Changes in the distribution of North Sea plaice (Pleuronectes platessa)

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Internal Report 04.023

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Publication Date: 31-08-2004

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Summary

The North Sea flatfish fisheries generate considerable numbers of discards, especially of plaice (*Pleuronectes platessa*). Their survival is very low. To reduce discard mortality, a partially closed area was established ("plaice box") in 1989. The beam trawl fishery in this area was prohibited for vessels larger than 300 hp. Because the Plaice Box encompassed the major nursery grounds of North Sea plaice, it was expected that, at the same rate of exploitation, the introduction of the plaice box would enhance recruitment, yield and spawning stock biomass.

During an evaluation of the plaice box in 1999, it became clear that since 1989, the yield and spawning stock biomass had declined by about 40%. A possible explanation for this decline is that there has been a shift in the spatial distribution of North Sea plaice. It is possible that the young undersized plaice inhabit places further away from the coast so that the plaice box is not offering as much protection against discarding as originally supposed.

In this research we tested if the spatial distribution of plaice has changed in time. This study consisted of two parts. In the first part we analyzed the distribution of individual cohorts with the help of a generalized linear model. The effects of temperature and growth on the distribution were also tested. In the second part we studied the spatial distribution of different length groups in three different periods, 1902-1909, 1983-1987 and 1999-2003. We used the total mean crowding to test if the intraspecific competition changed in time.

The results showed that the spatial distribution of plaice has changed in time. The model showed that the distribution of mainly the 0- and 1-group plaice has changed in the period 1970-2002. This change seems to have started around 1993. The model did not give significant effects of temperature en growth on the distribution. The first part supposed that the change in the spatial distribution started around 1993, but the results of the second part showed that the change already took place ever since the beginning of 1900. The intraspecific competition was high in the first period (1902-1909) for the length group 10-19 cm and clearly declined in the two succeeding periods. The rates of intraspecific competition for plaice bigger than 20 cm were much lower. Of these rates we can take on that no intraspecific competition took place. The intraspecific competition decreased considerably for the juvenile plaice. This could have had effect on the distribution. It is possible that they could extend their distribution due to the decreased intraspecific competition.

1. Introduction

Plaice (*Pleuronectes platessa*) is a flatfish species living in temperate waters. Plaice is mainly concentrated in the southern and south-eastern North Sea, but its complete distribution ranges from the Bay of Biscay to the Barents Sea and the waters around Iceland (Wimpenny, 1953; Harding *et al.,* 1978). The population consists of several subgroups that partially mix on the summer feeding grounds in the central North Sea but split up to spawn over different grounds in winter (de Veen, 1978a). After spawning, the pelagic eggs and larvae drift with the residual current in the open sea. At the end of the larval stage, plaice settle in shallow nursery areas on sandy beaches in estuarine areas. Adult plaice are distributed in deeper offshore waters. During the first years of their life, juveniles migrate seasonally between offshore and inshore and only after maturation plaice participate in distinct migrations between feeding and spawning areas (Wimpenny, 1953; Rijnsdorp & van Beek, 1991).

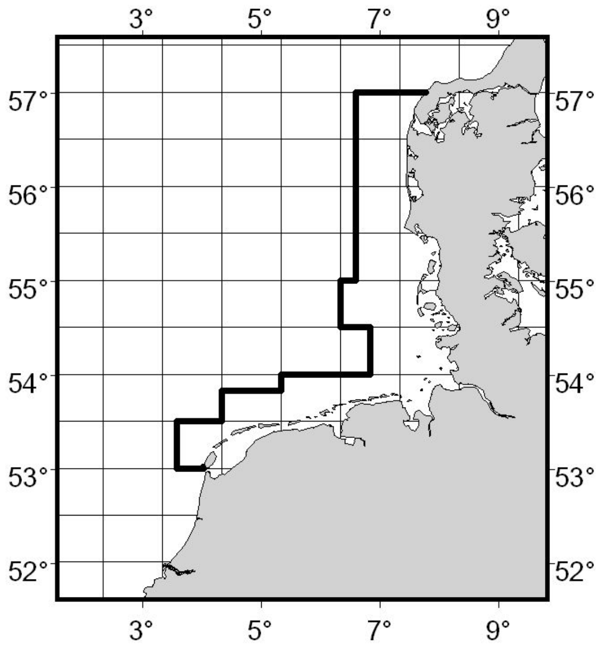

Figure 1. Map of the plaice box

Plaice is an important species in the commercial trawl fishery. The rate of discarding is high (van Beek, 1998) and the undersized fish are restricted to coastal waters. Because of that, a protected area was proposed to improve the exploitation pattern of the stock (ICES, 1987).
In 1987 the North Sea Flatfish Workgroup was asked to give advice to improve the exploitation pattern of plaice in the North Sea using the annual data about the distribution of plaice, data considering discards of plaice per area and season, and data about other species like sole (ICES, 1987).
The working group analyzed the effects of a closed area for all fisheries on plaice. This area along the coast of Denmark, Germany and the Netherlands encompassed the major nursery grounds of North Sea plaice. Historical information on the distribution of plaice, the fisheries effort and simulation models showed that closing the area would enhance recruitment, yield and spawning stock biomass (ICES, 1987).
In 1989, the plaice box was established as a partially closed area along the Dutch, German and Danish coast with the aim to reduce discarding of undersized plaice (figure 1). Beam and otter trawlers larger than 300 hp were expelled from the area during the second and third

quarter. The regulation was extended to the fourth quarter in 1994. Since 1995, the plaice box has been closed during the entire year for vessels larger than 300 hp.

In contrast to the expectation the yield and spawning stock biomass had declined by about 40% since 1989 (ICES, 1999).
A possible explanation for this decline is that there has been a shift in the spatial distribution of plaice. It is possible that the young undersized plaice inhabit places further away from the coast so that the plaice box is not offering as much protection against discarding as originally supposed.
The main question to be answered in this research will be:

“Has there been a shift in the spatial distribution of plaice?”

And when there has actually taken place a change in the spatial distribution of plaice additional questions follow:

“Is the change in distribution observable in all different age/length groups?”

“Which factors are responsible for the changed spatial distribution?”

“Is the changed distribution a phenomenon which occurred in the last decades or did it start earlier?”

It is obvious from the life cycle that different physical parameters may influence the distribution and abundance of North Sea plaice. Talbot (1978) described that predation, water drift and temperature variability as well as wind influence the mortality of plaice during the first life stages. Gibson (1994) named food, predators, temperature, salinity, oxygen, habitat structure, water depth and hydrodynamics to be the major factors contributing to growth and survival of juvenile stages of flatfish.
To explain an eventual change in de spatial distribution we will focus on three factors, namely growth, temperature and intraspecific competition.
Growth may play a role in the distribution of plaice as results of Borley (1923) showed that in periods of high population abundance and low growth the movement away from the coast was less observable. In North Sea plaice the relation between growth and stock size is not very clear. In the period after the Second World War, the weight at age of 10 to 13-year-old fish was reduced by about 20%, whereas stock size increased almost threefold (Beverton & Holt, 1957). Bannister (1978) did not find a relation between growth and stock abundance although he showed that the length at age of the very strong year class 1963 was lower throughout its life time. A significant negative correlation between growth of 0-group plaice and year class strength was found by Rauck and Zijlstra (1978) and they concluded that juvenile growth was density dependent. In 1982 Zijlstra *et al.* showed that this negative relation could at least partly be explained by the shorter growing season of strong year classes due to a delay in the immigration of larvae into the nursery areas at low water temperatures.
The specified factors, which are studied, are affected by each other. The strength of a year class is dependent of the temperature during the spawning period, while the growth of plaice seems to be affected by the stock size as well as temperature. It is likely that intraspecific competition may play a role in the distribution pattern of plaice. When the densities are high, older and larger plaice may prevent the smaller individuals to move into deeper water. When there is less competition as a result of decreased presence of larger plaice, it would be possible for the smaller plaice to extend their distribution to places further offshore.

We named temperature as a factor affecting the strength of a year class, but it could also influence the distribution of juvenile plaice. As a cue for timing movement, temperature plays a role in the seasonal movement between onshore and offshore habitat, in particular in shallow waters where temperature fluctuations are wider than at greater depths.
There is some evidence that juvenile plaice have an endogenous annual rhythm of temperature preference (Zahn, 1963). One clear example of temperature as a cue for movement is provided by the mass ‘exodus’ of newly settled plaice from intertidal pools in the Wadden Sea when the temperature exceeds critical levels of about 24^{o}C (Van der Veer & Bergman, 1986; Berghahn *et al.*, 1993).
So temperatures may have a direct and indirect effect on the distribution of plaice.

It is expected that there has taken place a shift in the distribution of plaice as was already stated by ICES in 1999. This change will be most obvious in the smaller length groups because their distribution is restricted to shallow coastal waters. The larger plaice are more equally distributed over the North Sea.
To learn more about the distribution of undersized North Sea plaice, we analyzed the following survey data:

- Beam Trawl Survey (BTS) (1985-1987, 1999-2003)
- KW34 en KW36 (precursor of BTS) (1983, 85, 86, (KW34) and 1987 (KW36))
- Sole Net Survey (SNS) (1970-2002)
- Historical data (1902-1909)

We will use these survey data to compare the distribution of North Sea plaice during three different periods. The distribution of individual cohorts will be analysed in detail using the data of the Sole Net Survey.

2. Materials and methods

2.1 Analysis of the spatial distribution of plaice during the period 1970-2002
In this part of the research we analyzed the relation between numbers of plaice and distance from the coast during the period 1970-2002. A generalized linear model was used to statistically test for a shift in the distribution of young plaice.

2.1.1 Survey
To study if the relationship of the abundances of different age groups of plaice and distance from the coast changed in time, we used data derived from the Sole Net Survey (SNS).
This survey started in 1970 and is being performed annually in September and October. The SNS survey consists of more or less fixed stations on transects which run parallel or perpendicular to the coast in Dutch and Danish waters.
The SNS covers a depth range from 10 to 40 m. The gear used is a 6-m beam trawl with a standard ground rope and four tickler chains and a cod-end stretched mesh size of 40 mm. Standard haul duration is 15 minutes at a towing speed of approximately 2.0 m s^{-1}.
The stations consists of ten transects. The number of hauls varies per transect, but at least four hauls are performed. An overview of the positions of the transects is shown in figure 2.1.
In this study we concentrated on 3 different transects, e.g. 601, 606 and 660 (figure 2.1). Transect 606 and 660 are combined into one transect (666) because 606 lies prolonged from transect 660.

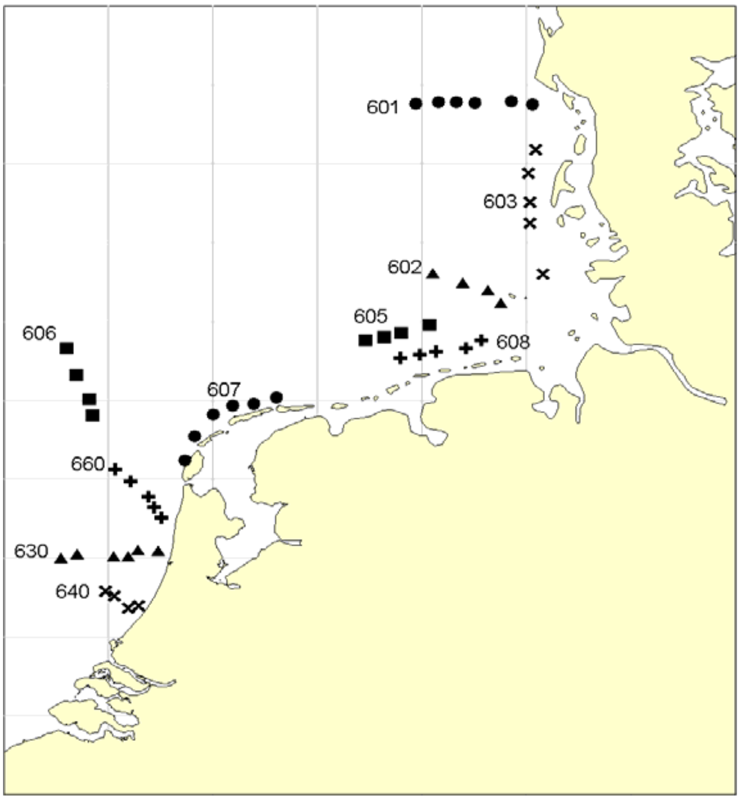

Figure 2.1. Map of the transects of the SNS survey. In this analysis, transects 601 and 666 (combination of 660 and 606) were used.

2.1.2 Data analysis

Age is determined from otoliths. Age-length keys were established for each year, and used to convert the size frequency into age compositions.

The catches per haul were converted to numbers per fishing hour.

The distance from the coast was determined by converting the differences in degrees between the longitude of the sampling stations and the longitude of the coast into kilometres. The longitude of the coast for transect 666 was specified as 4.8°E and for transect 601 as 8.35°E.

A generalised linear model of log-transformed (log +1) catch rates (numbers hour^{-1}) was used for the statistical analysis of the variation in catch rates:

$$\log(C_R + 1) = A + D + YC + D*A + D*Y + D*Y*A, \quad (1)$$

in which C = catch rate (numbers hour^{-1}), R = transect, A = age group, D = distance from coast (km), YC = year-class and Y = year, where A and YC are class variables. D and Y are continuous variables. A and YC correct for the difference in catch rate induced by age groups and year-classes. The parameter estimate for D represents the slope of the decline in numbers with distance. This slope is different for each age group which is accounted for by the parameter $D*A$. For age 1 and age 2 plaice the parameter will be negative, as the numbers will decrease with increasing distance from the coast. The interaction term $D*Y$ examines whether the slope of the numbers with distance has changed in time ($D*Y$). If this term is significant, the slope has changed over the years and we may conclude that the distribution of plaice over distance has also changed over years. A type 1 analysis was used to test whether the parameters included in the model significantly contribute to the explained variation in catch rates.

Because we included year as a continuous variable in this model, a significant result for the terms $D*Y$ and $D*Y*A$ suggests a linear trend in the change of the slope. A separate model was ran with Y as class variable to estimate the slope of the relation between log catch numbers and distance for individual years.

When the type I analysis gave significant rates for the factors $D*Y$ and $D*Y*A$, which indicates that there has been a change in the distribution of plaice, the model was expanded to explain this change.

Two more factors, e.g. growth and water temperature, were separately added to model 1.

A growth index derived from back-calculated mean length at age 2 of female plaice was used to test whether growth had a significant effect on the distribution of plaice:

$$\log(C_R + 1) = A + D + YC + D*G + D*A + D*Y + D*A*G + D*Y*A \quad (2)$$

in which C = catch rate (numbers hour^{-1}), R = transect, A = age group, D = distance from coast (km), G = growth index, YC = year-class and Y = year.

A significant interaction term $D*G$ indicates that the slope of the relationship between catch rate and distance from coast is affected by the growth index. The term $D*A*G$ indicates that the effect of the growth differs across age groups.

To test whether water temperature had a significant effect on the distribution we added temperature measurements to the model (1). These measurements are taken daily at "'t Horntje", Texel since 1947.

We presumed two possible effects of water temperature. First, high water temperatures during spring (March – June) could negatively affect the food availability for plaice which would enhance the migration to deeper water further away from the coast.

Secondly, high water temperatures during summer could directly cause a shift to deeper water further away from the coast due to temperature preference.
Because the water temperature of preceding years could also affect the distribution of plaice of age 1 and older, the model was performed for each age group separately. Age group 4 was not modelled because no water temperature effects were expected.
The model for age group 1 to 3 was now as follows:

Age 0: $\log(C_{R,A}+1) = D + Y + D*T_x + D*Y$ (3)

Age 1: $\log(C_R+1) = D + Y + D*T_x + D*T_{x-1} + D*Y$ (4)

Age 2: $\log(C_R+1) = D + Y + D*T_x + D*T_{x-1} + D*T_{x-2} + D*Y$ (5)

Age 3: $\log(C_R+1) = D + Y + D*T_x + D*T_{x-1} + D*T_{x-2} + D*T_{x-3} + D*Y$ (6)

in which C = catch rate (numbers hour^{-1}), R = transect, A = age group, D = distance from coast (km), Y = year, T_x = water temperature (spring or summer) in current year and T_{x-i} = water temperature in year x-i.

2.2 Comparison of three periods

In this part we compared data originating from three different periods. Unique data obtained in the period 1902-1909 is compared with data from the periods 1983-1987 and 1999-2003 to find out the distribution already changed after the turn of the century.
We analyzed the relationship between the catch rates of different length groups and the distance from the coast and analyzed possible changes in competitive interactions.

2.2.1 Surveys

1902-1909

Trawl surveys using three different gear types were carried out in the first decade of the 20th century by fisheries laboratories in England (Garstang, 1905; Anon., 1912) and the Netherlands (Anon., 1908, 1909, 1910). The English research vessel RV “Huxley” used either a 26.5 m headline otter trawl (OT90), with a ground rope of 38.5 m consisting of a wire core without a chain, or a 13 m beam trawl (BT13).
Tow duration varied between 1 and 3 h for both gears. For each hall, the numbers of the larger fish species caught are available and for the principal species (flatfish, roundfish, gurnards, rays, skates, sharks, dogfish) size distribution data are available by 10-cm groups. Station information includes position, depth, date, time of day, and haul duration.
The Dutch vessel RV “Wodan” used a similar 26.5 m otter trawl to RV “Huxley”. The same station information was collected as for the RV “Huxley” surveys and a record of all fish species and invertebrate species caught was maintained.
In this analysis only the data from the surveys which used a 26.5 m headline otter trawl or a 13 m beam trawl were used.

1983-1987

Data for this period were collected in the offshore waters (1983, 1985-1987) by two chartered commercial fishing ships ("KW34" and "KW36") and in the coastal waters (1985-1987) by "Isis" (Beam Trawl Survey).

"KW34" collected data in the years 1983, 1985 and 1986. "KW36" only did this in 1987. The ships both used a 12 m beam trawl except for the year 1983 when "KW34" used a 14 m beam trawl. Mesh size was 85 mm. Tow duration 30 minutes (range 10-40 min.) with a towing speed of 5-5.5 nm/hr. Eight tickler chains ran in front of the groundrope.

Fishing methods for RV "Isis" are described below.

1999-2003

The data for this period was collected during the BTS survey. This survey makes use of an 8 m beam trawl (BT8) and is conducted by the RV "Isis" and RV "Tridens".

The BT8 survey is carried out in August-September and covers the southern and south-eastern North Sea. The sampling area is stratified by ices rectangles of 0.5^{o} latitude and 1^{o} longitude (± 30 x 30 mile) in which one to four hauls are made. The beam trawl is equipped with a ground rope consisting of a chain with rubber discs (20 cm diameter) in the central part. Eight tickler chains run in front of the ground rope. Haul duration is 30 minutes and towing speed 4 nm/hr.

The procedures for recording fish catches were the same for the two surveys. The catch was sorted by species, sub-sampled if necessary, and the numbers caught and their distributions (cm below) were recorded.

Swept area correction factors

Different fishing gears vary in efficiency in catching individual species of fish (or even in catching different sizes of fish within one species) due to a multitude of factors (Gunderson, 1993). Rijnsdorp *et al.* (1996) used the swept area as a correction factor for the catch rates obtained with any one gear. In this study the same approach was used.

The area swept by the gear was estimated from the towing speed and the horizontal net opening. The resulting factors were used to standardize roughly the trawl catches in approximately similar units. The details of survey gear used and the correction factors are given in table 2.1.

Table 2.1. Details of survey gear used in the trawl surveys

	1902-1909 BT13	1902-1909 OT90	1983-1987 BT14	1983-1987 BT12	1983-1987 1999-2003 BT8
Haul duration (min)	60-180	60-180	10-40	10-40	30
Codend mesh (mm)	63	68	85	85	40
Tickler chains	0	0	8	8	8
Towing speed (nm/hr)	2	2	5-5.5	5-5.5	4
Sweep (m)	13	17	14	12	8
Swept area (1000 m^2 h^{-1})	50	60	140	120	60
Relative catch efficiency	0.85	1	2.3	2	1

2.2.2 Analysis

In all three periods most of the hauls were taken in the third quarter, so the third quarter data was used in this analysis.

For all periods catch numbers per haul were converted to numbers per hour of fishing corrected for the swept area. Then the average numbers per hour of fishing were averaged per ICES rectangle and used in the further analyses.

The plaice were grouped into four 10 centimetre size classes (10-19 cm, 20-29 cm, 30-39 cm and 40-49 cm) and one rest group (> 50 cm).

2.2.2.1 Distribution maps

With the use of "The SAS system for Windows" maps with numbers per hour of fishing per ICES square, length group and period were made. In these maps the sizes of black dots indicate for the amounts of plaice of a specific length group. An "x" indicates that there has been fished in the rectangle, but that no fish of the concerning length group was caught.

2.2.2.2 Cumulative mean catch rates per length group over the distance from coast

The distances from the continental coast for each haul were calculated making use of "Arc View". Hauls west of longitude 2^{o}E were not used in this analysis assuming that only plaice east of that longitude originate from the continental nursery areas.

For each period the cumulative mean catch rates (N.hr^{-1}) over 20 kilometre distance classes per length group were calculated and displayed in a diagram.

2.2.2.3 Population structure over distance from coast

The same data as described in 2.2.2.2 was used to calculate the proportions of each length group in a specific distance class. For each period the compositions of the population over the complete range of distance classes were displayed in a diagram. The proportions are based on the mean catch rates (N.hr^{-1}) and not on absolute numbers, so we can not speak of the actual population structure.

2.2.2.4 Coefficient of overlap and total mean crowding

This analysis was based on the numbers per fishing hour per ICES rectangle. Only the rectangles sampled in all three periods were included.

An index of the competitive interaction between individuals was estimated using the index of 'mean crowding' as proposed by Lloyd (1967).

Lloyd's index of mean crowding (*m*) is defined as:

$$m = \frac{\sum_i x_i^{\;2}}{\sum_i x_i} - 1 \qquad (7)$$

where *m* is the index of mean crowding and x_i is the number of individuals in the *i*th spatial unit.

The index of mean crowding gives the average number of individuals with which an individual has to share the spatial unit. Lloyd (1967) developed this index for terrestrial ecological studies where the interacting individuals have a similar size. In our case we are not only interested in the interaction within an age group but also in the interaction within a length group and in the interaction between different length groups.

Lloyd (1967) showed that equation (7) can be extended to apply to mean crowding between length groups or species. A crude estimate for the mean crowding by length group *b* on length group *a* is:

$$_{b}m_{a} = \frac{\sum_i x_{a_i} \cdot x_{b_i}}{\sum_i x_{a_i}} \qquad (8)$$

where ${}_b m_a$ is the index of mean crowding by length group *b* on length group *a*, and x_{ai} and x_{bi} are the numbers of length group *a* and *b* respectively in the *i*th spatial unit.
The total mean crowding on length groups *a* by all length groups *b* is (Rijnsdorp & van Beek, 1991):

$$m_a = \sum_b {}_b m_a \tag{9}$$

3. Results

3.1 Analysis of the spatial distribution of plaice during the period 1970-2002

All parameters included in the model explain a significant proportion of the variance in the catch rates (Table 2.1). The total model explains 63.2% of the variance in transect 601 and 60.3% in transect 666. Age, year-class and the interaction term distance*age explain most of the variance in catch rates. The parameter *D* is significant and explains 4.7% of the variation in catch rates in both transects, so there is a relationship between the catch rates and distance from the coast. This relationship differs between different age groups (*D*A*). Together these parameters (*D* + *D*A*) explain a considerable part of the variance. In transect 601 these parameters together explain 24.7% of the variance and 15.3% in transect 666.

*D*Y* and *D*Y*A* are significant too, which means that the relationship between the catch rates and distance from the coast has changed in time and that this change is different for various age groups. The parameter *D*Y* explains 1.2% and 0.8% in transects 601 and 666, respectively. This means that the change in the relationship is stronger in transect 601. The explained variation by interaction term *D*Y*A* is bigger for transect 601 as well.

Table 3.1. Statistical evaluation of the influence of age (*A*), distance (*D*) and year (*Y*) on the catch rates in the transects 601 and 666.

Area	Source	SS	%	df	MS	F	p
601	*A*	1861.1	23.5	4	465.3	202.1	<.0001
	D	371.3	4.7	1	371.3	161.3	<.0001
	YC	907.5	11.5	36	25.2	10.9	<.0001
	*D*A*	1580.6	20.0	4	395.1	171.6	<.0001
	*D*Y*	98.4	1.2	1	98.4	42.7	<.0001
	*D*Y*A*	182.2	2.3	4	45.5	19.8	<.0001
	Explained	5001.0	63.2	50	100.0		
	Unexplained	2912.4	36.8	1265	2.3		
	Total	7913.4	100.0				

Area	Source	SS	%	df	MS	F	p
666	*A*	2053.3	33.5	4	513.3	389.0	<.0001
	D	290.2	4.7	1	290.2	219.9	<.0001
	YC	568.1	9.3	36	15.8	12.0	<.0001
	*D*A*	648.3	10.6	4	162.1	122.8	<.0001
	*D*Y*	47.3	0.8	1	47.3	35.8	<.0001
	*D*Y*A*	86.0	1.4	4	21.5	16.3	<.0001
	Explained	3693.3	60.3	50	73.9		
	Unexplained	2428.2	39.7	1840	1.3		
	Total	6121.5	100.0				

The type I analysis gives parameter estimates. With these estimates the slopes of the relationship between the catch rates and distance can be calculated. Figure 3.1 shows that the slopes of all age groups seem to change in time. The change is most obvious for age group 1 in both transects, but the change is stronger in transect 601.

To get a more precise view on the change in the slopes in the period 1970-2002, the same model was analyzed with year as a class variable. The calcu-lated slopes from the parameter estimates are shown in figure 3.2.

It is clear from figure 3.2 that the change in the slope is most obvious for age groups 0 and 1. The change is less visible for age group 2. The change of the slope is strongest in transect 601.

In figure 3.1 a linear change of the slopes is shown, but when we look at figure 3.2 we can see that the slopes stays at a same rate until 1993, with small increasing rates around 1985, and ever since 1993 the slopes are at higher rates. This means that the slopes became less negative, or in the case of age group 2, more positive.

All these patterns are visible, though less clear, in transect 666.

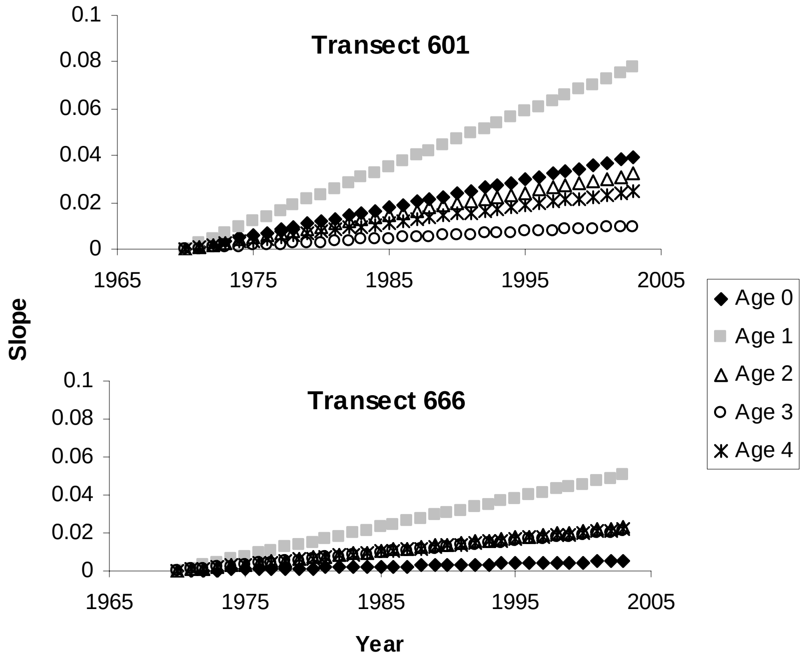

Figure 3.1. Change of the slope of the relationship between catch rates and distance from the coast in the period 1970-2002 per age group for transects 601 and 666. The slopes of year 1970 have been set to zero.

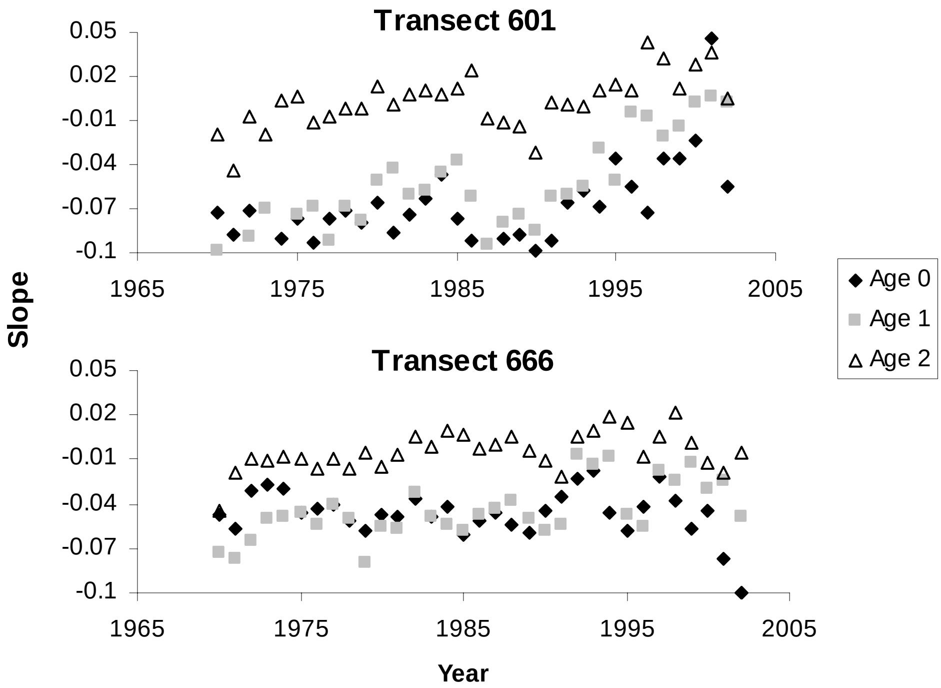

Figure 3.2. Estimated slopes of the relationship between catch rate and distance from coast for age groups 0, 1 and 2 in the period 1970-2002 for transects 601 and 666. A negative slope indicates that abundance decreases with distance; a slope of 0 indicates that there is no relationship between distance and abundance; a positive slope indicates that abundance increases with distance.

3.1.1 Effects of growth and temperature on the distribution of plaice

The models for both growth and water temperature gave no satisfying results. For the growth index no significant results were found. The water temperature in spring and summer gave some significant results, but when we looked at the parameter estimates, the results were very inconsistent. From the results no clear relationships could be determined.

The cause of these inconsistence is probably the great variation in the slopes as well as in the growth index and temperatures. Another problem is the increasing complexity of the model.

To still get a view on the relationship between the water temperature and the distribution of plaice, we plotted the average slopes of 3-year periods with the average water temperature (summer and winter) of 3-year periods. We also did this for the growth-index. The results are shown in figure 3.3 and figure 3.4.

In transect 601 it can be seen that the water temperature in summer shows a relationship with the slopes of age groups 0 and 1 and in a lesser extent with age group 2. Especially ever since around 1993 the slopes show a similar trend as the summer water temperature. In transect 666 the relationship is less visible as a result of a less changing slope. The winter water temperature shows a peak around the beginning of the 1990s, but no clear effect of these high temperatures can be seen on the slopes. Thus no relationships can be deduced from these figures with winter temperature.

When we look at the plots with growth index, no clear patterns can be discovered. Only at the 0-group plaice in transect 666, the slopes seem to have the same pattern as the growth index. For the other age groups no clear effects of high or low growth indices can be observed.

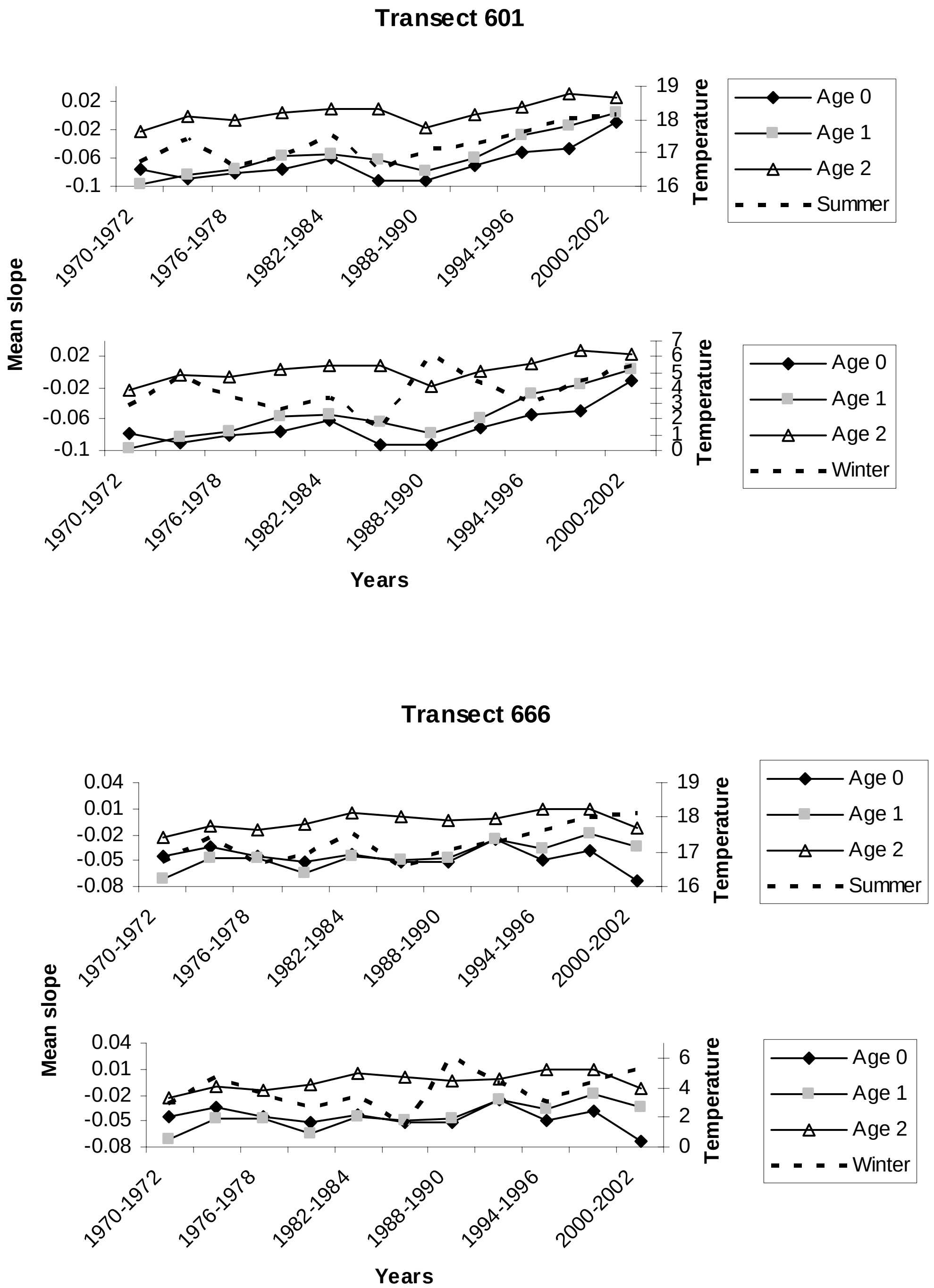

Figure 3.3. Mean slopes of 3-year periods with mean summer and winter water temperatures for ages 0, 1 and 2 in transects 601 and 666.

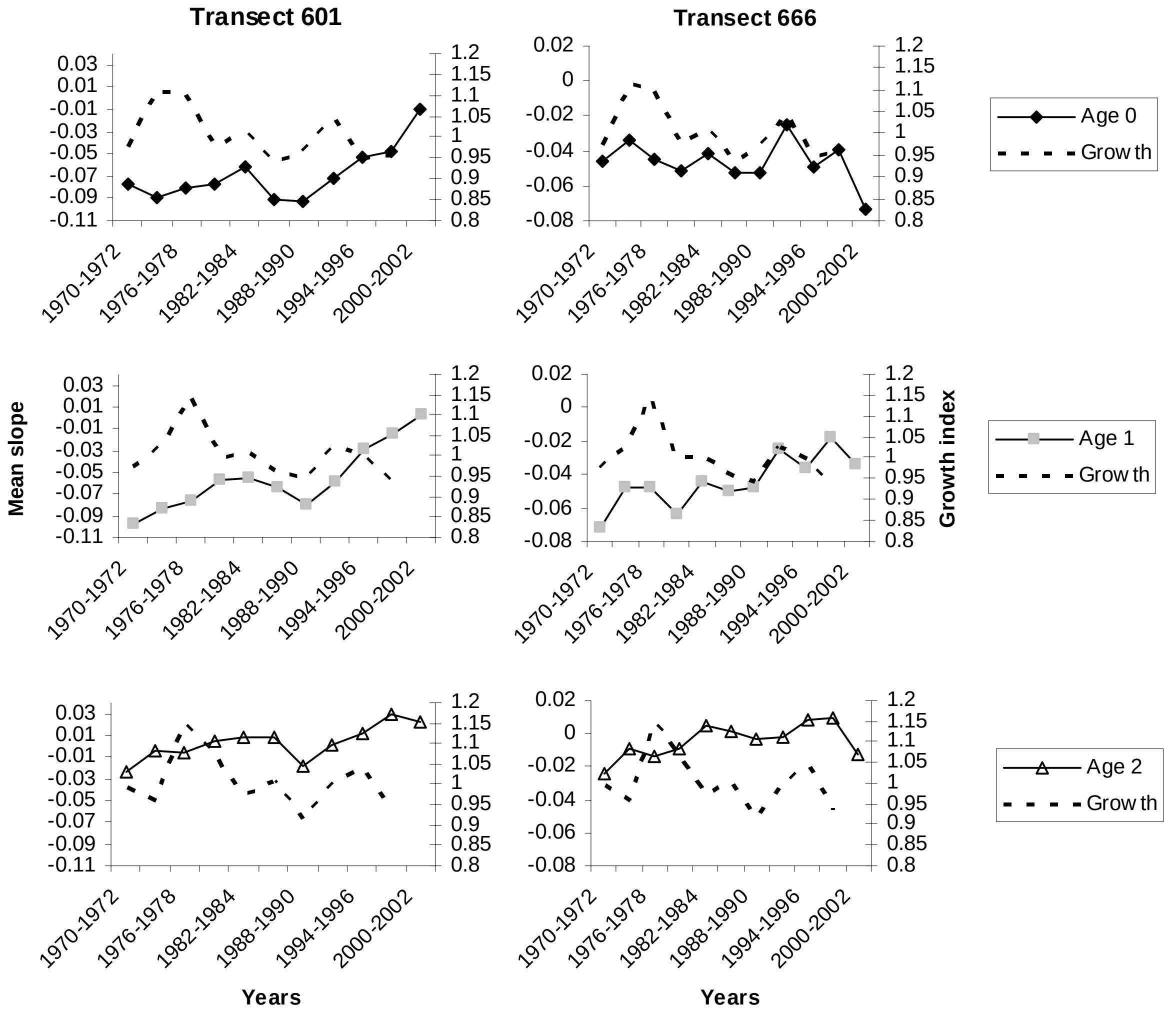

Figure 3.4. Mean slopes of 3-year periods with mean growth index for ages 0, 1 and 2 in transects 601 and 666.

3.2 Comparison of three periods

In figure 3.5, 3.6 and 3.7 the distribution maps of the different length groups are shown for the periods 1902-1909, 1983-1987 and 1999-2003. When we look at the general pattern of the distribution, we can see that this is the same for all periods. The smallest length group (10-19 cm) is strictly bounded to the coastal zones and with increasing lengths plaice gradually moves to places further away from the coast. Plaice of 50 cm and larger are barely found in the coastal zones.

When we compare the distribution of specific length groups in the three different periods, there are clear changes visible. Length group 10-19 cm shows a similar distribution pattern in the first two periods, but in the period 1999-2003 plaice of that length group have spread out to places further away from the coast. Looking at length group 20-29 cm, we can see that the distribution is slightly different in the second period compared to the first and that the distribution is completely different in the most recent period. In the last period plaice of that length group also occur in the central North Sea, while this was not the case in the two previous periods. Plaice of 30-39 cm show difference in distribution between the first and the last two periods. Plaice of 40 cm and larger do not show different patterns between the three periods. The overall catch rates, especially those of the larger length groups, are much lower in the first period compared to the period 1983-1987. This is also the case for the last period, 1999-2003.

The patterns which can be seen in the distribution maps can be confirmed by the cumulative numbers in figure 3.8. In that figure the cumulative mean catch rates of a specific length group over the total range of distance classes are given for each period. For the length group 10-19 cm no big differences can be seen. In all periods 50% of the cumulative numbers of that length group can be found within 60 km from the coast. Furthermore no clear differences can be found, although in the last period it appears that a small part of the cumulative numbers occurs at distance classes further away from the coast compared to the preceding periods.

Looking at the 20-29 cm length group, big differences can be found. The first two periods have similar cumulative numbers, but in the last period larger proportions are found further away from the coast. In the first two periods around 80% of the cumulative numbers is within 100 km from the coast, while in the last period that percentage is reached at 180 km from the coast. The line of the cumulative numbers in the last period is more smoothly. This means that plaice of this length group is kind of evenly distributed over the complete range of distance classes which are occupied.

This is completely the case for plaice of length group 30-39 cm. The cumulative numbers follows a straight line, so the numbers are evenly distributed over the complete range of distance classes. For this length group it is not only obvious in the latest period, but also in the period 1983-1987. For these periods the distribution is similar.

For plaice bigger than 40 cm no differences in the cumulative frequencies between the three periods can be found. All periods show similar patterns. Plaice of these lengths are evenly distributed over the distance classes which are occupied. Only in the latest period for plaice bigger than 50 cm larger amounts are found further away from the coast compared to the two preceding periods.

Till now we only have been looking at the level of specific length groups. It is also important to look at all length groups together. In figure 3.9 we can see the proportions of each length group on the total numbers per distance class for each period.

Comparing the three periods, we can see that the length group 10-19 cm takes larger proportions of the total numbers in the second and last period. It can also be seen that this length group extends its distribution to places further away from the coast. For the length group 20-29 cm, the proportions in the first two periods are the same, but in the last period this length group accounts for a bigger proportion in the distance classes further away from the coast. The proportions of plaice larger than 30 cm are considerably reduced in the latest period.

We used the total mean crowding as an index for the intraspecific competition. The total mean crowding is based on the mean catch rates ($N.hr^{-1}$) per ICES square. We used the swept area as a correction factor for the catch rates obtained with any one gear. We used the BT8 gear as the standard. In table 2.1 it can be seen that the swept area is 60.000 m^2 per hour for this gear type. The total mean crowding gives the total individuals with which an individual of a specific length group has to share the spatial unit, which is in this case 60.000 m^2.
It is clear from figure 3.10 that the total mean crowding on length groups 10-19 cm and 20-29 cm is highest in the first period and that these rates decreased in the two following periods. The levels of total mean crowding in the last period are more than a factor two lower as compared to the first period. The decline in these rates is considerable as well when we compare the periods 1983-1987 and 1999-2003.
It is necessary to take a closer look to the rates of total mean crowding to understand what these rates really mean. We have to take the swept area in to account. In the period 1902-1909 the rate of total mean crowding for length class 10-19 cm was 2400, which means that 100 m^2 has to be shared by 4 individuals. In the period 1983-1987 3 individuals have to share 100 m^2 and in the last period this number is 1.8.
For the length class 20-29 cm the rates of total mean crowding are much lower. In 1902-1909 100 m^2 has to be shared with 2.8 individuals. In the second period this number is 1.7 and in the most recent period the number of individuals is 1.
For the other length groups no big changes can be observed although the total mean crowding on plaice of length 40 cm and bigger increased a little bit in the two latest periods compared to 1983-1987, but this change can be disregarded.
Figure 3.11 shows the percentage of the total mean crowding of each length group which crowds on a specific length group. We can see that the proportions of plaice of length group 10-19 cm crowding on other length groups has become bigger in the two last periods compared to the first one. This is especially the case for crowding on the larger length groups. The proportions of length 30 cm and larger crowding on its own length group and other length groups has declined.

Figure 3.5. Catch rates (numbers hour^{-1}) per ICES square in the period 1902-1909 for plaice of length group 10-19 cm (upper left), 20-29 cm (upper right), 30-39 cm (middle left), 40-49 cm (middle right) and >50 cm (lower left).

Figure 3.6. Catch rates (numbers hour^{-1}) per ICES square in the period 1983-1987 for plaice of length group 10-19 cm (upper left), 20-29 cm (upper right), 30-39 cm (middle left), 40-49 cm (middle right) and >50 cm (lower left).

Figure 3.7. Catch rates (numbers hour^{-1}) per ICES square in the period 1999-2003 for plaice of length group 10-19 cm (upper left), 20-29 cm (upper right), 30-39 cm (middle left), 40-49 cm (middle right) and >50 cm (lower left).

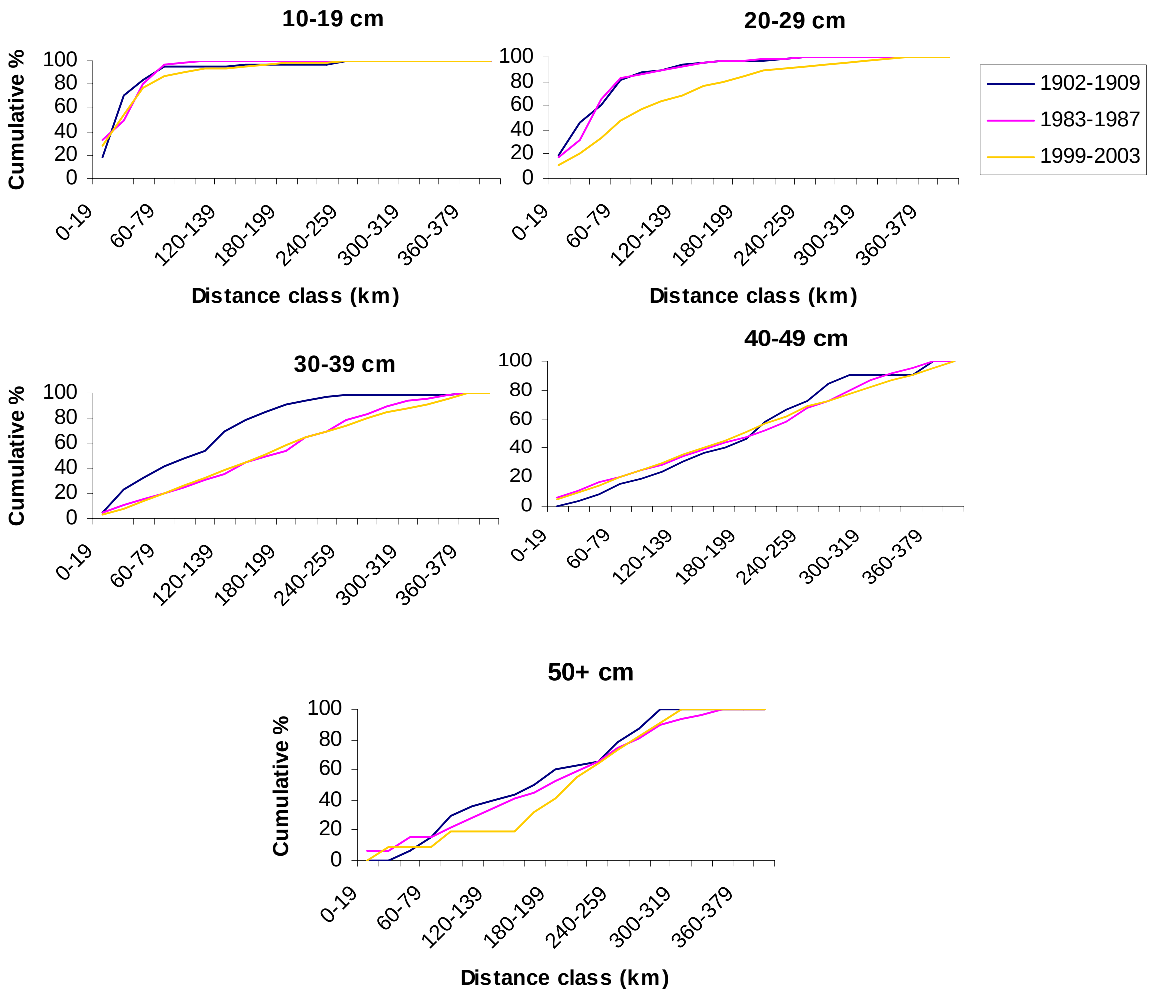

Figure 3.8. Cumulative mean catch rates (N.hr^{-1}) of different length groups over 20 km distance classes per period.

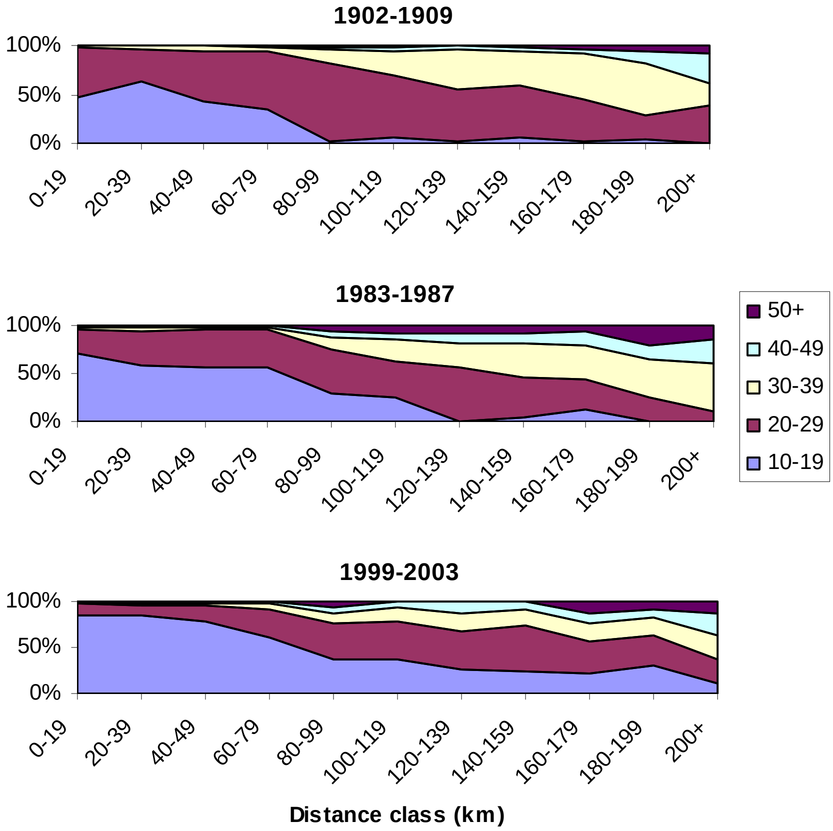

Figure 3.9. Proportions of specific length groups in 20 km distance classes, per period, based on mean catch rates ($N.hr^{-1}$).

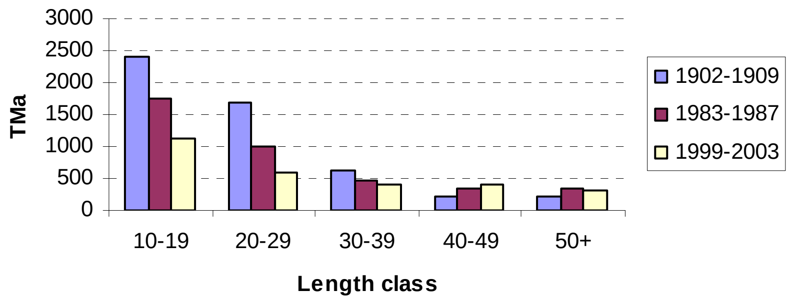

Figure 3.10. Total mean crowding on each length group by all length groups, per period.

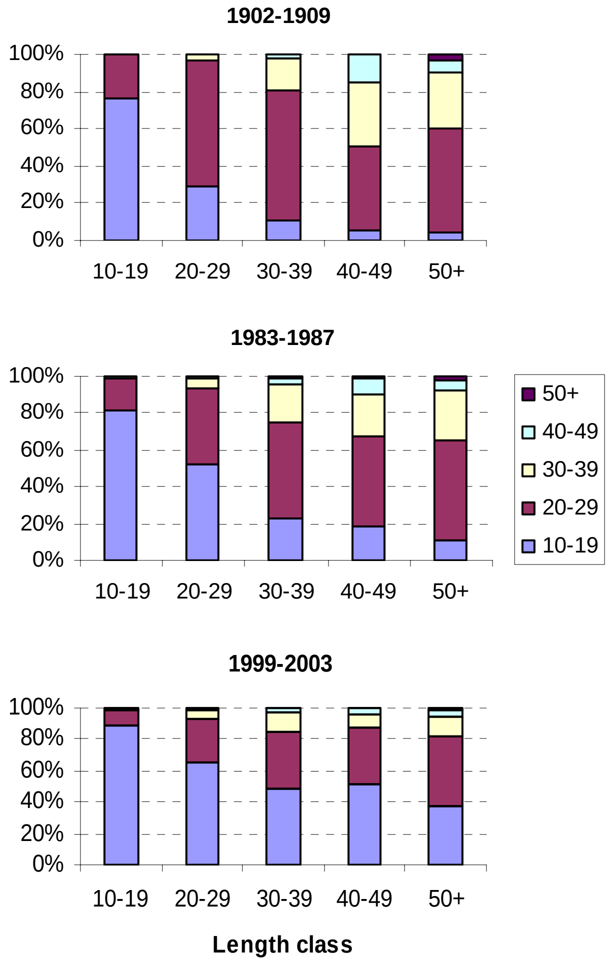

Figure 3.11. Composition of the total mean crowding on each length group.

4. Discussion

4.1 Changes in the spatial distribution of plaice

It is very clear from the results of this research that the spatial distribution of plaice changed in time. Both parts of the research clearly showed that there has actually been a change in the distribution of plaice.

In the first part we statistically proved this. We saw that especially for age groups 0 and 1 and to a lesser extent for age group 2 the slopes of the relation between the catch rates and distance from the coast have become less steep (figure 3.1). This means that young plaice are no longer restricted to the coastal areas, but have moved further offshore. In both transects a significant change in distribution pattern of juvenile plaice was observed. The change in the spatial distribution of young plaice seems to have started around 1993. The trend is more pronounced in transect 601, which is situated in the plaice box, than in transect 666, which is situated just south of the plaice box.

From this we could conclude that there may be an effect of the plaice box on the distribution of young plaice, but we have to take into account that the working method is not completely precise.

A better method to use is the one we used for calculating the distances in the second part of the research, at which the distances were calculated in “Arc View” as the nearest distance to the coastal line on the base of longitude as well as latitude.

Using that method to calculate the distances and applying these distances in the model could make it possible to say more about differences between the two transects. But we have to be very careful taking conclusions about this. The transects lie at complete different positions, so different processes determining the distribution may play a role. Comparing just these two transects makes it difficult to say something with certainty.

The first part of the research showed that there was a shift in the distribution of plaice, especially for age groups 0 and 1. We first saw a linear trend (figure 3.1), but when we calculated the slope for each year apart, we saw the slopes change especially ever since 1993 (figure 3.2). This suggested that the change in distribution was something which occurred in the last decade. In the second part we discovered that this was not the case.

The distribution maps of the three periods (figure 3.5, 3.6 and 3.7) and the figures with the cumulative frequencies (figure 3.7) and the compositions of the population (figure 3.8), all clearly showed changed distribution patterns in the middle 1980s already, compared to the period 1902-1909. These changes were only more visible in the last period. The change in distribution thus started earlier and is not a phenomenon which occurred in the last decade, although the change seems to occur faster.

Notable fact was that the overall catch rates were much lower in the first period compared to the second one. This difference is possible a result of different fishing gears used in the different periods. It is generally accepted that trawl catches made with the same gear reflect relative differences in abundance of demersal fish species. However, problems arise when different species caught with the same trawl are compared, or when different gears are used for a single spe-cies, because all fishing gears are more or less selective and catchabilities vary accordingly. Standardization to swept areas per unit of time does not resolve the gear differences in this respect, and relative catch efficiencies of different gears can only be estimated when they have been employed simultaneously within the same area (Knijn *et al.*, 1993).

In the two recent periods, tickler chains have been deployed which increase the catch efficiency for flatfish which are often buried in the sediment (Creutzberg *et al.*, 1987). Beside this, the higher towing speed in recent years may have reduced the chance to escape.
So the gear characteristics could have had effects on the catch rates, but this probably can not totally explain the difference in catch rates. It is possible that the total numbers were indeed lower in the period 1902-1909. When collection of international fisheries statistics started, total international landings of plaice had stabilized around 50 000 t. This level was maintained until the 1950s, with excep-tion of the period during the two world wars. Catch data reported by some countries suggested that total plaice landings between 1892 and 1905 would have been at least 50 000 t. During both war-time periods (1914-1918; 1940-1945), landings were reduced due to restricted fishing activities, but extremely good catches were made in the first year thereafter, followed by a gradual decline to pre-war levels (Borley, 1923; Bannister, 1978). From the early 1950s, landings increased to record high levels of more than 150 000 t by the early 1980s, followed by a sharp decline to about 80.000 t at the beginning of 2000 (ICES, 2003).

4.2 The effect of water temperature on the spatial distribution of plaice
Several independent time series have shown an ongoing increase in water temperature. Effects of a change in water temperature can be expressed in recruitment (effect on egg and larval survival), growth rate and spatial distribution. Apart from water temperature, the spatial distribution and growth of plaice may also be affected by low oxygen concentrations.
Oxygen depletion can occur in summer periods after water column stratification with limited exchange of dissolved oxygen between the water layers. Periods of low oxygen concentrations seem to be restricted to the German Bight, where hypoxia events have been observed (OSPAR, 1993; Zevenboom, 1994). Also in stratified waters like the Kattegat, oxygen depletion problems are important (Christensen et al., 1998). Since the beginning of the 1990s, no severe oxygen depletion has occurred in the German Bight. Hence the results of transect 601 may be influenced by oxygen depletion.
Effects of changes in water temperature on fish abundance and distribution have been shown in many studies. North Atlantic Oscillation fluctuations have had differential effects on the ecosystems in the North Atlantic (Parsons & Lear, 2001). For several species such as gadoids (ICES, 1999), Herring *Clupea harengus* (Alheit & Hagen, 1997) and plankton (Planque & Fromentin, 1996) in the North Atlantic, indications of a link between population developments and long-term trends in the NOA have been described (Parsons *et al.*, 2001). Climatic change has had dramatic effects on community composition in Britain (Genner et al., 2004). Responses of species composition and the occurrence of warm-water species to increasing sea surface temperature were also observed in the English Channel (Hawkins et al., 2003).
In this study no statistical evidence for a relationship between the water temperature and the distribution of plaice was found. When we plotted the mean summer water temperatures of 3-year periods with the mean slopes of 3-year periods, we saw that the mean water temperature in summer did show a relationship with the mean slopes (figure 3.3). This relationship was most obvious in transect 601 for age groups 0 and 1 and to a lesser extent for age group 2.
At high water temperatures during summer the slopes are less negative. Thus at high water temperatures in summer plaice of age 0 and 1 seem to extend their distribution to places further away from the coast into deeper water. It is reasonable that effects would occur at plaice of age groups 0 and 1 because these age groups inhabit shallow water where temperature will reach its highest values.
Apparently plaice have a temperature preference and it looks like they react to raising water temperatures immediately. All of this cannot be concluded with certainty because there is no

statistical evidence. There is some evidence that juvenile plaice have an endogenous annual rhythm of temperature preference (Zahn, 1963). One clear example of temperature as a cue for movement is provi-ded by the mass ‘exodus’ of newly settled plaice from intertidal pools in the Dutch Wadden Sea when the temperature exceeds critical levels of about 24^{o}C (Van der Veer & Bergman, 1986; Berghahn *et al.*, 1993). Plaice is a cold-water species, which means that the optimum temperature is relatively low (Fonds et al., 1992), so increasing water temperatures due to continuous global warming could lead to a further shift in the distribution of plaice.

4.3 The effect of growth on the spatial distribution of plaice

In an evaluation of the plaice box (ICES, 1999) it was concluded that there has been an increase in the growth of the smaller size classes of Plaice (<35 cm) in the 1960s and early 1970s. In the mid 1960s and the mid 1980s a period of reduced growth was observed which could be related to the presence of the outstanding year classes of 1963, 1981 and 1985. Although, growth rate seems to be depressed at high population densities, there is no indication that the establishment of the plaice box in 1989 was followed by a decrease in growth rate (ICES, 1999).

In this study, no relationships between the growth index and the distribution of North Sea plaice, based on the back calculated mean length at age 2 of plaice, were found. Both the statistical research as the plots with the mean growth indices of 3-year periods did not give any indication (figure 3.4). Peaks in the growth index did not have an effect on the distribution of plaice. We have to mention that only growth indices up to year class 1997 were available. Considering that the slopes increased considerably after 1993, we can not completely exclude an effect of the growth on the distribution of plaice.

The mechanism how growth could influence the distribution is not completely understood. In fact growth rate itself is affected by several processes. Van der Veer *et al.* (1990) stated that density-dependent effects of growth due to food limitation seem to be restricted to only minor parts of the plaice population. The growth of plaice on the nursery grounds is not food-limited according to Milner & Whiting (1996). On the other hand, Berghahn *et al.* (1995) found individual and local growth rates of 0-group plaice determined by differences in food quantity and quality due to bottom conditions.

Despite local food limitations and hence reduced growth due to high concentrations of juvenile plaice in a restricted area, Bergman *et al.* (1988) found growth of juvenile plaice to depend only on water temperature. However, Rijnsdorp and van Leeuwen (1996) showed that growth changes in smaller size classes of North Sea plaice were significantly correlated with their density, eutrophication and seabed disturbances by beam trawling, but not with temperature.

If food is not limited, growth rate will increase with temperature up to a maximum beyond which growth rate will decrease. Small juvenile fish eat more and grow faster at higher temperatures than larger older fish. Large fish grow better in colder conditions. (Fonds et al., 1992).

4.4 Changes in intraspecific competition

In the second part of the research we looked at the intraspecific competition. We took the total mean crowding as an indication for this factor. We expected that the intraspecific competition had decreased in time. We supposed that the larger length groups controlled the distribution of the smaller length groups by restricting those length groups to the coastal zone. As the plaice became larger, the control became less and they could extend their distribution. With decreasing numbers of the larger length groups, as a result of the increased fisheries, a shift in the distribution of the smaller length groups could take place.

Figure 3.10 shows that the total mean crowding for the length groups 10-19 cm and 20-29 cm was considerably lower in the periods 1983-1987 and 1999-2003. The last period has the lowest values.
It is likely that the rates of total mean crowding for the two smallest length groups truly mean that intraspecific competition took place. The rates of total mean crowding for the larger length groups are much lower and it is unlikely that at these rates intraspecific competition is taking place. The proportions of length 30 cm and larger crowding on its own length group and other length groups became smaller. The observed offshore movement of the smaller length groups is consistent with the competitive hypothesis.

4.5 Different factors affecting the spatial distribution of plaice
In this research we discussed the effects of temperature, growth and intraspecific competition on the spatial distribution of plaice. Beside these factors there could also be other things which may play a role, like predation, oxygen depletion, or fisheries.
Two main predator groups on early juvenile plaice cause substantial mortality (van der Veer *et al.*, 1990): while fish predation during summer and autumn has only little impact on the recruitment, the influence of the predatory crustaceans brown shrimp and shore crab on the just settled fish is temperature-dependent during spring. After severe winters the number of predatory crustaceans are reduced, and the early juveniles grow to sizes which are too large for the recovered crustacean stocks in June (van der Veer *et al.*, 2000b) because the brown shrimp, e.g., has only a limited food size window (van der Veer *et al.*, 1994).
With changing water temperatures changes in the number of predatory crustaceans can be expected, which can lead to a change in the distribution of plaice. With higher rates of predation by these crustaceans, the 0- and 1-group plaice may be forced to migrate to places further offshore.
In 1998 Piet and Rijnsdorp reported that an increase in number of species already had started in the late 1980s. They suggested that the increase in number of species seemed to be a climate driven development inferring from the increase in number of southern species.
These southern species may act as food competitors, causing the small plaice to migrate offshore.

As well as changes in environmental variables, changes in the biotic environment have also taken place. The diet of both plaice and sole consists mainly of short-lived highly productive benthic organisms such as annelids. Bivalves and echinodermata are of secondary importance. Among the annelids the polychaetes predominate. Important bivalve species are spisula and ensis. Diet does not differ between areas differing in trawling intensity (Rijnsdorp *et al.*, 2001). Recently, the composition of the benthic community the Wadden Sea changed rapidly as a result of sediment change due to intensive shellfisheries and a reduction in primary production (Brinkman & Smaal, 2003). In general, the density of bivalves decreased, while densities of polychaetes increased. In the Dutch coastal zone major changes also took place. Spisula that occurred in dense banks just offshore the islands and North Sea coast disappeared (Craeymeersch & Perdon, 2004). Concurrently, densities of ensis increased dramatically. Any changes in the distribution or abundance of benthic food organisms may therefore be expected to have an impact on flatfish distributions. Short-term changes which can effect benthos include severe winter weather and periods of oxygen deficiency (Beukema & Dekker, 2003; Honkoop & Van der Meer, 1997). Although, recovery appears to be rapid and biomass may reach pre-impact levels within two years, this can still affect food availability for flatfish if a significant proportion of the feeding area has been affected.

4.6 Further recommendations

Returning to the question which factors are responsible for the change in the spatial distribution of plaice, it became clear that no single factor can be held responsible and that several factors may play a role and these factors are linked to each other.

Higher water temperatures cause a shift in the distribution due to the temperature preference of plaice. Beside this direct effect the temperature can affect the growth rate and thus have an indirect effect on the distribution. The effect of growth is not completely determined. We would expect that lower growth indices would cause plaice to distribute to places further off-shore on smaller lengths. In this research we did not find such a relationship.

Other factors which influence the growth are eutrophication and seabed disturbance by beam trawling, but these factors may also directly influence the distribution of plaice and in further study they should be taken into account.

This study revealed the changes in the distribution of plaice. We could not really assign the causes to these changes. Further research will have to be focused on the factors which determine the distribution of plaice. It is also necessary to look at the effects of the increase in total species numbers and the effects of predators on the distribution. It is possible that specific predators changed in abundance which may affect the distribution.

Because most effect on the distribution can be expected by water temperature, better series of water temperature are necessary. Measurements are needed which are more specific for the area where the fish are distributed.

Acknowledgements

In the first place, I would like to thank Dr. Adriaan Rijnsdorp for his help during the complete training period. He always had enough time to clarify things I could not deal with and always was critical so no mistakes were made.
In second place I would like to thank Olvin van Keeken. He mainly helped me finding my way into the computer program “SAS” and I could always ask my questions to him when Adriaan was not there.
I also like to thank Bastiaan Star for his help computing the distances from the coast in “Arc View”.
Finally I would like to thank the Netherlands Institute for Fisheries Research for offering me a training period and a good working place.

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