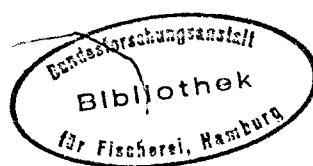


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CHANGES IN GROWTH OF NORTH SEA PLAICE SINCE 1950 AND ITS RELATION TO DENSITY, EUTROPHICATION, BEAM TRAWL EFFORT AND TEMPERATURE

by

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Abstract

Changes in somatic growth of female North Sea plaice were studied from annual length increments back-calculated from otoliths. Annual length increments of size classes <25 cm increased since the mid 1950s and decreased in the 1980s. Length increments of larger size classes varied without a trend in time. The changes in growth of the smaller size classes correlated with indices of plaice density, eutrophication and beam trawl effort. No correlation was observed with temperature. The changes in growth were analysed in relation to the spatial and temporal patterns in eutrophication and beam trawling. The analysis led to a consistent interpretation suggesting that plaice density, eutrophication and beam trawling affected the growth rate of plaice. Their contributions, however, differed in space. Density was restricted to plaice <25 cm. Eutrophication dominated in the shallow coastal waters, whereas beam trawling dominated in the waters further offshore. In the open North Sea no effect of eutrophication and beam trawling could be detected.

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1. Introduction

The marine ecosystem is influenced by a multitude of antropogenic activities. Evaluation of these effects is often difficult because of the complexity of the marine ecosystem, and because various antropogenic activities develop simultaneously.

In the 1960s and 1970s a major increase in growth rate has been reported for both plaice and sole in the North Sea (de Veen, 1976; 1978; Bannister, 1978; Rijnsdorp & Beek, 1991; Rijnsdorp & Leeuwen, 1992). The increased growth could not be related to a change in temperature, but coincided with an increase in eutrophication and an increase in the intensity of beam trawling. Both factors have been hypothesised to explain the increase in growth (Veen, 1976; 1978; Rijnsdorp & van Beek, 1991; Boddeke & Hagel, 1991).

Plaice and sole feed mainly on macro-zoobenthos species such as molluscs and polychaetes, which are characterised by a small body size, a short life span and high productivity. These organisms appear to be particularly able to take advantage of the increased primary production in the coastal waters of the North Sea, that is well documented (Cadée, 1986; Gerlach, 1987; Salomons et al. 1988; Cadée & Hegeman, 1993). Enhanced production of macro-zoobenthos has indeed been reported for tidal flats (Beukema & Cadée, 1988; Beukema, 1989) and sublittoral areas in the German Bight (Rachor, 1990).

However, the same opportunistic macro-zoobenthos species are candidates which may benefit from disturbance of the sea bed due to the beam trawl fishery. Beam trawling thus may have led to a shift in the benthic community from low productive, long lived, species to high productive, short lived, species (Rijnsdorp & Beek, 1991). In addition, beam trawling has been shown to enhance the feeding conditions directly by damaging benthic organisms in the path of the trawl (Veen, 1976; Bergman & Santbrink, 1994; Santbrink & Bergman, 1994).

Since time series data on changes in the macro-zoobenthic community in the North Sea are scarce, the potential effects of eutrophication and beam trawling on the growth rate of plaice cannot be studied directly. Therefore, an indirect approach has been followed to unravel the significance of these two factors. The starting point is the notion that effects of beam trawling and eutrophication will have different spatial patterns. Eutrophication, which is mainly due to the load of nutrients in the run off of major European rivers, decreases with an increasing distance from the coast. Beam trawling occurs over a large area in the southern and south-eastern North Sea, but does not occur in estuaries and is of minor importance within the 12-miles zone.

The spatial distribution of plaice changes during its life (Wimpenny, 1953). As 0-groups, plaice inhabit the shallow waters of estuaries and of sandy beaches. With increasing age their distribution gradually spreads out over deeper off shore areas. Because of the differences in spatial patterns between size classes of plaice, and the different spatial patterns in eutrophication and beam trawling, we hypothesise that the degree to which the growth rate of plaice has changed, and its pattern through time, will differ between size-classes. A comparison of the change in growth through time of different size classes may therefore provide indirect evidence about the contribution of the two antropogenic factors. However, other factors may be involved as well. Growth rate may also be affected by intra- and inter-specific competition, and by natural changes in the ecosystem that affect the production of suitable food for plaice.

This paper presents the changes in the average annual growth of 5-cm size classes of plaice for each year between 1950 and 1991 as estimated from otoliths of female

plaice. The patterns of change are compared with time series information of eutrophication, beam trawl fishing, temperature and intra-specific competition. In order to facilitate the interpretation of the data the spatial pattern of the various size classes and antropogenic effects will be analysed.

Acknowledgement. This study forms a part of the project 'Aquatic Outlook Project' (Schol-case) in which the National Institute for Coastal and Marine Management (RIKZ, RWS), Netherlands Institute for Fisheries Research (RIVO-DLO) and the Agricultural Economics Institute (LEI-DLO) participate to develop a bio-economic simulation model of North Sea plaice and its fisheries. Comments on an earlier draft by Niels Daan, Gerard Janssen and Wanda Zeevenboom is appreciated.

2. Methods.

2.1. Back-calculation of growth from otoliths.

The back-calculation method applied is described in several earlier papers, including an analysis of its validity, accuracy and precision (Rijnsdorp, et al., 1990; Rijnsdorp & van Leeuwen, 1992). For the present study, we have extended the otolith samples reported in the earlier papers with additional length stratified samples to allow the analysis of yearly changes in growth since 1950.

Otoliths of females were randomly selected within each cm-group up to a total of 4 fish per cm-group. The otoliths were taken from market samples that were collected during the spawning period (January - March) in the southern North Sea between 20 and 54° N and 10 and 40° E. A summary of these samples is given in Table 1. These samples comprised about 100 fish of 27-55 cm and were evenly spaced in time. By this procedure, the number of growth estimates should be evenly distributed over the 5-cm size classes by year. However, due to differences in year class strength, and because part of the available samples from earlier studies were selected from single year classes throughout their life (year classes 1955-1961, 1963, 1969, 1972-1974) the number of observations per cell range from 0 - 187 (Table 2).

One otolith per fish was cut along the lateral plane through the nucleus, polished and burned above a gas flame on a brass plate above a Bunsen gas flame. The burned otoliths were mounted in plasticine and read with a binocular microscope under reflected light. The outer tips of the annuli were drawn on paper using a drawing mirror at a magnification of 24x. The maximum diameter of each annulus was measured. The length at the time of annulus formation $w(L_i)$ was calculated according to

$$L_i/L_t = a (O_i/O_t)^b$$

where L_t is the length at capture; O_i is the otolith diameter of the i th annulus, O_t is the diameter of the total otolith; a is the proportionality coefficient and b is the back-calculation coefficient. A value of $b = 1.364$ was estimated from a log-log regression of otolith size on fish size (Rijnsdorp, et al., 1990).

The rationale for sampling during the spawning period is that in this period the mature population has returned to its spawning ground (de Veen, 1962, 1964, 1978b). Thus, at this time period, a fairly homogeneous population could be obtained over a number of years. Tagging experiments of juvenile plaice has shown that the majority of adult fish in the Southern Bight area originates from the nursery grounds of the Wadden Sea from Texel to Heligoland (ICES, 1992).

2.2. Environmental variables

2.2.1. Eutrophication.

Dissolved inorganic phosphate and nitrate represent the basic nutrients for the primary production which have been affected by antropogenic activities. Nutrient levels in sea will be affected by the inflow of nutrient rich Atlantic water and by the run off of the major rivers. The effect of the enhanced nutrient load of the rivers will be restricted to coastal waters. In the southern North Sea off the Dutch coast the enhanced levels are restricted to a small band along the coast, but in the German Bight the enhanced nutrients levels are apparent in waters further offshore (Fig.1). The nutrient levels in the open North Sea will be mainly affected by the Atlantic inflow.

Time series information on eutrophication is shown in Fig.2. Since 1950 data were available on the load of ortho-phosphate (PO_4 in kg/s) in the river Rhine at Lobith (German - Netherlands border). Similar data on concentrations of ortho-phosphate and nitrate ($\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ in mg N/l) are available for Maassluis near the outlet of the Rhine in the North Sea (Heymen, 1992). The load of ortho-phosphate of the Rhine at Lobith increased considerably since 1950 until 1980-1981. Since then, it decreased to a level similar to that of the early 1960s (Fig.2a). The decrease in nutrients since 1980 is also apparent in the concentrations of phosphate and nitrate, although to a smaller extend. Concentrations of dissolved phosphate and nitrate in waters off the Dutch coast (<10 km) increased since the early 1960s, reached a peak in the late 1970s and early 1980s. In the late 1980s, nutrient concentrations tend to show a slight decrease, but not at all stations (van der Meyden, 1992; Fig.2b). Nutrient concentrations in winter at offshore stations tend to be rather stable between 1960 and 1990, although a slight decrease since 1979 is apparent north off Terschelling. Nitrate concentrations in the inner German Bight near Helgoland show have shown a marked increase since the late 1970s (Fig.2c). Phosphate concentrations show a different trend with an increase upto the late 1970s and a decrease during the 1980s.

Comparison of the various time series indicate a general increase in nutrient levels upto the 1970s - early 1980s. Nitrate levels remained at a high level or showed a slight decrease, whereas the phosphate levels appears to have decreased. Since the load of PO_4 at Lobith was the only time series encompassing the full time period of growth data, we have used this series in the ANOVA of growth. This approximation will be acceptable for the period up to 1980. However, the steady decrease in the PO_4 load of the Rhine at Lobith is much stronger than that of the concentrations observed in the coastal waters, and therefore may underestimate the nutrients available for primary production in coastal waters in recent years. This should be born in mind when interpreting the results of the statistical analysis.

2.2.2. Temperature.

The temperature data used were recorded at Den Helder. From daily readings of sea water temperature at a fixed time of the day, after correction for tidal cycle, the average monthly temperature was calculated (van der Hoeven, 1982). Average temperature between April and September were used in the analysis as these reflect the temperature conditions during the main growing period. The temperature record refers to coastal waters where the smaller size classes of plaice occur. No time series data on temperature are available for the distribution area of larger plaice in the offshore waters in the southern and central North Sea.

The plots of average temperature by quarter shows the years with exceptional temperature conditions are restricted to the winter, with relatively cold winters in 1963, 1979, 1985, 1986 and 1987 (Fig.3b). The winters after 1988 have been particularly mild. Average temperatures in other quarters are rather stable, although the annual differences observed during the main growing period ($\pm 1-2^{\circ}\text{C}$) are large enough to influence the growth rate of plaice (Fonds et al. , 1992).

2.2.3. Beam trawling.

Beam trawling is a very efficient method in catching sole, due to the large number of tickler chains that can be attached to the shoes and ground rope to activate the flatfish. Application of a large number of tickler chains in an otter trawl reduced the spread of the otter boards and reduced the efficiency of the net. After its introduction in the early 1960s, beam trawling quickly out competed the traditional method of otter trawling. For two decades, the expansion of beam trawling was restricted to The Netherlands and Belgium. Only in the 1980s beam trawling also expanded in the UK and Germany.

No consistent time series of international beam trawl effort is available that can be used as an index of the disturbance of the sea bed by tickler chains. The number of beam trawl fishing hours was registered in The Netherlands on a routine basis upto 1983. No statistics were collected between 1983 and 1988, but since 1989 the numbers of days at sea are available from EC-logbooks. The actual increase in fishing power will be larger than reflected in the number of beam trawl hours or days at sea, because the horse power of the beam trawl fleet showed a continuous increase since 1962. Therefore, we used the number of horse power days of the Dutch beam trawl fleet, estimated from a representative sample of vessels by LEI-DLO, to construct a time series of beam trawling by extrapolating backwards in time according to the time series of annual beam trawl fishing days which was available for the period 1962 - 1982 (Table 3).

A second time series of Dutch beam trawl effort was derived from the partial fishing mortality of the Dutch beam trawl fleet. The partial fishing mortality F_{ij} of age group i by fleet j is given by $F_{ij} = C_{ij}/C_i * F_i$ where C_{ij} is the catch number of age i by fleet j , C_i is the total number of age group i caught, and F_i is the VPA estimate of fishing mortality of age group i . The partial exploitation pattern of Dutch beam trawlers shows a peak in fishing mortality on the age groups 3 to 5. The age of maximum exploitation differs among years which will be partly due to differences in age of recruitment because of differences in growth.

The partial beam trawl fishing mortality will more accurately reflect of the sea bed disturbance of beam trawling than horsepower days because it is an age-specific measure and thus takes account for changes in the spatial distribution of the beam trawl fishery. A measure for the beam trawl effort in the distribution area of the size classes <30 cm is given by the peak in the partial F . This peak reflects the beam trawl mortality on the age groups which have just recruited to the fishery. The partial fishing mortality of the older age groups reflects the effect of beam trawling in the distribution area of these older and larger size classes. Because, the partial beam trawl fishing mortality is an age-specific measure of beam trawling, it is a priori a better measure of the effect of beam trawling on the availability of food for particular size- or age-classes of plaice.

The two time series of beam trawling effort show the same overall increase, but differ in some details (Fig.3c). The timeseries of horse-power days shows a steady increase of beam trawling in the first half of the 1970s, whereas the F_{peak} index levelled off. A second period of increase occurred in the early 1980s. In the last four years between 1988-1992 the HP-index remained high, whereas the F_{peak} -index

decreased. For this period, the F_{peak} -index, however, may not be accurate because the VPA-estimates have not yet converged.

The spatial distribution of beam trawling in the early 1970s does not differ substantially with that in the early 1990s (Fig.4). There is only a small increase in beam trawling in more northern offshore waters in the Central North Sea. Throughout the period the heaviest beam trawling occurred on the fishing grounds of the southern and south-eastern North Sea.

2.3. Plaice abundance.

Because of differences in spatial distribution of size- and age-groups of plaice, the intensity of intra-specific competition will be a function of the spatial distribution. In an earlier paper we estimated indices of competition between age-groups from their degree of spatial overlap (Rijnsdorp & van Beek, 1991). Indices of proportional crowding (P_{ab}) were estimated which were based on the overlap in spatial distribution during the main growing period between age-group a and b. The index mean crowding (Lloyd, 1967), reflecting the intra-specific competition on age-group a ($\bar{b}m_a$) can be estimated as $\bar{b}m_a = P_{ab} * S_b$, where S_b is the population number or biomass of age-group b. Assuming a constant age-specific distribution, we then can estimate time series of intra-specific competition from population numbers (VPA), observed weight-at-age data and the P_{ab} indices. P_{ab} indices applied were taken from (Rijnsdorp & van Beek, 1991). Population numbers of plaice at age were taken from a modified assessment (Rijnsdorp, in prep).

The index of mean crowding thus reflects the interaction which a particular age group has with its conspecifics, taking account for the overlap in spatial distribution and the number of weight of the conspecifics. In this report we have calculated the index of mean crowding in terms of numbers.

Time series of plaice abundance indicate two distinct periods of an increased index of mean crowding, which are both related to the recruitment of strong year classes (Fig.1). The first increase occurred after the recruitment of the exceptionally strong 1963 year class which was about 2-3 times the average strength. This year class increased the index of mean crowding on 1-, 2- and 3-group plaice in the period 1964-1966. After 1966 the index quickly dropped to a level similar to that in the 1950s. For the 4- and 5-year and older plaice, the index of mean crowding peaked later, respectively in 1967 and 1968. A second period of high indices of mean crowding occurred in the 1980s. In this period however the peak was broader due to the contribution of several strong year classes which were born in 1979, 1981 and 1985. Since 1988 the index rapidly decreased to a level of the mid 1970s.

Spatial distributions of plaice by size class derived from beam trawl surveys carried out in summer between 1983-1992 clearly show the gradual spread from the shallow coastal nursery grounds over the offshore grounds of the southern and central North Sea (Fig.5).

2.4. Statistical analysis

Estimated annual growth rates were correlated with environmental variables and indices of intra-specific competition using the NAG statistical package GLIM (Baker & Nelder, 1978). GLM models were analysed of the form

$$Y = \%GM + aX1 + bX2 + cX3 + dX4 + e$$

where Y is the dependent variable growth rate, X1, X2, X3 and X4 are the independent covariables temperature, PO4, index of mean crowding and index of beam trawling, and e is a normally distributed error term. The term %GM is the average growth rate at X1=X2=X3=X4=0. Because the number of observations of growth rate per size class and year were different, the analysis was carried out by weighting over the number of observations.

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

3. Results

3.1. Changes in growth by size class

The average annual length increment and the approximate 95% confidence limits were calculated for 5-cm size classes and expressed relative to the average growth rate in the period 1950-1990 (Fig.6). In order to reduce the variance, due to data points based on relatively small number of observations, 3-pt running averages are shown. Fig.6 clearly illustrates the increase in growth rate between 1960 and 1980. This increase is mainly restricted to the size classes <30 cm. In larger plaice no clear pattern is apparent, although a slight increase might be inferred. Superimposed on the general increase in growth, a temporary decrease occurred in the mid-1960s. The year in which the lowest growth rate occurred shifted from 1966 in the <10 cm and 10-15 cm size classes to 1968 and 1969 in the size classes 15-20 cm and 20-25 cm respectively. Even in the growth of 25-30 cm and 30-35 cm plaice a dip in growth is apparent around 1970. This shift followed the growth of the slowly growing strong 1963 year class through the successive size classes in successive years. In the second half of the 1980s a decrease in growth of plaice < 30 cm occurred. The decrease in growth rate was strongest in the smallest size classes.

The observed patterns of change in growth corroborates the patterns published earlier, but gives more detail in the timing of the change. Closer inspection of Fig.6 suggests that growth rate in the smallest size classes (<10 cm, 10-15 cm) gradually increased and reached a peak around 1978. The increase in growth of size classes 15-20 cm and 20-25 cm, however, was abrupt and already reached a peak in 1970, just after the dip in growth due to the 1963 year class passed away. The increase in growth of these size classes might indicate a switch from a low to a higher level in 1970. The decrease in growth in the 1980s started in the smallest size classes and was followed in later years in larger size classes.

3.2. Statistical analysis

For each size class, the annual estimates of growth rate were correlated with environmental variables and the index of intra-specific competition. We started with the full model $Y = \text{Temp} + \text{PO4} + F_{\text{peak}} + \text{PX}$, and eliminated backwards the various covariables. The residual sums of squares of the various models are given in Table 5. The explained sums of squares (SS_{exp}) of the covariables and the corresponding F-statistic, which tested the significance of the contribution to the full model, showed that in none of the size classes temperature was significant (Table 6). Indices of eutrophication, beam trawling and intra-specific competition were

generally significant in the four smallest size classes (up to 20-25 cm). In contrast, none of the environmental covariables nor index of intra-specific competition were significant in size classes 25-30 cm and 30-35 cm.

The multicollinearity term in Table 6 shows that a substantial part of the variance in growth could not be ascribed to a single covariable. This multicollinearity particularly affected the analysis of the effect of PO4 and Fpeak (Table 5), which are themselves significantly correlated (Fig.2 and 3).

The significant intra-specific competition suggests that growth is reduced at high level of population density. The shape of the relationship between growth rate and intra-specific competition was explored by plotting the residual growth rate RG against the index of intra-specific competition (Fig.7). The residual growth was calculated as the difference between observed (G_{obs}) and predicted growth rate (G_{pred}): $RG = G_{obs} - G_{pred}$. For none of the size-classes do the scatter plots provide evidence for another than the simplest relationship of a straight linear regression.

A plot of RG against year indicates the reduction in growth rate in the mid 1960s when the strong 1963 year class dominated the plaice population (Fig.8) However, no clear decrease in growth is apparent in the late 1980s when population density and the index of intra-specific competition increased following the recruitment of the strong 1981 and 1985 year class. This may be due to the correlation between the various covariables that may have ascribed part of the decrease in growth in this period to the reduction in PO4 and reduction in Fpeak.

ANOVA of the growth rate of plaice size groups against the index of intra-specific competition, index of beam trawling and other measures of eutrophication than PO4 at Lobith was explored. The results are presented in Table 7. The mean square error explained by the eutrophication index is the part of the variance explained with Fpeak and PX still included in the model. The variances given thus reflect the contribution of the eutrophication index above the part which was already explained by Fpeak and PX. In all cases the eutrophication index did explain a part of the variance in growth, but in only a few cases the contribution was significant. Given the rather low number of observations and the multicollinearity in eutrophication indices and Fpeak, the lack of statistical power could be expected.

4. Discussion

The ANOVA of growth as a function of environmental variables and an index of intra-specific competition provided strong evidence for density dependence of growth, corroborating our earlier analysis (Rijnsdorp & van Leeuwen, 1992). On theoretical grounds, one would expect that growth rate is depressed if intra-specific competition increases above a threshold level. However, the plots of the residual growth, after correcting for PO4 and Fpeak, against indices of intra-specific competition did not provide evidence for such a relationship.

The parameter estimates of the density-dependent effect suggested a negative relationship between density-dependence of growth and fish size. Density dependent was not statistically significant for the size classes >25 cm, although the time series plots still suggested a small decrease in growth around 1970 coinciding with the strong 1963 year class.

The evidence for density-dependent growth in the late 1980s, following the recruitment of the strong 1981 and 1985 year classes, is not convincing (Fig.8). However, the growth rate plotted in this figure is corrected for the PO₄ load of the Rhine at Lobith and index of beam trawling. Since the PO₄ load at Lobith showed a much stronger decline than that at Maasluis or in the coastal waters, this may have led to an underestimate of the expected growth rate, and hence in an overestimate of the residual growth. This tentative interpretation is supported by the slight increase in growth rate of the smallest size classes in 1989 and 1990, concurrently with a rapid decline in the index of intra-specific competition (Fig.6). Also the mean length at age of plaice observed in the summer and autumn pre-recruit surveys suggested that the growth rate bounced back from the substantial reduction in the late 1980s.

The strength of the density-dependence in growth appeared to be positively correlated with the absolute level of intra-specific competition, although the index of intra-specific competition did not differ between the three youngest age groups. However, the indices of intra-specific competition were derived from distribution data with a spatial resolution of ICES rectangles of 30x30 miles. This spatial resolution is less appropriate for the smaller size classes which show a strong depth-related distribution and occur in high densities in a relatively small depth band. The ICES-rectangle based indices, therefore may underestimate the absolute level of intraspecific competition, and improving the positive relationship between density-dependence and index of intra-specific competition.

Our interest in the beam trawl is in its potential effect on the availability of food for flatfish through the disturbance of the benthos by the tickler chains. As argued in 2.2.3, the introduction of the beam trawl followed a period in which the number of tickler chains used in the otter trawl fishery in The Netherlands was increased. Hence, the potential effect of the disturbance of the benthos by tickler chains may have started earlier than 1962. This effect however, is considered not to have affected our statistical analysis, since this may have raised the F_{peak} -index from a value of zero to a value of less than 0.015 (Table 3).

Statistical analysis of growth showed that both PO₄ and F_{peak} explained a significant part of the variance in growth. The effects of these environmental variables were less easy to interpret, because they were mutually correlated. When tested separately, each explained a significant part of the variance in growth, but when tested together a substantial part of the variance in growth could not be ascribed to the individual covariables (Table 5). Statistical analysis, thus cannot help us further in disentangling the possible causal effects of eutrophication and beam trawling.

However, including the spatial and temporal patterns may be of help. From the spatial patterns in eutrophication, beam trawl activity and plaice distribution, we may infer that beam trawling is less likely to be involved in the changes in growth of the size classes <10 cm and 10-15 cm which are predominantly distributed in shallow inshore waters where no heavy beam trawling takes place. This shallow area is only fished by shrimpers which employ much lighter beam trawls with a bobbin rope and without tickler chains. In these areas, however, eutrophication has led to an enhanced primary production and to an increase in the production of macro zoobenthos (Beukema & Cadée, 1988; Beukema, 1989; Rachor, 1990). Hence, the changes in growth of the two smallest size classes may be related to eutrophication but is unlikely to be affected by beam trawling.

For the intermediate size classes, both eutrophication and beam trawling may be involved. The effect of eutrophication is likely to decrease with increasing distance from the coast, whereas that of beam trawling will be maximum at some distance from the coast. Fig.9 shows a tentative graph of the level of eutrophication and beam

trawling in relation to the distance from the coast¹. Hence the increase in growth of plaice of 15-25 cm may be due to an increase in food availability as a result of both eutrophication and beam trawling. The relative contribution of both factors will shift from predominantly eutrophication in the smaller size classes to predominantly beam trawling for the larger size classes. For the size classes >30 cm no increase in growth rate is apparent. This observation is consistent with the above interpretation for the other size classes, because both the level of eutrophication and beam trawling is relatively small in the area of distribution of the larger size classes.

The above interpretation is further supported by the difference in timing of the increase in growth between the smallest and intermediate size classes, and by the timing of the increase in eutrophication and beam trawling. For both the smallest two size classes (<10, 10-15 cm) somatic growth gradually increased to a peak in the late 1970s. In the intermediate size classes (15-30 cm) the increase in growth occurred suddenly in 1970 when the strong 1963 year class had grown into the larger size classes. The difference in timing and shape of the relationship, corresponded to the gradual increase in eutrophication between 1950 and 1980 and the relatively steep increase in beam trawling between 1964 - 1969 and between 1975-1980.

This study revealed that both eutrophication and beam trawling (disturbance of the sea bed) significantly correlated to the annual variations in the growth of plaice. The statistical analysis, however, was unable to distinguish between eutrophication and beam trawling. Combining the statistical analysis with a detailed study of the spatial and temporal patterns in the changes in growth and environmental variables however, yielded a consistent pattern. The break down of the temporal resolution to one year suggested, and the break down of the spatial resolution to areas with increasing distance from the coast, provided strong indirect evidence that eutrophication may be involved in the inshore areas with a decreasing effect when moving going offshore, whereas beam trawling may be involved in the areas at a distance between 12-50 miles from the coast. In the areas further offshore both beam trawl activity and eutrophication effects are small and no changes in growth have been observed.

The evidence presented in this study does not provide any proof that both eutrophication and beam trawling are causally involved. Other factors may be involved as well. For instance, the substantial decrease in growth rate of plaice in the 1980s coincided with similar decreases in growth rate of other fish in other areas (herring, ICES, 1993), which may be related to large scaled changes in the hydrography in the North-east Atlantic. Concurrent shifts in the benthic community have been described for various areas in the Northeast Atlantic (Austen et al., 1991; Josefson et al. 1993). Whether the decrease in growth of plaice in the 1980s is due to the decrease in PO₄ as claimed by Boddeke & Hagel (1991) is still open to debate. Time series data on primary production, chlorophyll-a concentrations, Phaeocystis concentrations and macrofaunal biomass remained at a high level between 1980 and 1990 (Cadeé & Hegeman, 1993; Janssen, 1993; I. de Vries, pers. comm.). Further, part of the decrease in growth is likely to be related to the peak in intra-specific competition in the mid 1980s due to the recruitment of the strong 1981 and 1985 year classes. In 1990, the growth of size classes 10-15 and 15-20 cm again increased coinciding with the strong decrease in intra-specific competition. Also the mean length of the pre-recruit plaice as observed in the autumn surveys tentatively suggests that growth rate again increased in the early 1990s.

¹ The relationship of beam trawl activity and distance from the coast will be affected by fisheries management regulation. In the past, the larger trawlers (>300 HP) were excluded from the 12-miles zone. In 1989, this regulation was extended to the coastal area between Texel and the Skagerrak upto about 30 miles from the coast (plaice box).

The results of the present study illustrates that a back-calculation study of changes in somatic growth may provide detailed information on the temporal and spatial pattern in the changes in growth. This approach may prove even more fruitful if it is extended to other species. North Sea sole and dab seems to be the obvious candidates to test the hypothesis based on the observed changes in plaice. Further a study on the temporal changes in growth of plaice in other parts of the North Sea (Flamborough, off the Scottish coast) which are differently affected by beam trawling and eutrophication may also be worth pursuing.

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6. Tables

Table 1. Summary of otolith samples analysed. Two types of samples were taken. The Year class samples were taken of selected year class(es) during a number of successive years. Length stratified samples were taken in a particular year and comprised of upto 4 randomly selected otoliths per cm-group between 27-50+ cm. The number (#x-) preceding the year/year class notation refers to the set number. Otolith sets upto #10 have been included in the analysis of Rijnsdorp & van Leeuwen (1992). Otolith sets \geq #11 were particularly prepared and analysed to increase the temporal resolution to one year.

	Age groups sampled:											
Year/ Year class	III	IV	V	VI	VII	VIII	IX	X	XI- XIV	XV- IXX	XX+	Total
Year class samples												
#4-1955-61	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
#7-1972-74	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
#8-1982-85	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

Table 2. The number of observations in each year - size class cell. Waves of large sample sizes can be observed which are due to strong year classes passing through successive size classes during subsequent years. This is particularly pronounced for year class 1963, which was also sampled deliberately (see Table 1).

year	size class (cm)									
	<10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	>50
1950	20	15	13	18	11	17	10	6	16	26
1951	21	16	17	21	16	12	19	8	11	13
1952	7	11	19	25	24	17	17	17	10	16
1953	27	8	8	20	28	32	19	22	12	19
1954	20	13	22	14	23	32	33	26	17	22
1955	33	16	17	22	17	23	39	31	16	21
1956	13	18	29	18	22	27	35	41	26	23
1957	15	7	12	32	27	26	43	43	33	30
1958	27	7	11	12	38	33	36	56	42	36
1959	75	25	21	10	17	28	23	30	29	35
1960	78	45	55	37	14	16	17	14	22	15
1961	45	39	72	60	50	22	23	17	23	20
1962	26	19	57	68	70	60	31	28	21	24
1963	22	13	26	42	85	76	67	38	25	29
1964	187	25	16	23	43	96	86	53	32	32
1965	10	110	89	17	25	51	121	75	41	38
1966	5	9	80	91	37	42	83	103	49	47
1967	13	2	11	68	89	48	57	58	34	19
1968	1	6	8	9	57	76	56	45	32	23
1969	13	1	3	10	16	64	52	36	28	23
1970	124	41	9	1	11	32	82	52	26	30
1971	8	48	87	27	11	11	40	29	21	21
1972	16	0	26	53	67	29	34	46	23	25
1973	34	19	7	7	36	93	50	32	27	27
1974	88	42	30	13	12	27	82	24	17	5
1975	18	29	76	50	21	16	50	41	21	7
1976	7	7	14	56	66	54	39	61	24	14
1977	19	8	6	6	41	85	66	47	26	19
1978	11	13	12	12	9	34	63	39	26	13
1979	22	7	7	15	17	14	36	34	8	3
1980	24	8	14	12	13	26	27	44	21	3
1981	14	11	19	9	19	19	35	40	17	5
1982	13	9	8	15	22	19	27	40	23	6
1983	18	12	8	12	14	30	27	25	14	5
1984	24	18	14	15	15	16	31	19	7	5
1985	20	22	25	20	14	21	21	15	5	5
1986	57	47	21	22	31	23	27	28	7	6
1987	12	21	60	41	26	41	28	41	14	7
1988	5	10	22	39	60	33	51	45	25	12
1989	0	1	6	20	40	57	70	49	45	14
1990	0	0	1	1	20	24	35	35	24	18

Table 3. Time series of environmental variables and indices of intra-specific competition. IIP is the Dutch beam trawl effort in horse power days; I_{peak} is the peak in the partial fishing mortality rate of the Dutch beam trawl fleet; PO4 is the load of ortho-phosphate at Lobith (kg/s); TQ2 and TQ3 are the mean temperatures in the 2nd and 3rd quarter, respectively; P1, P2, P3, P4 and P5+ are the indices of mean crowding in numbers of age groups 1, 2, 3, 4 and 5 and older.

year	IIP	I_{peak}	PO4	TQ2	TQ3	P1	P2	P3	P4	P5+
1950	0.0	0.00	0.044	11.8	17.3	42.0	44.6	45.8	19.5	14.3
1951	0.0	0.00	0.050	11.0	16.9	41.3	44.0	43.5	20.0	15.3
1952	0.0	0.00	0.066	11.8	16.8	37.6	41.5	42.2	19.2	15.4
1953	0.0	0.00	0.063	11.6	17.0	38.0	40.2	41.4	19.4	15.4
1954	0.0	0.00	0.090	11.1	15.9	39.1	41.4	40.1	18.8	15.2
1955	0.0	0.00	0.086	9.9	17.6	45.6	47.3	45.6	19.7	15.6
1956	0.0	0.00	0.145	10.5	15.8	38.0	43.6	43.6	19.8	15.8
1957	0.0	0.00	0.150	12.1	16.9	37.8	40.2	44.0	20.6	16.4
1958	0.0	0.00	0.138	10.5	17.3	44.5	45.1	42.4	20.9	17.1
1959	0.0	0.00	0.120	12.6	18.3	51.5	54.3	50.5	21.5	17.4
1960	0.0	0.00	0.225	12.2	16.8	53.6	57.5	56.7	23.7	17.9
1961	0.0	0.00	0.290	12.3	16.7	50.8	55.1	56.1	24.5	18.5
1962	10.7	0.02	0.220	10.0	15.3	46.4	50.7	52.8	24.8	19.2
1963	20.4	0.04	0.255	10.5	16.5	43.3	47.0	48.9	24.1	19.7
1964	32.9	0.03	0.280	11.6	16.8	81.7	75.7	68.6	29.0	21.6
1965	53.4	0.06	0.495	11.3	15.9	68.3	80.2	69.6	27.8	21.6
1966	68.8	0.06	0.463	11.8	16.5	58.6	66.3	80.1	31.0	21.9
1967	63.0	0.08	0.425	11.6	17.5	42.6	46.8	51.5	31.3	23.6
1968	161.8	0.09	0.468	11.6	17.0	36.7	40.9	43.4	25.1	24.3
1969	266.0	0.13	0.480	10.7	17.9	38.8	41.1	42.1	23.2	21.7
1970	285.0	0.22	0.518	11.4	16.5	42.8	45.0	43.0	21.5	19.4
1971	325.0	0.14	0.428	11.6	17.1	40.4	44.6	43.8	19.5	16.3
1972	349.0	0.16	0.500	10.9	16.5	35.4	39.0	41.1	19.0	15.1
1973	432.0	0.23	0.590	11.5	18.0	48.3	46.7	43.9	19.6	15.0
1974	522.0	0.24	0.640	11.8	16.7	53.6	56.5	48.6	18.9	14.2
1975	556.0	0.25	0.730	10.9	17.8	51.3	56.5	57.0	20.4	13.9
1976	498.0	0.19	0.590	12.0	18.0	45.4	48.9	51.3	22.2	14.8
1977	462.0	0.26	0.790	10.7	16.4	49.6	50.4	48.6	21.4	15.9
1978	404.0	0.16	0.910	10.9	15.8	51.4	54.3	49.5	20.6	15.5
1979	443.0	0.27	0.890	10.6	16.8	53.8	56.7	54.7	21.0	15.1
1980	448.0	0.37	0.980	11.7	16.9	66.5	66.4	61.1	22.7	14.9
1981	472.0	0.37	1.030	11.7	17.1	61.4	67.1	60.9	21.8	14.6
1982	541.0	0.45	0.910	12.3	18.0	90.8	86.8	80.8	27.4	16.5
1983	656.0	0.40	0.870	11.1	17.9	85.3	93.4	80.2	27.4	17.2
1984	708.0	0.34	0.870	10.8	16.7	82.4	88.2	91.1	30.6	18.3
1985	703.0	0.38	0.700	11.1	16.9	70.8	75.9	74.3	29.9	19.1
1986	681.0	0.38	0.640	10.8	16.7	109.0	103.2	93.5	33.6	21.1
1987	684.0	0.48	0.510	11.1	17.3	94.4	107.0	92.6	32.3	21.2
1988	762.0	0.38	0.460	11.9	16.4	84.3	92.4	103.0	35.6	21.5
1989	725.0	0.28	0.240	12.6	17.9	60.7	67.6	71.0	33.8	22.5
1990	710.0	0.32	0.200	13.0	17.2	52.1	56.2	59.2	27.3	21.3

Table 4. Exploitation pattern of plaice by the Netherlands beam trawl fishery. The exploitation pattern gives the partial fishing mortality rates by age group for the years between 1962 and 1991.

	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971
Age										
1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
2	0.001	0.002	0.011	0.003	0.004	0.006	0.022	0.042	0.040	0.062
3	0.010	0.010	0.023	0.033	0.021	0.044	0.089	0.131	0.182	0.112
4	0.016	0.038	0.029	0.041	0.060	0.036	0.075	0.090	0.218	0.130
5	0.016	0.022	0.034	0.038	0.039	0.078	0.062	0.076	0.135	0.145
6	0.006	0.015	0.023	0.039	0.039	0.035	0.056	0.075	0.146	0.114
7	0.009	0.005	0.014	0.029	0.039	0.032	0.026	0.050	0.155	0.143
8	0.005	0.012	0.008	0.018	0.025	0.021	0.063	0.023	0.075	0.078
9	0.004	0.011	0.012	0.015	0.030	0.024	0.010	0.097	0.036	0.138
10	0.003	0.010	0.006	0.055	0.017	0.015	0.040	0.005	0.118	0.106
11	0.003	0.009	0.007	0.016	0.026	0.021	0.010	0.054	0.023	0.121
12	0.002	0.008	0.005	0.029	0.026	0.033	0.038	0.015	0.079	0.056
13	0.002	0.005	0.006	0.024	0.027	0.019	0.024	0.040	0.026	0.071
14	0.001	0.005	0.003	0.020	0.025	0.027	0.031	0.014	0.048	0.053
15	0.001	0.001	0.002	0.009	0.010	0.015	0.020	0.027	0.028	0.064
Fpeak	0.016	0.038	0.034	0.055	0.060	0.078	0.089	0.131	0.218	0.145

Year	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981
Age										
1	0.008	0.002	0.004	0.002	0.003	0.005	0.003	0.003	0.002	0.000
2	0.117	0.123	0.031	0.043	0.081	0.136	0.128	0.132	0.146	0.144
3	0.153	0.223	0.240	0.057	0.146	0.114	0.159	0.267	0.372	0.365
4	0.118	0.233	0.216	0.209	0.150	0.145	0.121	0.191	0.273	0.245
5	0.131	0.127	0.224	0.230	0.143	0.255	0.119	0.236	0.166	0.287
6	0.155	0.130	0.137	0.244	0.148	0.164	0.149	0.218	0.213	0.210
7	0.155	0.150	0.151	0.154	0.148	0.153	0.153	0.224	0.181	0.214
8	0.160	0.126	0.214	0.187	0.094	0.116	0.123	0.198	0.134	0.217
9	0.087	0.156	0.183	0.239	0.127	0.075	0.121	0.199	0.110	0.151
10	0.134	0.102	0.234	0.190	0.171	0.096	0.074	0.176	0.137	0.145
11	0.085	0.127	0.160	0.193	0.134	0.148	0.095	0.127	0.090	0.168
12	0.100	0.070	0.201	0.245	0.084	0.131	0.119	0.158	0.057	0.126
13	0.046	0.085	0.143	0.176	0.191	0.013	0.097	0.272	0.069	0.123
14	0.068	0.085	0.185	0.219	0.055	0.132	0.013	0.167	0.106	0.115
15	0.046	0.058	0.062	0.050	0.013	0.002	0.051	0.002	0.020	0.013
Fpeak	0.160	0.233	0.240	0.245	0.191	0.255	0.159	0.272	0.372	0.365

Table 4 continued. Partial fishing mortality of Dutch beam trawl fleet

Year	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
Age										
1	0.003	0.002	0.000	0.000	0.001	0.000	0.000	0.003	0.000	0.001
2	0.117	0.118	0.112	0.136	0.143	0.062	0.024	0.093	0.008	0.090
3	0.448	0.350	0.331	0.327	0.378	0.269	0.203	0.213	0.186	0.208
4	0.331	0.400	0.239	0.379	0.316	0.485	0.223	0.279	0.240	0.281
5	0.283	0.278	0.341	0.231	0.371	0.450	0.379	0.248	0.316	0.299
6	0.264	0.255	0.240	0.276	0.305	0.282	0.353	0.278	0.255	0.307
7	0.281	0.234	0.211	0.232	0.288	0.303	0.285	0.253	0.194	0.288
8	0.245	0.234	0.258	0.208	0.237	0.193	0.297	0.163	0.149	0.175
9	0.173	0.206	0.235	0.210	0.241	0.148	0.258	0.144	0.117	0.157
10	0.189	0.237	0.204	0.191	0.277	0.220	0.223	0.143	0.111	0.108
11	0.155	0.194	0.168	0.157	0.262	0.183	0.162	0.106	0.087	0.097
12	0.157	0.307	0.149	0.200	0.233	0.178	0.197	0.097	0.088	0.064
13	0.164	0.184	0.112	0.147	0.289	0.120	0.191	0.139	0.090	0.050
14	0.099	0.164	0.130	0.170	0.149	0.129	0.160	0.090	0.097	0.103
15	0.040	0.032	0.023	0.018	0.034	0.076	0.083	0.040	0.035	0.040
F _{peak}	0.448	0.400	0.341	0.379	0.378	0.485	0.379	0.279	0.316	0.307

Table 5. Results of the analysis of variance of growth rate as a function of environmental variables mean temperature in 2nd and 3rd quarter (Temp), index of eutrophication (PO4), index of beam trawling (F_{peak}), and index of intra-specific competition (PX). The table gives the residual sum of squares (SS) and degrees of freedom (df) of various models. The full model is $Y = \text{Temp} + \text{PO4} + \text{F}_{\text{peak}} + \text{PX}$. For the index of mean crowding (PX) was used: P1 for size class <10 cm; P2 for size class 10-15cm and 15-20 cm; P3 for size class 20-25 cm and 25-30 cm; and P4 for size class 30-35 cm, where P1 is the mean crowding on age group 1, P2 on age group 2 ect.

Size class	< 10 cm		10-15 cm		15-20 cm	
	SS	df	SS	df	SS	df
Total SS	1537	38	1281	38	1147	40
Full model	485.6	34	452.2	34	527.3	36
Full - Temp	511.3	35	463.7	35	529.7	37
Full - PO4	613.6	35	479.5	35	582.8	37
Full - F _{peak}	499.6	35	648.2	35	687.6	37
Full - PX	750.9	35	847.1	35	785.3	37
PO4 + F _{peak}	768.3	36	919.6	36	785.8	38
PO4 + PX	524.6	36	702.1	36	688.5	38
F _{peak} + PX	633.2	36	486.0	36	586.2	38
PO4	769.7	37	986.6	37	806	39
F _{peak}	948.1	37	935.9	37	871.8	39
PX	1491	37	1232	37	1142	39

Size class	20-25 cm		25-30 cm		30-35 cm	
	SS	df	SS	df	SS	df
Total SS	967.9	40	704.6	40	393.3	40
Full model	376.3	36	375.7	36	334.4	36
Full - Temp	380.5	37	383.2	37	335.4	37
Full - PO4	497.9	37	410.0	37	349.4	37
Full - F _{peak}	441.9	37	410.8	37	334.4	37
Full - PX	501.5	37	376.5	37	349.6	37
PO4 + F _{peak}	503.5	38	383.5	38	353.6	38
PO4 + PX	442.7	38	412.1	38	335.4	38
F _{peak} + PX	502.3	38	422.7	38	350.7	38
PO4	508.0	39	426.1	39	353.9	39
F _{peak}	666.4	39	428.9	39	360.7	39
PX	966.7	39	642.2	39	374.2	39

Table 6. Summary of the mean square error (MS= SSexp/df) of the various covariables when tested against the full model, and the corresponding F-statistic and P-value.

	MS	df	F	P	MS	df	F	P
size class	<10 cm				10 - 15 cm			
Temp	25.63	1	1.795	NS	11.51	1	0.86	NS
PO4	128.0	1	8.96	<0.01	27.51	1	2.07	NS
Fpeak	13.99	1	0.98	NS	195.9	1	14.73	<0.01
PX	265.3	1	18.57	<0.01	394.8	1	29.68	<0.01
multicollinearity	618.5				199.1			
MS error	14.28	34			13.30	34		
SS total	1537	38			1281	38		
size class	15 - 20 cm				20 - 25 cm			
Temp	2.476	1	0.17	NS	4.168	1	0.40	NS
PO4	55.54	1	3.79	NS	121.6	1	11.64	<0.01
Fpeak	160.4	1	10.95	<0.01	65.57	1	6.27	<0.05
PX	258.0	1	17.61	<0.01	125.2	1	11.98	<0.01
multicollinearity	143.3				275.1			
MS error	14.65	36			10.45	36		
SS total	1147	40			967.9	40		
size class	25 - 30 cm				30 - 35 cm			
Temp	7.476	1	0.72	NS	1.053	1	0.11	NS
PO4	34.30	1	3.29	NS	15.05	1	1.62	NS
Fpeak	35.04	1	3.36	NS	0.035	1	0.004	NS
PX	0.827	1	0.07	NS	15.23	1	1.64	NS
multicollinearity	251.3				361.9			
MS error	10.44	36			9.288	36		
SS total	704.6	40			393.3	40		

Table 7. ANOVA results the contribution to the variance in growth rate explained by various indices eutrophication after correcting for beam trawling (F_{peak}), and intra-specific competition (PX). Model: $Y = F_{\text{peak}} + \text{PX} + \text{NUTRIENTS}$

	MS	df	F	P
SIZE CLASS <10 CM				
PO4-Lobith	119.1	1,35	8.22	<0.01
DIN-Noordwijk	41.77	1,12	3.85	NS
DIP-Noordwijk	52.41	1,13	3.99	NS
DIN-Terschelling	4.82	1,11	0.33	NS
DIP-Terschelling	21.38	1,12	1.30	NS
DIN Helgoland	38.86	1,20	2.26	NS
DIP Helgoland	34.38	1,20	1.85	NS
SIZE CLASS 10-15 CM				
PO4-Lobith	25.96	1,35	1.97	NS
DIN-Noordwijk	14.71	1,13	1.46	NS
DIP-Noordwijk	7.438	1,14	0.62	NS
DIN-Terschelling	3.305	1,12	0.35	NS
DIP-Terschelling	16.93	1,13	1.69	NS
DIN Helgoland	69.33	1,20	5.75	<0.05
DIP Helgoland	45.96	1,20	4.28	± 0.05
SIZE CLASS 15-20 CM				
PO4-Lobith	63.35	1,35	4.41	<0.01
DIN-Noordwijk	2.528	1,14	0.48	NS
DIP-Noordwijk	14.84	1,15	3.02	NS
DIN-Terschelling	3.575	1,12	0.68	NS
DIP-Terschelling	17.56	1,13	3.83	NS
DIN Helgoland	9.884	1,21	0.87	NS
DIP Helgoland	28.91	1,20	1.40	NS
SIZE CLASS 20-25 CM				
PO4-Lobith	128.6	1,35	12.55	<0.01
DIN-Noordwijk	2.198	1,14	0.24	NS
DIP-Noordwijk	2.205	1,15	0.26	NS
DIN-Terschelling	3.259	1,12	0.31	NS
DIP-Terschelling	6.439	1,13	0.67	NS
DIN Helgoland	15.73	1,21	1.14	NS
DIP Helgoland	32.87	1,20	2.13	NS

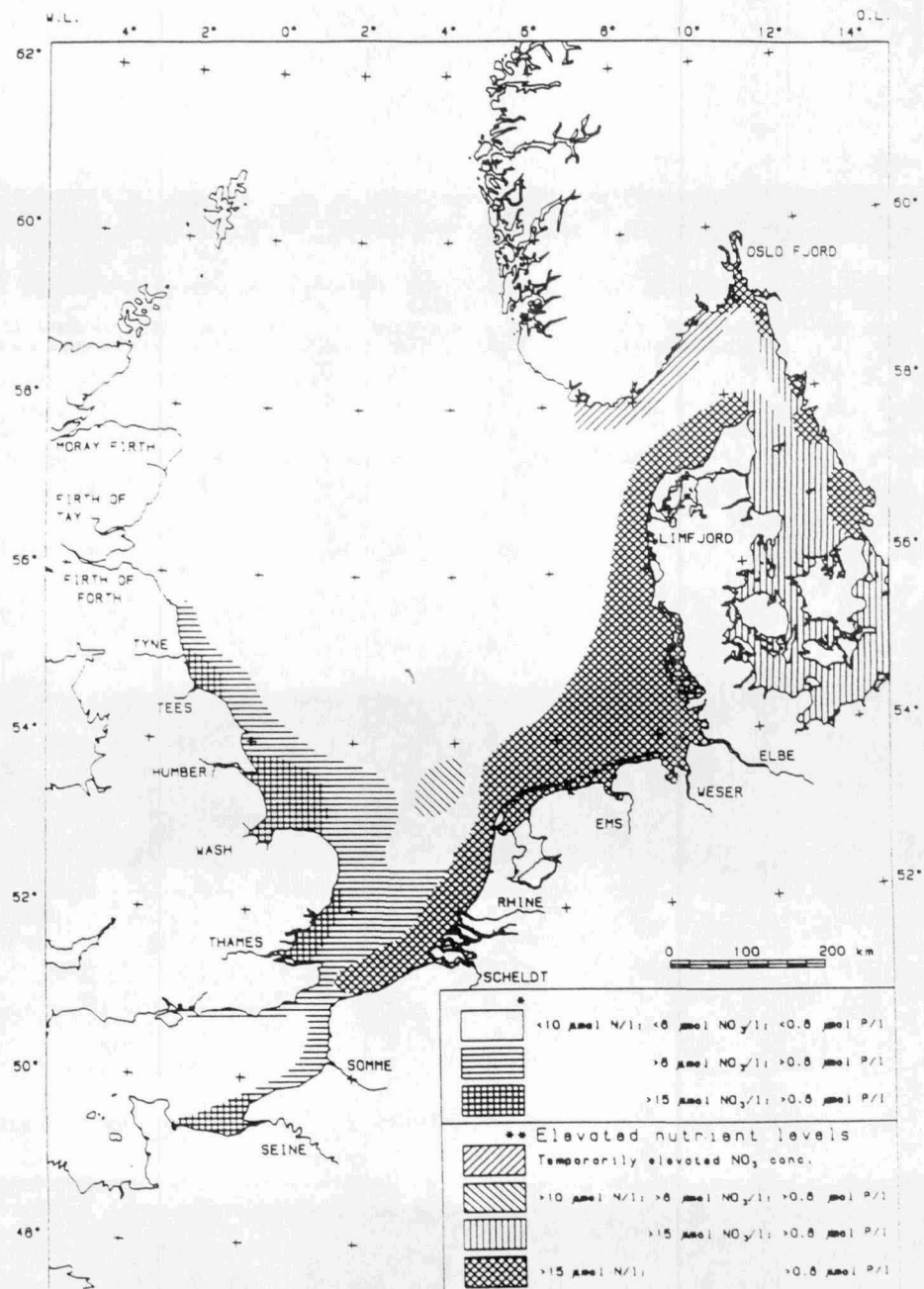


Figure 1. Distribution of eutrophicated waters in the southern North Sea (from Zevenboom, 1993)

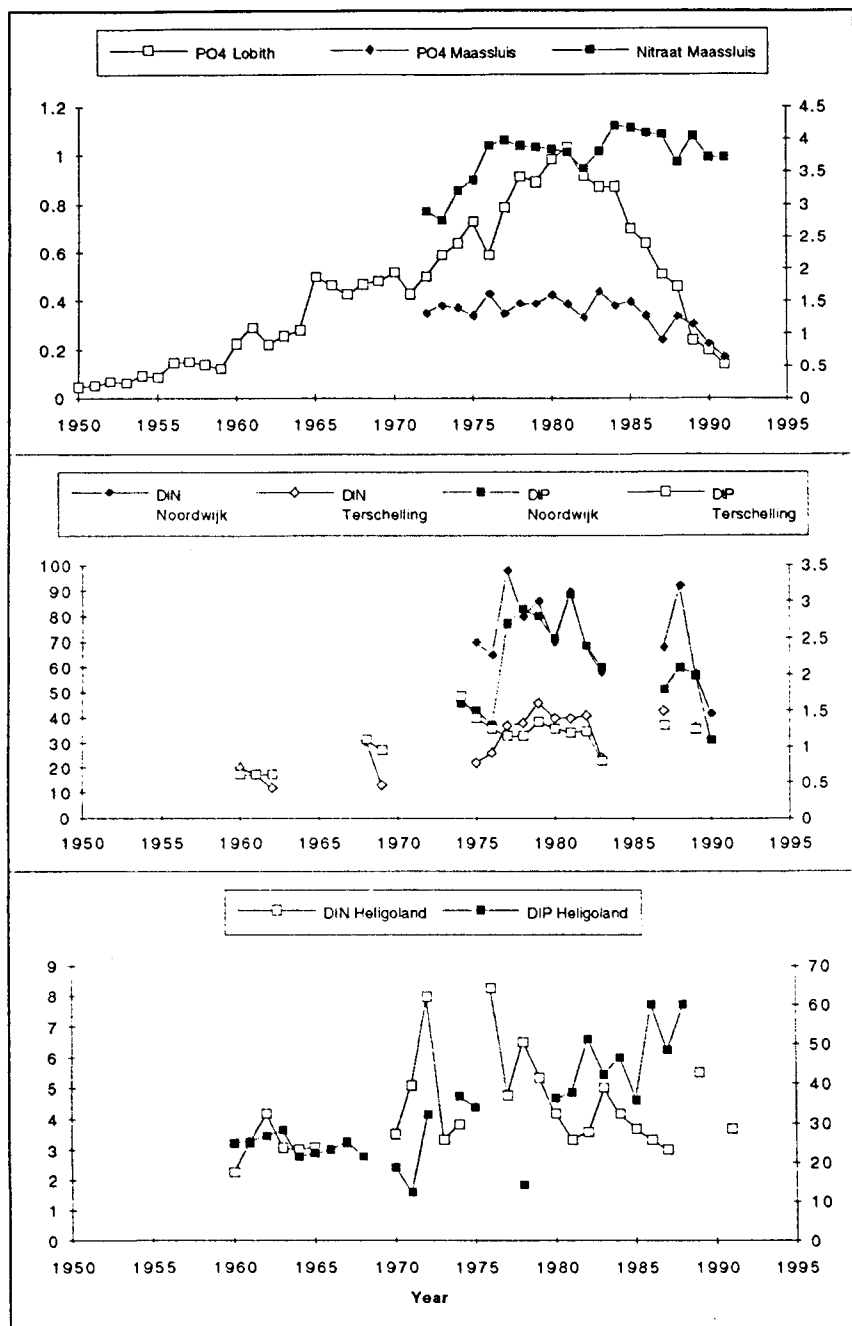


Figure 2. Time series of eutrophication. A - phosphate and nitrate loads of the river Rhine at Lobith (PO4 in kg/s), Maassluis (PO4 and NO3-N + NO2-N in mg P/l and N/l respectively); B - DIN and DIP concentrations in winter at ≤ 10 km off Noordwijk and off Terschelling ($\mu\text{mol/l}$); C - DIN and DIP concentrations in winter near Helgoland ($\mu\text{mol/l}$). Data sources: A from Heymen (1992); B from Meyden (1992); C from Anon (1993).

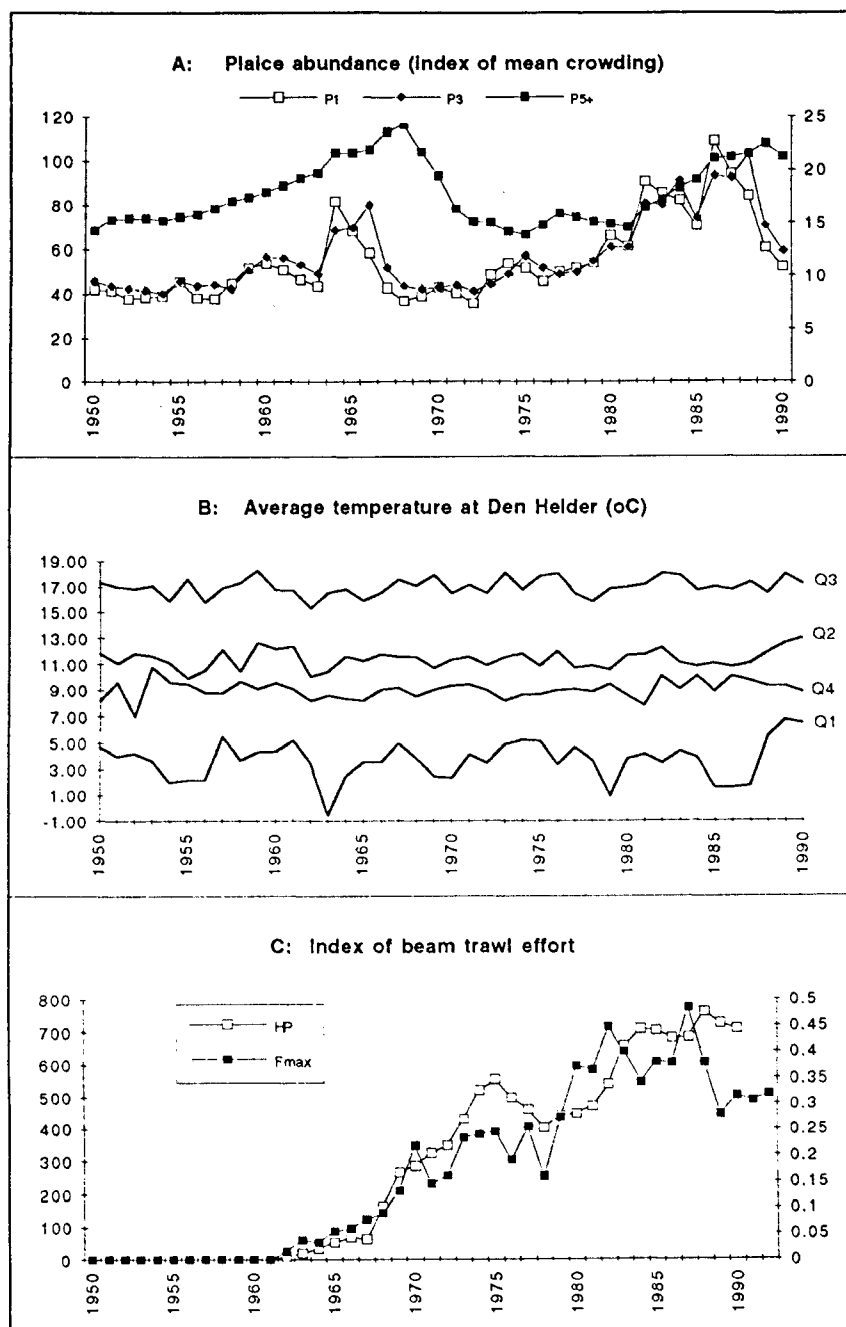


Figure 3. Time series of an index for intra-specific competition and of environmental variables. A - index of mean crowding (kg) on age-group 1 (P1), age-group 2 (P2), age-group 3 (P3), age-group 4 (P4) and age-groups 5 and older (P5); B - average temperature by quarter at a coastal station (Den Helder); C - index of Dutch beam trawl fishing: HP = number of horsepower days, F_{peak} = the peak in the partial fishing mortality of Dutch beam trawlers.

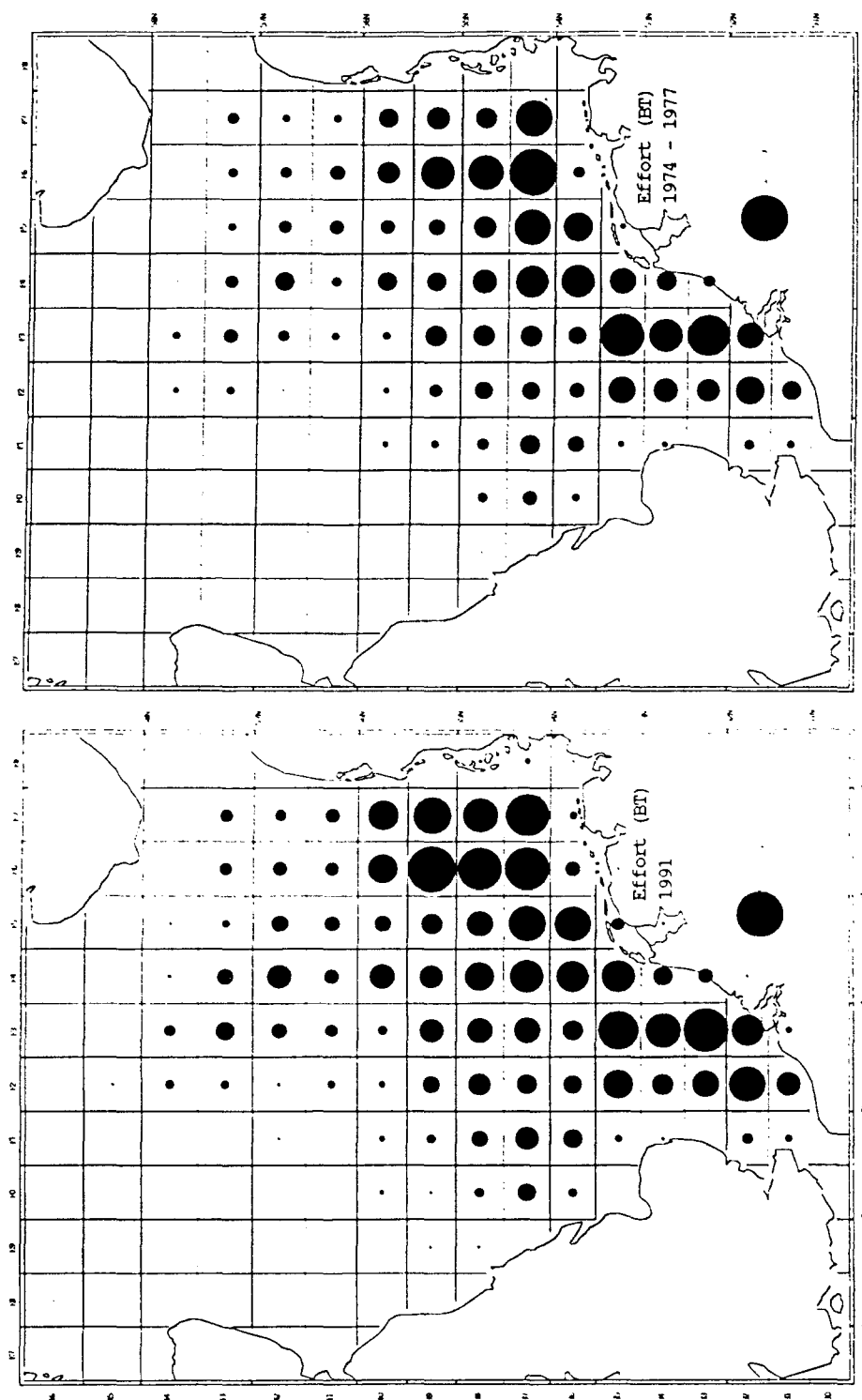


Figure 4. Relative distribution of Dutch beam trawl effort in the 1974 and in 1991.

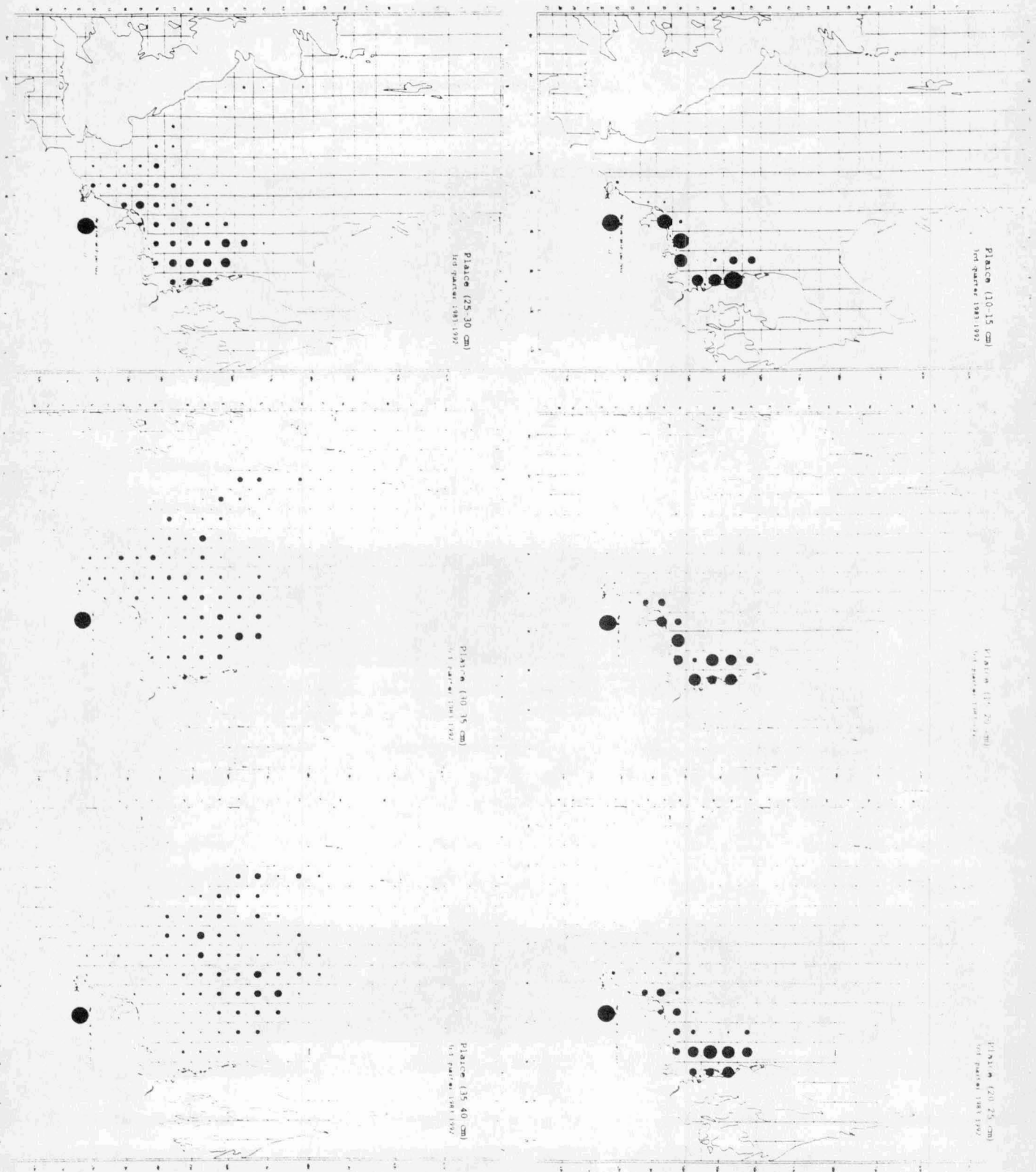


Figure 5. Distribution of plaice during the summer feeding period in relation to its size illustrating the progressive offshore movement with age and size. Data Beam Trawl Surveys 1983-1992.

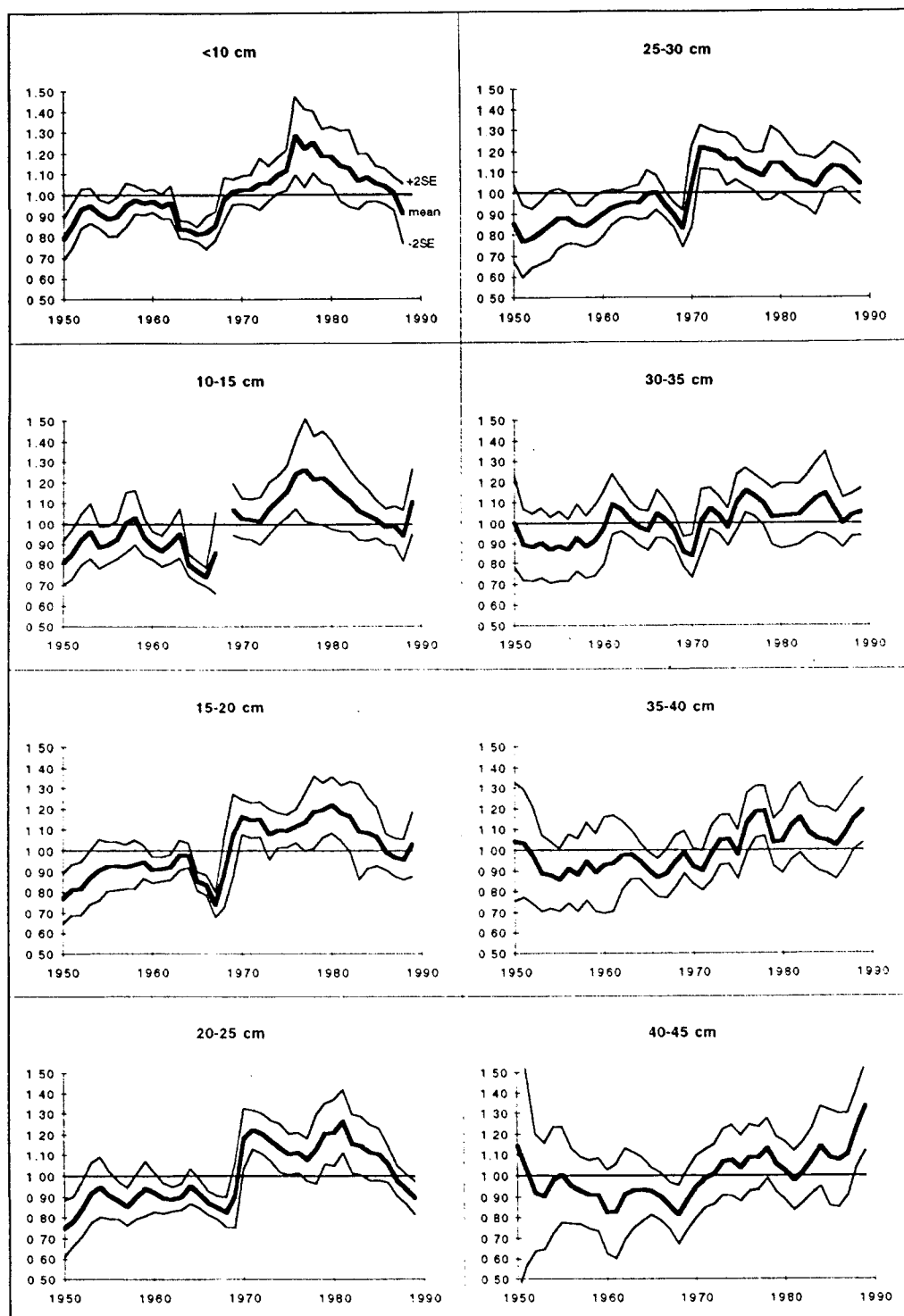


Figure 6. Timeseries of back-calculated growth rates of various 5-cm size classes of female plaice between 1950 and 1990. The heavy line shows the mean growth rate. The two thin lines show the approximate 95% confidence limit ($\pm 2 \times$ S.E.). The growth rate is shown as a 3-pnt running mean to smooth the variance due to heterogeneous sampling levels.

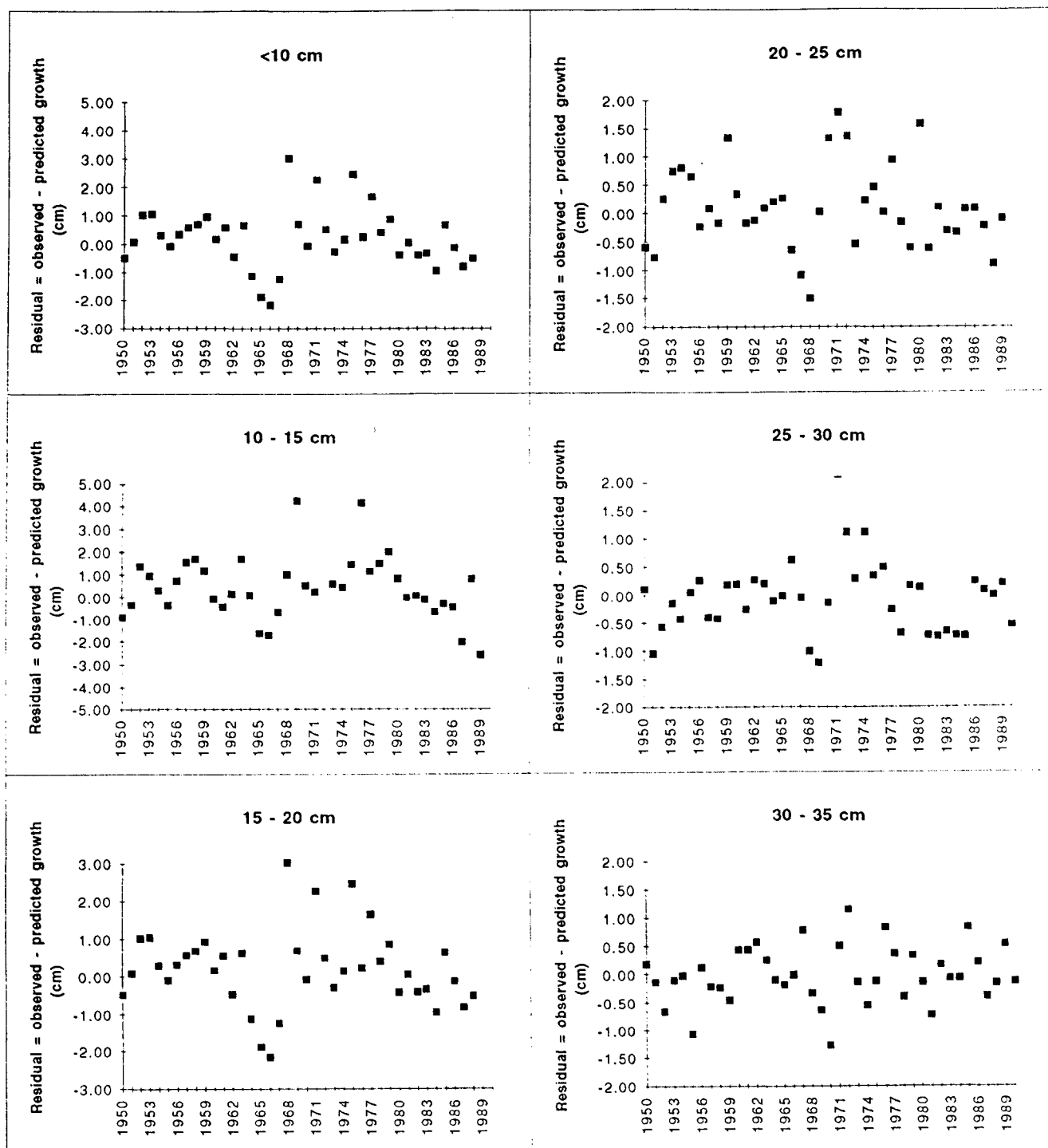


Figure 7. Time series plot of the residual growth rate ($RG = G_{obs} - G_{pred}$) after correcting for the correlation between growth and PO_4 and F_{peak} or various 5-cm size classes.

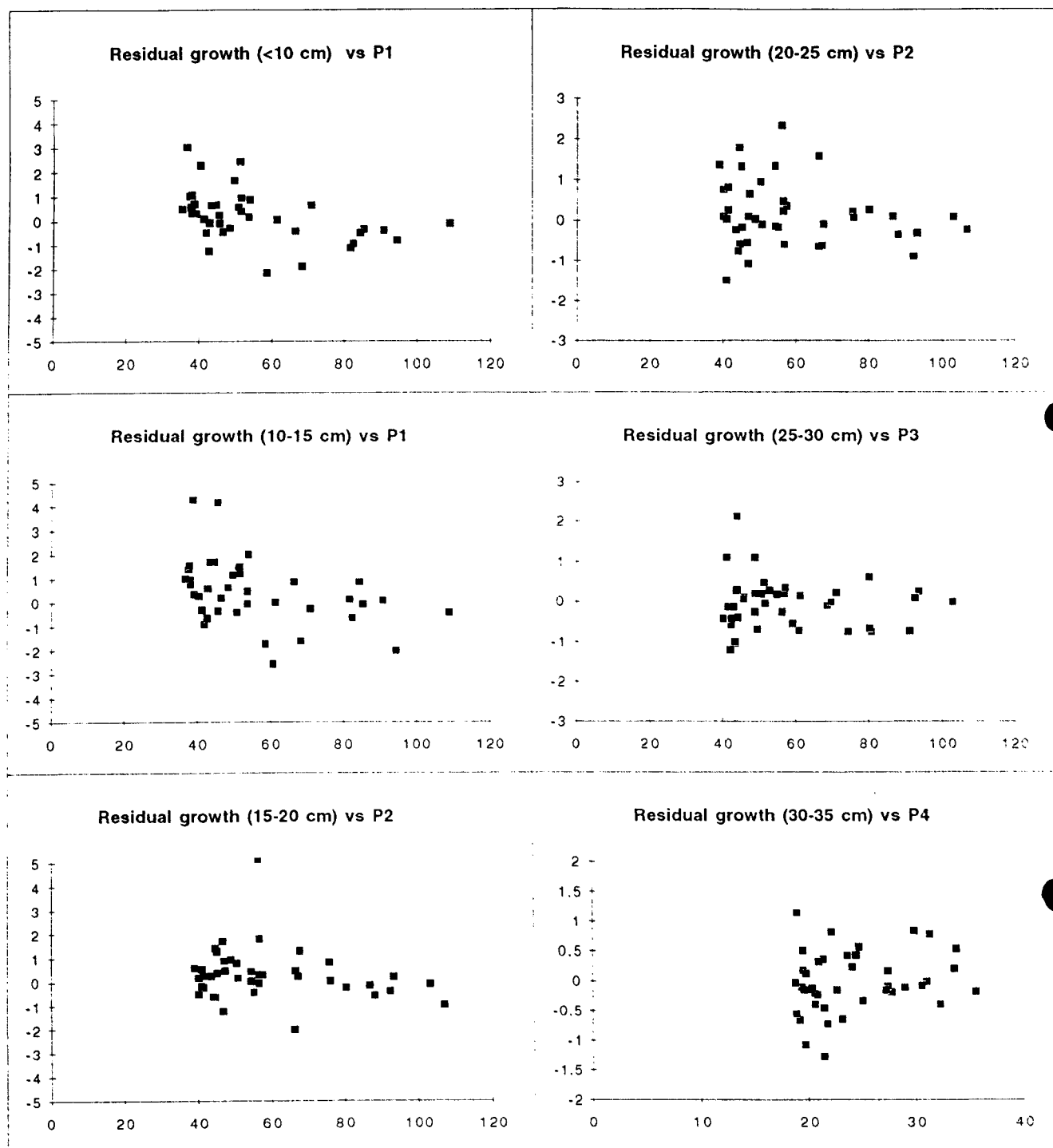


Figure 8. Scatter plot of the residual growth rate ($RG = G_{obs} - G_{pred}$) after correcting for the correlation between growth and PO_4 and F_{peak} against the index of intra-specific competition for various 5-cm size classes.

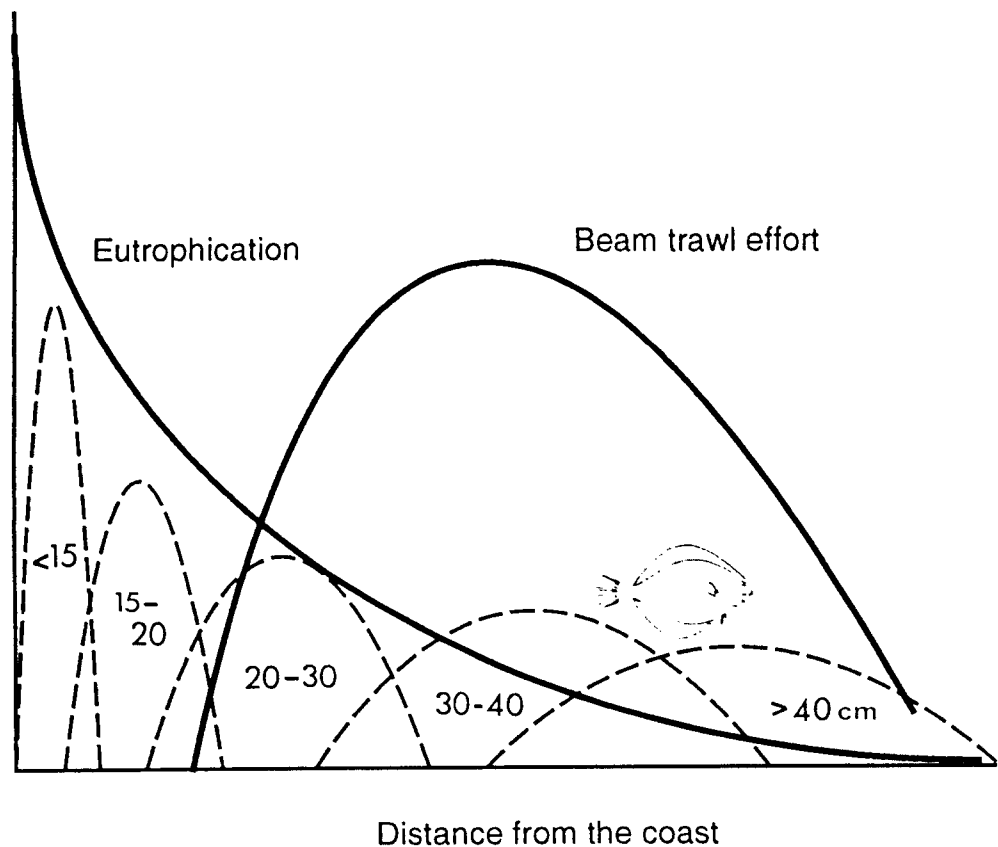


Figure 9. Schematic relationship between the effects of eutrophication and beam trawling in relation to the distance from the coast. The eutrophication decreases with the distance from the coast. Intensity of heavy beam trawling is zero within the 3-miles zone and reaches a peak in offshore waters along the 12 miles zone or along the borders of closed areas such as the plaice box. The dashed lines indicate the length-frequency distributions indicate the offshore movement of groups of plaice.