

CHAPTER 8

Responses of phytoplankton communities to climate variability

Andrea Belgrano, Mauricio Lima, Nils Chr. Stenseth, and Odd Lindahl

8.1 Introduction	109
8.2 A statistical approach	109
8.3 Phytoplankton diversity and dynamics, an example	110
8.4 Outlook	112

8.1 Introduction

The potential connections between climate and phytoplankton community composition dates back to the work by Hutchinson (1967). More recently, studies by Lehman (1992, 2000) and Jassby *et al.* (1996) suggest that climate variability may be linked directly and indirectly to phytoplankton in relation to streamflow as well as changes in biomass and chlorophyll-*a* (Lehman 1996). Shifts in phytoplankton species composition in relation to climate forcing have been reported for the California coast by Tont (1989) observing that dinoflagellates abundance was higher than diatoms in relation to a reduced upwelling during the El-Niño years.

The 1977 climate regime shift along the California coast was also related to a decrease in diatom density (Lange *et al.* 1990). Barber and Chavez (1983) reported a change in the phytoplankton species composition from diatoms to dinoflagellates in relation to changes in the upwelling region off the Peruvian coast linked to El Niño. In the North Sea and neighbouring areas, changes in phytoplankton density and species composition have been observed in relation to the climate shift around 1977 (Dickson and Reid 1983; Colebrook 1986; Aebischer *et al.* 1990) as well as in the late 1980s. Furthermore, long-term fluctuations have been related to the North Atlantic Oscillation (NAO), as reported by Reid *et al.* (1998), Beaugrand *et al.* (2000), Edwards *et al.* (2001), and Edwards *et al.* (2002). Data from the continuous plankton recorder (CPR) survey were fundamental for these studies (see Chapter 5 for description of the CPR data). The anomalous periods in the late 1970s and late 1980s seem to be largely synchronous with unusual ocean climate conditions that have occurred

episodically over a timescale of decades. The unusual ocean climate conditions prevailing at these two time periods appear to contain important hydrographical elements that involve oceanic incursions into the North Sea (Edwards *et al.* 2002).

When analysing the effects of climate on community dynamics we need to disentangle the impact of abiotic and exogenous biotic factors, as well as factors internal to the population. In this chapter, we first present a general statistical approach to studying changes in phytoplankton species abundance in relation to climate variability. Thereafter we apply this method to an example where changes in phytoplankton species diversity, the dynamics of three phytoplankton species in a Swedish fjord, are related to the NAO and other abiotic factors. Finally, we conclude with a general outlook underlining the importance of further studies of changes in phytoplankton biovolume.

8.2 A statistical approach

Population dynamics of phytoplankton species are considered the result of feedback and exogenous structure (see also Chapter 1). We can represent these ecological relationships using a very general model in terms of reproduction and survival of individuals (Berryman 1999), which represent a variant of the Ricker (1954) discrete-time logistic model influenced by climate and stochastic forces:

$$N_t = N_{t-1} \cdot e^{[a_N + f_1(N_{t-1}) + f_2(C_t^i) + K + f_3(C_t^{i+1}) + \epsilon_t]} \quad (8.1)$$

Here N_t is the phytoplankton abundance at time t and C_t^{i+1} is the a variable representing the exogenous factors. The functions $f_i(\bullet)$ represents

the effects of density-dependence and exogenous factors on phytoplankton population dynamics and ε_t represent normal distributed stochastic perturbations. An alternative way to express Eq. (8.1) is in terms of the realized per capita population growth rates, which represent the processes of individual survival and reproduction that drive population dynamics, this is the R -function (*sensu* Berryman 1999). Defining $R_t = \log(N_t) - \log(N_{t-1})$ Eq. (8.1) can be expressed as a R -function (*sensu* Berryman 1999):

$$R_t = a_N + f_1(N_{t-1}) + f_2(C_t^i) + K + f_i(C_t^{i+1}) + \varepsilon_t \quad (8.2)$$

This model represents the basic feedback structure and integrates the exogenous and stochastic forces that drive population dynamics in nature. The basic idea for population analysis is to choose a family of functional forms for f to fit time-series data. This model formulates Eq. (8.2) as an additive non-linear model (see Bjørnstad *et al.* 1998 for an ecological example). Model (8.2) represents a Generalized Additive Model (GAM; Hastie and Tibshirani 1990). The choice of the functional form of the f_i functions can be approached using natural cubic splines (Green and Silvermann 1994; see Stenseth *et al.* (1997) and Bjørnstad *et al.* (1998, 1999) for ecological examples). The most parsimonious

model can be selected by criteria like the Akaike Information Criterion (AIC) or Schwartz's Bayesian Criterion (SBC).

8.3 Phytoplankton diversity and dynamics, an example

The data used in this example consist of abundance estimates of 40 phytoplankton species (cell counts), with a focus on the three species *Skeletonema costatum* (diatom), *Ceratium tripos*, and *Ceratium furca* (dinoflagellate), and abiotic factors including the NAO and local winds (Belgrano *et al.* 1999, 2001). Measurements were made on a monthly basis from 1986–96 at a station located at the mouth of the Gullmar Fjord on the Swedish West Coast (58° 15' N 11° 26' E; Fig. 8.1).

The NAO fluctuations (Fig. 8.2(a)) shows a switch in the late 1980s and early 1990s from a negative to a positive phase concomitant with warmer winter sea surface temperature (SST) as reported by Belgrano *et al.* (1999). This is a good indication that during the end of the 1980s, as shown by Reid *et al.* (1998), the seasonal pattern of phytoplankton has been extended in the North Sea and adjacent area beyond the usual pattern of spring/summer/autumn due to the warmer SST condition that possibly forced by the shift in the NAO from a negative to a positive

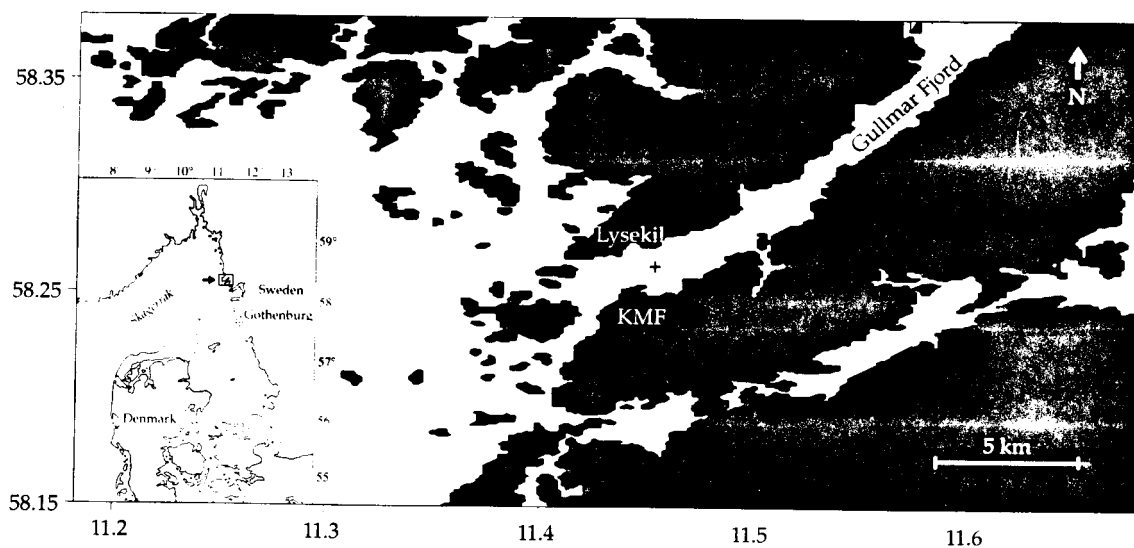


Figure 8.1 Location of the sampling station in the Gullmar Fjord, Sweden (58°N, 11°E) indicating Kristineberg Marine Research Station (KMF).

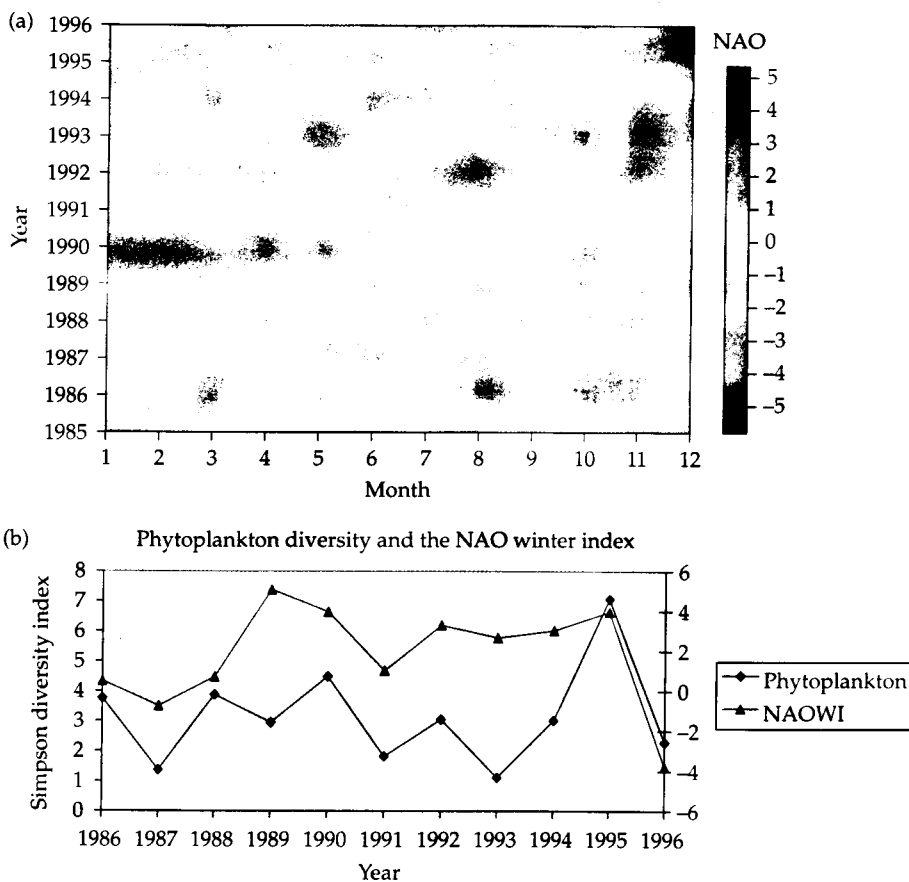


Figure 8.2 (a) NAO distribution covering the period 1985–96, indicating the strong positive phase during winters in the late 1980s and (b) Simpson's diversity index together with the NAO winter index (called NAOWI in panel b). (See Plate 7.)

phase in 1988 (Rodwell *et al.* 1999). The Simpson's diversity index (D ; Simpson 1949) (Fig. 8.2(b)), was correlated ($r = 0.41$; $p < 0.01$) with the NAO winter index. This indicates that higher diversity in phytoplankton species composition may be related to the positive phase of the NAO. A closer look at the changes in species composition showed that phytoplankton diversity was low during 1987 due to a large dominance of *S. costatum*. The increased number of cells of the dinoflagellate species *Ceratium furca* in 1992 coincided with the absence of two diatoms species *Chaetoceros socialis*, and *Thalassiosira nordenskiöldii* between 1990 and 1993. *Thalassiosira nordenskiöldii* can be regarded as an important species in terms of biomass for the spring bloom due to its size (Tiselius and Kuylenstierna 1996). *Chaetoceros socialis* can be regarded as an important food source for

copepods and its absence might have caused a shift in their grazing habits. These temporal changes in the species compositions during the spring bloom may result in an increase in the grazing activity by heterotrophic dinoflagellates. This may in turn prevent an increase in the diatom concentrations and as reported by Tiselius and Kuylenstierna (1996) disrupt the phytoplankton spring bloom. A plausible explanation (Lindahl *et al.* 1998) is that stronger winds during the high NAO years lead to more vertical mixing, which in turn enhanced nutrient concentrations in the surface layers, thus favouring an increase in dinoflagellate abundance. The relationship observed between the NAO, diatoms, and dinoflagellates on the Swedish west coast seems to be a general pattern very similar to the one observed for the northeast Atlantic by Edwards *et al.* (2001).

Phytoplankton diversity related to a number of limiting resources may be generated by non-linear dynamics (Huisman and Weissing 1999). A first order density dependence was detected in the three species of phytoplankton (Figs 8.3(a), 8.4(a) and 8.5(a)). The results presented in Fig. 8.3 shows the response of that changes in the abundance of the diatom *S. costatum* where strongly related to the variability in nitrates NO_3 , salinity and density associated with the southwest winds. These changes in the abiotic condition along the Swedish west coast have earlier been observed by Lindahl *et al.* (1998). They suggested that a transport of nutrients associated with stronger SW winds from the Kattegat area directly linked to a typical positive NAO scenario, could be related to large phytoplankton blooms as the one observed for *S. costatum* in 1987. The model for *S. costatum* including the covariates in (SC, Fig. 8.3) explained 95% of the observed variance, however, no direct relation with NAO was found for this species. The models obtained for the dinoflagellate *C. furca* (CF, Fig. 8.4) showed that this species was directly

related to changes in the NAO, SW winds and density. *Ceratium tripos* (CT, Fig. 8.5), showed a direct relation to changes in temperature, nitrate concentrations, southeast wind and northwest wind. The model that included nitrates explained 75% of the variance, reflecting the direct dependence of this species for nitrates availability. The abiotic conditions for the formation of dinoflagellates blooms along the Swedish west coast (Belgrano *et al.* 1999) suggest that the covariates selected by the models for CF and CT may be regarded as the explanatory variables underlying the changes in the abundance of these species. The use of GAMs models in the analysis of ecological time-series provided important information on the effect of both exogenous and stochastic forcing of the dynamics of marine phytoplankton.

8.4 Outlook

Species abundance models have been discussed in great detail by May (1975). However, the results

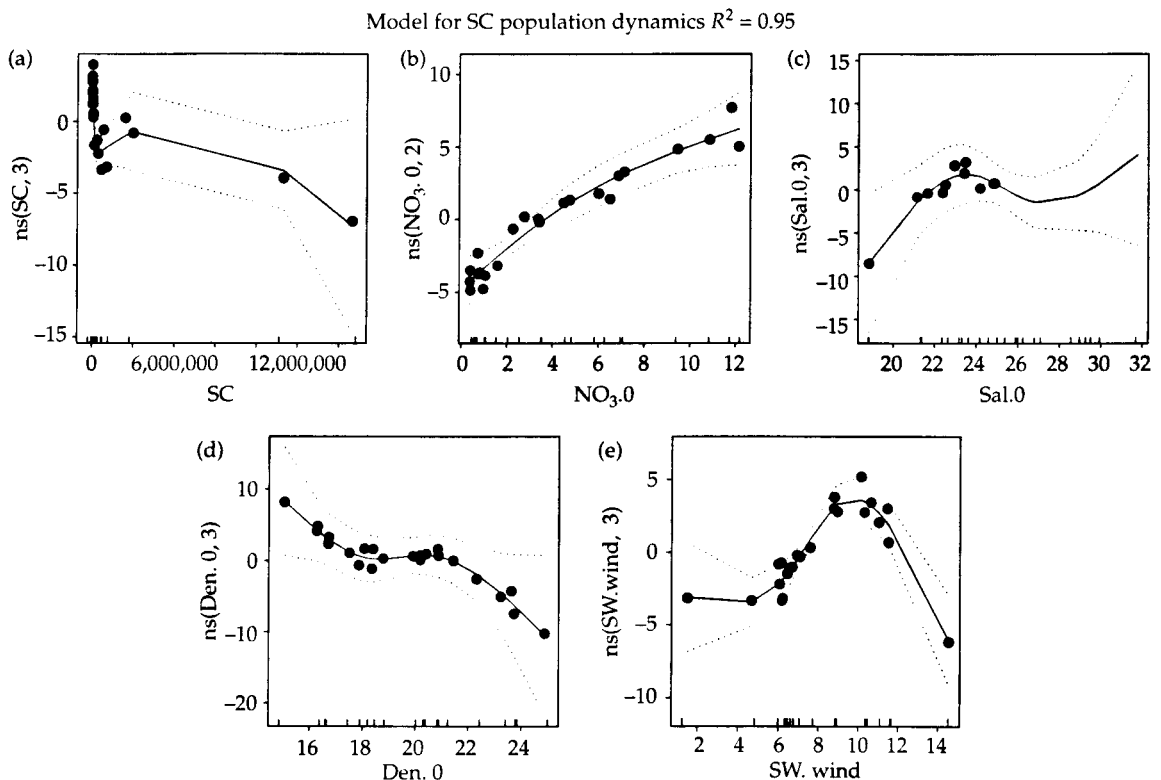


Figure 8.3 GAM Model for *S. costatum* population N_{t-1} (a), nitrates NO_3 (b), salinity (c), density (d), and southwest wind (e).

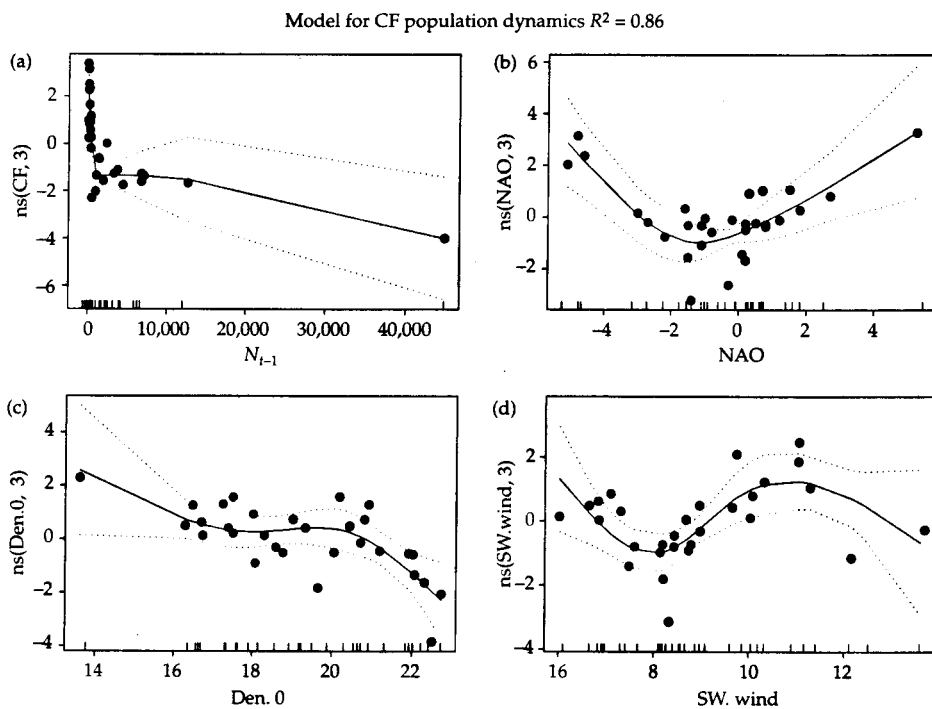


Figure 8.4 GAM Model for *C. furca* population N_{t-1} (a), NAO (b), density (c), and southwest wind (d).

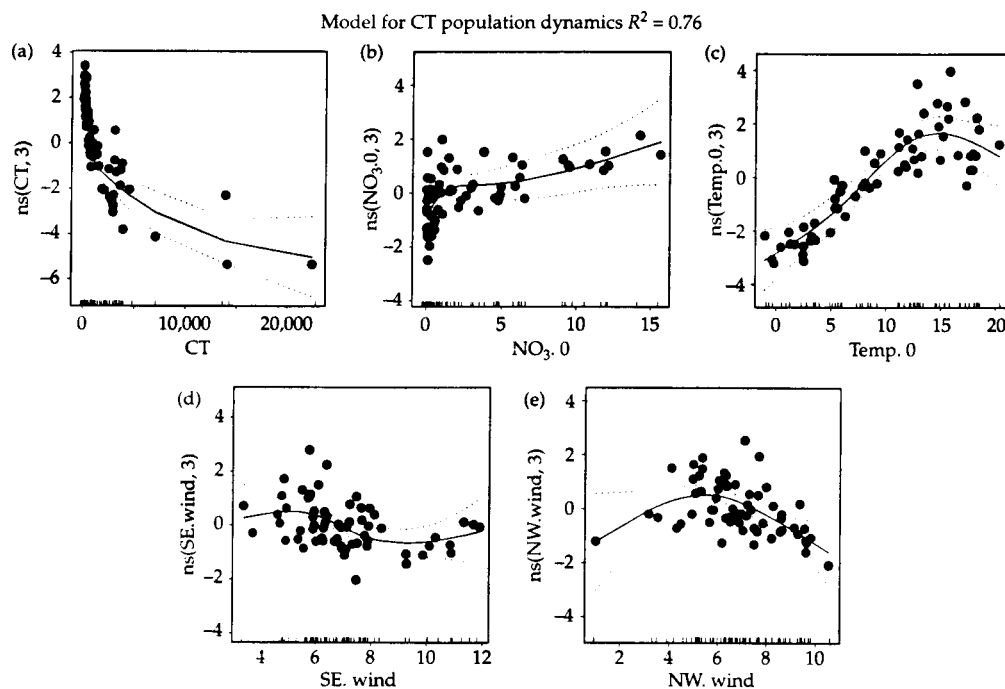


Figure 8.5 GAM Model for *C. tripos* population N_{t-1} (a), nitrates NO_3 (b), temperature (c), southeast wind (d), and northwest wind (e).

presented here suggest the importance of considering non-linear dynamics to investigate the relationships between changes in phytoplankton species abundance and a high number of covariates. At the interface of a dynamic system (Lindahl 1987; Tiselius and Kuylenstierna 1996) we can expect high phytoplankton variability, although species composition and coexistence may reflect well-defined assemblages that are taxonomically related. This is suggested by the Connell (1978) hypothesis of intermediate disturbance and the role of disturbance acting at a variety of scales. Phytoplankton species have a unique covariance relationship, resulting in a transfer function that indicates that each species can react to the same environmental fluctuations in different ways. As suggested by Harris (1986) the amplitude of this

transfer function may increase at longer timescales providing an indication of the integrative properties of cellular physiology. A reduction in the vertical mixing from a few days to a period of about two weeks may reduce the vertical mixing leading to increased biomass (Harris 1983). Therefore an increase in diversity (as the one observed in our example) may be related to the variance in the physical structure.

Climate variability has been shown to be potentially linked to changes in phytoplankton biovolume in relation to primary productivity and upwelling of nutrients. This aspect, as pointed out by Lehman (2000), needs further attention since changes in phytoplankton biovolume are linked to the fate of biogenic carbon in the pelagic food web.