Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature

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Annual length increments of female North Sea plaice were back-calculated from distances between rings in otoliths. Growth of the smaller size classes (<25 cm) increased from the mid-1950s and decreased in the 1980s. Length increments of intermediate size classes varied more or less randomly, and those of the larger size classes (>35 cm) increased from 1970. Growth changes of the smaller size classes were significantly correlated with indices of plaice density, eutrophication, and seabed disturbance by beam trawling. Moreover, they could be related to spatial and temporal patterns in variations in eutrophication and beam trawling. No correlation was observed with temperature. The analysis led to a consistent interpretation suggesting that eutrophication and beam trawling have both affected the growth rate of plaice. The contributions of these factors differed in space. Effects of eutrophication dominated in the shallow coastal waters, whereas beam trawling dominated in the waters further offshore.

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Introduction

Although the marine ecosystem is undoubtedly influenced by anthropogenic activities, evaluation of these effects is difficult because of the complexity of the system, and because different anthropogenic activities have developed simultaneously and may interact. In the 1960s and 1970s, a major increase in growth rate was reported for both plaice and sole in the North Sea (de Veen, 1976, 1978a,b; Bannister, 1978; Rijnsdorp and van Beek, 1991; Rijnsdorp and van Leeuwen, 1992). This increase could not be related to changes in temperature, but coincided with an increase in both eutrophication and intensity of beam trawling. Hypothetically, both factors may explain increases in growth (de Veen, 1976, 1978a,b; Rijnsdorp and van Beek, 1991; Boddeke and Hagel, 1991). Both flatfish species feed mainly on macro-zoobenthos species such as molluscs and polychaetes, which are characterized by a small body size, a short lifespan and high productivity. These organisms may be expected to have taken advantage of the well-documented increase in primary production in the coastal waters (Cadée, 1986; Gerlach, 1987; Salomons et al., 1988; Cadée and Hegeman, 1993). Enhanced production of macro-zoobenthos has indeed been

reported for tidal flats (Reise, 1982; Beukema and Cadée, 1988; Beukema, 1989) and for sublittoral areas in the German Bight (Rachor, 1990).

However, beam trawling may also have caused a shift in the benthic community from low-productive, long-lived, species to high-productive, short-lived species (Rijnsdorp and van Beek, 1991). Thus, opportunistic macro-zoobenthos species may have benefited from both eutrophication and disturbance of the seabed. In addition, beam trawling has been shown to enhance food availability directly by damaging benthic organisms in the trawl path (de Veen, 1976; Bergman and Santbrink, 1994; Santbrink and Bergman, 1994).

Since time-series data on changes in the macro-zoobenthic community are scarce, the potential effects of eutrophication and beam trawling on growth rate of plaice cannot be studied directly. An indirect approach has therefore been followed to unravel the significance of these two factors. A starting point is the notion that effects of beam trawling and eutrophication will follow different spatial patterns. Eutrophication is mainly due to nutrient loads in the run-off of major European rivers and its effects should decrease with increasing distance from the coast. Heavy beam trawls are widely used over a large area in the southern and south-eastern North

Table 1. Summary of otolith samples analysed. Year-class samples consist of otoliths of selected year class(es) collected during successive years; length stratified samples were taken in a particular year and comprised up to four randomly selected otoliths per cm group between 27–50 cm. The number (#) preceding the year/year-class notation refers to set number. Otolith sets 1–10 have been included in earlier analyses by Rijnsdorp and van Leeuwen (1992). Otolith sets 11–20 were added to increase the temporal resolution to one year.

Year/ year class	Age groups sampled											
	III	IV	V	VI	VII	VIII	IX	X	XI–XIV	XV–IXX	XX+	Total
Year-class samples												
#4-1955–1961	2	51	23	35	48	43	41	26	23	0	0	292
#5-1963	0	39	43	33	0	36	0	33	0	18	0	202
#6-1969	0	40	43	41	0	39	0	28	0	0	0	191
#7-1972–1974	4	50	50	47	9	15	20	14	6	0	0	215
Length-stratified samples												
#3-1955	0	2	2	4	5	6	0	1	6	0	3	29
#8-1982–1985	8	35	28	28	22	9	9	8	5	0	0	152
#9-1960	0	6	7	10	11	9	2	7	24	5	5	86
#10-1974	12	6	7	9	3	5	1	2	24	15	5	89
#11-1959	8	0	17	10	14	6	5	5	30	8	4	107
#12-1967	7	12	10	17	8	5	5	10	21	29	12	136
#13-1971	22	3	6	4	3	23	6	2	21	8	4	102
#14-1978	28	7	16	19	7	7	3	3	4	9	2	105
#15-1990	23	22	55	17	17	21	12	7	12	3	0	189
#16-1991	1	11	7	25	11	7	5	5	11	4	3	102
#17-1992	26	17	11	15	21	10	16	1	4	2	0	123
#18-1993	10	10	13	19	14	16	4	2	5	4	1	98
#19-1994	12	15	16	6	14	7	12	7	8	1	0	98
#20-1995	15	23	21	11	5	10	14	8	10	2	0	119

Sea, but beam trawling is of minor importance in estuaries and within the 12-mile zone.

The distribution of plaice changes markedly with age and size (Wimpenny, 1953). 0-group fish inhabit shallow waters of estuaries and sandy beaches, but the distribution gradually spreads out over deeper offshore areas when they grow older. Because of differences in distribution between size classes and of spatial differences in impact caused by eutrophication and beam trawling, we put forward the hypothesis that the degree to which growth rate has changed over time will differ between size classes. An analysis of these patterns may thus provide indirect evidence for the relative contribution of the two anthropogenic factors. However, other factors may be involved as well. Growth rate may also be affected by intra- and interspecific competition, and by natural changes in the production of suitable food for plaice.

This paper presents information on changes in the average annual length increment by 5 cm size classes of female plaice for each year between 1950 and 1992 as estimated from otoliths. The emerging patterns are compared with time-series information on eutrophication, beam trawling, temperature, and intraspecific competition. To facilitate interpretation of the results, aspects of spatial distribution are incorporated.

Methods

Otolith back-calculations

Details of the back-calculation method applied, including validation and determination of accuracy and precision, have been described in earlier papers (Rijnsdorp *et al.*, 1990; Rijnsdorp and van Leeuwen, 1992). For the present study, the number of otolith samples investigated has been extended to allow an analysis of annual growth changes since 1950.

Otoliths of up to four female fish per cm group were randomly selected from length-stratified market samples collected during the spawning period (January–March) in the southern North Sea (52°–54°N; 1°–4°E). Samples were evenly spaced in time and comprised about 100 fish of 27–55 cm (Table 1). Information has been combined in 5 cm size classes (<10 cm; 10–14.9 cm; etc.). Fish >45 cm have been excluded, because numbers were generally too low. Because of differences in year-class strength, and because samples from earlier studies had partly been selected from single year classes (1955–1961, 1963, 1969, 1972–1974) at different ages, the numbers of observations per cell range from 0 to 187 (Table 2).

The rationale for choosing the spawning period for sampling is that the different sub-populations have returned to their specific spawning grounds at this time

of year (de Veen, 1962, 1964, 1978b), enhancing comparability between years. Tagging experiments of juvenile plaice have shown that the majority of adult fish in the Southern Bight area originate from the nursery grounds in the Wadden Sea between Texel and Helgoland (ICES, 1992).

Abundance

Spatial distributions of plaice by size class, derived from beam trawl surveys carried out in summer between 1983 and 1992 (RIVO, unpubl. data), show the gradual spreading from shallow coastal areas over offshore grounds (Fig. 1). These differences in distribution affect the intensity of intraspecific competition. Because time-series information on changes in abundance is only readily available by age groups, indices of mean crowding (Lloyd, 1967) was calculated for individual age groups following the approach of Rijnsdorp and van Beek (1991). The index of mean crowding m_a reflects the number of conspecifics per unit area of 30×30 mile and was calculated according to

$$m_a = \sum_b P_{ab} * N_b \tag{1}$$

where P_{ab} represents the index of proportional crowding of age group b on age group a (Rijnsdorp and van Beek, 1991) and N_b is the population number of age group b from Rijnsdorp and Millner (1996). In the present analysis, m_1 has been assumed to apply to size class <10 cm, m_2 to size class 10–14.9 and 15–19.9 cm, m_3 to size class 20–24.9 and 25–29.9 cm, m_4 to size class 30–34.9 cm, and m_5 to size classes $>=35$ cm.

Time series of mean crowding indices indicate two distinct periods of increased values, which are related to the recruitment of strong year classes (Fig. 2a). The first increase occurred after the recruitment of the exceptionally strong 1963 year class. A second period of high indices during the 1980s reflected the presence of several strong year classes born in 1979, 1981, and 1985, resulting in a much broader peak. Since 1988, the index rapidly decreased to the level of the mid-1970s.

Temperature

Average monthly seawater temperatures were calculated from daily readings at a fixed time of day at Den Helder after correction for tidal phase (van der Hoeven, 1982). Annual variation in average temperature by quarter has been relatively small during all seasons except winter (Fig. 2b). Exceptionally cold winters occurred in 1963, 1979, 1985, 1986, and 1987. Winters after 1988 have been particularly mild.

Although average temperatures during spring and summer were fairly stable, annual differences (± 1–2°C)

are large enough to influence growth rates (Fonds *et al.*, 1992). Average values for the months between April and September were used here since these reflect temperature conditions during the main growing period in coastal waters inhabited by the smaller size classes. No time series of temperature data are available for offshore waters.

Seabed disturbance

Demersal trawls disturb the seabed mainly by the use of tickler chains which run in front of the groundrope to activate flatfish. Although tickler chains had been used on otter trawls, their number was limited, because they reduced the spread of the boards. In beam trawls, the opening is fixed and more chains can be added when horse power is increased. Since more powerful engines result in higher catch rates, beam trawl effort is best expressed in terms of HP days of the total fleet.

Beam trawling for flatfish was introduced in the early 1960s and soon outcompeted the otter trawl. For two decades, use of this gear was largely restricted to The Netherlands and Belgium. Only in the late 1980s did beam trawling also expand in the United Kingdom and Germany. The expansion of the total international beam trawl effort is reflected in the steady increase in horse power days of the Dutch fleet since 1962 (Fig. 2c), which accounts for about two-thirds of the international landings of flatfish.

Since tickler chains were already employed by otter trawlers in the preceding period, the time series of HP days underestimates the level of seabed disturbance before beam trawling was introduced. A more appropriate measure of seabed disturbance might be fishing mortality on sole (Fsole, Fig. 2c; from Millner, 1996), because catchability of this species is particularly affected by the use of tickler chains. However, this measure is not without problems either, because at high levels of exploitation further increases in effort apparently do not result in proportional increases in fishing mortality. We therefore constructed an index of seabed disturbance (SBD) based on fishing mortality for sole but extrapolating values for years after 1974 from the linear regression of fishing mortality on HP days for the period 1962–1974. Over this period both indices increased in concert ($r=0.84$, $p<0.01$, $n=14$). This procedure raised the disturbance index in the late 1980s by about 25% above the estimated fishing mortality (Fig. 2c).

Dutch beam trawl effort is concentrated on the fishing grounds of the southern and south-eastern North Sea. The pattern has not changed substantially since the mid-1960s, except for a relatively small increase in effort in offshore waters of the Central North Sea since the late 1970s. Recent automated recordings of fishing positions from a representative sample of 10% of the Dutch fleet

Table 2. Mean length increment, standard deviation, and number of observations of female plaice by size class and year (1950–1992) estimated by back-calculation of otoliths.

Size	<10 cm			10–14.9 cm			15–19.9 cm			20–24.9 cm		
Year	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.	n
1950	7.25	1.98	20	6.31	1.89	15	5.96	1.53	13	4.89	2.00	18
1951	7.83	1.77	21	6.89	1.55	16	5.98	2.21	17	4.73	1.75	21
1952	8.83	2.24	7	8.61	2.41	11	6.41	1.82	19	5.79	1.80	25
1953	8.84	1.76	27	8.19	1.58	8	6.10	1.59	8	6.28	2.58	20
1954	8.18	1.17	20	7.57	1.60	13	6.93	2.46	22	6.41	2.03	14
1955	7.78	1.91	33	6.90	1.50	16	7.14	2.50	17	6.24	1.62	22
1956	8.38	2.21	13	8.06	1.57	18	6.99	1.68	29	5.49	1.20	18
1957	8.66	1.75	15	8.86	1.47	7	6.93	1.88	12	5.83	1.61	32
1958	8.73	2.19	27	8.99	3.48	7	7.11	1.68	11	5.54	1.37	12
1959	8.93	2.12	75	8.48	1.73	25	7.16	1.66	21	7.00	1.67	10
1960	8.50	1.97	78	7.31	1.84	45	7.20	1.80	55	6.27	2.56	37
1961	9.11	2.03	45	7.03	1.74	39	6.58	1.79	72	5.91	1.69	60
1962	7.84	1.65	26	7.61	2.31	19	7.08	1.72	57	5.80	1.36	68
1963	9.05	2.28	22	9.22	2.38	13	7.89	1.58	26	6.11	1.32	42
1964	7.37	1.91	187	7.64	2.02	25	7.87	1.51	16	6.29	1.53	23
1965	7.30	1.29	10	6.19	1.38	110	7.20	1.59	89	6.89	1.67	17
1966	6.92	0.67	5	6.08	1.95	9	5.39	1.19	80	5.89	1.67	91
1967	7.71	1.19	13	7.15	1.34	2	6.13	2.34	11	5.37	1.34	68
1968	12.10	0.00	1	8.90	2.59	6	7.25	1.54	8	5.07	1.58	9
1969	9.79	2.38	13	12.30	0.00	1	8.07	1.10	3	6.65	1.72	10
1970	9.11	2.62	124	8.91	2.92	41	8.98	2.95	9	8.10	0.00	1
1971	11.18	2.28	8	8.30	2.67	48	8.84	2.26	87	8.29	2.46	27
1972	9.64	3.32	16	—	—	0	8.17	1.98	26	8.05	1.73	53
1973	8.99	2.31	35	9.09	3.30	19	9.54	2.81	7	6.41	1.03	7
1974	9.72	2.69	88	8.91	2.76	43	7.89	2.09	30	7.31	2.39	13
1975	12.31	4.04	18	10.08	2.22	29	8.37	1.99	77	7.77	2.26	50
1976	9.67	2.94	7	12.49	4.16	7	8.74	1.85	14	6.95	1.98	57
1977	11.71	2.93	19	9.78	2.73	9	9.00	2.22	6	8.40	2.20	6
1978	11.09	3.15	12	10.03	2.70	13	8.36	1.24	13	7.53	1.37	12
1979	11.24	2.43	22	10.05	2.81	10	10.21	2.53	7	6.89	2.15	16
1980	10.00	2.50	25	10.13	3.54	8	9.56	1.74	16	9.16	2.34	13
1981	10.64	4.15	16	9.30	1.92	11	9.01	2.02	19	7.49	1.60	9
1982	9.96	3.17	14	9.53	1.63	9	8.31	2.51	10	7.98	1.83	15
1983	9.40	2.63	22	9.73	2.57	15	8.86	2.40	9	7.13	1.74	13
1984	9.41	2.15	30	8.73	2.30	25	7.85	3.18	15	7.10	2.20	18
1985	10.36	2.35	33	8.83	1.80	27	8.26	2.48	32	7.27	1.83	24
1986	9.24	2.18	82	8.77	2.44	58	7.79	2.39	33	7.26	2.31	30
1987	8.29	2.15	35	7.12	2.38	41	6.84	2.12	78	6.50	1.47	53
1988	8.83	2.50	34	7.81	2.37	35	7.12	2.55	45	6.03	1.52	62
1989	8.94	3.49	19	7.33	2.76	18	7.32	2.44	32	6.58	1.70	52
1990	8.51	2.18	18	7.35	2.45	18	7.79	2.80	18	6.18	1.99	26
1991	9.89	2.28	14	9.79	1.84	10	7.59	1.94	24	7.51	1.66	19
1992	—	—	0	7.75	2.19	2	8.07	1.80	15	6.77	2.14	19
1993	—	—	0	—	—	0	—	—	0	6.41	2.14	7
1994	—	—	0	—	—	0	—	—	0	—	—	0

(Rijnsdorp *et al.*, 1994) show the typical pattern of intensive fishing in a narrow band along the coast (Fig. 3a). The pattern in the area north-east of 53°N is probably not representative for the period prior to 1989 due to the installation of a protected area which expelled beam trawling of vessels >=300 HP from the shallow coastal waters in the German Bight ("plaice box"). In earlier years intensive beam trawling occurred just outside the 12-mile zone, but detailed information is lacking.

Eutrophication

Dissolved inorganic phosphate and nitrate represent essential nutrients which have been affected by anthropogenic land-based activities. Nutrient advection depends on the inflow of Atlantic water and on river run-off. Enhanced nutrient loading in the south-eastern North Sea originating from discharge by rivers is restricted to a small band along the Dutch coast (Zevenboom, 1993), but spreads further offshore in the

25–29.9 cm			30–34.9 cm			35–39.9 cm			40–44.9 cm		
Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.	n
4.86	2.96	11	4.08	1.33	17	2.70	1.59	10	2.05	1.99	6
3.71	1.43	16	3.76	1.71	12	3.00	1.49	19	2.61	1.95	8
4.20	1.71	24	3.25	1.29	17	2.64	1.15	17	1.69	0.89	17
4.63	2.28	28	3.80	1.69	32	2.30	1.42	19	1.54	0.79	22
4.38	2.15	23	3.89	2.45	32	2.36	1.08	33	1.95	1.70	26
4.85	1.88	17	2.84	1.14	23	2.45	1.19	39	2.10	1.29	31
5.14	1.27	22	4.06	1.85	27	2.15	1.38	35	1.82	0.94	41
4.47	1.54	27	3.73	1.68	26	2.74	1.66	43	1.67	1.08	43
4.44	1.32	38	3.70	1.93	33	2.19	1.33	36	1.87	1.17	56
5.03	1.38	17	3.47	1.48	28	2.80	1.49	23	1.67	0.86	30
5.15	2.03	14	4.41	2.14	16	2.38	1.02	17	1.49	0.96	14
4.77	1.44	50	4.44	1.73	22	2.33	1.77	23	1.56	0.89	17
5.26	1.51	70	4.55	1.68	60	2.79	1.70	31	1.69	1.08	28
5.26	1.49	85	4.25	1.47	76	2.69	1.12	67	1.92	1.33	38
4.97	1.79	43	3.91	1.50	96	2.59	1.20	86	1.78	0.95	53
5.35	1.84	25	3.94	1.67	51	2.50	1.13	121	1.77	1.04	75
5.95	1.99	37	4.10	1.68	42	2.24	1.18	83	1.82	0.91	103
5.28	1.32	89	4.88	1.59	48	2.21	1.28	57	1.58	0.99	58
4.38	0.98	57	3.80	1.16	76	2.86	1.47	56	1.40	0.85	45
4.28	1.59	16	3.51	1.18	64	2.64	0.99	52	1.79	0.94	36
5.55	1.92	11	2.93	1.35	32	2.59	0.90	82	1.93	1.02	52
7.57	2.16	11	4.64	1.88	11	2.13	0.76	40	1.72	0.70	29
6.67	1.48	67	5.32	1.68	29	2.47	1.27	34	2.02	0.88	46
6.09	1.74	36	4.10	1.26	93	3.24	1.40	50	2.07	0.91	32
6.98	1.79	12	3.72	1.32	27	2.75	1.05	82	2.15	0.93	24
6.32	1.54	21	4.19	1.64	16	2.63	1.41	50	2.05	0.97	41
6.21	1.73	66	5.05	1.84	54	2.49	1.27	39	1.92	1.09	61
5.70	1.55	42	4.71	1.57	85	3.73	1.51	66	2.39	1.21	47
5.33	1.88	9	3.95	1.35	35	3.11	1.05	63	2.03	0.75	39
6.23	1.60	18	4.66	1.67	15	2.48	1.05	36	2.09	0.63	34
6.43	1.90	14	4.32	1.33	27	2.55	0.93	28	2.01	1.01	44
5.65	1.45	21	4.10	1.66	21	3.37	1.53	36	1.84	0.85	41
5.81	1.21	22	4.58	1.67	21	3.13	1.12	30	1.80	0.75	41
5.73	1.42	15	4.37	1.31	30	2.91	1.02	29	2.36	0.89	29
5.68	1.55	17	4.31	1.46	17	2.86	1.08	32	2.12	0.74	22
5.44	1.85	18	5.21	2.20	24	2.81	1.04	22	1.85	0.73	18
6.08	1.41	39	4.68	1.72	28	2.85	1.12	30	2.17	1.33	31
6.00	2.05	40	4.02	1.21	51	2.72	0.99	33	2.15	1.23	46
5.63	1.80	77	4.35	1.79	44	3.16	1.57	66	2.19	0.96	51
5.60	1.70	66	4.61	1.59	80	3.25	1.53	84	2.80	1.32	62
4.98	1.57	55	4.22	1.69	62	3.33	1.44	58	2.61	1.48	51
5.48	1.92	28	3.83	1.37	54	3.33	1.35	64	2.59	1.21	52
5.27	1.18	24	3.66	1.35	34	3.42	1.24	54	2.80	1.07	45
5.26	1.65	19	4.33	1.48	25	3.36	1.43	32	2.49	0.96	33
4.86	1.19	5	4.91	2.90	14	3.46	1.64	19	2.78	1.44	17

German Bight (Fig. 3b). Nutrient levels in the open North Sea are largely determined by the Atlantic inflow.

Time-series information on nutrient loads and concentrations is shown in Fig. 2d. The load of orthophosphate of the river Rhine at Lobith (German–Netherlands border; data from RIZA-RWS) increased by a factor of 20 between 1950 and 1980–1981, followed by a decrease to 20% of the peak level in 1990. Nutrient concentrations in waters off Helgoland are available since 1962 (Hickel *et al.*, 1993). The change in phosphate concentration in these coastal waters was less pronounced than in the river Rhine load. Concentrations doubled between 1963 and the mid-1970s and in 1990 had decreased to about 75% of the peak level. Nitrate concentrations were rather more variable and showed a fourfold increase between the 1960s and the 1980s.
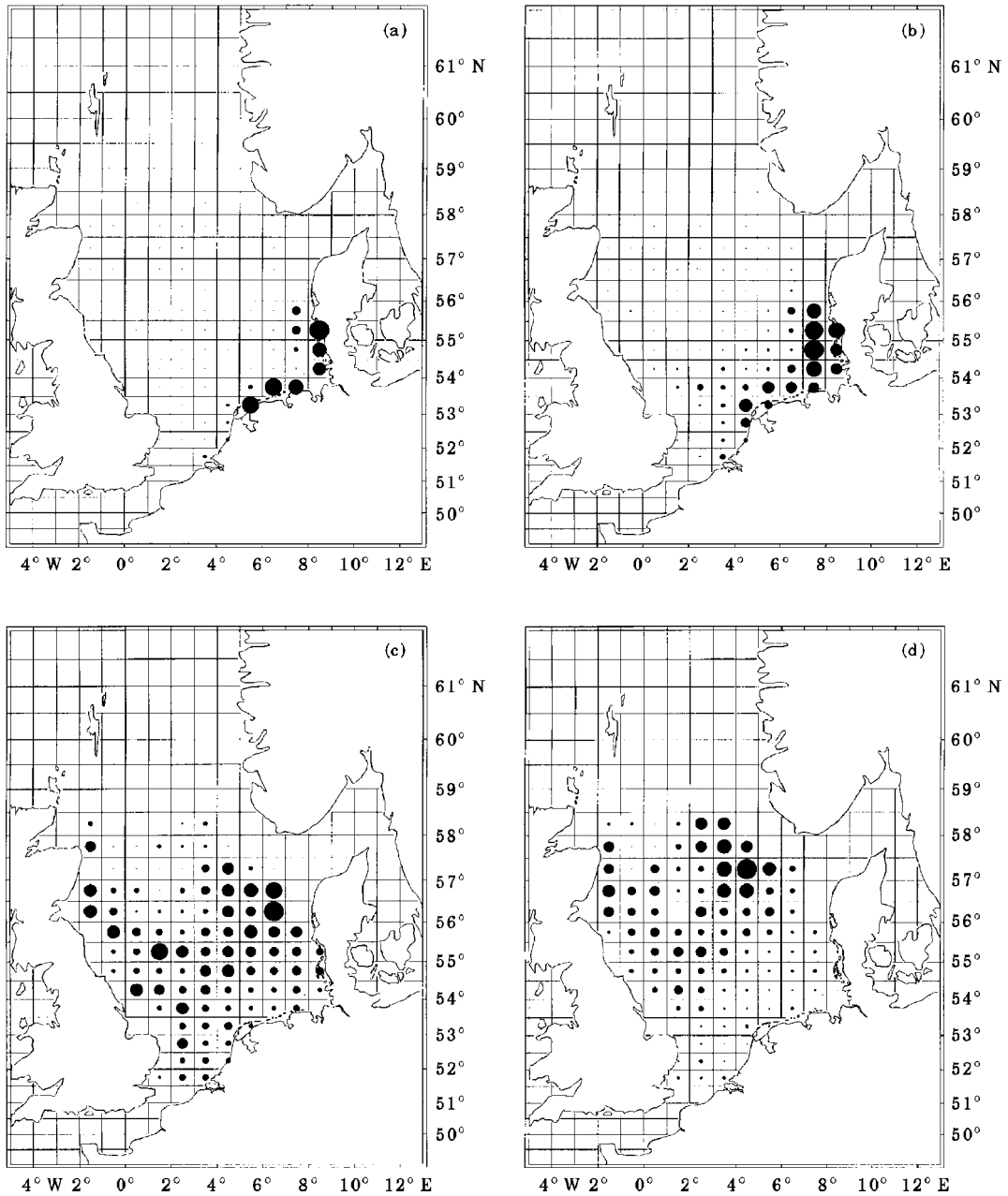
Figure 1. Distribution of plaice by 5 cm size class during the summer feeding period illustrating the progressive offshore movement with age and size: (a) 10–14.9 cm; (b) 20–24.9 cm; (c) 30–34.9 cm; (d) 40–44.9 cm. Data: August–September Beam Trawl Surveys 1983–1992.

Since plankton production in coastal waters appears to be limited by phosphate (Brockmann *et al.*, 1990), phosphate concentration off Helgoland was selected as an appropriate eutrophication index. Values for years before 1963 were extrapolated backwards to 1950 based on the linear regression of phosphate concentration off Helgoland and phosphate load of the river Rhine between 1963 and 1975, when both levels increased synchronously ($r=0.72$, $p<0.01$, $n=13$).

Statistical analysis

Estimated annual length increments were correlated with environmental variables and indices of intraspecific
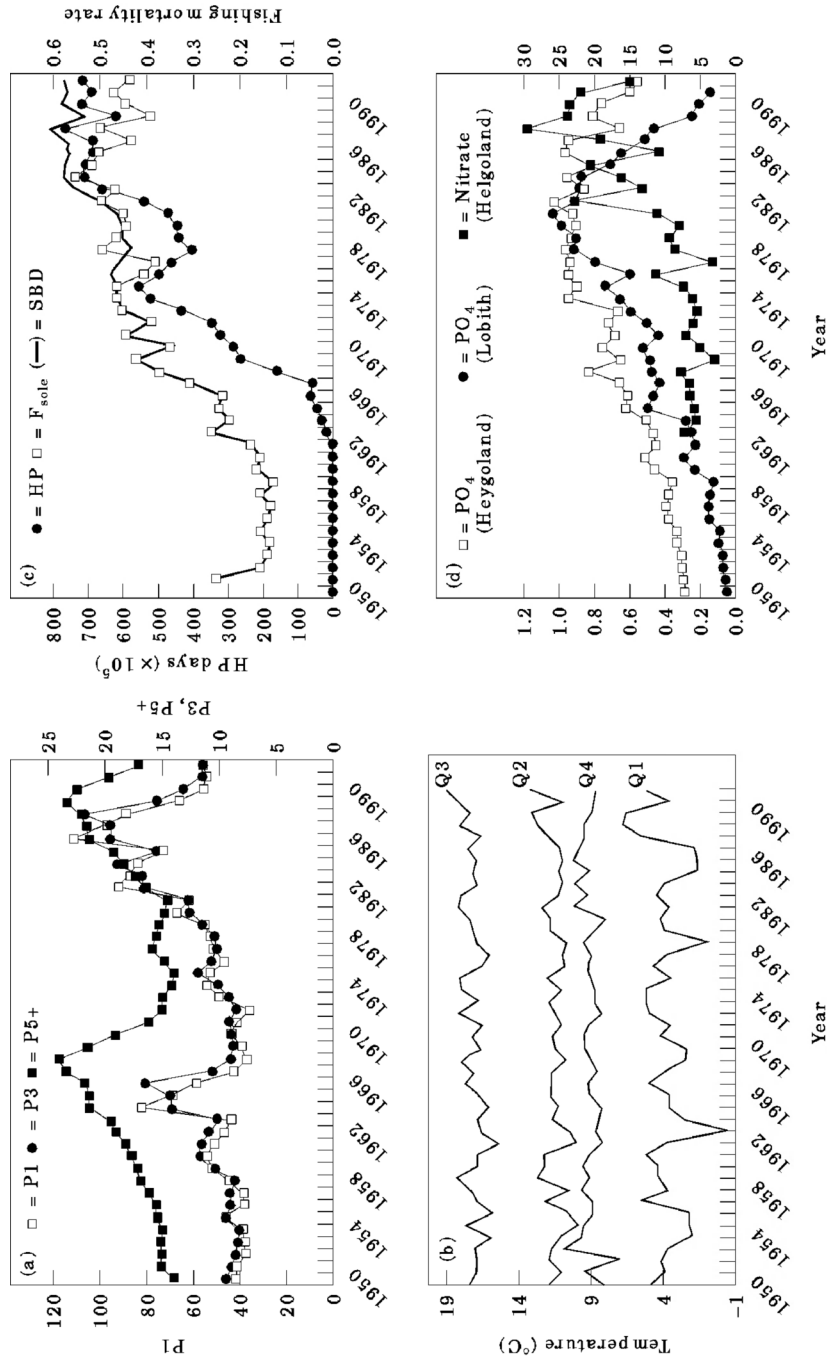
Figure 2. Time series of plaice abundance and environmental variables between 1950 and 1992. (a) Index of mean crowding (m) on age groups 1, 3, and 5 and older; (b) average temperature by quarter at Den Helder; (c) indices of seabed disturbance: HP=total HP days of the Dutch beam trawl fleet $\times 10^{-5}$; F_{sole}=instantaneous fishing mortality rate (from Millner, 1996); SBD=F_{sole} corrected for decrease in catchability between 1962 and 1974; (d) eutrophication: PO_4 (extrapolated for years before 1963) and NO_3 concentration near Helgoland (μmol l^{-1}) from Hickel *et al.* (1993), PO_4 load in the river Rhine at Lobith (kg s^{-1}) from Rijkswaterstaat-RIZA.
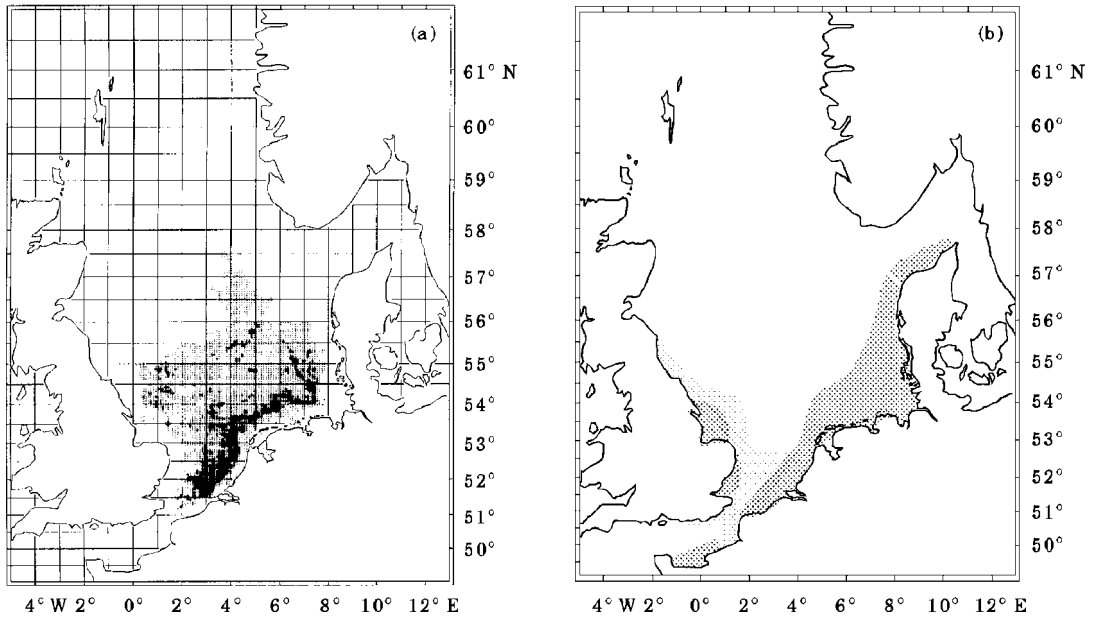
Figure 3. Distribution of (a) Dutch beam trawl effort of vessels >300 HP in 1993 on a scale of 3 × 3 mile (Rijnsdorp *et al.*, 1994); (b) eutrophicated waters in the southern North Sea (from Zevenboom, 1993).

competition (Table 3) using the NAG statistical package GLIM (Baker and Nelder, 1978). GLM models analysed were of the form

$$Y = \%GM + aX1 + bX2 + cX1X2 + \varepsilon \qquad (2)$$

where Y is the dependent variable length increment, X1 and X2 are independent covariables, X1X2 is the inter-action term and ε is a normally distributed error term. The term %GM is the average length increment at X1=X2=0. Number of observations was used as a weighting factor.

The variance explained by the independent covariables was estimated by backwards elimination. The contribution of each covariable was tested against the full model. The variance that could not be ascribed to a single covariable is indicated as multicolinearity factor.

Results

The average annual length increment and approximate 95% confidence limits were calculated in 5 cm size classes and expressed as relative values to the average over the period 1950–1992 (Table 2). To reduce variations due to the sometimes relatively small number of observations, 3-pt running averages are shown in Fig. 4.

In size classes <30 cm, growth rate generally showed an upward trend until the 1970s and a downward trend in the 1980s. Superimposed on this pattern, a temporary

dip occurred in the mid-1960s and late-1980s. The dip in the 1960s shifted to later years in the larger size classes, tracing the slowly growing strong 1963 year class through successive size classes in consecutive years. The dip in the late-1980s coincided with the strong 1985 year class. Closer inspection of Fig. 4 suggests that growth rate in the two smallest size classes (<15 cm) increased gradually, reaching a peak in the late 1970s. Intermedi-ate size classes (15–30 cm), however, showed a sharp increase following the passage of the 1963 year class, suggesting a switch from a low to a high level around 1970 rather than a gradual change. In the mid-1970s, growth rate decreased slightly followed by a second peak in the late 1970s. The decrease thereafter started off in the smallest size class, followed in later years by larger size classes. No overall trend is apparent in the inter-mediate size class 30–34.9 cm, but length increments in the larger size classes (>35 cm) increased since the 1970s, particularly in the late 1980s.

Regression of annual length increments against the environmental variables revealed significant relation-ships with indices of eutrophication and seabed distur-bance (SBD), but not with the index of mean crowding nor with temperature (Table 4). Because various environmental variables were mutually correlated (Table 5), a multiple regression was conducted including the environmental variables and their interaction terms. In none of the analyses did the interaction terms con-tribute significantly to the explained variance, except for the interaction of eutrophication and SBD (A · B) in size

Table 3. Time series of environmental variables and indices of intraspecific competiton. PO_4 is an index of eutrophication ($\mu mol\ l^{-1}$); SBD is an index of seabed disturbance based on F_{sole} (yr^{-1}); m_1, m_2, m_3, m_4, and m_5 are indices of mean crowding in numbers of age groups 1, 2, 3, 4, and 5 and older, and Temp is the average temperature (°C) in the second and third quarters.

Year	PO_4	SBD	m_1	m_2	m_3	m_4	m_5	Temp.
1950	0.282	—	42.0	44.6	45.8	19.5	14.3	14.6
1951	0.288	0.254	41.3	44.0	43.5	20.0	15.3	14.0
1952	0.303	0.160	37.6	41.5	42.2	19.2	15.4	14.3
1953	0.300	0.144	38.0	40.2	41.4	19.4	15.4	14.3
1954	0.325	0.142	39.2	41.4	40.1	18.8	15.2	13.5
1955	0.321	0.160	45.6	47.3	45.6	19.7	15.6	13.8
1956	0.375	0.146	38.0	43.6	43.6	19.8	15.8	13.2
1957	0.380	0.137	37.8	40.2	44.0	20.6	16.4	14.5
1958	0.369	0.160	44.5	45.1	42.4	20.9	17.1	13.9
1959	0.352	0.132	51.5	54.3	50.5	21.5	17.4	15.5
1960	0.449	0.167	53.6	57.5	56.7	23.7	17.9	14.5
1961	0.509	0.160	50.8	55.1	56.1	24.5	18.5	14.5
1962	0.444	0.181	46.4	50.7	52.8	24.8	19.2	12.7
1963	0.462	0.261	43.4	47.0	48.9	24.1	19.7	13.5
1964	0.490	0.228	81.7	75.7	68.7	29.0	21.6	14.2
1965	0.622	0.246	68.3	80.2	69.6	27.8	21.6	13.6
1966	0.608	0.240	58.6	66.3	80.1	31.1	21.9	14.2
1967	0.650	0.308	42.6	46.8	51.5	31.3	23.6	14.6
1968	0.825	0.373	36.7	40.9	43.4	25.1	24.3	14.3
1969	0.643	0.423	38.8	41.1	42.1	23.2	21.7	14.3
1970	0.748	0.351	42.9	45.1	43.1	21.5	19.3	13.9
1971	0.671	0.444	40.5	44.7	44.0	19.6	16.4	14.4
1972	0.713	0.393	35.5	39.1	41.2	19.0	15.2	13.7
1973	0.657	0.452	48.5	46.8	44.1	19.7	15.1	14.8
1974	0.937	0.463	53.7	56.6	48.8	19.0	14.4	14.3
1975	0.895	0.462	51.6	56.8	57.3	20.6	14.1	14.3
1976	0.937	0.474	45.8	49.3	51.6	22.4	14.9	15.0
1977	0.923	0.457	50.1	50.9	49.1	21.6	16.0	13.6
1978	0.951	0.429	52.0	54.9	50.1	20.8	15.7	13.3
1979	0.923	0.448	54.5	57.5	55.4	21.3	15.4	13.7
1980	0.895	0.450	66.4	66.4	61.1	22.7	14.9	14.3
1981	0.909	0.462	61.4	67.1	61.0	21.9	14.7	14.4
1982	1.021	0.494	90.8	86.9	80.8	27.5	16.6	15.2
1983	0.853	0.549	85.6	93.6	80.4	27.6	17.3	14.5
1984	0.944	0.574	82.8	88.6	91.4	30.7	18.4	13.8
1985	0.755	0.571	71.7	76.7	75.0	30.2	19.3	14.0
1986	0.951	0.561	109.6	104.0	94.3	33.9	21.5	13.8
1987	0.937	0.563	95.6	108.1	93.8	32.9	21.7	14.2
1988	0.643	0.600	87.3	95.1	105.1	36.6	22.2	14.2
1989	0.797	0.530	64.8	71.8	74.6	35.1	23.5	15.3
1990	0.755	0.576	54.8	59.7	63.0	28.9	22.5	15.1
1991	0.587	0.563	53.6	56.2	55.6	25.7	19.7	14.3
1992	0.559	0.575	54.9	57.8	54.6	22.7	17.1	16.0

class 15–19.9 cm, which explained about 6% of the variance (Table 6). The parameter estimate of this interaction term indicated that the two factors had a synergistic effect. However, no significant effect was observed in other size classes.

After removing the interaction terms the analysis showed that temperature effect was not significant in any size class (Table 6). The index of mean crowding was significant in size classes up to 25 cm, explaining 12–26% of the variance. The eutrophication index explained 6–10% and was significant in size classes up to 30 cm with the exception of size class 15–19.9 cm, where SBD

explained a significant part of the variance (9%). Results for size classes beyond 35 cm are not shown, because they were generally not significant.

Since the contribution of each factor was estimated by backwards elimination, the variances explained represent minimum estimates, with a substantial part of the total variance not being ascribable to a single covariable. This multi-colinearity particularly affected the effects of eutrophication and SBD, which were significantly correlated among themselves (Table 4). The full model was significant at the 1% or 5% level for all size classes up to 35 cm (Table 6).
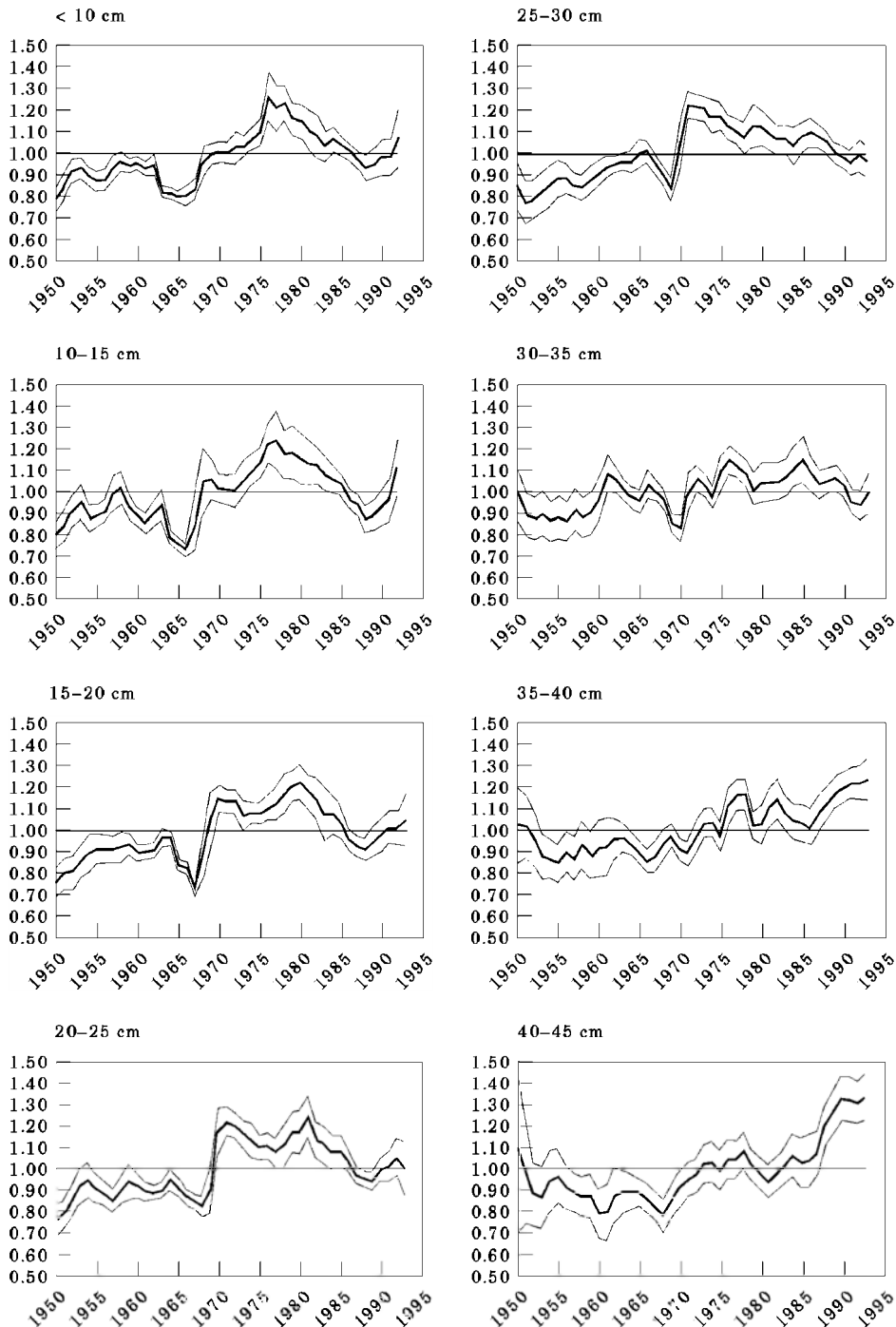
Figure 4. Time series of back-calculated growth rates by 5 cm size class of female plaice between 1950 and 1993. The heavy line shows the mean growth rate as a 3-pnt running mean; the two thin lines show the approximate 95% confidence limits (± 2 × s.e.).

The significant effect of intraspecific competition suggests that growth is reduced at high population densities. The shape of the relationship was explored by plotting length increment, after correction for effects of eutrophication and SBD, against the index of mean crowding (Fig. 5). Corrected length increment was calculated as the residual between observed growth and growth predicted from the model:

Table 4. Correlation coefficients (r) of annual length increment and entrophication (A), seabed disturbance (B), intra-specific competition (C), and temperature (D) by 5 cm size classes of female plaice. N denotes the number of observations. For intra-specific competition the indices of mean crowding were used: m_1 for size class <10 cm; m_2 for 10–15 cm and 15–20 cm; m_3 for 20–25 cm and 25–30 cm; and m_4 for 30–35 cm. Significance levels are indicated as * for $p<0.05$ and ** for $p<0.01$.

Size class	N	A	B	C	D
<10	41	0.61**	0.53**	0.18	0.00
10–14.9	41	0.45**	0.44**	0.21	0.18
15–19.9	42	0.46**	0.49**	0.13	0.10
20–24.9	42	0.59**	0.50**	0.00	0.09
25–29.9	42	0.61**	0.52**	0.28	0.03
30–34.9	42	0.41**	0.31*	0.29	0.00
25–29.9	42	0.37*	0.65**	0.00	0.31*
40–44.9	42	0.25	0.66**	0.00	0.34*

Growth=%GM+a*Eutrophication+b*SBD. For none of the size classes do the scatter plots provide evidence of other than a simple linear relationship.

Discussion

The indices of intraspecific competition used in this study may underestimate the absolute level of mean crowding in the smaller size classes, because their distribution varies strongly with depth at much smaller scales than the 30 × 30 miles grid used here (Wimpenny, 1953). Nevertheless, the ANOVA provides strong evidence of density-dependent growth among the juveniles, corroborating earlier analyses (Rijnsdorp and van Leeuwen, 1992). The lack of density-dependent effects in the larger sizes coincides with a substantial reduction in the index of mean crowding due to the dispersion of the larger and older fish over offshore grounds (Fig. 1). On theoretical grounds, one might expect growth rate to become depressed when intraspecific competition increases above a threshold level. However, plots of residual growth, after correcting for other factors, against indices of mean crowding did not provide evidence for a threshold relationship (Fig. 5).

The indices of both eutrophication and seabed disturbance explained a significant part of the variance, but the true effects of these two variables were less easy to determine, because they were mutually correlated. When tested together, a substantial part of the variance could not be ascribed to individual covariables as reflected in the multi-colinearity factor accounting for 20–70% of the explained variance of the full model (Table 6). Statistical analyses thus cannot be used in disentangling the possible causal factors further.

However, reference to spatial and temporal patterns may be of help here. From the spatial distribution patterns of eutrophication, beam trawl activity, and plaice, we may infer that beam trawling is less likely to be involved in causing growth changes in size classes up to 15 cm, because these are largely distributed in shallow inshore waters where no heavy beam trawling takes place. These shallow areas are only fished by shrimpers employing light beam trawls with a bobbin rope and without tickler chains. However, effects of eutrophication are probably strongest in the shallow areas, for which evidence of enhanced primary production and enhanced production of macro-zoobenthos has been reported (Reise, 1982; Beukema and Cadée, 1988; Beukema, 1989; Rachor, 1990). Hence, growth changes in the two smallest size classes are probably related to eutrophication rather than to beam trawling.

For the intermediate size classes (15–30 cm), both eutrophication and beam trawling may be involved. Effects of eutrophication are likely to decrease with increasing distance from the coast, whereas maximum effects of beam trawling are expected at some distance from the coast. Figure 6 shows a tentative picture of the levels of eutrophication and beam trawling in relation to the distance from the coast. The true picture has probably varied because of management regulations. Originally, larger trawlers (>300 HP) were excluded only from the 12-mile zone, but locally this regulation was extended in 1989 to about 30 miles from the coast ("plaice box"). The relative impact of the two factors will shift from predominantly eutrophication in the smaller size classes to predominantly beam trawling in

Table 5. Correlation matrix (r) of the environmental factors for 1951–1992 (n=42). Level of significance is indicated by * for $p<0.05$ and ** for $p<0.01$.

	PO_4	F_{sole}	m_1	m_2	m_3	m_4	m_5
SBD	0.799**	—	—	—	—	—	—
m_1	0.513**	0.550**	—	—	—	—	—
m_2	0.514**	0.560**	0.981**	—	—	—	—
m_3	0.468**	0.552**	0.928**	0.958**	—	—	—
m_4	0.333*	0.460**	0.741**	0.776**	0.868**	—	—
m_5	0.068	0.177	0.321*	0.361*	0.455**	0.798**	—
Temp.	0.100	0.284	0.110	0.095	0.107	0.147	0.088

Table 6. Results (ANOVA) of length increment by size class as a function of eutrophication (A), seabed disturbance (B), intra-specific competition (C), and temperature (D) when tested by backward elimination. The multi-colinearity factor represents the explained variance that cannot be ascribed to a single covariable when no interaction terms are included.

Size class	<10 cm				10–14.9 cm			
	SS	df	F	p	SS	df	F	p
A – PO$_4$	133.1	1	7.86	<0.01	74.6	1	4.24	<0.05
B – SBD	20.5	1	1.21	NS	67.1	1	3.82	NS
C – m$_a$	334.0	1	19.72	<0.01	372.4	1	21.2	<0.01
D – TEMP	11.3	1	0.67	NS	0.7	1	0.04	NS
A+B+C+D	910.2	4	13.4	<0.01	679.5	4	9.13	<0.01
Multicolinearity	411.3				164.7			
Error	609.8	36			632.5	34		
A.B	36.2	1	2.24	NS	47.0	1	3.25	NS
A.C.	12.7	1	0.79	NS	32.4	1	2.24	NS
B.C	10.3	1	0.63	NS	20.6	1	1.42	NS
A.B.C	5.17	1	0.31	NS	1.5	1	0.10	NS
Error	528.1	32			475.9	30		
SS$_{total}$	1520	40			1312	38		

Size class	15–19.9 cm				20–24.9 cm			
	SS	df	F	p	SS	df	F	p
A – PO$_4$	54.6	1	3.59	NS	87.8	1	6.92	<0.05
B – SBD	107.3	1	7.06	<0.05	36.6	1	2.88	NS
C – m$_a$	293.9	1	19.34	<0.01	106.8	1	8.42	<0.05
D – TEMP	13.5	1	0.89	NS	13.9	1	1.09	NS
A+B+C+D	587.7	4	9.67	<0.01	431.4	4	8.50	<0.01
Multicolinearity	118.4				186.3			
Error	562.3	37			469.4	37		
A.B	67.0	1	4.77	<0.05	17.2	1	1.33	NS
A.C.	9.6	1	0.69	NS	2.5	1	0.19	NS
B.C	49.4	1	3.51	NS	24.3	1	1.87	NS
A.B.C	6.5	1	0.46	NS	1.0	1	0.07	NS
Error	471.3	33			439.7	33		
SS$_{total}$	1150	41			900.8	41		

Size class	25–29.9 cm				30–34.9 cm			
	SS	df	F	p	SS	df	F	p
A – PO$_4$	67.6	1	6.37	<0.05	25.5	1	2.94	NS
B – SBD	8.4	1	0.80	NS	2.1	1	2.06	NS
C – m$_a$	0.07	1	0.07	NS	0.03	1	0.003	NS
D – TEMP	21.1	1	0.89	NS	0.7	1	0.66	NS
A+B+C+D	275.6	4	6.50	<0.01	93.5	4	2.70	<0.05
Multicolinearity	178.4				65.2			
Error	392.5	37			320.2	37		
A.B	0.02	1	0.002	NS	1.3	1	1.32	NS
A.C.	0.02	1	0.002	NS	0.9	1	0.86	NS
B.C	15.2	1	1.41	NS	0.2	1	0.19	NS
A.B.C	1.23	1	0.11	NS	0.09	1	0.09	NS
Error	364.9	33			304.3	33		
SS$_{total}$	668.1	41			413.7	41		

the larger size classes. Hence we suggest that the growth increase in plaice of 15–25 cm may be due to an increase in food availability as a result of the combined effect of eutrophication and beam trawling.

This interpretation is further supported by the differences in timing of the observed growth changes between the smaller and intermediate size classes, and by the timing of the increases in eutrophication and beam
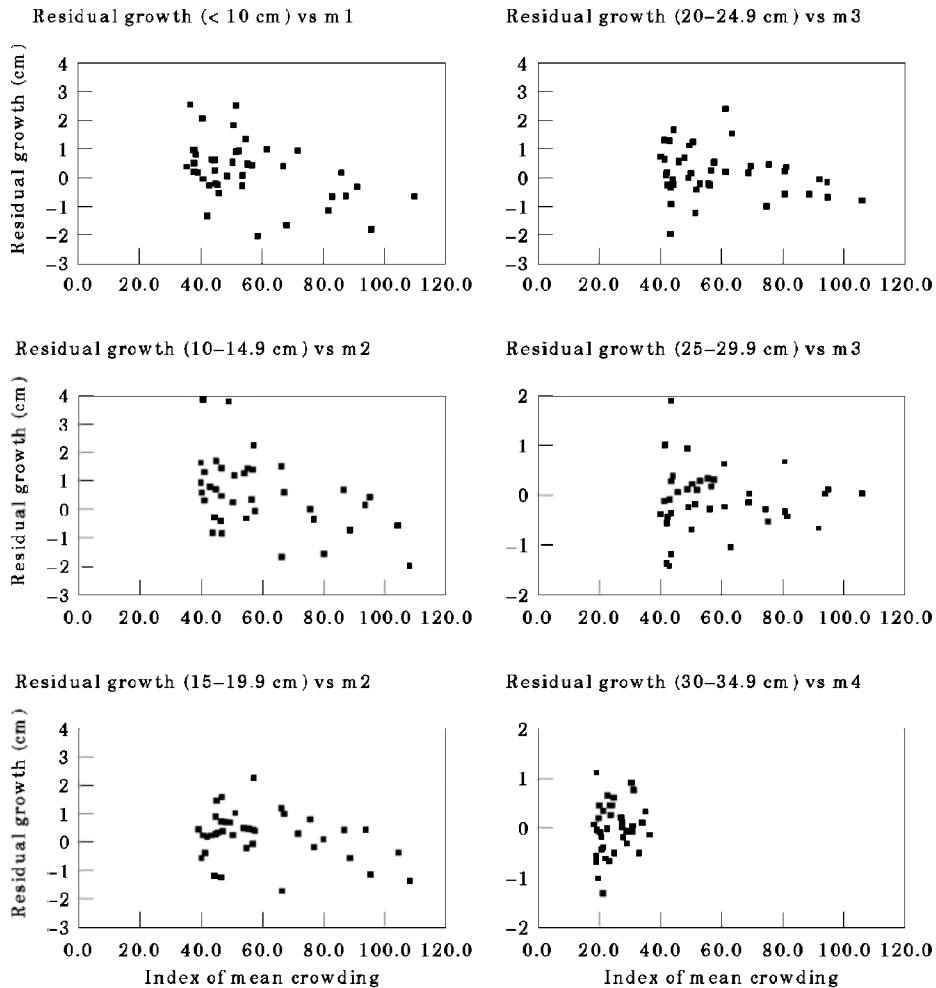
Figure 5. Scatter plots of residual growth rate corrected for effects of eutrophication and seabed disturbance versus the index of mean crowding.

trawling. Growth in the two smaller size classes gradually increased to a peak in the late 1970s when phosphate load of the Rhine reached its maximum (Fig. 2d), whereas growth in the intermediate size classes (15–30 cm) suddenly increased in 1970, just after the steep increase in beam trawling between 1962 and 1969 (Fig. 2c). An explanation why the growth change was delayed in this case may be found in the 1963 year class, which apparently was so strong that density-dependent effects overruled the positive effects of seabed disturbance. By 1970 this year class had grown into the larger size classes and thus made room for a response to beam trawling.

From the significant positive interaction between seabed disturbance and eutrophication in size class 15–19.9 cm (Table 6), we may speculate that production of suitable benthic food could be enhanced under eutrophic conditions when the rate of nutrient regeneration is increased through beam trawling (Dr I. de Vries, pers. comm.). This interpretation is consistent with the fact that this size class is distributed in the coastal zone which is under influence of eutrophication and where beam trawling is heavy.

For size classes >35 cm, growth changes were significantly correlated with seabed disturbance and/or eutrophication. However, it would seem unlikely that either factor could have had a substantial direct effect, because increased nutrient levels and intensive beam trawling were both restricted to the coastal zone, unless primary production from coastal waters had been advected to offshore areas. An alternative explanation might be found in the increased fishing mortality of plaice and the corresponding decrease in the number of older and larger fish in recent years (Rijnsdorp and Millner, 1996). If fishing mortality increases, a length-stratified otolith sampling programme may result in
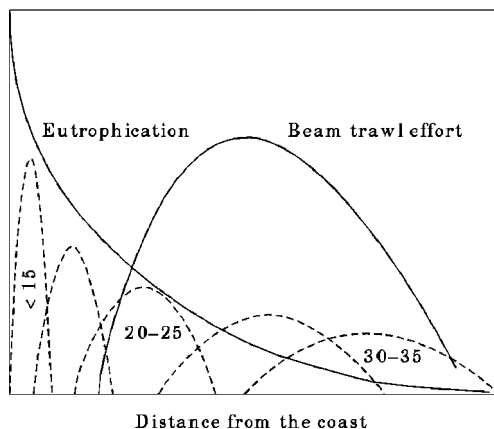
Figure 6. Schematic distribution of size classes and of the effects of eutrophication and beam trawling in relation to distance from the coast. Eutrophication is highest in inshore areas. Intensity of heavy beam trawling is zero within the 3-mile zone and reaches a peak in offshore waters along the areas closed for beam trawling (12-mile zone and plaice box). Dashed lines indicate the offshore movement of larger sizes.

overestimates of the growth rate of larger fish, because only fast-growing individuals will get a chance to attain a large size. A comparison of the back-calculated length increments of females of a year class sampled at different ages did not reveal differences over the time period 1967–1979 (cf. Figure 7 in Rijnsdorp and van Leeuwen, 1992). Whether this conclusion holds true for the years after 1980 remains to be tested.

Whether the lower growth rates in plaice during the 1980s are due to reduced phosphate loading from the river Rhine, as claimed by Boddeke and Hagel (1991), is still open to debate. Time-series data on primary production, chlorophyll *a*, *Phaeocystis* concentrations, and macrofaunal biomass revealed that all these parameters have remained at high levels between 1980 and 1990 (Cadée and Hegeman, 1993; Janssen, 1993; I. de Vries, pers. comm.). Furthermore, at least part of the growth reduction can be explained by the peak in intraspecific competition in the late-1980s due to the recruitment of the strong 1981 and 1985 year classes. Also, the growth of the smallest size classes has increased again in the early 1990s and it is not yet clear at what level growth rates will stabilize at average levels of intraspecific competition.

The combination of a statistical analysis with a study of the spatial and temporal patterns in relation to growth changes and environmental variables appears to have yielded a consistent interpretation. The overall changes in growth can be broken down into the effects of eutrophication on the juveniles in inshore areas and of beam trawling on the older fish, whereas both factors may play a role during an intermediate life phase.

However, these effects may become overruled by density-dependent effects under influence of strong year classes in the population.

Nevertheless, the evidence presented cannot provide definite proof that either eutrophication or beam trawling are causally involved. Other factors may still be responsible or at least play a significant role. For instance, the substantial decrease in growth rate of plaice in the North Sea in the 1980s coincided with similar reductions in growth rate of plaice and sole in other areas (Millner *et al.*, 1996), suggesting that large-scale hydrographical factors in the North-east Atlantic might be involved. Also, the coincidence of the sudden increase in growth of the intermediate size classes around 1970 and reported shifts in the benthic community in the western North Sea and Skagerrak (Austen *et al.*, 1991; Josefson *et al.*, 1993) and phytoplankton (Hickel *et al.*, 1994) is intriguing.

The results illustrate that a back-calculation study of length increments may provide detailed information on temporal and spatial patterns in growth changes. This approach may prove even more fruitful when extended to other species to further test the validity of the explanation derived. Sole (see also Millner, 1996) and dab are obvious candidates in this respect because, although they inhabit the same general area, environmental factors would affect them differentially due to different life histories. Furthermore, a study on temporal changes in growth of plaice in other areas, less affected by beam trawling and eutrophication, might also be worth pursuing.

Acknowledgements

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