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Temporal and spatial variability of phytoplankton and chlorophyll *a*: lessons from the south coast of Norway and the Skagerrak

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Regular monitoring of phytoplankton has been carried out on the Norwegian Skagerrak coast three times a week since 1989, and samples from the upper 3 m of the water column have been analysed for chlorophyll *a* (Chl *a*) concentrations and dominant species. Selected potentially toxic or harmful species of phytoplankton have also been quantified. Chl *a* appears to fluctuate considerably on a short time scale (2–3 days), and simple analyses suggest that Chl *a* should be measured at least twice a week to obtain reliable annual estimates. By contrast, at the inshore monitoring station Chl *a* is significantly correlated with transect measurements across most of the Skagerrak, indicating a high spatial homogeneity. Hence, measurements at the inshore stations are likely to reflect concentrations over a large area and meteorological conditions are suggested to be the most likely driving force controlling the variability. The traditional view of a marked spring and autumn bloom in temperate stratified waters does not seem to be a predominant feature of the production cycle in the Skagerrak. In fact, Chl *a* concentrations $>4\ \mu g\ l^{-1}$ rarely last for more than a week. In addition to short-term variability, there is also high inter-annual variability in the production cycle. This picture is reinforced by large variations in species composition of the phytoplankton community; the abundance of all species analysed varies substantially from one year to the next.

Key words: Chlorophyll *a*, phytoplankton, Skagerrak, variability.

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Introduction

Systematic monitoring of phytoplankton in Norway began in the early 1980s as a service to the fast-growing fish-farming industry. The main objective of the monitoring programme is to provide an early warning of algal blooms that may be a threat to caged fish or cause toxicity in shellfish. Initially, the toxic dinoflagellate *Gyrodinium aureolum* was the target species (Dahl and Tangen, 1993), but additional algal species were included in the programme as they proved to be a threat to the fish-farming industry or were demonstrated to induce toxicity in wild and cultivated shellfish (Aune *et al.*, 1995; Dahl, 1989). Today, algal surveillance includes many different taxa, three of which have caused significant losses in caged fish (viz. *G. aureolum*, Dahl and Tangen, 1993; *Chrysochromulina* spp., Underdal *et al.*, 1989; *Prymnesium* spp.), and two have caused toxicity in shellfish (viz. *Dinophysis* spp. and *Alexandrium* spp., Aune *et al.*, 1995). Monitoring is carried out during the period March–October and includes 24 stations covering the entire Norwegian coast.

One of the stations is situated in Flødevigen Bay on the south coast (Fig. 1), where extended monitoring of algae and Chl *a* has been carried out since 1984, with a sampling frequency of three times a week throughout the year. Initially, samples were taken at a depth of 1 m, but since 1989 a hose has been used from the surface to a depth of 3 m. On the basis of this latter time series (1989–1996), we describe inter- and intra-annual variability in Chl *a* and in cell concentrations of selected taxa. The spatial relevance of the monitoring is evaluated by correlating Chl *a* in Flødevigen Bay with simultaneous measurements carried out approximately monthly on a transect across the Skagerrak (Fig. 1) between Arendal (Norway) and Hirtshals (Denmark). In

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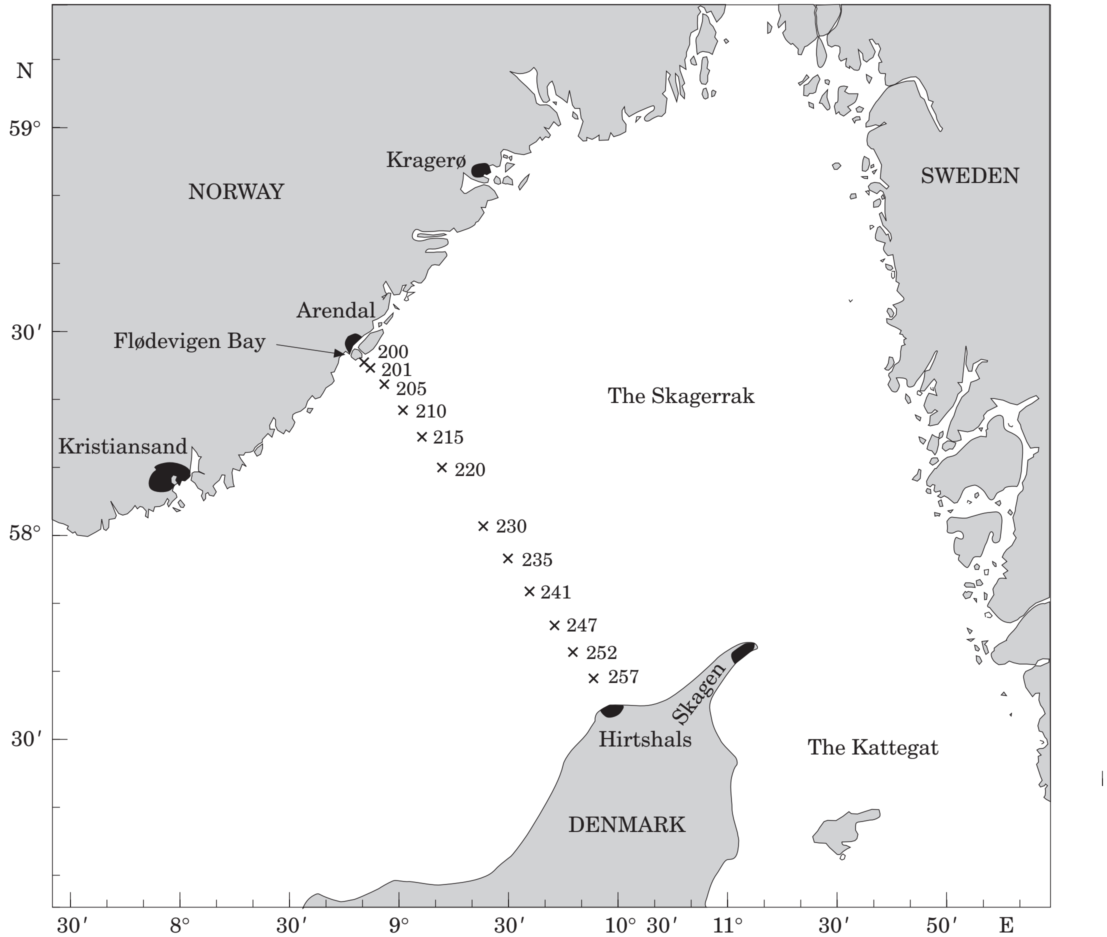


Figure 1. The Skagerrak area with Flødevigen Bay and stations (200–257) along the transect Arendal–Hirtshals indicated.

addition, temporal and spatial variability in Chl *a* are compared, and the effect of reducing sampling frequency from three times to once a week is evaluated.

The algae for which data are presented are: *Dinophysis* spp., which may contain diarrhetic shellfish toxins (DST), *G. aureolum*, *Chrysochromulina* spp., and two non-toxic genera of thecate dinoflagellates, *Ceratium* spp. and *Protoperidinium* spp. Blooms of *Ceratium* spp. have been associated with episodes of low oxygen in the sea (Falkowski *et al*., 1980; Edler, 1984). *Protoperidinium* spp. are heterotrophic. The occurrences of both genera may relate to the trophic status in the area and to decreasing oxygen concentrations along the Norwegian Skagerrak coast (Johannessen and Dahl, 1996a, b).

Materials and methods

Flødevigen Bay (Fig. 1) water has been sampled every Monday, Wednesday, and Friday at 9 a.m., and Chl *a* concentrations analysed after extraction with 90% acetone using the standard fluorescence method of Strickland and Parsons (1968).

Gyrodinium and *Chrysochromulina* were fixed by iodine and then counted using counting chambers with a detection limit of 10 000 and 50 000 cells l^{-1}, respectively. *Dinophysis, Ceratium*, and *Protoperidinium* were concentrated on membrane filters and counted under a microscope using an epifluorescence attachment. Among the *Protoperidinium* spp. only those that have green autofluorescence are detected by this method. The detection limit for these three genera was 20 cells l^{-1}.

The Chl *a* measurements and algal counts are positively skewed (many low values, fewer high values, and a few very high values). Because of the high sampling frequency, the annual average was in all cases estimated on the basis of the raw data (integrated over the year and divided by 365). Inter-annual variability in Chl *a* during the spring (Feb–Apr) and autumn (Aug–Sept) periods was also studied on the basis of integrated raw data (μg Chl *a* l^{-1}). Intra-annual

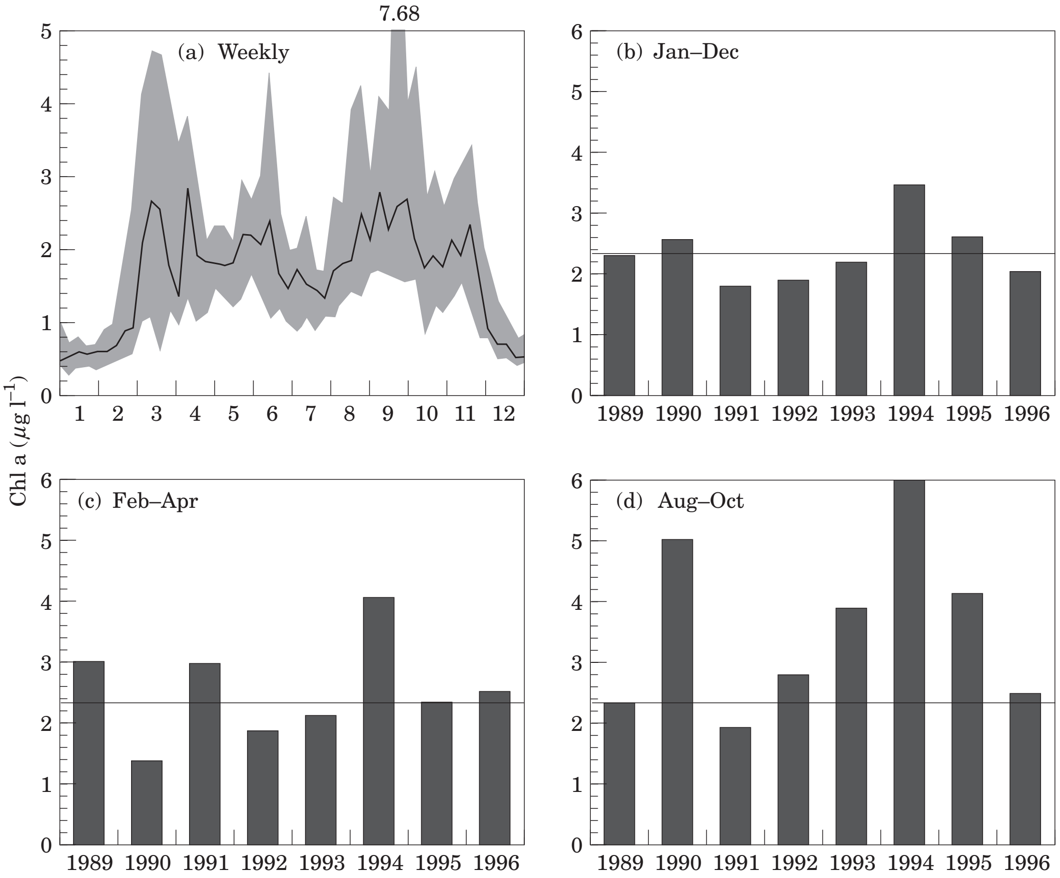


Figure 2. Chl *a* concentrations in Flødevigen Bay (0–3 m), 1989–1996: (a) Weekly medians and inter-quartile range (shaded); (b) annual averages; (c) spring averages by year; (d) autumn averages by year.

variability, however, was studied by pooling all data (1989–1996) and estimating the median and quartiles on a weekly basis (1–7 Jan, 8–14 Jan, etc.). Pearson correlation coefficients were obtained on log-transformed data ($\log_{10}(\text{value}+1)$). Chl *a* concentrations on the Arendal–Hirtshals transect were correlated with those in Flødevigen Bay either from the same day or from the days before and after averaged.

Results

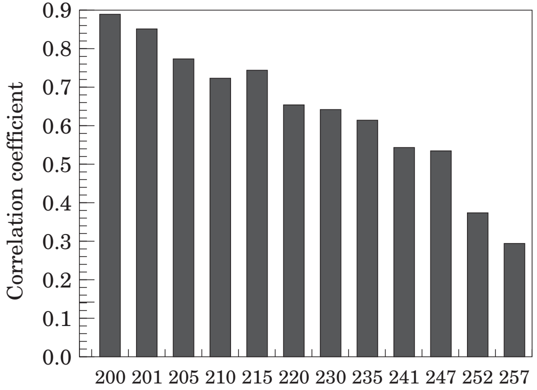
Temporal and spatial variability in Chl *a*

The intra-annual fluctuation in Chl *a* in the upper 3 m of the water column in Flødevigen Bay is presented in Fig. 2. Primary production generally starts in late February or the beginning of March. The median indicates a fairly stable level from March to November. However, the upper quartile shows a higher proportion of high concentrations in March and April, indicating the most likely period of the spring bloom. In June, there is often a smaller bloom, which coincides with flooding of the rivers due to melting snow in the mountains. An increased frequency of high concentrations is again observed from August to mid-November, with a peak in September.

The annual average concentration in Flødevigen Bay varied between 1.77 μg l^{-1} in 1991 and 3.45 μg l^{-1} in 1994, with an overall average for 1989–1996 of 2.34 μg l^{-1} (Fig. 2). The inter-annual Chl *a* concentrations varied by a factor of 2, whereas during the spring (Feb–Apr) and autumn periods (Aug–Oct) they varied by a factor of 3. In 1990, the average concentration during spring was well below the average for the period (2.51 μg l^{-1}), whereas 1994 was characterized by high spring concentrations. The highest concentrations generally occur in the autumn, with an overall average of 3.56 μg l^{-1}. However, just as in the spring, there is not always a marked phytoplankton bloom in the autumn.

The Chl *a* concentration in the upper 3 m in Flødevigen Bay is significantly and positively correlated with the measurements obtained all across the Skagerrak (Fig. 3; $p<0.005$ for the lowest correlation, Stn 257), both for the upper 5 m (measurements at 0 and 5 m) and

(a) 0–5 m depth



(b) 0–30 m depth

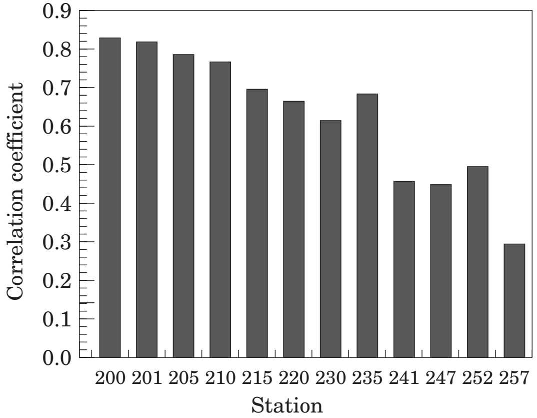


Figure 3. Correlation coefficients between simultaneous measurements of Chl *a* in Flødevigen Bay and at the different stations (200–257) along the transect Arendal–Hirtshals (n=89 for all pairs): (a) average transect values 0–5 m depth; (b) integrated transect values 0–30 m depth.

for the integrated values over the euphotic zone (measurements at 0, 5, 10, 20, and 30 m). The lag-one autocorrelation in Flødevigen Bay (i.e., the correlation between consecutive measurements; all data included) is 0.62. The spatial correlation between the bay and the transect stations for the upper 5 m is significantly higher than the temporal autocorrelation for stations 200–215 ($p<0.05$; according to the method of Zar, 1974); it is about the same for stations 220–247 and for stations 252 and 257, which are situated in the Jutland Current just outside the Danish coast, the spatial correlation is significantly lower than the temporal correlation. For the euphotic zone (0–30 m), the spatial correlation is higher for stations 200–210, about the same for stations 215–235, and significantly lower for stations 241–257. The mean correlation coefficient of Chl *a* between neighbouring stations along the transect is 0.87, with a range of 0.64–0.94.

These results show that there is a high degree of spatial homogeneity across the Skagerrak. Measurements in the upper 3 m in Flødevigen Bay seem more representative of Chl *a* in the euphotic layer (0–30 m) along the first part of the transect Arendal–Hirtshals on the same day than for the Chl *a* concentration 2–3 days later in Flødevigen. Hence, in addition to spatial homogeneity, there seems to be a high degree of short-term temporal variability.

To test the effect of reducing the sampling frequency (Table 1), we estimated the annual average Chl *a* concentrations based on: (1) all the samples (three times a week), (2) twice a week (Monday and Friday), and (3) once a week (estimates for Monday, Wednesday, and Friday, separately). There was no marked difference between sampling three times a week and twice a week. In contrast, sampling once a week resulted in markedly different annual estimates in some years (e.g., ≥35% in 1989 and 1995).

Algal concentrations

The potential ichthyotoxic algae *Chrysochromulina* spp. and *Gyrodinium aureolum* have distinct seasonal occurrences along the Norwegian Skagerrak coast, with their highest abundance in May–July and August–October, respectively (Fig. 4). *Chrysochromulina* spp. recurs regularly each year, although the peak concentration may vary from one year to the next (not shown). *G. aureolum*

Table 1. Estimated annual average Chl *a* concentrations ($\mu g\ l^{-1}$) based on sampling data on all days (Monday, Wednesday, Friday), two days (Monday and Friday), and individual days of the week. The percentage difference between the lowest and the highest values obtained from individual days is also given.

	1989	1990	1991	1992	1993	1994	1995	1996
All days	2.33	2.58	1.80	1.91	2.23	3.33	2.62	2.12
Mon./Fri.	2.13	2.55	1.74	1.87	2.10	3.25	2.81	1.98
Mon.	2.23	2.39	1.70	1.81	2.15	3.29	2.54	1.90
Wed.	2.72	2.63	1.91	1.99	2.49	3.49	2.24	2.39
Fri.	2.02	2.72	1.78	1.93	2.04	3.20	3.07	2.05
Diff. (%)	35	14	12	9	22	9	37	25

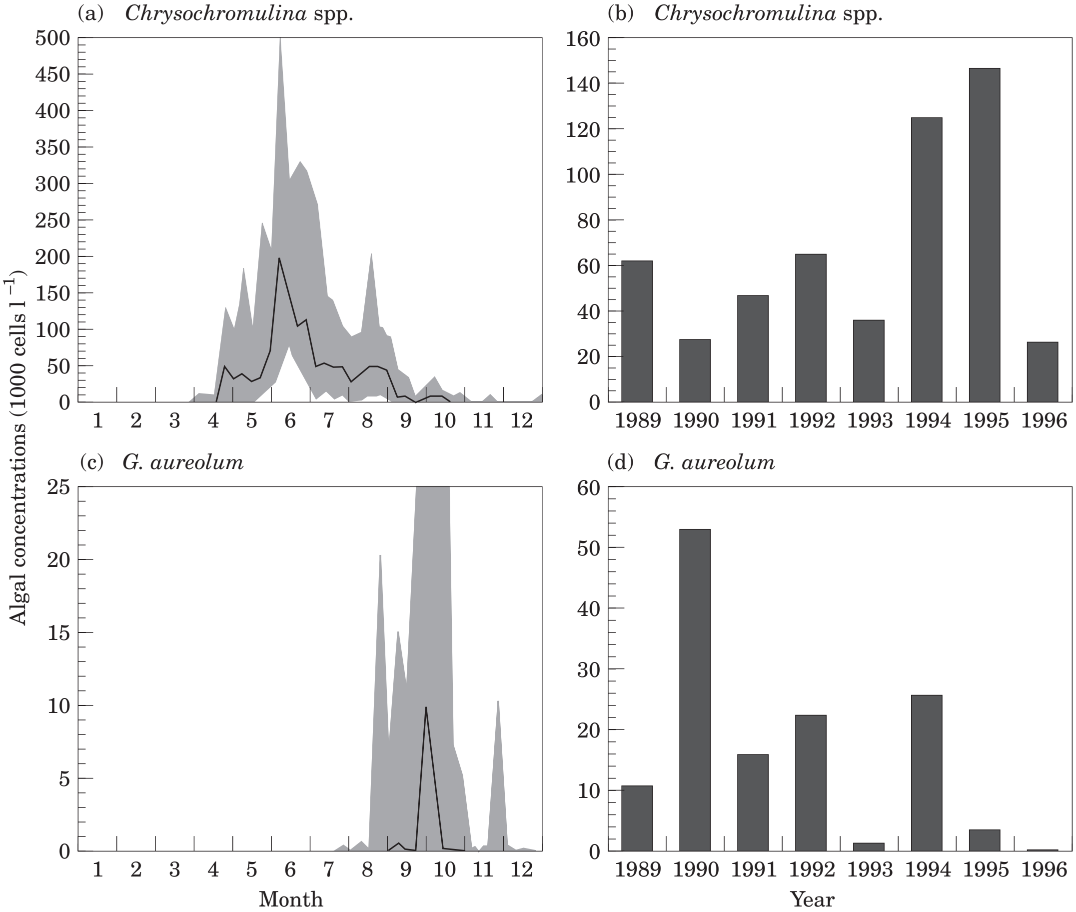


Figure 4. Intra-annual (a, c: weekly medians and, shaded, inter-quartile range) and inter-annual variation (b, d: annual averages) in concentrations of phytoplankton species in Flødevigen Bay, 1989–1996: (a, b) *Chrysochromulina* spp. (c, d) *Gyrodinium aureolum*.

concentrations vary considerably inter-annually, from being virtually absent to colouring the water brownish as in 1994. The two years with the highest concentrations of Chl *a* during August–October (1990 and 1994) are both peak "*Gyrodinium* years".

Species belonging to the genus *Dinophysis* are usually found in low concentrations with blooms seldom exceeding 10 000 cells l^{-1} (Fig. 5). The most common species, *D. norvegica*, has its main occurrence in May–August, but can be present in relatively high numbers in all seasons. *D. acuminata* has its main season in May–July, but may appear in relatively high concentrations all through the period March–November. *D. acuta* has a pronounced seasonal occurrence with the highest concentrations in August–November (the low concentrations in parts of October probably reflect the still relatively low number of monitoring years). Because *D. acuta* is the most toxic among the *Dinophysis* species in Norwegian coastal waters (Dahl *et al*., 1995), the risk of accumulation of DST in mussels is highest in the autumn. The occurrence of *Dinophysis* spp. from one year to the next may vary considerably. In 1993 the concentrations of *D. acuta* and *D. norvegica* were exceptionally high in the autumn. In a bay near Flødevigen, reddish water due to mass occurrence of these species was observed, and concentrations of about 25 million cells l^{-1} were recorded, consisting mostly of *D. norvegica* (Dahl *et al*., 1996). This is probably the highest concentration of *Dinophysis* spp. ever reported.

Both *Ceratium* spp. and *Protoperidinium* spp. appear to increase steadily from spring/early summer, reaching peak concentrations in August–September (Fig. 5). The inter-annual variability seems to be considerably higher for the autotrophic *Ceratium* spp. than for the heterotrophic *Protoperidinium* spp. A reasonable explanation for this difference in variability may be their different modes of feeding. The highest concentrations of both genera were recorded in 1993, coinciding with the highest concentrations of *Dinophysis*.

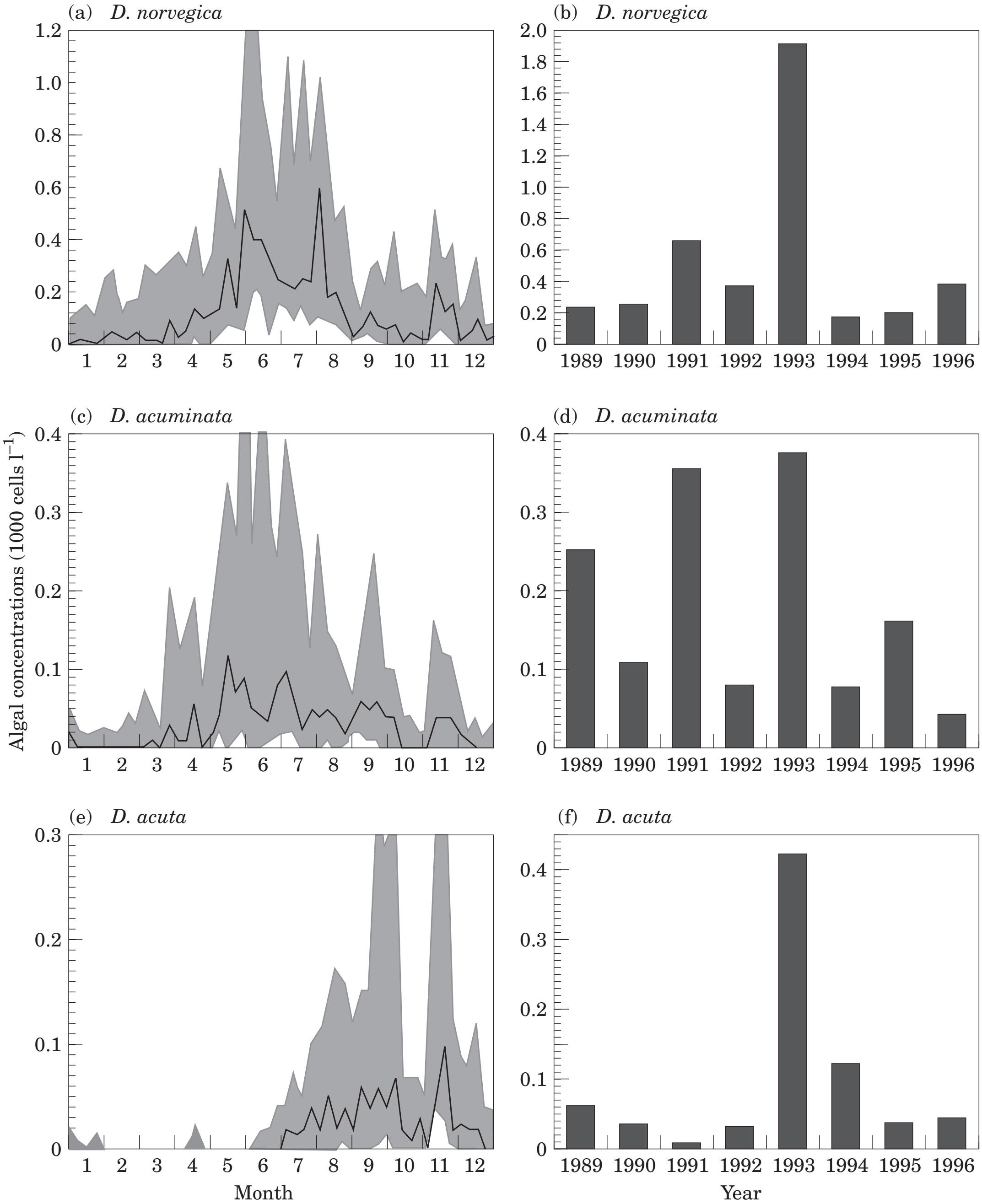
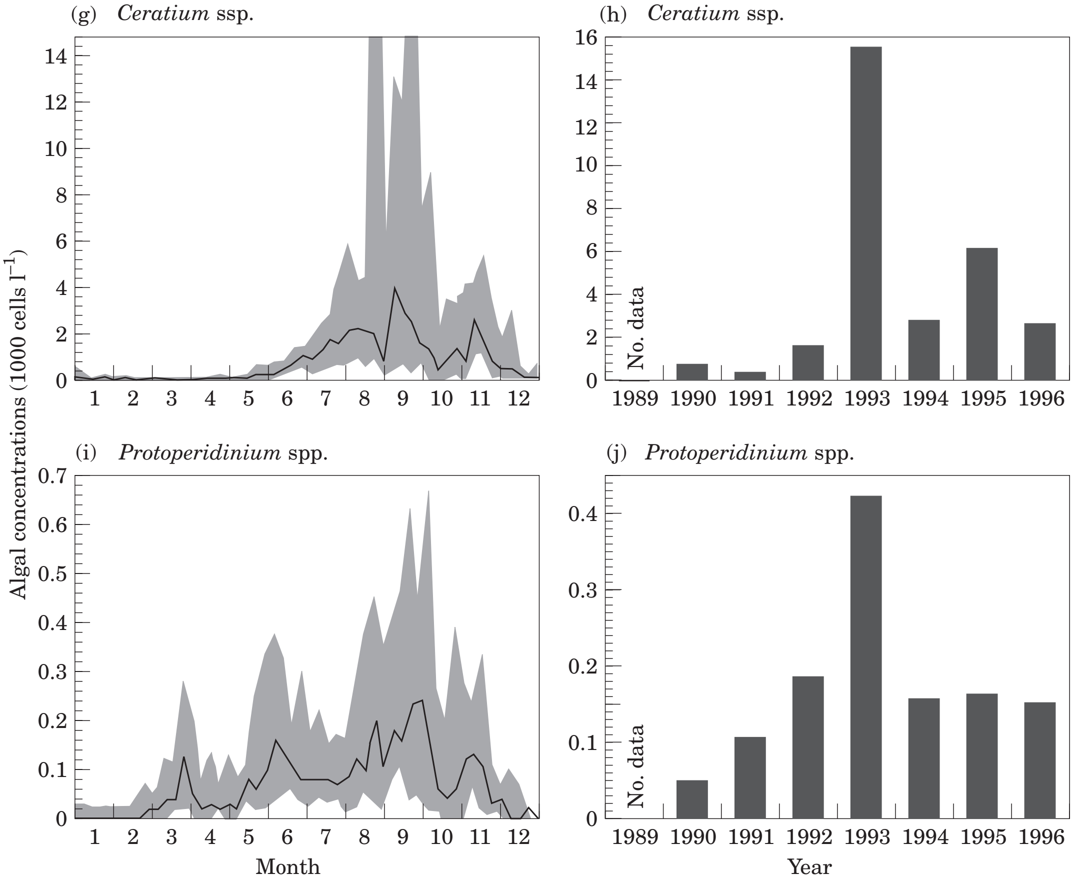


Figure 5. a to f.

Discussion

The results from Flødevigen Bay show that there is high short-term variability (within a few days) in Chl *a* concentrations. Consequently, to obtain relatively precise estimates over a period, frequent measurements are needed. Our simple analysis suggests at least twice a week. However, because of high spatial homogeneity in Chl *a* across the Skagerrak, the measurements in Flødevigen probably give a fairly good estimate of the annual variability in the euphotic layer over a large area. Chl *a* measurements in the Gullmar fjord on the west coast of Sweden show similar intra-annual variability (Lindahl, 1995) as in Flødevigen Bay.

The high spatial homogeneity combined with relatively high short-term temporal variability suggests that



(g) *Ceratium* ssp.

(h) *Ceratium* ssp.

(i) *Protoperidinium* spp.

(j) *Protoperidinium* spp.

Figure 5. g to j.

Figure 5. Intra-annual (a, c, e, g, i: weekly medians and, shaded, inter-quartile range) and inter-annual variation (b, d, f, h, j: annual averages) in concentrations of phytoplankton species in Flødevigen Bay, 1989–1996: (a, b) *Dinophysis norvegica.* (c, d) *Dinophysis acuminata.* (e, f) *Dinophysis acuta.* (g, h) *Ceratium* spp. (i, j) *Protoperidinium* spp.

the main regulating mechanism operates on larger scales, e.g. of the Skagerrak or even larger. Hence, meteorological conditions seem to be the most likely driving force controlling the variability in Chl *a* concentrations.

The Skagerrak is a highly dynamic area with regard to hydrographical conditions. Therefore, one explanation which should be considered for the relatively high short-term variability is advection of water masses with variable Chl *a* concentrations. However, this hypothesis assumes relatively high spatial variability, which does not seem to be the case. On the other hand, advective processes related to blocking and subsequent massive outflow of water masses (e.g., Aure and Sætre, 1981) can contribute to both spatial homogeneity during the blocking phase and to temporal variability during the outflow phase. Other meteorological variables that are likely to affect Chl *a* concentrations are wind and light. Little wind during spring, for example, may give rise to an early start of the production season (see Cushing, 1995), whereas strong winds may cause turbulence and thereby limit primary production. Turbulence caused by strong winds during summer and autumn may cause the flagellates to become evenly distributed above the pycnocline, whereas during calm periods motile phytoplankton may concentrate at favourable depths, for instance near the pycnocline where nutrients may be available. During such periods, light may become unfavourable during cloudy days, thus "forcing" the flagellates to migrate closer to the surface. Knowledge about the mechanisms causing the spatial homogeneity and the relatively high short-term temporal variability is likely to be important to our understanding the production cycle in the Skagerrak.

The traditional view of a marked spring and autumn bloom in temperate stratified waters (e.g., Cushing, 1975) does not seem to be a predominant feature of the production cycle in Flødevigen Bay and, by extrapolation, in the Skagerrak. In fact, Chl *a* concentrations >4 μg l^{-1} rarely last for more than a week. In addition to short-term variability, there is also high inter-annual variability in the production cycle. This picture of high variability is reinforced by the large variations in the species composition of the phytoplankton community; the abundance of all species analysed here varies substantially from one year to the next.

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