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Studies on the Covariation between Physical Factors and the Long-Term Variation of the Marine Soft Bottom Macrofauna in Western Sweden

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A seven to 13 year data series of yearly macrobenthic (infaunal) mean abundance data from eight stations in, or adjacent to Gullmarsfjorden, on the Swedish west coast were compared to the freshwater runoff to the fjord, temperature at 600 m depth in the Skagerrak (temp 600) and to the North Atlantic Oscillation (NAO) index. The NAO index was positively correlated with temperature at 600 m depth in the Skagerrak and negatively correlated to the runoff. Macrobenthic abundances at the three stations outside the fjord (depth range 40–100 m) and two stations inside the fjord (118 m and 44 m), correlated negatively to temperature at 600 m depth in the Skagerrak. This study indicates that the correlation may be caused by a NAO influenced, periodically increased upwelling of deep water, rich in dissolved inorganic nutrients, resulting in a corresponding primary production and food input increase to the benthos. There was a positive correlation of macrobenthic abundances at these stations to runoff, probably caused by the input of depositing organic detritus. Macrobenthic abundances at the three stations in the inner part of the fjord (depth range 25–65 m) correlated positively to the NAO index. This is proposed to be an effect of strong stratification when the NAO index is low, which causes low primary production.

Keywords: benthos; NAO; oscillation; climate; upwelling; runoff; infauna; Skagerrak; Sweden coast

Introduction

Background

Gullmarsfjorden is situated on the Swedish Skagerrak coast. The fjord has a maximum depth of 118 m and a sill depth of approximately 40 m. The soft bottom macrobenthos (infauna) of the fjord has experienced a number of severe community crashes since the National Benthic Monitoring Program of the Swedish west coast started in the beginning of the 1970s (Tunberg, 1998). The crashes have earlier been blamed primarily on excessive dissolved inorganic nutrient input causing strong algal blooms which created hypoxic conditions in the bottom water. Recent studies have revealed that macrobenthic (infaunal) abundances at a number of stations along the Swedish Skagerrak coast, including stations in Gullmarsfjorden, correlate positively to the changes of the North Atlantic Oscillation (NAO) index (Tunberg & Nelson, 1998). The macrobenthic community crashes in Gullmarsfjorden were therefore suspected to be influenced by large scale climatic forcing, probably connected to the NAO.

In order to look for possible explanations for the correlation of the soft bottom macrobenthos and the NAO, benthic data from five stations in Gullmarsfjorden and three stations outside the fjord were studied and compared with hydrological and climatic data.

The North Atlantic Oscillation (NAO)

The NAO is a climatic pressure anomaly which is measured as the atmospheric sea level pressure difference between the Icelandic low and the Azores high (Rogers, 1984). The NAO has a period of 7·3–8 years (Rogers, 1984; Tunberg & Nelson, 1998). The index is considered high when the atmospheric sea-level pressure is low at Iceland and high at the Azores. According to Hurrell (1995) this condition results in increased westerlies in the North Atlantic which causes an increased transport of warm air and moisture onto northern Europe, including Scandinavia, resulting in milder winters as opposed to the more continental climate during low NAO periods. The NAO has been found to correlate to zooplankton abundances in the North Sea (Fromentin & Planque, 1996), the position of the North Wall of the Gulf Stream (Taylor, 1995), macrobenthic abundances Kröncke *et al.*, 1998; Tunberg & Nelson, 1998) and

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TABLE 1. Sampling stations, their positions, depths, sampled years and number of replicates taken in different years

Station	Lat.	Long.	Depth (m)	Sample period	No. of replicates
L6	58°15.20′N	11°03.50′E	100	1983–1995	5 (94–95, 4 repl.)
L5	58°14.40′N	11°15.00′E	49	1983–1995	5 (94–95, 4 repl.)
L4	58°14.68′N	11°25.58′E	40	1983–1995	5 (94–95, 4 repl.)
AL	58°19.38′N	11°32.75′E	118	1983–1995	5 (94–95, 4 repl.)
S2	58°24.20′N	11°37.74′E	65	1988, 1990–1995	3 (94–95, 4 repl.)
SF	58°24.97′N	11°38.65′E	44	1983–1995	5 (94–95, 4 repl.)
S1	58°25.91′N	11°40.52′E	25	1988, 1990–1995	3 (94–95, 4 repl.)
S3	58°25.15′N	11°35.59′E	25	1988, 1990–1995	3 (94–95, 4 repl.)

the temperature at 600 m depth in the Skagerrak, as well as runoff to this region (Tunberg & Nelson, 1998).

Water exchange in the Skagerrak

The major part of the water exchange in the Skagerrak takes place along the Norwegian trench with two secondary surface currents, the Jutland Current and the Baltic Current. The intermediate depth water (50–500 m) enters the Skagerrak along the southern slope of the Norwegian trench, passes Skagen, the northern tip of Denmark, turns north along the Swedish coast and exits the Skagerrak along the northern slope of the trench (Svansson, 1975; Rodhe, 1987). The current motion creates an anticlockwise gyre with a residence time of approximately 100 days (Rodhe, 1987). However, the exchange of the Skagerrak bottom water (>500 m, maximum depth 700 m) is the result of occasional inflows rather than due to a continual current, from the North Sea (Ljøen & Svansson, 1972). Stagnation periods between deep water inflows are known to vary from 1 to 3 years (North Sea Task Force, 1993).

Materials and methods

Data material

Five stations in Gullmarsfjorden and three stations outside the fjord have been sampled for soft bottom macrobenthos (infauna) as part of either Swedish national or regional monitoring programmes (Table 1; Figure 1). All stations were sampled in April–May every year. Faunal samples were collected with a modified Smith-McIntyre grab (0·1 m^2, 70 kg), washed on a 1-mm mesh sieve, and material retained was preserved in the field (4% buffered formalin–sea water solution) (Tunberg & Nelson, 1998). Mean abundance of the replicates were used for the analyses.

Additionally the following hydrological and climatic variables were used in the study:
(1) The NAO winter index (December–February) during the period 1970 to 1995 (Rogers, 1984).
(2) The temperature in May at 600 m depth (temp 600) in the Skagerrak between Torungen (Norway) and Hirtshals (Denmark) from 1970 to 1994.
(3) The freshwater runoff to Gullmarsfjorden (river Örekilsälven) measured as yearly mean flow ($m^3 s^{-1}$) during the period 1980 to 1995 calculated from monthly means.
(4) The yearly mean precipitation to the Norwegian part of the Skagerrak catchment area (98 000) km^2) calculated from monthly means.

Statistical procedures

The PRIMER (Plymouth Routines In Multivariate Ecological Research) software package was used for multi dimensional scaling (MDS) analyses (Carr, 1993; Clarke & Warwick, 1994; Carr, 1996). The MDS analyses were performed to compare the benthic communities between different years and stations in order to clarify whether community composition changes had occurred simultaneously at different stations. Plots were made separately for each station. The data were double root transformed in order to decrease the influence of dominating species (Field, *et al.*, 1982). The program RELATE in the PRIMER package was used to correlate abundance changes at the different stations. The method basically relates the position of the points between the different MDS plots and compares the change over time. The program calculates Spearman correlation coefficients computed on the corresponding elements of two

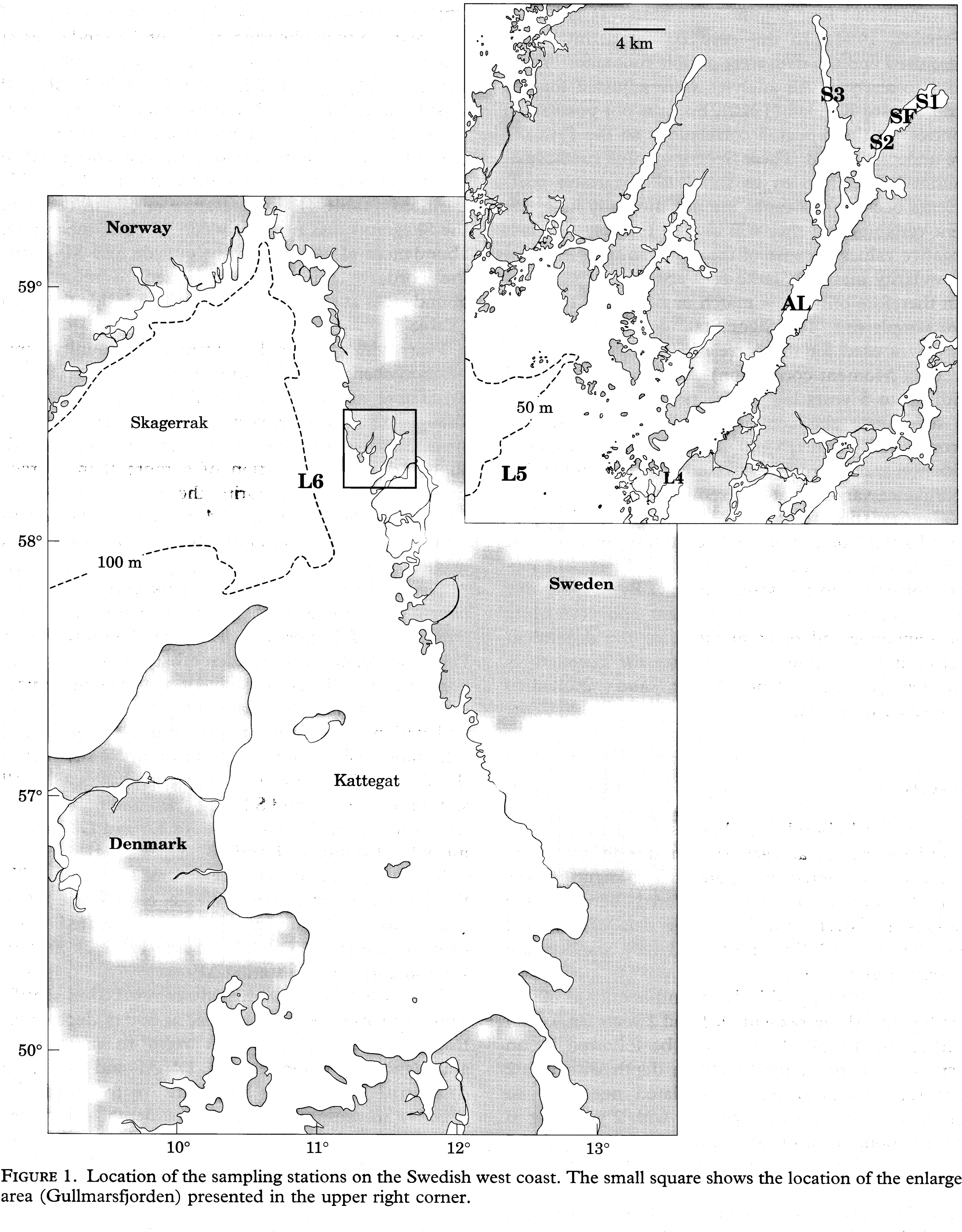


FIGURE 1. Location of the sampling stations on the Swedish west coast. The small square shows the location of the enlarged area (Gullmarsfjorden) presented in the upper right corner.

triangular matrices of rank similarities based on Bray-Curtis similarity matrices and uses Monte Carlo permutations for significance tests (Clarke & Warwick, 1994). In this case 20 000 permutations were used and the data were double root transformed prior to analysis. All analyses were adjusted for ties according to Kendall (1970), but it is not possible to control for the repeated correlations so the *P*-values are underestimated. These Spearman rank coefficients cannot be referred to as standard Spearman coefficients because the ranks are not mutually independent variables and they will also be unlikely to attain negative values because of the constraints inherent in a similarity matrix (Clarke & Warwick, 1994). They can therefore only show match or no match between two sample sets. The SigmaStat® for Windows software was used for the correlation analyses (Pearson Product Moment correlation) which were performed with up to 5 years lag. These procedures were used to investigate the covariation of (a) different environmental factors; (b) macrobenthic abundance variation and environmental factors; (c) macrobenthic abundance variation at different stations.

The Statistica® software package was used to perform Partial Correlation analyses to test the individual correlations in cases where several independent factors correlated to the same variable. By keeping one of the independent factors constant and correlating the remaining independent factor to the dependent factor, it is possible to investigate the correlations between a dependent factor and individual independent factors.

Results

The temporal abundance changes for the four most abundant species at each station during the study period are presented in Figure 2. This figure shows that the dominant species differed between the stations and over time. The basic data of the total abundance variability at the different stations are presented in Table 2.

NAO correlated positively to temperature at 600 m depth in the Skagerrak with 0, 1 and 2 years lag, i.e. an increase of the NAO index will be followed by an increase in temperature at 600 m depth with a 0–2 year lag. However, NAO correlated negatively to runoff with no lag and, negatively with 2 years lag to precipitation. Runoff and precipitation correlated positively with no lag (Table 3). Using Partial Correlations, precipitation correlated positively to runoff, if the variation of NAO was controlled for showing the association of the two irrespectively of the variation due to NAO. Runoff also correlated positively to NAO, controlling for precipitation (Table 4).

The NAO index correlated positively with delays of 0–1 years to macrobenthic mean total abundances at stations S1, S2 and S3 but not to mean total abundances at L6, L5, L4, AL and SF (Table 5). Runoff was positively correlated to mean total abundances at stations L4 and L5 at the mouth and outside the fjord (L6, $r=0{\cdot}51$, $P=0{\cdot}066$), and negatively correlated to mean total abundances at stations AL and S3, inside the fjord (Table 5). Temperature at 600 m depth in the Skagerrak was negatively correlated to mean total abundances at all the stations outside and SF inside the fjord, but positively correlated to mean total abundances at stations AL, S1 and S3 inside the fjord (Table 5).

Years with a larger than average community composition change were identified on MDS plots (Figure 3). These analyses indicate that large community changes occurred between 1988 and 1990 at the studied stations except for station SF and L4. SF showed a weak indication of a more than average change between years during the periods 1983–1984 and 1987–1988. At station L4, these plots showed no years when the community change was larger than average.

The multivariate Spearman rank correlations between the stations resulted in 18 significant correlations out of 28 possible (Table 6). The three outer L-stations all correlate to each other. Fjord station S3 correlates to all stations except the two outermost stations L5 and L6. Station S2 correlates to L6 and S3 and station S1 correlates to all stations except L5 and S2. Station SF, the only station from the inner part of the fjord with a long time series, correlates with all stations except AL and S2. The deep mid fjord station AL correlates to the outer stations L6 and L4 and the inner fjord stations S1 and S3.

Mean total abundances at the three stations outside the fjord correlated positively to each other while abundance at the inner station S3 correlated negatively to that at stations L5 and L4 (Table 7). Station L5 also correlates to station SF.

The Partial Correlation analyses resulted in significant correlations of temperature at 600 m depth controlling for runoff and vice versa to mean total abundances at stations L6, L5, L4, AL and S3 (Table 4). Partial Correlations were positive to runoff but negative to temperature at 600 m depth, except for station S3, where the situation was the opposite. When separating correlations of NAO and runoff to mean total abundance at station S3 we found that S3 correlated negatively to runoff, controlling for NAO and positively to NAO, controlling for runoff.

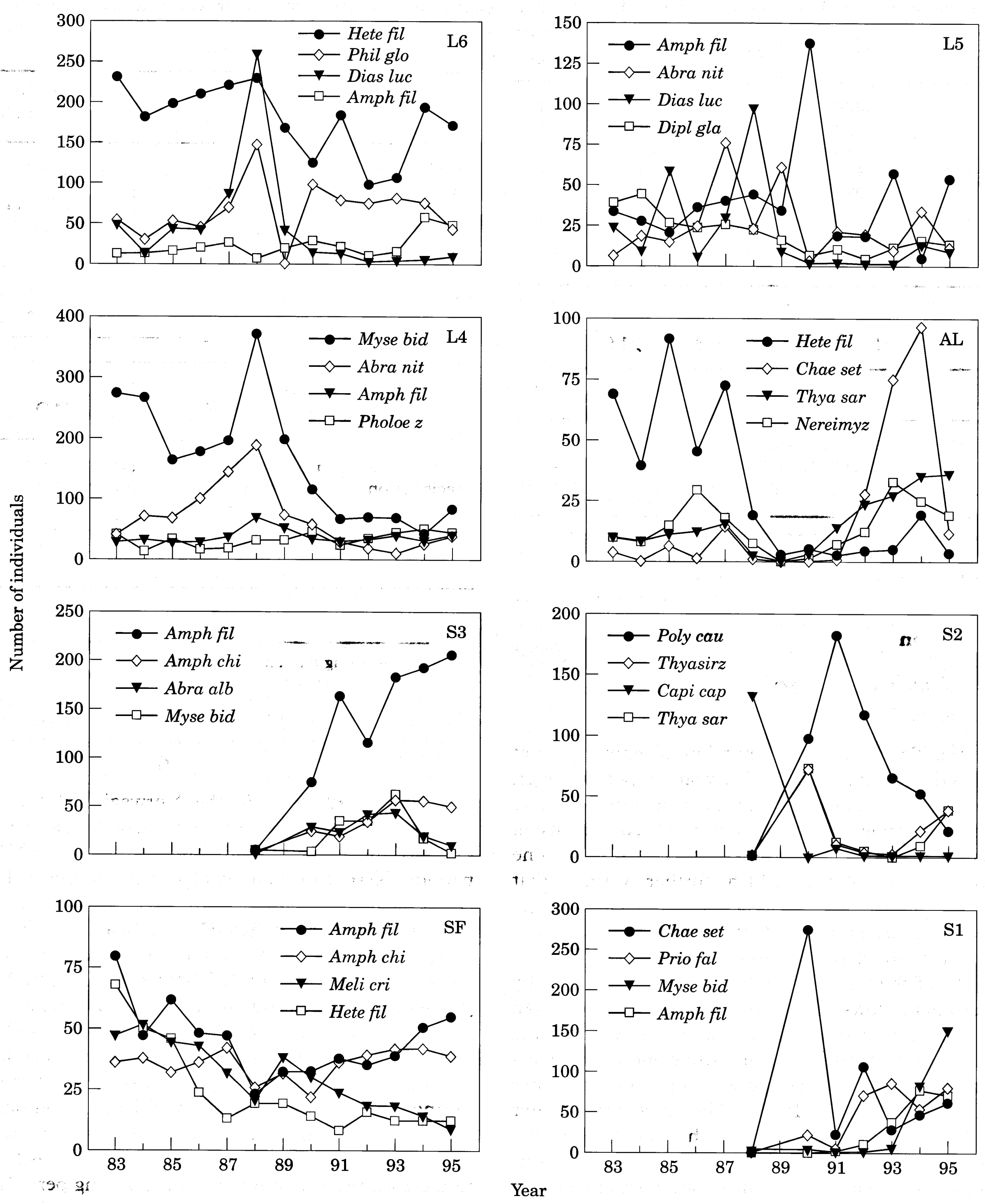


FIGURE 2. Abundance pattern of the four most abundant species at each station during the study periods. *Abra alb*: *Abra alba*; *Abra nit*: *Abra nitida*; *Amph chi*: *Amphiura chiajei*; *Amph fil*: *Amphiura filiformis*; *Capi cap*: *Capitella capitata*; *Chae set*: *Chaetozone setosa*; *Dias luc*: *Diastylis lucifera*; *Dipl gla*: *Diplocirrus glaucus*; *Hete fil*: *Heteromastus filiformis*; *Meli cri*: *Melinna cristata*; *Myse bid*: *Mysella bidentata*; *Nereimyz*: *Nereimyra* sp.; *Phil glo*: *Philomedes globosus*; *Pholoe z*: *Pholoe* sp.; *Poly cau*: *Polydora caulleryi*; *Prio fal*: *Prionospio fallax*; *Thya sar*: *Thyasira sarsi*; *Thyasirz*: *Thyasira* sp.

TABLE 2. Descriptive statistics of the mean total abundance variations at the sampling stations during the study period

Station	Mean	SD	Max.	Min.
L6	480	149	761	244
L5	254	93	462	107
L4	589	174	979	326
AL	165	116	429	21
S2	285	134	495	105
SF	294	82	536	216
S1	406	175	623	104
S3	327	125	480	27

TABLE 3. Correlations between tested physical factors

	NAO	Runoff
Runoff	− 0·56* (0)	
Temp 600	0·41* (0), 0·51* (1), 0·48* (2)	–
Precipitation	− 0·64* (2)	0·71** (0)

r values are presented with significance level marked with *
(*P=<0·05, **P=<0·01, ***P=<0·001).
Time lags in years are presented in brackets.

TABLE 4. Partial correlation analysis of cases where more than one independent factor correlate to macrobenthic abundance variation. Time lags with the best significance value in Table 5 have been used

	Runoff contr. Temp600	Temp600 contr. Runoff
L6	pcc=0·61	pcc= − 0·69*
L5	pcc=0·72*	pcc= − 0·75**
L4	pcc=0·80**	pcc= − 0·85***
AL	pcc=0·61*	pcc= − 0·64*
S2		
SF		
S1		
S3	pcc= − 0·92***	pcc=0·90***

	NAO contr. Runoff	Runoff contr. NAO
S3	pcc=0·89**	pcc= − 0·91**
Precipitation	irrelevant	pcc=0·73**

	NAO contr. Precipitation
Runoff	pcc=0·95***

Contr. =controlling for . . .; pcc=Partial Correlation Coefficient.
Significance level marked with *
(*P=<0·05, **P=<0·01, ***P=<0·001).
NAO and temp 600 (*r*=0·51, *P*=0·012) can not be controlled for against each other, without losing all significant correlations.

Discussion

Relationship between NAO and temperature at 600 m depth in the Skagerrak

The significant positive correlation of temperature at 600 m depth with NAO (with 1 year temperature lag), described by Tunberg and Nelson (1998) using smoothed values for NAO was repeated, but using unsmoothed raw data. This resulted in the same significant correlation which further verifies that changes in the NAO index are associated with changes in temperature at 600 m depth in the Skagerrak. The bottom water of the Skagerrak is replaced either by cooling of the water on the North Sea plateau or by occasional inflows of deep water from the Norwegian Sea. When these inflows occur, it results in decreasing temperature at 600 m depth, while increasing temperature occurs during periods of stagnant water (Ljøen & Svansson, 1972). The exchanging water reaches the 600 m level in March, judging from the raw data. The mechanisms causing favourable conditions for water exchange have not been elucidated. However one possible explanation is that when the NAO index decreases, the winters get colder and consequently the water temperature in the North Sea decreases. The cool surface water sinks and replaces the Skagerrak bottom water (Ljøen & Svansson, 1972; Svansson, 1975). Another possible explanation is that a weaker stratification in the Norwegian Sea could develop during low NAO index periods, caused by colder water (weaker Gulf Stream during low NAO periods (Kerr, 1997) and cooler winter weather. This could facilitate the inflow of high density deep water from the Norwegian Sea (North Sea Task Force, 1993). The NAO index and the temperature at 600 m are presented in Figure 4. These plots indicate that the temperature at 600 m decreases at occasional inflows and also that the inflows occur during periods of 2–3 years when NAO is low. These inflows occur in February to March followed by a temperature increase during the year until next inflow. When inflows occur for several subsequent years, it appears that the temperature decreases further for each inflow. This leads to the conclusion that inflows occur during periods of low NAO and that the longer time NAO is low the lower the temperature at 600 m. The shortest stagnation periods occur during periods of cold winters (North Sea Task Force, 1993), which agrees with the positive correlations found between the NAO index and the temperature at 600 m depth. Our results are

TABLE 5. Correlations of mean total abundance at the different stations to hydrological and climatic factors

Station	NAO	Runoff	Temp 600
L6	n.s.	n.s.	− 0·60* (0)
L5	n.s.	0·68** (1)	− 0·66* (0), − 0·77** (1)
L4	n.s.	0·76** (0), 0·73** (1)	− 0·79** (0), − 0·79** (1), − 0·59* (2)
AL	n.s.	− 0·62* (3)	0·64* (3)
S2	0·82* (1)	n.s.	n.s.
SF	n.s.	n.s.	− 0·54* (3)
S1	0·83* (1)	n.s.	0·77* (5)
S3	0·77* (0)	− 0·85** (1)	0·71* (2)

r values are presented with significance level marked with *
(**P*=<0·05, ***P*=<0·01, ****P*=<0·001).
Time lag in years is presented in brackets.
n.s.: not significant.

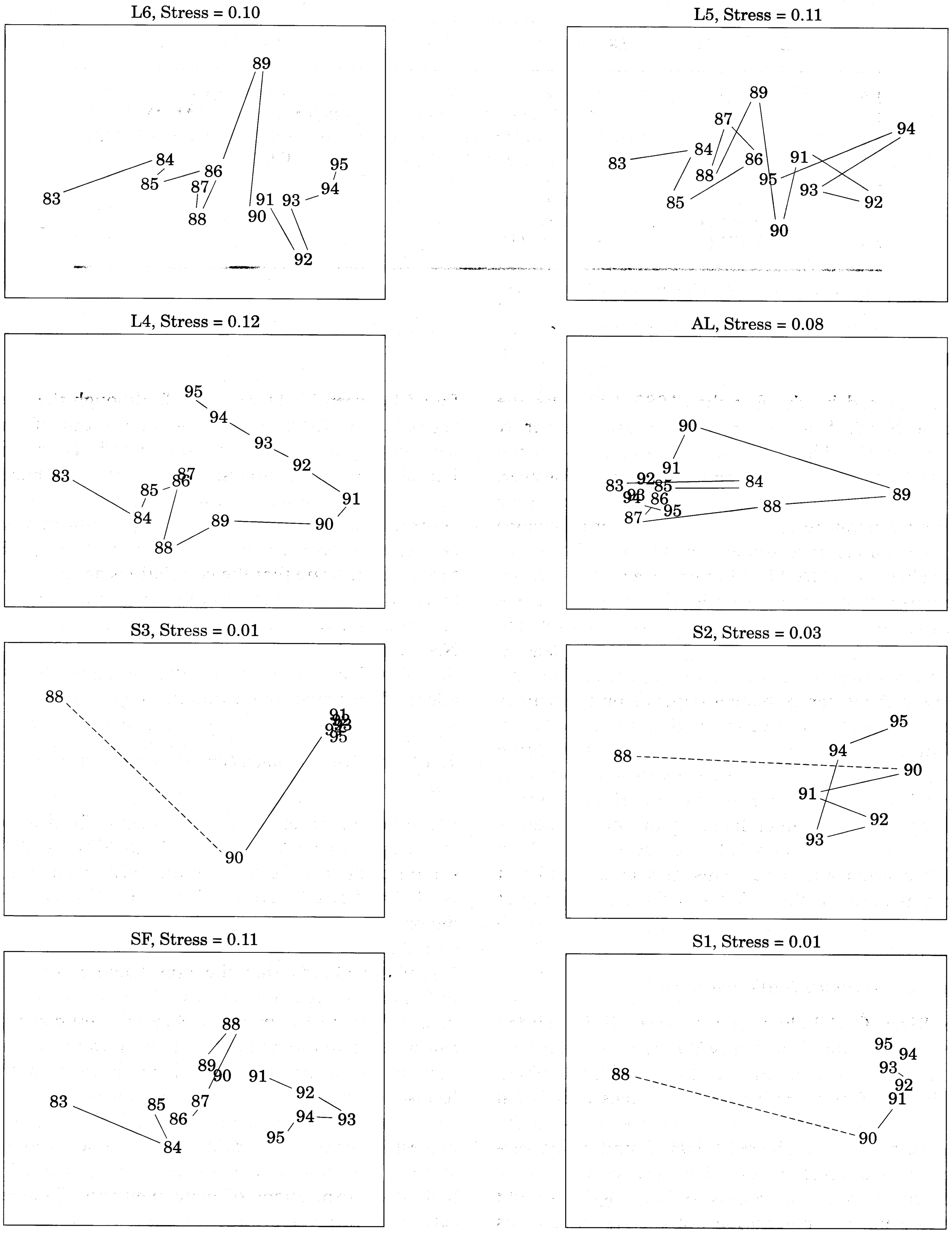
also supported by the fact that 1989–1990 was the mildest North Sea winter in 50 years (Becker & Dooley, 1995). The temperature lag of 1 year is too long to be explained by these mechanisms. However, when comparing the NAO index curve with the curve for the temperature at 600 m (Figure 4) it is obvious that the temperature sometimes also reacts without lag to changes in NAO in addition to lags of 1–2 years. The correlation lag of 1 year is of course an average over the whole study period and this is most likely the main reason for the different significant time lags. If the mechanisms suggested above operate, then the timing of the water exchanges depends on the density of the deep water relative to the density of the North Sea surface water. If the deep water is very dense (cold), the NAO index needs to be very low to cool the North Sea surface water enough to trigger a water exchange. On the other hand, if the deep water is warmer, then the NAO only has to decrease slightly to trigger a water exchange. This may create different time lags between the NAO and the temperature at 600 m.

Relationship between NAO and runoff

The River Örekilsälven runoff to Gullmarsfjorden correlated negatively to the NAO index with no time lag. A similar correlation was also found by Tunberg and Nelson (1998) with 0 to 2 year lags using total annual combined flow from all major streams on the Swedish west coast. Hurrell (1995) found, using vector plots, that a high NAO index increases the atmospheric moisture transport to Scandinavia. This should lead to a positive correlation but the reason for this disagreement is not known. The significant positive correlations between precipitation and runoff with no time lag supports the negative correlation that we found between NAO and runoff, although the 2 year lag between NAO and precipitation is out of phase with no lag between NAO and runoff. However, a Partial Correlation analysis shows that precipitation correlates with runoff with no lag if the correlation is controlled for NAO (Table 4). The significant correlations between precipitation and runoff, controlling for NAO, indicate that the correlations are not caused by covariation with the other variables but represent a separate variation. The Partial Correlation between NAO and runoff controlling for precipitation indicates that NAO has a covariation with runoff apart from the effect of precipitation on runoff.

Total abundance of macrobenthos versus NAO and runoff

Macrobenthic abundances at three inner fjord stations (S1, S2, S3) correlated positively to NAO while the station in the middle of the fjord (AL) or outside the fjord (L6, L5, L4) did not (Table 5). This is contradictory to the assumption that NAO influences the abundance at all stations. It has earlier been shown by Rosenberg (1995) that the polychaete *Heteromastus filiformis* may reach densities of 3000 ind. m^{-2} at depths down to 100 m on the Swedish west coast, and can be expected to be food-limited up to this density. Similar maximum densities have been found by Josefson and Conley (1997) for *Amphiura filiformis*. They also showed that the benthic biomass was the highest in areas where primary production was high and that the benthic macrofauna here contained the highest concentrations of plant pigments. This indicates that primary production may be an important factor for macrobenthic abundance variations. The maximum density of *H. filiformis* in the present study was 2300 ind. m^{-2} and that of *A. filiformis*



L6, Stress = 0.10

L5, Stress = 0.11

L4, Stress = 0.12

AL, Stress = 0.08

S3, Stress = 0.01

S2, Stress = 0.03

SF, Stress = 0.11

S1, Stress = 0.01

FIGURE 3. MDS plots of community changes at the different stations based on mean abundance of all species. Numbers on plots represent years.

Table 6. Multivariate Spearman rank correlations between Bray-Curtis similarity matrices of each station during the sampling period

	L5	L4	AL	S2	SF	S1	S3
L6	**0·545*****	**0·482*****	**0·411***	**0·451***	**0·527****	**0·575***	0·500 n.s.
L5		**0·364****	0·192 n.s.	0·018 n.s.	**0·359***	0·375 n.s.	0·174 n.s.
L4			**0·268***	0·321 n.s.	**0·418****	**0·660*****	**0·481***
AL				0·387 n.s.	0·176 n.s.	**0·900*****	**0·838****
S2					0·452 n.s.	0·595 n.s.	**0·668***
SF						**0·671****	**0·584***
S1							**0·883****

R values are presented with significance level marked with *
(**P*=<0·05, ***P*=<0·01, ****P*=<0·001).

Table 7. Correlations of mean total abundance between the stations without time lag. Significant correlations are highlighted

	L5	L4	AL	S2	SF	S1	S3
L6	**0·72****	**0·75****	0·18	0·05	0·28	−0·11	−0·57
L5		**0·87*****	−0·17	0·24	**0·58***	−0·05	**−0·69***
L4			−0·08	0·04	0·37	−0·26	**−0·84****
AL					−0·18	0·34	0·39
S2						0·62	0·16
SF							0·07
S1							0·46

R values are presented with significance level marked with *
(**P*=<0·05, ***P*=<0·01, ****P*=<0·001).

2040 ind. m^{-2} on one occasion, suggesting that the studied populations may have been food limited, and explanations should therefore be sought with this in mind. The climate pattern of high NAO index values is associated with cooler summers and milder winters, generating less stratified surface water (no, or limited, ice cover in the winter and weak thermocline in the summer) which may affect the inner, shallow stations to a higher degree compared to the outer stations. Decreased stratification may result in an increased flux of dissolved inorganic nutrients to the euphotic zone which increases primary production (Levinton, 1995) and therefore also food input to the benthos (Josefson & Conley, 1997). The short time lag of 0 to 1 years between the NAO and the effect on the bottom fauna at S1, S2 and S3 may seem too short for benthic abundances to increase. Figure 2 shows that different species are responsible for the major abundance changes at different times and stations. In spite of this, time lags to NAO and other factors are equal for several stations. It is therefore difficult to explain the lags in terms of the species responsible for the changes, such that certain abundant species common to all stations are responsible for the changes. However, as discussed above concerning deep water temperature lags, NAO may change gradually (Figure 4). The benthos will therefore experience a decreasing or increasing NAO several years before it reaches its peak and the peak in abundances will therefore be the result of the change in NAO that started a few years earlier. A lag of 0 years between NAO and the benthos is therefore equal to a lag of 1–2 years between the benthos and the beginning of the NAO change. The significant Partial Correlation between S3 and NAO, keeping runoff constant, suggests an effect of NAO in addition to runoff at station S3. However, the time series at these stations are short (8 (7) years) and correspond to only one period of the NAO cycle, which makes interpretation difficult.

Abundances at L5 and L4 correlated positively to runoff (Table 5), while a positive correlation at L6 was nearly significant (P=0.066). This may be due to the increase of dissolved inorganic nutrients caused by the runoff water which results in increased primary production and benthic food input. Positive correlations between dissolved inorganic nutrient concentrations in the Skagerrak coastal water and runoff were found by Josefson *et al.* (1993). Partial correlation analysis of L4, L5 and L6 to runoff were significant if temperature at 600 m was kept constant. This excludes the

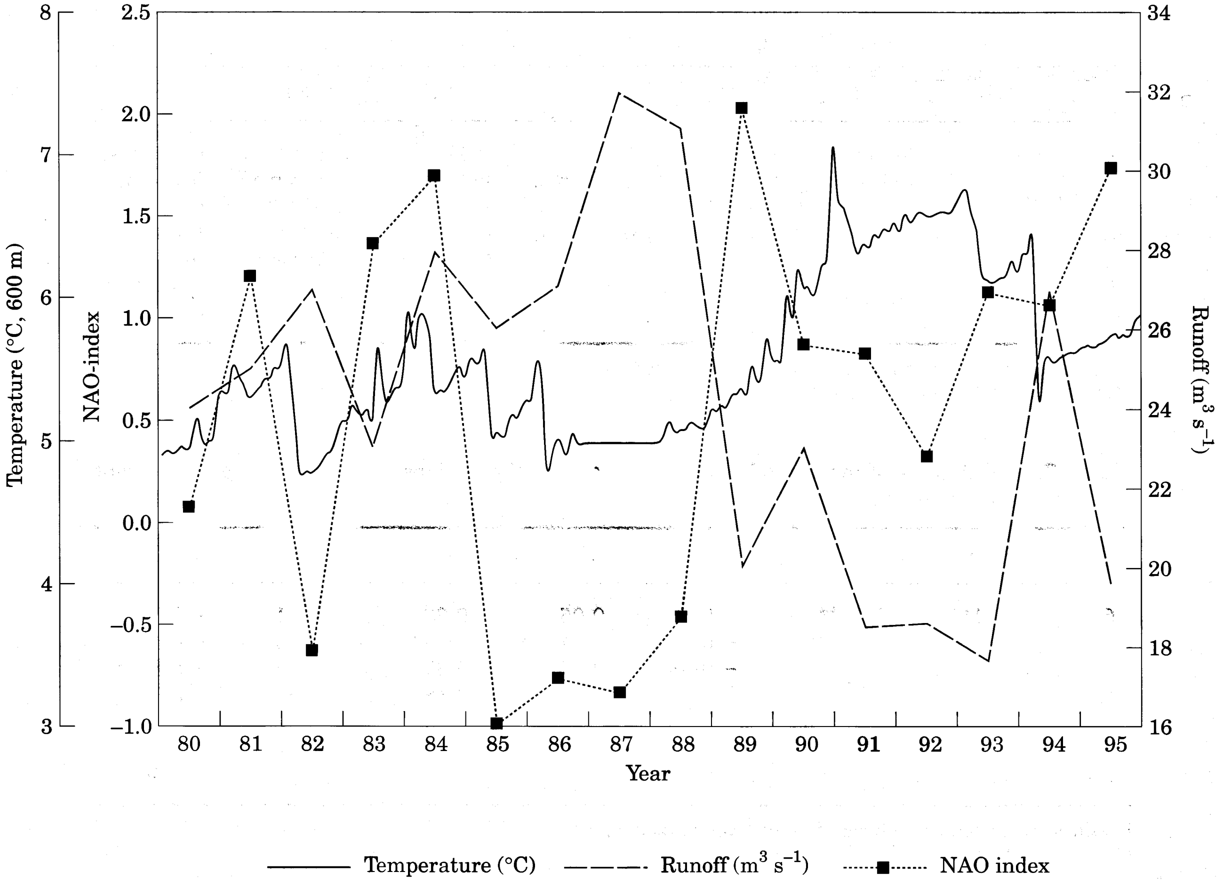


FIGURE 4. Temperature at 600 m in the Skagerrak (monthly measurements), the yearly mean runoff to Gullmarsfjorden and the mean NAO winter index (December to February).

possibility that the correlation is due to a covariation between runoff and temperature at 600 m depth and supports the almost significant correlation between runoff and L6 abundance. Runoff also changes gradually (Figure 4) which means that the benthos experiences the effects of a changing runoff a few years before runoff reaches its maximum/minimum (cf. NAO and temperature). This results in the 0 year lag in the correlation analyses equalling a lag of 1–2 years between the benthos and the start of the runoff change.

Intuitively one would expect the macrobenthic abundances at the inner stations to be more affected by runoff than the outer stations, since they are situated closer to the source. This hypothesis was not supported by our results for reasons which are currently unknown. However, possible effects of runoff at the inner stations are shading from turbidity and increased stratification, which may lead to decreased primary production at the inner stations, and thus to decreased benthic abundances. If such mechanisms operate, then a negative correlation of the inner stations to runoff might occur, which was the case at station S3. Partial Correlation of S3 to runoff, keeping NAO constant, still results in a significant negative correlation. This negative correlation is also supported by the negative correlations of benthic abundances between the inner station S3 and the outer stations L4 and L5 (Table 7) since runoff is positively correlated to the mean total abundance at stations L4 and L5. However, it is also possible to expect a positive effect of runoff on the benthos at stations inside the fjord, by the same reasoning as for the outer stations. However, the effect of low NAO (increased water stratification) and increased runoff will be co-occurring since NAO and runoff correlated negatively without time lag. A positive effect of runoff on total abundance would then lessen the effect of NAO, while a negative effect (stratification or shading by turbidity) would strengthen the effect of NAO. Since we do find consistent positive correlations between NAO and the S-stations, and the results of the partial correlation analysis show that low NAO index values as well as high runoff had a negative effect at S3, we suggest that

NAO is the most important factor of the three for macrobenthic variability in the inner part of the fjord.

The MDS analyses further support a covariation of the S-stations by showing that the community composition changed between 1988 and 1990 at these stations. A similar change also occurs at the other stations but is weak at SF and L4. The MDS plots also indicate a serial change of the communities over time but the reason for this change is unknown and could be due to anthropogenic and/or natural changes. However, this does not alter the discussion concerning the timing of the disturbances as well as the timing of the total abundance variations, dealt with in this paper. The results from the multivariate Spearman rank correlations also indicate a covariation of most stations (Table 6). R values are lower than those from the univariate correlations of total abundances (Table 7), but this may be due to the fact that the macrobenthic communities differ at the separate sites, and changes in the community composition are probably different although occurring at the same time. (Note that these correlations will most likely only attain positive values.) Eighteen out of 28 possible correlations were significant in this analysis and five of the non significant correlations were connected with station S2. At this stage it is only possible to speculate about the reasons for the apparent random correlations found to the S-stations in some cases. However, they have the shortest time series and no data exist for 1989, when large community changes were recorded at the other stations (see above). It is therefore likely that more significant correlations would have been found to these stations if the data sets were more complete. Station S1, S2 and SF are all situated relatively close to the mouth of River Örekilsälven and this part of the fjord has also earlier (until 1966) been exposed to heavy pollution from a pulp mill (Pearson & Rosenberg, 1978). This may lead to increased disturbance in this part of the fjord and may be a contributing factor for the different ‘ behaviour ’ of these stations compared to the other inner fjord station S3. Station SF is the only station in the inner part of the fjord with a long time series and it correlates to all stations except AL and S2. The univariate correlations (Table 7) show that SF correlates to L5. This indicates that SF behaves as most of the other stations and the positive sign of the univariate correlations indicates a behaviour at SF similar to the outer stations. SF also correlates negatively to temperature at 600 m as the outer stations do. Station S2 therefore seems to be the station with the most deviating temporal pattern. The lack of covariation to AL is probably due to the fact that it is the deep fjord station and is affected by oxygen depletion to a higher degree than the other stations. The same probably applies to S2, which is situated in a depression behind a sill. However, all these data combined indicate that the benthic community composition covaries at both offshore stations and within the fjord and that most stations showed a major disturbance during the period of 1988–1990. It is important to note that in 1989 to 1990 there was a high salinity and temperature anomaly (surface observations) in the North Sea (Becker & Dooley, 1995) and there were also large toxic algal blooms in the Skagerrak in 1988 (Underdal *et al.*, 1989).

The abundance at SF decreased from 1983 to 1988 while runoff increased. Macrobenthic mean total abundance at SF increased again between 1988 and 1989 (*c.* 30% total abundance increase) when runoff decreased to *c.* 50% of that of 1988. However, SF continued to decrease in spite of much lower runoff after 1990. Abundance at SF did not correlate to either NAO or runoff. Abundances at SF as well as at S1, S2 and S3 reacted negatively to the runoff peak in 1988 and positively to the decreased runoff in 1989. However, SF did not seem to recover from the low abundances in 1988 as the S-stations did.

Total abundance of macrobenthos versus temperature at 600 m depth in the Skagerrak

The equal time lags of 0–2 years between temperature at 600 m depth and macrobenthic mean total abundances at the outer stations is an indication of an association, important for benthic control at the outer stations (Table 4). The covariation of the outer stations shown in Table 7 as well as in Table 6, also supports the hypothesis of a large scale factor controlling abundances at these stations. One possible mechanism could be that an increase of a slow upwelling of bottom water, rich in dissolved inorganic nutrients (at times of water exchange in the Skagerrak deep water), increases the primary production and consequently increases the input of depositing organic detritus to the benthos. It has earlier been found that the Atlantic is the main source of dissolved inorganic nutrients to the North Sea (Becker & Dooley, 1995) so it is therefore reasonable to assume that the North Sea may have a similar effect on the Skagerrak. Belgrano *et al.* (1999) found indications of an association between increased densities of phytoplankton (*Dinophysis*) and high salinity surface water at the mouth of Gullmarsfjorden. The hypothesis is also supported by the time lags of 0–2 years between temperature at 600 m and the benthic abundance increase which is a reasonable time for the benthos to respond to an increase of depositing organic detritus. A zero year lag may here seem too limited for the benthos to react to an increase of depositing organic detritus. However, considering the behaviour of the inflows described above (inflows beginning 2–3 years before the temperature has reached its minimum) this means that if the benthic abundance peak coincides with the temperature minimum (0 year lag), the benthos has experienced increased deposition of organic detritus for 2 years when it reaches the abundance peak. The upwelling in the Skagerrak has been investigated by Rodhe (1989) who estimated the mean upwelling, associated with the estuarine circulation, to correspond to a horizontal entrainment velocity of 2 m day^{-1}. He also demonstrates that there is a peak in the vertically integrated mean velocity at about 100 m depth which decreases dramatically toward shallower areas, agreeing with our findings of shortest lags to the 100 m station L6. To our knowledge, however, there are no estimates of the yearly upwelling variation. The Partial Correlation analyses of the correlation between the L6, L5, L4 stations and temperature at 600 m depth, controlling for runoff, confirm the correlations. It is hard to draw any further conclusions from the correlations of temperature to the inner stations due to the differing time lags. However, the fact that the time lags differ is an indication that an effect, connected to the temperature at 600 m depth, probably is weak at the inner stations. Partial Correlation analyses do not result in a correlation between station S3 or S1 and temperature at 600 m depth if the variation of NAO is controlled for, indicating that temperature at 600 m depth describe the same variation. Due to the different time lags of correlations between S3 or S1 and temperature at 600 m we suspect that these correlations are formed because of the covariation of NAO and temperature at 600 m.

Abundance at station AL correlates negatively to runoff and positively to temperature at 600 m, indicating an abundance reaction similar to the reaction of the inner S-stations (Table 5). However, the Partial Correlation analyses result in opposite signs indicating a closer connection to the stations outside the fjord (Table 4). The latter analysis should better reveal the covariations and considering the lag of 3 years (the same as SF), it follows the pattern of increasing lags to temperature at 600 m, further away from the 100 m station L6 (Table 5). It is important to emphasize that lags with best *P*-value in Table 5 have been used for the Partial Correlation analysis (Table 4).

Conclusion

During periods of low NAO index values and high runoff, benthic abundances at the inner, shallow (25 m) fjord stations tend to decrease. The suggested mechanism is an effect of the cold winters with ice cover and warm summers resulting in strong stratification during times of low NAO index values. This may decrease primary production due to increased stratification in the inner parts of the fjord. High turbidity due to the high runoff may further decrease primary production. In contrast, benthic abundances at the outer stations increase during periods of high runoff and low NAO index values. When the NAO index is high and runoff is low, the benthic abundances tend to increase at the inner stations and decrease at the outer. The benthic decrease at the outer stations may be caused by a decreased primary production (due to the lower runoff) as opposed to the inner stations where decreased stratification during high NAO/low runoff periods may result in increased primary production.

The temperature at 600 m depth has the most consistent covariations to benthic abundances at the outer stations. The temperature at 600 m depth reflects the water exchange of the Skagerrak deep water and the covariation is therefore suggested to be due to an increase of the transport of deep water, rich in dissolved inorganic nutrients to the coast at times of deep water exchange. This may be followed by an increased primary production and thereby also increased input of depositing organic detritus to the macrobenthos on the Skagerrak coast.

The three suggested hypotheses concerning NAO, runoff and temperature at 600 m depth and their associations to benthic abundance variations in the inner and outer parts of Gullmarsfjorden will theoretically result in the obtained correlation patterns. A low NAO index will be associated with high runoff and low temperature at 600 m depth which may be associated with stratified water in the inner part of the fjord and low benthic abundances. Simultaneously, the upwelling of deep water and the runoff, both rich in inorganic dissolved nutrients will be high at the outer stations, resulting in high macrobenthic abundances and vice versa.

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