

Increase of benthic biomass in the Skagerrak-Kattegat during the 1970s and 1980s – effects of organic enrichment?

Alf B. Josefson

National Environmental Research Institute, Jaegersborg Alle 1B, DK-2920 Charlottenlund, Denmark

ABSTRACT: Biomass and abundance of macrobenthos was monitored from 1972 to 1988 at 14 soft-sediment stations below the halocline in the Skagerrak-Kattegat area. Year-to-year variations in fauna were analysed. Clear general trends were demonstrated over the study area, which is > 170 km long. Total biomasses showed linear increases by a median factor of 1.8, primarily from 1981 to 1988, and biomasses excluding some large species, notably echinoids, increased by a median factor of 1.7 from 1972 to 1988. The changes were primarily due to echinoderms, notably the amphipod *Amphiura filiformis*, and polychaetes. Polychaetes contributed more to the increase at the deepest stations, and the absolute increase of this group was positively related with water depth. The relative increases in 'biomass without large species' as well as biomass of amphipods and polychaetes were positively related to water depth. Parallel to the biomass change, land freshwater run-off from western Sweden and to Danish inner waters have increased, and this has influenced the input of nutrients to the sea. Although reliable data on primary production and sedimentation of organic material are largely lacking, the present results are in accordance with hypotheses that soft-sediment infauna in the area is food limited, and that the area is being affected by organic enrichment.

INTRODUCTION

During the last decade much interest among ecologists has been focused on whether the coastal marine ecosystems in the northeastern Atlantic are disturbed by human activities or not. Incidents with faunal kills due to oxygen deficiency appear to be more frequent in recent years (e.g. Rosenberg 1985). Increased frequencies of intensive algal blooms (Nielsen & Årtebjerg 1984), increased nutrient concentrations (Andersson & Rydberg 1988) and changes in benthic biomass and structure (Rosenberg & Möller 1979, Pearson et al. 1985, Rosenberg et al. 1987, Josefson & Rosenberg 1988) support the contention that the coastal ecosystems are experiencing eutrophication.

Of the many biological components in these ecosystems, the composition of the soft-sediment benthos is a useful tool for evaluating long-term temporal changes in the environment. Many benthic species have sessile habits and life spans > 1 yr which make it relatively easy to quantify changes in abundances and biomasses. Furthermore, much is known about the

environmental demands of many species in this faunal category. Particularly good historical data on macrobenthos are available from the Scandinavian seas, the Kattegat and the Skagerrak, which have been studied for many years. Previous work in these areas has involved comparisons of biomass and species composition between dates, widely separated in time (Rosenberg & Möller 1979, Pearson et al. 1985, Rosenberg et al. 1987, Josefson & Rosenberg 1988). Clear differences were reported which suggest organic enrichment and in some areas oxygen deficiency. It is not known from these studies, however, whether the changes are gradual trends over a long time, or merely fluctuations over a few years.

This paper presents a benthic data set that illustrates environmental changes over a 16 yr period (1972 to 1988) in a large area of the Skagerrak and northern Kattegat based on samples taken annually. It is demonstrated that benthic biomass showed a general linear increase within this time period. It is argued that the most probable major cause of this change is increased sedimentation of degradable organic matter. The pre-

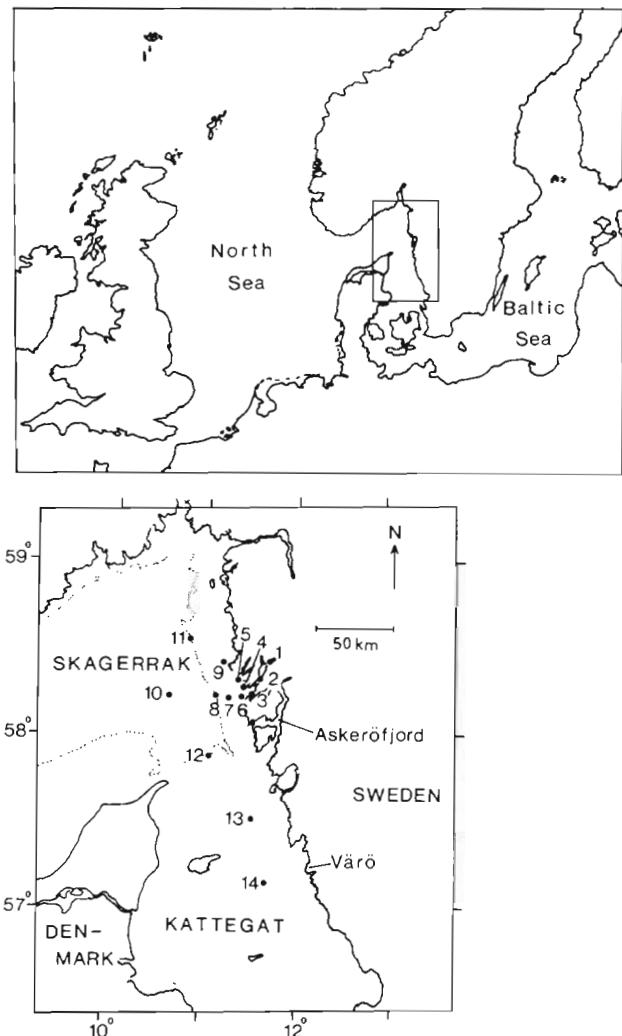


Fig. 1. Upper: position of the investigation area (rectangle). Lower: sampling stations. Dotted line indicates the 100 m isobath

sent results further corroborate the contention that several coastal areas in the North Sea region are being affected by eutrophication.

STUDY AREA

The Kattegat-Skagerrak is a transition area between the Baltic Sea and the North Sea (Fig. 1). The area is influenced both by currents from the North Sea, such as the Jutland Current, and by the low saline Baltic Current from the Baltic Sea. In the Skagerrak the latter current is likely to be of most importance close to the Swedish coast where the water masses are stratified with a halocline at ca 15 m depth (e.g. Svansson 1975). In addition to the water currents, the area receives land run-off directly from the surrounding countries; namely

Denmark, Sweden and Norway. It has been suggested that the deeper part of the study area is the major sink for organic material from the southern North Sea (Weering et al. 1987).

MATERIAL AND METHODS

Quantitative benthic samples were taken at 14 stations over the period 1972 to 1988 (Fig. 1, Table 1). The stations were situated below the halocline at water depths from 18 to 300 m and distributed over a distance of more than 170 km in length. Sediment characteristics for most of these stations are given in Josefson (1987). Except for the station in the Gullmar Fjord Basin (Stn 2) and Stn 1 in the innermost part of the same fjord, where intermittent hypoxia has affected the fauna (Josefson & Widbom 1988, Josefson unpubl.), all stations are situated in well-flushed areas.

In general 5 replicate samples were taken on each date. Three replicates, however, were taken in the Kattegat, Stns 13 and 14; in Gullmar fjord, Stn 2, during 1977 to 1980; and at Stn 12 in 1973. The sampling dates, at most one per year, are shown in Table 1. In most years sampling was carried out in May or adjacent months.

The samples were taken with a modified 0.1 m² Smith-McIntyre grab except at Stns 13 and 14 where a 0.1 m² Van Veen grab was used. Samples were sieved on board the ship on a 1 mm screen and preserved in 4% buffered formalin. In the laboratory samples were split into 2 size fractions: 1 to 2 mm and > 2 mm. The former fraction was sorted using a stereomicroscope and the latter by eye under a strong lamp. Biomass determinations were made after blotting dry on filter paper. Each species was weighed separately. Molluscs were weighed including shells and tube-dwellers without their tubes, except for *Myiochela* spp. and *Phoronis* spp. The contribution of these 2 taxa to total biomass was however negligible. *Amphiura* species were weighed together because of difficulties in separating arm-fragments. From 1981 onwards, echinoids were weighed after being punctured in order to treat samples in a consistent way. Earlier, a significant source of variation in biomass was due to whether the individuals contained body fluid or not. This is the main reason for excluding echinoids from the total biomass values and the biomass values of Echinodermata when analysing trends from the whole 16 yr period. In addition to echinoids a few species are excluded which are rare, and thereby inaccurately quantified, and had a disproportional influence on total biomass because of their large individual size. These are the Ocean quahog *Arctica islandica*, the Norway lobster *Nephrops norvegicus* and pennatulid antho-

Table 1. Station list showing station positions, depths and dates of observation. Unless otherwise stated each year was sampled in May

Station No.	Lat. N	Long. E	Depth (m)	Sampling dates
1	58° 25'	11° 39'	44	1981–1984, Apr 1985, 1986–1988
2	58° 19.2'	11° 32.8'	115	Sep 1977, Dec 1978, Nov 1979, Jun 1980, 1981–1984, Apr 1985, 1986–1988
3	58° 15.8'	11° 28.7'	30	Dec 1977, 1979, Oct 1980, 1981, Jun 1982, 1983–1988
4	58° 18.45'	11° 24'	18	1983–1988
5	58° 20.3'	11° 21.6'	27	1972, 1983–1988
6	58° 14.72'	11° 25.8'	40	1983–1988
7	58° 14.4'	11° 15'	49	1983–1988
8	58° 15.2'	11° 03.5'	100	1983–1988
9	58° 23'	11° 09.3'	49	Jun 1974, 1975, Jun 1976, 1981–1988
10	58° 14.9'	10° 34.3'	300	Mar 1973, Jun 1974, 1975, Jun 1976, Jul 1977, Feb 1978, Feb 1979, Feb 1980, 1981–1988
11	58° 32.5'	10° 47.5'	100	Mar 1973, Jun 1974, 1975, Jun 1976, Jul 1977, Feb 1978, Feb 1979, Feb 1980, 1981–1988
12	57° 55.9'	11° 02.2'	100	Mar 1973, Feb 1977, 1981–1982, 1984–1988
13	57° 33'	11° 31'	75	Oct 1979, Nov 1980, Dec 1981, 1982–1986
14	57° 11'	11° 40'	75	1979, Nov 1980, Nov 1981, 1982–1986

zoans. The category excluding these taxa is hereafter called 'biomass without large species'.

As a measure of nutrient input to the sea, and eventually to the benthos, data on land run-off from Sweden and Denmark were used. The annual mean water flows ($m^3 s^{-1}$), in turn based on mean flows from each month, in 10 major streams (Nedre Bullaren, Örekilsälven, Göta älv, Rolfsån, Viskan, Åtran, Nissan, Fylleå, Lagan and Rönneå) were added and used as a measure of land run-off from western Sweden (Swedish Meteorological and Hydrological Institute, SMHI). Run-off data from Denmark to the area were obtained from Det Danske Hedeselskab, Hydrometriske Undersøgelser.

Numerical treatment. The data, biomasses and abundances from individual replicate grab samples, were subjected to the following statistical treatments.

To evaluate if there were significant linear long-term trends at individual stations, the values from individual grabs were regressed against time (yr) at each of the stations, using the model ($y = a + bx$). Correlations with time were tested with the non-parametric Spearman's rank.

Prior to regression analysis the following procedure was performed to fulfill the criterion of homoscedasticity. Data on total biomass and on total abundance in the period 1983 to 1988, from all the stations sampled annually in this period, were transformed using $\ln(x+1)$ and \sqrt{x} . Correlations between annual means and standard errors (all stations) were computed using Spearman's rank for each of the 2 variables and using

each of the 2 transformations, as well as no transformation. For biomass $\ln(x+1)$, and for abundance \sqrt{x} transformations gave the least evidence of relations between means and standard errors, and were therefore consistently used across all data within each of the 2 groups of variables.

To evaluate if there were general trends among stations, the results from the regression analysis were tested with a 2-tailed sign test. The probability was calculated of obtaining a certain frequency of positive or negative regression line slopes in a random situation, using both all the signs and the significant ($p < 0.05$) ones only.

RESULTS

The following faunal variables were subjected to linear regression analysis at each of the 14 stations: total biomass and abundance; biomass without large species; biomass and abundance for the taxonomic groups Polychaeta, Mollusca, Echinodermata, Crustacea and Miscellaneous; biomass of amphipods; and abundance of the 2 species *Amphiura filiformis* and *A. chiajei*. Results for biomass are given in Table 2 and for abundance in Table 3. Results for biomass without large species are also shown graphically in Fig. 2. Because of the change in method of weighing sea urchins in 1981, total biomass and biomass of echinoderms were only analysed from the period 1981 to 1988 at Stns 3, 9, 11, and 12.

Table 2. Results of statistical analysis for trends in biomass with time at 14 stations, in order of increasing water depth, in the Skagerrak-Kattegat area over the period 1972 to 1988. Signs of slopes are given for linear regression lines ($y = a + bx$) as well as the p-values and levels of significance (Sig.) for the contribution of the linear model to the sum of squares. Regression analysis was made on $\ln(x+1)$ -transformed data. Correlations between biomasses and time (yr) were also tested with Spearman's rank: r, rank correlation coefficient; p, likelihood of no correlation; Sig., level of significance. n: number of observations; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; NS: $p > 0.05$

Station No.	n	Linear regression			Spearman's rank		
		Slope	p	Sig.	r	p	Sig.
Total biomass							
4	30	—	0.136	NS	-0.52	0.005	**
5	35	+	0.002	**	+0.49	0.004	**
3	40	—	0.625	NS	-0.10	0.528	NS
6	30	+	0.278	NS	+0.23	0.222	NS
1	40	+	0.897	NS	-0.06	0.701	NS
7	29	+	0.003	**	+0.53	0.005	**
9	40	+	0.005	**	+0.43	0.008	**
13	24	+	0.011	*	+0.52	0.013	*
14	24	+	0.118	NS	+0.28	0.174	NS
8	30	+	0.149	NS	+0.26	0.168	NS
11	40	+	0.047	*	+0.31	0.052	NS
12	35	+	0.000	***	+0.68	0.000	***
2	52	+	0.013	*	+0.30	0.032	*
10	80	+	0.001	***	+0.39	0.001	***
Biomass without large species							
4	30	—	0.224	NS	-0.37	0.048	*
5	35	+	0.000	***	+0.62	0.000	***
3	55	—	0.557	NS	-0.08	0.532	NS
6	30	+	0.024	*	+0.36	0.051	NS
1	40	—	0.882	NS	-0.05	0.775	NS
7	30	+	0.006	**	+0.48	0.010	**
9	55	+	0.154	NS	+0.12	0.366	NS
13	24	+	0.003	**	+0.59	0.005	**
14	24	+	0.048	*	+0.55	0.009	**
8	30	+	0.010	*	+0.47	0.012	*
11	80	+	0.000	***	+0.74	0.000	***
12	43	+	0.000	***	+0.84	0.000	***
2	52	+	0.013	*	+0.30	0.032	*
10	80	+	0.001	***	+0.39	0.001	***
Polychaeta							
4	30	+	0.989	NS	+0.02	0.913	NS
5	35	+	0.631	NS	-0.07	0.686	NS
3	55	—	0.537	NS	-0.14	0.299	NS
6	30	+	0.916	NS	+0.03	0.879	NS
1	40	—	0.002	**	-0.46	0.004	**
7	29	+	0.192	NS	+0.23	0.213	NS
9	55	+	0.093	NS	+0.16	0.254	NS
13	24	+	0.297	NS	+0.18	0.378	NS
14	24	+	0.003	**	+0.53	0.011	*
8	30	+	0.094	NS	+0.26	0.161	NS
11	80	+	0.000	***	+0.74	0.000	***
12	43	+	0.000	***	+0.80	0.000	***
2	52	+	0.004	**	+0.33	0.017	*
10	80	+	0.052	NS	+0.22	0.047	*
Mollusca							
4	30	—	0.206	NS	-0.26	0.164	NS
5	35	+	0.060	NS	+0.51	0.003	**
3	55	+	0.437	NS	+0.20	0.138	NS
6	30	+	0.017	*	+0.43	0.020	*
1	40	—	0.004	**	-0.45	0.005	**
7	30	+	0.022	*	+0.46	0.016	*
9	55	—	0.556	NS	-0.01	0.933	NS
13	24	—	0.761	NS	-0.15	0.484	NS
14	24	—	0.373	NS	-0.19	0.358	NS
8	30	—	0.312	NS	-0.09	0.610	NS
11	79	—	0.300	NS	-0.26	0.023	*
12	43	—	0.759	NS	+0.23	0.133	NS
2	52	+	0.032	*	+0.28	0.043	*
10	80	+	0.000	***	+0.47	0.000	***

Table 2 (continued)

Station No.	n	Linear regression			Spearman's rank		
		Slope	p	Sig.	r	p	Sig.
Echinodermata							
4	30	—	0.429	NS	-0.15	0.426	NS
5	35	+	0.002	**	+0.49	0.004	**
3	40	—	0.646	NS	-0.10	0.516	NS
6	30	+	0.537	NS	+0.10	0.572	NS
1	40	+	0.091	NS	+0.23	0.153	NS
7	30	+	0.026	*	+0.36	0.053	NS
9	40	+	0.000	***	+0.61	0.000	***
13	24	+	0.025	*	+0.50	0.016	*
14	24	+	0.263	NS	+0.22	0.290	NS
8	30	+	0.795	NS	+0.01	0.966	NS
11	40	+	0.003	**	+0.49	0.002	**
12	35	+	0.059	NS	+0.42	0.015	*
10	80	+	0.113	NS	+0.30	0.007	**
Crustacea							
4	30	+	0.702	NS	-0.26	0.166	NS
5	35	—	0.001	***	+0.05	0.768	NS
3	55	—	0.113	NS	-0.24	0.075	NS
6	30	+	0.116	NS	+0.27	0.142	NS
1	40	+	0.313	NS	+0.13	0.423	NS
7	30	+	0.004	**	+0.40	0.029	*
9	55	—	0.536	NS	-0.15	0.280	NS
13	24	+	0.714	NS	+0.08	0.710	NS
14	24	+	0.558	NS	+0.10	0.641	NS
8	30	+	0.027	*	+0.32	0.085	NS
11	80	—	0.896	NS	+0.02	0.861	NS
12	43	+	0.028	*	+0.34	0.029	*
10	80	+	0.011	*	+0.55	0.000	***
Miscellaneous							
4	30	—	0.223	NS	-0.16	0.402	NS
5	35	—	0.654	NS	-0.13	0.462	NS
3	55	+	0.185	NS	+0.21	0.120	NS
6	30	+	0.832	NS	+0.07	0.711	NS
1	40	—	0.013	*	-0.22	0.161	NS
7	30	+	0.504	NS	+0.27	0.150	NS
9	55	+	0.667	NS	-0.11	0.667	NS
13	24	+	0.279	NS	+0.29	0.160	NS
14	24	—	0.110	NS	-0.38	0.085	NS
8	30	+	0.616	NS	+0.08	0.684	NS
11	80	+	0.169	NS	+0.24	0.031	*
12	43	—	0.562	NS	-0.10	0.517	NS
10	80	—	0.161	NS	-0.35	0.002	**
Amphiuroidea							
4	30	+	0.853	NS	+0.00	1.000	NS
5	35	+	0.000	***	+0.65	0.000	***
3	55	+	0.263	NS	+0.13	0.348	NS
6	40	+	0.054	**	+0.40	0.033	*
1	40	+	0.000	***	+0.66	0.000	***
7	30	+	0.252	NS	+0.24	0.200	NS
9	55	+	0.287	NS	+0.24	0.082	NS
13	24	+	0.021	*	+0.44	0.034	*
14	24	+	0.010	*	+0.50	0.016	*
8	30	+	0.028	*	+0.41	0.028	*
11	80	+	0.000	***	+0.65	0.000	***
12	43	+	0.000	***	+0.88	0.000	***
10	80	+	0.001	***	+0.36	0.001	**

Table 3. Results of statistical analysis for trends in abundance with time (yr) at 14 stations in the Skagerrak-Kattegat area over the period 1972 to 1988. Regression analysis was made on \sqrt{x} -transformed data. For further information see Table 2

Station No.	n	Linear regression			Spearman's rank		
		Slope	p	Sig.	r	p	Sig.
Total abundance							
4	30	—	0.008	..	-0.46	0.013	•
5	35	+	0.063	NS	+0.08	0.638	NS
3	55	+	0.544	NS	+0.04	0.748	NS
6	30	+	0.046	•	+0.28	0.131	NS
1	40	—	0.000	...	-0.67	0.000	...
7	30	—	0.559	NS	-0.06	0.752	NS
9	55	+	0.069	NS	+0.19	0.167	NS
13	24	+	0.000	...	+0.61	0.003	..
14	24	+	0.006	..	+0.51	0.015	•
8	30	+	0.400	NS	+0.12	0.527	NS
11	80	+	0.880	NS	+0.01	0.908	NS
12	43	+	0.004	..	+0.58	0.000	...
2	52	+	0.070	NS	+0.28	0.044	•
10	80	—	0.267	NS	-0.10	0.395	NS
Polychaeta							
4	30	—	0.000	...	-0.89	0.000	...
5	35	—	0.224	NS	-0.57	0.001	...
3	55	—	0.072	NS	-0.26	0.061	NS
6	30	—	0.031	NS	-0.31	0.099	NS
1	40	—	0.000	...	-0.65	0.000	...
7	30	—	0.000	...	-0.55	0.003	..
9	55	—	0.718	NS	-0.24	0.080	NS
13	24	+	0.000	...	+0.64	0.002	..
14	24	+	0.001	...	+0.62	0.003	..
8	30	—	0.224	NS	-0.19	0.305	NS
11	80	—	0.378	NS	-0.05	0.673	NS
12	43	—	0.039	NS	-0.12	0.425	NS
2	52	+	0.008	..	+0.40	0.004	..
10	80	—	0.005	..	-0.25	0.025	•
Mollusca							
4	30	+	0.102	NS	+0.31	0.100	NS
5	35	+	0.005	..	+0.49	0.005	..
3	55	+	0.090	NS	+0.19	0.157	NS
6	30	+	0.001	..	+0.56	0.003	..
1	40	—	0.000	...	-0.67	0.000	...
7	30	+	0.002	..	+0.57	0.002	..
9	55	+	0.190	NS	+0.28	0.038	•
13	24	—	0.068	NS	-0.40	0.053	NS
14	24	—	0.008	..	-0.48	0.021	•
8	30	—	0.302	NS	-0.18	0.330	NS
11	80	—	0.024	•	-0.32	0.004	..
12	43	+	0.012	NS	+0.44	0.005	..
2	52	—	0.418	NS	-0.05	0.745	NS
10	80	+	0.664	NS	+0.13	0.254	NS
Echinodermata							
4	30	+	0.794	NS	+0.04	0.831	NS
5	35	+	0.142	NS	+0.12	0.499	NS
3	55	+	0.166	NS	+0.16	0.251	NS
6	30	+	0.000	...	+0.63	0.001	...
1	40	—	0.879	NS	-0.02	0.904	NS
7	30	+	0.664	NS	+0.07	0.725	NS
9	55	+	0.000	..	+0.51	0.000	..
13	24	+	0.003	..	+0.59	0.005	..
14	24	+	0.414	NS	+0.15	0.472	NS
8	30	—	0.766	NS	-0.12	0.504	NS
11	80	+	0.000	...	+0.49	0.000	...
12	43	+	0.000	..	+0.70	0.000	...
10	80	+	0.000	..	+0.38	0.001	...

Table 3 (continued)

Station No.	n	Linear regression			Spearman's rank		
		Slope	p	Sig.	r	p	Sig.
Crustacea							
4	30	—	0.000	***	-0.57	0.002	••
5	35	+	0.188	NS	-0.04	0.804	NS
3	55	—	0.810	NS	-0.02	0.871	NS
6	30	—	0.470	NS	-0.19	0.315	NS
1	40	—	0.011	•	-0.29	0.082	NS
7	30	+	0.025	•	+0.34	0.069	NS
9	55	+	0.005	••	+0.32	0.019	•
13	24	+	0.361	NS	+0.29	0.170	NS
14	24	+	0.581	NS	+0.21	0.313	NS
8	30	+	0.061	NS	+0.31	0.095	NS
11	80	+	0.040	•	+0.28	0.014	•
12	43	+	0.001	•••	+0.46	0.003	••
10	80	+	0.000	•••	+0.54	0.000	•••
Miscellaneous							
4	30	—	0.040	•	-0.29	0.120	NS
5	35	—	0.956	NS	-0.33	0.058	NS
3	55	—	0.801	NS	-0.01	0.924	NS
6	30	—	0.012	•	-0.32	0.089	NS
1	40	—	0.150	NS	-0.20	0.204	NS
7	30	—	0.074	NS	-0.31	0.093	NS
9	55	—	0.328	NS	-0.30	0.029	•
13	24	+	0.267	NS	+0.25	0.233	NS
14	24	+	0.572	NS	+0.25	0.229	NS
8	30	—	0.004	••	-0.40	0.032	•
11	80	—	0.030	•	-0.27	0.015	•
12	43	—	0.000	•••	-0.68	0.000	•••
10	80	—	0.000	•••	-0.43	0.000	•••
<i>Amphiura filiformis</i>							
4	30	+	0.282	NS	+0.23	0.210	NS
5	35	+	0.486	NS	+0.05	0.763	NS
3	55	+	0.236	NS	+0.19	0.157	NS
6	30	+	0.007	••	+0.45	0.016	•
1	40	—	0.459	NS	-0.11	0.493	NS
7	30	+	0.128	NS	+0.29	0.119	NS
9	55	+	0.001	•••	+0.45	0.001	•••
13	24	+	0.000	•••	+0.72	0.001	•••
14	24	+	0.003	••	+0.56	0.007	••
8	30	—	0.990	NS	-0.04	0.827	NS
11	80	+	0.000	•••	+0.47	0.000	•••
12	43	+	0.000	•••	+0.73	0.000	•••
10 ^a	80	+	0.000	•••	+0.46	0.000	•••
<i>Amphiura chiajei</i>							
4	30	—	0.620	NS	-0.09	0.619	NS
5	35	+	0.000	•••	+0.57	0.001	•••
3	55	+	0.158	NS	+0.16	0.229	NS
6	30	+	0.134	NS	+0.31	0.097	NS
1	40	+	0.042	•	+0.29	0.071	NS
7	30	+	0.140	NS	+0.22	0.236	NS
9	55	—	0.008	••	-0.26	0.054	NS
13	24	+	0.095	NS	+0.39	0.064	NS
14	24	—	0.280	NS	+0.10	0.624	NS
8	30	+	0.424	NS	+0.17	0.353	NS
11	80	+	0.707	NS	+0.10	0.357	NS
12	43	—	0.044	•	-0.23	0.134	NS

^a Data for the amphipod species *Amphilepis norvegica*

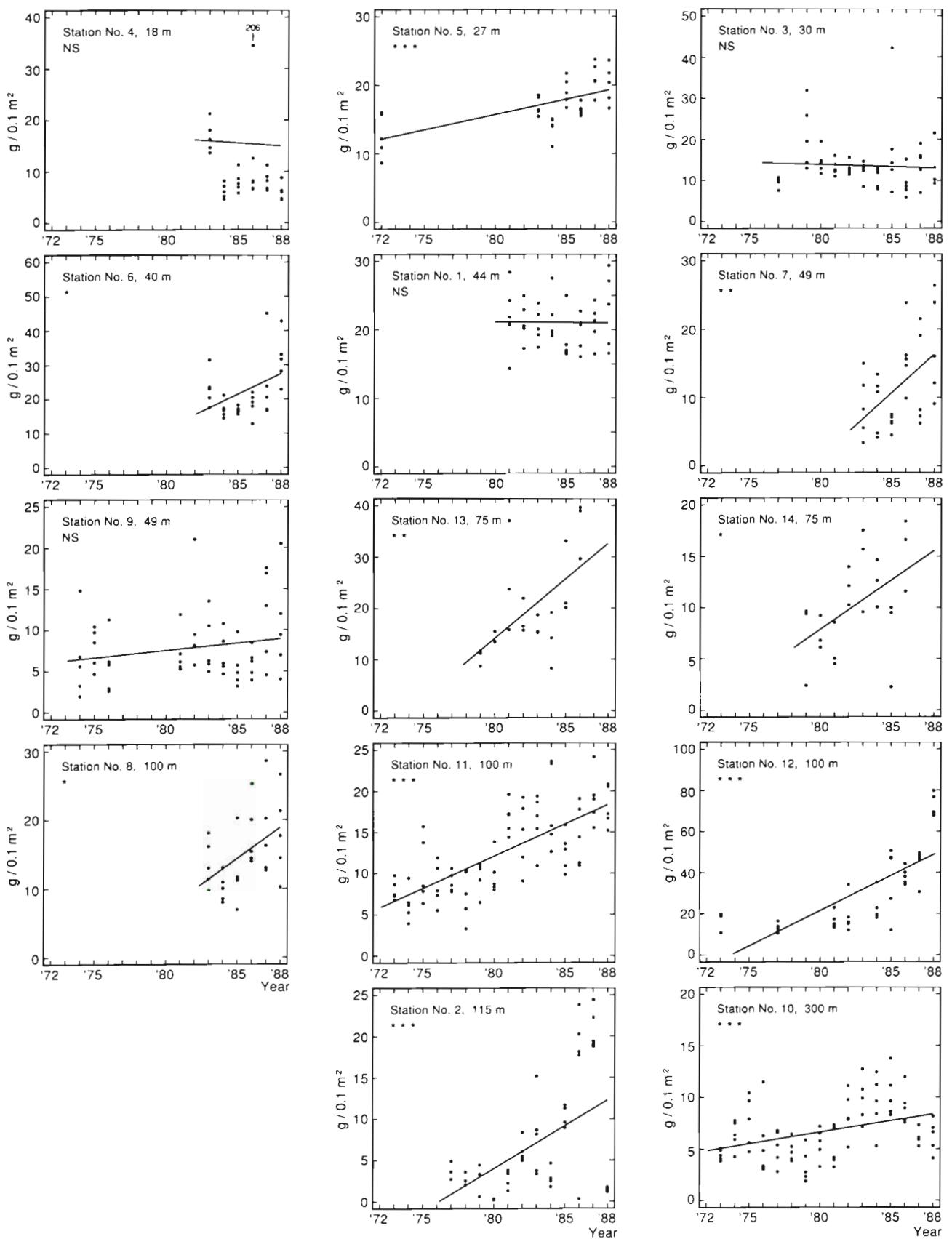


Fig. 2. Linear relationships with time for biomass without large species (see text for rationale) at 14 stations in the Skagerrak-Kattegat from 1972 to 1988. Data are values from individual grab samples. *** p < 0.001, ** p < 0.01; ns: p > 0.05 for the contribution of the linear model ($y = a + bx$) to the sum of squares

It is evident that there are significant changes at several stations for most categories except for biomass of Miscellaneous. To evaluate if there were general trends among the stations, that is if there is a basis for claiming that a change has occurred in the area, the results of regression analysis from individual stations were tested by the sign test (Table 4). The station set was viewed as a random sample of the area, that is the eastern part of Skagerrak and Kattegatt from Väderöarna in the north to Fladen in the south. The null hypothesis was that there was no general linear change in the area in the period 1972 to 1988. Total biomass showed a significant ($p < 0.05$) increase. At 12 out of 14 stations slopes of the regression lines were positive, and at 8 out of 8 stations where significant changes have occurred, the slopes were positive. Biomass without large species showed positive slopes at 11 out of 14 stations, which is on the border of significance ($p = 0.061$), and at the 10 stations where significant changes occurred all 10 slopes were positive, which is very significant ($p < 0.01$).

Polychaete biomass showed positive slopes at 12 out of 14 stations, which is significant ($p < 0.05$), whereas 4 positive slopes out of 5 significant changes is not significant ($p > 0.05$). Echinoderm biomass showed a significant positive trend ($p < 0.05$) using both approaches; 11 out of 13 and 6 out of 6 respectively. Abundance of the same category showed significant ($p < 0.05$) increases using both all slope signs and only the significant ones. Amphiuroid biomass showed positive slopes at all 13 stations ($p < 0.001$) and 8 of the 8

significant changes were positive ($p < 0.05$). Of the amphiuroids *Amphiura filiformis* showed significant ($p < 0.05$) increases with both approaches. The only tendency to decrease was shown by abundance of the group Miscellaneous, with 11 negative slopes out of 13 ($p < 0.05$) and with 6 negative ones out of 6 significant changes ($p < 0.05$).

The results of the nonparametric correlation analyses (Tables 2 and 3) essentially confirm the results of the parametric regression analysis. All significant results with the latter method were still significant with rank correlation ($p < 0.05$) except for total biomass ($p = 0.061$, $p = 0.077$) and Polychaeta biomass ($p = 0.061$) which were on the border of significance.

There is thus a basis for concluding that a positive trend exists for biomass in the area within the last 16 yr, and that a major part of this trend is due to echinoderms, notably amphiuroids, and polychaetes. To examine if there were differences within the area and between different depths, and to obtain an impression of the magnitude of the changes, absolute as well as relative changes were assessed in the following way. Using the regression equations on untransformed data the values in the first and the last year were calculated. The difference between the last and the first year yielded the absolute change, and the quotient between the last and the first yielded the factor of change.

In Fig. 3 the absolute changes in biomass are plotted against water depth. It is evident that at many of the stations shallower than 100 m a major part of the increase in total biomass was due to echinoderms. A

Table 4. Results of sign test applied to results from regression analysis of changes in benthic biomass and abundance at 14 stations in the Skagerrak-Kattegat area. The probabilities (p) were calculated for the outcomes of regression line slope signs and the outcomes of significant contributions of the linear model ($y = a + bx$) to the sum of squares. Biomass without = biomass without large species. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; NS: $p > 0.05$

Category	Sign of slope			Significance of regression line ($p < 0.05$)		
	+	-	p	+	-	p
Biomass						
Total biomass	12	2	0.016 *	8	0	0.013 *
Biomass without	11	3	0.061 NS	10	0	0.0044 **
Polychaeta	12	2	0.016 *	4	1	0.37 NS
Mollusca	6	8	0.79 NS	4	1	0.37 NS
Echinodermata	11	2	0.027 *	6	0	0.041 *
Amphiuroidea	13	0	0.00087 ***	8	0	0.013 *
Crustacea	9	4	0.27 NS	4	1	0.37 NS
Miscellaneous	7	6	1.00 NS	0	1	—
Abundance						
Total abundance	10	4	0.18 NS	4	2	0.68 NS
Polychaeta	3	11	0.061 NS	3	5	0.72 NS
Mollusca	8	6	0.79 NS	4	3	1.00 NS
Echinodermata	11	2	0.027 *	6	0	0.041 *
<i>Amphiura filiformis</i>	11	2	0.027 *	7	0	0.023 *
<i>Amphiura chiajei</i>	8	4	0.39 NS	2	2	0.62 NS
Crustacea	9	4	0.27 NS	5	2	0.76 NS
Miscellaneous	2	11	0.027 *	0	6	0.041 *

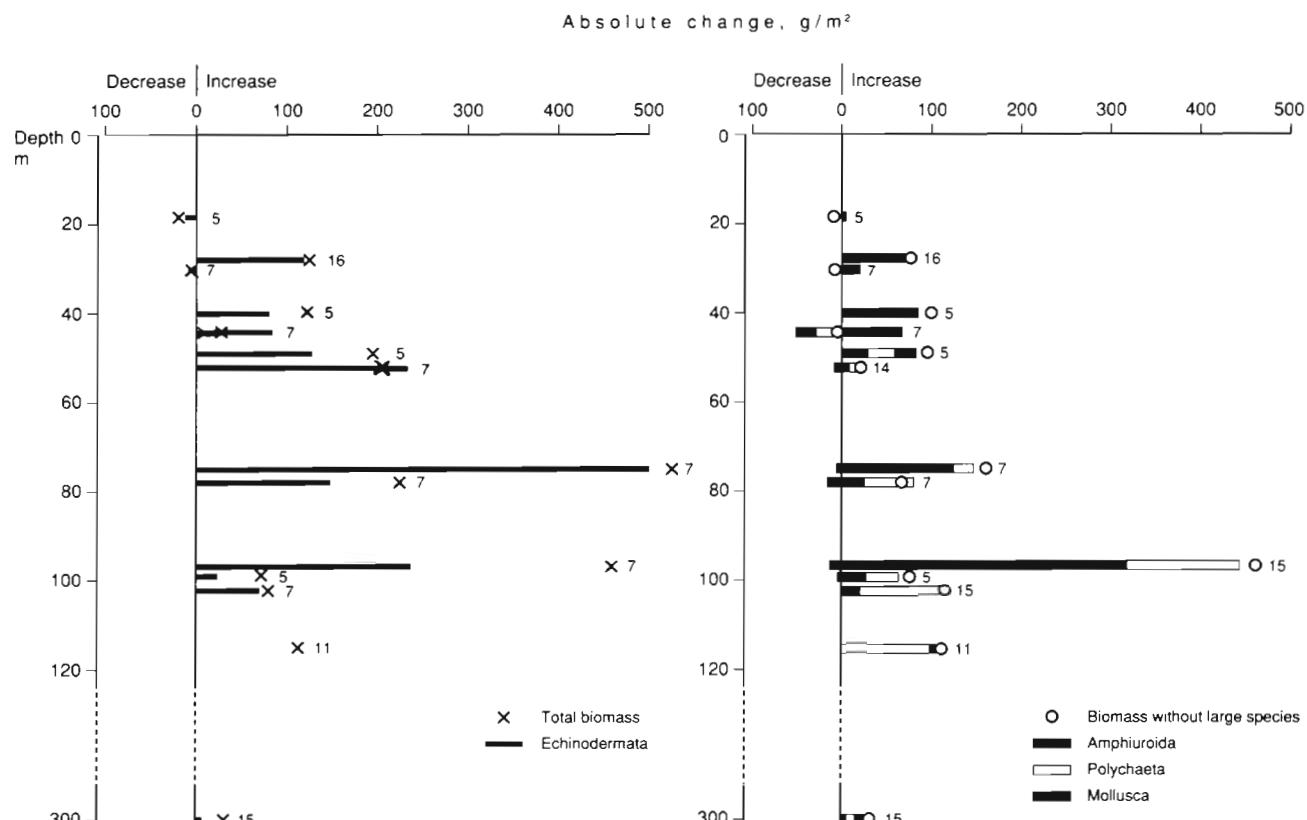


Fig. 3. Absolute change in total biomass and biomass of echinoderms (left) and change in biomass without large species and taxonomic groups (right) plotted against water depth. Figures in connection with symbols show the length of the observation periods (yr)

Table 5. Results of statistical testing for relations between water depth (m) and absolute magnitude of increase, as well as the factor of change, in biomass and abundance between the start and end of the observation period at each station. r: correlation coefficient; p: probability of no correlation using Spearman's rank analysis. n: = number of observations. See Table 4 for further information

Category	n	r	p
Absolute increase			
Total biomass	12	-0.17	0.58 NS
Biomass without	11	0.18	0.56 NS
Polychaeta biomass	12	0.69	0.022 *
Echinodermata: Biomass	11	-0.24	0.46 NS
Abundance	11	0.14	0.64 NS
Amphiuroidea biomass	13	0.01	0.97 NS
<i>Amphiura filiformis</i> abundance	11	0.26	0.39 NS
Factor of change			
Total biomass	14	0.47	0.092 NS
Biomass without	13	0.73	0.011 *
Polychaeta biomass	13	0.67	0.021 *
Echinodermata: Biomass	12	0.48	0.11 NS
Abundance	13	0.43	0.14 NS
Amphiuroidea biomass	12	0.79	0.0090 **
<i>Amphiura filiformis</i> abundance	13	0.61	0.035 *

major part of the increase in biomass without large species was due to amphiuroids and polychaetes. The latter category contributed more to the increases at the deepest stations. Of all categories showing significant general increases in biomass over time only polychaetes showed a significant ($p < 0.05$) relation between absolute increase in biomass and depth (Table 5).

The factor of change plotted against depth is shown for total biomass and biomass without large species in Fig. 4. The median factor of change was ca 1.8 for the former and ca 1.7 for the latter category. Total biomass did not change with depth ($p > 0.05$) whereas biomass without large species increased with depth ($p < 0.05$; Table 5). The same trend was evident for biomass of both polychaetes ($p < 0.05$) and amphiuroids ($p < 0.01$), and for abundance of *Amphiura filiformis* ($p < 0.05$; Table 5).

DISCUSSION

Previous benthic work in the study area has suggested that large-scale factors have been important in creating patterns of abundance during the period 1981 to 1986 (Josefson 1987). Variation in the sedimentation

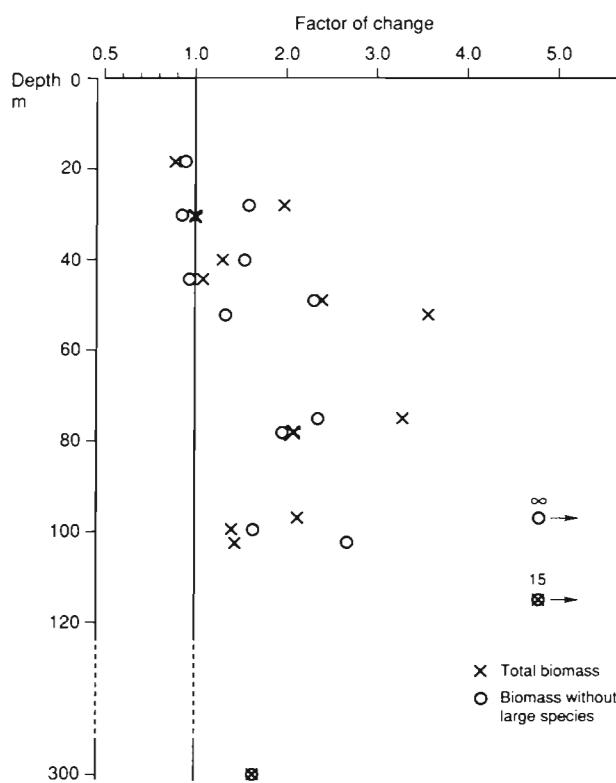


Fig. 4. Factors of change in biomass plotted against water depth

of organic material has been suggested to be an important factor affecting benthic dynamics. In this paper it is shown that while there is no long-term (> 10 yr) trend in total abundance, benthic biomass showed a general increase within the 16 yr 1972 to 1988. The greatest increase in relative terms occurred at the deeper stations, most of them situated offshore, in the Skagerrak. The increase was mainly due to an increase in the abundance of *Amphiura filiformis* and an increase in individual weight of polychaetes.

The generality of the results of this study is corroborated by results from a number of other local studies and comparisons with studies from the beginning of this century. Total biomass and polychaete biomass in particular increased over the period 1974 to 1986 in the Askeröfjord (see Fig. 1) (Smith 1982, Josefson & Smith 1984, Josefson 1986). In the Väro area in northeastern Kattegat total biomass increased at many of the stations below the halocline from the mid 1970s to 1985 (Smith 1986). Most of this increase was due to *Amphiura filiformis* and polychaetes.

In 1984 and 1985 comparisons were made with Petersen's benthic investigations in Kattegat and Skagerrak in 1911 to 1914. In the eastern part of Kattegat, deeper than 25 m, the biomass 'excluding echinoids' had increased, and again a major part of the increase was due to polychaetes and *Amphiura filiformis* (Pearson et al. 1985). The same taxa also formed a major part of the biomass increase in northern Skagerrak and Oslofjord (Rosenberg et al. 1987). In the latter study it was concluded that the difference by a factor of 1.8 over 71 yr was greater than that reported from the Skagerrak area during the 1970s, and the increase therefore could have been accumulated over a long time period. However the present data from the eastern Skagerrak for the same taxa indicate an increase of the same order of magnitude during 5 to 16 yr. It is therefore likely that much of the biomass difference noted by Rosenberg et al. (1987) was a relatively recent phenomenon.

Reports of increasing benthic biomass over time are now accumulating from areas other than the Kattegat-Skagerrak. In several of these reports the authors have considered eutrophication to be a likely cause. Cederwall & Elmgren (1980) and Persson (1981, 1987) described increases in benthic biomass over at least 50 yr (1920s to 1970/80s) in the Baltic Sea. Brey (1986) reported increases above the halocline over 20 yr (1960s to 1980s) in Kiel Bay. Beukema & Cadee (1986) reported increased benthic biomass and secondary production in the Dutch Waddensee over the period 1970 to 1984, which paralleled an increase in primary productivity, the majority of which occurred in the beginning of the 1980s. The ophiuroid *Amphiura filiformis* had increased in density over large areas of the North Sea between the 1930/50s and the 1980s (Duineveld et al. 1987).

One possible explanation to the large-scale change could be that conditions for recruitment of the important species, such as *Amphiura filiformis*, have been favourable for instance due to climatic changes. However, the biomass increase is not only due to changes in abundance in a single species. Furthermore a part of the increase is also due to an increase in body weight of polychaetes, such as *Heteromastus filiformis* (Josefson unpubl.). It is therefore not likely that this is the only explanation.

In addition there are essentially 2 possible explanations for the observed increase in biomass. The first assumes that the infauna is limited by predation. Decreased intensity of predation by mobile epifauna and/or demersal fish would therefore allow infaunal biomass to increase either through higher survivorship or through increased longevity reflected by greater individual size. The following reasons, however, contradict such an explanation for the Skagerrak-Kattegat area.

(1) There are no data showing a general decrease in stocks of demersal fish or other potential predators. The annual landings of cod, whiting, plaice and haddock from the Skagerrak and Kattegat combined appear not to have changed dramatically over the last 16 yr (data

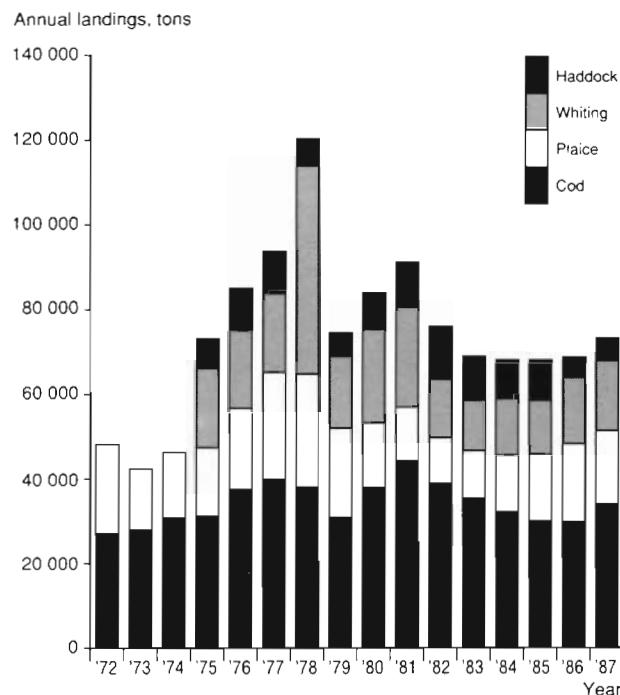


Fig. 5. Annual landings for 4 demersal fish species from the Kattegat and Skagerrak combined over the period 1972 to 1987. Figures for whiting and haddock are lacking from 1972 to 1974. (Data from ICES)

from ICES; Fig. 5). When taken separately, plaice landings from Kattegat decreased considerably during the 1980s whereas the landings from Skagerrak increased.

(2) A part of the increase in polychaete biomass was due to *Heteromastus filiformis* (Josefson unpubl.), a species which due to its deep burrowing habits is likely to be less affected by predation (e.g. Shaffer 1983).

(3) Different predators dominate in different areas, whereas the infaunal biomass change was more or less general. A general decrease of most potential predators seems unlikely.

The remaining possibility is increased sedimentation of organic material to the bottom. This explanation assumes that the infauna is food limited. Several studies, both correlative and experimental, have shown that benthic biomass often increases in response to organic enrichment (e.g. Pearson & Rosenberg 1978, Dauer & Conner 1980, Eleftheriou et al. 1982, Levin 1986). There is, in fact, circumstantial evidence that infauna in parts of the Skagerrak have been resource limited, for example decreased growth at high densities (Josefson 1982); decreased densities of subsurface feeders in areas with low content of buried organic material; and decreasing biomass with water depth (Josefson 1985).

Although there are few values on primary productivity available from the study area and period, those which exist suggest an increase (Nielsen & Årtebjerg

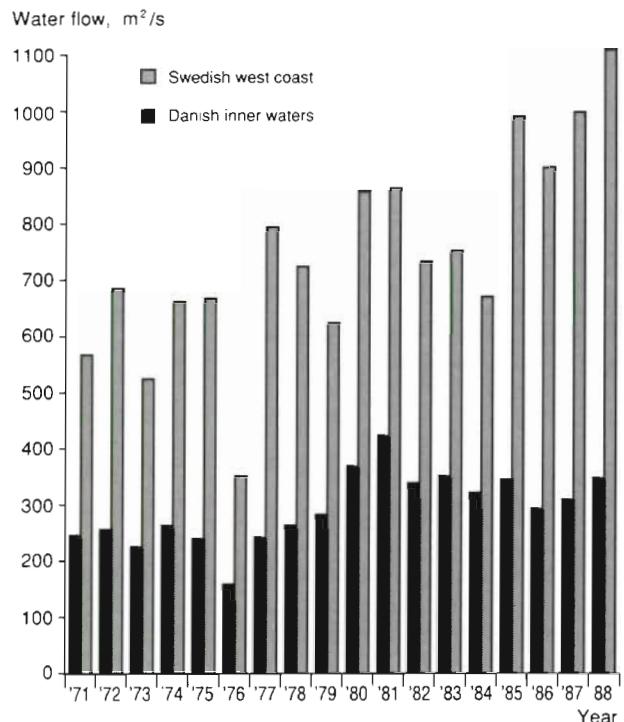


Fig. 6. Changes in annual mean water flow in the 10 largest waterways in western Sweden, and land runoff from Denmark to Danish inner waters in the period 1971 to 1988. (Data from the Swedish Meteorological and Hydrological Institute and Det Danske Hedeselskab, Hydrometriske Undersøgelser)

1984, Årtebjerg 1987). It is established that the input of nutrients to the Scandinavian seas has increased considerably over the last 15 yr (Fleischer et al. 1987, Andersson & Rydberg 1988, Wiederholm 1988). Nutrient concentrations in the seawater of both the Kattegat and the Skagerrak have increased over the last 2 decades (Svansson 1984, Andersson & Rydberg 1988). It is also well known that the nutrient input to the sea is strongly and positively correlated with land freshwater run-off (e.g. Nielsen & Årtebjerg 1984). Therefore, changes in river water flow should reflect changes in nutrient input. The annual mean water flow in the 10 major waterways of western Sweden and the land run-off from Denmark to inner Danish waters are shown in Fig. 6 for the period 1971 to 1988. Water flow from Sweden increased by ca 50 % over the period 1977 to 1988, and the flow from Denmark increased from the mid 70s to the beginning of the 80s, and remained at a high level throughout the 80s. The increase in water flow started before the observed increase in benthic biomass. A linear correlation analysis between the annual mean water flow and the mean infaunal biomass over the period 1973 to 1986 based on the 6 stations (2, 3, 9, 10, 11 and 12) in the Skagerrak showed significant positive results ($p < 0.05$) with 0, 1 and 2 yr time lag. The best correlation was obtained with a time

lag of 2 yr ($p = 0.01$). Two years is a reasonable time to allow for plankton production, sedimentation, recruitment and growth of benthic animals.

The correlation between biomass and land run-off from western Sweden is in accordance with the eutrophication hypothesis. In addition to Sweden the Skagerrak-Kattegat area receives nutrients and organic material from several other countries such as Denmark and the countries along the southern North Sea (Weering et al. 1987). The nutrient input to the southern North Sea has increased considerably over the last 2 decades (Berg & Radach 1985); for example through the river Rhine, which is the major nutrient source for the Southern Bight and the German Bight of the North Sea (Lancelot et al. 1987); similarly the plankton biomass and productivity have increased (e.g. Beukema & Cadee 1986, Cadee 1986).

In conclusion, it seems likely that the described changes in the Skagerrak-Kattegat area may be part of a large-scale environmental change. Changes in precipitation and in land use (such as clear felling in Sweden) act in concert with a human-generated input of nutrients both on land and directly to the sea through the air.

Acknowledgements. Thanks go to Jon Havenhand and Jørgen Nørrevang Jensen for critically reading the manuscript and to all at Kristineberg Marine Biological Station who have been involved in sample processing and field work. The samples from Stns 13 and 14 were collected and processed by Bengt Yhlen at the Swedish Meteorological and Hydrological Institute SMHI, and the Swedish water flow data were provided from the same institute. Financial support was given by the National Swedish Environmental Protection Board, and the data in this paper were collected within the Swedish Environmental Monitoring Program PMK.

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This article was submitted to the editor

Manuscript first received: February 12, 1990

Revised version accepted: June 5, 1990