in somatic growth. However, because changes in size at first maturity or in reproductive investment will affect somatic growth at constant surplus production, there is a one to one relationship between somatic growth and surplus production only in juvenile fish. It will be shown below that the size at first maturity has decreased by 3 - 6 cm to 30-35 cm since 1900, whereas reproductive investment remained the same. As the change in size at maturity was restricted to the size range 30 - 40 cm, somatic growth outside this range will directly reflect levels of surplus production.

Based on the changes in somatic growth (Fig.4), it can be inferred that the level of surplus production has increased since the 1950s for the size classes <30 cm, but remained the same for adult plaice >40 cm. The question now is whether the increase in juvenile growth could be due to a genetical selection for higher surplus production by the fisheries? There are three reasons why this explanation is less likely. Firstly, the increase in growth occurred over a short time period of about 20 years, corresponding with about four generations of males and less than three generations of females (Chapter 2). Secondly, the growth rate observed in the early 20th century in the transplantation experiments showed a close agreement with maximum growth rates observed in the laboratory (Borley 1916; Chapter 3). Thirdly, if there has been genetical selection for surplus production, one might expect similar trends in both the juvenile and adult phase, whereas the data indicate only juvenile growth has been affected.

CONCLUSION: the available evidence suggests that the changes in somatic growth observed during this century are related to density dependent effects in combination with possible increases in the food availability due to anthropogenic factors, but not to a genetical selection for surplus production among the available genotypes.

Maturation

A decrease in L_{mat} and A_{mat} between 1900 and 1985 have been reported for both males and females in all areas in the North Sea: in males by 10-13 cm and 3 years, respectively; in females by 4-8 cm and 2 years, respectively (Chapter 4).

For female plaice, the changes in length and age at first maturity can be studied into more detail by comparing the maturation envelope for the beginning of the century with the envelope for recent years (Fig.6), using data from the southern North Sea (area DWK and OG, see Chapter 4). The historic envelope is based on an ANCOVA of the maturity data collected between 1903 -1911 by Wallace (1909, 1914). Although the envelopes show some overlap, the recent envelope has clearly shifted to smaller sizes and present maturity occurs at a younger age. The difference in L_{mat} range between 8 cm at age IV to 4 cm at age V and VI. The shape of the envelopes is similar.

The question whether the observed change in juvenile growth may be responsible for the change in the position of the envelope was addressed by analysing maturity data of individual females in relation with the growth history obtained by back-calculation of otoliths (Chapter 6). The effect of different growth rates during previous years of life on the probability of maturation were quantified by fitting a general linearized regression model (GLM) through maturity data of individual females with ultimate size and relative growth rate during three previous years as explanatory variables. The relative growth rate

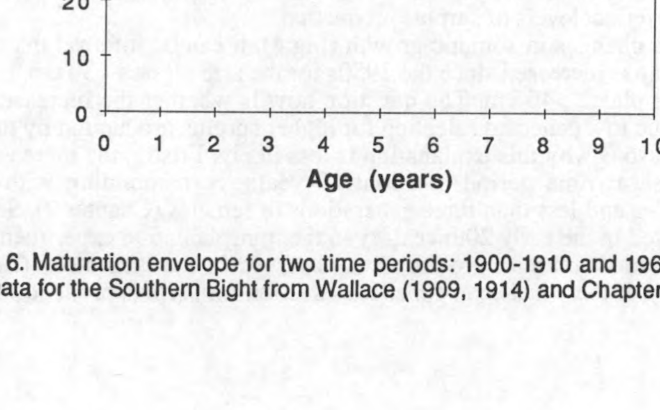


Figure 6. Maturation envelope for two time periods: 1900-1910 and 1960-1990. Data for the Southern Bight from Wallace (1909, 1914) and Chapter 6.

was calculated as the residual from the linear regression of successive length at age determined from otolith samples taken between 1963 and 1985. Table 1 reproduces the parameter estimates of this GLM model, which allows us to estimate the L_{mat} from growth curves. It was found that L_{mat} is affected by the ultimate length reached as well as by the growth rate back to three years prior to sampling (Chapter 6).

Changes in growth rate during the century were approximated by the mean length-at-age back-calculated from two sets of otoliths from females born before 1935 and born between 1970 and 1979. From these length-at-age data relative growth rates were calculated using the regression equation mentioned above (Table 2). Comparison of the length-at-age for the two time periods shows that the cumulative effect of the increased growth rate is substantial. From the relative growth rates during three years prior to sampling, and the parameter estimates of the GLM model from Table 1, the L_{mat} was

Table 1. Parameter estimates of the regression GLM model of the logit maturity probability as a function of ultimate length (L) and relative growth rate in three previous years (G-1, G-2, G-3): logit $Y = \alpha + \beta L + \gamma G\text{-}1 + \delta G\text{-}2 + \varepsilon G\text{-}3$. (from Chapter 3)

α	-8.244
β	0.2698
γ	-0.2406
δ	0.0374
ε	0.1141

Table 2. Back-calculated lengths at age I - VI (Li) of female plaice sampled in the southern North Sea of year classes born before 1935 and year classes born between 1970 and 1979 and the relative growth (Gi) compared to the standard linear regression of $L_{i+1} = 10.8 + 0.82\,L_i$ (from Chapter 3)

	<1935		1970-1979	
Age (i)	L_i (cm)	G_{i-1} (cm)	L_i (cm)	G_{i-1} (cm)
I	7.1	-1.2	8.6	+0.3
II	13.7	-2.9	20.1	+2.2
III	19.3	-2.7	28.5	+1.2
IV	24.7	-1.9	34.1	-0.1
V	29.5	-1.6	38.2	-0.6
VI	34.3	-0.7	41.2	-0.9

Table 3. The predicted L_{mat} values of the year classes <1935 and 1970-1979 according to the parameter estimates of the GLM model (Table 1) and the relative growth rates of (Table 2).

	Age	L_{mat} (cm)	95% C.L.
1935	IV	30.4	30.0-30.9
	V	30.6	30.2-30.8
	VI	31.0	30.7-31.2
1970-79	IV	29.4	28.9-29.8
	V	29.6	29.2-29.8
	VI	29.8	29.6-30.0

Table 4. The average L_{mat} in different parts of the North Sea and the approximate mean water temperatures by quarter in the coastal nursery grounds. L_{mat} from Chapter 4. Temperature data from Tomczak & Goedecke (1962).

		Temperature (°C)			
Area	L_{mat}	Q1	Q2	Q3	Q4
DWK	30	5.3	9.3	16.0	11.0
OG + DB	33	4.3	9.0	16.0	9.7
VB	33	3.3	7.3	15.0	9.3
FLAM	34	5.5	9.3	14.3	9.7

estimated for age groups IV, V and VI for the two periods. Table 3 shows that the estimated difference in L_{mat} between the historic and the recent period is about 1 cm for all age groups considered. This indicates that the growth change explains only 1 cm of the decrease in L_{mat} of 8 cm (13%) and 4 cm (25%) at age IV and at age V - VI, respectively (c.f. Fig.6).

This analysis is based on the assumption that the back-calculated growth rate of the year classes born before 1935 was representative for the period at the beginning of the century for which maturity - length data were available. This assumption is supported by the close correspondence between the back-calculated and the observed length increments in different data sets (Heincke 1907; Wallace 1914; Borley 1916; Chapter 3).

Since the change in growth rate explains less than 25% of the observed change in L_{mat}, other factors appear to be involved, of which we will consider temperature and genetical selection. According to Fig.5 the sea temperatures in summer around the turn of the century were about 1°C lower than in recent years. In Chapter 6 it was observed that L_{mat} increases with latitude and it was suggested that this spatial effect might be partly related with a geographical trend in temperature. Lower temperatures would thus lead to an increase in the length at first maturity. The temporal decrease in L_{mat} associated with increased sea temperatures on the nursery grounds would fit this hypothesis.

In an attempt to investigate the potential effect of temperature on L_{mat}, we studied the relation between L_{mat} of individual cohorts and the temperature on the nursery ground and the geographical differences in L_{mat} and temperature on the nursery grounds. Regression analysis of the L_{mat} of 4-year olds of individual cohorts (area DWK) and sea temperature on the coastal nursery grounds in the third quarter of the previous year showed a weak but significant negative relation (slope = -0.70, $r^2 = 0.146$, $n=30$, $P<0.05$), suggesting that a decrease in temperature of 1°C corresponds to a reduction in L_{mat} by 0.7 cm (Chapter 6). The correlations between L_{mat} and temperature in the other quarters were all highly insignificant.

Table 4 shows the differences in L_{mat} within the North Sea. The quantitative analysis of these geographical differences in L_{mat} in relation with sea temperature is complicated since this analysis should take account of the origin of plaice on the different spawning areas as well as of the seasonal cycle of water temperature experienced by plaice during their juvenile phase. A recent analysis of tagging experiments of juvenile plaice showed that the Southern Bight spawning group (area DWK) was dominated by recruits from the Dutch coast and western Wadden Sea; the German Bight spawning group from the German Bight nursery grounds; the area east of the Dogger Bank (area VB) from the nursery grounds along the Danish coast and Flamborough (area FLAM) from the Wash on the English east coast (ICES 1992). Ambient water temperatures, however, are much more difficult to infer. Besides our ignorance about the critical time period during the juvenile phase in which water temperature affects maturation, the substantial differences in temperature that occur over relative short distances (Tomczak & Goedecke 1962) emphasize the need for detailed information on the spatial distribution of plaice to estimate the temperature cycle of plaice during the juvenile phase. The approximate water temperatures given in Table 4, therefore serve as a necessarily crude and preliminary indication that the differences in temperature experienced by juvenile plaice in different parts of the North Sea is probably less than 2°C.

The 4-cm decrease in L_{mat} of age group V and VI, as observed between the periods 1903-1911 and 1960-1985, coincided with a temperature increase of about 1°C in the third quarter (Fig.5). The analysis of L_{mat} of individual cohorts indicates that a temperature increase of 1°C may reduce L_{mat} by about 0.7 cm. This reduction appears low compared to the geographical difference of up to 5 cm and differences in water temperatures of less than 2°C (Table 4).

Given these considerations, the effect of the temperature difference between 1903-1911 and 1960-1990 on the decrease in L_{mat} may be tentatively estimated at 0.7 cm. However, a firm quantitative assessment of the contribution of temperature differences to the decrease in L_{mat} is not possible because the precise temperature conditions experienced by juvenile plaice, as well as the critical time period during the juvenile phase, are not known.

Stearns & Koella (1986) analysed the expected shapes of reaction norms for maturation under various combinations of growth and mortality rates in the juvenile and adult phases. The trajectory observed in female plaice, indicating a fast decrease in L_{mat} at younger and a slower decline at older ages (Fig.2), corresponds to their L-shaped trajectory and in part also to their sigmoid trajectory (Fig.6 in Stearns & Koella 1986). These trajectories are characteristic when mortality is independent of growth rate, or when adult mortality is inversely proportional to growth rate, or when juvenile mortality increases slightly with decreasing growth rate. A completely different reaction norm would be expected if both juvenile and adult mortality rates are inversely proportional to growth rate or if growth rate has a large effect on juvenile mortality rate. The latter two conditions would yield a reaction norm in which size at maturation increases with age at maturation.

In plaice, it would seem likely that a decreased growth rate is associated with an increase in juvenile mortality, since size-selective predation mortality appears to be a predominant feature during the egg and early demersal phase (van der Veer & Bergman 1986; van der Veer *et al.* 1990; Rijnsdorp & Jaworski 1990; Hovenkamp 1991). Size-selective mortality might also occur during the later demersal stages, when mortality among the juveniles is still density dependent (Beverton & Iles 1992b). It is less likely that mortality rate in the adult phase will be a function of growth rate, since adults have outgrown most of their potential predators, although fishing mortality might be a size-selective. The observed and predicted shapes of reaction norms for maturation thus appear to be in agreement.

CONCLUSION: the evidence shows that L_{mat} and A_{mat} decreased substantially in males and females between 1900 and 1958-1990. For females it was shown that both an increase in juvenile growth and an increase in water temperature have contributed to the observed decrease in L_{mat}. The quantitative contribution of these two factors, which was estimated at 1.7 cm, was substantially smaller than the observed change (4-8 cm), suggesting that genetical selection for a reduced size at first maturity may also be involved. However, the contribution of genetical selection cannot be firmly inferred given uncertainties about the quantitative effects of temperature on maturation.

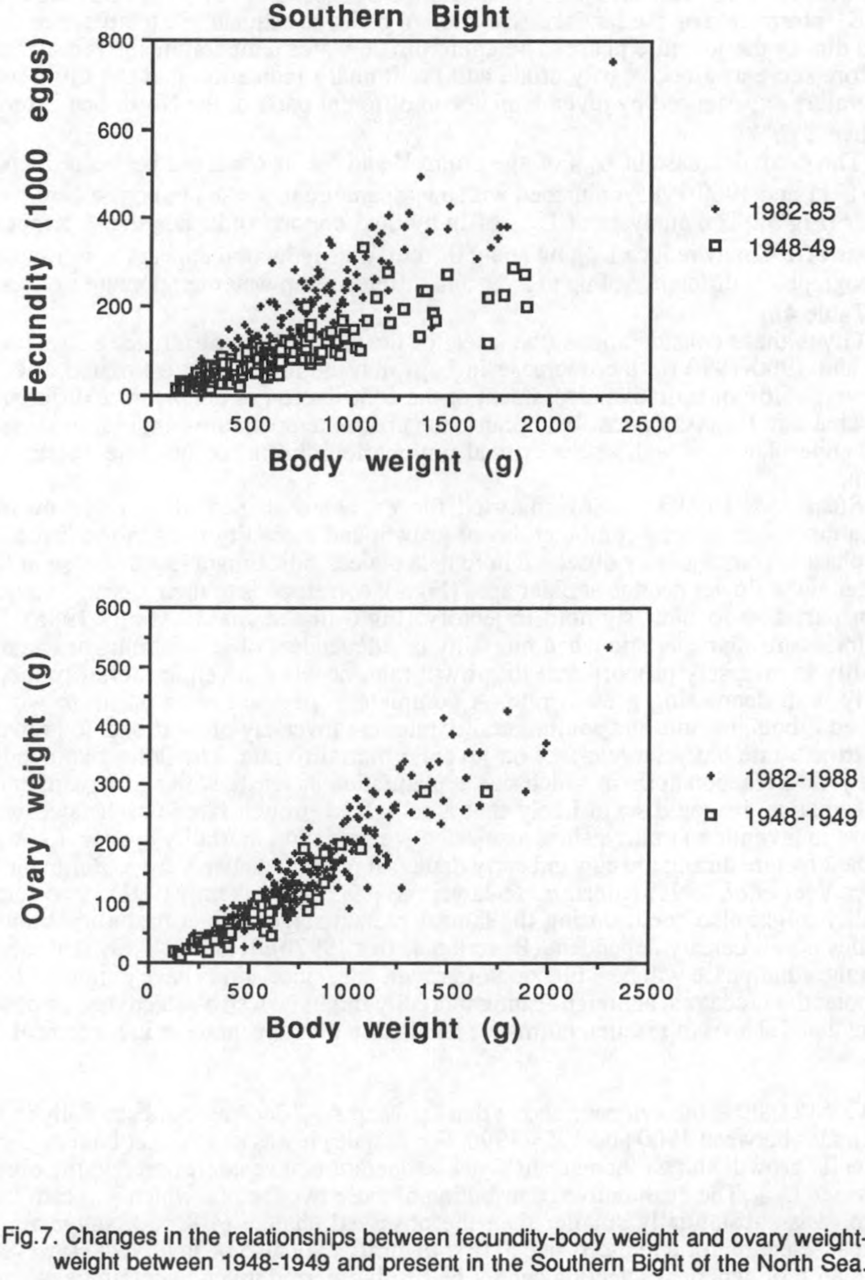


Fig.7. Changes in the relationships between fecundity-body weight and ovary weight-body weight between 1948-1949 and present in the Southern Bight of the North Sea.

Reproductive investment

Changes in fecundity and ovary weight between three periods since 1900 were reviewed in Chapter 5. Fecundity increased since the early 1900s and 1947-1949 (Table 5). In 30 cm females, the fecundity in recent years was about 30-100% higher compared to the first two periods, depending on the area in the North Sea. Fecundity of 50 cm females was similar to that in 1900, but was 30-60% higher than in 1947-1949. The substantial change in fecundity is in sharp contrast with the data on ovary weight, which suggest a much smaller change since 1947-1949 (Fig.7). This discrepancy suggests that there has been no change in the energy investment into reproduction, but in the allocation of available energy over a small number of large eggs versus a large number of small eggs.

In the southern North Sea, the scatter plots of individual ovary weights observed between 1982-1988 and between 1947-1949, show a substantial overlap. However, an analysis of variance indicated that the ovary weight - body length regression lines had similar slopes but significantly different intercepts. The ovary weight in 1947-1949 was on average 13% lower than in the recent period. In the western North Sea, the slopes differed significantly between both periods and differences between ovary weights were largest in large fish. Based on the estimates of the average somatic growth and the ovary weight - body length relationships for the southern North Sea, the surplus production - body size relationship for the two periods was calculated, indicating that reproductive investment has been relatively stable and has been only marginally affected by the change in the level of surplus production.

Further support for a relatively constant reproductive investment at different levels of surplus production has been provided by an analysis of fecundity or ovary weights of individual females in relation to the relative somatic growth in the penultimate year as estimated by back-calculation of otoliths. Females characterized by an above average somatic growth produced on average a similar number of eggs as females that had experienced a below average somatic growth (Chapter 7). A similar result has been obtained for sole (Millner *et al.* 1991). However, the variability between individual females was large and might have obscured a possible relationship. A weak but significant relationship has been observed between the average annual somatic growth in the population and the average pre-spawning condition factor, suggesting that a twofold increase in somatic growth would only result in a 2% increase in pre-spawning condition (Chapter 7).

Table 5. Predicted fecundity in thousand eggs for three size classes of plaice in three areas within the North Sea and three time period. The percentages indicate the percentage change from the historic period to the present period.

	30 cm		40 cm		50 cm	
German Bight						
1900-1910	33.6		104.8		252.8	
1977-1985	63.8	+90%	141.4	+35%	261.9	+4%
Southern Bight						
1947-1949	35.9		89.3		181.1	
1977-1985	72.8	+103%	159.8	+79%	294.0	+62%
Flamborough						
1947-1949	40.9		108.9		232.5	
1977-1985	51.7	+26%	137.6	+26%	293.8	+26%

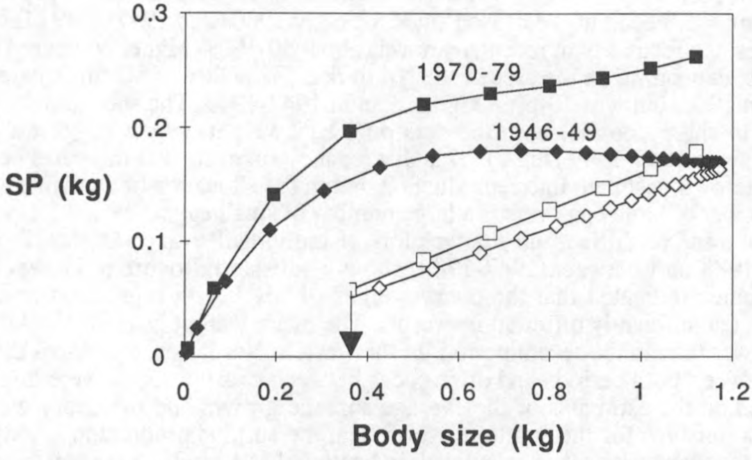


Figure.8. Comparison of the surplus production - body weight (full symbols) and reproduction - body weight relationships (open symbols) between two periods: 1946-1949 (diamonds) and 1970-1979 (squares). The arrow indicates the body weight at which the females became sexually mature.

The results of this descriptive field study suggests that reproductive investment in plaice is rather constant for large variations in surplus production. This conclusion appears to be in contrast with the results of various experimental studies in plaice (Horwood *et al.* 1989; Chapter 7) and other teleost species (Scott 1962; Bagenal 1969; Wootton 1973, 1977; Hislop *et al.* 1978; Waiwood 1982; Townshend & Wootton 1984; Springate *et al.* 1985; Knox *et al.* 1988; Kjesbu *et al.* 1992). Experiments with plaice showed that the development of the ovary was stopped at low food rations (Horwood *et al.* 1989; Chapter 7). At high food rations, fecundity was raised in some females but not in others. Females kept at a low ration early in the growing period and shifted to a higher ration in September did not develop their ovary, suggesting that a time window exists somewhere during the growing period when the decision to produce eggs during the next spawning period is made (Horwood *et al.* 1989; Horwood 1990). However, these experimental studies did not address the problem of energy allocation between reproduction and somatic growth in individual fish, and generally manipulated food ration only during part of the annual cycle. Since the temporal pattern of food availability appears to be an important factor causing individual variation in the energy allocation, this might explain part of the discrepancies between the different results.

The physiological mechanism that determines reproductive investment is a complicated one. Three types of oocytes can generally be recognized in ovaries representing cohorts that are assumed to mature in three successive years (Yamamoto 1956; Dunn & Tyler 1969; Hilge 1976; Burton & Idler 1984). Kjesbu *et al* (1992) suggested that in cod (*Gadus morhua*) at least three different mechanisms regulate fecundity: 1 - the number of previtellogenic oocytes entering the circum nuclear ring phase during the post-spawning period; 2- the increased production of previtellogenic oocytes in autumn that was closely related to the nutritional status; 3- the level of atresia during the spawning period in relation to feeding levels which led to a 20-80% reduction of the actual number of eggs in females deprived of food during spawning period. Mechanism 2 was also described for winter flounder (*Pseudopleuronectes platessa*) by Tyler & Dunn (1976) and might be responsible for the bimodal frequency distribution of oocyte diameters in autumn as observed in Irish Sea plaice by Horwood (1990). Levels of atresia in plaice have not been quantified in the sea, but appear to be low in tank experiments, even in females kept at low food rations (Horwood *et al.* 1989).

The experiments with plaice (Horwood *et al.* 1989) and cod (Kjesbu *et al.* 1992) clearly indicate that the timing of food availability may be an important factor causing variation in the allocation of energy and possibly also affect the energy allocation over a large number of small eggs or a small number of large eggs. A large phenotypic plasticity in the egg size - egg number relationship can be inferred from the comparison of the observed changes in fecundity and ovary weight. Experimental studies of the effect of food ration on the relation between egg numbers and egg size, have given very different results. Restriction of food ration before the spawning period resulted in a reduction of size-specific fecundity and lower egg weights (haddock, *Melanogrammus aeglefinus*, Hislop *et al.* 1978; rainbow trout, *Oncorhynchus mykiss*, Springate *et al.* 1985; Knox *et al.* 1988), a reduction of size-specific fecundity and constant egg weight (rainbow trout,Scott 1962; stickleback, *Gasterosteus aculeatus*, Wootton 1973, 1977), or a reduction in size-specific fecundity and increased egg weight (brown trout, *Salmo trutta*, Bagenal 1969). Work on rainbow trout by Ridelman *et al.* (1984) indicated that the duration and the timing of starvation prior to spawning indeed explained part of the differences in the trade-off between egg size and egg numbers.

The reduction in size-specific fecundity and constant size-specific ovary weight in the period 1947-1949 coincided with a substantial reduction in somatic growth (Fig.4) and surplus production (Fig.8) when the adult plaice stock in the southern North Sea tripled (Chapter 3). The plasticity in the trade-off between egg numbers and egg size in relation to density-dependent growth in the adult phase raises the question about the adaptive significance to produce fewer large eggs if adult growth rate is reduced at high adult biomass, although it cannot be ruled out that variation in egg size may be due to a constraint on the physiological mechanism to produce similar sized eggs in the relatively short spawning season.

The theory of egg size evolution predicts that the parental investment per egg is optimized and not the total number of eggs (Smith & Fretwell 1974; Winkler & Wallin 1987). McGinley *et al.* (1987) showed that environmental variability does not necessarily favour the production of a range of egg sizes. Most often, parental fitness is maximized by investing equally in all eggs. Only a large density-dependent fitness loss to eggs is a sufficient condition for variable egg sizes within one individual..

In many fish species egg sizes decrease in the course of the spawning period. This applies to subsequent batches spawned by individual females as well as to early spawners producing larger eggs than late spawners within the population (Bagenal 1971). This decrease in egg size is seen as an adaptation to the production cycle of the environment (Cushing 1975; Bagenal 1971). The large numbers of relatively small eggs produced by many fish species may be interpreted as a sampling strategy to find the scarce local patches of ample food (Rothschild 1986). Such hypotheses, however, do not offer an explanation why females should change their resource allocation to a smaller number of large eggs under conditions of density-dependent reduction in growth rate during the adult phase.

The success of an individual descendant will depend on its survival through the pelagic egg and larval phase, and survival through the demersal juvenile phase after successful settlement in a suitable nursery area. There is circumstantial evidence that mortality is size dependent during the egg and larval phase (Bailey 1984; van der Veer 1986; Bailey & Houde 1989; Rijnsdorp & Jaworski 1990; Hovenkamp 1991), which suggests an increase in fitness with egg size. However, the mortality in the pelagic phase appears to be density-independent (van der Veer *et al.* 1990) and as a consequence the number of surviving larvae will on average increase with the size of the spawning population. The adaptiveness of a relatively larger egg size when numbers are high may be sought in the supposed relatively higher competitive capability of larger descendants compared to smaller descendants. This should be most pronounced in the demersal habitat where post larval plaice settle in large numbers in the very localised tidal flats and shallow sandy bays (van der Veer *et al.* 1990). The trade-off between egg numbers and egg size, thus may be interpreted as a trade-off between the sampling of the habitat for salubrious feeding conditions of pelagic larvae (Rothshild 1986) and the competition for space between post-larval demersal juveniles (MacCall 1990). In periods of low adult biomass many small eggs and during periods of high adult biomass a small number of large eggs would be the optimal choice for the individual female to increase her reproductive success. This hypothesis implies that adult females use the adult competitive biomass as a proxy for the density-dependent processes in the juvenile phase.

CONCLUSION. The available evidence indicates that, despite the substantial differences in surplus production the relationship between reproductive investment and body size has remained remarkably stable since 1900, except for a perhaps small increase in plaice $<$ 40 cm. This increase, however, is uncertain because only fecundity data but no ovary weight data could compared between 1900 and present. The decrease in fecundity in 1947-1949 was not reflected in a similar change in ovary weight, indicating a trade-off between egg size and egg numbers in relation with density-dependent growth in the adult population.

SELECTION DIFFERENTIALS

The selection imposed by the fisheries on quantitative life history parameters such as length at first maturity and reproductive investment, can be predicted from the additional mortality due to fishing and the energy allocation over reproduction and somatic growth. The following account on selection differentials and the parameter estimates used in the calculations is based on Chapter 2.

The interaction between surplus production, maturation and reproduction was modelled according to equation 1. Fitness of a reproductive trait, taken as the combination of a reproductive investment (γ) and length at first maturity (L_{mat}), was calculated according to Fisher's reproductive value (Ricklefs 1979)

$$V_0 = \Sigma \lambda^{-x} l_x b_x \qquad (4)$$

where λ is the intrinsic rate of population increase, l_x is the survival to age x and b_x is the number of offspring born at age x. It is assumed that $\lambda = 1$ and b_x equals the reproductive investment m_x of equation 2. Survival was calculated according to

$$l_{x+1} = l_x \exp\{-(F_x + M_x)\} \qquad (5)$$

with F_x and M_x denoting the instantaneous rate of fishing and natural mortality respectively. Fig.9 shows that the relationship between F and age is flat-topped with a peak between ages II and V and that the level is higher in males than in females. In Chapter 2 evidence is presented for the natural mortality to decrease from $M_0 = 10.38$ during the first year of life (Beverton & Iles 1992a) to $M = 0.08$ (females) and $M = 0.14$ (males) for age group II - V (Beverton 1964), and is assumed to increase again in older plaice to reduce the life span to a realistic value of about 30 years (Fig.9).

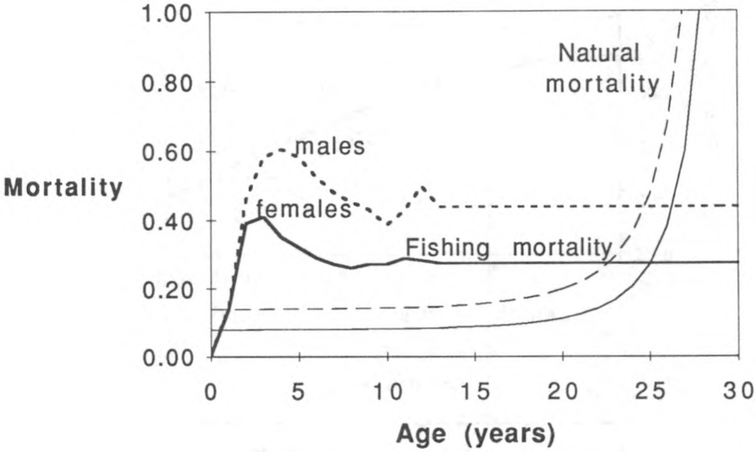


Figure.9. Instantaneous fishing (F) and natural mortality (M) coefficients in relation to age of male (dashed) and female (full line) plaice.

Fig.10 presents the fitness profiles for different combinations of length at first maturity and reproductive investment (γ), showing that under the current exploitation selection occurs for an increased reproductive investment and for a decrease in the length at first maturity.

These predictions can now be compared with the observed changes in reproductive investment and maturation. Contrary to the prediction, no evidence was obtained that reproductive investment changed since 1900, except perhaps for the increase in fecundity in smaller size groups since 1947-1949. One possible explanation for the lack of change in reproductive investment may be that morphology imposes a constraint on the maximum reproductive investment. Jones (1974) showed that the number of eggs per gram body weight varies substantially between flatfish species with a coefficient of variation CV=97% (range 142 - 4193 eggs.g^{-1}), while the volume of eggs per gram body weight is much less variable CV=20% (range 534 - 922 mm^3). This explanation, however, is only valid for females since gonad size in males is relatively small. Secondly, the simulation model only included a cost of reproduction in terms of a growth reduction but not in an increase in mortality rate. Although the latter is very difficult to measure, it is generally assumed in life history theory (Roff 1991; Reszcnik 1992). In plaice, a mortality cost is not unlikely since spawning causes a substantial reduction of the body condition of both males and females, which may make the fish more vulnerable for diseases and predation.

The direction of change in L_{mat} since 1900 agrees with the one predicted by the fitness simulation. The question now is whether there is also a quantitative agreement. From the fitness profiles a 'predicted' selection differential of L_{mat}, representing the average L_{mat} of the parents and that of the stock from which they were selected, can be assessed at $S_{pred} = 2.0$ cm and 0.3 cm for males and females, respectively (Chapter 2).

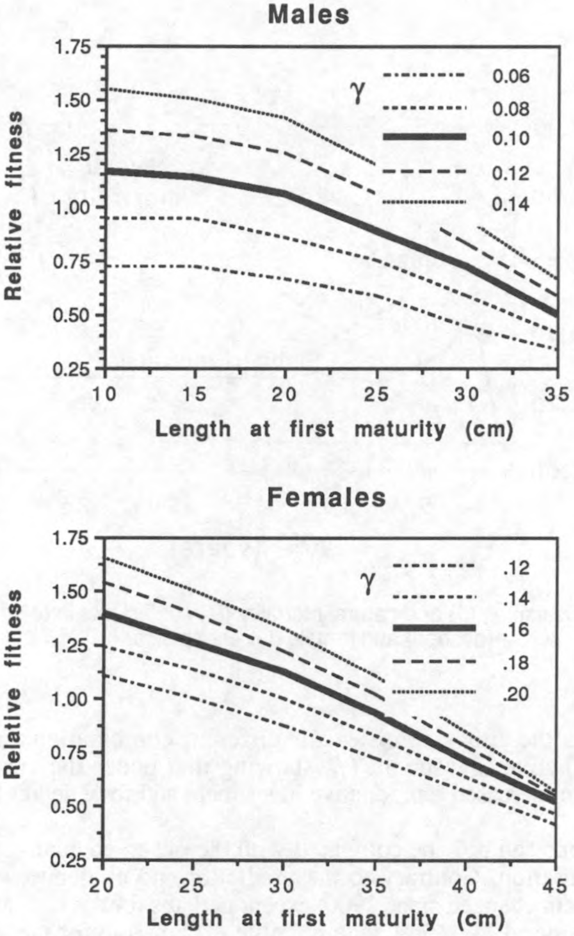


Figure.10. Fitness profiles for length at first maturity (L_{mat}) for different levels of reproductive investment (g) with λ=1.0. The fitness is expressed relative to the current reproductive strategy: males: L_{mat} = 22 cm, γ=0.10; females: L_{mat} = 33 cm, γ =0.16.

The 'observed' selection differential can be calculated from $S = h^{-2} R$, where R is the change in a quantitative trait per generation and h^2 is the heritability coefficient (Falconer 1989). At the current level of exploitation (Fig.9), which was assumed to be representative for the total period of exploitation since 1900, generation time was estimated at 4.8 and 7.7 years for males and females, respectively (Chapter 2). The data used in the calculation of the observed selection differentials are given in Table 6 and refer to the Southern Bight.

In females, the observed change in L_{mat} of age group V and VI was about 4 cm of which 1 cm could be ascribed to an increased growth rate and 0.7 cm to the difference in water temperature, leaving 2.3 cm of the change unexplained. The change in L_{mat} occurred over a period of 65 years (1910 - 1975) at an annual rate of 2.3/65=0.035 cm.year^{-1}, which equals to 7.7 x 0.035 = 0.27 cm per generation. Taking a mean heritability for life history traits of h^2 = 0.24 (Roff 1991), the 'observed' selection differential can be estimated at S_{obs} = 0.27/0.24 = 1.1 cm per generation.

In male plaice, L_{mat} decreased by 10 cm between 1910 and 1985 (Chapter 4), giving a decrease of 10/75=0.13 cm.year^{-1} and 0.13x4.8=0.64 cm per generation, and an 'observed' selection differential of S_{obs} = 0.64/0.24 = 2.7 cm per generation.

The 'predicted' selection differentials for female plaice were substantially smaller than 'observed' ones. This may be due to a number of uncertainties in the calculation of the predicted as well as of the observed selection differentials. Predicted selection differentials were based on fitness differences between different lengths at first maturity, assuming an exponential relation between surplus production and body size applying to the present as well as to the historic period. This relationship certainly did not give a perfect description of the average surplus production of female plaice at present (see Chapter 2) and did not take account of the changes in surplus production that occurred between 1910 and present.

Also, the predicted selection differential is sensitive for the variability in L_{mat}. S_{pred} will increase with variability in L_{mat}. This is illustrated by the larger S_{pred} for males which showed about the same slope in the fitness profiles between 20 and 30 cm as the females between 30 and 35 cm (Fig.10), but showed a standard deviation in L_{mat} of 5 cm compared to 2.5 cm in females. Further, if autosomal genes affect L_{mat}, selection on one sex will influence the other sex as well and different selection pressures on male and female may result in an average effect. The average 'observed' selection differential was S_{obs} = 1.9 cm compared to a predicted value of S_{pred} = 1.2 cm, neglecting differences in generation time and assuming an equal sex ratio.

Finally, the predicted selection differential is sensitive for the level of fishing mortality. If the fishing mortality prior to 1940 has been higher than the value of about F=0.5 and F=0.35 assumed in the calculation for males and females, respectively (Fig.9), the predicted selection differential will become higher due to a steeper slope of the fitness profiles and a reduced generation time. A higher fishing mortality (F=0.7) in the period 1928-1938 is indicated by the studies of Beverton and Holt (1957) and Gulland (1968), although Bannister (1978) estimated the fishing mortality in this period at F=0.3.

Table 6. Parameter estimates to calculate the 'observed' selection differential (S_{obs}) and the selection differential (S_{pred}) predicted from the fitness profiles in Fig.10

		Females	Males
a	Time span (years)	65	75
b	Total change in L_{mat} (cm)	4	10
c	ΔL_{mat} explained by growth (cm)	1	-
d	ΔL_{mat} explained by temperature (cm)	0.7	-
e	Unexplained change in L_{mat} (b-c-d)	2.3	10
f	Generation time (years)	7.7	4.8
g	ΔL_{mat}.year^{-1} (e/a)	0.035	0.13
h	ΔL_{mat}.generation^{-1} (g x f)	0.27	0.64
i	heritability	0.24	0.24
j	Observed selection differential S_{obs} (h/i in cm)	1.1	2.7
k	Predicted selection differential S_{pred} (cm)	0.3	2.0

The 'observed' selection differential (S_{obs}) was based on the observed change in L_{mat} (R), the generation time and h^2, the heritability coefficient. In this calculation the value of R will be most prone to uncertainty because of the phenotypic plasticity in L_{mat} in response to differences in surplus production and abiotic environmental factors such as temperature. Given the uncertainties about the accuracy of the temperature effect - which might be larger as suggested by the geographical differences in L_{mat} and temperature - the change in L_{mat} may be further reduced and the 'observed' selection differential would be closer to the predicted one.

It is obvious that the above discussion must be considered as highly speculative. Without a reanalysis of the fishing mortality estimates in the first half of the 20th century and a more detailed knowledge of abiotic factors driving the phenotypic plasticity in the onset of sexual maturity, in particular temperature, and knowledge of the genetics of maturation, in particular the autosomal or heterosomal effects, a final interpretation of the observed changes in length at first maturity is not possible. However, the predicted selection differentials are at least not contradicted by the observed changes. They suggest that selection is slow and therefore a more clearcut effect may only be revealed after a much longer period of exploitation. If over the next century exploitation of plaice is continued at the current level, L_{mat} in both male and female plaice is expected to decrease further as shown in Fig.11. The forward simulation was based on the fitness profiles of Fig.10 and used a generation time of 4.8 and 7.7 years for males and females respectively. The full lines show the results if the L_{mat} is coded by heterosomal genes, while the dashed lines show the result for autosomal coding. The latter simulation assumed an average selection differential by year for both males and females.

IMPLICATIONS FOR FISHERIES MANAGEMENT

Law & Grey (1989) explored the possible effects of genetical selection on the yield of Arcto-Norwegian cod. The evolution of total yield depends on the interplay between the yield from an individual over the course of its life and recruitment. Any future decrease in L_{mat} will affect the yield of the stock as well as the spawning stock biomass. In an equilibrium situation the annual yield per recruit (Y/R) can be calculated according to

$$Y = \Sigma F_x Z_x^{-1} l_x W_x q_x \qquad (6)$$

where F_x is the instantaneous rate of fishing mortality, $Z_x = F_x + M_x$ is the total instantaneous mortality rate, l_x is the fraction of plaice surviving to age x and W_x is the weight of age group x and q_x is the proportion of age group x recruited to the fisheries.
The spawning stock biomass (SSB) per recruit can be calculated according to

$$SSB = \Sigma l_x W_x p_x \qquad (7)$$

where p_x is the proportion mature fish at age x.

If we assume a current level of surplus production and the average exploitation pattern of 1958-1986 for male and female separately (Chapter 2), a decrease in L_{mat} due to genetical selection will result in a decrease in W_x. This will postpone the recruitment to the fisheries, which is size-dependent and was assumed to increase linearly from $q_x = 0$ at 22 cm to $q_x = 1$ at 32 cm with $q_x = 0.5$ at the minimum landing size of 27 cm.

Fig.12 shows that under these assumptions continuation of exploitation at the current level would result in a decrease in the yield and an increase in the spawning stock biomass per recruit of about minus 5% and plus 15%, respectively. The differences between the results for autosomal and heterosomal coding of maturation are relatively minor, although

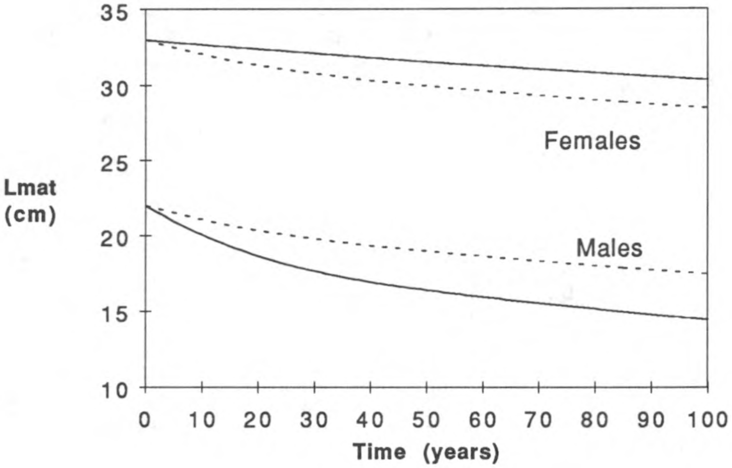


Fig.11. Predicted changes in L_{mat} if current exploitation is continued over the next 100 years. The full lines indicate the expected change if maturation is coded by heterosomal genes, the dashed line by autosomal genes.

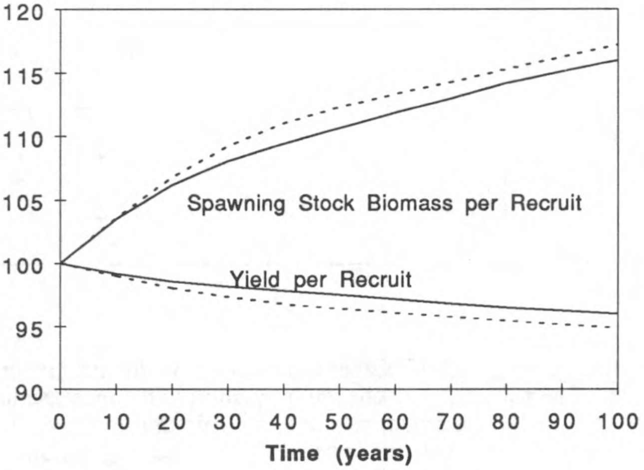


Fig. 12. The effect of current exploitation on the evolution of the equilibrium yield and spawning stock biomass per recruit if L_{mat} changes according the pattern shown in Fig.11. The dashed line indicate coding of maturation by autosomal genes the full line by heterosomal genes.

Table 7. Summary of the major changes in biological parameters of plaice that occurred since 1900 in the Southern Bight of the North Sea and differences in the average surface temperature on the nursery grounds by quarter. Fecundity data are given for the Southern and German Bight.

	1900-1910	1930-1940	1946-1949	1975-1985
Growth of females (cm.year^{-1})				
10-15 cm	-	5.6	6.9	10.1
25-30 cm	-	5.6	5.4	6.1
40-45 cm	-	2.1	1.2	2.1
Maturation				
males				
L_{mat} (cm)	30	-	-	20
A_{mat} (years)	5	-	-	2
females				
L_{mat} (cm)	34	-	-	30
A_{mat} (years)	6	-	-	4
Fecundity (thousand eggs)				
Southern Bight				
30 cm	-	-	35.9	72.8
40 cm	-	-	89.3	159.8
50 cm	-	-	181.1	294.0
German Bight				
30 cm	33.6	-	-	63.8
40 cm	104.8	-	-	141.4
50 cm	252.8	-	-	261.9
Ovary weight (g)				
30 cm	-	-	34.7	39.1
40 cm	-	-	100.3	113.5
50 cm	-	-	228.7	258.6
Mean surface temperature (^{o}C)				
Q1	3.4	4.0	3.1	3.4
Q2	10.9	11.6	11.8	11.3
Q3	16.2	17.3	17.6	17.1
Q4	8.6	9.0	9.2	9.1

heterosomal coding gave a slightly higher reduction in yield and higher increase in SSB. Whether the level of recruitment will change in relation to the increase in SSB will depend on the nature of the stock recruitment relation, in particular on the density dependence of recruitment. If there is no or only a minor density dependent regulation, an increase in SSB will lead to an increase in the average level of recruitment that may compensate for the decrease in the yield per recruit. However, if there occurs a strong density dependent mortality, a further decrease in yield may be expected. The nature of many of the processes underlying the stock-recruitment relation are still obscure making any such predictions highly speculative.

The sensitivity of the yield for genetical selection will depend on the level and pattern of exploitation, the surplus production relationship and recruitment. In plaice, the exploitation pattern is characterised by a peak on the younger age groups (Fig.9) which are partly undersized and discarded (van Beek 1990; van Beek *et al.* 1990; Chapter 2). In order to enhance the level of recruitment to the fisheries, the flatfish fisheries in coastal areas of the eastern North Sea was restricted since 1989 to reduce the discard mortality of undersized fish (plaice box). Additional to the expected gain in recruitment, a shift in the exploitation pattern to older age groups would also reduce the genetical selection for earlier maturation and a decrease in yield. Therefore, further improvements of the exploitation pattern might be considered by increasing the mesh size from the present level of 8 cm to 15 cm, which corresponds to an increase in the 50% retention length from 18 to 33 cm. This would shift the fishing mortality almost entirely to the adult phase of life and the discard problem of young plaice would be entirely solved. However, such an increase in mesh size is highly academic since plaice is mainly taken in a mixed trawl fishery for sole. Since the soles would largely escape through the meshes, a compromise is necessary, which involves a relatively small mesh size.

The results of the present study has shown that the current level and pattern of exploitation of North sea plaice may impose a genetical selection for a reduction in the size and age at first maturity, which will negatively affect the equilibrium yield. Although the decrease in yield of 5% as predicted seems rather small, it nevertheless emphasize the potential negative long term effects of exploitation. Further simulation studies can be used to explore the sensitivity of the equilibrium yield for various levels and patterns of exploitation, which may offer the fisheries manager some guideline's to formulate short term management advice within genetically safe long-term limits.

CONCLUSION

The present study showed that over the last century substantial changes were observed in growth and maturation but not in reproductive investment. A summary of the major changes in biological parameters and surface temperatures is given in Table 7. Growth rate increased since the 1950's in the smaller size classes but not in larger plaice, while in larger size classes a growth depression occurred during the 1940's coinciding with a threefold increase in the plaice stock. Fecundity appeared to be rather stable, except for the substantial decrease in the late 1940's and a perhaps small increase in smaller sized fish. The large reduction in fecundity in the late 1940's was not reflected in ovary weight, suggesting a trade-off between egg numbers and egg size in relation to the adult stock size. Length and age-at-first maturity decreased since 1900, which was partly related to the change in growth and water temperature. Simulation of the selective effects of fishing indicated that a genetical selection occurs for an increase in reproductive investment and a decrease in the length and age at first maturity. In contrast to this expectation, no evidence was obtained for a major change in reproductive investment. A quantitative analysis of the changes in the onset of maturation supported the hypothesis that fishing selected for a decrease in L_{mat}, but the observed decrease, after correction for changes in growth and temperature, was larger than expected from the simulation. Since there remain uncertainties in the quantitative analysis of the selection exerted by the fisheries in the beginning of the century, and in the analysis of phenotypic plasticity of maturation, in particular the temperature effect, no unequivocal interpretation in favour of genetical selection by the fisheries can be given. At the current level and pattern of exploitation the potential for genetical selection of the onset of maturation in plaice is relatively minor. The expected long term effects on the yield are estimated to be about 5%. Despite the uncertainty whether genetical selection is an important contributing factor to the dynamics of exploited fish populations, this study emphasizes that genetical reasoning can be incorporated in fisheries management and that advice can be provided on the possible long term effects of genetical selection on the yield and state of the stock.

SUMMARY

SUMMARY

This thesis studies possible genetical effects of fishing of North Sea plaice, which has been exploited intensively for more than a century and for which a wealth of literature information is available describing changes in basic biological parameters since 1900. From life-history theory we expect that exploitation, which may increases the mortality well above the natural level, pose a selection pressure for genotypes coding for higher reproductive investment or a reduced age at first reproduction. However, such changes, if they are observed over time, are not necessarily an indication of genetical selection, since they may equally well be related to phenotypic plasticity in response to a reduction of the stock biomass. Exploitation will reduce the stock biomass and as a result growth, maturation and reproduction rates may increase. Thus, a study of the genetical selection of fisheries is a study in which genetic and phenotypic plasticity must be enraveled. As no experimental approaches are feasible for commercial species which are characterized by a relatively large body size and long generation time, the indirect approach was adopted to study the phenotypic plasticity in the onset of maturation and in reproductive investment in response to variations in growth as can be observed at present. Observed changes in the onset of maturation and reproductive investment are compared to the expected changes which are predicted from the phenotypic plasticity and the changes in growth rate that were observed over time.

The thesis starts with a description of the interdependence of somatic growth, maturation and reproduction, and shows that males and females show distinct patterns of energy acquisition and allocation. This description, assuming that the energy allocated into somatic growth cannot be allocated to reproduction, serves as a conceptual framework for the study of the phenotypic plasticity in growth, maturation and reproductive investment.

The pattern of fishing mortality is then studied in relation to age in both males and females in order to examine the selective effects of fishing on maturation and reproductive investment and quantitative estimates of selection differentials for the size at first maturity is given.

The thesis then studies the changes in somatic growth, maturation and fecundity (ovary weight) which have occurred since 1900. Changes in somatic growth, reconstructed from the growth patterns in the otoliths, gave evidence for density-dependent growth in juvenile as well as adult plaice. Juvenile growth was below the maximal growth observed in the laboratory throughout the study period, although an increase was observed since the mid 1950's. This increase was most likely to be due to anthropogenic effects such as pollution or eutrophication. Adult growth was substantially reduced when the stock biomass tripled due to the substantial reduction of fishing in the Second World War.

Maturation of male and female plaice is studied in recent years and compared to literature data for 1900-1910, showing that length and age at first maturity in recent years were substantially lower than those observed in the beginning of the century. Comparison of the fecundity and ovary weight - body size relationships between three periods: 1900-1910, 1947-1949 and 1977-1985 shows substantial changes in the fecundity - body size relationships between the periods, but not in the ovary weight - body size relationship, suggesting that the reproductive investment has been rather stable and the trade-off between

egg numbers and egg size has changed in response to the increase in the plaice stock after the second World War.

Phenotypic plasticity is studied on the level of the population and that of the individual females. On the population level, the annual variability in maturation and reproductive investment is analysed in relation with growth. On the individual level, these parameters are related to the estimates of individual growth as obtained by back-calculation of otoliths. Maturation depends on the length reached within a certain year, but also on the rate in the three preceding years. Circumstantial evidence is further obtained that the temperature on the coastal nursery ground may affect the length at first maturity. Size-specific fecundity and ovary weight are highly variable between individual fish, but show only small variations between years. The variability in individual fecundity was not related to the individual growth rate in the previous year. The only indication of a growth effect on reproductive investment is given by the significant correlation between somatic growth and pre-spawning condition factor, which can be considered a proxy for the available resources for reproduction. Enhanced conditions for growth will result in a larger body size at the start of spawning and consequently a larger absolute fecundity, but not in an increased size-specific fecundity.

The lack of firm evidence for an increase in reproductive investment contradicts the expectations from the selective effects of fishing, which may be due to a constraint on reproductive investment imposed by morphology or by a mortality cost of reproduction. The reduction in the size (and age) at first maturity observed since 1900 corresponds to the change expected from genetical selection. However, the observed change was larger than the expected change, particularly in females. A part of this discrepancy can be explained by the phenotypic plasticity in length at first maturity (L_{mat}) in response to an increase in juvenile growth and to an increase in temperature on the nursery grounds. These two factors work in the same direction as genetical selection, but the analysis of their quantitative influence, in particular of temperature, is uncertain. Further, there is some uncertainty on the level of fishing mortality prior to 1940. Given these uncertainties no unequivocal conclusion that fishing has caused a genetical change in the L_{mat} can be drawn. Nevertheless, the qualitative agreement between the observed and predicted change indicates that genetical selection may be exerted. Continuation of the current exploitation may result in a further decrease in the length and the age at first maturity, which will result via a slower growth in a small decrease in yield but an increase in the spawning stock biomass.

Samenvatting

De mens heeft sinds mensenheugenis vis-bestanden geëxploiteerd als voedselbron. In de Noordzee was de visserij van bodem-vissoorten gericht op schol en kabeljauw, die door zeilschepen met een boomkor werden gevangen (1). Tijdens de industriële revolutie in de vorige eeuw breidde de visserij zich sterk uit zowel wat betreft de beviste gebieden, het aantal vissersschepen als het vangstvermogen (2). Aan het eind van de negentiende eeuw kwamen stoomtrawlers in de vaart. De mechanisering maakte het mogelijk om efficiëntere vistuigen te gebruiken zoals de bordentrawl. Dit leidde ertoe dat de vangsten per visreis, en daarmee de economische opbrengst, daalde. Het visserijbedrijf beklaagde zich hierover bij de overheid en vroeg om beschermende maatregelen. Dergelijke klachten zijn al oud. Zo beklaagden Engelse vissers zich al in de veertiende eeuw bij hun koning over het gebruik van de "Wondyrchon". Dit fijnmazige bodemnet, dat werd opengehouden door een zware boom van ongeveer 5 meter lengte, zou grote schade toebrengen aan het bodemleven (3,5). Mede door het voortdurende probleem van de overbevissing en de daarmee samenhangende vragen naar beheersmaatregelen werd in 1902 de Internationale Raad voor Onderzoek der Zee (ICES) werd opgericht, die tot op de dag van vandaag een belangrijke rol heeft gespeeld in de ontwikkeling van de visserijbiologie. Een van de hoofdpunten van het door de ICES gecoördineerde onderzoek richtte zich op de overbevissing van schol in de zuidelijke Noordzee. Het advies van de eerste generatie visserijbiologen was gericht op het verminderen van de visserij op kleine schol in de zuidoostelijke Noordzee (4,5). Het duurde echter tot 1989 voordat er daadwerkelijk maatregelen genomen werden ter bescherming van de jonge platvis door de instelling van een gesloten gebied in de zuidoostelijke Noordzee (de zogenaamde 'scholbox').

Uit deze korte historische schets moge duidelijk zijn dat de visserijbiologie traditioneel een sterk toegepast karakter heeft. Visserijbiologen hebben voor het beantwoorden van de vele beleidsvragen een gedegen kennis nodig van de biologie van de commercieel geëxploiteerde vissoorten zoals verspreiding, migratie, groei, voortplanting, leeftijdsopbouw. Hierdoor zijn veel biologische gegevens in de nationale en internationale literatuur bijeengebracht. Naast basale studies naar de biologie heeft het visserijonderzoek zich gericht op het in wiskundige formules beschrijven van de interactie tussen de visserij en de visbestanden. Na de tweede wereldoorlog leidde dit o.a. tot publicaties van Ricker (6) in Canada en van Beverton en Holt (7) in Europa, die tot op de dag van vandaag de basis vormen van het jaarlijkse beleidsadvies.

De vraag naar beheersadviezen heeft vaak een ad hoc karakter en is gericht op de korte termijn. De vraag naar de mogelijke gevolgen van langdurige exploitatie is pas de laatste jaren in de belangstelling komen te staan (8). Deze ontwikkeling gaat samen met het groeiend besef dat menselijke activiteiten ook in zee tot ingrijpende veranderingen (verstoringen) kunnen leiden (9). Vanuit de wetenschappelijke wereld is de vraag naar de effecten van langdurige exploitatie gestimuleerd door snelle vorderingen in de theoretische oecologie, met name in het onderzoek naar 'life-history' strategieën.

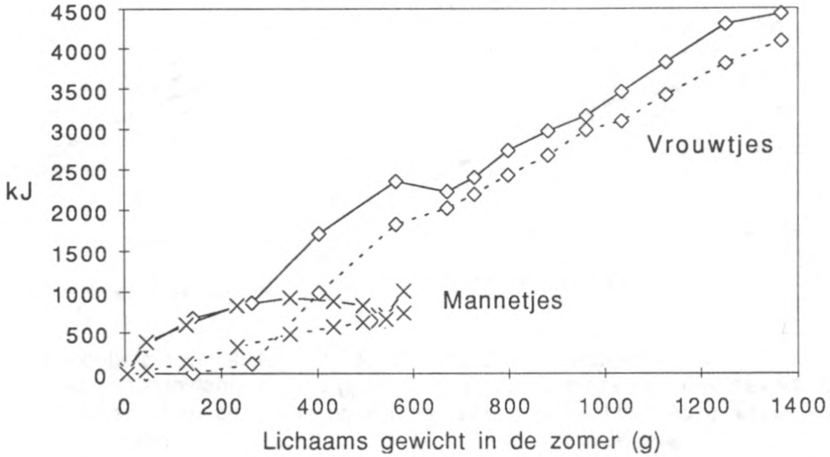
De 'life history' theorie houdt zich bezig met vragen zoals op welke leeftijd een dier zich gaat voortplanten (leeftijd van geslachtsrijpheid) en hoeveel energie er in voortplanting wordt geïnvesteerd (voortplantings-inspanning) (10). Het uitgangspunt bij het onderzoek naar 'life history' strategieën is dat de genetische eigenschappen van individuen, die het grootste aantal nakomelingen voortbrengen, voortbestaan, terwijl die van individuen, die minder nakomelingen voortbrengen, zullen verdwijnen. De optimale voortplantings-strategie, omschreven als de combinatie van de geslachtsrijpe leeftijd en voortplantings-inspanning waarbij een maximaal aantal nakomelingen wordt geproduceerd, wordt bepaald door de omstandigheden in de leefomgeving van een dier. Hierbij spelen factoren die de groei en sterfte bepalen een belangrijke rol. Het onderzoek heeft zich veelal beperkt tot een vergelijking van de voortplantings-strategieën van verschillende organismen, of verschillende populaties van één organisme, in relatie met verschillen in omgevings factoren. Zo leverde een vergelijking van de verschillende platvissoorten een duidelijk verband tussen leeftijd van geslachtsrijpheid en de natuurlijke sterfte (11,12). Hoe hoger de sterfte, hoe vroeger de dieren geslachtsrijp zijn. Een probleem bij dit vergelijkend onderzoek is dat het niet valt uit te maken of nu de leeftijd van geslachtsrijpheid een aanpassing is aan een hoge sterfte, of dat de hoge sterfte een gevolg is van de leeftijd van geslachtsrijpheid. Een kritische test van de 'life history' theorie is dan ook gewenst. De studie van geëxploiteerde visbestanden biedt deze mogelijkheid. De 'life-history' theorie voorspelt immers dat door een verhoging van de sterfte de leeftijd van geslachtsrijpheid en de voortplantings-inspanning zal toenemen (8,13).

Dit proefschrift beoogt deze kritische test te geven. Naast een betekenis voor de 'life-history' theorie heeft dit mogelijk ook belangrijke implicaties voor het visserijbeheer, omdat veranderingen in de voortplantings-strategie een verandering in de productiviteit van een visbestand kan veroorzaken (14,15). Een probleem is echter dat de door de 'life-history' theorie voorspelde veranderingen in voortplantings-strategie ook verklaard kunnen worden uit een afname van de visstand. Als gevolg van exploitatie zal de visstand afnemen en kan de groeisnelheid en daarmee de voortplantings-strategie veranderen. Een verandering in de voortplantings-strategie kan dus niet direkt als een aanwijzing voor genetische selectie worden gezien, maar zal moeten worden geanalyseerd tegen de achtergrond van de veranderingen die zich kunnen voordoen onder verschillende omgevingsomstandigheden (fenotypische plasticiteit, 16).

Het onderzoek is opgebouwd uit vier delen. In het eerste deel wordt een beschrijving gegeven van de samenhang tussen voortplantings-inspanning en lichaamsgroei en wordt onderzocht hoe groot de genetische selectie ten gevolge van de visserij is. In het tweede deel worden de veranderingen in groeisnelheid, lengte en leeftijd van geslachtsrijpheid en voortplantings-inspanning geanalyseerd, zoals deze zich sinds 1900 hebben voorgedaan. In deel 3 wordt de fenotypische plasticiteit in de lengte en leeftijd van geslachtsrijpheid en voortplantings-inspanning geanalyseerd. In het vierde deel, de synthese, worden de waargenomen veranderingen in lengte van geslachtsrijpheid gecorrigeerd voor de bijdrage van de fenotypische plasticiteit ten gevolge van veranderingen in groeisnelheid en temperatuur, waarna de gecorrigeerde veranderingen vergeleken worden met de te verwachte veranderingen als gevolg van genetische selectie door de visserij. Tenslotte worden de mogelijke konsekwenties van genetische veranderingen voor het visserijbeheer besproken.

1 a. De voortplantings-strategie

De jaar-cyclus van schol wordt gekenmerkt door een groei- en een voortplantings-periode. Gedurende de voortplantingsperiode (januari-maart) wordt er niet gegeten. De energie, die een schol gedurende het voortplantingsseizoen nodig heeft voor ei- of spermaproductie en verbranding, wordt onttrokken aan de lichaamsreserves. De lichaams conditie vertoont dan ook een maximum aan het eind van het groeiseizoen in de herfst en een minimum aan het eind van het paaiseizoen in februari - maart. De voortplantings-strategie wordt gekenmerkt door de verdeling van beschikbare energie over lichaamsgroei en voortplanting. Energie besteedt aan voortplanting kan niet worden besteed aan lichaamsgroei. Lichaamsgroei en voortplanting zijn dus onderling afhankelijk. Beide zijn echter ook afhankelijk van de totale hoeveelheid energie die een dier gedurende een jaar in zijn lichaam kan vastleggen: de surplus-productie (17,18). Zowel de voortplantings-strategie als surplus-productie verschillen tussen de sexen. De surplus-productie neemt toe met de grootte van de vis voor zowel mannetjes als vrouwtjes, maar bij een vis-grootte van ongeveer 300 g (± 30 cm) blijft die van mannetjes achter (Fig.1). Verschillen in voortplantings-strategie doen zich voor bij de lengte en leeftijd van geslachtsrijpheid en bij de voortplantings-inspanning. Mannetjes worden gemiddeld op tweejarige leeftijd geslachtsrijp bij een lengte van 20 cm, vrouwtjes 2 jaar later bij een lengte van 33 cm. Daarnaast is de voortplantings-inspanning van mannetjes kleiner dan die van vrouwtjes. Het verschil in lengtegroei tussen mannetjes en vrouwtjes kan dus niet alleen verklaard worden uit het eerder geslachtsrijp worden van mannetjes, maar wordt mede veroorzaakt door het achterblijven van de surplus-productie van grotere mannetjes. De oorzaak van het laatstgenoemde is waarschijnlijk een lagere voedselconsumptie dan van vrouwtjes.

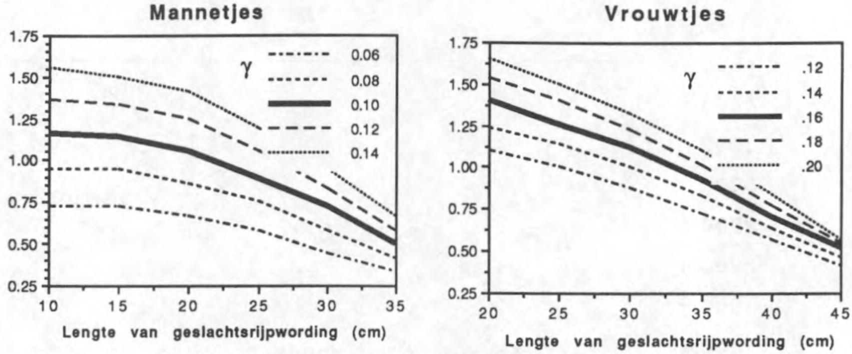


Figuur 1. Verschillen in de relatie tussen de jaarlijkse surplus productie (volle lijn) en voortplantings-inspanning (gebroken lijn) met het lichaamsgewicht in het groeiseizoen van mannetjes en vrouwtjes schol.

1 b. Selectie verschillen ten gevolge van de visserij

De visserij op bodemvis in de Noordzee veroorzaakt een aanzienlijke verhoging van de sterfte-kans van schol. De visserij vangt per jaar gemiddeld 30% van alle schollen van 18 cm en groter, terwijl er maar 10% een natuurlijke dood sterven. De kans om door de visserij gevangen te worden is niet voor iedere schol even groot. Volwassen mannetjes hebben een grotere kans dan volwassen vrouwtjes. Ook verschilt de visserijsterfte per leeftijds groep doordat deze een verschillende ruimtelijke verspreiding hebben. Jonge schol komt vooral in de ondiepe kustgebieden voor waar weinig gevist wordt en kan veelal door de mazen van het net ontsnappen. Naarmate de dieren ouder en groter worden, trekken zij weg uit het ondiepe kustgebied naar de intensiever beviste gebieden van de zuidelijke Noordzee. De visserijsterfte van de oudere leeftijdsgroepen neemt weer af omdat deze dieren 's zomers wegtrekken naar de relatief minder beviste centrale Noordzee.

In een model-studie is het gecombineerde effect van de leeftijd van geslachtsrijpheid en de jaarlijkse voortplantings-inspanning berekend op het totaal aantal nakomelingen dat een schol gedurende het gehele leven produceert (fitness). In het model betekent vroeg geslachtsrijp worden dat de lichaamsgroei, en daarmee de toekomstige voortplantings-inspanning, achterblijft. Het laat geslachtsrijp worden betekent dat de voortplantings-inspanning weliswaar groot is maar dat de kans om de hogere leeftijd van geslachtsrijpheid te bereiken klein is. Figuur 2 laat zien dat het aantal nakomelingen afneemt met een toenemende lengte van geslachtsrijpheid (L_{mat}) en met een afnemende voortplantings-inspanning (γ). Dit betekent dat de visserij een selectie-druk uitoefent ten gunste van dieren die een erfelijke aanleg hebben voor een grotere voorplantings-inspanning en een kleinere lengte van geslachtsrijpheid.

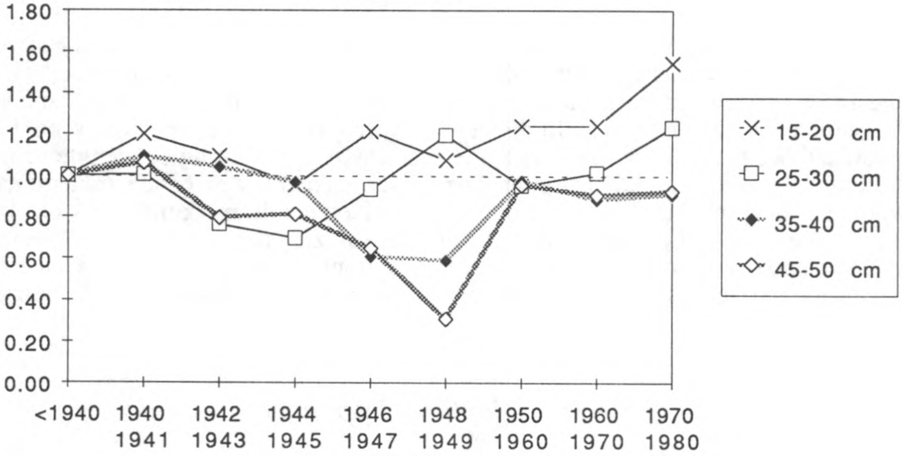


Figuur 2. Het aantal nakomelingen dat een schol in het gehele leven produceert (fitness) als functie van de lengte van geslachtsrijpheid (L_{mat}) en de voortplantings-inspanning (γ). De fitness is uitgedrukt ten opzichte van de huidige voortplantings-strategie: mannetjes: L_{mat}= 22 cm, γ = 0.10; vrouwtjes: L_{mat} = 33 cm, γ=0.16.

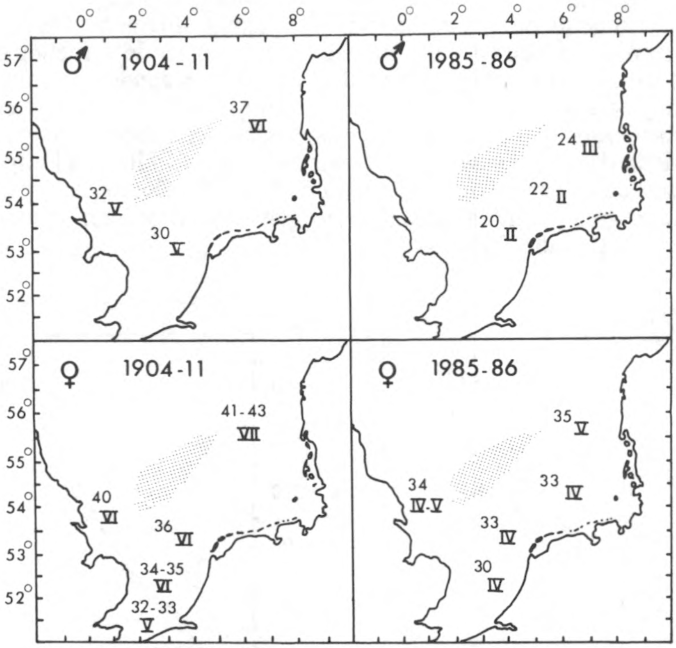
2. Waargenomen veranderingen in lichaamsgroei en voortplantings-strategie

Lichaamsgroei

Veranderingen in lichaamsgroei van vrouwtjes schol werden onderzocht aan de hand van de groeipatronen van de gehoorsteentjes (otolieten). Door meting van de afstanden tussen de jaarringen werd de individuele groei-geschiedenis van 1421 dieren gereconstrueerd. Mede dank zij de hulp van het visserij-laboratorium in Lowestoft (Engeland) konden otoliet monsters uit 1948 - 1955 onderzocht worden. Hierdoor was het mogelijk de groeiveranderingen te onderzoeken die zich ná 1930 hebben voorgedaan. De belangrijkste veranderingen waren een afname van de groeisnelheid tussen 1940 en 1949 en een groeitoename in de periode na 1955. De groeivertraging in 1940-1949 was beperkt tot de grotere dieren (>=30 cm), terwijl de groeiversnelling na 1955 beperkt was tot de kleinere lengte groepen (<30 cm). Door vergelijking van de veranderingen in groei met veranderingen in de scholstand en de temperatuur is het aannemelijk geworden dat de groeivertraging in de jaren veertig verband hield met de toename in de scholstand ten gevolge van de reductie in visserij gedurende de Tweede Wereld Oorlog, en dat de toename van de groeisnelheid na 1955 met een toename in het voedselaanbod. Verder werden er duidelijke aanwijzingen verkregen dat de groei van jonge schol beperkt is geweest door voedsel gedurende de gehele periode 1930-1985.



Figuur 3. Jaarlijkse lengte-groei in de periode 1930-1980 van verschillende lengte-groepen van vrouwtjes schol, gestandariseerd ten opzichte van de gemiddelde groei in de periode vóór 1940, die de afname in groeisnelheid in de jaren veertig en de toename in de jaren zestig en zeventig illustreert.



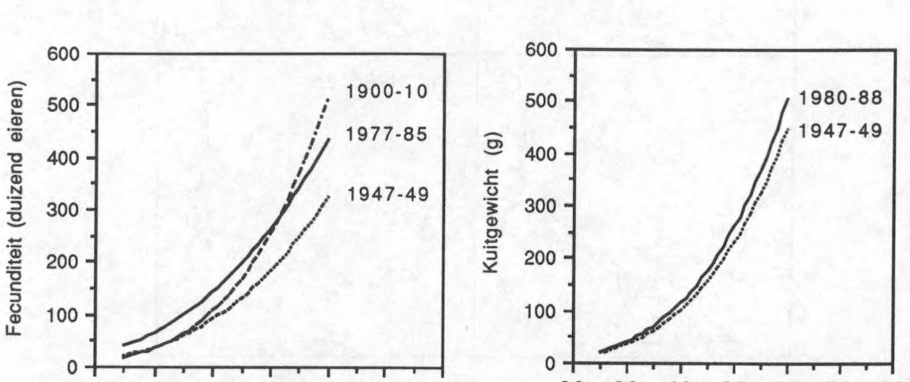
Figuur 4. Veranderingen in de lengte (L_{mat}) en leeftijd (A_{mat}) van geslachtsrijpheid van mannetjes en vrouwtjes schol tussen het begin van deze eeuw (1904-1911) en nu (1985-1986). De A_{mat} in 1904-1911 is niet gecorrigeerd voor verschillen in de methode van leeftijd-aflezing. Correctie zou de A_{mat} in 1904-1911 met gemiddeld een half jaar verhogen.

Geslachtsrijpheid

Het geslachtsrijp worden werd onderzocht aan de hand van vismonsters genomen van de commerciële visserij (marktmonsters) en verzameld tijdens onderzoeks-reizen. De onderzoeks-reizen hadden tot doel na te gaan of marktmonsters representatief zijn voor het vaststellen van de lengte en leeftijd van geslachtsrijpheid. Voor vrouwtjes schol bleek dit inderdaad het geval. Voor mannetjes, die geslachtsrijp worden bij een lengte beneden de minimum aanvoermaat, kon het geslachtsrijp worden niet aan de hand van marktmonsters worden onderzocht. Uit zowel de onderzoeksreizen als de marktmonsters bleek dat de lengte en leeftijd van geslachtsrijpheid toeneemt van zuid naar noord. Vergeleken met het begin van de eeuw worden zowel mannetjes als vrouwtjes schol nu op een kleinere lengte en een jongere leeftijd geslachtsrijp (Fig.4). De afname is het grootst in de noordelijker gebieden.

Voortplantings-inspanning

Veranderingen in de voortplantings-inspanning werden onderzocht door een vergelijking te maken van de eiproductie (fecunditeit) tussen drie perioden: I - 1900-1910; II - 1947-1949 en III - 1977 - 1988 (Fig.5a). De relatie tussen de eiproductie en de lichaams-lengte vertoonde aanzienlijke veranderingen. De grootste verandering deed zich voor in periode II, waarbij de eiproductie aanzienlijk lager was dan in periode I en III. Vergelijking van de eiproductie tussen periodes I en III toont een toename bij kleine vrouwtjes (<=40 cm), maar geen verandering bij grotere vrouwtjes. De aanzienlijke reductie in fecunditeit in periode II contrasteert met de geringe afname van het kuitgewicht (Fig.5b). Dit suggereert dat niet de voortplantings-inspanning maar de verdeling ervan over een klein aantal grote eieren of een groot aantal kleine eieren is veranderd. De plasticiteit in de afweging van ei-grootte en ei-aantal maakt het moeilijk veranderingen in ei-aantal te interpreteren als veranderingen in voortplantings-inspanning. Omdat de grote verschillen in ei-aantal tussen periode II en III niet worden weerspiegeld in verschillen in kuitgewicht, en de verschillen tussen de ei-aantallen tussen periode I en III relatief gering zijn wordt geconcludeerd dat er geen duidelijke aanwijzingen zijn voor een toename in de voortplantings-inspanning sinds 1900.

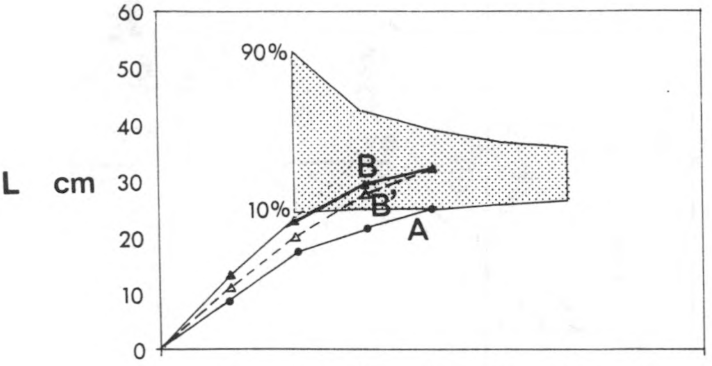


Figuur 5. Waargenomen veranderingen in de fecunditeit (links) en het kuitgewicht (rechts) tussen drie periodes: I - 1900-1910; I I - 1947-1949; I I I - 1977-1985

3. Fenotypische plasticiteit in het geslachtsrijp worden en in de voortplantings-inspanning

Het geslachtsrijp worden

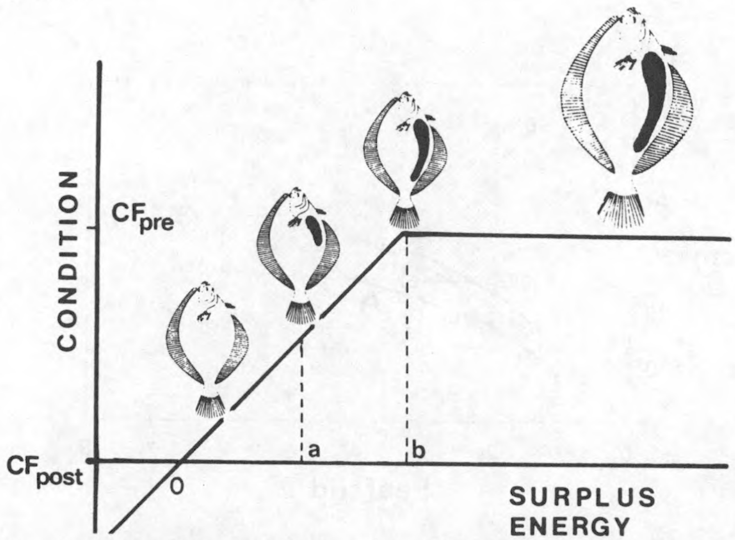
De invloed van lichaamsgroei op de lengte van geslachtsrijpheid werd onderzocht aan de hand van 1) verschillen in lichaamsgroei en geslachtsrijpheid van verschillende jaarklassen die geboren zijn in de periode 1958 - 1990 en 2) een analyse van het geslachtsrijp worden in relatie met de lichaamsgroei van individuele vrouwtjes. Figuur 6 geeft een beschrijving van het proces van geslachtsrijp worden. De gestippelde ruimte omvat de combinaties van de lengte en leeftijd waarop individuele vrouwtjes geslachtsrijp worden. Deze 'enveloppe' is geconstrueerd uit de berekende lengtes waarop 10% en 90% van de schol vrouwtjes van 2 tot 6 jaar geslachtsrijp worden. De enveloppe, die van links naar rechts gaand afloopt, illustreert dat langzaam groeiende dieren op een hogere leeftijd maar op een gemiddeld kleinere lengte geslachtsrijp worden. Anders gezegd, de in Figuur 6 getekende langzaam groeiende vis (A) heeft op 4-jarige leeftijd een kans van 10% om geslachtsrijp te zijn, terwijl het snel groeiende vrouwtje (B) een kans heeft van 50%. Geslachtsrijpheid wordt echter niet alleen door de bereikte lengte bepaald maar ook door de groei in de voorafgaande jaren. De invloed van de groei-geschiedenis wordt geïllustreerd door vergelijking van dier B met dier B'. Alhoewel beide op 4-jarige leeftijd éénzelfde lengte hebben bereikt , heeft dier B' als 0-jarige (tussen 0 en 1 jaar) een groeiachterstand opgelopen. Op 1 en 2 jarige leeftijd verschilt de groeisnelheid niet, maar op 3 jarige leeftijd groeit B' sneller dan B. Door deze verschillen in individuele groei geschiedenis is de kans op geslachtsrijpheid van B groter dan die van B'.



Figuur 6. Enveloppe (gestippeld) die de combinaties van de lengte en leeftijd van geslachtsrijpheid omvat van individuele schol vrouwtjes. De enveloppe wordt begrensd door de lengte waarop 10% en 90% van de schol vrouwtjes van 2 tot 6 jaar geslachtsrijp worden.

Voortplantings-inspanning

De voortplantings-inspanning van vrouwtjes kan worden geschat uit de fecunditeit, het kuitgewicht en de conditie factor aan het begin van het paaiseizoen. Analyse van deze parameters in relatie met de groei in het voorafgaande jaar van 5-8 jarige vrouwtjes in de periode 1965-1986 leverde geen duidelijke aanwijzingen voor een groeieffect op de voortplantings-inspanning. Alleen de conditie-factor bleek significant positief gecorreleerd te zijn met de lichaamsgroei. Lichaamsgroei bepaald aan de hand van de wijdte van de laatste jaarring, bleek niet gecorreleerd met fecunditeit, kuitgewicht, noch met conditie-factor. Deze resultaten kunnen worden samengevat in een 'fysiologisch' model van de energie verdeling over voortplanting en lichaamsgroei (Fig.7). Het model postuleert dat de lichaams conditie van een dier zo wordt gereguleerd dat ze niet beneden een minimum en niet boven een maximum zal uitkomen. Deze uitersten hangen samen met een optimale voortplantings-inspanning. De minimale conditie (CF_{post}) wordt bereikt aan het eind van het paaiseizoen en houdt verband met een maximale overlevingskans. Een verdere verlaging van de conditie ten gevolge van een grotere voortplantings-inspanning zou de overlevings-kansen onevenredig doen dalen. De maximale conditie aan het begin van het paaiseizoen (CF_{pre}) houdt verband met de benodigde reserves voor de voortplanting en het metabolisme gedurende het paaiseizoen waarin geen voedsel wordt opgenomen. Bij een lage surplus-productie ($SP<b$) zal het dier eerst zijn energie reserves aanvullen en niet in lengte groeien. Indien $SP<a$ zal een dier niet in staat zijn de voortplantingsverliezen van het vorig jaar aan te vullen en zal het zich in het eerstvolgende paaiseizoen niet voortplanten. Bij $a>SP>b$ zal de voortplantings-inspanning laag zijn teneinde te voorkomen dat de lichaams-conditie beneden het minimum waarde (CF_{post}) daalt. Indien de surplus-productie voldoende is om de voortplantings verliezen van vorig jaar te aan te vullen ($SP>b$) zal deze gebruikt voor lichaamsgroei en voor voortplanting, waarbij de voortplantings-inspanning proportioneel is met de grootte van de vis. Goede voedselomstandigheden zullen leiden tot een hoge surplus-productie en dus tot een grote lichaamsgroei. De voortplantings-inspanning zal in absolute zin eveneens toenemen maar constant zijn als percentage van het lichaamsgewicht.



Figuur 7. Hypothetische relatie tussen de conditie-factor aan het begin van het paaiseizoen (getrokken lijn), lichaamsgroei (visgrootte) en gonade ontwikkeling (kuit) van vrouwtjes schol met de beschikbare hoeveelheid surplus-productie (surplus energie).

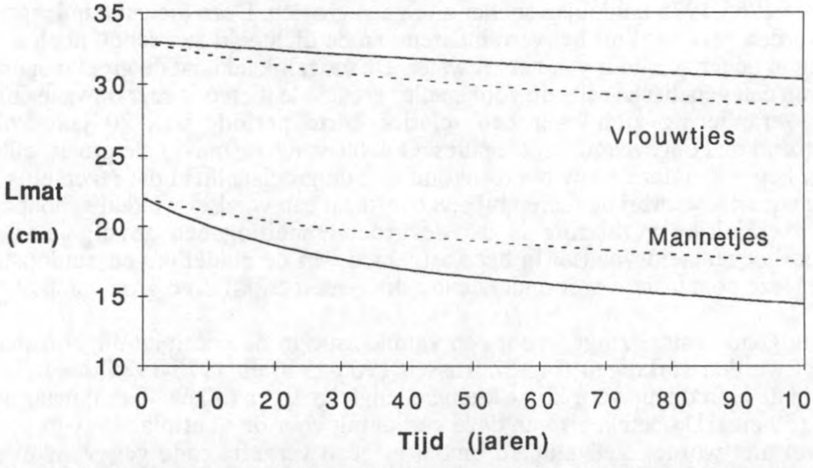
4. Synthese

Sinds 1900 hebben zich bij Noordzee schol een aantal belangrijke veranderingen voorgedaan in de groeisnelheid (Fig.3), de lengte en leeftijd van geslachtsrijpheid (Fig.4) en de voortplantings-inspanning (Fig.5). Wat betreft de groeisnelheid werd aangetoond dat deze voor de grotere lengte groepen niet is veranderd in tegenstelling tot de kleine dieren die in de periode 1955-1975 duidelijke sneller zijn gaan groeien. Deze toename in lengtegroei kon niet worden verklaard uit het verminderen van de dichtheid aan schol, noch aan een verandering in de temperatuur van het zeewater. De mogelijkheid dat de groeitoename een gevolg is van een genetische selectie voor sneller groeiende dieren is zeer onwaarschijnlijk omdat de verandering zich over een relatief korte periode van 20 jaar voltrok, overeenkomend met ongeveer drie generaties. Ook bleek dat de maximale groeisnelheid in zee aan het begin van deze eeuw overeenkomt met de groeisnelheid die recentelijk werd gemeten in aquaria, waarbij de dieren bij een overmaat aan voedsel werden gehouden. De meest waarschijnlijke verklaring is dat de groeiversnelling een gevolg is van een toegenomen hoeveelheid voedsel in het kustgebied van de zuidelijke en zuidoostelijke Noordzee. Deze conclusie wordt ondersteund door een gelijktijdige groeiversnelling bij tong.

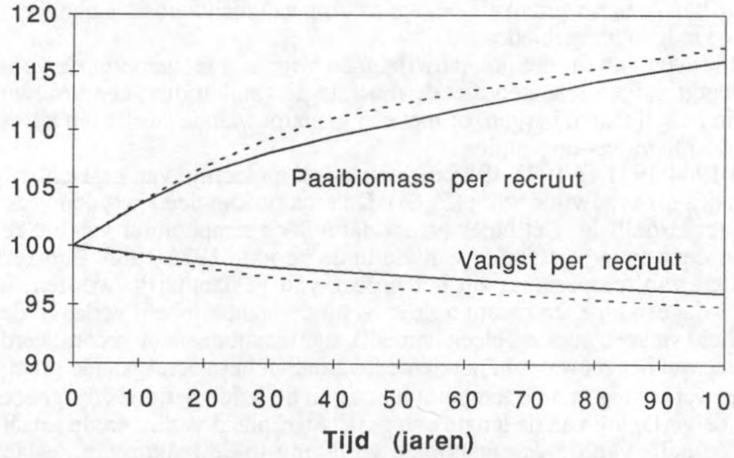
Overtuigende aanwijzingen voor een verandering in de voortplantings-inspanning konden niet worden verkregen (Fig.5). Tussen 1900-1910 en 1975-1985 deed zich een verhoging in de eiproductie voor bij de kleinere lengte-groepen (30 en 40 cm) maar niet bij de grotere (50 cm). De betekenis van deze verhoging voor de voortplantings-inspanning kan evenwel niet worden geëvalueerd omdat er geen vergelijkende gegevens over het kuitgewicht of eigroottes beschikbaar zijn voor het begin van deze eeuw. Vergelijking van de periodes 1947-1949 en 1975-1985 toonde dat de aanzienlijke verhoging van het aantal eieren niet optrad in het kuitgewicht zodat geconcludeerd kon worden dat de eigrootte en niet zozeer de totale voortplantings-inspanning veranderd was: weinig grote eieren in 1947-1949; veel kleine eieren in 1975-1985. Dit suggereert dat onder omstandigheden van een hoge volwassen stand, die aanleiding geeft tot dichtheids-afhankelijk reductie in groeisnelheid zoals in 1947-1949, scholvrouwtjes minder maar grotere eieren produceren. Deze strategie kan gezien worden als een aanpassing aan dichtheidsafhankelijke sterfte in de dichtbevolkte kinderkamergebieden.

Het ontbreken van duidelijke aanwijzingen voor een toename in de voortplantings-inspanning hangt mogelijk samen met de morfologie van het dier, een vrouwtje kan geen grotere kuit in haar lichaam bergen, of met een toename van de sterfte ten gevolge van een verhoogde voortplantings-inspanning.

Tussen 1904-1911 en 1975-1985 nam de lengte en leeftijd van geslachtsrijpheid af bij zowel mannetjes als vrouwtjes schol (Fig.4). De afname kan deels worden verklaard uit de toegenomen groeisnelheid. Het bleek echter dat ook de temperatuur van het zeewater aan het begin van deze eeuw verschilde van die in de periode 1975-1985. Een eerste analyse van de invloed van temperatuur op het proces van geslachtsrijp worden, leverde een aanwijzing op dat een lage temperatuur de kans op geslachtsrijpheid verlaagt: de lengte van geslachstrijpheid van een jaarklas bleek namelijk significant negatief gecorreleerd te zijn met de temperatuur van het zeewater in het derde kwartaal in het voorafgaande groeiseizoen. De waargenomen verhoging van de temperatuur tussen de beide periodes (ongeveer 1 °C) kan een deel van de verlaging van de lengte van geslachtsrijpheid verklaren. In totaal kon echter minder dan de helft van de waargenomen verlaging in de lengte van geslachtsrijpheid verklaard worden uit een toename in groeisnelheid en temperatuur. Het niet verklaarde deel komt wat betreft de richting (daling) overeen met de verwachtte afname als gevolg van een genetische selectie door de visserij. De waargenomen verandering, na correctie voor temperatuur en groeisnelheid, is echter groter dan de verwachte verandering. Het verschil tussen de waargenomen en de voorspelde verlaging hangt mogelijk samen met onnauwkeurigheden in model studie en in de analyse van de invloed van temperatuur op het proces van geslachtsrijp wording. De visserijsterfte in de periode vóór de Tweede Wereld Oorlog is mogelijk hoger geweest dan in de model studie is aangenomen. Directe experimentele informatie over de invloed van temperatuur op het proces van geslachtsrijp worden, en de periode in het leven waarop ze aangrijpt, is niet beschikbaar.



Figuur 8 Voorspelde verandering in de lengte van geslachtsrijpheid (L_{mat}) van mannetjes en vrouwtjes schol bij voortzetting van de huidige exploitatie gedurende de komende 100 jaar. De volle lijnen geven de voorspelde verandering aan indien het geslachtsrijp worden wordt bepaald door genen op het geslachts chromosoom. De gebroken lijnen geven de voorspelde verandering indien het geslachtsrijp worden wordt gecodeerd door autosomale genen.



Figuur 9. Het effect van de voorspelde verandering in de lengte van geslachtsrijpheid (L_{mat}) op de jaarlijkse vangst en paaibiomassa per recruut bij voortzetting van de huidige exploitatie over de komende 100 jaar. De volle lijnen geven de voorspelde verandering aan indien het geslachtsrijp worden wordt bepaald door genen op het geslachts chromosoom. De gebroken lijnen geven de voorspelde verandering indien het geslachtsrijp worden wordt gecodeerd door autosomale genen.

Door de onzekerheid over de invloed van een aantal grootheden, met name het effect van temperatuur op het geslachtsrijp worden, en het historische nivo van visserijsterfte, is het niet mogelijk een ondubbelzinnige conclusie over het optreden van genetische selectie door de visserij te trekken. Echter, het feit dat de richting van de waargenomen en voorspelde verandering overeenkomt, rechtvaardigt de conclusie dat dit onderzoek de hypothese van genetische selectie niet heeft kunne verwerpen. De modelstudie suggereert dat continuering van de huidige exploitatie een verdere afname in de lengte van geslachtsrijpheid kan veroorzaken (Fig.8). Een vervolg studie in de toekomst kan mogelijk met meer zekerheid het effect van genetische selectie kwantificeren.

Een verdere afname van de lengte van geslachtsrijpheid veroorzaakt een daling van de groeisnelheid en daarmee een daling van de productiviteit van de visstand. De voorspelde afname in de lengte van geslachstrijpheid ten gevolge van genetische selectie, zoals geïllustreerd in Fig.8, geeft in de komende eeuw een daling in de vangst van een 5%, terwijl de stand van volwassen vis zal met een 15% toenemen (Fig.9). De voorspelde veranderingen hangen echter af hoe het proces van geslachtsrijp-wording erfelijk is vastgelegd: op het geslachts-chromosoom of op de andere, autosomale, chromosomen.

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NAWOORD

Het ontstaan van dit proefschrift is nauw verweven met mijn werk als visserijbioloog aan het Rijksinstituut voor Visserijonderzoek. Na mijn studie Biologie aan de Rijks Universiteit van Groningen, waarbij ik mij met veel plezier met de oecologie van loopkevers en torenvalken had beziggehouden, vertrok ik op 1 september 1980 naar IJmuiden, enigszins onwennig met de zee en de visserij. Het toeval beschikte dat ik in plaats van onderzoek aan torenvalken, een subsidie aanvraag daarvoor was bij het BION afgewezen, toegepast onderzoek mocht gaan doen aan platvis. Mijn gevoelens waren tegenstrijdig. Aan de ene kant was ik blij een baan als onderzoeker te krijgen omdat er in die tijd veel biologen werkloos waren. De mogelijkheid 'maatschappelijk relevant' onderzoek uit te voeren was een uitdaging. Nu kon ik datgene in praktijk te brengen waarover wij als studenten zo vaak hadden gediscussieerd: een kritische wetenschapsbeoefening waarin het wetenschappelijk handelen mede bepaald zou worden door een maatschappelijke verantwoordelijkheid. Aan de andere kant was ik sceptisch over de mogelijkheden om fundamenteel wetenschappelijk onderzoek te doen. In IJmuiden aangekomen werd deze scepsis versterkt toen een aantal collega's mij verzekerde dat er geen, of maar weinig tijd, beschikbaar zou zijn voor fundamenteel onderzoek.

De primaire taak van de Nederlandse visserijbiologen bestaat uit het adviseren van de overheid en de EEG over een verantwoord visserijbeheer. De ruimtelijke schaal van de werkzaamheden en het feit dat vissen zich niet aan landsgrenzen houden, maken het noodzakelijk dat dit werk in internationaal verband wordt uitgevoerd. Zo wordt het biologisch advies ieder jaar voorbereid tijdens een werkgroep vergadering waarin een internationale groep visserijbiologen onder de paraplu van de ICES (Internationale Raad voor Onderzoek van de Zee) bijeenkomt. Voor mij was dit de “ICES North Sea Flatfish Working Group”. Op basis van onder andere de biologische rapporten stelt de ministerraad van de EEG een totale toegestane vangst (TAC) vast voor de verschillende vissoorten. Het werd me evenwel snel duidelijk dat de ontwikkelingen in de visserij zich volgens economische wetmatigheden voltrokken ongeacht de biologische adviezen. Het visserijbeleid dat erop gericht is de visserij-inspanning op platvis te verminderen door middel van TAC's, was in het begin van de tachtiger jaren van papier. In de periode 1977-1982 nam de visserij-intensiteit toe ondanks de vangstbeperkende maatregelen. Pas in de tweede helft van de jaren tachtig kwam de groei in visserij-intensiteit tot staan.

Onder deze omstandigheden 'verantwoord' wetenschappelijk onderzoek doen betekende voor mij persoonlijk dat ik in mijn werk de gevraagde rol moest spelen in het Brusselse toneelspel, maar dat ik óók een bijdrage wilde leveren aan een effectiever visserijbeleid. Daarnaast zouden de ontwikkelingen in de platvisbestanden in relatie tot de visserij zo nauwkeurig mogelijk moeten worden vastgelegd en wilde ik tijd kunnen besteden aan meer fundamenteel onderzoek naar oecologische processen in de Noordzee. Dit laatste betekende dat ik niet alleen *visserij*bioloog maar ook vooral visserij*bioloog* wilde zijn. Deze keuze werd gesteund door de toenmalige direkteur, Klaas Postuma, die mij een hart onder de riem stak door mij te verzekeren dat ik naast aandacht voor de beleidsgerichte 'assessment' biologie ook aandacht moest besteden aan fundamenteel onderzoek teneinde de geest fris en creatief te houden.

Na in de eerste jaren vooral veel gelezen en gevaren te hebben, ontwikkelden mijn ideeën zich in de richting van het bestuderen van lange-termijn veranderingen in vispopulaties. Hierin zou de invloed van de visserij kunnen worden bestudeerd, maar tevens de mogelijke invloed van andere menselijke activiteiten en van natuurlijke veranderingen (klimaat).

Het bestuderen van lange-termijn veranderingen in zeevispopulaties is goed mogelijk omdat de biologische onderbouwing van het visserijbeheer een uitgebreid routine onderzoek naar de biologie en de bestandsontwikkelingen van de commerciële vissoorten noodzakelijk maakt. De verzamelde gegevens hebben ook buiten de context van het visserijbeheer een waarde. Het visserijbiologisch onderzoek is als zodanig ongeveer 100 jaar oud. In Nederland is het platvis onderzoek vooral sinds het eind van de jaren vijftig tot ontwikkeling gekomen met het routinematig bemonsteren van de aanvoer van platvis (marktbemonstering). Sinds 1969 worden visserij-onafhankelijke gegevens verzameld door middel van bestandsopnames van jonge vis. In de tweede helft van de jaren tachtig werd de onderzoeks inspanning uitgebreid met aanvullend onderzoek naar de omvang van platvisbestanden door middel van eisurveys en bestandsopnames van volwassen vis. Dit was vooral bedoeld om het hoofd te bieden aan een afnemende betrouwbaarheid van de visserij-statistieken als gevolg van illegale visaanvoer en onjuiste rapportage van visserijinspanning en vangstgebieden.

Bij de selectie van een mogelijk onderzoeksprogramma heb ik mij laten leiden door drie overwegingen: 1) het onderzoek moet nauw aansluiten bij het bovengenoemde fundament van basisgegevens; 2) het onderzoek moet van betekenis zijn voor het visserijbeheer; 3) het onderzoek moet onze kennis en inzicht in oecologische processen vergroten. Mijn keuze is uiteindelijk gevallen op onderzoek naar de mogelijke genetische effecten van langdurige exploitatie. Dit onderzoek voldoet aan bovengenoemde voorwaarden en sluit nauw aan bij recente ontwikkelingen, zowel in de oecologie ("life-history" theorie) als in de maatschappij. In de loop van de jaren tachtig drong het besef door dat de zee naast een economische waarde ook een waarde heeft als natuur gebied. Als zodanig groeide de belangstelling voor de mogelijke effecten van de visserij op het oecosysteem.

Een studie naar de mogelijke genetische effecten van langdurige exploitatie bood een aantal voordelen. Ze sloot goed aan bij de sterk empirische onderzoekstraditie die het oecologisch onderzoek in Nederland kenmerkt en waarop het onderzoek van het RIVO geen uitzondering vormt. Joop de Veen en Niels Daan hadden al uitgebreid aandacht besteed aan de veranderingen die zich bij tong en kabeljauw hadden voorgedaan. Het gelukkige feit dat ik aan schol zou gaan werken gaf mij een voordelige uitgangspositie. Deze vissoort was al een eeuw lang uitgebreid bestudeerd. Een bijkomend voordeel was dat het onderzoek zich zou afspelen op het grensvlak van een aantal verschillende disciplines. In mijn studietijd in Groningen was me duidelijk geworden dat de voortgang in de wetenschap met name plaats vindt op de grensgebieden van bestaande disciplines.

De vraagstelling en de te volgen benadering van het probleem kristalliseerden zich uit in een periode van twee jaar en zijn in 1983 beschreven (ICES C.M.1983/G:53). Terugkijkend blijkt dat de gedurende de afgelopen tien jaar gevolgde lijn niet belangrijk afwijkt van de in 1983 uitgezette hoofdlijn, alhoewel de gedetailleerde uitwerking soms verrassend is geweest. Ook hier speelde het toeval een belangrijke rol. De uitnodiging om in 1991 deel te nemen aan een congres over de "Exploitation of Evolving Populations" vormde het kristallisatiepunt voor Hoofdstuk 2. Zonder dit congres zou ik de vraag naar de selectieve effecten van de visserij waarschijnlijk in een enkele alinea in de synthese hebben behandeld. Het beschikbaar stellen van een aantal monsters van gehoorsteentjes (otolieten) door mijn Engelse collega's Richard Millner en John Riley (Fisheries Laboratory Lowestoft) maakten het eind 1991 mogelijk om de veranderingen in groeisnelheid vanaf 1930 te reconstrueren (Hoofdstuk 3).

Een vergelijking van de plaats van de Hoofdstukken binnen dit proefschrift en de chronologische volgorde waarin ze geschreven zijn illustreert dat wetenschappelijk onderzoek zich niet in een rechte lijn van A naar B beweegt maar eerder de passen van een balletdanser volgt. Na een aantal verkennende pasjes, gepubliceerd als ICES papers[1], ben

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[1] *ICES C.M. 1983/G:53, 1984/G:52, 1985/G:53, 1986/L:9, 1987/G:53 -*

ik in 1987 'gericht' aan het proefschrift gaan schrijven. Hoofdstuk 1 en 4 ontstonden naast elkaar in 1987. Begin 1988 volgde Hoofdstuk 7 dat een verdere uitwerking was van ICES C.M. 1986/L:9 en dat in mei van dat jaar werd gepresenteerd op het Symposium "On the Ecology of the North Sea". In 1989-1990 volgde Hoofdstuk 5, in 1991 Hoofdstuk 2, en in 1991-1992 achtereenvolgens Hoofdstuk 3, 6 en 8. In 1989 heb ik veel tijd besteed aan de geldigheid en de nauwkeurigheid van de methode om aan de hand van de ringen in de gehoorsteentjes de groei-geschiedenis van individuele vissen te reconstrueren.

De voortgang bij het schrijven van het proefschrift is niet altijd maximaal geweest. Vaak heb ik mij, vanuit het proefschrift bezien, tot zijpaden laten verleiden. Ik denk evenwel dat deze zijpaden waardevolle verkenningen zijn geweest die uiteindelijk aan een verdieping van dit proefschrift hebben bijgedragen.

Achteraf kunnen we de vraag stellen of het onderzoek succesvol is geweest. Het antwoord hierop kan zowel positief als negatief zijn. Het antwoord is *nee* aan hen die de verwachting gekoesterd hebben dat dit onderzoek een bewijs voor genetische selectie zou kunnen leveren. Op voorhand kon echter al worden gesteld dat een onomstotelijk bewijs niet geleverd kon worden omdat het onderzoek noodzakelijkerwijs beschrijvend van aard was. Aquarium-experimenten met commercieel geëxploiteerde vissoorten zijn vanwege hun lichaamsgrootte en lange levensduur niet goed mogelijk. Ik geloof daarom dat de vraag met *ja* beantwoord kan worden. De analyse van de veranderingen in de voortplantingsstrategie ondersteunt de hypothese van genetische selectie en geeft een aantal specifieke hypothesen die in de toekomst experimenteel kunnen worden getoetst. Daarnaast is er een duidelijk beeld ontstaan van de witte plekken in onze kennis die richtinggevend kunnen zijn voor verder onderzoek. Het is dus mogelijk dat in de toekomst een op experimenteel onderzoek gebaseerde beschrijving van de fenotypische plasticiteit beschikbaar is die een nauwkeuriger interpretatie van de waargenomen veranderingen in voortplantingsstrategie mogelijk maakt.

Visserijonderzoek is doorgaans kostbaar door de voor het onderzoek noodzakelijke onderzoekings schepen. De gegevens die ik voor dit onderzoek nodig had konden echter verzameld worden door aanvullende metingen te verrichten - eitellingen, energiebepalingen, terugberekening van de individuele groei-geschiedenis aan de hand van gehoorsteentjes - aan materiaal dat uit de routine bemonsteringen beschikbaar was. Daardoor is het hier beschreven onderzoek relatief goedkoop geweest. In totaal zijn er slechts zes weken aan vaartijd geïnvesteerd: twee weken met de "Tridens" en vier weken met de "Isis".

Het onderzoek had evenwel niet uitgevoerd kunnen worden zonder de aanwezigheid een omvangrijke erfenis aan historische onderzoeksresultaten en bovenal ook van een veelheid aan basisgegevens, verzameld over een groot aantal jaren (marktbemonstering, bestandsopnames, merkexperimenten) en veelal dankzij de bereidwillige medewerking van het visserijbedrijf. Deze tijdreeks-informatie maakt het RIVO, evenals vele soortgelijke visserijonderzoeks instituten in andere landen, tot een goudmijn. De goudaders zijn gevormd door de inspanningen van al mijn collega's en hun voorgangers die met grote inzet en onder niet altijd even comfortabele omstandigheden hun werk hebben uitgevoerd.

Voor het RIVO moet ik speciaal mijn voorganger Joop de Veen noemen. Alhoewel ik hem persoonlijk niet heb gekend is het zonneklaar dat hij een belangrijke en stimulerende rol op het RIVO en binnen de ICES heeft gespeeld. Zijn publicaties ademen een wezenlijke interesse in biologische processen en zijn rol bij het opbouwen van de zeer omvangrijke databestanden is zeker zo belangrijk geweest. Daarnaast was de beschikbaarheid van vier goed uitgeruste onderzoekings schepen - Tridens, Isis, Stern en Schollevaar - met een gemotiveerde bemanning van eminent belang.

De werksfeer op het RIVO en in het internationale visserijonderzoek is altijd gekenmerkt door een grote openheid en hartelijkheid. Veel plezier heb ik beleefd aan de avonden van de Heren-Sociëteit waarop Frans van Beek, Niels Daan, Willem Dekker, Guus Eltink, Henk Heessen, Andries Kamstra en Frank Storbeck recente literatuur bespraken.

Niels Daan heeft geduldig en welwillend als uiterst kritisch klankbord gefungeerd. In een later stadium, na zijn benoeming als bijzonder hoogleraar in de Toegepaste Hydrobiologie aan de Universiteit van Amsterdam, heeft hij mede vorm gegeven aan het proefschrift.

Ray Beverton heeft het merendeel van mijn manuscripten als editor van het Journal du Conseil (later ICES Journal of Marine Science) of als referent van commentaar voorzien. Zijn opmerkingen resulteerden altijd in een verbetering van de artikelen. De interesse in de oorzaken achter de veranderingen in Noordzee schol en de invloed van de mens wordt door ons gedeeld. Ik hoop dat dit proefschrift een aanleiding vormt voor een verdere samenwerking bij de reconstructie van de historische veranderingen in Noordzee schol.

Willem Dekker heeft mij wegwijs gemaakt in de techniek van de variantie-analyse, in het bijzonder het gebruik van GLIM, en fungeerde eveneens als een kritisch klankbord.

Aan Frans van Beek, collega platvisbioloog, ben ik verschuldigd dat hij mij alle ruimte heeft gegeven mijn hart te volgen. Niet zonder strubbelingen hebben we, zeer verschillend als we zijn, een hecht teamverband gevonden, waarin wij ieder onze kwaliteiten kunnen ontplooien. In dit team moet zeker ook Piet van Leeuwen genoemd worden die loyaal en met interesse en grote precisie een veelheid van praktische werkzaamheden heeft uitgevoerd, in het bijzonder de interpretatie van de ringpatronen in de gehoorsteentjes. Het praktische werk is veelal uitgevoerd door Jan Apeldoorn, Kees Groeneveld, Peter Groot, Nico Molenaar, Dirk den Uijl en Bas Vingerhoed, alhoewel ook de assistenten van de pelagische afdeling regelmatig een bijdrage hebben geleverd.

Door het inzicht en de volharding van Frank Storbeck beschikt het RIVO al sinds 1988 over een goed funktionerend netwerk van personal computers, waardoor de wetenschappelijk productie aanzienlijk is verhoogd. Gerard Bais, Erik Visser en Marion Borghols droegen zorg voor het microcomputer systeem waarop wij onze uitgebreide databestanden beheren en vele analyses uitvoeren.

Bij de praktische uitvoering van de werkzaamheden heb ik verder veel steun gehad van studenten die in het kader van hun universitaire of HBO-studie een onderzoeks- of praktijk stage moesten lopen. In chronologische volgorde hebben Frances van Lent, Eric Maryniak, Bas Ibelings, Arno de Graaf, Theo Visser, Peter van der Wateren, Hans Verhagen en Feitzen Bijlsma een zeer wezenlijke bijdrage geleverd. Zonder hen zou het niet mogelijk zijn geweest om juist de extra metingen aan het routinematig verzamelde materiaal uit te voeren.

Suze Koudenburg en Cecile Huber vormden de altijd behulpzame ondersteuning in de bibliotheek.

Dr. Kees Kersting (IBN) bedank ik voor zijn hulp bij de energie-bepalingen met de bom-calorie meter, die hij tussen de motteballen op de het laboratorium van Aquatische Oecologie wist te vinden, en operationeel maakte.

Henk van der Veer (NIOZ) wil ik bedanken voor de uitnodiging in 1989 om zitting te nemen in het organisatie comité van het "International Symposium on Flatfish Ecology". Het accepteren van deze uitnodiging betekende weliswaar een verdere vertraging van de afronding van dit proefschrift, maar gaf mij de kans ervaring op te doen in het organiseren van een Symposium en de publicatie van de Proceedings. De hieruit voortvloeiende, inmiddels geformaliseerde, samenwerking tussen het NIOZ en RIVO zal de komende jaren, naar ik hoop, een stimulans voor het oecologisch onderzoek aan zeevissen betekenen.

Internationaal heb ik altijd zeer veel plezier beleefd aan de ICES aktiviteiten. Met de "North Sea Flatfish Working Group" als spil, hebben we naast de jaarlijks terugkerende bestands-beoordelingen, een aantal ondersteunende onderzoeksprojecten opgezet, vaak gecoördineerd via een "ad hoc ICES Study Group". Deze ondersteunende activiteiten hebben sterk tot het succes van de Platviswerkgroep bijgedragen en een belangrijke verdieping van ons inzicht in de oecologie van schol en tong gegeven. Binnen de Platviswerkgroep was Dick Houghton in het begin van de jaren tachtig de belangrijkste initiator. Merkexperimenten, eisurveys en een gemeenschappelijke databestand voor de leeftijdsamenstelling van de platvisaanvoer per kwartaal en per vloot werden op de rails gezet. In de tweede helft van de jaren tachtig volgden de start van een internationaal boomkor-survey in de Noordzee en het Kanaal, de analyse van de merkexperimenten van juveniele platvis, de analyse van de effecten van gesloten gebieden op de vangstmogelijkheden, eisurveys en hieraan gekoppeld een uitgebreid onderzoek naar de fecunditeit van tong. Al deze projecten hadden niet uitgevoerd kunnen worden zonder de inspanningen van: Frans van Beek, Rudy de Clerck, Uli Damm, Steve Flatman, Mark Giret, Mike Greer Walker, Dick Houghton, Richard Millner, Else Nielsen, Gert Rauck, John Riley, Wolfgang Weber en Peter Witthames.

Thuis vormden de ouderlijke zorgen voor Dirk en Joep, die zich uitstrekte van de luierwas tot het bouwen van ruimteschepen en het op tijd ophalen van het kinderdagverblijf, een bescherming tegen de aantrekkingskracht van het onderzoek. Ik denk niet dat zij mij hebben gemist. Voor Inge ligt dat anders; zij heeft mij vele avonden en soms in het weekend naar zolder zien vertrekken. Maar, zoals iedere promovendus, koester ik de (ijdele) hoop dat het leven na het verschijnen van het proefschrift wat rustiger wordt!

HOE NU VERDER ?

De boodschap van dit proefschrift, dat de schol niet meer is wat zij geweest is, zal niet voor iedereen nieuw zijn. Willem de Boer, een visser uit Urk, heeft mij al eens gekscherend gezegd, dat de tongstand niet zo sterk was afgenomen als de biologen dachten. De vissers konden de tongen immers moeilijker vangen omdat ze harder waren gaan zwemmen!

De vraag naar evolutionaire veranderingen tengevolge van de visserij is met dit proefschrift zeker niet beantwoord. Een aantal zaken kon niet volledig worden uitgewerkt omdat er nog veel onbekend is. Andere aspecten bleven onderbelicht. Zoals al is gesteld kunnen we in de komende jaren de waargenomen veranderingen mogelijk beter interpreteren, wanneer er nieuwe gegevens beschikbaar komen over bij voorbeeld de fenotypische plasticiteit en de genetische basis van het geslachtsrijp worden. Onderbelicht bleef de grootte-afhankelijke sterfte die de visserij mogelijk uitoefent. Een verdere reconstructie van de historische veranderingen in de visserij en in de populatie-dynamica van schol is zeker de moeite waard. Schol is een van de weinige kandidaten onder de zeevissen waarvoor een voldoende lange serie gegevens beschikbaar is om de lange-termijn effecten van exploitatie te kunnen bestuderen.

Of het RIVO zijn vooraanstaande rol in het visserijonderzoek zal kunnen handhaven is nog maar de vraag. Ook het RIVO is niet meer wat zij geweest is. De tendens tot een commercialisering van het visserijbiologisch onderzoek vormt een wezenlijke bedreiging van de noodzakelijke continuïteit in het verzamelen van gegevens betreffende de bestandsontwikkelingen en de veranderingen in biologische parameters van commercieel geëxploiteerde vissoorten. Onder het Regentschap van de Gulden kunnen de intenties tot een versterking van fundamenteel en oecosysteem onderzoek wel eens loze woorden blijken.

Ik hoop dat dit proefschrift aan allen die werkzaam zijn in de sfeer van het visserijbeleid, het milieubeleid én in het management van marien biologisch onderzoek duidelijk maakt, dat de lange tijdreeksen van "visserijbiologische" gegevens, voor groot scala aan vragen over de invloed die de mens op de veranderingen in de Noordzee uitoefent, onontbeerlijk zijn.

Santpoort september 1992

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