

Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present

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Sole stocks in the North Sea have shown a threefold variation in abundance over the past 50 years, largely as a result of fishing activity and variability in recruitment. Natural fluctuations in abundance have also occurred as a result of severe winter mortality as in 1962/1963 when the spawning stock biomass was reduced by more than half. Analysis of historical growth changes provides a means of assessing the causes of these variations in abundance. Changes in growth of female sole since the early 1940s were examined using back-calculated length increments from otoliths. Growth was lowest in the decade following the war and increased during the 1960s at a time of declining stock size. Growth of individual year classes appeared to be affected by the reduction in stock abundance in 1963. The extent to which these changes are related to eutrophication, beam trawl activity and density-dependent factors are discussed.

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Key words: sole, density dependence, fisheries, growth, North Sea, otoliths, stock abundance.

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Introduction

Sole (*Solea solea*) have been exploited in the southern North Sea as a by-catch in the demersal fisheries since at least the beginning of the century. However, it was not until the development of the modern heavy beam trawl in the early 1960s that a targeted fishery for sole began, initially in the coastal waters of the eastern North Sea and later spreading offshore to most of the southern North Sea south of latitude 56°N. The change in exploitation level is shown in Fig. 1. From 1951 to 1960, the fishing mortality rate (F) on ages 2–8 remained below 0.2. F rose sharply over the next 10 years to around 0.4 in 1970 and then continued to rise more slowly to a peak at just over 0.5 in the mid-1980s, since when it has declined slightly. Landings (Fig. 1) rose from less than 4000 t in 1905 to a peak of 33 000 t in 1966–1968 but then declined sharply and remained at around 20 000 t for the next 20 years, despite rising fishing effort, before increasing again in the early 1990s.

The changes in the sole fishery and in a number of biological parameters including growth and maturation during the period 1957 to 1973 were studied by de Veen (1976, 1978). On the basis of detailed studies of market and research vessel samples, he drew three major conclusions: (1) that there had been significant increases in length, weight, and condition factor at age; (2) that the

main growth change occurred in juveniles before the age of 3; and (3) that there was evidence that the growth change was a result of increased food availability caused by disturbance of the seabed by beam trawling. The changes in growth have subsequently been studied by Houghton (1979) and confirmed by van Beek (1988) and Rijnsdorp and van Beek (1991). Increases in length-at-age and weight-at-age of sole since the 1970s have also been reported from other areas such as the Bristol Channel, ICES Divisions VII f–g (Horwood, 1993).

Similar increases in growth of North Sea plaice (*Pleuronectes platessa*) have been reported by Bannister (1978) using market samples and research vessel data. Growth changes in plaice have been extensively studied by Rijnsdorp and van Leeuwen (1992, 1994) using length data derived from otolith measurements.

The availability of otoliths from North Sea sole over the period from 1940 to the present time provides an independent means of re-examining the reported growth changes and of assessing the likely factors involved.

Methods

Otoliths for back-calculation were selected mainly from Lowestoft market samples from the period 1951–1991.

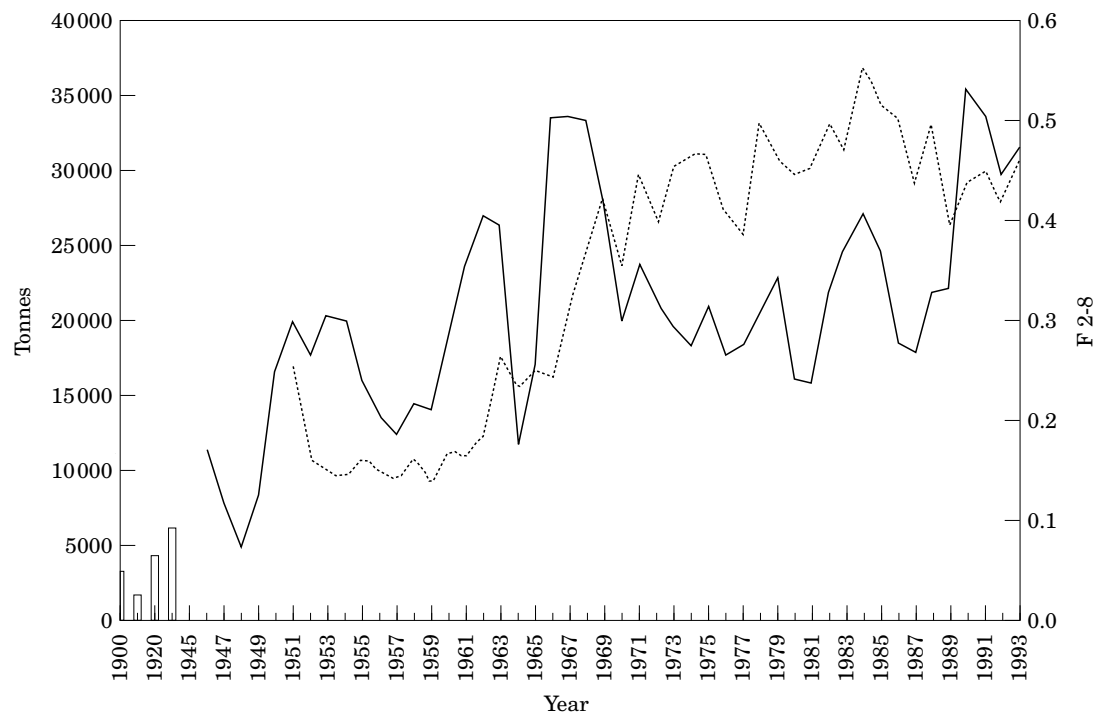


Figure 1. Trends in fishing mortality (---) and landings (—) for North Sea sole.

Table 1. Numbers of otoliths analysed by length group by selected groups of years during the period 1951–1991.

Length group (cm)	Selected years				
	1951–1955	1956–1961	1966–1971	1976–1981	1986–1991
25	17	8	15	18	40
27	15	17	17	20	40
29	19	17	16	20	40
31	20	17	20	20	40
33	18	19	18	20	40
35	10	18	20	20	38
37	11	19	17	19	38
39+	11	20	19	19	38
Total	121	135	142	156	314

Relatively few samples were available from the early 1950s and these were supplemented by otoliths collected from tagging cruises carried out in these years. Only females were randomly selected from each 2 cm length group from 25 cm to 37 cm, with fish of 39 cm and above grouped together. In order to have sufficient samples within each length group, all samples up to 1955 were grouped together; the remainder were grouped by 6-year periods from 1956 onwards. The number of samples in each period is given in Table 1.

Otolith processing

Otoliths were embedded in resin and sectioned through the centre of the nucleus using a diamond cutting blade (Bedford, 1983) before staining in acidified neutral red for up to 20 min (Richter and McDermott, 1990). The sections were viewed under reflected light using a Zeiss stereo microscope and the image projected on to a video screen using a VIDS 5 video analysis system (Analytical Instruments, Cambridge). Measurements of

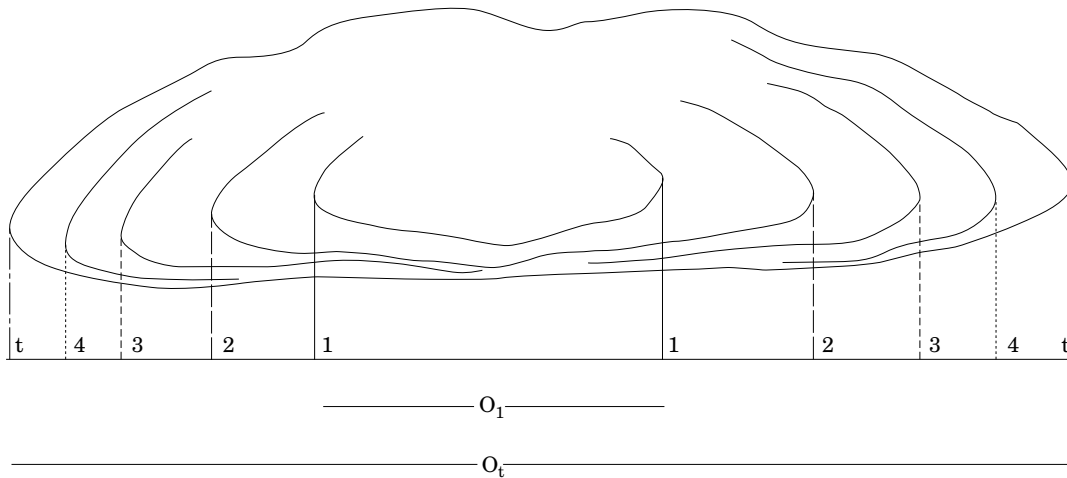


Figure 2. Otolith structure showing method of measuring along the main axis of growth. Four annual rings are shown and O_1 and O_t are measurements at age 1 and time of capture, respectively.

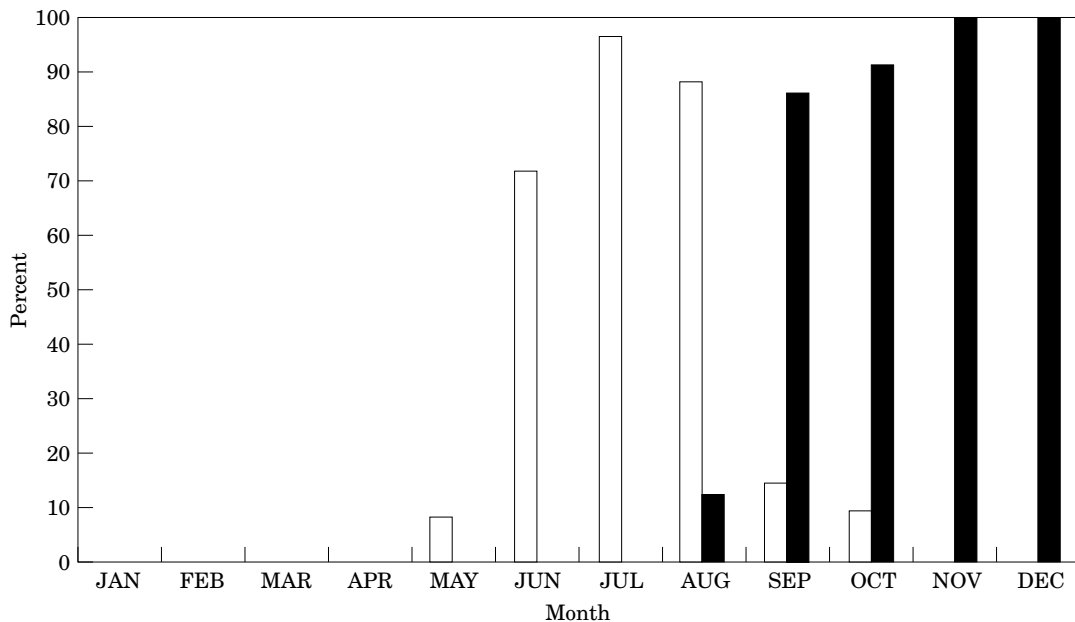


Figure 3. Seasonal pattern of growth in North Sea sole. New growth starts in May and more than 90% have completed growth by October. (new growth ring (□); ring complete (■).)

each annular ring were made along a single growth axis by measuring down to a parallel line as shown in Fig. 2. In old specimens it was not possible to separate the outer annual growth rings and measurements were made to the last reliable ring and to the outside edge. Validation of the pattern of opaque and hyaline rings as annual rings was made by recording the monthly pattern of growth over a period of one year. The results are shown in Fig. 3.

The relationship between otolith length (O) and fish length (L) appeared to be slightly curvilinear and

several models were examined to find the best fit to the data. A second degree polynomial of the form $L = a + b(O) + c(O)^2$ was found to minimize the residual variance but implied a relationship that is difficult to interpret biologically. A simplified linear model was therefore used and the length of fish at each age was calculated from

$$L_i = (O_i/O_t)b \times L_t$$

where L_i is the length-at-age i , L_t the length-at-capture, and O_i/O_t the ratio of the diameter of the annulus-at-age

Table 2. Numbers of measurements obtained by age and group of year classes.

Year class group	Age group								Total
	0	1	2	3	4	5	6	7+	
<1945	19	19	19	19	18	10	4	1	109
1945–1949	145	145	140	131	90	56	14	7	728
1950–1954	77	77	75	53	36	20	9	7	354
1955–1959	62	62	58	43	31	19	12	19	306
1960–1964	81	81	81	58	30	17	5	3	356
1965–1969	56	55	31	27	24	19	14	9	235
1970–1974	124	123	101	64	39	15	8	5	479
1975–1979	43	43	43	43	43	43	28	14	300
1980–1984	150	150	149	103	67	40	14	3	676
1985–1989	111	111	90	53	22	3	0	0	390
Total	868	866	787	594	400	242	108	68	3933

i to the diameter of the otolith at time of capture (Bagenal and Tesch, 1978; Rijnsdorp *et al.*, 1990). The slope b (1.331) was calculated from the fitted log–log plot of otolith length against fish length.

Environmental and anthropogenic factors

The temperature series used was from the “Smiths Knoll” lightvessel (52°43'N, 02°18'E) in the south-western North Sea for 1951–1988 (Jones and Jeffs, 1991). This series was extended by means of interpolated values from weekly surface temperature charts for 1989–1993 (Bundesamt für Seeschifffahrt und Hydrographie). The series is representative of the area from where most of the sole samples were taken. Mean temperatures from the second and third quarters were used, as these cover the main growth season of sole (Fig. 3).

Eutrophication and beam-trawl effort data were from Rijnsdorp and van Leeuwen (1994). The series for eutrophication was the load of orthophosphate ($\text{PO}_4\text{-P}$ in kg s^{-1}) in the river Rhine at the German/Dutch border. The total number of horsepower days fishing of the Dutch beam-trawl fleet, which constitutes the main fleet fishing for sole in the North Sea, was taken as a measure of beam trawling.

Results

The number of measurements by age and group of year classes is given in Table 2. Although the first year sampled was 1951, some of the fish in these samples were up to 20 years old and provided measurements from individual year classes as far back as 1932. The large 1947 year class was well represented in the samples and can be seen to boost the numbers in the 1945–1949 group of year classes.

The trends in mean back-calculated length-at-age for age groups 0–6+ by 5-year periods (Fig. 4) indicate that

there has been a decline in growth at all ages from the post-war years with a minimum in 1950–1954 for most age groups. The lengths for years before 1945 are based on less than 20 otoliths and should be regarded with caution. Mean length increased in nearly all ages up to 1965–1969 except at age 0. There was no clear trend at ages 0 and 1 but all other age groups show an overall increase over the whole period resulting in a peak during the last period.

Figure 5 shows the changes in length increment over the same time period, plotted as deviations from the long-term mean. The younger age groups show no overall trend with time but there appear to be significant differences between adjacent periods. There is a marked increase in length increment with time between ages 2–3 and 3–4. The trend is evident up to 1969 in the older fish but less well defined after that.

A two-way analysis of variance was used to examine the trends in length with age and time, using the model

$$\text{length} = \text{age}_a + \text{year}_y + (\text{age} * \text{year})_{ay}$$

where a is the age at each back-calculated length from 0 to 8+ and y is the year from 1932 to 1990 in which each annual ring was formed.

The age and year effects and the age*year interaction were all significant (Table 3). The significant age effect was to be expected, indicating that the average lengths over all years at each age are significantly different from each other. The significant year effect confirmed that there was a trend in length with time across all ages. However, this trend was not the same for all ages and the age*year interaction showed that some ages were increasing significantly more steeply than others (cf. Fig. 4). Similar results were obtained using year class instead of year in the analysis.

To check whether the significant trends were the result of variability in the data, a regression model was fitted, treating year as a covariate and fitting year as a

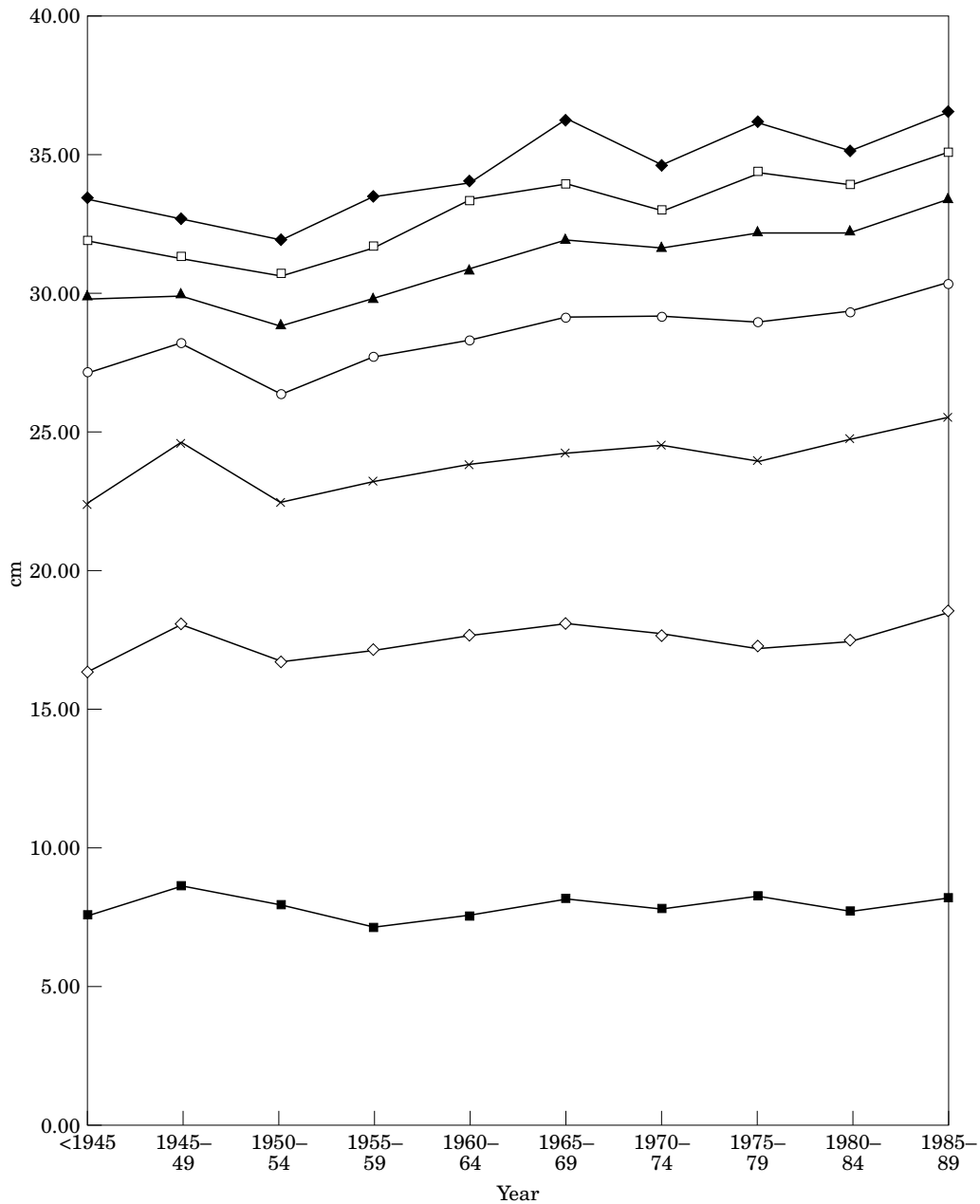


Figure 4. Trends in mean length-at-age by 5-year periods. Age is measured at the end of each year's growth for ages: 0 (—■—); 1 (—◇—); 2 (—×—); 3 (—○—); 4 (—▲—); 5 (—□—); 6 (—◆—).

quadratic function because of the time trends. The model used was

$$\text{Length} = \alpha_i + \beta_i \text{ year} + \gamma_i \text{ year}^2$$

where i = ages 0, . . . 7+.

The results of the ANOVA are summarized in Table 4 and the analysis confirmed that differences between ages were significant.

The increase in mean length-at-age by 10-year intervals (Fig. 6a) indicates a difference of about 20% between the slowest growth in 1950–1954 and the fastest growth in 1980–1984. Since the samples are dominated by four strong year classes (1947, 1958, 1963, and 1987), data for these years have been plotted separately (Fig. 6b). The 1947, 1958, and 1963 year classes show very similar trends in length-at-age, while the 1987 year

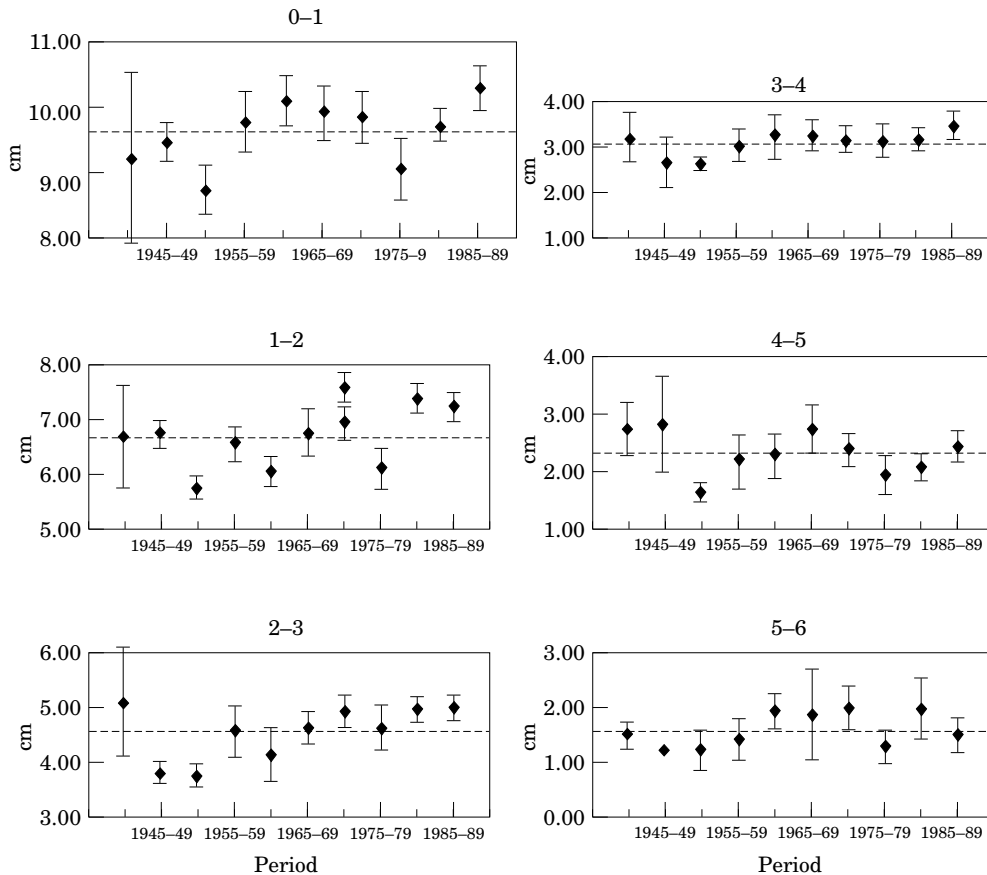


Figure 5. Trends in annual length increment plotted as deviations from the mean from 1945 to 1989. Error bars are $\pm 2 \times \text{SE}$.

class was growing markedly faster at age 4 than the other ones. Year-class 1958 was somewhat smaller than the other ones between ages 2 and 4. However, in 1963–1964, at ages 5 and 6, its mean length matched or even exceeded the 1947 and 1963 year classes. One explanation for this relative increase may be related to the more than 50% decrease in spawning-stock biomass that took place following the cold winter of 1963 (Fig. 8).

Changes in growth were examined in more detail by plotting length increments for year classes spawned

immediately before the 1963 stock reduction and comparing these with the 1963 year class which was spawned immediately afterwards (Figure 7). Enough measurements to allow a reliable comparison were available only for the 1958 and 1960 year classes. If stock density has affected growth, the first age at which changes would become apparent would be between ages 2 and 3 and ages 4 and 5 for the 1960 and 1958 year class, respectively. The figure indicates that the 1960 year class did show a strong growth increase after age 3–4. A similar but less marked increase occurs after ages 4–5 in the 1958 year class. However, as the error bars indicate, there was considerable variation and differences were not significant.

The changes in growth over time were examined in relation to observed trends in temperature, eutrophication, and beam-trawl effort, as well as spawning-stock biomass (Fig. 8). The mean length at ages 3–6 was used as a signal of the changes over the period from 1951 to 1991. Apart from a period of warmer years between 1959 and 1961, temperature has fluctuated with no apparent trend over the period. In contrast, both

Table 3. Results of a 2-way ANOVA of back-calculated length in relation to the associated age and year in which the ring was formed. The model used was: $\text{Length} = \text{age} + \text{year} + (\text{age} \times \text{year})$.

Source	df	SS	MS	F-value	p
Age	8	261 744	32 718	5869.1	0.0001
Year	58	3 168	55	9.8	0.0001
Age*year	312	3 036	10	1.8	0.0001

Table 4. Results of the regression model fitting year as a quadratic term to allow for the increasing trend with time. The model used was: $\text{Length} = \alpha_i + \beta_i \text{ year} + \gamma_i \text{ year}^2$.

Source	df	SS	MS	F value	p
Year (adj. for age)	1	758	758	56.9	0.0001
Year ² (adj. for year age)	1	151	151	11.4	0.0008
Age (adj. for year year ²)	7	309 289	44 184	3319.2	0.0001
Year*Age	7	696	99	7.5	0.0001
Year ² *Age	7	16	2	0.2	0.99
Between variation	342	4 553	13	2.4	0.0001
Residual	3 666	20 440	6		

phosphate and beam-trawl effort have shown marked increases peaking in 1981 and 1988, respectively. The sole spawning-stock biomass (estimated at the 1st of January) reached a peak of nearly 150 000 t in 1961 as a result of the recruitment of the very strong 1958 year class but decreased sharply in 1964 owing to high natural mortality during the severe preceding winter. The strong 1963 year class resulted in a temporary recovery of the stock, which then declined steadily to remain at a low level throughout much of the 1970s and 1980s. The strong 1987 year class again resulted in a temporary increase.

An analysis of covariance was carried out to test the relationship between mean length (L) and the four variables temperature (TEMP), eutrophication (PO₄), beam-trawl effort (BT), and spawning-stock biomass (SSB), using the model

$$L = \alpha \text{TEMP} + \beta \text{PO}_4 + \gamma \text{BT} + \delta \text{SSB} + e$$

Only beam-trawl effort was significantly correlated with mean length, explaining about 35% of the variance. The full model, with all four variables was not significantly better than one with beam-trawl effort on its own.

Discussion

The analysis of back-calculated lengths from otoliths confirms the growth changes reported earlier by de Veen (1978) and van Beek (1988). The trends in the mean length-at-age indicate that growth was at a minimum in the mid-1950s and has increased since then in several stages. There was no apparent trend in the 0- and 1-group fish, but an increasing slope up to at least age 6 indicates that effects were strongest in the older fish. These results are similar to changes observed in plaice in the North Sea (Rijnsdorp and van Leeuwen, 1992, 1994). In both species, a marked growth change started in the early 1960s and occurred in a number of age groups simultaneously, suggesting a common environmental factor affecting both stocks. Sea temperature, eutrophication, and beam trawling all operate over a scale large enough to have had an effect (de Veen, 1976,

1978; Rijnsdorp and van Leeuwen, 1994) and density is also a possibility.

Evidently, there is a strong signal in all the main factors except temperature, which makes it difficult to disentangle the influence of each. Moreover, all factors, with the possible exception of temperature, would be expected to influence growth through their effects on the availability of food. However, the fact that sole and plaice react similarly suggest that either the two species are competitors for the same food resource or their respective food resources are affected in the same way.

Temperature and eutrophication

Temperature can have a controlling effect on growth through its influence on metabolic rate and food consumption (Jobling, 1995; Wootton, 1990), providing food is not limiting. However, the trend in mean temperature during the main growing season is poorly correlated with mean length ($r^2=0.001$), indicating that this factor is not important.

Input of dissolved nutrients into the coastal zone of the southern North Sea from river discharges has increased substantially since the early 1960s. Concentrations of phosphate were two to four times higher and nitrate up to three times higher along the eastern coast (North Sea Task Force, 1993). The signal used here for eutrophication, the load of dissolved inorganic phosphate from the river Rhine (Rijnsdorp and van Leeuwen, 1994), indicates a fairly steady increase from the early 1950s until the beginning of the 1980s. The effects of an increase in nutrients would be to stimulate growth of phytoplankton and the increased production might be expected to find its way through the food chain to benthic organisms on which sole feed. Effects would be strongest in the coastal zone. Changes in benthos in the Dutch Wadden Sea have been monitored by Beukema (1989, 1991), who observed that biomass had doubled over the period 1970–1989 and attributed this to the effects of nutrient enrichment. Since these shallow coastal areas are the main nursery grounds of juvenile sole and plaice (Millner *et al.*, 1988; Dorel

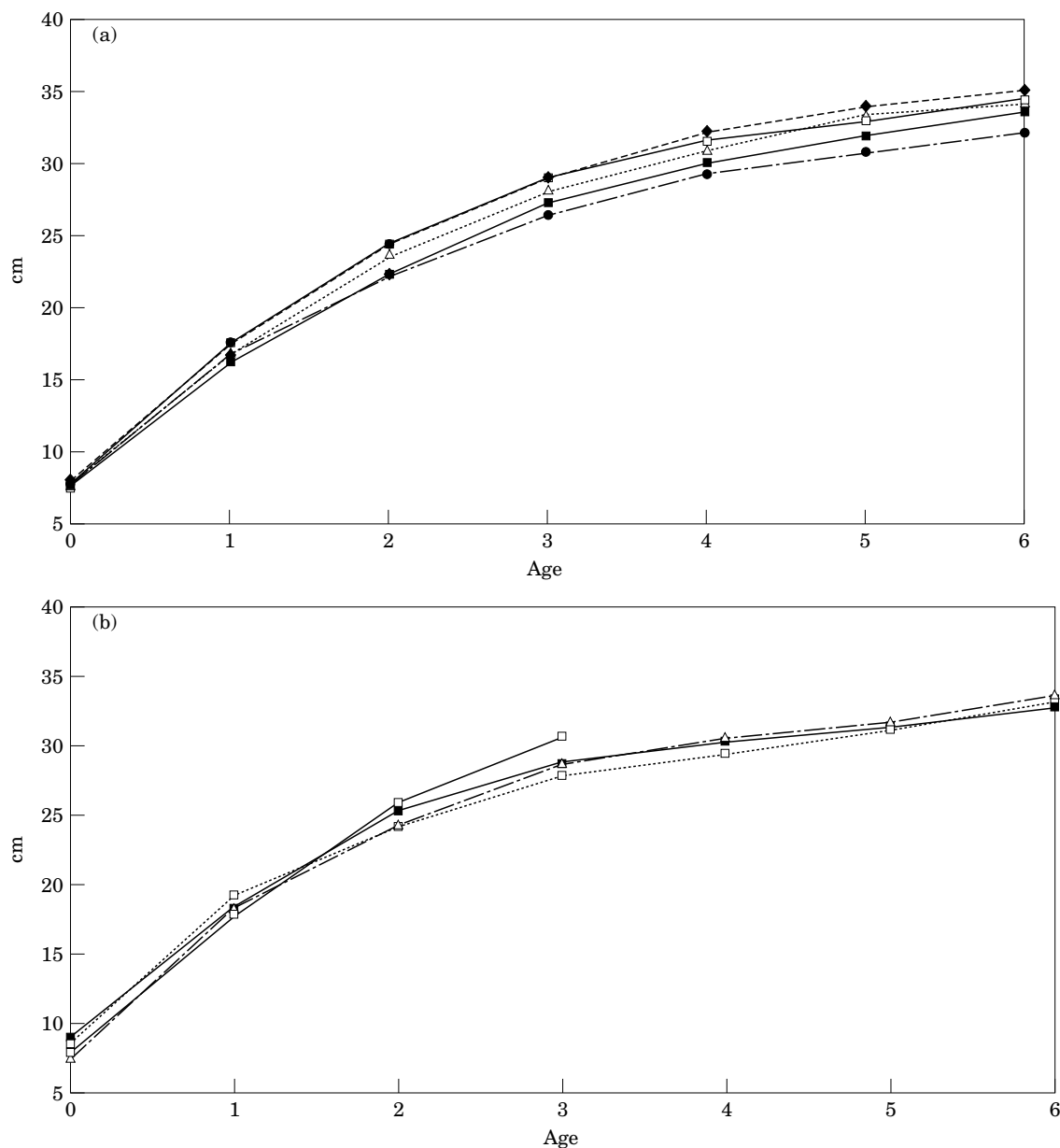


Figure 6. Mean length-at-age (a) 5-year averages <1945 (—■—); 1950–1954 (—●—); 1960–1964 (···△···), 1970–1974 (—□—); 1980–1984 (—◆—). (b) Strong year classes 1947 (—■—), 1958 (···□···), 1963 (—△—), and 1987 (—□—).

and Desaunay, 1991; Rijnsdorp *et al.*, 1992), the strongest effects would be expected on growth rates of the youngest age groups. However, back-calculated mean lengths suggest that there have been no significant trends in growth of juvenile sole and this conclusion supports earlier studies of 0- and 1-group fish from surveys covering the periods 1954–1970 (de Veen, 1976) and 1970–1990 (Rijnsdorp and van Beek, 1991). These results indicate that growth on the nursery grounds is not food-limited or that the increase in benthic produc-

tivity has affected species which are not used as food by sole. The latter possibility must be rejected, because species which have increased in abundance include polychaetes and bivalves (Beukema, 1989), which are typically those taken by sole (de Groot, 1971; Braber and de Groot, 1973; Mao, 1986; Lagardère, 1987). For sole, there is little information on food limitation in the nursery areas, but studies on plaice have found no evidence that growth has been limited by food availability (Kuipers, 1977; Kuipers *et al.*, 1986; Hovenkamp,

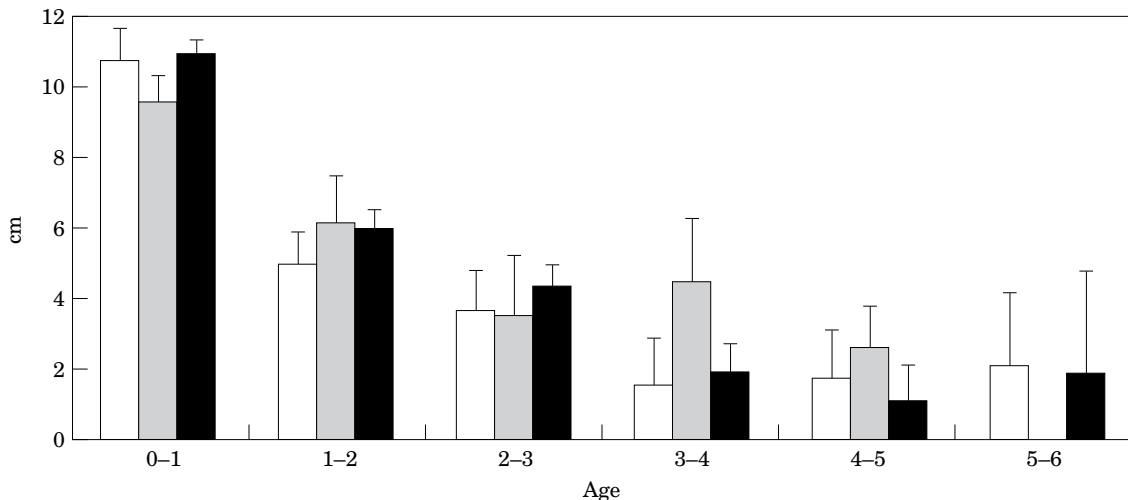


Figure 7. Annual growth increments of 1958 (□), 1960 (▒), and 1963 (■) year classes showing increase in growth at different ages following the stock decline in 1963. Error bars are $+2 \times \text{SE}$.

1989). Zijlstra *et al.* (1982) and Karakiri *et al.* (1991) maintained that growth was optimal and determined by ambient temperature conditions rather than lack of food. This study does not indicate that even the most abundant year classes exhibit reduced growth rates and therefore support this view, although effects of temperature also appear to be insignificant.

In older sole, too, no significant correlation was observed between mean length and the eutrophication index. Phosphate loads increased during a period when spawning biomass was decreasing and the peak in phosphate corresponded with a period of minimum stock abundance. Growth at low stock density would not be expected to be food-limited. Consequently, any increase in food supply caused by eutrophication could have had no effect until stock levels recovered.

Beam trawling

De Veen (1976) showed that beam trawl effort was strongly correlated with different growth parameters for North Sea sole and effort represented also a significant explanatory variable for some size groups of plaice (Rijnsdorp and van Leeuwen, 1994). In this study, beam-trawl effort was the only variable to be significantly correlated with length.

One of the effects of the tickler chains on sand or muddy sediments is that they dig out buried benthic organisms and the damaged animals are then left behind on the sediment (Anon., 1990). This process increases the availability of food to scavengers such as crabs and starfish and also to fish. Sole has a relatively small mouth and, therefore, may not be able to benefit from the larger material exposed by trawling (de Groot, 1971). However, beam trawling may result in changes in

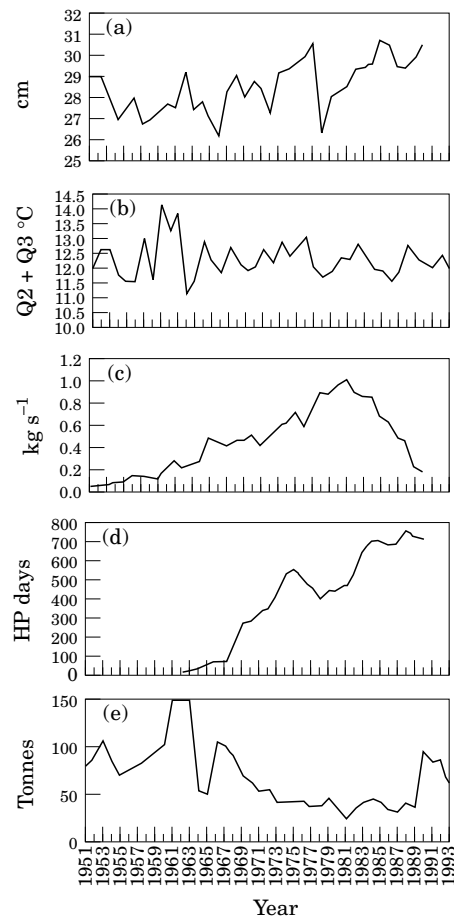


Figure 8. Trends in mean length of sole together with factors that potentially influence growth: (a) mean length of sole ages 3–6; (b) temperature; (c) inorganic phosphate; (d) beam-trawl horsepower; (e) spawning-stock biomass.

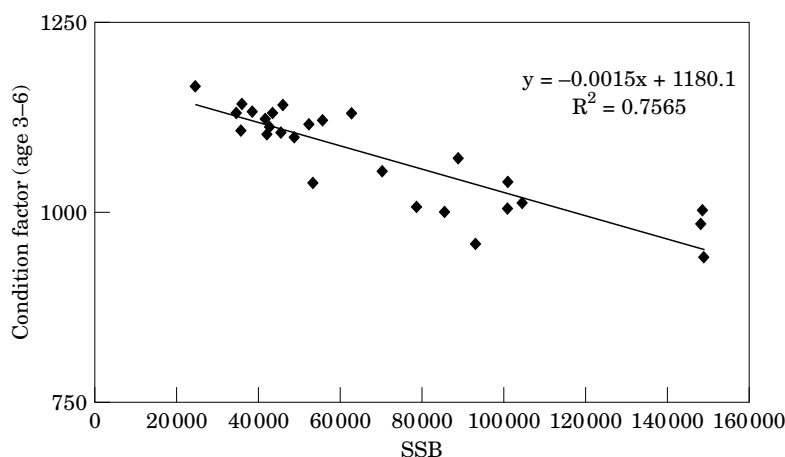


Figure 9. Relationship between spawning-stock biomass (SSB) and female condition factor for North Sea sole. Data for condition factors from van Beek (1988).

species composition by eliminating larger slow growing individuals and replacement with small opportunistic species (A. Rijnsdorp, pers. comm.). Since these are more suitable as food for sole, beam trawling might indirectly increase the food availability to sole. As the fishery operates mainly outside the 12-mile limit, the effects would preferentially benefit older sole. One problem with attributing changes in growth to beam trawling is the difference in timing between the two events. De Veen (1976) and this study (Fig. 4) indicate that the onset of growth started in the early 1960s before beam trawling had significantly expanded in the North Sea. However, otter trawlers were also using tickler chains and seabed disturbance had occurred before the introduction of the beam trawl. If the level of fishing mortality for sole (Fig. 1) is taken as an index of bottom disturbance, then this incongruity is largely resolved.

Stock abundance

Although de Veen (1976) did not observe a significant correlation between stock abundance and a variety of growth parameters over the period 1957–1973, Houghton (1979) reworked his data and showed that the changes in mean length were significantly correlated with estimates of stock abundance. Using an extended time series from van Beek (1988), the mean condition factor (Bagenal and Tesch, 1978) was significantly correlated with spawning-stock biomass (Fig. 9; $r^2=0.76$). Although these results provide evidence of a density-dependent relationship, the link is not necessarily a causal one.

Fish exhibit a large plasticity in growth. Beverton and Holt (1957) have shown empirically that growth can be related to population density but there are few un-

ambiguous instances in fish populations where this has been demonstrated. Rijnsdorp (1994) reviewed the literature on growth changes following the start of exploitation and concluded that growth rates generally increased, suggesting some density-dependent response. However, Horwood (1993) reported increases in weight of sole from the Bristol Channel (ICES Divisions VIIIf,g) of up to 14% during a period of very low abundance, which could not be explained as a response to population density. It was expected that the dramatic reduction in sole biomass after the severe winter of 1963 would serve as a test case for density-dependent growth changes, but in fact the data revealed only marginal effect. There is an indication of a growth spurt of the 1958 and 1960 year class after this winter, but the data were not conclusive.

Analysis of individual year classes has shown that growth may be reduced at high densities. Rijnsdorp and van Leeuwen (1992) found clear evidence of a growth reduction in the abundant 1963 year class of plaice in the North Sea and Jones (1983) demonstrated a marked reduction in mean length-at-age of haddock in two exceptionally strong year classes as well as in the year class immediately following these. In this study, there was no evidence for a reduced growth rate of the large 1963 year class of sole.

The results of this study indicate that there have been substantial changes in the growth of sole over a period of 30 years in the North Sea, which largely mirror the reported changes in plaice. The factor which appears to be most closely correlated with growth rates in both species is beam-trawl activity. However, there are also differences. For instance, growth rates of plaice were reduced in the 1970s, while growth rates of sole continued to increase. This suggests that a complex, multi-factorial response is involved.

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