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Long-term variation in phytoplankton productivity during spring in Icelandic waters

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Annual variations in primary productivity (uptake of ^{14}C) measurements in Icelandic waters during spring since 1958 are analysed for four geographically defined regions, which correspond to major hydrographical features. The overall means by region range from 4.3 to 9.2 mg C m^{-3} h^{-1}. Annual variation in the shelf region north-east of Iceland reflects the major changes observed in environmental conditions, especially during the 1970s. The seasonal development of phytoplankton productivity depends on surface salinity conditions and its effects on the stability of the water column. Given favourable conditions, the spring bloom may start to develop in late March/early April and usually has its peak in May. In the Arctic Water north-east of Iceland, there is a single, well-defined peak, whereas a sequence of peaks is frequently observed in the Atlantic Water of the south-western shelf. The differences between the regions show the importance of the physical factors affecting phytoplankton dynamics.

Key words: Arctic, environmental conditions, marine, North Atlantic, phytoplankton, productivity, seasonal cycles.

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Introduction

Annual biological oceanographic observations in the waters north of Iceland were initiated in the 1950s as part of a multinational research programme on Atlanto-Scandian herring (Jakobsson, 1978). The herring disappeared abruptly from the area in the mid-1960s simultaneously with major changes in environmental conditions in the northern shelf area (Malmberg and Svansson, 1982; Stefánsson and Jakobsson, 1989). Environmental research continued and gradually became the main objective of the annual spring surveys. Originally, the Icelandic surveys were focused on the fishing grounds to the north, but in 1974 they were expanded to cover all waters surrounding Iceland. The joint results of the multinational programme have been presented at ICES Council Meetings and reported in Annales Biologiques (see Astthorsson *et al*., 1983). The results of the Icelandic surveys regarding annual environmental conditions are published in Icelandic (see Astthorsson and Gislason, 1995).

The waters off Iceland are characterized by the cold Polar Water of the East Greenland Current and Arctic Water of the East Icelandic Current from the north, and the warm North Atlantic Water of the Irminger Current from the south (Fig. 1). The environmental conditions on the fishing grounds are highly variable. Extreme variation is observed north of Iceland, where the North Atlantic Water may shift from being almost negligible to the dominant water mass. Studies and reviews of changes in environmental conditions and their effects on the biota include hydrography (Malmberg, 1986; Malmberg and Kristmannsson, 1992), nutrients (Stefánsson and Ólafsson, 1991), phytoplankton (Thórdardóttir, 1976, 1977, 1984), zooplankton (Astthorsson *et al*., 1983; Astthorsson and Gislason, 1995) and fisheries (Jakobsson, 1978, 1992; Stefánsson and Jakobsson, 1989; Malmberg and Blindheim, 1994; Vilhjálmsson, 1997).

This paper is aimed at a description and analysis of extensive primary productivity measurements carried out annually since 1958 in relation to major hydrographical features of the waters around Iceland, with particular emphasis on spring-bloom development.

Material and methods

The station grid is based on sections (Fig. 2) transverse to the currents circulating clockwise around Iceland (Fig. 1), with transects running across the shelf from the

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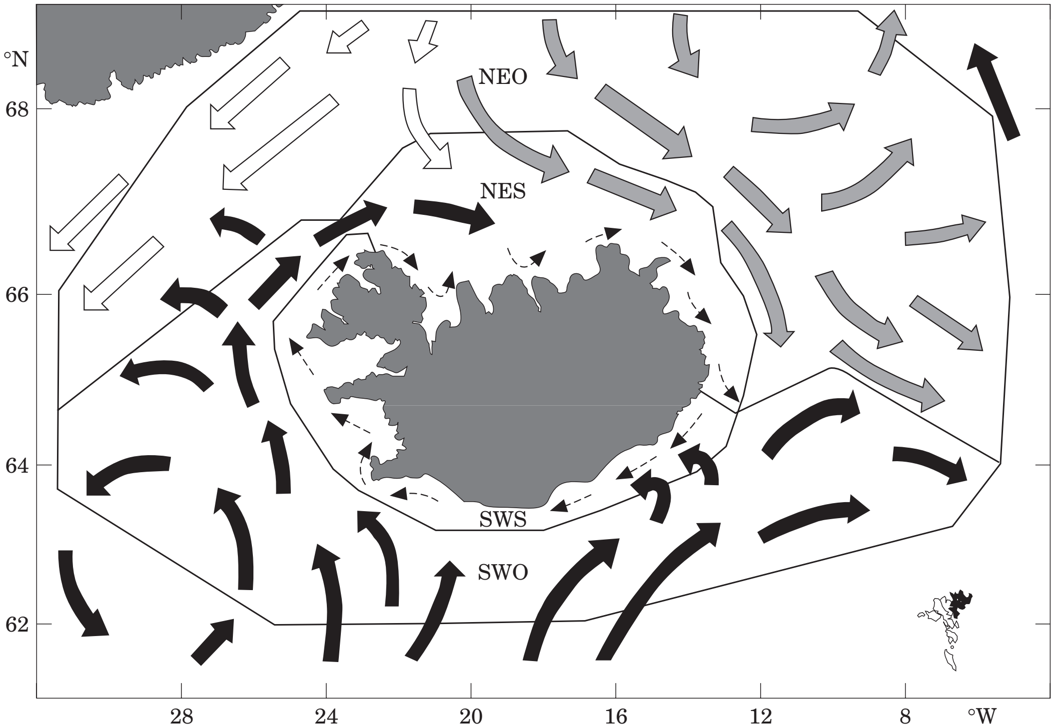

Figure 1. Map of Icelandic waters with the four regions distinguished and the main current system indicated. Currents (arrows) transporting Atlantic Water (black), Arctic Water (grey), and Polar Water (white) are modified from Gunnarsson (1991); coastal currents (broken lines) from Vilhjálmsson (1997). Regional acronyms are defined in the text.

coast into deep water. The area has been divided into two shelf regions (Fig. 1), approximately following the 200-m depth contour except to the north where it extends to roughly 500 m depth (Fig. 2), and two oceanic regions for the deeper stations. Shelf (S) and oceanic (O) regions were both split into a north-east (NE) and a south-west (SW) region. The division line between the two is situated close to the Greenland–Scotland ridge, and separates the domains of Atlantic and Arctic waters. These regions (referred to as SWS, NES, SWO, and NEO) match a division of the area used by Gislason and Astthorsson (1997); they apparently also correspond to contrasts in the averaged nutrient concentrations and in the index of stability (cf. Fig. 15 in Stefánsson and Ólafsson, 1991).

Water samples were taken from standard depths of 0, 10, 20, and 30 m. For measurement of the uptake of ^{14}C at light saturation and *in situ* temperatures as an index of photosynthetic activity, 50 ml borosilicate bottles were inoculated with 2 or 4 μCi $NaH^{14}CO_3$, and illuminated in an incubator for 4 h by fluorescent tubes (Philips TLF 20W/33) at approximately 220 μE m^{-2} s^{-1} (PAR). Light intensity was measured by means of a 2π-quantum sensor at the centre of the bottles, which were arranged along the edge of a vertically rotating wheel. Membrane filters (0.2 m) were used in all ^{14}C experiments. Post-incubation treatment followed standard procedures (Parsons *et al.*, 1984), with the exception of radioactivity counts. Geiger-counters were only exposed to the front side of the filters until 1983, but filters were counted from both sides thereafter and the result was corrected for variable penetration of ^{14}C into the filters (Theodórsson, 1975, 1984). Chl *a* measurements have remained unchanged since 1974. One litre subsamples were filtered on glass fibre filters (Whatman GF/C) and measured in a spectrophotometer following the trichromatic procedure on 90% acetone extracts (Parsons *et al.,* 1984).

The stations were fairly uniformly distributed geographically (Fig. 2), but the seasonal distribution of observations has been far from uniform. More than half of all data were collected during the annual spring surveys in late May and early June (Table 1). Therefore, inter-annual comparison of averaged productivity values has been restricted to observations made during the period from 16 May to 15 June, in spite of the obvious drawback that drastic changes in productivity values may occur on time scales of only a few days. Inter-annual comparison is further complicated because the annual cruises have changed to an earlier date over the years. The shift in sampling date at a selected station on the mid-northern shelf area is 2–3 weeks (Fig. 3). The

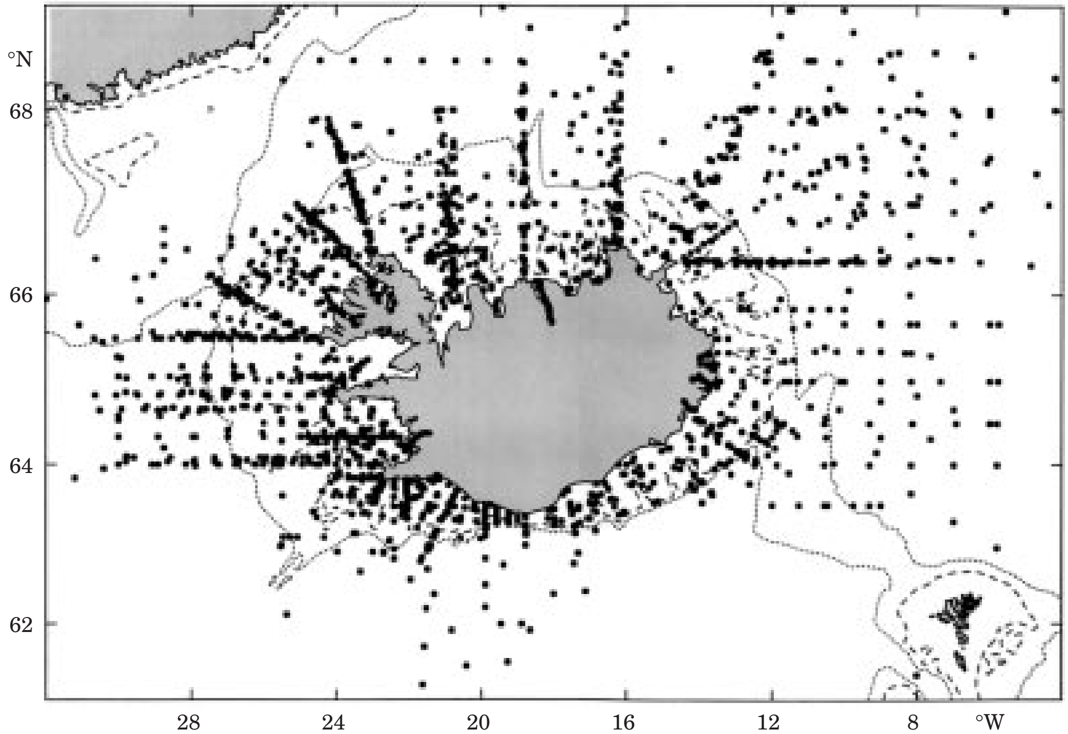

Figure 2. Distribution of sampling stations (dots) where primary productivity has been measured since 1958. A single dot may represent several observations; 200 m (broken lines) and 500 m (dotted lines) depth contours are indicated.

shift is not as marked for the SW regions, where some stations were monitored at both the beginning and the end of each cruise.

For the regions defined and spring period selected, the distribution of the number of observations in each year (Table 2) is quite evenly distributed between regions. Since the water column is relatively homogeneous down to 20 m, judged by hydrographical observations and nutrient concentrations (Stefánsson, 1962), and by phytoplankton productivity (Fig. 4a–f), annual productivity values were calculated as the means with standard errors of all measurements in the surface layer (0–20 m). Data are presented for all spring surveys between 1958 and 1994, with the exception of 1968 when ice-cover prohibited sampling north of Iceland.

Temporal variation is indicated as curved lines through the calculated means for every fortnight during the spring season. The close correlation between productivity and corresponding Chl *a* measurements in Icelandic waters (Thórdardóttir *et al.*, 1991) allows the use of the much more numerous productivity data for studying seasonal changes in phytoplankton biomass. Taking 1.0 mg m^{-3} Chl *a* as the biomass level marking the start of the spring bloom and using the average productivity to Chl *a* ratio in spring for each region (2.8, 2.7, 2.4, and 2.0 for SWS, SWO, NES, and NEO, respectively), the initiation of the spring bloom in the four regions can be compared.

Results and discussion

Productivity was generally higher in the SW regions than in the NE regions and also generally higher in the shelf regions than in the oceanic regions. The overall means for the shelf regions were 9.2 and 6.2 mg C m^{-3} h^{-1} for SWS and NES, respectively (Fig. 5a, b), and for the oceanic regions 7.1 and 4.3 mg C m^{-3} h^{-1} for SWO and NEO, respectively (Fig. 5c, d). The standard error for the mean productivity values ranged from 0.1 to 0.2 mg C m^{-3} h^{-1} and all means were significantly different (Student's t-test; $p<0.001$). One might argue on the basis of a $Q_{10}=2$ (Harris and Piccinin, 1977) that differences in ambient temperature (means 6.9 and 6.8°C in SWS and SWO, dominated by Atlantic Waters, compared to only 3.6 and 2.4°C in NES and NEO, influenced by Arctic waters) explain most of the differences in the averaged productivity values between the north-east and the south-west regions. However, the higher productivity found over the shelves compared to the open ocean cannot be explained by temperature differences.

Table 1. Frequency distribution of cumulative primary productivity measurements ('stations') by 2-weekly interval for the four regions (cf. Fig. 1), 1958–1994.

Period	Region SWS	SWO	NES	NEO
1	2	—	—	—
2	22	10	—	12
3	13	10	—	10
4	5	4	9	3
5	7	3	1	7
6	31	13	—	13
7	136	30	—	30
8	159	40	27	41
9	422	123	54	131
10	412	166	131	167
11	468	473	401	473
12	376	251	409	244
13	27	8	45	7
14	39	14	30	14
15	43	31	12	32
16	109	85	52	84
17	97	81	158	87
18	57	87	18	84
19	32	27	1	26
20	19	17	2	16
21	3	5	—	5
22	17	6	4	5
23	22	22	1	19
24	14	5	—	4
25	—	—	—	—
26	—	—	—	—

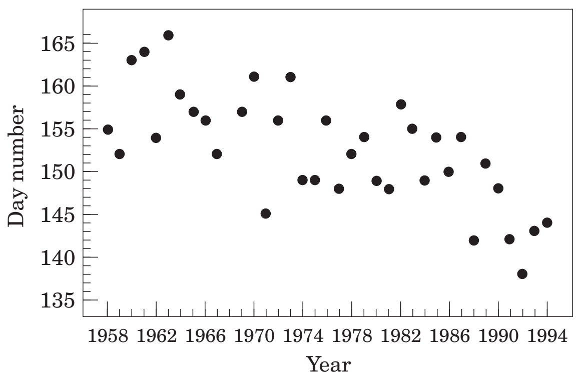

Figure 3. Change in timing (day number) of observations made at a reference station north of Iceland (66°32′N 18°15′W). 1958–1994.

Table 2. Frequency distribution of primary productivity measurements ('stations') between 16 May and 15 June by year for the four regions (cf. Fig. 1), 1958–1994.

	Region SWS	SWO	NES	NEO
1958	10	21	33	31
1959	19	47	14	8
1960	2	—	1	1
1961	8	17	7	6
1962	2	2	6	1
1963	2	—	6	—
1964	7	14	20	6
1965	10	15	37	24
1966	21	5	36	32
1967	7	12	18	13
1968	—	—	15	—
1969	2	—	—	9
1970	4	4	20	5
1971	20	20	16	6
1972	18	19	25	19
1973	26	21	21	6
1974	29	27	34	18
1975	47	37	28	116
1976	28	25	29	26
1977	38	50	37	25
1978	44	30	31	25
1979	34	29	36	23
1980	25	22	28	23
1981	63	36	46	32
1982	30	35	31	21
1983	39	32	25	22
1984	23	35	24	21
1985	24	24	23	22
1986	23	27	18	26
1987	25	19	22	15
1988	25	20	25	21
1989	27	17	14	41
1990	59	23	26	12
1991	49	27	21	25
1992	57	28	20	21
1993	25	18	22	18
1994	22	20	28	44

The annual mean spring productivity by region varies considerably (Fig. 5). In some instances, these variations can be ascribed to changes in environmental conditions, which are most pronounced in the NE region, due to the variable strength of the main currents around Iceland and their effects on the inflow of Atlantic Water. In the mid-1960s, temperature and salinity north of Iceland dropped abruptly (Fig. 6). This severe change marked a transfer of a massive body of cold and low salinity water by the East Greenland Current, which kept circulating in the North Atlantic and the sub-Arctic region during the following decades (Dickson *et al.,* 1988). This event had a major effect on the stability of the surface layers in the NES region and thereby on the pelagic biota (Thórdardóttir, 1977). During the 1970s, salinity fluctuated from being typical of Polar Water in one year to typical of Atlantic Water in the next. Similar changes were observed in water temperature and years have been categorized accordingly into "cold" and "warm" years (Malmberg and Svansson, 1982). Salinity, however, is a more appropriate parameter to distinguish different water masses in the NES region, since surface water temperatures depend on air temperature and wind force.

A comparison of the relative annual variations in average salinity and productivity for the NES region (Fig. 7) reveals the strong covariance during the

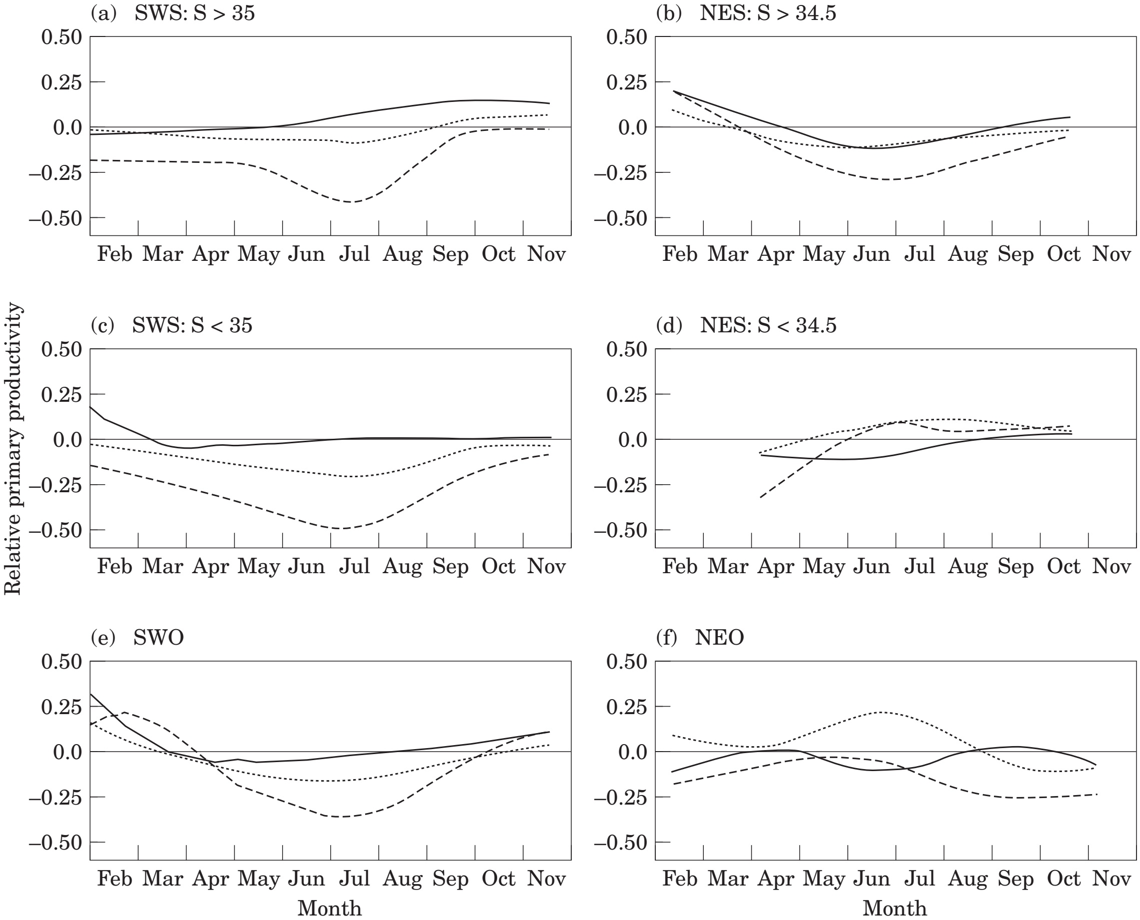

Figure 4. Seasonal change in phytoplankton productivity at 0 m (drawn line), 20 m (dotted line), and 30 m (broken line) relative to productivity at 10 m by region. For the shelf regions, data have been split in stations with surface salinity above and below 35.

1970s. The highs and lows in spring productivity measurements have been explained by differences in spring bloom development in "cold" versus "warm" years due to differences in stability of the water column (Thórdardóttir, 1984). At first sight, the low productivities prior to 1964 appear to contradict this explanation, but the conflicting results have been explained by the change in grazing pressure (Thórdardóttir, 1977; Astthorsson *et al*., 1983; Stefánsson and Jakobsson 1989), in accordance with the marked decline of zooplankton biomass during the mid-1960s (Astthorsson *et al*., 1983; Astthorsson and Gislason, 1995). The apparent increase in annual mean productivity along with higher salinity since the mid-1980s may be explained by an earlier timing of the surveys (cf. Fig. 3). This will be considered further when dealing with the seasonal changes in phytoplankton biomass.

It has to be emphasized that mean productivity has not increased homogeneously among all stations, but only at stations characterized by a relatively high surface salinity, indicative of Atlantic Water and a turbulent water column in spring (Fig. 7). A salinity criterion of 34.5 has been used here to distinguish between stations with a dominance of Atlantic Water and stations influenced by Polar Water, meltwater from drift-ice or fresh water run-off, which are indicative of a stable surface layer. The timing of the spring bloom is affected by prevailing environmental conditions (Thórdardóttir, 1977, 1984, 1986) and the stability of the water column in particular (Stefánsson and Ólafsson, 1991).

Given favourable conditions for phytoplankton growth, a spring bloom at these latitudes may develop in mid-March (Sakshaug and Slagstad, 1991), but is frequently delayed for at least one month. Smoothed curves of 2-week mean productivity values and nitrate concentrations (Fig. 8) illustrate the seasonal cycles in phytoplankton biomass and growth in the four different regions. The data from the shelf regions were split according to surface salinity (34.5) at each station.

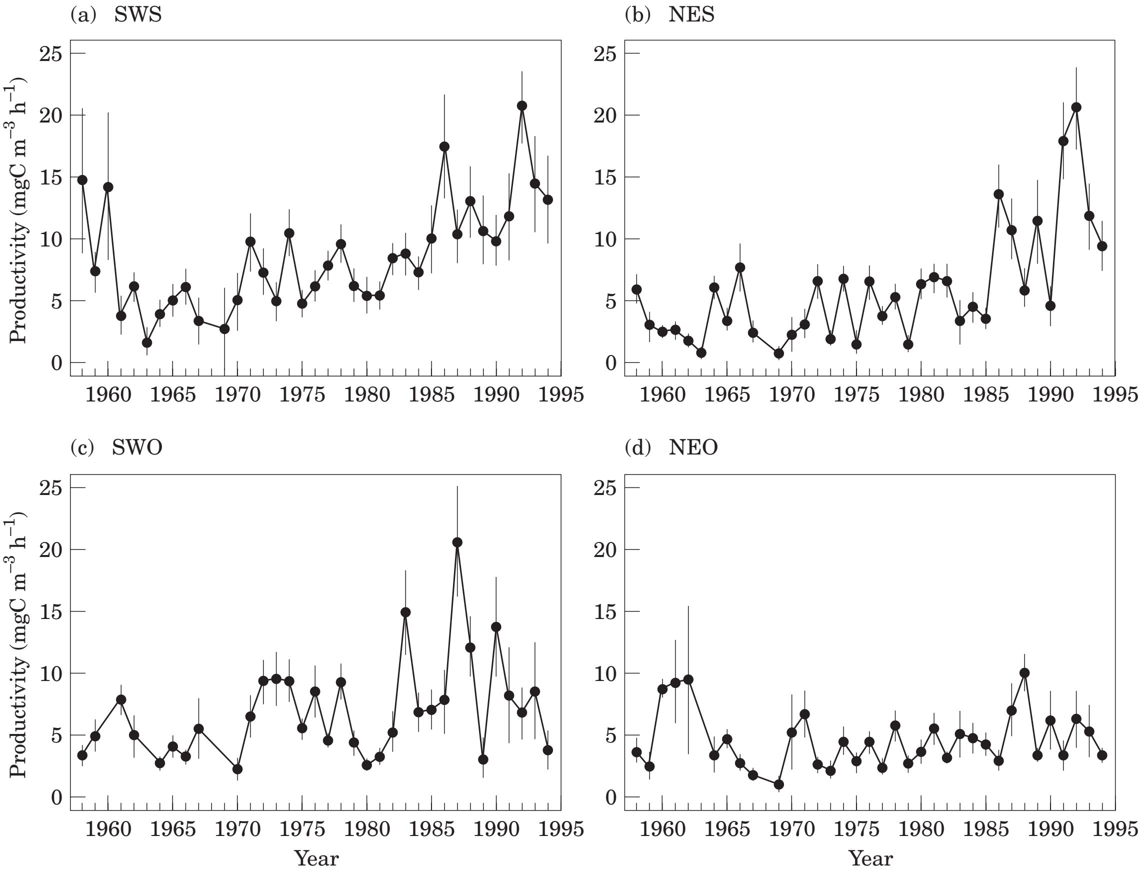

Figure 5. Mean productivity (mg C m^{-3} h^{-1}) during spring with error bars ($\pm 2 \times$ s.e.) by year and region, 1958–1994.

In low salinity waters of the NES region, the spring bloom starts in early April and lasts about one month, having a maximum in late April or the beginning of May. A steep decrease follows until mid-May, when a plateau of fairly low summer values is reached. At higher salinities, the bloom is delayed by about 2–3 weeks but the general pattern is broadly similar. The average summer values are higher than at low-salinity stations. In the NEO region, the timing is approximately as at the high-salinity stations of the shelf region, but the peak values are only half the level. The development during the summer is uncertain due to limited observations. In the SW regions, the spring blooms appear to develop as a sequence of peaks with maxima corresponding to those observed in the NE regions. The bloom starts as early as late March in low salinity shelf waters, in mid-April at higher salinities, and as late as early May in oceanic waters. Levels of productivity during summer are higher in SWS than in NES. To different degrees, the nitrate concentrations reflect the development of phytoplankton growth in each region.

The differences in seasonal development between the NE and SW regions of Iceland reflect the prevailing conditions, particularly with respect to the stability of the water column. The atmospheric low pressures frequently approaching the SW coast and the wind forced mixing of surface layers (Thórdardóttir, 1986) may explain both the observed increase in productivity in early March at high salinity stations and the elevated productivity during summer in SWS compared to NES.

Especially during "cold" years, the prevailing stability of the water column in the NES region effectively limits the admixture of deep water into the surface layer. When the initial concentration of the nutrients becomes exhausted, the bloom ends abruptly and the biomass remains low throughout the summer. Thus, a post-bloom situation of low biomass (Fig. 8d) may be expected in "cold" years, regardless of the timing of observations within the period between 16 May and 15 June. In "warm" years, however, the end of the spring bloom is not to be expected before the second week of June (Fig. 8b). Apparently, the shift in sampling date from early June to late May (Fig. 3) may have brought the observations in "warm" years closer to the peak in recent years (Fig. 7). This argumentation may also apply to SWS (Fig. 4a).

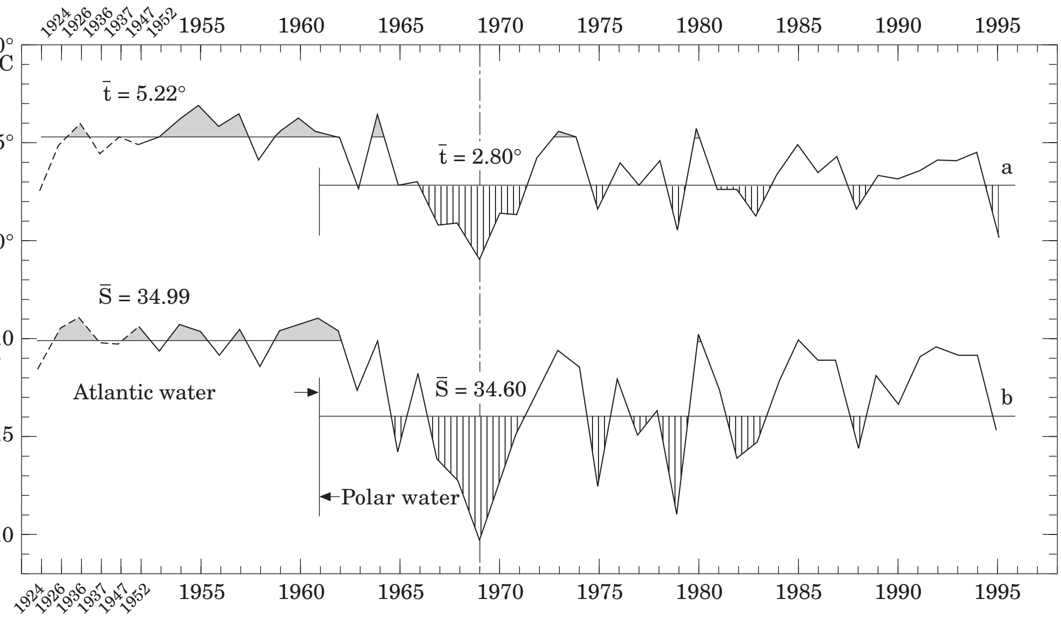

Figure 6. Time series of mean temperature and salinity recorded at a station north of Iceland (66°32′N 18°15′W) at 50 m depth during spring, 1952–1995; long-term means for the periods before and after 1961 are indicated (from Anonymous, 1996).

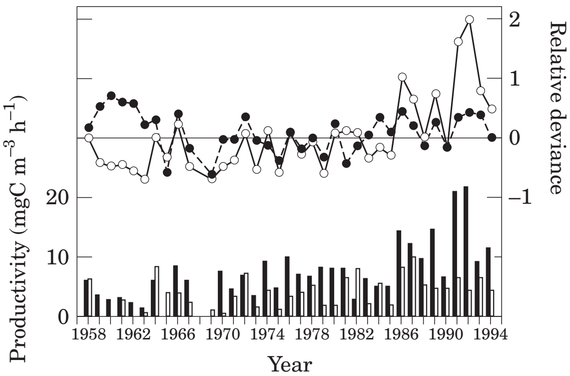

Figure 7. Comparison of average productivity during spring in the NES region, 1958–1994: (top) the productivity (○) and the salinity (●) as relative deviance (zero mean; standard deviation=1), and (bottom) average productivity (mg C m^{-3} h^{-1}) for stations with surface salinity >34.5 (filled bars) and ≤34.5 (open bars) separately.

The annual average spring productivity in the other three regions too varies considerably, but in contrast to NES a simple explanation appears to be lacking. Unexpectedly, simple linear regression analysis among the different regional pairings of productivity data revealed a highly significant correlation ($p<0.001$) only between regions SWS and NES. Similarly, a significant correlation was found between measurements of surface temperature in SWS and NES. It remains to be established whether such common patterns are linked to changes in weather conditions.

Although the annual phytoplankton observations around Iceland in spring have in the past been interpreted in relation to hydrography and zooplankton biomass, such interpretations may be misleading because of differences in timing of the surveys in relation to the seasonal development of phytoplankton blooms. In particular, the timing and the degree of stabilization of the surface layer, which depends on surface salinity, appears to be an important factor controlling phytoplankton development. If low salinity water is found at the surface in the shelf regions north and east of Iceland, the spring bloom peak may be expected in late April, whereas the peak is delayed until after mid-May if Atlantic Water prevails. Thus, although under Atlantic Water conditions the spring bloom on the south-western shelf may start earlier than on the north-eastern shelf, the peak is expected at approximately the same time due to turbulence in the surface layer. Given all the regional and temporal variation in spring-bloom development, it is obvious that productivity measurements obtained during intensive surveys within a restricted period (between 16 May and 15 June) cannot elucidate the entire story of annual variation in primary productivity over a wide area.

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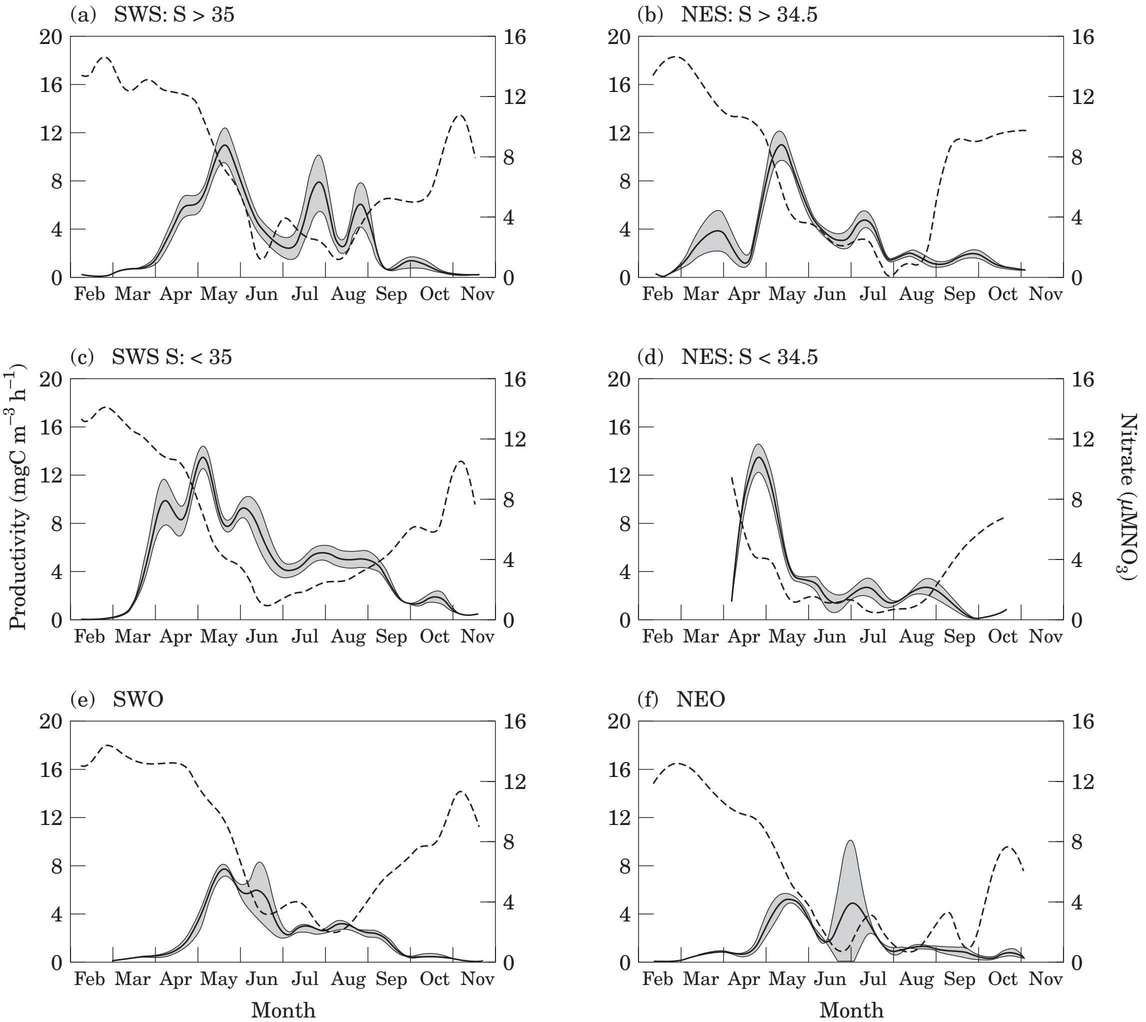

Figure 8. Smoothed patterns of average seasonal development of phytoplankton productivity (drawn line; mg C m^{-3} h^{-1}) and nitrate concentration (broken line; μM NO_3) by region, 1958–1994. Data for the shelf regions (SWS and NES) are presented for surface salinity conditions >34.5 and ≤34.5 separately. The grey area indicates the 95% confidence limits of the productivity line.

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