

Do climatic oscillations influence cyclical patterns of soft bottom macrobenthic communities on the Swedish west coast?

Björn G. Tunberg^{1,*}, Walter G. Nelson^{2,**}

¹Kristineberg Marine Research Station, Kristineberg 2130, S-450 34 Fiskebäckskil, Sweden

²Division of Marine and Environmental Systems, Florida Institute of Technology, Melbourne, Florida 32901, USA

ABSTRACT: Soft sediment macrofauna has been monitored at 10 stations (10 to 300 m) off the west coast of Sweden for periods of 12 to 20 yr. Macrobenthic abundance and biomass in this region show a distinct cyclical pattern of approximately 7 to 8 yr. Macrobenthic oscillation patterns down to 100 m depth are generally in phase, suggesting a causative mechanism operating at a regional scale. At the 300 m deep station, the cycles did not appear to be in phase with the stations in shallower water. Spectral analysis of the 130 yr record of the North Atlantic Oscillation (NAO) index indicated that the dominant component of the index occurred at a period of 7.9 yr. The NAO index over the period 1970 to 1990 was significantly positively correlated with Skagerrak deep water (600 m) temperature and significantly negatively correlated with stream flow from western Sweden. Stream flow was significantly positively correlated with benthic abundance and biomass at stations down to 100 m depth, but negatively correlated with bottom water oxygen content. We therefore propose that climatological linkages affecting primarily surface primary production result in bottom-up control of benthic population changes. We suggest that climatic variability in the region may be a more basic causative factor for benthic disturbance than eutrophication and other possible factors which have previously been proposed.

KEY WORDS: Benthos · Infauna · Cycles · Oscillation · Climate · NAO index

INTRODUCTION

Variability of population abundances is a typical feature of marine pelagic and benthic ecosystems at a variety of temporal scales (Cushing 1981, Botsford et al. 1982, Gray & Christie 1983, Baumgartner et al. 1992). Climatological factors are believed to be responsible for many aspects of temporal variability of marine communities (Aebischer et al. 1990, Francis & Hare 1994, Beamish et al. 1995, Stein & Lloret 1995, Ware 1995), including cyclical patterns of variation in some populations (Gray & Christie 1983). The El Niño South-

ern Oscillation (ENSO) is a well known source of climatologically driven variation in marine populations (Barber & Chavez 1983, Cane 1983, Dayton & Tegner 1984, Tarazona et al. 1988a, b, Philander 1989). The comparable role of periodic climatological variation in regulating physical and biological oceanographic processes in the North Atlantic region has been increasingly studied in recent years. Recent modeling suggests that there may be predictable climatic influences on North Atlantic sea surface temperature at time scales of a decade or longer (Hansen & Bezdek 1996, Griffies & Bryan 1997, Sutton & Allen 1997). Proposed linkages of climate to biological processes include the long-term increase in the northerly wind component over the eastern North Atlantic in recent years as an influence on phytoplankton and zooplankton biomass (Dickson et al. 1988), and the relation of westerly weather in the North Atlantic to long-term

*E-mail: b.tunberg@kmf.gu.se

**Present address: Coastal Ecology Branch, Western Ecology Division, US Environmental Protection Agency, Hatfield Marine Science Center, 2111 S.E. Marine Science Drive, Newport, Oregon 97365-5260, USA

trends in phytoplankton, zooplankton and seabird colonies (Aebischer et al. 1990).

The large scale ocean-atmosphere variation associated with the ENSO in the southern hemisphere appears to be linked to similar periodic variation in the North Atlantic region (Rogers 1984). The North Atlantic Oscillation (NAO) was described by Walker in the 1920s, and is defined by Rogers (1984) as 'the temporal fluctuation of the zonal wind strength across the Atlantic Ocean due to pressure variations in both the subtropical anticyclone belt and in the subpolar low near Iceland'. Consequences of the NAO include periodic variation in the winter temperatures and precipitation levels of northern Europe. Periodic alteration of sea surface temperature and coastal runoff provide potential linkages of climate variation to changes in pelagic and benthic populations of the coastal zone in this region.

The National Marine Monitoring Program of the Swedish Environmental Protection Agency has sam-

pled a network of soft-sediment community stations off the west coast of Sweden since 1983, with collections from selected stations extending from 1973. Analysis of data collected by this program up to the 1980s (Josefson 1990) found significant increases in benthic community abundance and biomass which were positively correlated with nutrient discharge from Swedish rivers to the coastal ocean. However, subsequent to the mid-1980s these benthic parameters decreased, only to rebound again in the 1990s (Tunberg unpubl. data).

Based on statistical analysis of the long-term benthic monitoring data, we present evidence that there is a periodic component for benthic community parameters, and that this periodicity is generally temporally synchronized among stations within different depth ranges. We propose that the periodic behavior of benthic community parameters is driven by periodicity at similar time scales for meteorological conditions within the North Atlantic region.

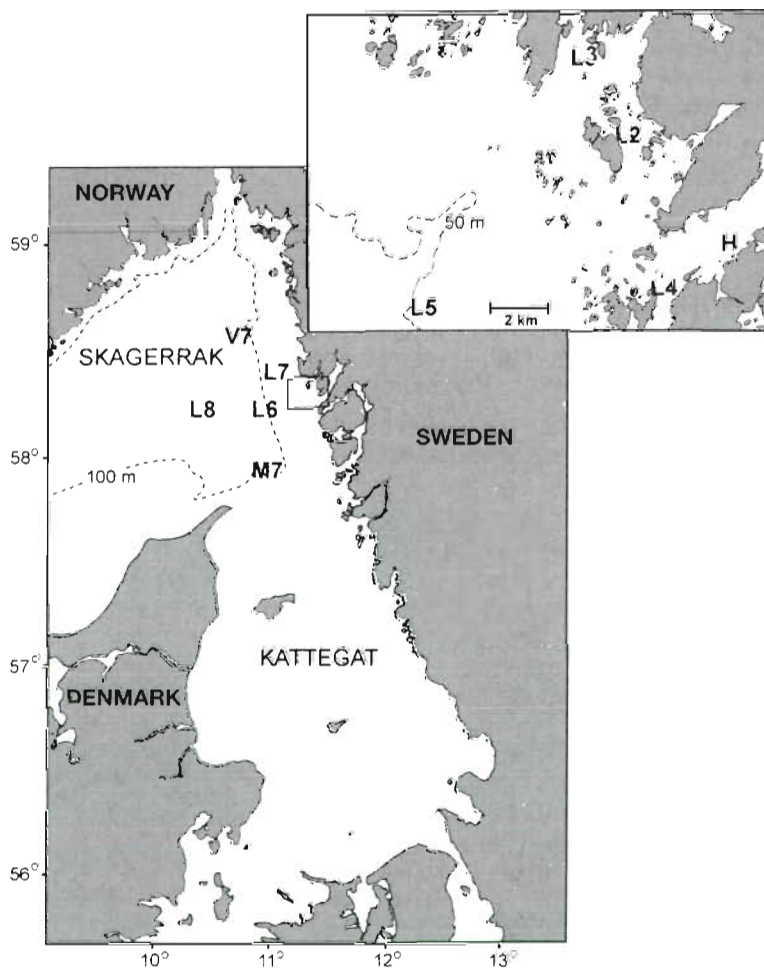


Fig. 1. Location of sampling stations along the Swedish west coast. The small rectangle shows the location of the enlarged area (at the mouth of Gullmarsfjorden) presented in the upper right corner

MATERIALS AND METHODS

Ten stations were sampled within varying depth zones off the central west coast of Sweden (Fig. 1). Data from 9 stations (L2, L3, L4, H, L5, L7, L6, M7, V7) sampled once per year in May in the 12 yr period from 1983 through 1994 (except M7 in 1983) and data from 1 additional deep (300 m) station (L8) sampled over the 20 yr period from 1973 to 1993 were analyzed. Stn L8 was sampled quarterly from 1973 to 1976, biannually in 1977, 1981 and 1982, and once per year in 1978 to 1980 and 1983 to 1993. Sampling was discontinued at Stn L8 subsequent to 1993 due to financial limitations.

At each station 5 quantitative sediment samples for biological analysis were collected with a modified Smith-McIntyre grab (0.1 m²) weighing 70 kg. The faunal samples were washed on a 1 mm mesh sieve, and material retained was preserved in the field (4% buffered formalin-sea water solution).

In the laboratory, each grab sample was divided into 2 size fractions (≥ 2 mm, 1 to 2 mm) by resieving in fresh water with nested sieves. The larger fraction was sorted by hand in a large white pan, while the smaller fraction was sorted under a stereo microscope ($\times 6$ magnification). All animals were generally identified to the species level, counted, and total wet

Table 1. Position and description of long-term benthic monitoring stations on the west coast of Sweden

Station	Lat. (N)	Long. (E)	Depth (m)	Substrate
L2	58° 18.48'	11° 24.13'	18	Clayey mud
L3	58° 20.36'	11° 21.44'	27	Clayey mud
L4	58° 14.68'	11° 25.58'	40	Sandy mud
H	58° 15.81'	11° 28.66'	30	Sandy mud
L5	58° 14.40'	11° 15.00'	50	Sandy mud
L7	58° 22.90'	11° 09.20'	50	Sandy mud
V7	58° 32.50'	10° 47.50'	100	Clayey mud
L6	58° 15.20'	11° 03.50'	100	Sandy mud
M7	57° 55.90'	11° 02.50'	100	Clayey mud
L8	58° 14.90'	10° 34.30'	300	Mud

weight of each species was determined after blotting to remove excess water. For practical reasons biomass was always expressed without certain very large species (e.g. *Nephrops norvegicus*, *Arctica islandica*, *Brisopsis lyrifera*, *Ecinocardium* spp.) that completely obscured the biomass contributions of other species. Sorted and identified samples were transferred to 70% ethanol and archived.

In order to detect trends which were most representative of regional processes, stations were combined for analysis into groups based on similar depths (Table 1). The groups were (1) L2, L3, L4, H (inshore <40 m), (2) L5, L7 (50 m), (3) L6, M7, V7 (100 m), and Stn L8 (300 m). For a group of stations the mean abundance values, representing all replicate grabs at a single station, were first averaged for all stations within a given sampling year to form a single time series for the group. Time series were 12 yr (1983 to 1994) for inshore and 50 m groups, and 11 yr (1984 to 1994) for the 100 m group because no sample was obtained from Stn M7 in 1983. The mean and standard deviation for all dates for the combined time series were computed, and these values were used to convert the abundance for each year into a standard normal deviate value (see e.g. Sokal & Rohlf 1981). Conversion of all data into standard deviates allows data from sites differing substantially in absolute abundance to be presented on the same abundance axis and allows a more ready visual comparison of trends. Abundance or biomass data were analyzed by least squares polynomial regressions using SigmaPlot® for Windows software. The best fit polynomial regression was determined from the *F* tests of the incremental and overall residual mean squares for each order of the regression using SigmaStat® for Windows software (see Table 2 for an example).

An index of the magnitude of the NAO, the NAO index, is calculated as the difference between the normalized mean winter (Dec, Jan, Feb) atmospheric pressure anomalies at Ponta Delgadas, Azores and Akureyri, Iceland (Rogers 1984). Index values were

Table 2. Example of incremental and overall stepwise polynomial regression results for regression orders 0 to 8 for the inshore (<40 m) stations

Regression order	Incremental		Overall		
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>r</i> ²
0	0.00	0.00	0.00	0.00	0.00
1	7.55	0.02	7.55	0.02	0.43
2	0.00	0.95	3.40	0.10	0.43
3	0.09	0.77	2.07	0.19	0.44
4	13.03	0.01	7.15	0.03	0.80
5	0.16	0.71	5.06	0.07	0.81
6	0.01	0.93	3.52	0.12	0.81
7	0.03	0.88	2.43	0.19	0.81
8	0.79	0.44	2.12	0.24	0.85

computed for the period 1875 to 1995 from data kindly provided by Dr J. C. Rogers. Periods when the NAO index is below the long-term mean (Fig. 2) are associated with lower winter temperatures in Scandinavia and with a greater intensity of the westerlies during spring over the northeast Atlantic (van Loon & Rogers 1978, Rogers 1984, Kerr 1997). The time series of the NAO index was subjected to Fourier analysis to determine the major periodic components of this climatological index.

Cross correlation analysis between abundance or biomass and a variety of either climatological or biological variables were conducted for time lags between -15 and +15 yr using Statistica® for Windows software.

Physical data for cross correlation analyses were obtained from a variety of sources. Data for total annual combined flow from all major streams along the

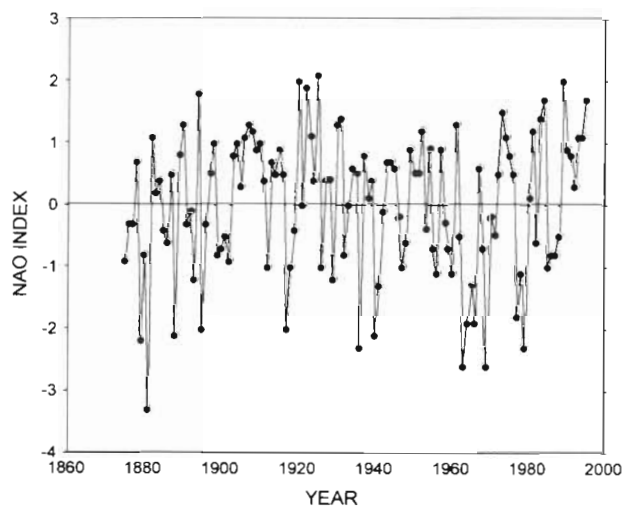


Fig. 2. North Atlantic Oscillation (NAO) index values between 1875 and 1995 calculated as the difference between the normalized mean winter (Dec, Jan, Feb) atmospheric pressure anomalies at Ponta Delgadas (Azores) and Akureyri (Iceland)

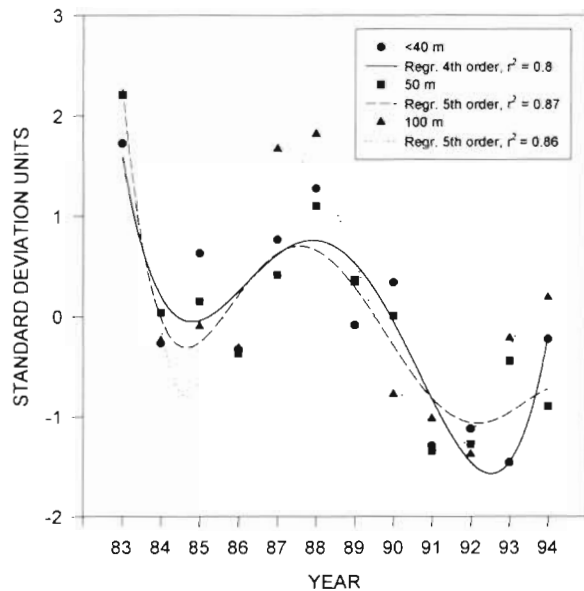


Fig. 3. Least squares polynomial regressions for normalized total abundance of macrobenthos between 1983 and 1994 for 3 sets of stations grouped by depth intervals (<40 m = L2, L3, L4, H; 50 m = L5, L7; 100 m = L6, M7, V7)

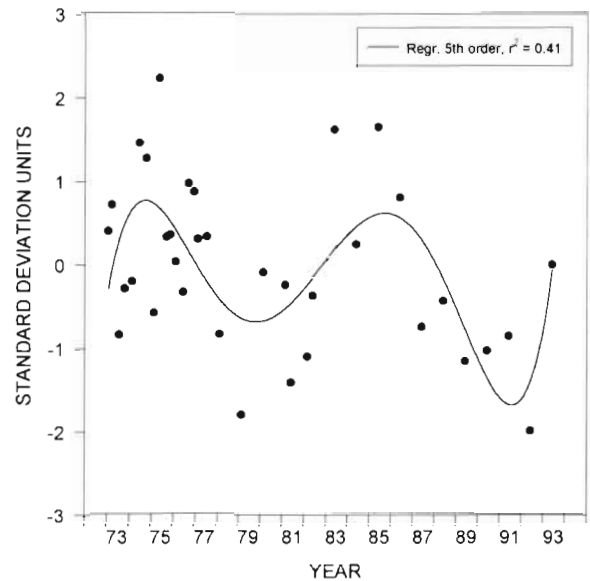


Fig. 4. Least squares polynomial regression for normalized total abundance of macrobenthos between 1973 and 1993 for Stn L8 (300 m)

west coast of Sweden for the period 1970 to 1994 were obtained from the Swedish Meteorological and Hydrological Institute. Stream flow data were first converted to standard normal deviates, and then smoothed by a 3 point moving average. The data were then detrended to remove a linear trend from the data set using the empirically calculated transformation for the stream flow data set ($Y_{\text{detrended}} = Y - 0.925 - 0.062 \times \text{time}$). Smaller subsets of the stream flow data for the time periods corresponding to benthic sample data were smoothed with 2 point moving averages.

Data for temperature in the Skagerrak deep water (600 m) off the coast of Norway were obtained for the period 1947 to 1990 from a publication of the North Sea Task Force (1993). The water at this depth is located below the sill depth of the Skagerrak (270 m) and variations in temperature are indicative of climatic variations (North Sea Task Force 1993). A subset of the data from 1970 to 1990, covering most of the period of benthic sampling in this study, was used in analyses. Published values of mean bottom water oxygen concentration from 31 stations along the Skagerrak coast of Norway were obtained from Fig. 6 of Johannessen & Dahl (1996) for the period 1977 to 1993 and were smoothed with a 2 point moving average.

Fish and shellfish landing data for the west coast of Sweden over the period 1980 to 1995 were obtained from the Swedish Statistical Central Bureau (SCB), Örebro. Data on crustacean landings were smoothed with a 2 point running average prior to cross correlation analysis.

RESULTS

In all cases the best fit polynomial regression analyses for abundance at the 3 groups of stations were non linear (Fig. 3), either a 4th order polynomial (inshore stations) ($r^2 = 0.80$, $p = 0.03$), or a 5th order polynomial function (50 m: $r^2 = 0.87$, $p = 0.03$; 100 m: $r^2 = 0.86$, $p = 0.056$), accounting for $\geq 80\%$ of total variance in the data sets. Peak benthic abundances at all stations occurred in 1988, followed by a decrease to a minimum in 1991 to 1992, and a subsequent increase through 1994, suggesting a cycle with a period of approximately 7 to 8 yr.

Abundance at Stn L8 showed a significant fit to a 5th order polynomial regression (Fig. 4), although the intraannual variation present during the first decade of sampling greatly reduced the goodness of fit compared to the other groups of stations ($r^2 = 0.41$, $p = 0.056$). Peaks of abundance were seen in the periods 1975 to 1976 and 1983 to 1985, suggesting a cycle length of approximately 7 to 9 yr. The lack of samples subsequent to 1993 at Stn L8 prevents the confirmation of a suggested upturn in abundance at this time. Comparison of the timing of peaks at Stn L8 versus other stations showed a temporal offset of about minus 3 yr.

The temporal pattern of change in biomass at the inshore stations differed both from the abundance data and from the biomass data at all other sets of stations (Fig. 5). The 50 and 100 m stations showed clear minima in the periods 1983 to 1985 and 1991 to 1992, and maxima in the periods 1988 to 1989 and 1993, a pattern

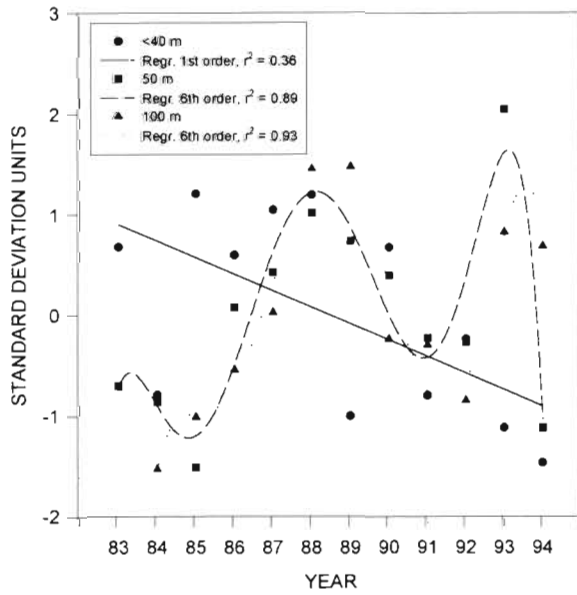


Fig. 5. Least squares polynomial regressions for normalized total biomass of macrobenthos between 1983 and 1994 for 3 sets of stations grouped by depth intervals (<40 m = L2, L3, L4, H; 50 m = L5, L7; 100 m = L6, M7, V7)

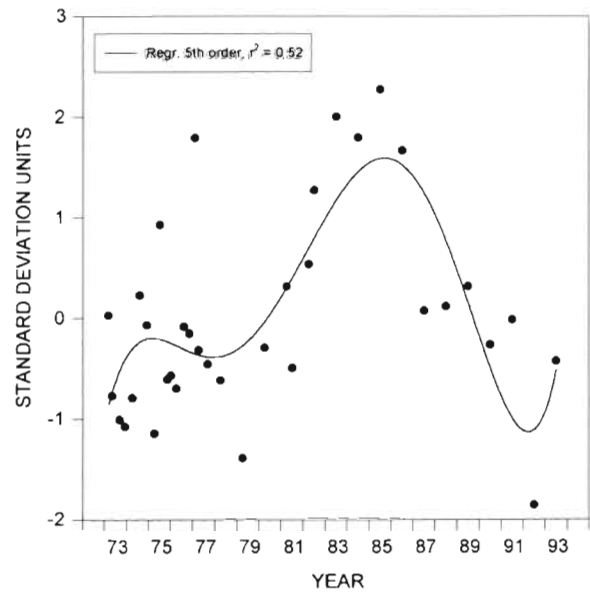


Fig. 6. Least squares polynomial regression for normalized total biomass of macrobenthos between 1973 and 1993 for Stn L8 (300 m)

consistent with a cyclical component of period 7 to 9 yr. Oscillations at both sets of stations showed significant fits to 6th order polynomial regressions ($r^2 = 0.89$, $p = 0.048$ and $r^2 = 0.93$, $p = 0.041$) explaining $\geq 89\%$ of total variance in the data sets. In contrast, the biomass at the inshore stations was best fit by a 1st order (linear) regression ($r^2 = 0.36$, $p = 0.04$) explaining relatively little of total variation in the data. Stn L2 biomass showed the highest deviation from the general pattern of the other 3 shallow stations. When Stn L2 was excluded from the calculations the best fit was achieved by a 2nd order polynomial regression ($r^2 = 0.61$, $p = 0.03$), with a peak value in 1987 to 1988.

Biomass at the deep station (L8) was best fit by a 5th order polynomial regression (Fig. 6), although again the intraannual variation present during the first decade of sampling greatly reduced the goodness of fit compared to the other stations ($r^2 = 0.52$, $p = 0.018$). Peaks in biomass occurred in 1976 to 1977 and 1983 to 1986, again consistent with an oscillatory component with a 7 to 9 yr period. Biomass peaks at Stn L8 were in phase with those for abundance at this station, but approximately minus 3 yr out of phase with the 50 and 100 m stations.

Spectral analysis of the 130 yr record of the NAO index indicated that the dominant oscillatory component of the index occurred at a period of 7.9 yr.

The NAO index over the period 1970 to 1990 was significantly positively correlated with lag -1 yr Skagerrak deep water (600 m) temperature (Fig. 7). Over

the same time period the smoothed NAO index was significantly negatively correlated with stream flow from western Sweden at lags of 0, -1 and -2 yr, with the largest correlation occurring for stream flow at lag -1 yr (Fig. 8). In turn, mean bottom water oxygen concentration from the Norwegian coast of the Skagerrak was significantly negatively correlated with stream flow at lags of 0 and +1 yr (Fig. 9).

Stream flow was significantly positively correlated with benthic abundance and biomass at inshore, 50 and 100 m stations at lags of either 0 or -1 yr (Table 3).

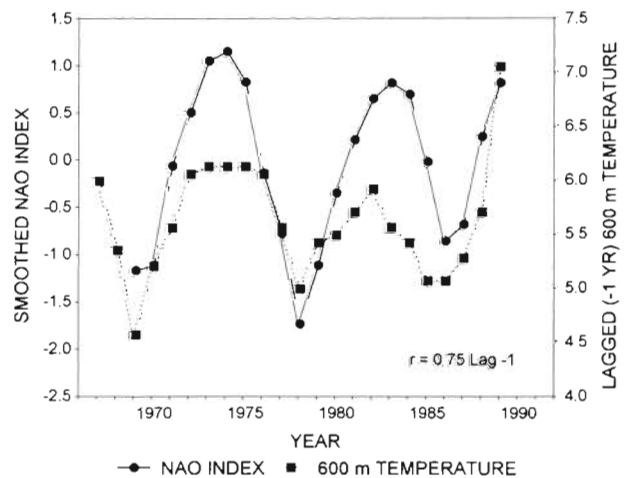


Fig. 7. Correlation between the NAO index values (smoothed) and 600 m temperature values in the Skagerrak (lag -1 yr)

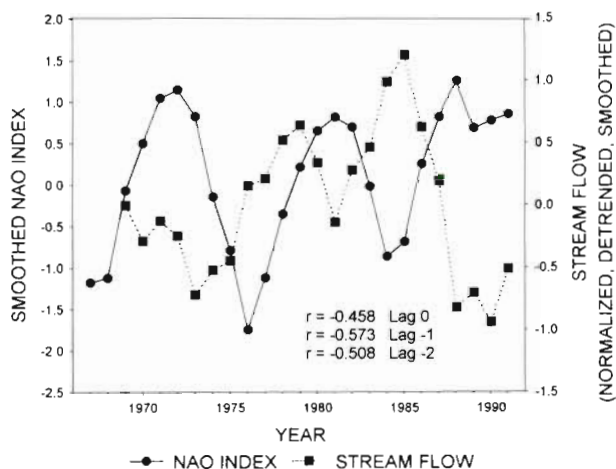


Fig. 8. Correlation between the NAO index values (smoothed) and the total stream flow data (normalized, detrended, smoothed) from the rivers on the Swedish west coast

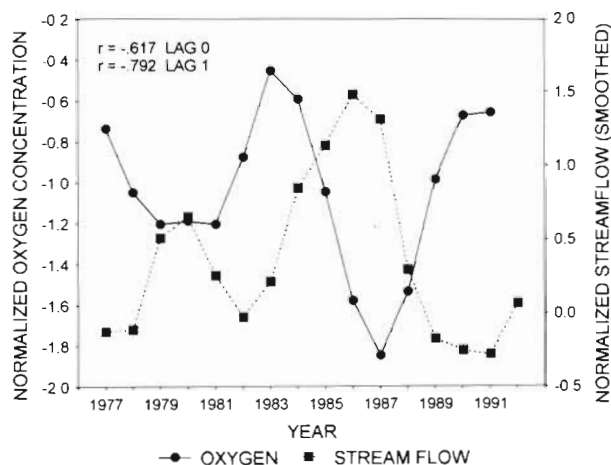


Fig. 9. Correlation between mean oxygen concentrations (normalized) from 31 stations along the Skagerrak coast of Norway and normalized stream flow data (see Fig. 8)

There were significant correlations of stream flow with abundance and biomass at the deep station L8, but these correlations were for lag + 2 yr, and were thus out of phase with the stations closer to the coast (Table 3).

Abundance and biomass values were significantly correlated with the NAO index, but with different time lags at different depth intervals (Table 4).

In order to elucidate possible interactions between benthic infauna and other available biological long-term data series a comparison was made with fish landing data (total yearly catches along the Swedish west coast). These preliminary analyses showed e.g. that there was a strong positive correlation between benthic inshore abundances and cod landings (Fig. 10), and a strong negative correlation between benthic inshore abun-

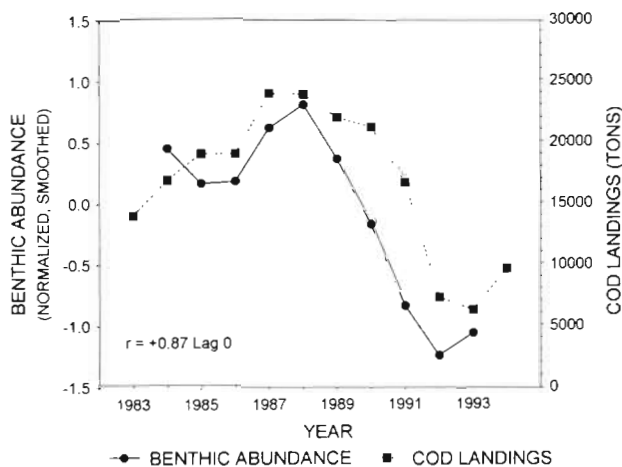


Fig. 10. Correlation between total abundance values (normalized, smoothed) at the 4 inshore stations L2, L3, L4, H combined and cod landings on the Swedish west coast

Table 3. Time lags associated with significant ($p < 0.05$) correlations between total annual flow from all major streams along the Swedish west coast with mean macrobenthic community abundance and biomass from long-term monitoring stations. Letters indicate transformations applied to the stream flow variable. S = smoothed by 2 point moving average, D = linear trend removed from data

Stns	Abundance	Biomass
Inshore		
L2, L3, L4, H	0.60 (lag 0)	0.70 (lag 0)
50 m		
L5, L7	0.85 (lag -1) S	0.82 (lag -1) S, D
	0.68 (lag 0) S	
100 m		
L6, M7, V7	0.72 (lag 0)	0.74 (lag -1) S, D
300 m		
L8	0.75 (lag +2)	0.72 (lag +2)

Table 4. Time lags associated with significant ($p < 0.05$) correlations between NAO index values with mean macrobenthic community abundance and biomass from long-term monitoring stations

Stns	Abundance	Biomass
Inshore		
L2, L3, L4, H	-0.88 (lag -2)	-0.70 (lag 0)
50 m		
L5, L7	-0.59 (lag +3)	+0.72 (lag +2)
100 m		
L6, M7, V7	-0.62 (lag -2)	+0.73 (lag +1)
300 m		
L8	-0.72 (lag +2)	-0.80 (lag +2)

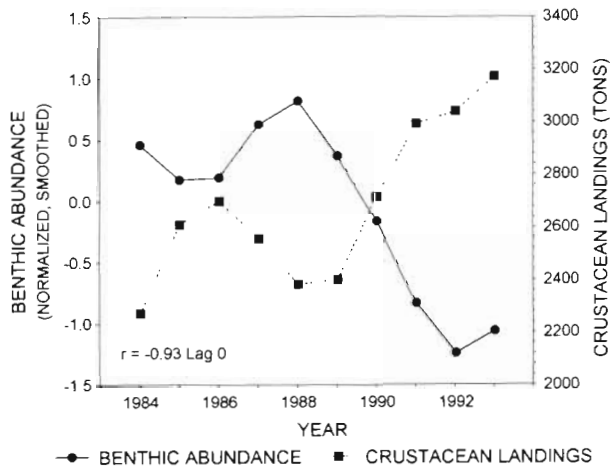


Fig. 11. Correlation between total abundance values (normalized, smoothed) at the 4 inshore stations L2, L3, L4, H combined and commercial crustacean landings on the Swedish west coast

dances with crustacean landings (Fig. 11). However, no significant correlation was found between cod landings and crustacean landings (directly or at any time lag).

DISCUSSION

The fact that many marine benthic populations exhibit periodic variation in abundance at a variety of temporal scales was clearly summarized by Gray & Christie (1983). Further examples are the temporal trends of abundance and biomass of benthos off the Swedish west coast over the period 1983 through 1993, which are best described at most stations by higher polynomial functions indicating an important periodic component to these macrobenthic community parameters. The simple linear regression models previously used (Josefson 1990) to describe temporal trends in earlier segments of the data from these stations may not have been adequate to describe the complex temporal behavior of abundance and biomass trends, a point partly reflected in the criticism by Gray (1990) on the interpretation of these data.

With the exception of biomass at the inshore stations, groups of stations from 18 m down to 100 m depth all showed cyclical patterns of abundance and biomass with periods of approximately 7 to 8 yr, and the cycles were in phase. That oscillations were in phase at stations spread over an area of more than 1500 km² indicates that large scale processes are important drivers of the pattern. A similar oscillatory pattern with a 7 yr period has been reported for the abundance of the benthic amphipod *Pontoporeia affinis* in the Bothnian Sea of the Baltic over the period 1961 to 1974 (Gray & Christie 1983).

Abundance and biomass of the deepest station (300 m) also showed evidence of cyclical patterns, although the cycles did not appear to be in phase with those of the stations in depths of 100 m or less. While it is tempting to attribute this difference to some function of depth, the fact that only 1 deep station was sampled greatly limits the ability to generalize.

The correlations noted in this paper between the NAO index as an indicator of climatic variation, variations of physical parameters in the marine environment, and variation patterns in biological populations offer potentially important insight into the regulation of coastal nearshore communities. However, when correlations between benthic populations parameters and the NAO index are directly calculated, significant correlations are found but the sign and lag of these correlations are variable and difficult to interpret (Table 4). This may be partly due to the limited number of sample stations available at some depths (e.g. 50 m), but it is also probable that a variety of mechanisms which vary across the depth gradient may be important in transmitting climatological variation to the benthic populations.

Correlation of winter air temperatures in Scandinavia with the NAO index has been shown by van Loon & Rogers (1978). Similarly, Alheit & Hagen (1996) have shown a significant positive correlation between the NAO index and west European air temperature anomalies, as well as a relation of the January air temperature in England to the NAO index. Cushing (1982, Fig. 82) has published data from Betin (1957) on long-term winter ice cover in the Baltic. Superimposing the pattern of the NAO index shows a virtually complete correspondence of periods of low NAO index with high Baltic ice cover over the period 1880 to 1950. The positive correlation between the NAO index and deep water temperature in the Skagerrak is demonstrated in Fig. 7 with temperature lagging the NAO index by 1 yr. Thus there exists a clear association of winter atmospheric temperature variation to ocean water temperature variation in the Skagerrak region, although the mechanisms driving this linkage may be complex (Alheit & Hagen 1996).

Winter temperature variation may be one potential linkage from climate to the biological systems of the Skagerrak. Alheit & Hagen (1996) have concluded that long-term climatic variation associated with severe winters drives variation in abundance patterns of herring (and alternating populations of sardines) along the Swedish coast. Long-term shifts in oceanic temperature regimes of coastal waters have also been implicated in variations of spawning pattern of a variety of pelagic species off California (MacCall & Praeger 1988). Josefson et al. (1993) also noted the potential role of water temperature variation on the benthos of the

Skagerrak-Kattegat. How low winter temperatures would be directly favorable to benthic populations is not clear. An indirect connection might occur if winter conditions are severe enough to cause mortality of bottom feeding fishes or macrocrustaceans, as was the case in the winter of 1962/63 in portions of the North Sea (Cushing 1982). Benthic populations might respond favorably to a release of predation pressure. Whether the strong negative correlation of crustacean landings and benthic population abundance (Fig. 11) is partially or wholly a result of trophic interactions or, as is probably the case for the positive correlation with cod landings (Fig. 10), is largely an independent response to climatic driven variation in the biological systems of the Skagerrak, cannot be determined at this time.

The potential for climatic variation to be an important influence on trophic interactions in coastal systems is suggested by both modeling (Robinson 1994) and empirical data (Aebischer et al. 1990), but the interactions are likely to be very complex. For example, Fromentin et al. (1998) found no correlation between abundance of 0-groups of cod or pollack and the NAO, while the fluctuations of *Calanus finmarchicus* in the Skagerrak were closely associated with the NAO.

The negative correlation between NAO index and stream flow (Fig. 8) provides the most probable mechanistic connection of climatic variation to variation in benthic populations. Josefson (1990) and Josefson et al. (1993) have previously demonstrated the positive relationship of nutrient input to the Skagerrak and Kattegat to flow volumes of coastal rivers in Sweden and land runoff in Denmark. Positive correlations were also shown between runoff and primary production levels in the Kattegat from 1970 to 1990. Josefson (1990) proposed that increased nutrients increased surface primary production in coastal waters and hence the food supply to benthic populations. During periods of low NAO values, winter precipitation in Scandinavia (Rogers 1984) is higher than average, and thus flow of nutrients into coastal waters will be increased. Increased production of phytoplankton with rapid sinking of production to the bottom in the shallower waters close to the coast (Smetacek 1980) should be reflected in a higher chemical oxygen demand in the bottom waters with some lag period. The negative correlation between oxygen concentration and stream flow (Fig. 9) is therefore consistent with this scenario. Table 3 also demonstrates the direct (or 1 yr lagged) positive correlation of the benthic communities in the Skagerrak with stream flow predicted by this mechanism. Smith (1996) has also shown that strong recruitment of the suspension feeding brittle star *Amphiura filiformis* at inshore stations (20 m) tends to follow periods of high river flow from Swedish rivers into the Kattegat.

Similar relationships appear to occur in the coastal embayments on the Swedish coast. Hagberg (1997) compared benthic infaunal data from a number of sites within Gullmarsfjorden over the 1980s and 1990s with measurements of yearly primary production between 1983 and 1992 from 1 site at the mouth of the fjord (Lindahl 1995). There was a positive correlation between NAO and primary production in this area, with a 1 yr lag of primary production (Hagberg 1997). These findings are consistent with the hypothesis that there is a linkage between the NAO, runoff driven primary production, and benthic community response at the offshore stations of the Skagerrak.

Preliminary examination of benthic data from the monitoring stations collected during the period 1995 to 1996 shows increases at most stations which is consistent with the pattern predicted from the 7 to 8 yr cycle within the Skagerrak benthic communities observed over the last 25 yr. In the summer of 1997 the benthos in the deep basin of Gullmarsfjorden was severely disturbed by extremely low oxygen values due to a lack of water exchange. The last serious hypoxic disturbance occurred in 1989 to 1990, i.e. 7 to 8 yr before the 1997 crash in the fjord macrobenthos. We do not mean to imply that there is a fixed temporal cycle to the NAO of 7 to 8 yr, merely that this has been the approximate cycle length over the recent period, which is not unexpected given the fact that the dominant oscillatory component of the index over 130 yr is 7.9 yr.

The hypoxia events within Gullmarsfjorden have generally been attributed to increased local and regional eutrophication. However, the data presented within this study strongly suggest that periodic problems within the fjord may have an important component related to regional climatological variation which may influence stream flow and surface productivity, as well as deep water exchange, within the fjord.

In 1985 Rosenberg et al. (1987) revisited 23 of the benthic stations established by C. G. J. Petersen (Petersen 1913) in the northern Skagerrak and the Oslofjord and showed that a dramatic increase in biomass had occurred during the intervening period. The conclusion was that these changes pointed toward a general enrichment of the area, even though other potential causes also were discussed. Other studies in the 1970s and 1980s (Josefson & Smith 1984, Josefson 1990) also demonstrated large biomass increases in the region during these periods. Josefson (1987, 1990) concluded that the investigated area most likely was being affected by anthropogenic organic enrichment. However, our results suggest the importance of climatological oscillatory patterns as an influence on these benthic systems. Cyclical climatic changes may interact strongly with, or even overshadow, changes from

anthropogenic alterations such as eutrophication. If the role of climatic variation is not considered, it may lead to incorrect conclusions regarding the relative contribution of anthropogenic versus naturally generated disturbances in regulating marine biological systems. The development of appropriate methods to separate climatic and anthropogenic contributions to long-term changes in benthic communities is a significant challenge for future research.

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