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Uncertain biotic and abiotic interactions in benthic communities

Jacob Hagberg, Niclas Jonzén, Per Lundberg and Jörgen Ripa

We analyze marine benthic communities at different sites in Skagerrak with the purpose of understanding the role of exogenous and endogenous factors in explaining the species' temporal dynamics. The previous finding that the dynamics of these species communities are mainly driven and synchronized by environmental (temperature) forcing was only weakly supported when analyzing single-species dynamics at five sites where four of the species were present every year. There was no consistent pattern in how the temperature affected the realized per capita growth rate, either across species at a given site, or among sites for a given species. Furthermore, there was no net-interaction from the community on a given species strong enough to give rise to second-order dynamics. However, when implementing a Multi Dimensional Scaling (MDS) analysis and incorporating all sampling sites and species -we found that the different communities clustered in relation to depth, hence, communities at the same depth were more "similar" than communities at different depth. Revealing the underlying interactions shaping these marine benthic communities is a challenge that calls for an array of various and complementary approaches.

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Most, if not all, species are sharing their physical environment with other species. To what extent the species in such a "community" are independent components or actually interacting, is the field of community dynamics (Morin 1999). However, to investigate how species interact with each other and the surrounding abiotic environment lies at the heart of ecology and evolution in general, and current work emphasizes the importance of both endogenous and exogenous factors in explaining the temporal dynamics of populations (Higgins et al. 1997, Stenseth et al. 1999a, b, Lundberg et al. 2000) and community change (Belyea and Lancaster 1999). The role of exogenous factors in population and community dynamics is receiving a lot of interest because global climate change is an important scientific issue (Hurrell et al. 2001), but also due to the observation of synchronous dynamics across large spacial scale as a general pattern in a variety of different organisms (Ranta et al. 1995, Koenig 1999, Bjørnstad et al. 1999). Spatial synchrony is a striking feature also in the marine study system in Skagerrak analyzed in this paper.

The macrobenthic fauna abundance of eastern Skagerrak shows a high degree of synchrony (Josefson 1987, Austen et al. 1991, Tunberg and Nelson 1998) with an interannual variation of up to 300% (Hagberg and Tunberg 2000) (Fig. 1). The abundance has been cyclic with a period of 7–8 years since 1980 (Tunberg and Nelson 1998) and the community composition differs within the area (Josefson 1987). Hagberg and Tunberg (2000) showed that the most abundant species at three adjacent sites – L4, L5 and L6 – are not the same. This suggests that the synchrony is caused by a large scale abiotic factor that overrides effects of intrinsic factors such as predation and competition (Josefson 1987, Josefson et al. 1993, Tunberg and Nelson 1998,

Hagberg and Tunberg 2000). Runoff (Josefson 1990) and /or upwelling (Hagberg and Tunberg 2000) have been suggested as the synchronizing factors. Both factors assume that the dynamics are controlled through benthic-pelagic coupling (Josefson 1987, Hagberg and Tunberg 2000). The regulating factor is thus dissolved inorganic nutrient availability for the primary production.

In this paper we have used single species autoregressive (AR) models including temperature as a covariate, to identify the dynamics of four macrobenthic animals from five sites on the Swedish Skagerrak coast. The dynamics of the species have been compared between the sites and contrasted to the synchronized behaviour of the total abundance at these sites.

Materials and methods

Data material

Five sites along the Swedish west coast have been sampled for soft bottom macrobenthos (infauna) as part of either Swedish national or regional monitoring programs. For details on positions and time-series, see Table 1. All stations were sampled in April–May every year. Faunal samples were collected with a modified Smith-McIntyre grab (0.1 m², 70 kg), washed on a 1-mm mesh sieve, and material retained was preserved in the field (4% buffered formalin-sea water solution) (Tunberg and Nelson 1998). Mean abundance of the replicates were used for the analyses. The two dominating species with respect to abundance at each sampling station were: L4; *Mysella bidentata* (Montagu) and *Abra nitida* (Müller), L5: *Amphura filiformis* (Müller) and *Diplocirrus glaucus* (Malmgren), L6: *Heteromastus filiformis* (Claparéde) and *Philomedes globosus* (Lilljeborg), L7: *Amphura filiformis* and *Diplocirrus glaucus*, V7: *Heteromastus filiformis* and *Diastylis lucifera* (Kröyer). There are about 200 species recorded over 20 years at each site and more that 400 species in total. The total abundance within the area varies between 2000–10 000 ind. m⁻².

Species, present in all years and at all sites were needed to make AR-models that could be compared between sites and species. There were four species that applied to these criteria: *Amphiura filiformis* (Echinodermata), *Diplocirrus glaucus*, (Annelida), *Pholoe* sp.,

Johnston (Annelida) and *Abra nitida*, (Bivalvia). The abundance of these species is presented in Fig. 1. All samples (means of replicates) of the entire community from all sites and years were included in the Multi Dimensional Scaling (MDS) analyses. The community recorded at one sampling site and occasion is thereby represented by one point on the MDS plot.

The temperature at 600 m depth in the Skagerrak without lag have been found to correlate with the long term benthic abundance variation (Hagberg and Tunberg 2000). The Skagerrak deep water (600 m) has been suggested to be exchanged when the North Atlantic Oscillation Index (NAOI) (December to March) is low (Hagberg and Tunberg 2000), due to the cold weather that follows the northerly winds that prevail during low NAOI periods (Hurrell 1995). The temperature is therefore a good representation of years (late winter-early spring) with northerly winds. Northerly winds are known to induce upwelling (Rodhe 1998) which is suggested to increase the primary production (Hagberg and Tunberg 2000) but periods of low NAOI are also dominated by calmer weather (Planque and Taylor 1998) which could induce an earlier onset of the spring bloom due to earlier stratification (Taylor 1995, Dahl and Johannessen 1998). Dahl and Johannessen (1998) also found indications of synchronized blooms across the Skagerrak indicating effects of a climatic forcing on scales larger than the Skagerrak. Temperature at 600 m depth in the Skagerrak is therefore thought of as a food proxy for the benthic fauna, although the exact mechanisms are not fully understood. However, correlations between benthos and temperature have been found with temperature lagged 0–2 years (Hagberg and Tunberg 2000). It was therefore included in the models, with 0–1 years lag, as the most important factor for the synchronised dynamics exhibited by the macrobenthic total abundance in the Skagerrak (Hagberg and Tunberg 2000). The reasoning for the lag is that increased food availability would increase the successful settling of benthic larvae. These larvae would not be retained on a 1mm mesh sieve until the following year and thereby give a lag of approximately one year.

Statistical procedures

A general single-species model in discrete time can be written

Table 1. Sampling sites, their positions, depth, sampled period and number of replicates collected each year.

Station	Latitude	Longitude	Depth (m)	Sample period	No. of replicates
L4	58 14.68′ N	11 25.58′ E	40	1983–1999	5 (95–99, 4 repl)
L5	58 14.40′ N	11 15.00′ E	49	1983–1999	5 (95–99, 4 repl)
L6	58 15.20′ N	11 03.50′ E	100	1983–1999	5 (95–99, 4 repl)
L7	58 22.90′ N	11 47.50′ E	49	1981–1999	5 (95–99, 4 repl)
V7	58 32.50′ N	10 47.50′ E	100	1980–1999	5 (95–99, 4 repl)

Fig. 1. Total abundance and abundance of four separate species of benthic fauna at the five study sites.
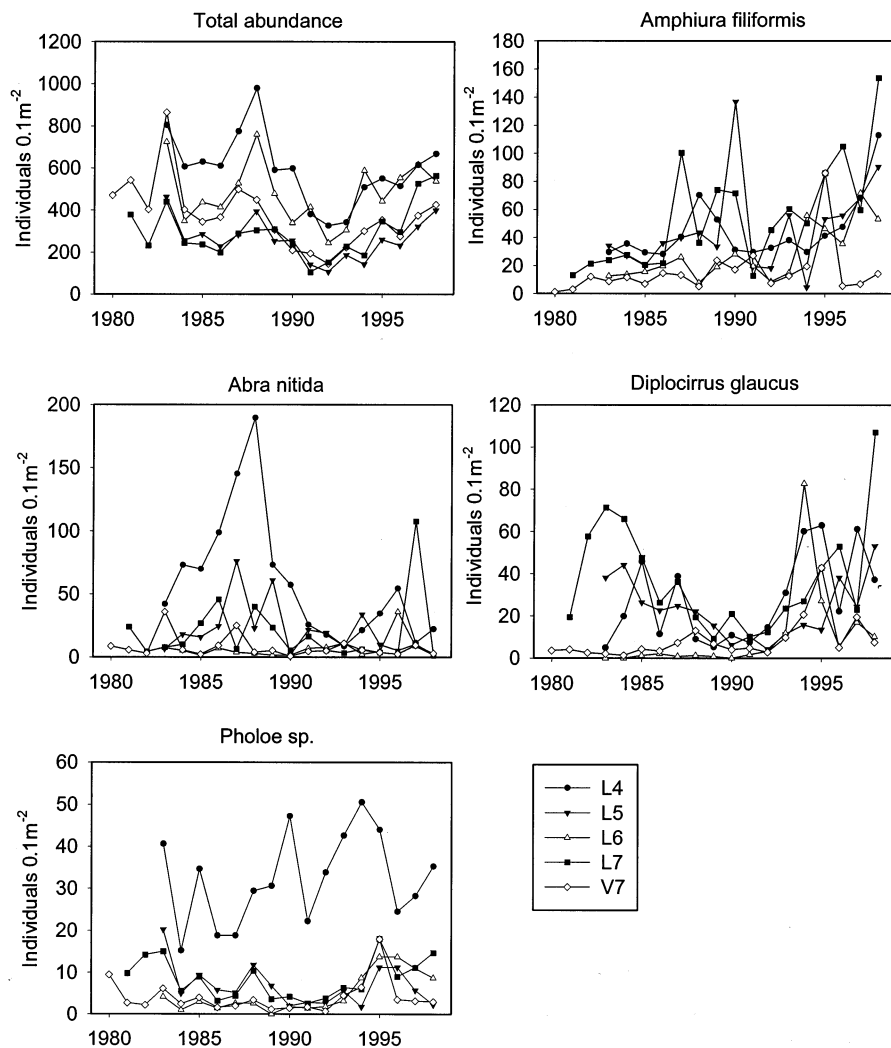
$$N_t = N_{t-1}g. \quad (1)$$

where N_t is population density at time t, and g may contain previous densities (so called density dependence), as well as other biotic or abiotic input. The logarithmic per-capita rate of change is defined as

$$r_t = \log_e(N_t) - \log_e(N_{t-1}) = \log_e(g.) = f. \quad (2)$$

We will assume r_t to be a linear function of log density. Hence, we regress r_t on log density as

$$r_t = a_0 + a_1 x_{t-1} + a_2 x_{t-2} + \varepsilon_t \quad (3)$$

where x_{t-k} is $\log_e(N_{t-k})$, a_1 and a_2 are estimates of the strength of direct and delayed density dependence, respectively, and ε_t is a series of uncorrelated noise. Eq. (3) (in combination with eq. (2)) can be rearranged to an autoregressive (AR) model of order 2, and we

will use the notation of eq. (3) throughout the paper. There are many possible ecological mechanisms that may give rise to delayed density dependence (or second order dynamics; Royama 1992), including strong dynamic interactions with parasites or predators (Royama 1977). In this paper, we are interested in estimating the role of both biotic and abiotic factors in shaping the temporal dynamics of a number of species. Due to the short time series and relatively high number of species (see above), we will restrict the analysis to univariate time series rather than estimating the parameters of a community matrix (Maurer 1999). Hence, we will interpret eventual second-order effects (a_2) as an indication of strong net interactions from the biotic feedback environment not described by a_1 (Royama 1992, Berryman 2001).

However, many abiotic factors tend to be positively autocorrelated in marine environments (Steele 1985) and neglecting this may lead to biased estimates of a_1

and a_2 and, hence, erroneous conclusions about the relative importance of endogenous and exogenous factors (Jonzén et al. 2002). We will therefore try to avoid that problem by explicitly including temperature as a covariate in the estimation framework (Forchhammer et al. 1998) giving the model

$$r_t = a_0 + a_1 x_{t-1} + a_2 x_{t-2} + b T_{t-u} \varepsilon_t \qquad (4)$$

where b is the regression coefficient with respect to temperature with (u = 1) or without (u = 0) delay, and ε_t is a noise term lumping together all factors not included in the model.

The models were fitted to data by the method of least squares. Observation error is of course present which could potentially bias the parameter estimates. However, we are not interested in the exact point estimates, but rather in comparing estimates between species. Furthermore, we have no reason to believe that observation error differs significantly between the selected species. Relative differences therefore remain. After a first inspection of the parameter estimates, we also compared the full model (eq. 4) with simpler nested models including or excluding the effect of temperature. The Akaike information criterion corrected for small sample, AIC_c, (Hurvich and Tsai 1989), will guide model selection. The appropriate expression for AIC_c to use when fitting models to data with least squares is

$$AIC_c = n \log_e(\sigma^2) + 2K(K+1)/(n-K-1) \qquad (5)$$

where n is the length of the time series, $\sigma^2 = \Sigma \varepsilon_t^2/n$, and K is the number of estimated parameters including the standard deviation of the noise, σ (Burnham and Anderson 1998). We then calculated AIC_c differences (Δ_i) for each model such that $\Delta_i = AIC_c(i) - \min(AIC)$, scaling the AIC_c values to give the model with minimum AIC_c a value of zero. Finally, for each of the r models, we calculated the likelihood of the model given data and normalized each value according to

$$w_i = \exp(-0.5\Delta_i)/\Sigma \exp(-0.5\Delta_r) \qquad (6)$$

The normalized likelihood for each model, w_i, is the Akaike weight (Burnham and Anderson 1998).

The resulting models were plotted in a $(1 + a_1, a_2)$ space to indicate the type of dynamics exhibited by the four species at the five stations using AR(2) models with the temperature included or excluded. Parameter combinations below the semi-circle (Fig. 4) give rise to damped fluctuations, and the presence of noise keeps the fluctuations persistent and we get so called quasi-cyclic dynamics (Royama 1992). If the dynamic is cyclic due to environmental forcing (i.e. temperature in this case), the point estimates of $(1 + a_1)$ and a_2 should be above (below) the semicircle if temperature is included (excluded) in the model.

The PRIMER (Plymouth Routines In Multivariate Ecological Research) software package was used for the Multi Dimensional Scaling (MDS) analyses (Carr 1993, 1996, Clarke and Warwick 1994). The MDS was based on a Bray-Curtis similarity matrix with untransformed data. The structure of dominating species is thereby important for the ranking of the samples. The similarity matrix is built up as a distance map with the Bray-Curtis ranks as a measure of the distance between the samples. The community composition, abundance of the species and the total abundance are taken into account but the Bray-Curtis index disregards zeros which makes it suitable for species data. The calculation of the minimum stress value was based on 100 iterations.

Results

A general result when fitting autoregressive models of different order is the very low AIC_c values of all second order models (Fig. 2). This indicates that there is no strong net-interaction from the community that give rise to delayed density-dependence in any of the four species. Each of the four species is best explained by different models at the five sites. That is, the same species exhibits different dynamics at different sites, excluding *Pholoe* sp. for which there is a slight tendency for first order models at all sites. The different species show no strong preference for a certain model at one site, except at V7, where there is a weak preference for first order models for all species. The variance-covariance models (AR0) have, with a few exceptions very low values. The r^2-values (Fig. 2) indicates on the other hand, that first and second order models explains the observed abundance equally well and much better than the variance/covariance models. That is, there is no significant model improvement between first and second order models, again suggesting that there are no dominating second order interactions.

The temperature at 600 m depth in the Skagerrak had earlier been shown to explain a large part of the benthic decadal total abundance variation and was therefore thought to improve these models. However, there are no consistent indications of higher AIC_c values for models including temperature, compared to models without temperature (Fig. 2). Figure 3 shows the b-values (model coefficient for temperature) for the four species using different models. For two of the four species *Abra nitida* and *Amphiura filiformis*, there is no consistent pattern in strength nor sign of the b-value. The other two species, *Diplocirrus glaucus* and *Pholoe* sp. show a tendency for positive b-values, although the model selection analysis of the *Pholoe* sp. data shows no consistent preference for models including temperature (Fig. 2). For *D. glaucus*, however, temperature

Fig. 2. The Akaike weights (Aw) for nine autoregressive models applied to four species at five sampling stations (M, L5, L6, L7 and V7). The r²-values for the correlation between the model and the observed data are presented above each Aw-bar.
AR0 = autoregressive variance-covariance model,
AR1 = first order autoregressive model,
AR2 = second order autoregressive model,
T = temperature included in the AR-model,
Tlag = temperature lagged one year included in the AR-model.
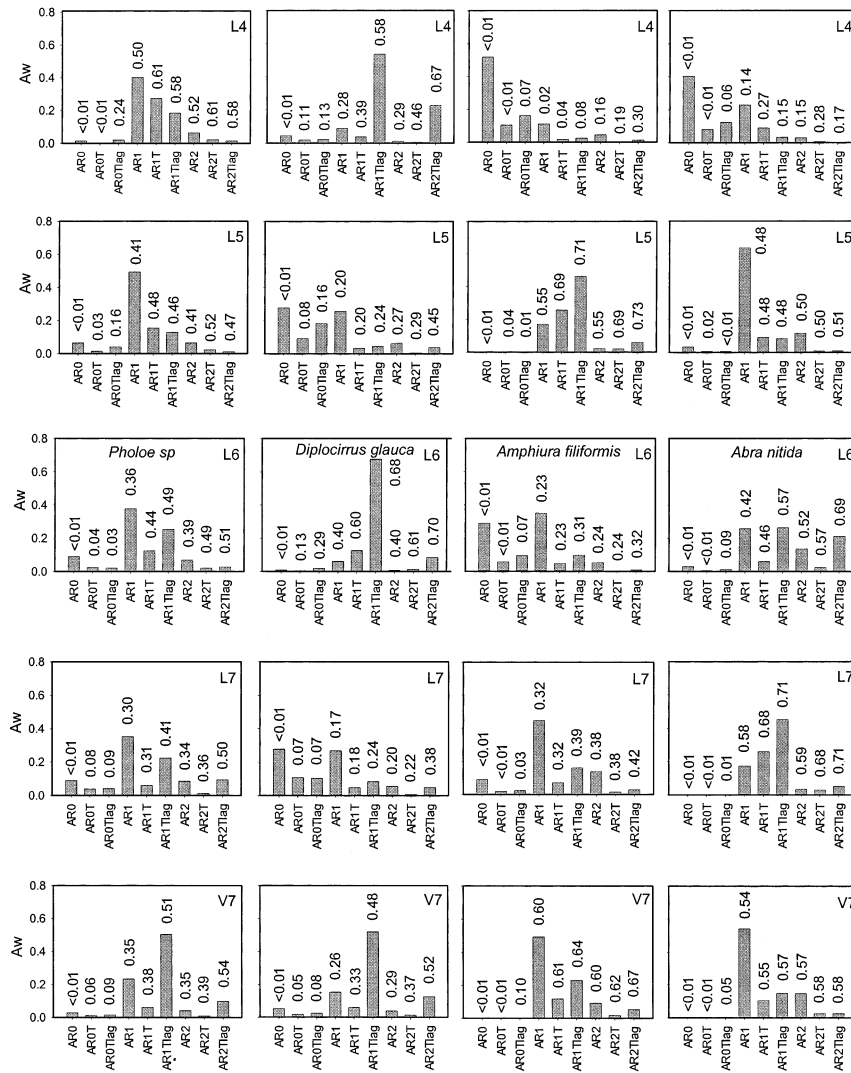
(lagged) is included in the preferred model at three of the five sites (L4, L6 and V7). This does indicate a true temperature dependence (Fig. 2), although *D. glaucus* is not among the most abundant species at the sites where the preferred model is temperature dependent. Thus, we can not conclude that the temperature effect on the total community is due to the apparent effect on *D. glaucus*. The r²-values are often, but not consistently, higher for models with temperature included which supports that temperature has some effect but that this varies between sites and species.

The second order, single species models did not show the cyclicity found for the total abundance and there were no stabilizing effects on the models by the inclusion of the food proxy, temperature, as a covariate (Fig. 4). The total abundance of the four species used for the AR models did not correlate significantly to the total abundance at the five stations (Table 2). However,

the total of the seven most abundant species at each station correlated significantly with the total abundance at the 5 stations (Table 3). This indicated a strong contribution from the most abundant species (4% of the species) on the total abundance. We therefore analysed the most common species (being different from the four species present everywhere) at the locations L4, L6 and V7. Again, there were no consistent results and temperature was included in the best model of the most common species at L4 and V7, but not at L6. To summarize, we only find an effect of temperature in the most common species at three of the five locations sampled. When analysing the four species being present at all locations, we find an ambiguous effect of temperature on a given species across locations as well as among species at a given location.

A Spearman rank correlation of the total abundance at all sites indicates very synchronized benthic commu-
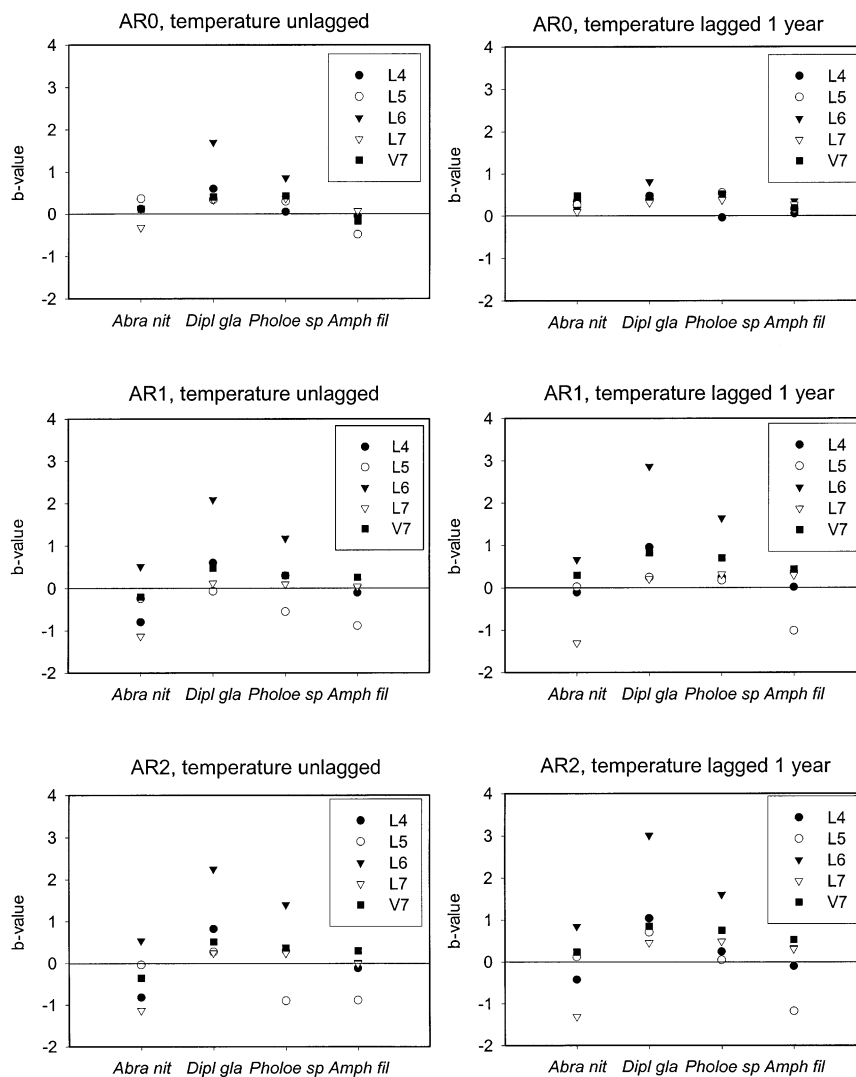
Fig. 3. Model coefficients for temperature and temperature lagged one year (b-values) when included in variance-covariance, first and second order autoregressive models (AR0, AR1 and AR2 respectively). The models have been applied to four species/species groups, present at five sampling stations (L4, L5, L6, L7 and V7). Abra nit = *Abra nitida*, Dipl gla = *Diplocirrus glaucus*, Amph fil = *Amphiura filiformis*.

nity dynamics for the entire area (Table 4, Fig. 2). The MDS plot on the benthic community (Fig. 5) indicates that the community shows some similarities with regard to depth. The communities at the 100m sites (L6 and V7) form a mixed cluster that is separated from the other sites. The same applies to the 50 m sites (L5 and L7) and the 40 m site (L4). The similarity refers both to species composition and abundance. The minimum stress value was 0.12, indicating that only minor alterations were needed to plot the MDS in two dimensions.

Discussion

The dynamics of populations and communities is the combined result of endogenous (demography and trophic interactions) and exogenous (e.g. climate) processes. Several recent studies have shown that the inter-play between such factors can be intricate, but also sometimes revealed by more sophisticated time series techniques (Post et al. 1999, 2001, Stenseth et al. 1999b, Fox and Morin 2001, Post and Forchhammer 2001). Previous studies of the benthic communities in the Skagerrak have shown that one large-scale factor (deep water temperature) indeed plays a major role in the overall community dynamics (Hagberg and Tunberg 2000). Among other factors such as runoff, fish predation and recruitment, only runoff has showed consistent agreement to the benthic variation, though weaker than temperature (Josefson 1990, Hagberg and Tunberg 2000). Our results show that temperature is also discernable in the dynamics of individual species but in a far more complicated way. Although the overall community dynamics seems to be strongly affected by temperature to the extent that total abundance variation in time is synchronized over large distances, individual species seem to respond very differently.

Fig. 4. Second order autoregressive models for four species, present at five sampling stations, plotted with respect to their coefficients for direct and indirect density dependence. The temperature is either included or excluded from the models of each sampling station (e.g. L4T or L4). Models plotted in the bottom part of the triangular parametric space display cyclic dynamics while those in the upper part display stable dynamics. The sampling stations are LA, L5, L6, L7 and V7.
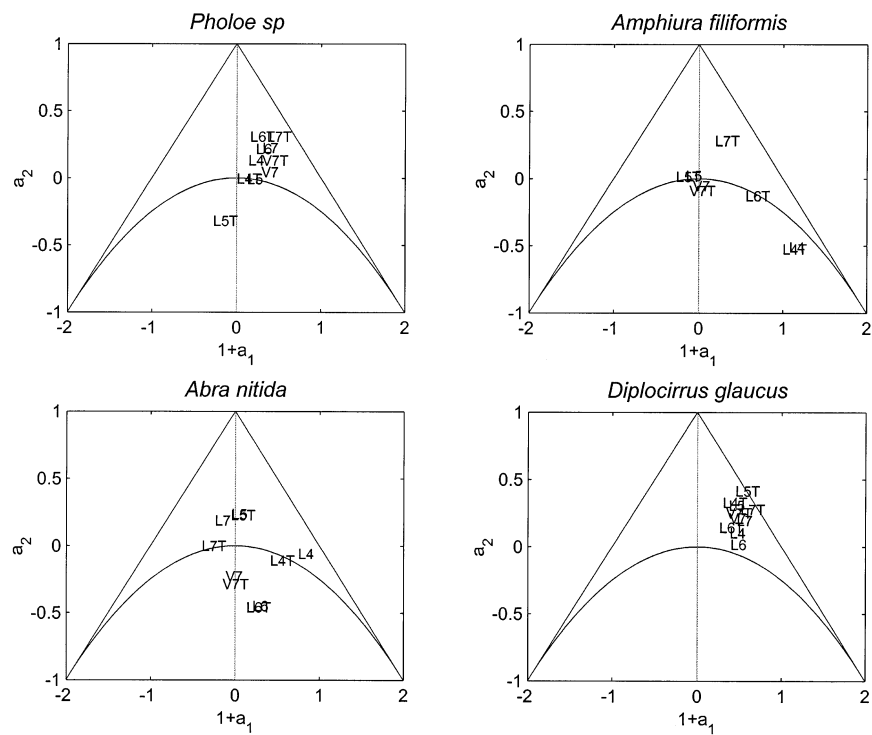
The benthic communities at different depths and with different species compositions seem to respond similarly to the dominating environmental variable (Tunberg and Nelson 1998, Hagberg and Tunberg 2000). The lack of response in individual species to that same variable may seem enigmatic at first. However, assuming that most of the (dominating) species in the community respond similarly to the input of nutrients mirrored by temperature fluctuations, then a likely interpretation is that the species are substituting each other over time. That is, the identity of the dominating species varies temporally for example due to chance events in the settling dynamics and that competition for space is a critical process leading to pre-emptive competitive interactions. No matter what species happens to dominate, it responds to the nutrient input in similar ways as all the others, it is just that species composition is not determined by the large-scale environmental fluctuations but rather by local condictions.

Our results also indicate that the trophic interactions other than the pre-emptive competition ones are weak in the Skagerrak benthic communities. This is also supported by the fact that we did not find any strong lagged density-dependent responses in any of the species investigated (Fig. 2). Strong interspecific interactions are known to generate second order dynamics (Bjørnstad et al. 2001). This indicates that the soft-bot-

Table 2. Spearman rank order correlations between total of four selected species (*Amphiura filiformis*, *Abra nitida*, *Diplocirrus glaucus*, *Pholoe* sp.) at each station and total abundance of all species.

Site	Correlation coefficient (r)
L4	0.12
L5	−0.44
L6	0.19
L7	0.56
V7	0.07

Table 3. Spearman rank order correlations between total of the seven most abundant species at each station and total abundance of all species. Correlations significant after Bonferroni correction (p ≤ 0.01) printed in bold face.

Site	Correlation coefficient (r)	Percent of total abundance (%)
L4	**0.67**	37
L5	**0.96**	56
L6	**0.87**	75
L7	**0.78**	60
V7	**0.86**	63

Table 4. Spearman rank order correlation coefficients (r) between benthic total abundance at all sites from 1983 to 1999. Correlations significant after Bonferroni correction (p ≤ 0.005) are printed in bold face.

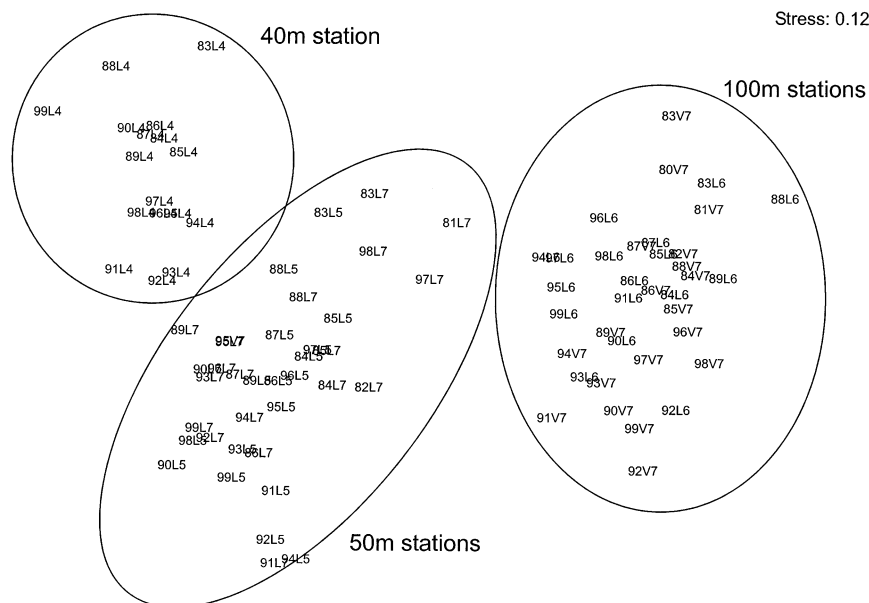|	L4	L5	L6	L7	V7
L5	**0.90**	–	–	–	–
L6	0.59	0.59	–	–	–
L7	**0.65**	**0.85**	0.63	–	–
V7	**0.90**	**0.85**	0.61	**0.65**	–

Fig. 5. Multi dimensional scaling plot of the macrobenthic faunal community at five different stations over the sampling period. First two digits of each point refers to the sampling year and the following to the sampling station.

tom communities in Skagerrak are rather loosely coupled entities largely driven by large-scale environmental variation rather than biotic assembly rules. Note though, that the more general species composition at different depths (Fig. 5) and sites is stable over time and probably determined by local conditions. Hence, a "community" under such conditions is merely the (random) collection of species sampled from a large pool of potential members (determined by local conditions) whose identity will be determined by dispersal and settling dynamics, and whose dynamics will be driven by external large-scale environmental variables, such as deep water temperature (here as a proxy for nutrient availability). This underscores the importance of the combined consideration of both biotic and abiotic variables when interpreting the dynamics of natural communities.

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