

Long-term fluctuations in fish recruit abundance in the western Wadden Sea in relation to variation in the marine environment

Catharina J. M. Philippart, Han J. Lindeboom,
Jaap van der Meer, Henk W. van der Veer, and
Johannes IJ. Witte



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Fyke catches from the westernmost tidal inlet of the Wadden Sea were analysed for inter-annual variability in recruit numbers of several commercial and non-commercial fish species between 1972 and 1994. Year-to-year variability in recruits ranged between 0.28 and 1.13 standard deviation. Variability was relatively low for species such as turbot, plaice, and sole, which concentrate in nursery areas during their early life history. Correlations between species were generally low, although a few clusters of species tended to show similar patterns. Pollack and whiting decreased during the study period, whilst sole, flounder, herring, and lumpsucker became more abundant. Part of the observed inter-annual variability in recruits appears to be related to fluctuations in the environment, such as transport rate of larvae across the North Sea and quality of the nurseries, i.e. temperature, food availability, and predation pressure.

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Key words: estuarine environment, fish recruits, population variability, time series, Wadden Sea.

C. J. M. Philippart, H. J. Lindeboom, J. van der Meer, H. W. van der Veer, and J. IJ. Witte: Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands.

Introduction

Recruitment studies of marine fish species represent a major topic in fishery research. The number of recruits of any given species may vary greatly between years. Although no general hypothesis on the cause of the observed inter-annual variability in recruitment has emerged so far from the extensive literature (e.g. Bakun *et al.*, 1982; Shepherd *et al.*, 1984; Leggett, 1986; Anderson, 1988; Houde, 1989; Wooster and Bailey, 1989; Miller *et al.*, 1991; Leggett and DeBlois, 1994; Beverton, 1995), some common patterns have been suggested.

Long-term dynamics of fish populations are thought to be controlled by a combination of density-independent and density-dependent processes. The latter aspect is stressed in the “concentration hypothesis” (Beverton, 1995), which rests on the premise that species concentrating spatially during their early life history, relative to their adult distribution range, are likely to be subject to stronger density-dependent forces than species without such concentrating tendencies. This implies that

year-to-year variations in recruitment should on average be smaller for species with restricted nursery areas than for those without. Thus, the concentration hypothesis emphasizes differences in annual variability in recruitment among species.

Yet, when trying to fit a stock–recruitment relationship, residuals usually remain highly variable, indicating that the density-dependent component is not very strong. This has led to the search for effects of fluctuations in the marine environment on recruitment as an additional source of variability (e.g. Mysak *et al.*, 1982). For example, successful transport of herring larvae has been related to hydrographical conditions, which may deviate strongly from year to year (e.g. Corten, 1990). For juvenile flatfish, Gibson (1994) stated that recruitment levels depend on the quality of the nurseries, i.e. food abundance, water temperature, and predation pressure. Although not much is known about annual variation in food availability for fish recruits, water temperature and predator abundance vary strongly between years. The main predators of flatfish recruits after settlement in the Wadden Sea are brown shrimp

and crabs (van der Veer and Bergman, 1987; van der Veer *et al.*, 1990, 1991), which are rare on the tidal flats after severe winters (Beukema, 1991b) as a result of either increased mortality or migration to deeper waters (Pihl, 1989).

In this article, long-term variability in recruit abundance of various fish species in the Dutch Wadden Sea is analysed. The Wadden Sea accommodates large numbers of fish species which use the area primarily during their early life stages. A long-term sampling programme was started in the early 1960s in the Marsdiep, the westernmost and largest tidal inlet between the North Sea and the Wadden Sea (Fig. 1). A kom-fyke trap has been employed at the same location for almost 35 years. Most investigations on fish abundance are restricted to commercially exploited species. However, the fyke catches have resulted in time series of both commercial and non-commercial fish species. Time series of recruit (0-group) abundance in the Marsdiep are (1) compared for differences in year-to-year variability among species, (2) analysed for the existence of covariability between species as an indication that recruit numbers may be related to common environmental factors, and (3) examined for relationships with environmental variables, i.e. North Sea circulation, water temperature, productivity, and predation pressure in the Dutch coastal zone.

Material and methods

Fyke catches

The kom-fyke has been in operation between April and October from 1960 until the present day, being emptied almost every morning from Monday to Friday. Catches are sorted immediately and identified to species level. For the present analysis, only samples were selected which relate to fishing periods of approximately 1 day (24 ± 12 h), since longer periods may have resulted in losses due to decay or consumption by crustaceans.

A selection was made for those species for which (1) the assumption seemed reasonable that a constant fraction of the western Wadden Sea populations had been sampled (van der Meer *et al.*, 1995), and (2) the recruits could be identified in the catch (Table 1). Fish were divided into length classes from 1972 onwards, and lengths were individually measured from 1979 onwards. Catches sampled between 1960 and 1971 had to be rejected because information on size was insufficient to discriminate between recruits and older fish.

For each of the selected fish species, the average abundance of recruits in the fyke catches was calculated for every month (in numbers per month) by dividing the

total monthly catch by the fraction of the time that the fyke was operated. Missing values (11) within every data set (23 years times 7 months) were predicted under the assumption that the expected monthly catches were a product of a year effect and a month effect. These effects were estimated using a log-linear Poisson regression (McCullagh and Nelder, 1989). For each species, a period of 2 months was selected to calculate an annual index of recruit abundance (Table 1). This selection was based on the observed seasonal change in relative abundance of the 0-group and 1-group fish within the selected size groups (see Fig. 2). Before further analysis, abundance values were logarithmically transformed to approximate normality: $\log_e(\text{numbers per month} + 1)$. For each species, year-to-year variability in recruitment was indexed by means of the standard deviation of the log-transformed time series (McArdle, 1995).

Covariability between species was examined by performing principal components analysis (PCA) on the correlation matrix by means of SYSTAT (Wilkinson, 1988). The results were visualized in so-called biplots (Gabriel, 1971). Correlations between each pair of species (or environmental variables) are indicated by the product of the cosine of the angle between and the length of two species vectors. Thus, long vectors pointing in the same direction indicate a high positive correlation between species, whilst orthogonal vectors indicate a zero correlation. In addition, the orthogonal projection of each annual observation on a species vector approximates the relative number of that species in that particular year. The reliability of this approximation is indicated by the length of the vector: the approximation is perfect when a vector approaches the unit circle.

Environmental variables

The North Atlantic Oscillation (NAO) index, i.e. sea-level pressure at Ponta Delgada on the Azores during winter (average of December, January, and February) minus the comparable value at Akureyi in Iceland, provides a measure of the strength of the mid-latitude westerly circulation over the North Atlantic (Dickson and Brander, 1993). It can also be interpreted as an indication of the strength of the wind-driven North Sea circulation (Reid *et al.*, 1992) during winter. Most of the selected species start to spawn in winter/spring. For fish spawning in the North Sea and using the Wadden Sea only as a nursery area, the NAO index is assumed to reflect the transport rate of eggs and larvae across the North Sea.

Figure 1. Location of the kom-fyke (open square), the jetty (open circle) used for measuring chlorophyll and water temperatures, and the Balgzand zoobenthos sampling stations (closed circles) in the western Wadden Sea.

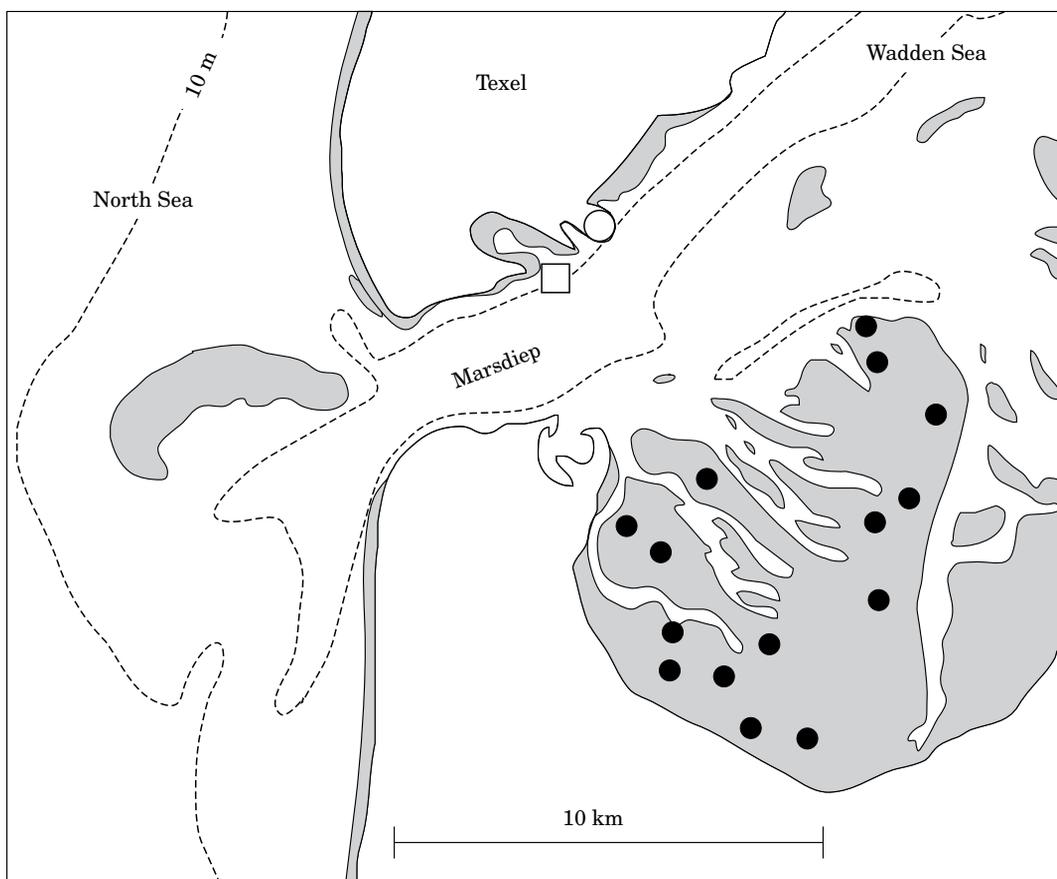
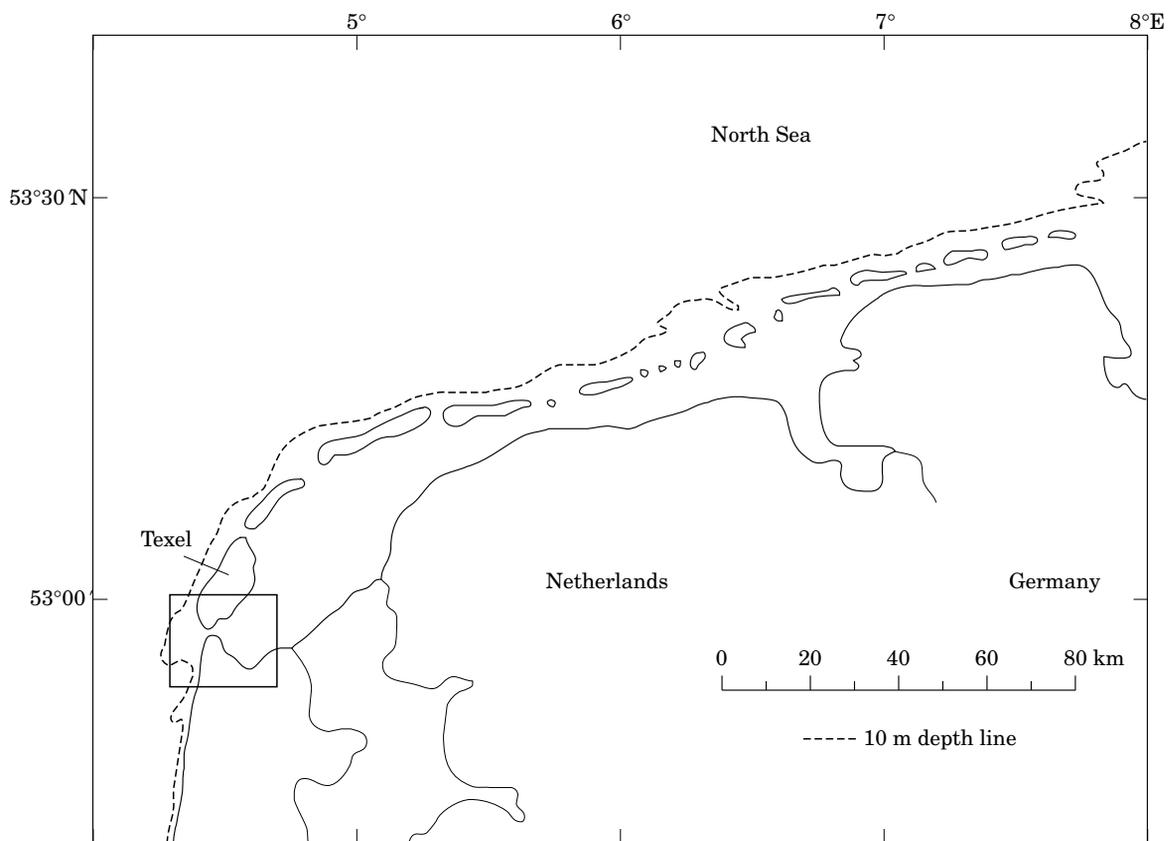


Table 1. Family name, species name, common name, maximum size (cm) of fish classified as recruits, and 2-month period selected for the calculation of the annual index of recruit abundance of 12 fish species

Family	Species	Common name	Size	Period
Clupeidae	<i>Clupea harengus</i>	Herring	10	Sep–Oct
	<i>Alosa fallax</i>	Twaite shad	20	Sep–Oct
Gadidae	<i>Gadus morhua</i>	Cod	20	Jul–Aug
	<i>Merlangius merlangus</i>	Whiting	20	Sep–Oct
	<i>Pollachius pollachius</i>	Pollack	20	Aug–Sep
Cyclopteridae	<i>Cyclopterus lumpus</i>	Lumpsucker	10	Sep–Oct
Carangidae	<i>Trachurus trachurus</i>	Scad	20	Aug–Sep
Mugilidae	<i>Chelon labrosus</i>	Grey mullet	20	Sep–Oct
Bothidae	<i>Scophthalmus maximus</i>	Turbot	20	Sep–Oct
Pleuronectidae	<i>Pleuronectes platessa</i>	Plaice	15	Aug–Sep
	<i>Platichthys flesus</i>	Flounder	15	Aug–Sep
Soleidae	<i>Solea solea</i>	Sole	15	Sep–Oct

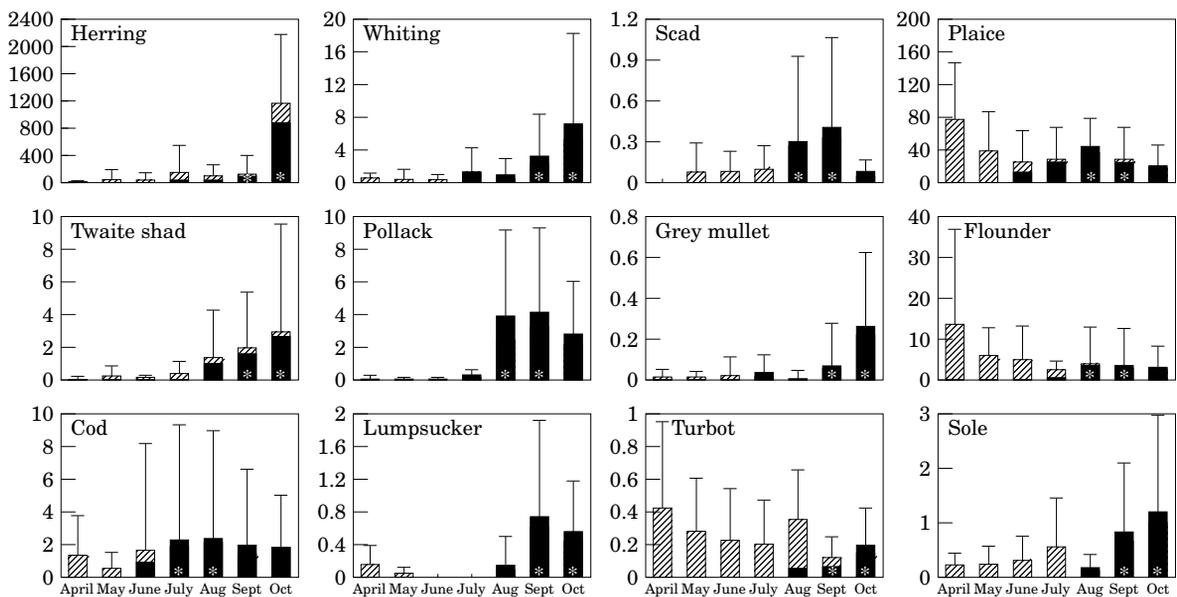


Figure 2. Seasonal variation in average numbers of 0-group (black bars) and 1-group (hatched bars) of selected species (in numbers per day) with standard deviations (thin vertical lines). White asterisks indicate the 2 months used to calculate annual indices of recruit abundance.

Water temperature and chlorophyll concentration have been measured from a jetty in the Marsdiep tidal inlet in close proximity to the kom-fyke (Fig. 1). Temperature has been measured daily at 0800 since 1948 (van der Hoeven, 1982). Winter temperatures were obtained by averaging the monthly means of water temperature of December, January, and February.

Little is known about the diet of fish recruits and no long-term records of potential food items were available. However, food supply for fish recruits, i.e. secondary production for all species with the exception of the herbivore grey mullet, might be positively related to primary productivity during the entire year. In the western

Wadden Sea, an increase in chlorophyll and primary production has indeed been accompanied by an increase in zoobenthos biomass and changes in zoobenthos species composition (Beukema and Cadée, 1986; Beukema, 1991a). Annual productivity of the Wadden Sea was expressed as the average chlorophyll content of the water, which is related to the annual primary production in this area (Cadée and Hegeman, 1991). Sampling of phytoplankton took place during high tide almost every week in spring and summer and less frequently during the rest of the year (Cadée and Hegeman, 1974; Cadée, 1992). For 1974 to 1994, annual values of chlorophyll *a* concentrations were calculated from 12 monthly averages.

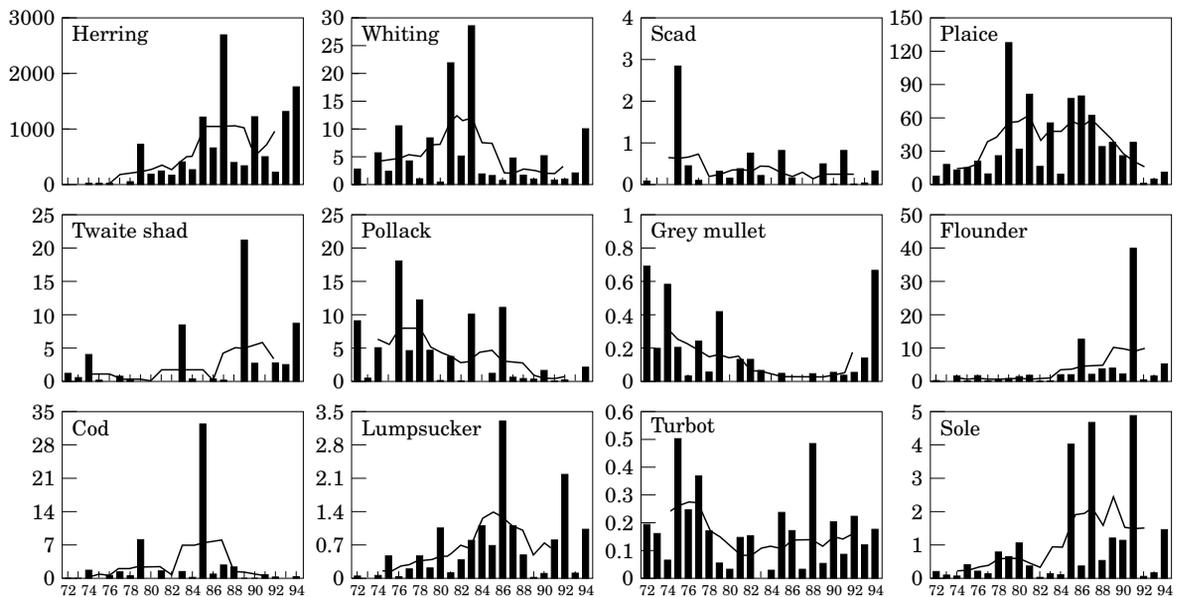


Figure 3. Inter-annual variation (bars) and 5-year running mean (line) of the average numbers of recruits (in numbers per day) by species.

Zoobenthos has been sampled in late winter, i.e. February–March, at 15 fixed stations on Balgzand, a 50 km² tidal-flat area in the western Wadden Sea (Fig. 1). Biomass of shore crabs (*Carcinus maenas*) and brown shrimps (*Crangon crangon*) has been determined as the ash-free dry mass (Beukema, 1993).

Covariability between the four environmental variables was examined by means of PCA using the correlation matrix. To compare the values of the environmental variables with the inter-annual variability in recruitment, each variable was standardized to mean 0 and variance 1. The standardized values (V) were subsequently divided into four classes, i.e. $V \geq 1$ standardized unit (su), $1 > V > 0$ su, $0 \geq V > -1$ su, and $V \leq -1$ su. Circles indicating the values of the standardized environmental variables were projected on the principal component scores in the biplot of recruit abundance.

Results

Year-to-year variability among species

Herring recruits were the most abundant in the fyke catches, followed by plaice, whereas catches of juveniles of turbot and grey mullet were very low (Fig. 3). Inter-annual variability was lowest for turbot and plaice (Table 2), both flatfish species spawning offshore and using the coastal zone only as a nursery area. Young herring and twaite shad showed a high year-to-year variability. Both are pelagic species but the Wadden Sea plays a different role in their life history. Herring, like

turbot and plaice, uses the Dutch coastal zone as a nursery area. Twaite shad belongs to the group of species which spend most of their lives in the Wadden Sea but move out to spawn either offshore (flounder) or in freshwater environments (twaite shad).

Covariability between species

The first two principal components (PCs) of the PCA of the fyke catch data (Fig. 4) accounted for 46% of the total variance of the logarithmically transformed and

Table 2. Standard deviations (s.d.) of log-transformed annual recruit abundance, and functional groups (after McHugh, 1967; Zijlstra, 1978), bio-geographical distribution (S: southern; I: intermediate; N: northern) and depth preference of the selected fish species

Species	s.d.	Functional group	Distribution	Depth preference
Turbot	0.28	Nursery type	S	Demersal
Plaice	0.43	Nursery type	N	Demersal
Grey mullet	0.44	Nursery type	S	Pelagic
Lump sucker	0.56	Spawning	N	Demersal
Sole	0.56	Nursery type	S	Demersal
Scad	0.59	Seasonal visitor	S	Pelagic
Whiting	0.63	Nursery type	N	Dem/pel
Flounder	0.64	Near-resident	I	Demersal
Pollack	0.75	Nursery type	I	Dem/pel
Cod	0.82	Nursery type	N	Dem/pel
Twaite shad	0.87	Near resident	S	Pelagic
Herring	1.13	Nursery type	N	Pelagic

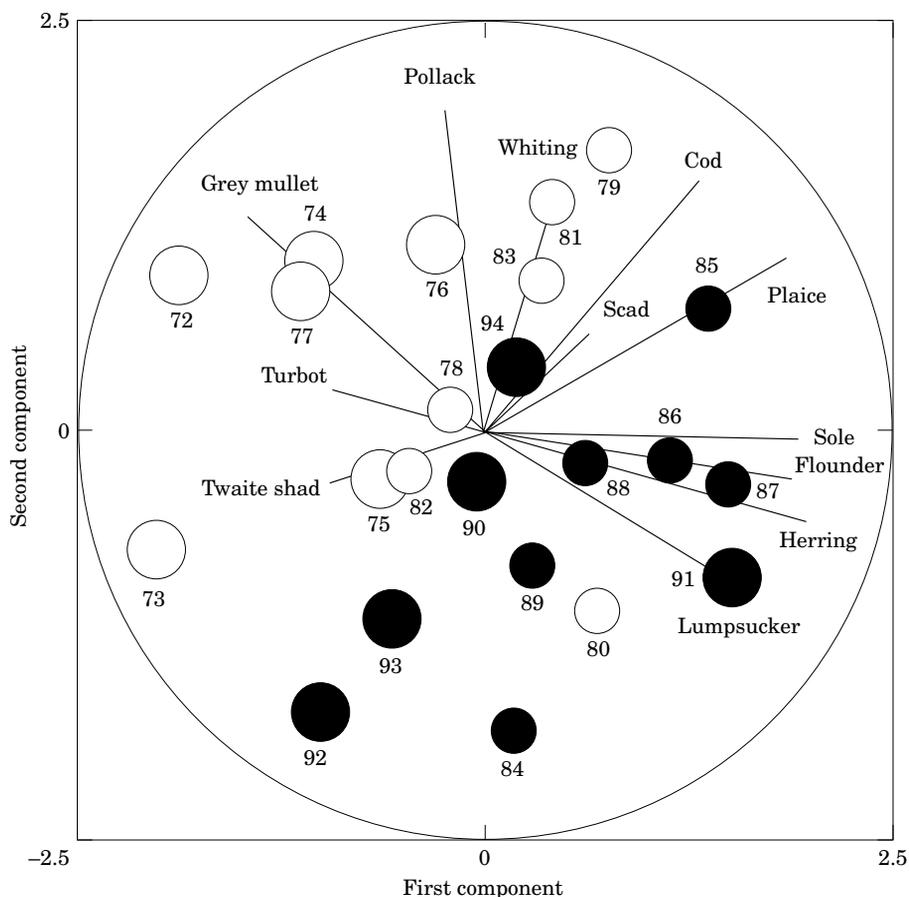


Figure 4. Covariance biplot (1st and 2nd axis) based on PCA of log-transformed and standardized recruit numbers per month by species. Large circles: 1972–1977; small circles: 1978–1983; small dots: 1984–1989; large dots: 1990–1994.

standardized recruitment indices. Covariability between species is relatively low because the explained variance is not much higher than the minimum value of the variance explained by the first two PCs in the event all species were uncorrelated (i.e. $2/12 \approx 17\%$).

Based on the biplot of the first two PCs, the study period can be roughly divided into two periods, i.e. 1974–1983 and 1984–1994, with the exception of 1980 and 1994 (Fig. 4). Recruit abundance of sole, flounder, herring, and lumpsucker generally increased during the study period. These species are characterized by low numbers during the beginning of the 1970s and high numbers at the end of the 1980s. Plaice and cod show similar patterns with relatively high numbers in the centre of the study period, i.e. highest values around the 1980s. Grey mullet, pollack, and whiting show a general decline, with the highest values during the first half of the study period. Turbot, twaite shad, and scad are not very well represented in the biplot of the first two PCs, as indicated by their location close to the origin.

Relationships with the environment

Owing to missing values of chlorophyll in 1972 and 1973, PCA was restricted to the period between 1974 and 1994. The first two PCs of the environmental data (Fig. 5) accounted for 73% of the total variance of the untransformed and standardized values of NAO index, water temperature, chlorophyll concentration, and crustacean abundance. In the biplot, NAO index and winter temperature are positively correlated. No correlation appears to exist between winter temperature and crustacean abundance. These conclusions are in agreement with the correlation structure between the environmental factors for the entire study period (excluding chlorophyll concentrations): a significant linear correlation was found only between NAO index and water temperature in winter ($n=23$, $r=0.71$, $p<0.05$).

In general, high recruit numbers for most species, in particular herring, flounder, sole, plaice, and whiting,

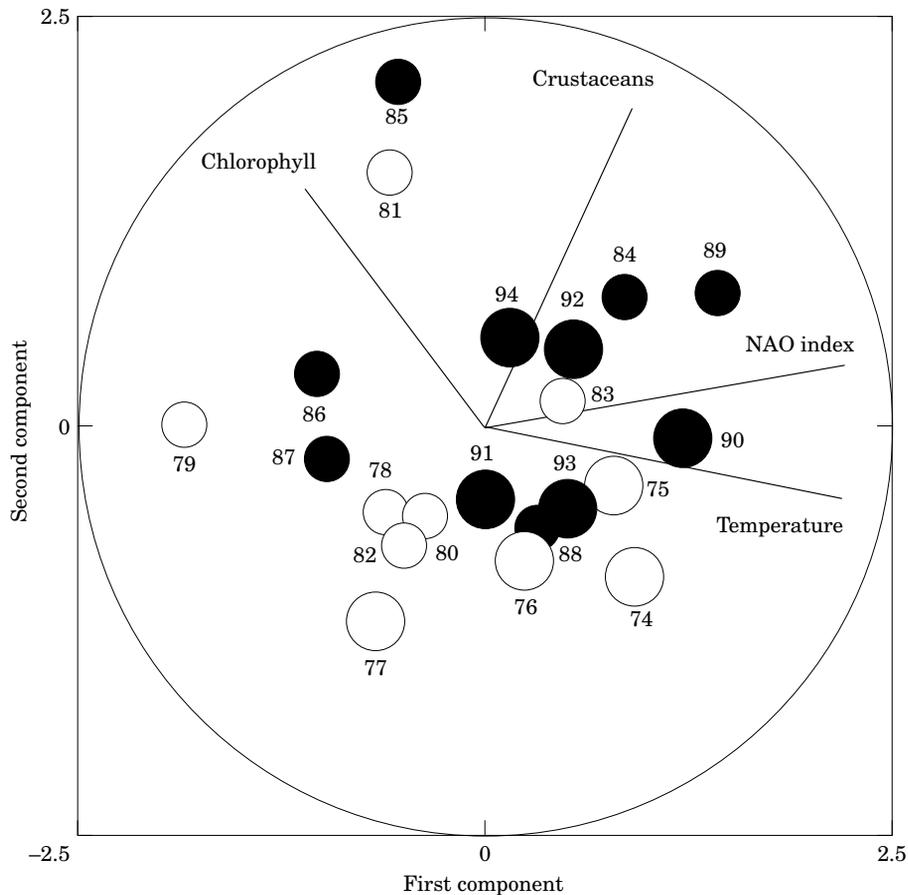


Figure 5. Covariance biplot (1st and 2nd axis) based on PCA of standardized values of NAO index, winter temperature, annual chlorophyll concentration, and predation pressure by crustaceans. Large circles: 1974–1977, small circles: 1978–1983; small dots: 1984–1989; large dots: 1990–1994.

were observed in years characterized by low values of the NAO index and by severe winters, i.e. 1979 and 1985–1987 (Fig. 6). Recruits of whiting, cod, plaice, sole, flounder, and herring were abundant in periods when chlorophyll levels were above average and in years with low densities of predatory crustaceans.

Discussion

Within the study period, nursery-type flatfish species (i.e. turbot, plaice, and sole) showed a below average variability in recruit numbers. This is in agreement with the concentration hypothesis of Beverton (1995). Recruits of these species concentrate from a large area (North Sea) in a narrow zone along the coast. Based on the actual size of the nursery areas of the three species, Beverton (1995) predicted that the concentration tendency would be strongest, and thus variability would be lowest, for turbot, followed by plaice and sole, respectively. Our results support his prediction.

Covariation between species was not very high. Variation in recruits was dissimilar for species within the functional groups identified or for species with a similar geographical distribution (Table 2). However, some similarities were observed between species showing a similar depth distribution. Recruits of all three gadoids (cod, whiting, and pollack) that feed pelagically as well as close to the seabed showed a more or less similar variation in abundance with high numbers in 1979 and 1980, and almost zero densities in 1984 and the beginning of the 1990s. Number of recruits of the common flatfish species (plaice, flounder, and sole) was high at the end of the 1980s and low at the beginning of the 1970s.

The relatively low explained variance in the abundance biplot indicates that inter-annual variation in recruits cannot be explained by one or two environmental factors. Because of the strong correlation between NAO index and winter temperature, as also found at other locations in Europe (Hurrell, 1995), no

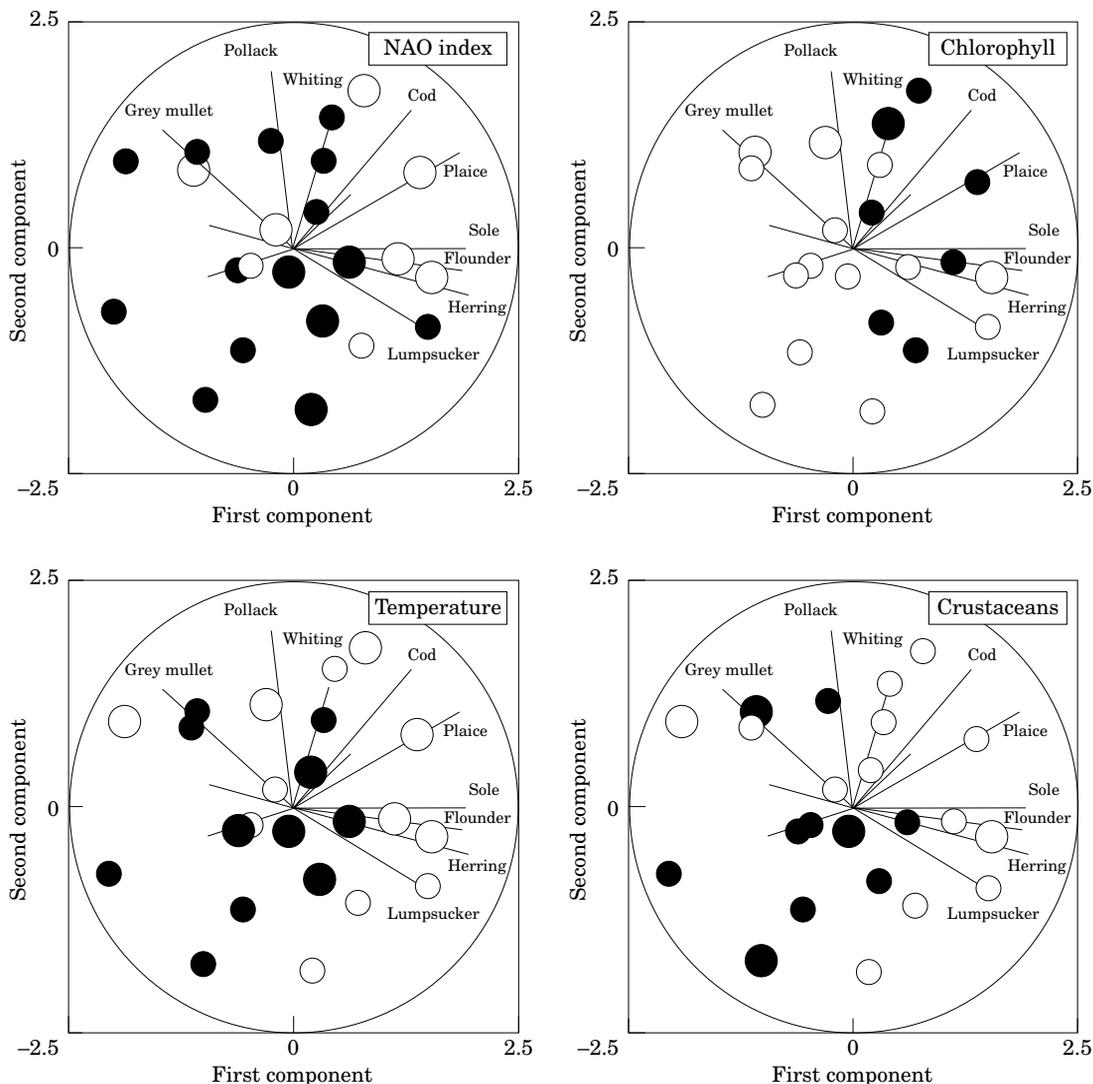


Figure 6. Covariance biplots of recruit abundance in relation to the four environmental variables between 1972 and 1994. Circles refer to below average values of the environmental variable and dots to above average values. Symbol diameter indicates deviation from the average value. Chlorophyll data were not available for 1972 and 1973.

distinction can be made between the effects of these two variables. Coinciding high recruit numbers of herring, flounder, sole, plaice, and whiting in years with a low NAO index and low water temperatures in winter can therefore be caused by an enhancement of eastward transport of fish larvae across the North Sea (Corten and Van der Kamp, 1992) as well as by a decrease in mortality after severe winters (Rijnsdorp *et al.*, 1992; van der Veer, 1986; Zijlstra and Witte, 1985).

Recruits of whiting, cod, plaice, sole, flounder, and herring seem to prosper in years with high chlorophyll concentrations and low numbers of predatory shrimps and crabs. High abundance of flatfish recruits at low predation pressure is in agreement with the predation

hypothesis for flatfish (van der Veer *et al.*, 1990, 1991). For cod and whiting, crustacean predation was not expected to be an important factor for recruit survival. However, these roundfish have a demersal life style and may, therefore, also be affected by benthic predators.

In conclusion, our results suggest that recruit numbers in the Wadden Sea are influenced by a combination of density-dependent processes in the nurseries and year-to-year variations in the estuarine environment. However, based on the low covariability between the species it is expected that no single environmental factor caused the observed inter-annual variability in recruits in the Dutch coastal zone.

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