

On changes in some biological parameters in the North Sea sole (*Solea solea* L.)

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Biological parameters such as length and weight-at-age, fecundity and length at first maturation, derived from market sampling in Dutch ports, showed significant changes in the period under observation 1957–1973. An attempt was made to correlate these changes with environmental factors such as the density of the sole stock, temperature in the growth-season, eutrophication, and fishing effort. Of these factors significant correlations were only found with fishing effort and with indices of the disturbance of bottom layers by active gears. Additional evidence points to the possibility that the amount of beam-trawling with chains has a positive effect on the growth rate and on other biological parameters of the sole.

Introduction

The sole fishery in the North Sea is a matter of great concern both to fishermen and to administrators. A fast expansion in the sole fishing fleet in the Netherlands since 1966 has led to a situation of increasing overfishing. The ICES North Sea Flatfish Working Group has reported repeatedly on the situation (ICES, 1970; 1973a and 1973b; 1974; 1975) and has given advice on measures to improve the situation in the fishery.

The sole stock has declined markedly since 1967–1968, when the very strong 1963 year class, responsible for the high stock level in 1966, started to lose its importance and recruitment fell to a lower level. The unfavourable situation in the sole fisheries has ultimately led to restrictions of fishing by means of catch quota imposed by the North East Atlantic Fisheries Commission from the 1 January 1975 onwards. The aim is to bring the fisheries back to more favourable conditions and give the sole stock an opportunity to recover by setting appropriate Total Allowable Catches annually.

Overfishing in the North Sea sole stock is only a relatively recent feature. In general terms the stock has been under-exploited in the period before 1963–1964 and moved quickly through a period of optimum fishing effort in 1965–1966 to ever increasing overfishing in the years after 1966.

For the Netherlands the sole has become the major fish species and an extensive sampling pro-

gramme has made it possible to follow the developments in the sole stock closely. Dutch fishermen catch soles all over the southern and central North Sea and the sampling has been spaced in time and place to cover all parts of the exploitation area. Since 1957 sole landings at IJmuiden, and in later years in other ports, have been sampled weekly on a routine basis in order to follow the length and age compositions of the various sole substocks exploited by the Dutch fishermen. Data on the maturation of female soles have been collected from 1962 onwards including the weight of the ovaries as an index of fecundity. Prior to market sampling length-at-age data were available for the second quarter of the year from research ship sampling along lines of stations perpendicular to the Dutch coast from 1951–1956 (Boerema, unpublished). In the years concerned the available data showed changes in growth, maturation and fecundity which will be discussed here.

Variations in length-at-age

Generally Dutch fishermen tend to concentrate on small to medium-sized soles although a number of them go to fishing grounds where the large soles are taken. Growth data from the landings may be biased by the dominance of the smaller soles. During the spawning season soles of all lengths and ages aggregate in the shallow coastal waters for spawning and length-age data from this period supposedly

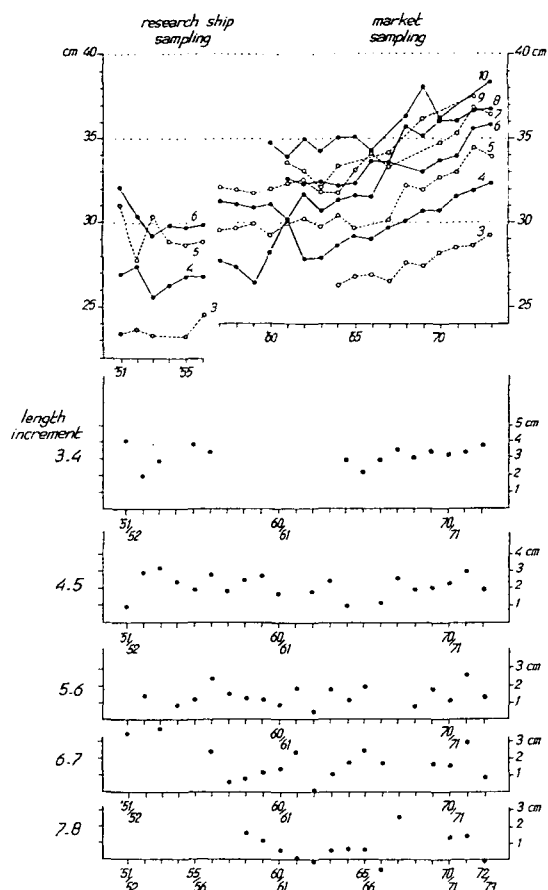


Figure 1. Top diagram, average length-at-age for North Sea sole, sexes combined, in the second quarter, based on research ship sampling 1951–65 and commercial ship sampling in the fish market 1957–73; other diagrams, annual length increments by years.

provide a more adequate picture of the real growth in the sole stock. Therefore, the second quarter – the months of April, May, and June – was selected as a basis for calculating average length-at-age for males and females. Table 1 gives these values together with the standard error and the total number of otoliths in the length-age keys used in the conversion of length into age distributions. Figure 1 shows the average lengths for sexes combined in the upper diagram together with the values derived from research ship sampling at fixed stations in 1951–1956. To make research vessel data and market data comparable a correction for shrinkage has been applied (ICES, 1965, Fig. 20) of 1.5 mm for soles of 20 cm, 3.5 mm for 25 cm, 4.5 mm for 30 cm and 5 mm for 35 cm.

It is obvious from the upper diagram of Figure 1

that the average length-at-age for the soles sampled in the fish market is not constant but shows a steady increase from about 1963 onwards. The influence of the individual year classes cannot be traced easily. In order to study the growth curves for each year class Figure 2 shows the length-at-age in the second quarter by year class. It is apparent that the growth curves of the individual year classes do differ and that the more recent year classes have increasingly steeper growth curves.

The average lengths from the sampling on fixed stations in the period 1951–1956 appear to be at a somewhat lower level than the corresponding values in the market sampling from 1957–1962. It is possible that a change in growth had started before 1962. On the other hand the research ship data cover only a small part of the total exploitation area and the observed differences may reflect differences in growth in different sole sub-stocks. From 1968 onwards the sampling has been intensified in order to cover all different sole sub-stocks more adequately as shown in Figure 3. The average length-at-age for the sub-stocks in the second quarter of the years 1968–1973 is given in Table 2 for males and females. For the age-groups 4, 5 and 6 the length values for sexes combined are shown in Figure 4 for the most important sub-stocks.

Apparently all four sole sub-stocks demonstrated an increase in growth and no significant difference in length-at-age values exists between the sub-stocks in the period 1968–1973. This implies that the factors responsible for the observed increase in growth are not restricted to certain areas. Their influence extends all over the part of the North Sea under consideration. Although insufficient data are available for the pre-1968 years, it seems reasonable to assume that the growth of the various sole sub-stocks were identical not only for 1968–1973 but also for the preceding years. Thus in our search for the factors responsible for the increase in growth the length-at-age data for all sub-stocks combined as given in Table 1 and Figures 1 and 2 may be used as representative for all sub-stocks.

When investigating the annual increments of length (Fig. 1, lower diagrams) it is obvious that for the age-groups 3 and older no significant increases in increments took place from 1951 onwards. Consequently the increase in growth must have taken place in the youngest age-groups. Unfortunately long term data on the lengths of soles younger than 3 years are lacking. However, length data of 0-group soles can be derived by the Petersen method from the data given by Meyer-Waarden and Tiews (1965) and Tiews (1971) for the German nurseries for the period 1954–1967 and data from the Netherlands–

Table 1. Average length (\bar{l}), standard error ($S\bar{l}$), and number of otoliths used in

Year	Age-group	3*		4		5		6		7		8	
		\bar{l}	$S\bar{l}$	\bar{l}	$S\bar{l}$	\bar{l}	$S\bar{l}$	\bar{l}	$S\bar{l}$	\bar{l}	$S\bar{l}$	\bar{l}	$S\bar{l}$
1957.....	♂	25.0	0.4	25.9	0.4	28.8	0.7	29.8	0.6	29.4	0.4	31.1	0.5
	♀	26.0	0.2	28.6	0.3	31.0	0.8	33.1	0.6	34.8	0.4	37.4	0.6
1958.....	♂	26.0	0.4	27.4	0.6	27.5	0.4	28.2	0.6	29.4	1.0	30.7	0.5
	♀	26.9	0.6	29.5	0.3	31.9	0.3	32.4	0.6	35.1	0.8	33.6	0.8
1959.....	♂	25.5	0.4	25.7	0.3	27.5	0.4	28.7	0.6	28.4	—	31.2	0.7
	♀	26.5	0.2	29.0	0.4	32.2	0.4	33.0	0.7	35.2	1.6	36.1	0.7
1960.....	♂	26.7	0.4	26.4	0.3	26.8	0.5	28.1	0.4	28.9	0.5	29.4	1.0
	♀	26.9	0.4	29.9	0.3	31.6	0.6	34.0	0.3	35.1	0.4	—	—
1961.....	♂	25.8	0.2	28.9	0.3	27.9	0.6	27.9	0.9	30.5	0.5	29.4	0.7
	♀	26.5	0.2	31.6	0.5	32.0	0.5	32.3	0.5	34.2	0.7	35.7	0.7
1962.....	♂	26.2	0.6	26.4	0.1	27.8	0.5	29.1	0.5	29.5	0.7	29.6	0.5
	♀	26.0	0.2	29.2	0.2	32.6	0.5	34.4	0.3	35.4	0.4	35.2	0.6
1963.....	♂	25.4	0.4	27.1	0.5	27.7	0.2	28.1	0.4	29.4	0.4	29.3	0.9
	♀	26.2	0.2	28.6	0.5	31.7	0.2	33.2	0.4	34.2	0.5	35.4	0.7
1964.....	♂	26.5	0.3	26.9	0.2	28.0	0.3	29.2	0.2	29.4	1.4	30.1	0.6
	♀	26.1	0.2	30.3	0.4	32.7	0.4	33.5	0.1	33.9	0.3	34.3	0.9
1965.....	♂	25.4	0.5	28.7	0.5	27.8	0.2	29.7	0.7	31.0	0.3	29.2	0.7
	♀	28.2	0.8	29.6	0.5	31.4	0.6	33.5	0.6	35.1	0.3	35.4	0.6
1966.....	♂	26.3	0.2	—	—	—	—	27.8	0.7	31.8	0.5	31.3	0.3
	♀	27.4	0.1	29.4	0.4	35.0	1.4	35.2	0.4	36.4	1.0	36.0	0.3
1967.....	♂	25.7	0.2	28.3	0.1	29.6	0.3	30.2	1.1	30.3	0.5	29.4	0.8
	♀	27.2	0.2	31.0	0.1	30.6	0.4	36.8	1.1	36.3	0.4	37.5	0.8
1968.....	♂	26.2	0.2	27.9	0.2	30.2	0.2	—	—	—	—	33.1	0.7
	♀	29.0	0.4	32.1	0.2	34.1	0.1	32.7	1.2	40.3	0.5	38.2	0.5
1969.....	♂	26.3	0.1	28.6	0.2	29.8	0.2	30.9	0.1	—	—	31.5	1.2
	♀	28.4	0.1	32.5	0.3	33.9	0.2	35.1	0.1	38.4	0.7	38.6	0.8
1970.....	♂	27.3	0.1	29.0	0.2	30.7	0.4	31.5	0.2	32.2	0.1	—	—
	♀	29.1	0.1	32.3	0.1	34.7	0.3	35.8	0.3	37.1	0.1	37.7	1.0
1971.....	♂	27.9	0.1	30.1	0.1	31.4	0.2	31.2	0.4	33.2	0.3	33.6	0.2
	♀	29.0	0.1	32.8	0.1	34.5	0.2	36.6	0.3	37.3	0.3	38.4	0.1
1972.....	♂	27.8	0.1	30.6	0.2	32.4	0.2	33.6	0.5	34.6	1.5	34.1	0.6
	♀	29.4	0.1	33.1	0.2	36.6	0.2	37.5	0.3	39.0	0.4	39.3	0.4
1973.....	♂	28.2	0.1	30.4	0.1	31.6	0.4	33.3	0.4	33.0	0.5	33.1	0.7
	♀	30.5	0.2	34.2	0.1	36.2	0.4	38.2	0.3	39.8	0.5	40.2	0.6

* This age-group only partly recruited in the period 1957–1967 and average length can thus be assumed to be biased in these years.

Belgian–German Waddensea programme for 1969 onwards. Additional data on 0-group length is given by De Clerck (1974) for the Belgian coast and for the pre-war situation by Tesch (1913) and Bückmann (1934) for the Dutch and German nurseries respectively.

Figure 5 shows the modal length of 0-group soles in the German coastal area in 1954–1967 and in the Dutch Waddensea and the Belgian coast in 1969–1972. Tesch (1913) and Bückmann (1934) give about 9 cm as the average length after one year. It may be concluded that no significant change took place in the average length until about 1964. After that time a small increase can be observed to 10 cm at present. This increase is only 1 to 1½ cm over the last ten years whereas, for example the 4 year old soles

changed from 28 cm to 32½ cm, an increase of 4½ cm in the same period. Therefore, the main increase in length-at-age should have taken place in the second and the third year of life. Soles of that age are not distributed all over the North Sea. After having left the nurseries their distribution is limited. The factors responsible for the increase in growth in the sole have to be localised in the coastal waters of the North Sea but outside the estuaries and the Waddensea.

Variations in weight-at-age

Table 3 gives the gutted weight-at-age with gonads for males and females in the second quarter. For

length-age key for North Sea sole in the second quarter, derived from market-sampling

9		10		11		12		13		14		15		Total number of otoliths (<i>n</i>) in length-age keys (including age-groups 15+)
\bar{l}	<i>S\bar{l}</i>	\bar{l}	<i>S\bar{l}</i>	\bar{l}	<i>S\bar{l}</i>	\bar{l}	<i>S\bar{l}</i>	\bar{l}	<i>S\bar{l}</i>	\bar{l}	<i>S\bar{l}</i>	\bar{l}	<i>S\bar{l}</i>	
32.3	0.4	32.1	0.6	-	-	-	-	-	-	-	-	-	-	94
37.6	0.7	38.0	0.5	-	-	42.0	2.0	43.1	2.0	-	-	37.0	2.2	203
32.1	1.3	31.0	1.4	31.7	0.6	-	-	-	-	-	-	-	-	127
34.7	1.3	37.6	0.7	38.4	0.5	-	-	-	-	-	-	-	-	176
30.5	0.2	29.5	2.2	-	-	31.8	1.3	-	-	-	-	-	-	49
34.3	0.5	38.2	1.1	38.3	1.4	39.1	0.8	37.5	0.3	-	-	-	-	142
-	-	30.8	0.7	-	-	-	-	32.7	0.7	-	-	-	-	114
40.1	0.6	38.7	0.5	37.8	0.9	37.7	0.9	40.6	0.7	-	-	-	-	183
32.7	0.7	31.2	0.8	31.8	0.5	34.5	0.7	34.4	1.4	35.5	0.8	-	-	97
34.4	1.3	36.5	0.9	37.8	0.9	39.0	1.0	31.8	1.7	39.9	0.7	-	-	252
28.3	0.7	-	-	31.2	1.0	30.5	0.7	33.1	1.0	34.7	1.3	35.4	0.9	184
37.8	0.4	38.5	1.5	37.7	0.7	41.5	0.8	40.0	0.7	41.5	0.5	40.8	0.4	318
30.7	0.7	30.3	1.0	32.7	1.2	33.3	0.8	34.1	1.1	34.1	1.6	34.4	1.6	252
33.4	1.4	38.0	0.6	38.9	0.6	-	-	40.8	0.9	38.8	0.3	40.5	1.6	354
30.9	0.4	32.4	1.2	32.4	0.8	33.5	2.3	36.8	0.6	31.7	0.8	33.8	1.4	344
35.8	0.5	37.8	0.4	36.2	0.9	38.7	0.8	38.5	0.5	39.0	0.7	42.3	0.4	504
-	-	31.6	1.2	-	-	31.6	1.4	33.9	0.4	34.5	1.0	-	-	120
40.3	0.8	38.6	0.7	37.1	0.6	42.0	0.8	37.3	1.8	-	-	41.7	1.5	146
-	-	31.7	0.4	-	-	-	-	32.0	0.8	-	-	-	-	147
36.5	0.6	36.7	0.7	41.1	1.2	38.2	0.8	42.2	0.8	-	-	42.8	0.3	381
31.2	0.3	-	-	31.1	1.2	30.2	1.9	32.7	1.3	33.2	1.1	-	-	423
36.9	0.3	36.9	0.6	38.7	0.5	38.4	1.3	39.4	0.4	41.0	0.5	41.2	1.7	773
-	-	33.0	0.4	-	-	34.2	0.6	-	-	-	-	-	-	400
38.0	1.1	39.5	0.4	42.9	1.1	42.0	0.5	39.2	1.5	41.0	0.6	-	-	502
33.3	0.5	-	-	34.2	0.5	-	-	33.5	0.9	33.5	1.2	34.8	1.2	934
39.1	0.3	39.6	0.4	40.2	0.3	39.7	1.2	42.3	0.4	44.2	0.8	44.2	0.7	1248
-	-	33.3	0.4	35.3	0.4	34.1	0.1	35.7	0.9	32.4	0.1	34.6	1.0	1301
-	-	39.0	0.2	38.6	0.7	40.1	0.2	43.0	0.7	41.2	0.5	42.0	0.6	1736
-	-	-	-	35.0	0.1	-	-	36.3	0.4	-	-	-	-	936
-	-	-	-	39.5	0.2	-	-	40.5	0.4	39.7	1.9	40.4	1.0	1170
34.6	0.2	-	-	-	-	33.7	0.7	-	-	36.6	0.4	-	-	978
40.3	0.2	40.8	1.9	40.8	3.9	41.5	0.9	40.3	1.8	41.2	0.4	39.6	0.9	1226
31.7	0.7	34.9	0.4	-	-	-	-	35.0	1.7	-	-	34.2	1.5	631
40.9	0.5	41.8	0.3	41.0	1.5	-	-	44.0	1.2	-	-	42.8	0.5	758

sexes combined the weight data are shown in the upper diagram of Figure 6. As with length, the weight-at-age more or less remained constant until about 1963 and increased in all age-groups since 1964. The annual increments in weight also show a tendency to increase over the period but the major increase is again to be found in soles of three years old or younger. The increase in weight-at-age is most pronounced in the females (Fig. 7). From 1957 to 1973 the weight of four year old female soles in April increased from 200 g to 380 g, an increase of 90%; six year old females increased from 300 to 600 g, a 100% increase. Male soles increased some 50% in weight over the same 16 years. In order to exclude the length increment from the weight effect, changes in the condition factor have to be considered.

Variations in the condition factor

In sole the weight-length relationship can be described by $W = ql^a$, in which q is the condition factor¹. In sole larger than 24 cm the exponent a equals 3, thus we use this value for our market samples. Table 4 gives the average condition factor for males and females per month and per year for gutted soles with gonads. Inspection of Table 4 reveals that the condition factor remained more or less constant from 1957-1963 and increased stepwise to a higher level

¹ The condition factor usually given as k is here described as q to avoid confusion with the Von Bertalanffy coefficient of catabolism k .

Table 2. Average length (\bar{l}), standard error ($S\bar{l}$) and number of otoliths (n) used in length-age key

Year	Age-group	Sub-stock (see Fig. 3)	3		4		5		6		7		8		
			\bar{l}	$S\bar{l}$	\bar{l}	$S\bar{l}$	\bar{l}	$S\bar{l}$	\bar{l}	$S\bar{l}$	\bar{l}	$S\bar{l}$	\bar{l}	$S\bar{l}$	
1968	1	♂	25.9	0.3	27.4	0.3	29.2	0.4	—	—	—	—	35.2	0.4	
		♀	27.0	0.3	31.8	0.3	33.8	0.3	—	—	—	—	38.9	0.4	
	2	♂	25.9	0.3	27.2	0.2	31.5	0.4	—	—	—	—	—	—	
		♀	29.6	1.2	31.5	0.3	34.3	0.2	—	—	—	—	39.1	0.5	
	3	♂	26.8	0.3	29.2	0.3	29.8	0.2	—	—	—	—	31.0	0.8	
		♀	30.4	0.5	33.0	0.5	34.2	0.2	32.7	1.8	40.3	0.6	36.7	0.9	
1969	1	♂	25.9	0.1	28.7	0.3	29.6	0.3	30.5	0.3	—	—	—	—	
		♀	27.6	0.2	31.4	0.4	33.8	0.2	34.4	0.3	—	—	40.9	0.3	
	2	♂	25.6	0.1	27.1	0.3	29.2	0.3	30.4	0.3	—	—	—	—	
		♀	27.7	0.2	32.4	0.4	34.2	0.3	35.2	0.2	—	—	37.6	0.6	
	3	♂	27.4	0.2	27.9	0.5	30.3	0.3	30.5	0.2	—	—	—	—	
		♀	28.9	0.4	32.9	1.3	34.8	0.4	35.7	0.2	37.1	0.7	—	—	
	4	♂	25.9	0.2	28.4	0.5	29.2	0.3	31.1	0.3	—	—	—	—	
		♀	27.7	0.2	32.5	0.5	33.3	0.3	35.6	0.2	39.3	0.6	—	—	
	6	♂	26.7	0.2	30.7	0.6	31.5	0.4	32.0	0.2	—	—	—	—	
		♀	30.0	0.5	33.1	1.3	33.5	0.4	34.8	0.3	—	—	—	—	
	1970	1	♂	27.5	0.2	29.4	0.5	31.3	1.0	31.9	0.4	32.6	0.2	—	—
			♀	29.1	0.2	32.5	0.5	36.3	0.8	34.5	0.4	37.1	0.2	35.1	1.5
2		♂	26.5	0.1	28.0	0.2	29.0	0.8	31.2	0.4	31.8	0.3	—	—	
		♀	28.5	0.2	32.2	0.2	34.4	0.5	35.6	0.5	37.4	0.2	—	—	
3		♂	27.5	0.1	30.2	0.4	29.8	0.6	31.6	0.5	32.0	0.2	—	—	
		♀	29.7	0.2	32.9	0.3	34.0	0.8	36.4	0.5	37.1	0.2	41.5	2.0	
4		♂	26.9	0.2	29.0	0.3	32.1	1.0	31.8	0.3	33.1	0.3	—	—	
		♀	28.5	0.1	30.8	0.3	34.2	0.5	36.5	0.4	37.2	0.2	—	—	
5		♂	27.7	0.2	28.6	0.4	31.4	0.7	30.6	0.6	30.6	0.2	—	—	
		♀	30.2	0.3	33.6	0.9	36.1	1.0	36.3	0.6	37.3	0.3	—	—	
6		♂	27.7	0.2	28.8	0.4	—	—	31.8	0.6	32.8	0.2	—	—	
		♀	28.7	0.2	31.9	0.6	33.3	0.6	35.3	1.4	36.7	0.2	36.5	0.7	
1971		1	♂	27.9	0.3	29.9	0.3	31.2	1.0	30.7	0.8	34.1	0.4	34.2	0.5
			♀	28.9	0.3	33.6	0.3	34.9	0.4	37.1	0.9	37.5	0.9	39.0	0.3
		2	♂	27.7	0.2	29.7	0.2	31.1	0.3	29.9	0.7	32.7	1.0	33.1	0.5
			♀	29.5	0.3	33.7	0.2	35.2	0.3	37.7	0.4	38.1	0.4	38.6	0.3
		3	♂	28.0	0.2	30.5	0.2	31.9	0.4	31.2	0.6	34.0	0.5	33.3	0.3
			♀	29.2	0.3	33.7	0.2	34.9	0.9	37.6	0.6	37.6	0.5	38.8	0.2
	4	♂	27.2	0.3	28.9	0.4	29.2	0.8	31.0	0.4	32.6	0.3	33.5	0.4	
		♀	28.9	0.4	32.8	0.6	—	—	36.2	1.3	37.3	1.2	40.8	0.4	
	6	♂	27.9	0.3	30.2	0.3	31.4	0.8	32.8	2.0	32.0	0.4	33.9	0.3	
		♀	28.4	0.2	30.1	0.4	32.9	0.6	34.1	1.3	35.9	0.6	37.1	0.4	
	1972	1	♂	27.2	0.2	30.9	0.4	32.6	0.4	33.4	0.6	—	—	34.4	0.6
			♀	28.9	0.2	33.2	0.5	36.5	0.4	37.5	0.3	39.6	0.5	38.7	0.7
2		♂	27.4	0.1	30.2	0.6	31.4	0.4	33.7	1.3	—	—	—	—	
		♀	29.7	0.2	34.1	0.3	36.5	0.3	38.5	0.6	38.5	0.5	40.3	0.8	
3		♂	28.0	0.1	30.0	0.5	32.4	0.5	33.5	0.7	—	—	32.6	0.4	
		♀	29.7	0.1	33.0	0.4	36.2	0.4	36.6	0.8	—	—	38.9	0.9	
4		♂	27.9	0.1	29.5	0.4	32.1	0.3	33.1	0.6	—	—	35.2	0.5	
		♀	29.2	0.3	33.2	0.5	35.7	0.4	39.4	0.7	38.3	0.7	38.7	0.5	
5		♂	28.5	0.2	30.1	0.3	30.7	0.4	31.4	0.7	—	—	33.0	0.8	
		♀	30.3	0.3	33.1	0.4	35.0	0.6	36.8	0.6	39.6	1.0	38.3	1.1	
6		♂	28.1	0.1	31.1	0.1	33.1	0.4	33.7	0.7	34.6	1.0	35.4	0.8	
		♀	29.3	0.2	32.0	0.5	37.0	0.5	38.0	0.9	38.9	1.0	—	—	
1973	1	♂	27.9	0.3	29.5	0.3	31.2	0.3	33.3	0.6	31.9	0.3	—	—	
		♀	31.2	1.1	33.9	0.5	37.3	0.7	38.3	0.4	39.2	0.4	39.9	0.5	
	2	♂	27.1	0.2	29.6	0.3	31.8	1.0	32.4	0.9	33.1	1.2	33.1	1.3	
		♀	30.3	0.4	34.2	0.3	36.2	0.6	39.8	0.5	39.9	0.7	41.3	2.1	
	3	♂	28.2	0.2	30.6	0.2	31.0	0.5	32.5	0.4	33.9	0.4	—	—	
		♀	30.0	0.3	33.8	0.2	35.7	0.7	38.2	0.5	40.5	0.8	39.1	1.1	
	4	♂	28.2	0.3	30.5	0.2	—	—	32.9	0.8	—	—	—	—	
		♀	30.7	0.6	34.7	0.3	37.4	0.5	39.5	0.4	39.4	0.8	40.5	0.6	
	6	♂	29.4	0.5	31.7	0.4	32.2	0.4	35.2	1.3	—	—	—	—	
		♀	30.2	0.3	34.2	0.4	34.6	0.8	35.2	2.1	—	—	—	—	

for various sub-stocks of North Sea sole in the second quarter, derived from market-sampling

9		10		11		12		13		14		15		Total number of otoliths (<i>n</i>) in length-age keys (including age-groups 15+)
\bar{l}	<i>S\bar{l}</i>	\bar{l}	<i>S\bar{l}</i>	\bar{l}	<i>S\bar{l}</i>	\bar{l}	<i>S\bar{l}</i>	\bar{l}	<i>S\bar{l}</i>	\bar{l}	<i>S\bar{l}</i>	\bar{l}	<i>S\bar{l}</i>	
-	-	34.0	0.9	-	-	-	-	-	-	-	-	-	-	68
38.0	0.9	40.4	0.4	-	-	43.6	0.7	39.2	1.2	41.0	0.3	-	-	109
-	-	33.3	0.6	-	-	35.7	0.4	-	-	-	-	-	-	138
-	-	40.6	0.2	-	-	42.6	0.8	-	-	-	-	-	-	152
-	-	31.7	1.1	-	-	32.6	1.4	-	-	-	-	-	-	194
-	-	37.4	0.7	42.9	1.0	39.9	0.6	-	-	-	-	-	-	239
33.5	0.9	-	-	34.2	0.9	-	-	-	-	-	-	-	-	223
37.8	0.7	40.7	0.7	41.1	0.2	41.1	0.3	44.0	0.9	45.8	1.7	43.0	1.0	307
-	-	-	-	33.4	0.5	-	-	-	-	-	-	-	-	197
40.4	0.6	39.5	0.0	41.7	0.4	40.1	1.4	42.6	0.7	-	-	-	-	285
-	-	-	-	33.4	0.9	-	-	-	-	-	-	34.4	2.4	218
40.6	0.5	42.0	1.4	39.1	0.7	-	-	43.3	0.9	-	-	-	-	244
35.3	1.2	-	-	36.0	0.4	-	-	-	-	-	-	-	-	120
-	-	-	-	40.7	0.4	-	-	40.7	0.5	41.9	0.4	-	-	205
31.8	0.4	-	-	34.1	0.3	-	-	32.6	0.6	-	-	32.9	0.8	176
37.5	0.6	37.2	1.1	38.2	0.4	43.0	0.5	41.0	0.8	-	-	41.7	0.8	207
-	-	34.9	0.9	-	-	34.8	0.3	-	-	34.0	0.4	-	-	238
-	-	39.7	0.5	-	-	37.6	0.5	42.3	2.0	40.8	0.9	41.4	1.1	281
-	-	33.4	0.5	-	-	34.4	0.6	-	-	-	-	-	-	250
-	-	39.7	0.5	-	-	42.0	0.3	-	-	42.1	0.9	42.0	0.8	357
-	-	-	-	36.5	0.7	34.3	0.7	-	-	32.0	0.4	31.8	1.1	248
-	-	37.4	0.9	-	-	39.4	0.5	44.0	0.4	40.1	0.5	42.0	1.0	308
-	-	-	-	-	-	36.2	1.4	-	-	-	-	-	-	186
-	-	39.0	0.8	-	-	39.9	0.3	-	-	39.6	2.0	41.8	0.7	336
-	-	33.0	0.6	-	-	32.5	0.6	-	-	32.7	1.7	-	-	146
-	-	-	-	-	-	41.2	1.0	43.0	1.5	42.0	0.4	-	-	144
-	-	33.8	0.7	-	-	32.2	0.4	-	-	-	-	-	-	238
-	-	39.4	0.5	38.7	0.8	40.2	0.3	39.8	1.5	42.8	2.0	43.2	1.2	314
-	-	-	-	-	-	-	-	35.9	0.8	-	-	-	-	191
-	-	-	-	39.8	1.7	-	-	39.5	1.0	-	-	-	-	237
-	-	-	-	-	-	-	-	37.3	1.1	-	-	-	-	235
-	-	-	-	41.3	1.0	-	-	42.4	0.4	-	-	41.7	0.8	247
-	-	-	-	-	-	-	-	34.8	0.6	-	-	-	-	268
-	-	-	-	-	-	-	-	40.8	0.6	-	-	-	-	342
-	-	-	-	33.9	0.7	-	-	-	-	-	-	-	-	89
-	-	-	-	-	-	-	-	42.5	1.0	-	-	-	-	111
34.7	0.7	-	-	35.0	0.2	-	-	37.0	0.1	-	-	-	-	242
-	-	-	-	37.5	0.2	-	-	39.1	0.1	39.7	0.4	39.0	0.3	344
35.1	0.3	-	-	-	-	-	-	-	-	37.8	0.5	-	-	250
40.5	0.3	-	-	-	-	45.9	1.2	-	-	43.3	0.5	-	-	273
34.7	0.4	-	-	-	-	-	-	-	-	35.9	1.5	-	-	213
40.6	0.3	-	-	-	-	39.5	1.2	-	-	37.8	2.3	-	-	271
34.0	0.5	-	-	-	-	-	-	-	-	-	-	-	-	257
40.3	0.3	-	-	-	-	41.5	0.5	-	-	42.0	0.5	-	-	376
35.2	0.2	-	-	-	-	35.4	0.5	-	-	36.8	0.5	-	-	243
41.3	0.4	-	-	-	-	-	-	-	-	43.0	0.7	-	-	170
32.8	0.3	-	-	-	-	-	-	-	-	33.3	1.7	-	-	200
38.7	0.3	-	-	-	-	39.9	0.4	-	-	41.4	1.6	42.5	1.4	156
34.6	0.3	-	-	-	-	33.7	1.0	-	-	36.1	0.4	-	-	258
39.9	0.3	40.8	0.9	40.8	1.1	38.9	1.5	40.3	1.7	41.5	0.4	39.6	0.9	310
-	-	32.5	1.1	-	-	-	-	-	-	-	-	-	-	77
42.2	0.3	42.5	0.7	-	-	-	-	-	-	-	-	-	-	64
-	-	33.8	1.8	-	-	-	-	-	-	-	-	-	-	112
42.0	0.4	43.3	0.6	-	-	-	-	-	-	-	-	-	-	136
-	-	34.4	0.5	-	-	-	-	-	-	-	-	-	-	229
41.9	0.4	41.6	0.4	-	-	-	-	45.6	0.7	42.4	1.3	43.0	0.6	312
31.7	1.4	37.5	0.7	-	-	33.5	-	-	-	-	-	-	-	151
37.7	1.0	40.9	1.1	41.0	0.4	43.5	-	-	-	-	-	-	-	95
-	-	36.4	0.5	-	-	-	-	35.0	0.4	-	-	34.2	0.3	75
40.6	1.5	40.9	0.5	-	-	-	-	42.3	0.3	-	-	42.5	0.7	171

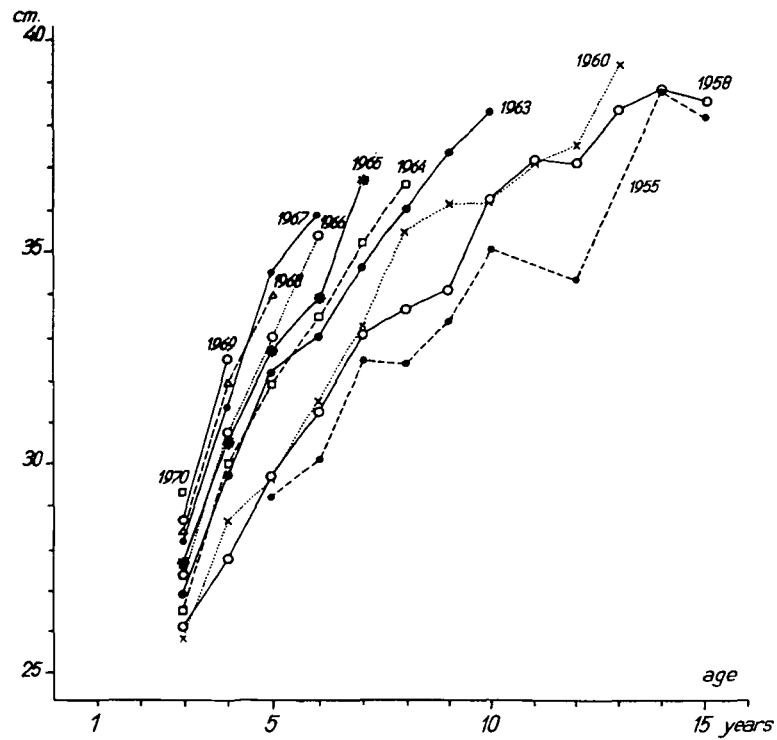


Figure 2. Average lengths for different year classes by age of North Sea sole, sexes combined, based on market sampling 1957–73.

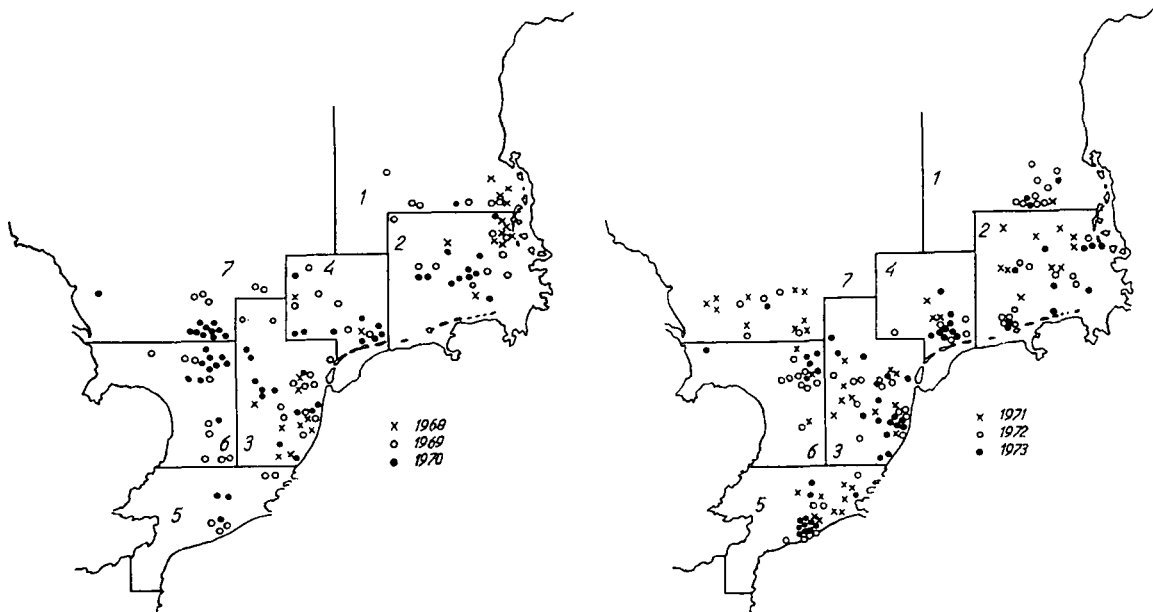


Figure 3. Positions of commercial ship samples in the second quarter 1968–1973; area-breakdown used for sampling, defining sub-stocks.

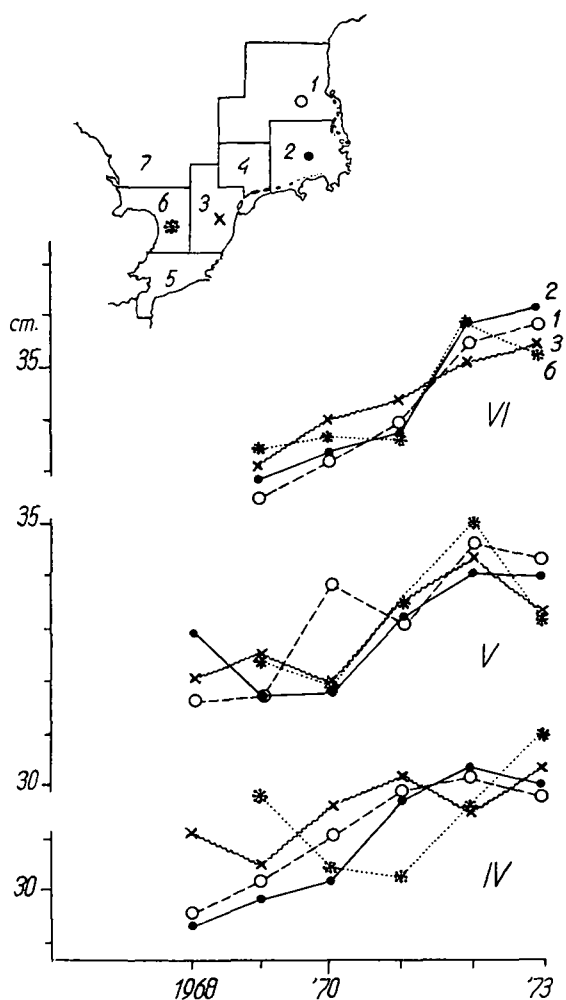


Figure 4. Average length in the second quarter for North Sea sole sub-stocks 1, 2, 3 and 6, sexes combined, in the period 1968-73.

in 1964. Since 1971 the annual condition factors are again at an even higher level. The amplitude of the monthly variation in the condition factor has also increased (Fig. 8). In 1957-1962 the amplitude in the condition factor of male soles was 10.7% of the minimum value in spring, but increased to 19% in 1968-1973. In females the amplitudes slightly increased from 15.8% to 16.5%.

Variations in the weight of the ovaries

Weighing ovaries on a routine basis was started in 1962. The weight of the ovary is a function of length, smaller soles having small and large soles having big ovaries. In order to compare variations in ovary weight of soles of different sizes, the weight of the ovary can be expressed as percentage of the gutted weight including gonads. This is shown in Figure 9 in which the monthly relative ovary weights have been given for four length groups. The diagrams show, that over the period concerned several changes have taken place.

Ovaries of soles of 25 cm developed to a weight of 5% of the gutted weight including gonads in 1962 but this decreased to some 1% in later years. This decrease in the relative weight of the fully developed ovary is also present in soles of 30 cm in which a change from 9% in 1962 to 5% in 1966 took place. Gonad weights of female soles of 35 cm remained constant and for soles of 40 cm they increased from 10% in 1962 to about 15% later on. These changes indicate that the relationship between relative ovary weight and length has become steeper and that this change took place in 1965-1966. In the following we will use ovary weight as an index of fecundity. In

Figure 5. Modal length of 0-group sole at the age of $\frac{1}{2}$ and 1 year. Open circle 1913, from Tesch (1913) from Dutch coastal area; open circle 1934, from Bückmann (1934) from German coastal areas; black circles 1954-1967, from Meyer-Waarden and Tiews (1965), and Tiews (1971) from the German coastal areas; open circles 1969-1972, from Dutch Waddensea surveys; and crosses 1971-72 from De Clerck (1974) for the Belgian coast.

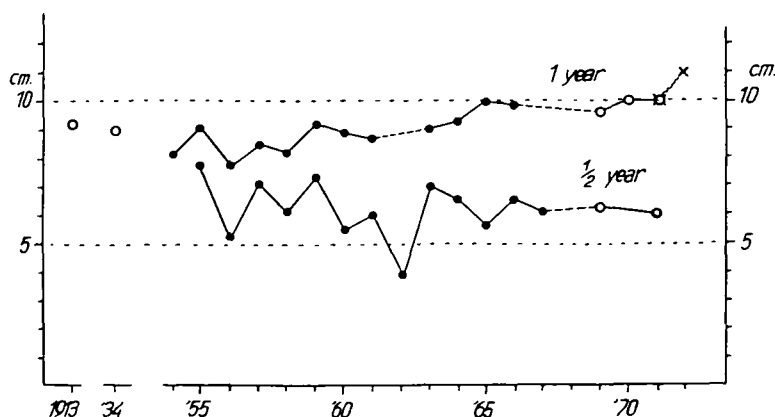


Table 3. Average gutted weight (\bar{W}) in g and number of otoliths (n) used in length-age key for North Sea sole in the

Year	Age-group	3*		4		5		6		7		8	
		\bar{W}	n	\bar{W}	n	\bar{W}	n	\bar{W}	n	\bar{W}	n	\bar{W}	n
1957...	♂	118.1	7	129.8	12	178.4	5	203.0	9	192.9	18	234.0	6
	♀	135.3	23	184.6	41	251.4	10	295.2	13	339.7	32	440.0	15
1958...	♂	130.4	11	151.4	15	153.1	29	164.6	11	188.3	5	217.6	18
	♀	155.3	12	205.9	33	265.9	31	281.6	3	377.1	8	322.1	22
1959...	♂	125.4	7	128.0	9	154.1	9	177.1	7	170.7	1	240.5	3
	♀	152.8	18	200.2	27	275.8	29	299.0	13	373.8	3	407.9	6
1960...	♂	145.4	8	140.2	17	147.3	12	170.8	25	186.6	19	196.7	6
	♀	156.5	24	219.7	29	261.0	28	328.2	20	363.7	18	—	—
1961...	♂	123.6	20	176.2	3	155.7	9	155.7	11	216.8	15	188.3	13
	♀	140.1	63	249.9	28	262.1	28	270.9	23	329.6	15	367.2	21
1962...	♂	134.5	6	138.2	87	163.7	17	189.5	18	198.0	12	200.0	9
	♀	139.9	6	204.7	112	301.4	25	359.0	38	392.2	22	385.6	16
1963...	♂	119.6	10	146.5	14	157.3	134	164.6	30	191.1	22	188.9	7
	♀	144.2	39	188.1	21	266.3	132	309.6	34	340.4	29	382.0	19
1964...	♂	143.5	19	150.3	56	170.1	49	193.2	165	197.2	2	211.4	20
	♀	145.6	22	243.7	46	305.3	33	326.7	210	338.6	47	351.1	22
1965...	♂	136.8	3	195.7	16	176.2	16	219.5	9	250.5	55	207.4	7
	♀	195.6	4	231.9	5	280.8	15	338.0	12	384.9	65	393.5	11
1966...	♂	135.2	71	174.3	1	220.5	1	160.7	6	257.9	5	241.6	51
	♀	160.7	184	204.6	3	356.7	3	363.3	18	406.1	8	391.4	101
1967...	♂	124.1	68	169.3	271	197.4	6	211.3	3	214.2	13	192.9	5
	♀	165.6	79	250.8	391	240.4	9	427.1	5	409.4	48	452.5	10
1968...	♂	136.3	63	167.2	109	210.7	175	—	—	—	—	287.2	8
	♀	204.7	27	285.5	78	343.8	237	302.1	3	587.8	3	495.0	24
1969...	♂	141.5	261	185.3	80	212.0	152	237.8	352	—	—	252.2	4
	♀	191.7	259	306.2	76	347.5	169	388.3	438	511.9	12	518.8	8
1970...	♂	161.1	570	196.8	140	238.4	40	258.2	72	275.4	357	339.2	1
	♀	211.7	567	298.9	160	375.2	50	417.1	82	467.2	571	489.2	7
1971...	♂	183.1	245	234.2	243	274.4	89	205.6	14	327.7	39	329.9	193
	♀	225.7	272	338.2	250	391.1	69	505.3	25	485.1	53	547.7	261
1972...	♂	178.1	539	240.9	100	287.9	98	325.7	28	356.2	5	341.4	14
	♀	227.2	490	343.0	153	466.8	143	476.9	46	563.5	12	594.0	29
1973...	♂	183.9	177	227.8	281	255.5	38	316.8	23	293.9	10	299.8	8
	♀	249.7	147	366.7	246	436.1	55	528.8	49	592.2	25	628.5	10

* This age-group only partly recruited in the period 1957–1967 and average weight was thus assumed to be biased in these years.

Figure 9 the role of the individual year classes is masked. It is possible to follow the year class influence by plotting the weights of the ovaries per year class.

Variations in ovary weight per year class

In Figure 10 the relationship between ovary weight in grammes and length per age-group is given for the month of maximum ovary development (April). Not all age-groups are represented every year owing to differences in year class strength. Thus the poorer year classes yielding too few points are omitted from the graphs. This figure shows that the change in fecundity took place rather abruptly from 1964 to 1965. The change affected all age groups at the same time. Apart from the change in the slope of the curves

the already mentioned increase in length-at-age can be observed in Figure 10 as a shift of the age group curves to the right. The diagrams suggest that the change in fecundity is rather distinct. Except for the shift to the right the situation in April 1973 closely resembles that of 1966. The fact that all year classes demonstrated the change more or less in the same year indicates that environmental rather than genetic factors are responsible.

A typical feature in Figure 10 is the fact that the year group curves do not fall on the same overlapping line, but that each year group has its own line, the relationship being fan-like in some years. This may be the result of a small but continuous increase in the ovary weight – age relationship. It may, however, also mean that within one single year class the slow growing individuals develop ovaries too small for their size and the fast growing soles ovaries of ex-

second quarter derived from market sampling per age-group for males and females per year for the second quarter

9		10		11		12		13		14		15	
\bar{W}	<i>n</i>	\bar{W}	<i>n</i>	\bar{W}	<i>n</i>	\bar{W}	<i>n</i>	\bar{W}	<i>n</i>	\bar{W}	<i>n</i>	\bar{W}	<i>n</i>
262.5	13	257.7	22	292.1	1	—	—	472.8	1	—	—	—	—
448.7	12	467.5	47	580.6	1	644.6	3	691.7	2	707.1	1	423.0	2
253.4	10	224.6	5	242.4	21	—	—	—	—	—	—	415.8	1
362.3	15	482.1	6	516.4	43	600.5	1	478.3	1	600.5	1	—	—
221.9	8	196.1	2	261.8	1	256.3	2	—	—	—	—	—	—
341.0	7	483.3	9	485.4	8	512.9	18	456.7	2	641.0	2	—	—
—	—	227.6	10	445.5	1	220.7	1	278.0	12	—	—	—	—
589.4	5	522.2	18	477.4	10	472.6	6	609.0	25	—	—	—	—
274.5	3	234.5	4	250.2	5	330.6	2	327.3	4	369.1	8	—	—
334.6	10	388.5	5	434.8	16	487.0	12	256.0	3	530.4	28	—	—
173.6	7	243.8	1	236.0	4	219.6	5	288.7	5	339.3	3	363.8	10
480.2	15	510.2	3	476.4	14	656.1	10	580.5	15	656.1	6	620.1	34
220.5	10	210.6	5	268.5	3	283.6	6	303.7	3	303.7	3	311.8	2
315.6	13	479.6	15	516.2	5	—	—	604.5	16	512.3	2	588.6	3
229.0	8	277.9	4	277.9	4	320.3	2	385.2	5	251.7	4	330.2	2
400.6	21	467.7	31	413.7	19	497.3	4	490.8	15	508.4	11	629.0	18
—	—	263.2	3	—	—	263.2	4	315.6	2	335.9	2	377.2	1
598.2	8	519.9	4	450.9	6	657.9	8	459.3	3	—	—	647.6	3
220.5	1	254.2	5	470.8	1	—	—	264.4	3	—	—	374.5	1
409.9	11	417.7	18	613.0	9	479.4	17	668.9	5	536.8	1	701.7	2
239.3	31	—	—	234.0	5	211.3	3	277.3	3	291.3	4	—	—
431.1	149	431.1	11	499.6	19	488.1	7	530.3	25	601.7	15	611.2	3
—	—	284.3	18	—	—	315.6	6	—	—	—	—	—	—
486.2	2	553.4	83	701.9	6	662.4	14	540.3	2	618.9	3	—	—
298.7	22	408.5	1	324.8	43	408.5	1	304.2	7	304.2	4	344.7	6
538.0	54	557.0	14	582.7	153	561.3	10	681.2	28	781.5	7	781.5	12
296.1	2	304.3	24	366.0	5	326.3	61	379.9	5	280.6	12	342.1	4
405.3	2	538.6	41	523.4	9	581.6	175	702.8	14	625.2	27	657.9	23
—	—	—	—	374.5	14	—	—	431.3	35	—	—	—	—
—	—	—	—	583.6	18	—	—	642.1	84	—	—	610.9	13
373.0	130	—	—	—	—	461.6	12	—	—	470.7	29	—	—
640.8	209	—	—	—	—	862.0	16	518.7	3	669.0	73	809.2	7
250.1	6	348.4	35	—	—	—	—	341.1	2	—	—	328.6	2
623.4	23	676.7	84	697.8	2	—	—	755.0	7	747.4	2	712.7	24

cessive weight. Very probably it is the last assumption which is correct.

When ovary weight in April per year class is plotted against age (Fig. 11) it is obvious that the number of years needed to reach, for example an ovary weight of 100 g, has decreased since 1962. It took the 1965 and 1966 year classes only 7 to 8 years to achieve this, whereas the 1963 year class reached this level after 8–9 years. For the 1958 year class the interval was 12–13 years. Older year classes needed even more than 15 years to attain the 100 g level. If ovary weight can be taken as an index for fecundity, as has been proved for the lemon sole (Newton and Armstrong, 1974), the observed increase in gonad weight-at-age undoubtedly will influence the egg-production of the sole stock.

Earlier the condition factor was considered in relation to gutted weight including gonads. The observed

increases might be completely due to the increase in ovary weight. This cannot be checked for the males because of lack of information on male gonad weights. For the females the somatic gutted weight can be calculated by subtracting ovary weight from gutted weight including gonads. Thus the annual weight increment per age can be split into a somatic and a reproductive component. In Figure 12 the annual increments by age determined from April to April are given for four periods for somatic tissue weight (hatched columns) and reproductive tissue weight (black columns). With increasing age less weight increment goes to somatic tissue and more to reproductive tissue. The ratio of somatic to reproductive increment is 1:1 at about 7–8 years of age. Both somatic and reproductive increments increased over the period and, therefore, the changes in total weight mentioned before are not restricted to the gonads

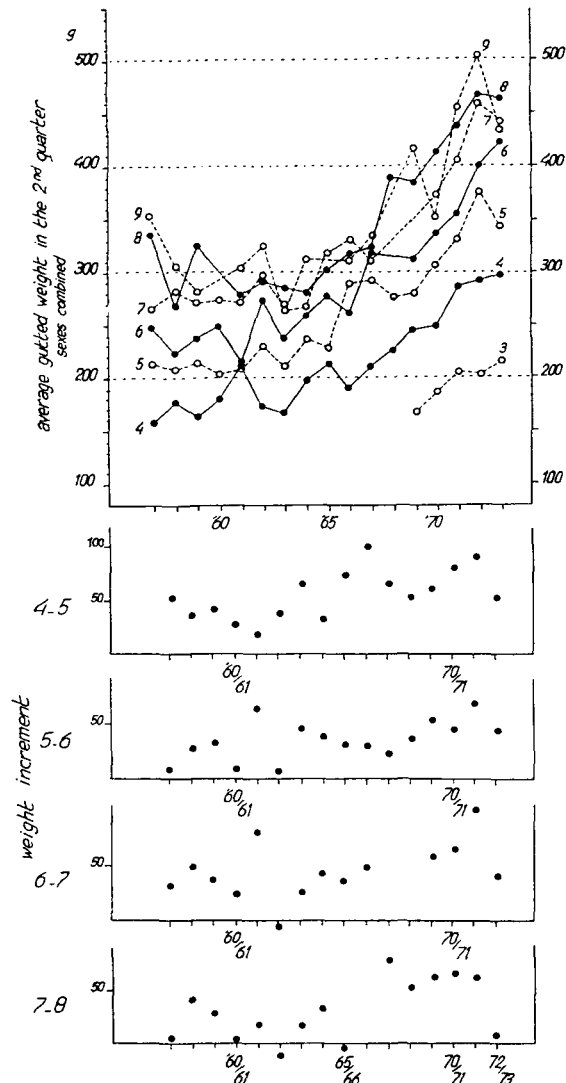


Figure 6. Top diagram, average gutted weight-per-age for North Sea sole with gonads, sexes combined, in the second quarter, based on market sampling 1957-73; other diagrams, annual weight increments by years.

only. It is not clear, whether the point of equal increment in both components changed from 1962-1964 to 1971-1973 owing to the large variations in the data.

Changes in recruitment to the spawning stock

The maturity - length ogive for female soles can be derived from the monthly data on maturation collected since 1964. The criterion used is that mature

female soles must have reached at least stage 4 in May and June. I have shown (de Veen, 1970) that the gonads of age-group II may develop in May up to stage 3 but stop developing further in June. These soles are not considered to be mature for the present calculations. De Veen (1970) demonstrated that in the period 1964-1969 the length at which 50% of the females mature - the 50% point of the maturity ogive - was 27.5 cm for North Sea sole. Compared with the data for North Sea sole given by Holt (1892) and Bückmann (1934) this value appeared to be remarkably constant over a long period, Holt's 50% length being 27.5 cm and that given by Bückmann 27.2 cm.

Very recently, however, this picture changed. In 1969 the ogive was raised by some 2.5 cm and this remained so in the following years. Figure 13 gives the annual ogives in which the data for the years 1964 and 1965 were pooled for lack of sufficient data in the ogive length range owing to poor year classes. The diagrams show clearly the shift to the higher level in 1969. Figure 14a gives the 50% points of the ogives of Figure 13 together with the values given by Holt and Bückmann. Figure 14b shows the average maturity - length ogives for 1964 to 1968 and for 1969 to 1973. In the preceding section fecundity was shown to have started to change in 1965 and we have just discussed an abrupt change in maturity - length in 1969, 4 years later. It might be possible that the change started with one particular year class which was born for example in 1966 and matured for the first time in 1969. We have to consider therefore the 50% lengths of the ogives per age-group.

From Figure 15 it is evident that the 4 year old and the 3 year old soles simultaneously changed their maturity-length relationship in 1969 and the conclusion must be drawn that an unknown factor affected the maturity - length relationship of all year classes in one particular year, 1969. The other diagrams in Figure 15 give the average ogives for 1964-1968 and for 1969-1973 for the age-groups 3, 4 and 5 and older. The change in the 50% length is greatest in the 3 year old soles, nearly 3 cm, whereas in the 5 year and older fish the change is less than 2 cm. Another feature is the increasing steepness of the ogives with age, which has not been affected by the change.

Did the change in the maturity - length relationship take place in the whole North Sea stock to the same extent or are there differences between the sub-stocks? Figure 16 gives the answer to this question. Apparently the distinct change in 1969 took place in sub-stocks 1, 2 and 3 and probably in sub-stocks 4 and 5, although no complete data are available. For sub-stock 6 only data for 1969, 1970, 1972 and

Table 4. Average condition factors ($q \times 10^2$) of gutted North Sea sole

Year	Males												Aver. year
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
1957	0.8208	0.8405	0.8090	0.8035	0.7749	0.6994	0.8209	0.8810	0.8669	0.8729	0.8372	0.8423	0.8224
1958	0.8295	0.8649	0.8155	0.7717	0.8150	0.7299	0.6814	0.7118	0.8033	0.7524	0.8172	0.8507	0.7869
1959	0.7777	0.7640	0.7992	0.8076	0.7419	0.7720	0.8222	0.8485	0.8055	0.8169	0.8629	0.8428	0.8051
1960	0.8192	0.8386	0.7668	0.8166	0.7953	0.8040	0.7699	0.7708	0.7411	0.8017	0.8012	0.8173	0.7952
1961	0.8045	0.7718	0.8280	0.7840	0.8081	0.7349	0.7829	0.7754	0.7571	0.8093	0.8236	0.8140	0.7911
1962	0.8617	0.8959	0.8351	0.8238	0.7742	0.7958	0.7494	0.7569	0.7602	0.8419	0.8695	-	0.8149
1963	0.8848	0.7832	0.7872	0.7743	0.7920	0.7176	0.7378	0.7857	0.8135	0.8548	0.8785	0.8986	0.8090
1964	0.8791	0.8516	0.8496	0.8055	0.8156	0.7493	0.8375	0.8344	0.8937	0.8839	0.8963	0.8983	0.8496
1965	0.9475	0.8724	0.8867	0.8689	0.8568	0.7840	0.7932	0.8342	0.8982	0.8762	0.8936	0.8590	0.8642
1966	0.8779	0.8910	0.7897	0.7412	0.8029	0.7927	0.8361	0.8130	0.8350	0.8801	0.8407	0.8866	0.8322
1967	0.8091	0.8691	0.7792	0.8084	0.7484	0.7945	0.7670	0.8178	0.9020	0.8822	0.8960	0.8649	0.8284
1968	0.8926	0.8894	0.7963	0.7782	0.7751	0.7399	0.8076	0.7720	0.9162	0.8801	0.8929	0.9025	0.8369
1969	0.8625	0.8215	0.7721	0.8094	0.8213	0.8118	0.7001	0.7855	0.8958	0.9010	0.9101	0.8802	0.8309
1970	0.9072	0.8485	0.8158	0.8267	0.7846	0.8221	0.7588	0.8624	0.9224	0.8320	0.8869	0.8606	0.8440
1971	0.9236	0.8927	0.8434	0.8947	0.8665	0.8925	0.8233	0.9026	0.9424	0.9107	0.9104	0.9575	0.8967
1972	0.9376	0.9583	0.9004	0.9073	0.8506	0.8306	0.8410	0.7703	0.9370	0.9151	0.9243	0.8729	0.8871
1973	0.8720	0.8493	0.9156	0.8659	0.8078	0.7872	-	0.8531	0.9520	0.9503	0.9478	0.8654	0.8788

Year	Females												Aver. year
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
1957	0.8930	0.9329	0.9388	0.8997	0.8125	0.7588	0.8317	0.8850	0.9036	0.9538	0.8981	0.9222	0.8858
1958	0.9320	0.9747	0.8865	0.8626	0.9053	0.7791	0.7432	0.7857	0.8319	0.8379	0.8859	0.9091	0.8612
1959	0.8784	0.9039	0.9099	0.8983	0.8779	0.8177	0.8358	0.8213	0.8356	0.9118	0.8899	0.9735	0.8795
1960	0.8997	0.9287	0.9167	0.9139	0.8378	0.8138	0.8045	0.8112	0.7985	0.8548	0.8762	0.8773	0.8611
1961	0.8838	0.8883	0.9011	0.8431	0.8159	0.7652	0.7932	0.8296	0.8379	0.8848	0.8796	0.8761	0.8499
1962	0.9443	0.8756	0.9315	0.9415	0.9041	0.7985	0.7674	0.8157	0.7865	0.8594	0.8902	-	0.8646
1963	0.9403	0.8924	0.8733	0.9200	0.8204	0.7899	0.7373	0.8179	0.8284	0.8834	0.9272	0.9448	0.8646
1964	0.9393	0.9298	0.9422	0.8765	0.8419	0.8101	0.8599	0.8396	0.8912	0.9117	0.9421	0.9664	0.8958
1965	1.0540	0.9566	0.9774	0.9497	0.9241	0.8205	0.8308	0.8370	0.9180	0.9105	0.8880	0.9277	0.9162
1966	0.9311	0.9315	0.8914	0.8318	0.8645	0.8252	0.8606	0.8622	0.9195	0.9083	0.9358	0.9313	0.8911
1967	0.8901	0.9245	0.8576	0.8951	0.8228	0.8176	0.8152	0.8724	0.9776	0.9288	0.9765	0.9685	0.9102
1968	0.9778	0.9710	0.9500	0.9016	0.8510	0.7929	0.8655	0.8077	0.9311	0.9288	0.9765	0.9685	0.9102
1969	0.9338	0.9199	0.9440	0.9243	0.8758	0.8444	0.7435	0.8387	0.9735	0.9641	0.9687	0.9893	0.9100
1970	0.9831	0.9614	0.8794	0.8924	0.8585	0.8413	0.8603	0.8760	0.9412	0.9143	0.9854	0.9680	0.9093
1971	0.9995	0.9870	0.9750	1.0352	0.9724	0.9159	0.8162	0.8949	0.9695	1.0031	0.9816	1.0013	0.9694
1972	1.0669	1.0455	1.0897	1.0044	0.9330	0.8672	0.9789	0.8670	0.9003	0.9404	1.0226	0.9984	0.9762
1973	0.9897	1.0040	1.0219	0.9963	0.9141	0.8543	-	0.9000	0.9673	0.9981	0.9895	1.0205	0.9687

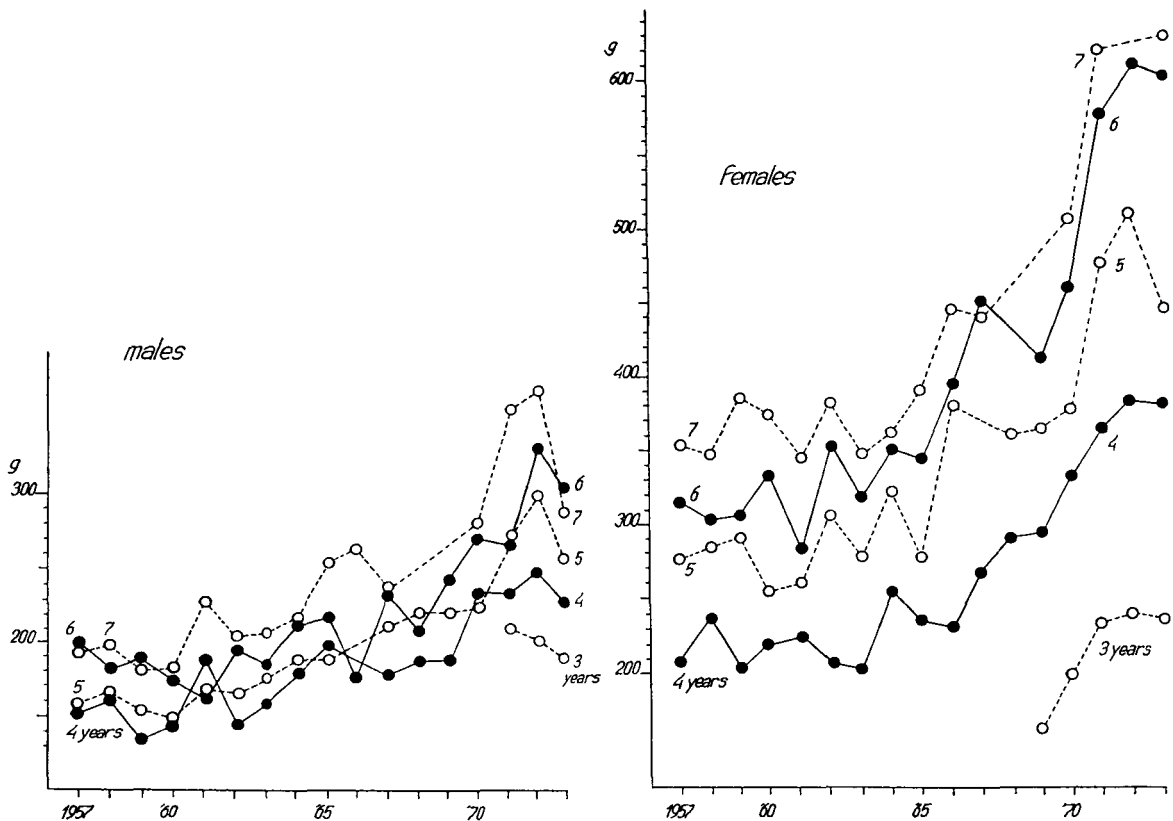


Figure 7. Average gutted weight-per-age of male and female North Sea sole with gonads in April by years.

1973 are present, which are all in line with the higher level of 50% lengths of the other sub-stocks. Apparently the change in 1969 affected all sub-stocks to the same extent and the factor responsible is not restricted to parts of the central or southern North Sea but covers the whole area.

Changes in recruitment to the spawning stock as a function of age

In the preceding section the maturity – length relationship was discussed. Reaching maturity for the first time is not only a matter of length but also of age. In Figure 17 the maturity ogives for female soles are given per year as a function of age. The 50% ages of the ogives are shown in the lower right hand corner. In contrast to the length ogives which changed to another level in 1969, the age ogives give a more complex figure. In the years 1966–1970 the 50% age increases but falls in 1971. The 50% age for 1964–

1965 is higher than that in 1966. There is variation around a constant level, which is about 3.2 years.

Each ogive contains several year classes. In order to find out what the effect per year class is, maturity-age ogives were constructed per year class (Fig. 18). From this diagram the same conclusion can be drawn as from Figure 17: variation around a constant level of 3.2 years.

Unfortunately data on maturity – age for Holt's and Bückmann's prewar ogives are not available because there was no reliable age determination in their periods. Thus there is no indication that age at first maturity is influenced by the factors responsible for the other changes in biological parameters that have been discussed.

Variations in the Von Bertalanffy growth parameters

The Von Bertalanffy growth parameters L_{∞} , W_{∞} , K and t_0 were calculated from Table 1 and the aver-

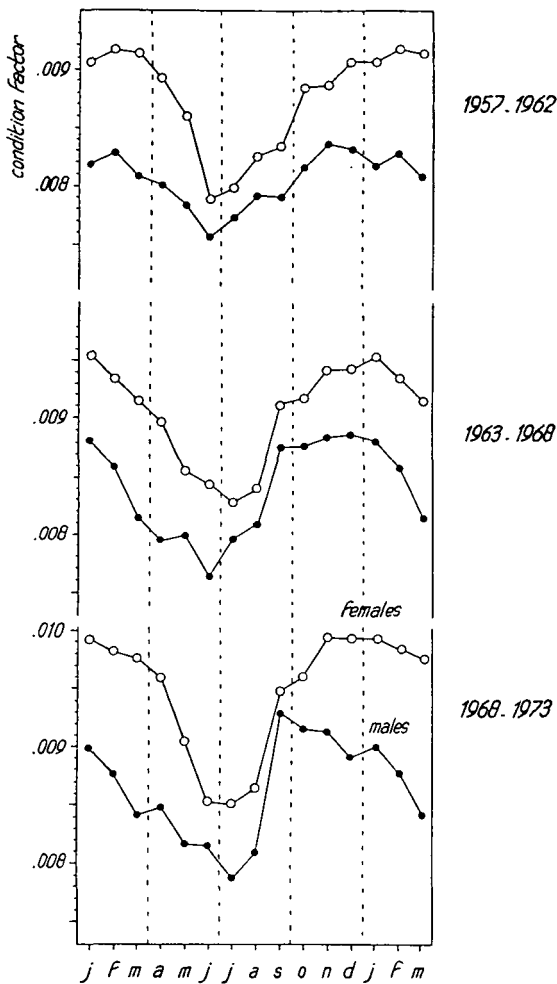


Figure 8. Average condition factor for males and females with gonads per month for the periods 1957-62, 1963-68 and 1968-73.

age annual condition factors calculated for the sexes separately. In order to determine L_∞ and K the functional or geometric mean regression of L_{t+1} over L_t has been calculated (Ricker, 1972, p. 412). Table 5 summarises the annual growth parameters.

Both L_∞ and W_∞ show an increase which is significant for both sexes ($P < 0.01$, Spearman's rank correlation coefficient). But K as well as t_0 tend to decrease. However, the decrease in these parameters is only probably significant ($P = 0.02$) for females and is not significant for males.

Another way of expressing growth is to use the Von Bertalanffy equation in its original form:

$$dW/dt = HW^{2/3} - kW^n$$

where $HW^{2/3}$ is the anabolic and kW^n the catabolic

term, as has been discussed by Nielsen (1973). It should be noticed that the catabolic coefficient k is not identical to the Von Bertalanffy growth parameter K .

The observed annual increment in weight ΔW depends largely on the season or month in which it was determined owing to fluctuations in weight-at-age throughout the year. The Von Bertalanffy approach does not take account of this seasonal fluctuation but assumes continuous growth throughout the year.

In Figure 19 the average monthly gutted weight including gonads and the weight of the ovary (in black, and repeated separately on a larger scale at the bottom of the Figure) are given for North Sea sole as a function of age. It is based on data from 1962-1973. Although the seasonal variation in gutted weight including gonads increases with age there is a strict timing of the curves for each age. Somatic weight reaches its maximum around the 1 of January and ovary weight in March-April. Reproductive tissue appears to be formed at the expense of somatic tissue each year. The seasonal variation in somatic and reproductive weight is very regular.

It is reasonable to assume that we may use the data from corresponding months to estimate ΔW , so that we calculate the weight increment from January to January in the next year, February to February and so on. This results in 12 estimates per age group per year. The calculations were made for females only in order to see whether this method of analysing growth would yield results which are better interpretable than determining L_∞ , W_∞ , K and t_0 .

The equation

$$dW/dt = HW^{2/3} - kW^n$$

can be written as

$$dW/dt = HpL^2 - kqL^{3n} \text{ with } n = 1$$

in which p is a physiological factor equal to $q^{2/3}$ and q is the condition factor.

Monthly condition factors have been tabulated in Table 4. The length value in the equation is the average between the length at the beginning and at the end of the 12-month period concerned:

$$(L_{ij} + L_{i+1j})/2$$

in which i stands for month and j for year.

The coefficients H and k were determined by least squares regression of

$$\Delta W_{ij} = a_{ij}L^2_{ij} + b_{ij}L^3_{ij}$$

in which $a = Hp = Hq^{2/3}$ and $b = -kq$.

Table 6 and Figure 20 give the annual average estimates of H and k for the years 1957-1973. The coefficient of anabolism H is more or less constant from 1957 to 1964, thereafter rising to a higher level.

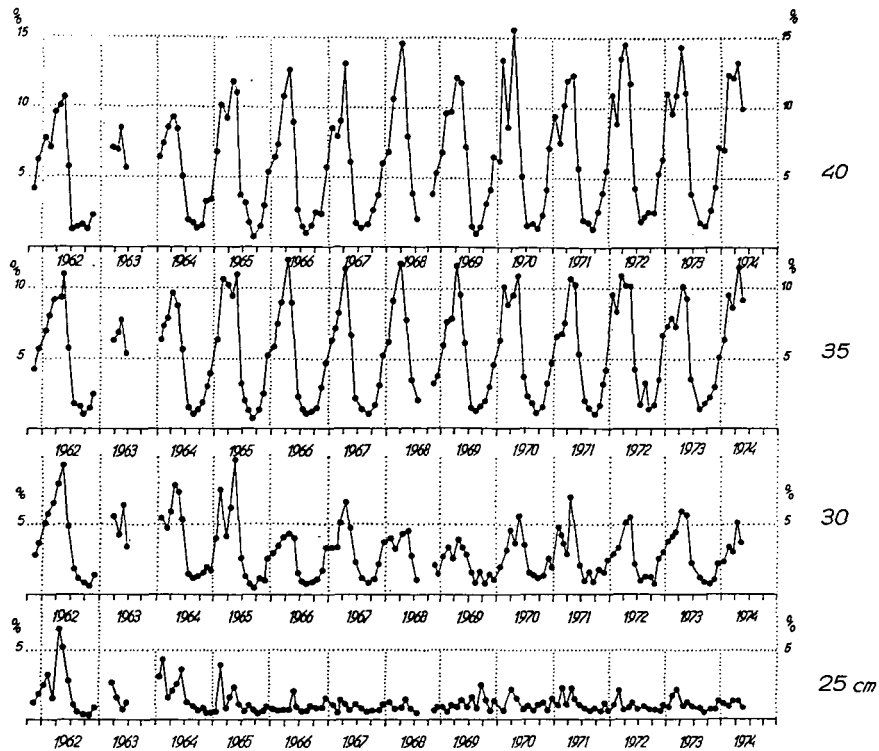


Figure 9. Relative weight of female gonads (as % of gutted weight including gonads) per month for the years 1962-74 for 4 length categories.

Table 5. North Sea sole: the Von Bertalanffy growth parameters estimated for the years 1958-1973

Year	L_{∞} cm		W_{∞} g		K		t_0 years	
	♂	♀	♂	♀	♂	♀	♂	♀
1958.....	30.2	35.6	217.4	387.6	0.393	0.380	-2.0	-0.5
1959.....	29.9	36.9	215.0	441.2	0.377	0.362	-2.1	-0.3
1960.....	31.2	39.3	241.1	525.5	0.180	0.339	-	+0.1
1961.....	24.5	35.0	-	364.1	-0.582	0.495	-	+0.1
1962.....	30.1	38.5	222.5	492.3	0.289	0.503	-4.2	+1.2
1963.....	32.0	36.6	265.6	424.6	0.378	0.230	-0.7	-3.4
1964.....	33.0	38.1	305.0	493.5	0.415	0.394	+0.04	+0.2
1965.....	31.6	38.6	274.0	526.5	0.337	0.437	-2.1	+0.8
1966.....	28.2	38.0	-	490.1	-0.252	0.425	-	-0.1
1967.....	30.7	38.4	240.3	505.9	0.556	0.306	-0.8	-1.7
1968.....	19.6	46.5	-	915.2	-0.279	0.230	-	-0.6
1969.....	33.5	41.7	311.3	658.0	0.302	0.213	-2.3	-2.8
1970.....	34.2	39.6	337.6	521.5	0.359	0.352	-1.3	-0.8
1971.....	36.2	40.2	424.0	629.8	0.294	0.286	-1.7	-1.9
1972.....	36.9	46.6	445.4	867.8	0.282	0.255	-2.3	-1.4
1973.....	33.9	44.4	340.9	846.2	0.353	0.264	-3.2	-1.5

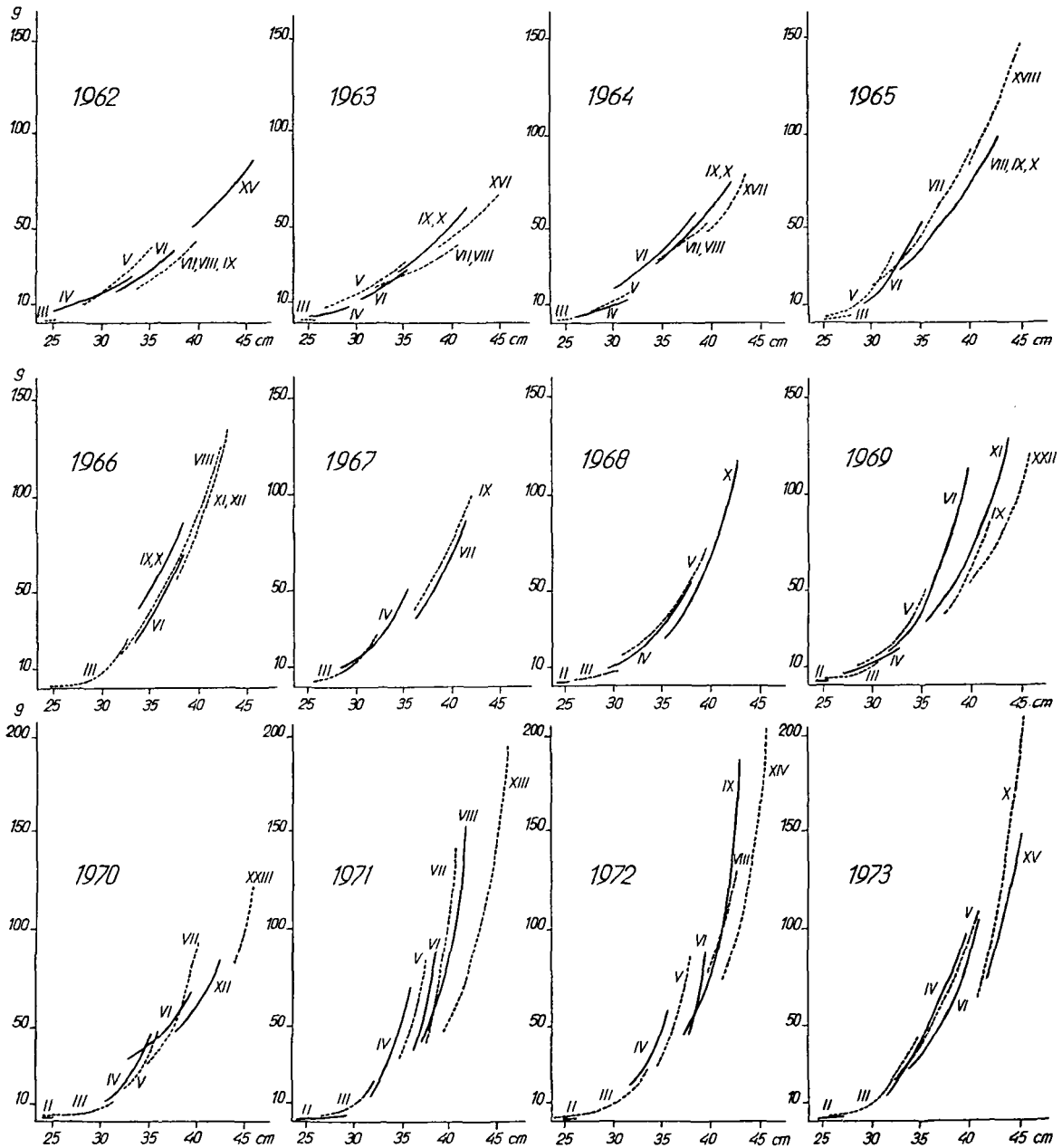


Figure 10. Relationship between female gonad weight per age-group and length for the years 1962–1973.

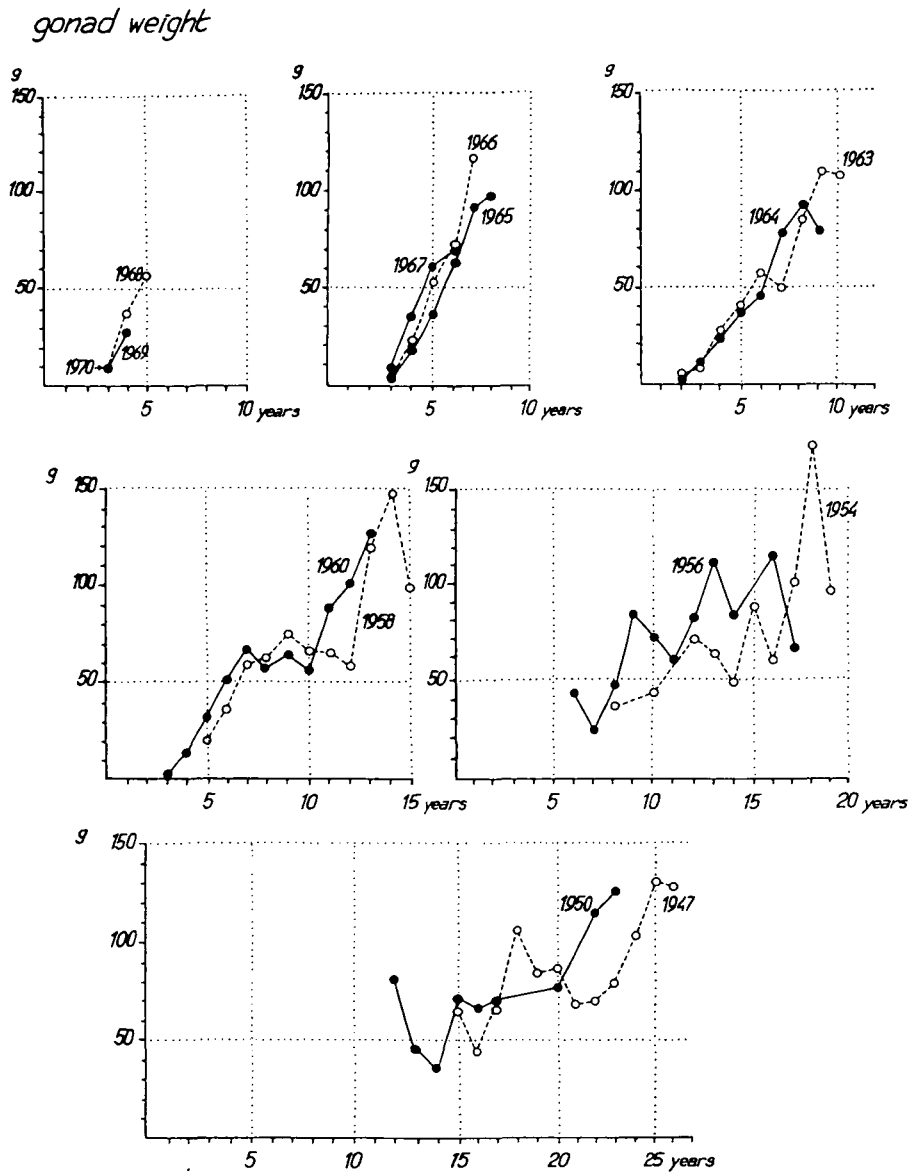


Figure 11. Relationship between female gonad weight per year class and age for a number of year classes.

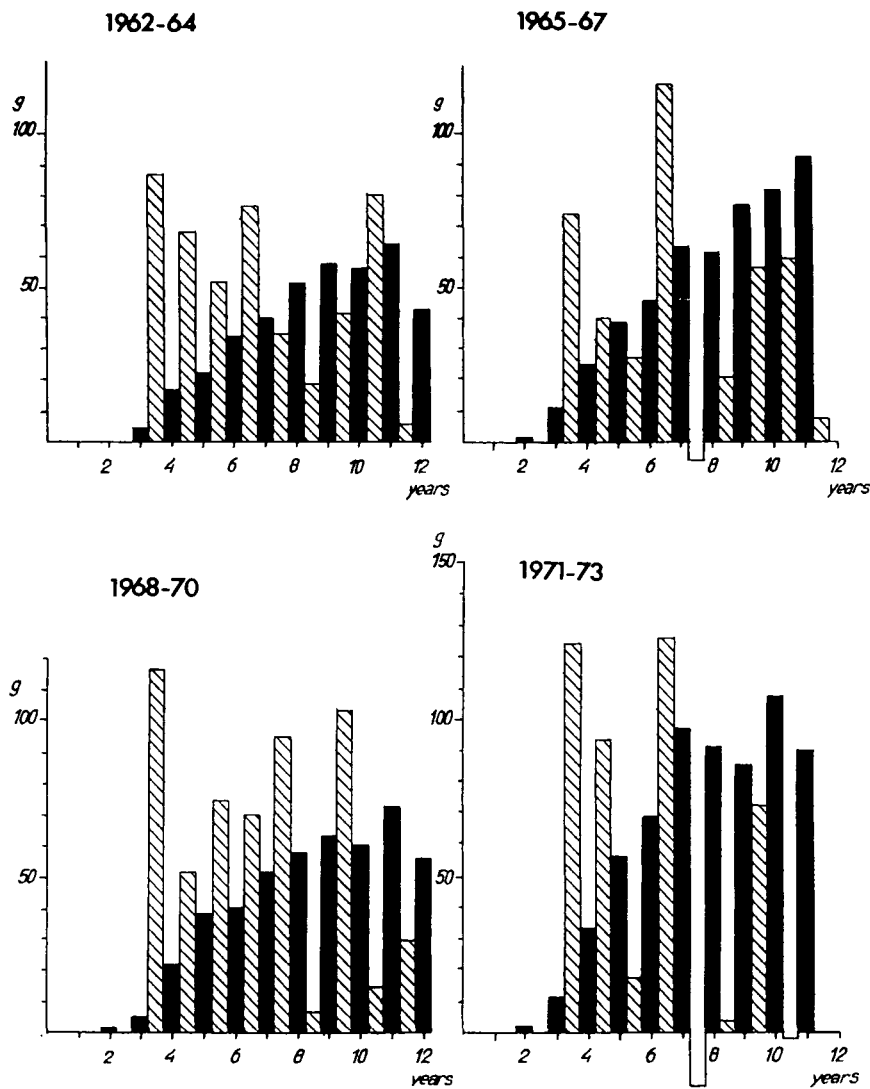


Figure 12. Annual increments in somatic weight (hatched) and female gonad weight (black) per age for the periods 1962-64, 1965-67, 1968-70 and 1971-73.

The coefficient of catabolism follows the same trend as H . When comparing the W_{∞} estimates with those of H it is apparent that both show the same trends.

Correlations of the observed changes in biological parameters with the environment

Comparison of the observed changes in the sole stock with indices of the environment might give some insight as to the possible underlying factors.

However, a correlation by itself does not prove that a relationship is causal and we have to look for additional evidence for direct causal factors.

The first possibility to be considered is a density dependent mechanism in growth. By means of Virtual Population Analysis (Gulland, 1956) the total number and total weight of the sole stock has been calculated per year (VPA, de Veen, 1974 unpublished; ICES, 1975). One year old soles were excluded for occupying different areas than older fish. Thus the sole stock was assumed to consist of 2-15 year old fish. Stock densities in number and weight were cal-

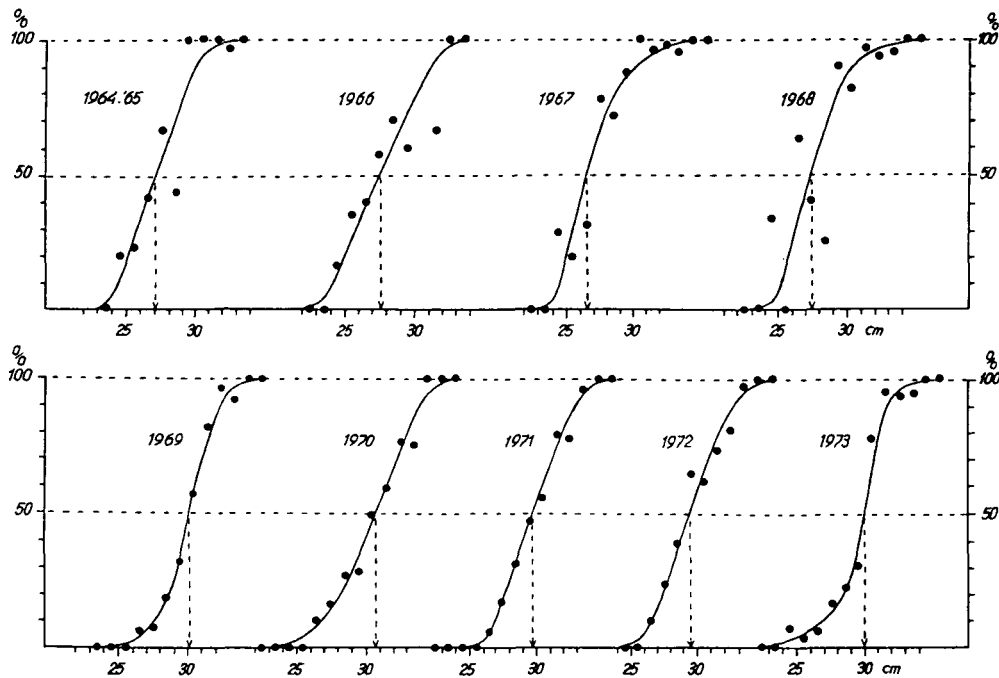


Figure 13. Maturity-ogives in May-June for female soles reaching at least stage 4, by years against length.

Table 6. Average annual coefficients of anabolism (H) and catabolism (k) for female North Sea sole.

Year	Coefficient of anabolism (H)	Coefficient of catabolism (k)
1957/58.....	5.98	0.65
1958/59.....	5.55	0.94
1959/60.....	6.15	0.89
1960/61.....	6.18	0.75
1961/62.....	4.26	0.68
1962/63.....	4.48	0.45
1963/64.....	6.31	0.64
1964/65.....	3.12	0.30
1965/66.....	10.66	1.20
1966/67.....	9.90	1.15
1967/68.....	9.24	1.07
1968/69.....	14.34	1.67
1969/70.....	6.84	0.77
1970/71.....	18.03	2.08
1971/72.....	17.76	1.98
1972/73.....	8.33	1.07

culated for the sexes separately. Table 7 gives the data for the sexes combined. We have found that the changes in growth were mainly apparent in 2 and 3 year old soles. Stock density in number and weight was therefore calculated for these two age groups alone.

A second possibility is the influence of temperature on growth phenomena (Weatherly, 1972). A difficulty

is that there is no long term series of observations of bottom temperatures representative for the whole area occupied by the North Sea sole. The best data

Table 7. North Sea sole. Stock size in numbers and gutted weight of 2-15 year old fish and of 2 and 3 year old fish for 1 July derived from Virtual Population Analysis with $M = 0.10$

Years	2-15 years	2-15 years	2+3 years	2+3 years
	stock size	stock size	stock size	stock size
	in	in	in	in
	numbers	weight	numbers	weight
	$\times 10^{-8}$	$\times 10^{-5}$ kg	$\times 10^{-5}$	$\times 10^{-6}$ kg
1957...	4 228	80.0	1 807	17.5
1958...	4 821	90.5	1 963	19.0
1959...	6 345	110.4	2 275	21.9
1960...	7 300	126.0	4 771	50.8
1961...	6 515	126.5	3 787	49.2
1962...	5 333	120.2	1 073	11.9
1963...	3 914	101.0	825	12.6
1964...	5 334	108.8	389	6.0
1965...	8 113	135.6	6 131	69.8
1966...	7 759	145.0	6 691	90.1
1967...	6 521	150.9	1 836	24.6
1968...	5 196	136.7	1 240	18.6
1969...	4 064	109.7	1 596	20.9
1970...	3 596	99.7	1 410	23.4
1971...	3 518	99.4	1 959	31.9
1972...	3 069	89.5	1 901	36.3
1973...	2 628	84.6	1 156	18.8

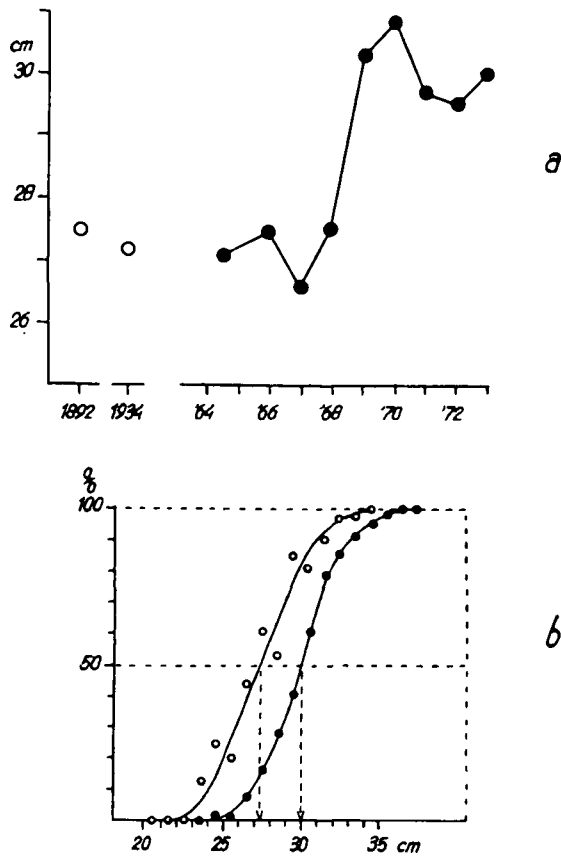


Figure 14. a, The 50% points of the ogives of Figure 13 together with Holt's (1892) and Bückmann's (1934) 50% length, by years; b, average maturity ogives for 1964-68 (open circles) and 1969-73 (black circles) against length.

available were the series of monthly surface water temperatures collected at the light-vessels "Vyl" and "Texel". From the combined data the number of days with temperatures above 14°C and above 15°C have been calculated together with the average August + September surface temperatures in the period of rapid growth of the sole. These data are given in Table 8.

Another important factor might be the average density of bottom animals serving as food for soles. The sole is a typical polychaete - molluscs feeder, searching for food in the night using olfactory stimuli (de Groot, 1971). No long term series of bottom fauna densities in the North Sea, representative for the sole area, exists, thus making it impossible to study this essential possibility.

It is a fact that eutrophication takes place in the North Sea. This might result in a richer supply of food animals. The major source for this eutrophication in the southern and central North Sea is the

river Rhine. Unfortunately no long term series of, for example total phosphate in the coastal areas exists. Instead of total P a series of observations on orthophosphate in the Dutch part of the river Rhine (van Bennekom, Gieskes and Thijssen, 1975) from 1957 to 1970 was used as a rather poor index of eutrophication of the North Sea coastal areas (Table 9).

A major factor is the sole fishery itself. Changes in the sole fishery may have had its influence on the biological characteristics of the sole stock. Table 10 gives the estimates of the fishing mortality coefficient *F* of 4, 5 and 6 year old male and female soles by years derived from Virtual Population Analysis. These age groups have been chosen because the fishery tends to concentrate on these rather than on younger or older soles. Relevant to the problem of fishing intensity is the type of gear used. In a number of countries fishermen and biologists worry about the possible ill-effects of disturbing bottom layers by active gears (ICES, 1971; 1972a; 1973c). It is claimed that the use of heavy chains attached to beam trawls may kill valuable food animals and turn rich feeding

Table 8. Monthly surface water temperatures of the lightvessels "Texel" and "Vyl" combined, by years

Year	Numbers of days with surface temperatures		Average surface temperature August + September in °C
	> 14°C	> 15°C	
1957 ...	105	81	16.0
1958 ...	109	86	16.7
1959 ...	121	103	17.5
1960 ...	100	70	16.4
1961 ...	129	107	16.2
1962 ...	87	41	15.3
1963 ...	93	67	16.0
1964 ...	99	72	16.1
1965 ...	90	58	15.7
1966 ...	103	76	16.0
1967 ...	117	93	16.9
1968 ...	111	83	16.4
1969 ...	115	91	17.4
1970 ...	116	85	16.5
1971 ...	122	88	16.7
1972 ...	95	76	16.1
1973 ...	120	95	17.0

grounds into waste lands. Chains are in use in active gear such as otter trawls and beam trawls, but it is the heavy beam trawl that makes it possible to carry a large number of chains (up to 12) on one gear in twin beam trawling.

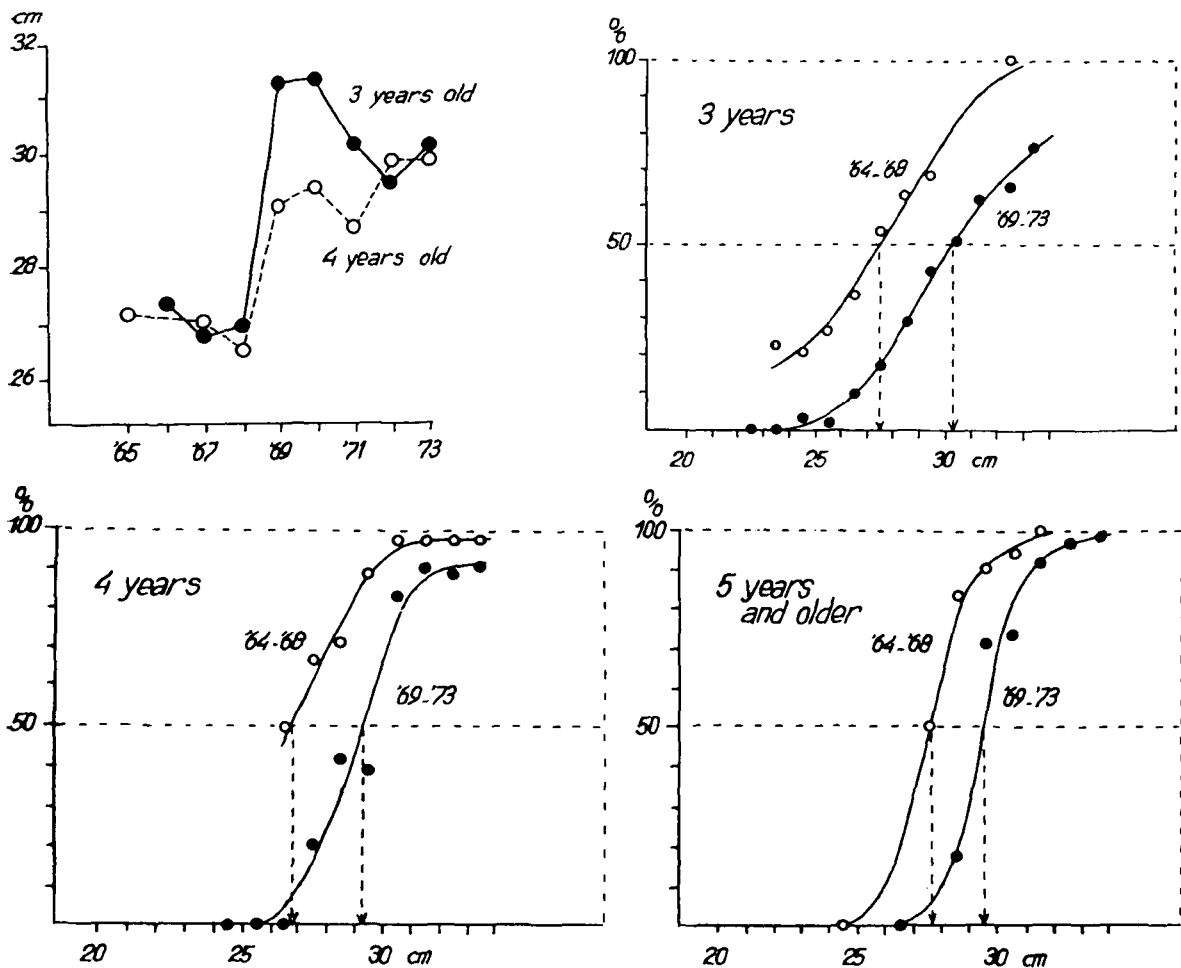


Figure 15. The 50% points of ogives of 3 year and 4 year old female soles by years; and the average ogives for 1964–68 and 1969–73 for 3 year old, 4 year old and 5 year and older soles.

The total number of fishing hours by Dutch beam trawlers (catching over 80% of all landings of sole in the North Sea) can be taken as an index of the disturbance of the bottom layer (Table 11). Not only beam trawlers disturb the bottom; the otter trawl can dig into the bottom with its chains although the effect is much less pronounced. In order to have an index for the number of "chain fishing hours" the beam trawl hours must be converted into otter trawl hours to take account of the larger amount of chains on the beam trawl.

Since 1962 the ratio between the catch-per-effort of the beam trawl to that of the otter trawl on the same fishing grounds in the Dutch sole fisheries rose from 2 to 1 to 3 to 1 in 1968. Thus the number of hours fishing by a beam trawler is now equivalent to

three times the number of hours fishing by an otter trawler on the same ground.

The total hours fishing of the Dutch beam trawlers can be expressed in equivalent otter trawl hours and together with the existing otter trawl hours will give a more complete index of the impact of chains on the bottom than the beam trawl hours alone. Table 12 gives the totals of otter trawl hours and converted beam trawl hours of the Dutch fisheries.

For the comparison between the changes in stock parameters described earlier with the above mentioned environmental factors only quantitative biological characteristics have been used such as L_{∞} , W_{∞} , K , t_0 , H and k , the condition factors q and the annual weight increments of 3–6 year-old soles, sexes combined. Qualitative features remaining un-

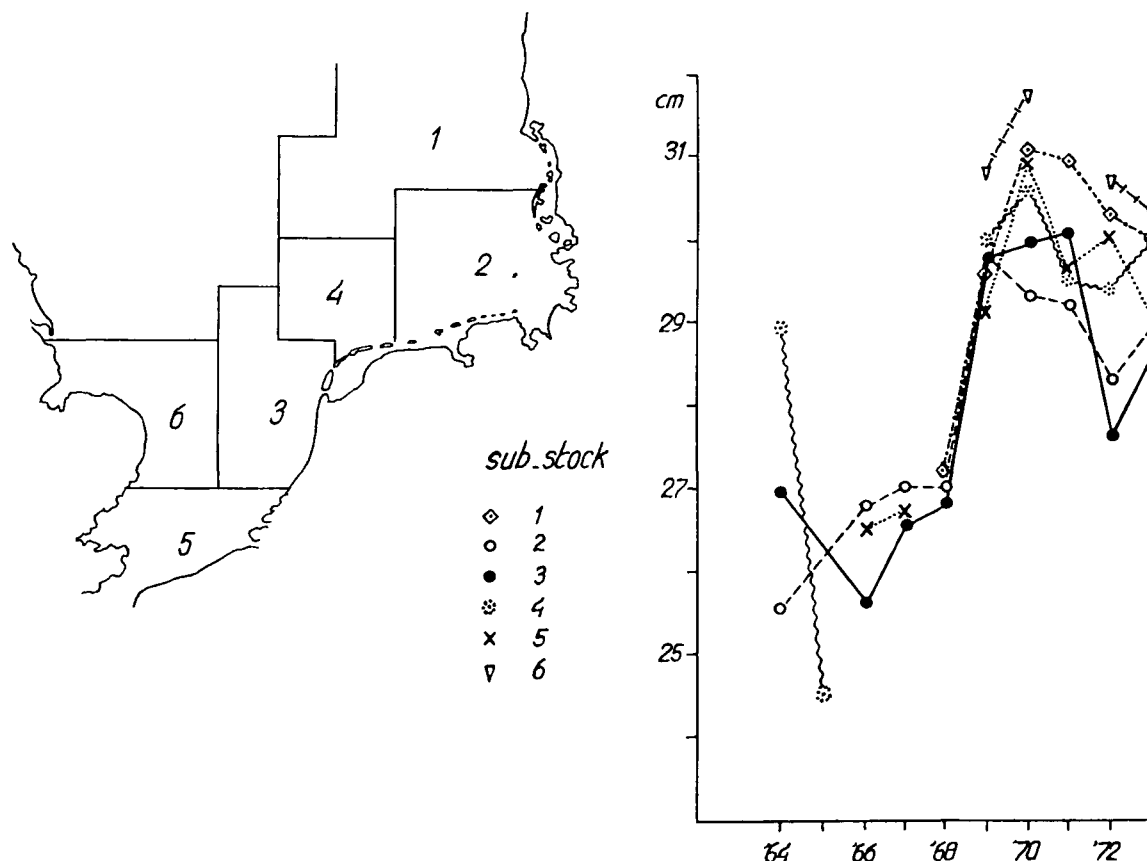


Figure 16. The 50% points of ogives for the 6 sub-stocks shown in the left hand figure.

changed (maturity-age) or showing two levels (maturity-length) were not considered in the comparison. Spearman's rank order correlation coefficients were determined for the variables summarised in Table 13 and the results of these calculations are discussed in the next section.

Discussion

In the preceding sections a number of changes have been considered. Summarized they are as follows:

1. In the period 1957–1973 *length-at-age* started to increase in 1963–1964 and continued to increase up to the present.

2. The annual length increments for age groups 4 and older did not change.
3. In the 0-group soles a small increase in length took place only, too small to account for the observed large increase in older soles.
4. Consequently the observed change was induced in the 2 and 3 year old soles and the factors responsible for it have to be looked for in the more inshore areas where these age groups occur.
5. In 1968–1973 length-at-age values for different sub-stocks were identical, all showing the same increase. This implies that the responsible factors are not local but involve all coastal areas.
6. *Weight-at-age* started to increase in 1963–1964.

Table 9. Index of eutrophication of the Dutch coastal area: average orthophosphate content of the river Rhine, near the Dutch–German frontier in metric tons per year

Year	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971
PO ₄ -P	4793	4257	3879	7159	9272	6780	8042	8925	15 547	14 538	13 403	14 196	15 137	16 241	13 403

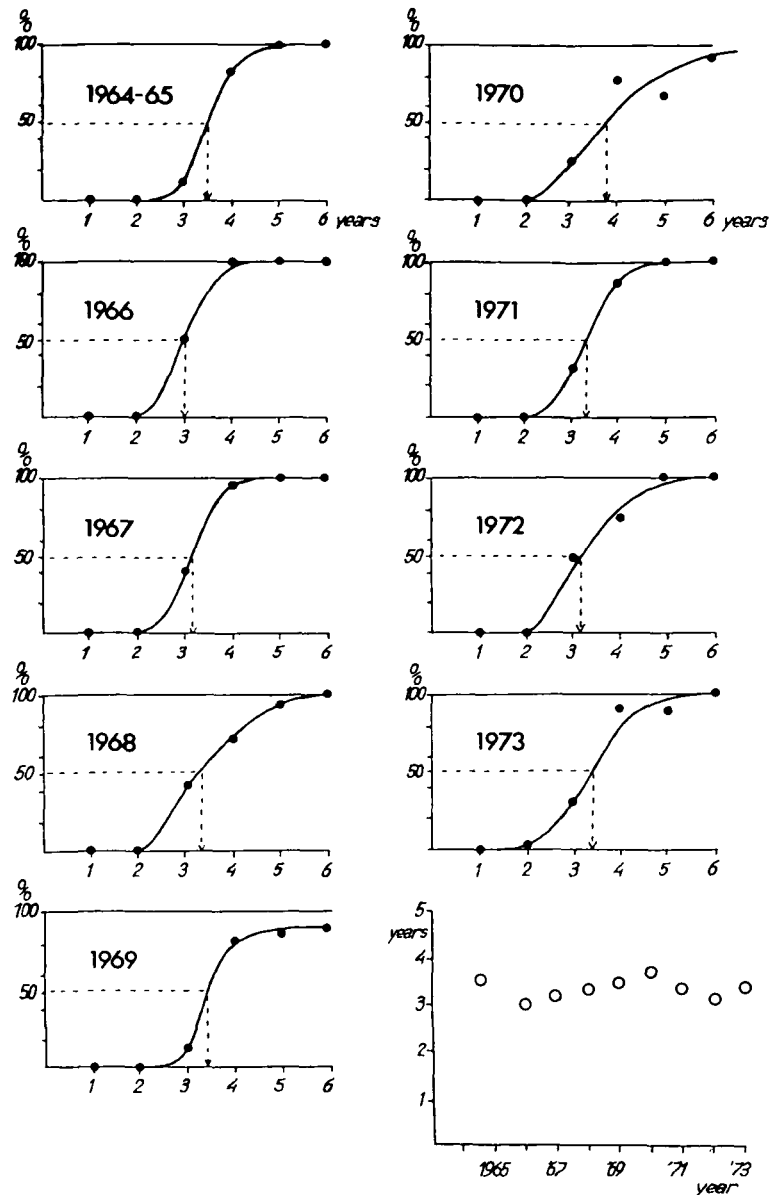


Figure 17. Maturity-ogives in May-June for female soles reaching at least stage 4, by years against age; 50% ages of these ogives.

This was caused by the increase in length-at-age and a significant increase in the condition factor which also started in 1963-1964.

7. The relationship between ovary weight and age of female soles started to change in 1965.
8. Maturity-length constant for a long period (1892-1968), changed in 1969 to a $2\frac{1}{2}$ cm higher level and has remained there since.
9. Maturity-age, apart from fluctuations, stayed at a constant level.

10. The Von Bertalanffy growth parameters L_{∞} and W_{∞} showed a significant increase both for males and females. The decrease in K and t_0 in females is doubtful and is not significant for males.
11. The coefficients of anabolism (H) and catabolism (k), derived from the original Von Bertalanffy equation, as used by Nielsen (1973), showed a significant increase since 1965-1966.

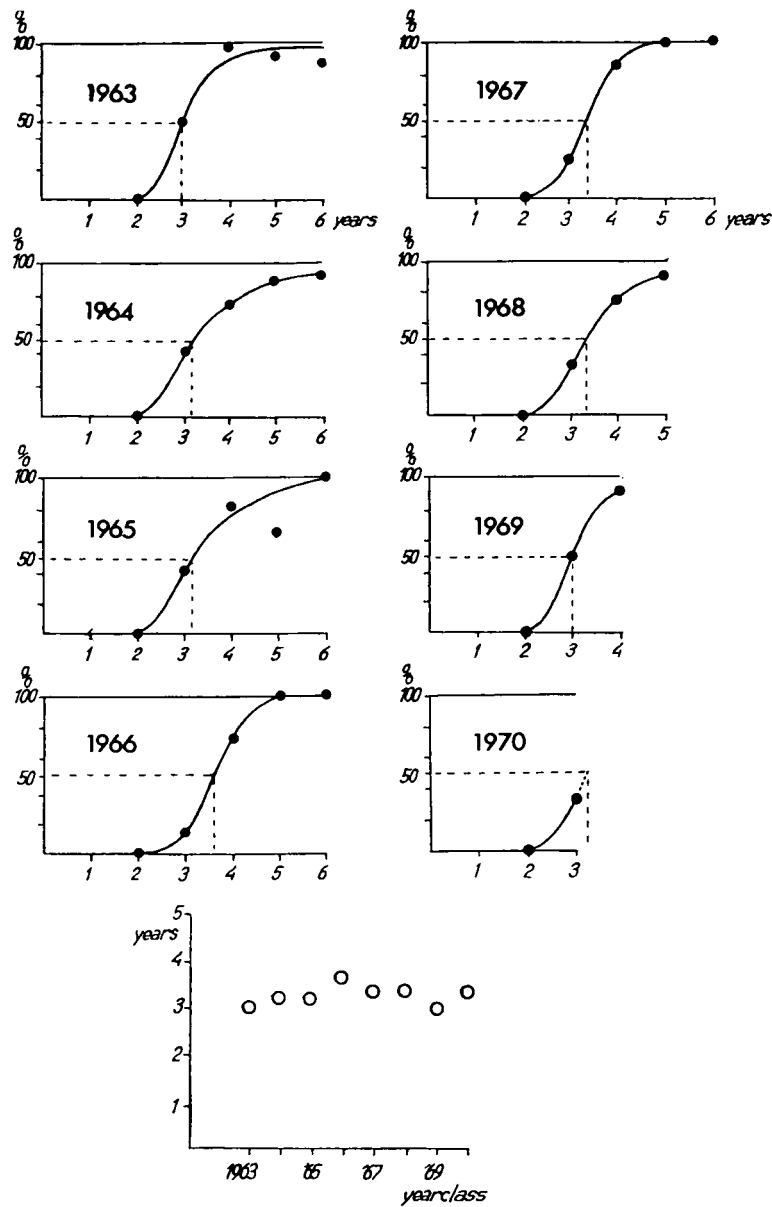


Figure 18. Maturity-ogives in May-June for female soles per year class; 50% ages of these ogives.

The results show that in general the biological parameters started to change in the years 1963-1969. However, length, weight and condition factors demonstrated this change already in 1963-1964, whereas the change in fecundity came one year later and the change in the maturity - length relationship in 1969. The reasons for these time lags is still obscure. It is possible that the increase in length and weight-at-age has to exceed a given threshold value before

fecundity starts to react. The fact that in 1965 the ovary length and age relationships changed rather abruptly instead of gradually over a number of years may imply there was a fixed relationship in the pre-1963 period and that after two years increase in length and weight the sole had to change to another fixed relationship which remained constant from 1965 to 1973. In these years length and weight-at-age still continued to increase. If our conclusion

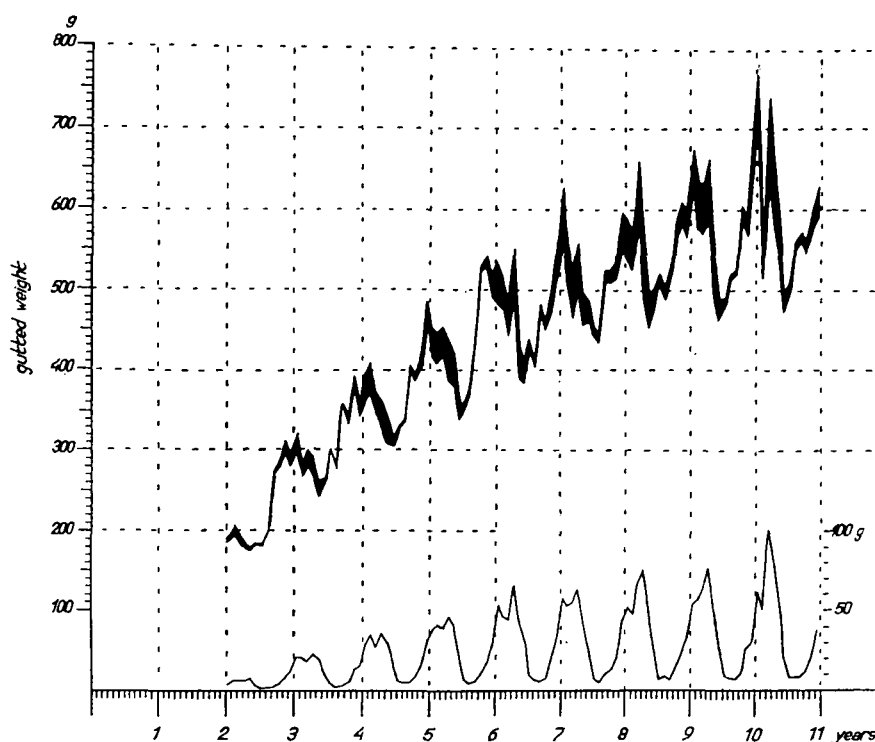


Figure 19. Average monthly gutted weight with gonads (upper curve) and female gonad weight (black) at age based on 1962–73 data. In the lower diagram gonad weight is shown separately on a larger scale.

Table 10. Estimates of the fishing mortality coefficient F for male and female 4–6 year old soles derived from Virtual Population Analysis. $M = 0.10$

Year	Value of F	
	males	females
1957.....	0.13	0.21
1958.....	0.13	0.21
1959.....	0.17	0.21
1960.....	0.19	0.27
1961.....	0.29	0.27
1962.....	0.26	0.39
1963.....	0.37	0.37
1964.....	0.34	0.43
1965.....	0.26	0.28
1966.....	0.12	0.13
1967.....	0.18	0.19
1968.....	0.37	0.42
1969.....	0.89	0.65
1970.....	0.67	0.50
1971.....	0.52	0.54
1972.....	0.72	0.55
1973.....	0.77	0.66

on fixed fecundity–length and–age relationship levels is correct, another abrupt change may occur in the

future when length and weight continue to increase at the present rate. At the moment (1973) there is no sign of such a new change.

The same reasoning may be applied to the change in the 50% maturity length. From Figures 17 and 18 it follows that the 50% age at first maturity remained more or less constant at 3.2 years. The increase in length-at-age normally should have led to a continuous decrease in the 50% age and if no change in the 50% length had taken place, recruitment to the spawning stock would have now been at an earlier age. It may be that this is an impossible physiological change for the sole and that for some unknown reason the sole is not able to mature at an age earlier than roughly three years.

In favour of this idea is our observation that in the years 1962 to the present, soles of age group II start to develop gonads but fail to reach maturity in that year. The partially developed gonads are resorbed at the end of the spawning season (de Veen, 1970).

Possible changes in the future concerning fecundity and length at first maturity can only be considered by extrapolating on present trends when more is known about the factors responsible for the observed changes that have been discussed.

Table 11. Total number of beam-trawl-fishing hours fished by Dutch beam trawlers, $n \times 10^{-3}$.

Year	Number of beam-trawl fishing hours $\times 10^{-3}$
1957	0
1958	0
1959	0
1960	0
1961	0
1962	97
1963	152
1964	289
1965	424
1966	515
1967	1015
1968	829
1969	673
1970	723
1971	841
1972	834
1973	946

The matrix of correlation coefficients in Table 13 may help in this respect. Although significant correlations alone do not tell us anything of causal relationships, a non-significant correlation at least implies that the relevant factor can be dismissed from the list of potential factors. When looking at Table 13 it is obvious that most of the correlation coefficients are not significant. Those which are probably significant ($P < 0.05 > 0.01$) are given in bold types and those which are significant ($P < 0.01$), are underlined bold types. There is no correlation between stock density in numbers and weight of the 2–15 year-old soles, and of the 2 and 3 year-old fish with the biological parameters. Nielsen (1973), using sole length-at-age data from the Danish coastal area and comparing these with stock densities in the southern and central North Sea sole failed to find any density dependent growth. A limitation of her comparison is that she could only use length-at-age data from a restricted area, namely the northern part of the area occupied by the North Sea sole. But when using length and weight data representative for the whole area there is no indication of any density-dependent mechanism as our study reveals.

In another flatfish species in the North Sea, the plaice, density-dependent growth was assumed by Beverton and Holt (1956). Hempel (1957) failed to find this mechanism in the adult plaice using empirical German data and recently the ICES North Sea Flatfish Working Group (ICES, 1972b) could only demonstrate retarded growth in the exceptionally strong year class of 1963, but not in other year

classes and concluded that in general there is no evidence in plaice supporting a density-dependent mechanism in growth.

The next factor to be considered is temperature. In Table 13 no single significant correlation can be found for the relationships of temperature in the growth season and the biological parameters. This may be partly due to the fact that no representative series of bottom temperatures was available and that data of surface temperatures of two light-vessels have been used instead. For the moment we can disregard any effect of temperature on growth and fecundity.

The probably significant correlation between the index of eutrophication used and W_{∞} for males may be understood as indicating an increased level of abundance of food animals. However, the rate of eutrophication, although restricted mainly to the coastal areas and thus agreeing well with the observed changes in length and weight in the 2 and 3 year old soles, is decreasing with increasing distance from the mouth of the river Rhine and does not explain why the increase in length is the same for all sole sub-stocks. The fishing mortality coefficient of 4–6 year old soles is probably significantly correlated with W_{∞} and L_{∞} but not with K , t_0 , H , k , and the condition factor q .

In the period under consideration changes in fishing mortality were mainly caused by changes in the Netherlands fishing effort. This changed from otter trawling with at most four to five chains to beam

Table 12. Total number of equivalent otter-trawl fishing hours fished by Dutch otter and beam trawlers, $n \times 10^{-3}$.

Year	Number of equivalent otter-trawl fishing hours $\times 10^{-3}$
1957	480
1958	500
1959	550
1960	678
1961	770
1962	989
1963	1002
1964	1229
1965	1485
1966	1985
1967	3504
1968	2981
1969	2448
1970	2357
1971	2700
1972	3541
1973	3958

Table 13. A matrix of Spearman's rank correlation coefficients of the biological parameters with environmental factors bold underlined type – significant.

		Eutro- phica- tion	Fishing effort	Fishing mortality		Temperature			Stock		
		PO ₄ -P in the river Rhine	Number Dutch equivalent otter trawlhours	Number Dutch beam trawlhours	F ♂ 4–6 years	F ♀ 4–6 years	Average Aug– Sep surface temp. Vyl, Texel	Temperature sum > 15°C	Temperature sum > 14°C	2–3 years in weight	do, in numbers
Von Bertalanffy growth parameters	$W_{\infty} \delta$	0.72	0.87	0.82	–	0.64	0.42	0.38	0.38	0.06	–0.17
	$W_{\infty} \text{♀}$	0.56	0.70	0.65	0.78	–	0.39	0.29	0.28	–0.20	–0.40
	$L_{\infty} \delta$	0.33	0.48	0.48	–	0.67	0.12	0.05	0.10	–0.02	–0.29
	$L_{\infty} \text{♀}$	0.60	0.76	0.69	0.72	–	0.54	0.54	0.53	0.00	–0.22
	$K \delta$	–0.27	–0.10	–0.03	–	–0.15	–0.40	–0.26	–0.35	–0.45	–0.37
	$K \text{♀}$	0.22	–0.55	–0.49	–0.49	–	–0.17	–0.10	–0.11	0.22	0.36
	$t_0 \text{♀}$	–0.23	–0.52	–0.54	–0.37	–	0.07	0.11	0.07	0.13	0.29
	$H \text{♀}$	0.50	0.74	0.74	0.41	–	0.11	0.03	0.17	0.19	–0.04
	$k \text{♀}$	0.25	0.61	0.61	0.24	–	0.32	0.24	0.38	0.30	0.17
Condition factor	$q \delta$	0.43	0.47	0.41	–	0.13	–0.11	0.06	0.08	0.35	0.30
	$q \text{♀}$	0.49	0.77	0.73	0.39	–	0.06	0.20	0.25	0.14	0.01
Annual weight- increment	3–6 year old soles trend eliminated	0.67	0.74	0.71	0.73	0.65	0.29	0.24	0.29	0.03	–0.22
		–0.24	–0.29	–0.29	–0.02	–0.21	0.14	0.22	0.33	0.12	0.19
Stock density	2–15 year numbers	0.06	–0.24	–0.20	–0.70	–0.57	–0.17	–0.13	–0.10	–	0.34
	2–15 year weight	0.39	0.18	0.20	–0.20	–0.03	0.00	0.00	0.06	0.04	–
	2 + 3 year numbers	0.06	–0.28	–0.26	–0.56	–0.54	0.14	–0.06	0.01	0.90	–
	2 + 3 year weight	0.35	0.03	0.06	–0.36	–0.29	0.19	–0.08	0.02	–	–
Temperature	Sum > 14°C	–0.06	0.06	0.04	0.26	0.22	0.76	0.61			
	Sum > 15°C	–0.10	0.02	–0.01	0.24	0.19	0.80				
	Average temp. Aug–Sep	0.17	0.05	0.03	0.29	0.33					
Fishing mortality	F ♂ 4–6 years	0.52	0.63	0.55	0.96						
	F ♀ 4–6 years	0.43	0.57	0.49							
Fishing effort	Number Dutch beam trawl hours	0.78	0.98								
	Number Dutch equivalent otter trawl hours	0.76									
PO ₄ -P in river Rhine											

trawling with more than ten chains. Thus the number of Dutch beam trawl fishing hours is not only an indication of this increased fishing effort but of the effect of chains on the bottom layers as well. A still better index of this effect is the equivalent otter trawl hours.

The significant correlation coefficients for both the beam trawl fishing hours and the equivalent otter trawl hours with W_{∞} for both sexes and probably significant for L_{∞} and H and the female condition factor, implies that we may have traced a significant factor.

When plotting the condition factor values against equivalent otter trawl hours (see Fig. 21) a close relationship seems to exist in the females but less so

in the males. Still this does not tell us much, the more so because the correlation is based on variables in two time series.

Additional evidence should be collected before we may identify causal relationships. In the case of the condition factor the curves in Figure 21 show an intercept on the Y-axis of 0.0076–0.0078. This could be the situation in an area without any influence of chains on the bottom layers. El-Zarka (1963), reporting on Mediterranean soles near Egypt and on soles transplanted from the Nile delta to Lake Quarun gives length and weight-at-age data sampled throughout the year. The average annual condition factor for these soles was 0.0085 for the Mediterranean and 0.0082 for the Lake Quarun soles.

such as stock density, temperature, fishing mortality, fishing effort and eutrophication. Bold type – probably significant,

density		Annual weight increment		Condition factor		Von Bertalanffy growth parameters								
2-15 years in weight	do, in numbers	Trend eliminated	3-6 years old soles	$q \text{ } \varphi$	$q \text{ } \delta$	$k \text{ } \varphi$	$H \text{ } \varphi$	$t_0 \text{ } \varphi$	$K \text{ } \varphi$	$K \text{ } \delta$	$L_{\infty} \text{ } \varphi$	$L_{\infty} \text{ } \delta$	$W_{\infty} \text{ } \varphi$	$W_{\infty} \text{ } \delta$
0.12	-0.31	-0.14	0.79	-	0.52	-	-	-	-	-0.22	-	0.47	-	-
-0.14	-0.61	-0.01	0.74	0.60	-	0.36	0.50	-0.49	-0.69	-	0.84	-	-	-
-0.44	-0.79	0.16	0.67	-	0.34	-	-	-	-	0.27	-	-	-	-
0.05	-0.39	-0.03	0.79	0.69	-	0.56	0.56	-0.31	-0.56	-	-	-	-	-
-0.35	-0.32	-0.07	-0.16	-	-0.13	-	-	-	-	-	-	-	-	-
-0.09	0.33	0.43	-0.27	-0.44	-	-0.49	-0.51	0.87	-	-	-	-	-	-
-0.03	0.31	0.47	-0.21	-0.40	-	-0.51	-0.56	-	-	-	-	-	-	-
0.21	-0.17	0.06	0.70	0.63	-	0.86	-	-	-	-	-	-	-	-
0.16	-0.09	-0.04	0.52	0.58	-	-	-	-	-	-	-	-	-	-
-0.27	-0.29	0.28	0.54	0.81	-	-	-	-	-	-	-	-	-	-
-	-	-0.53	0.60	-	-	-	-	-	-	-	-	-	-	-
-0.14	-0.55	0.31	-	-	-	-	-	-	-	-	-	-	-	-
-0.40	-0.27	-	-	-	-	-	-	-	-	-	-	-	-	-
0.79	-	-	-	-	-	-	-	-	-	-	-	-	-	-

To make these values comparable to those for the North Sea we have to apply a factor for gutting. Using the factor of 1.125, common in use for the European sole, gives the values of 0.0076 and 0.0073 for "gutted" Egyptian soles. These values agree well with the values at the intercept in Figure 21. However, the Egyptian data were collected before 1963 and the North Sea sole condition factors of 1957-1963 were at about the same levels. Thus this example cannot be used as evidence for a causal influence of bottom disturbance and growth-rate changes.

The changes in growth were mainly imposed in the 2 and 3 year old soles occupying the coastal areas. When considering the local distribution of the Dutch beam trawl effort (Fig. 22) it is obvious that effort

is maximal in the coastal areas and that from 1963-1965 to 1971-1973 there was an overall increase in this effort. Contrary to the effect of eutrophication which decrease with increasing distance from the mouth of the Rhine the average number of beam trawl fishing hours is more or less the same in all continental coastal areas fished by the Dutch at present.

Other evidence in support of a causal relationship is the observation that dabs concentrate in the path of a trawl, apparently looking for injured or excavated food animals (Margetts and Bridger, 1971). Bannister and Lee (personal communication) have observed the occurrence of the gonads of *Echinocardium* in the stomach contents of the dab in the North Sea,

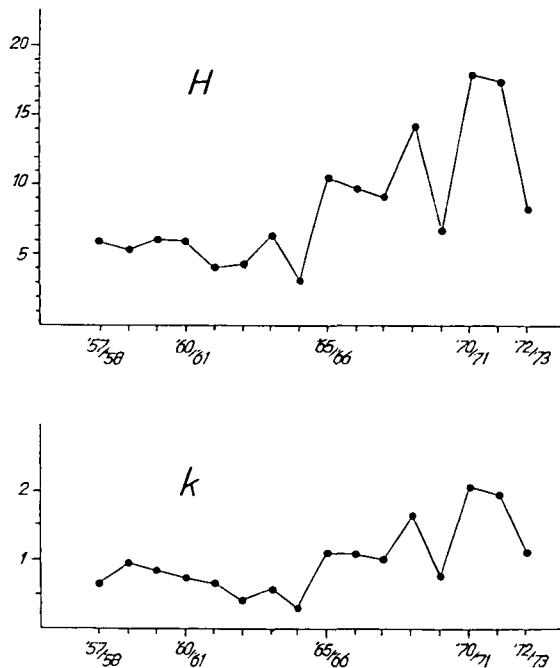


Figure 20. The coefficients of rate of anabolism H and of the rate of catabolism k for female sole by years.

an unlikely occurrence if the *Echinocardium* had not already been damaged by gear. Arntz and Weber (1970) have discussed the importance of *Cyprina islandica* L. as food animal for cod and flounder in Kiel Bay and considered the damaging of buried *Cyprina* by the digging action of trawl doors as a possible explanation of the increased quantities in the stomach of both species. Daan (1973) assumes that the same is true for the North Sea, where *Cyprina* is tossed about first and partly broken up before being an easy food supply for cod.

Up to the present there is no direct evidence of an increased availability of molluscs and polychaetes for sole. De Groot and Apeldoorn (1971) have studied the damage to beam trawl caught zoobenthos and demonstrated heavy damage to most bottom organisms. The sole is not an active feeder and has to rely on its chemical receptors for locating food. Under normal conditions it has to spend a certain amount of energy to find and dig out its prey. In a situation where beam trawl chains have damaged bottom animals, location of food might be made easier by stronger olfactory stimuli from the injured zoobenthos and less digging is needed. Thus, hypothetically, less energy would then go into searching for food and more could be transformed into growth.

To prove that this is a correct assumption needs further research, mainly through controlled ex-

periments. However, there is a good chance that the answer will be given in a few years. The regulation by NEAFC of the demersal fisheries in the North Sea by setting Total Allowable Catches for 1975 and 1976 implies a substantial decrease in the fishing effort and provided this reduction is effectively realised the influence of beam-trawling with chains will diminish. The values of the biological parameters in the coming years will no doubt tell us if our assumptions are right or wrong.

Summary

In the period from 1957 to the present market sampling has made it possible to follow biological parameters in the North Sea sole stock continuously. Changes in a number of these parameters have taken place together with changes in the fishing effort. The sole stock was in a situation of under-exploitation in 1957 which remained to 1963, then passed the point of optimum exploitation quickly in 1964–1965 and entered increasing overfishing in 1966 which led to the present serious problems.

In the various sole sub-stocks in the North Sea an increase in growth took place, at first slowly but more

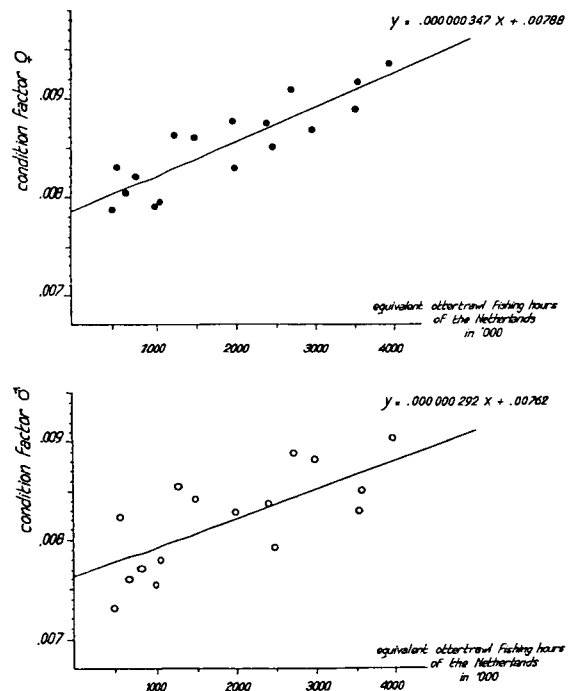


Figure 21. The relationship between condition factor for males and females and the index of disturbance of the seabed by heavy chains in the Dutch beam trawl fisheries.

rapidly since 1963–1964. Length and weight-at-age together with the condition factor continued to increase regularly, as did the weight of the ovary.

The 50% length at first maturity, for a very long period constant, changed to a 2.5 cm higher level in 1969 and remained at that level since. The 50% age at first maturity did not change.

The relationship between ovary-weight per year group and age changed in 1965 to another form of relation which remained constant since that year.

The Von Bertalanffy growth parameters L_{∞} and W_{∞} increased in both sexes, K and t_0 probably decreased in females but remained constant in males. Both the coefficients of anabolism and catabolism changed in females.

No correlation could be demonstrated between the biological parameters and stock size in numbers or weight. The same was true for water temperatures in the growth season.

For W_{∞} in males only there was a correlation with the index of eutrophication used – the amount of orthophosphate in the river Rhine.

A significant correlation was found for condition factors, L_{∞} for females, W_{∞} for both sexes, and the coefficient of anabolism for females with the number of beam trawl fishing hours and with the index of bottom disturbance – the number of equivalent otter trawl fishing hours. Additional evidence on distribution of fishing effort by beam trawlers points to the possibility that the amount of bottom disturbance by heavy chained beam trawls may have a positive effect on growth in soles. Food organisms are injured by the gear and made more easily available for soles, which may economize on energy for searching, locating and digging out food and may thus transform more energy into growth.

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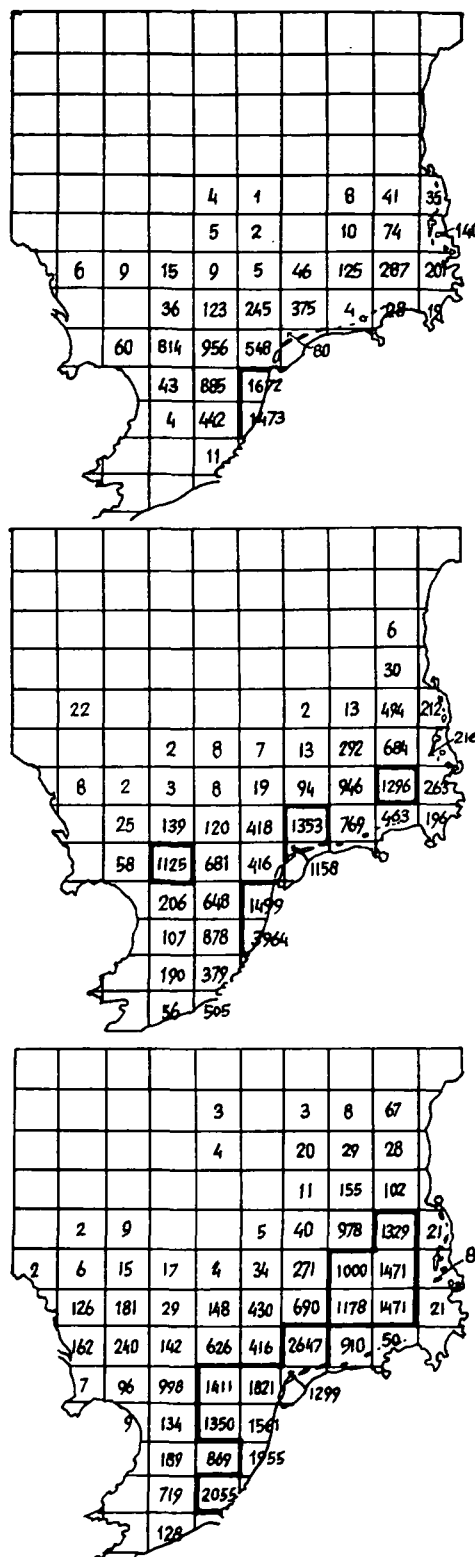


Figure 22. Average numbers of hours fishing by Dutch beam trawlers in the growth season of the sole (3rd quarter) by rectangles for the periods 1963–65 (top), 1967–69 (centre) and 1971–73 (bottom). Rectangles where fishing effort exceeded 1000 h are indicated.

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