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Interannual variability in the spring phytoplankton bloom in Auke Bay, Alaska

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Abstract. Data on phytoplankton primary production, biomass, and species composition were collected during a 5 yr (1985–1989) study of Auke Bay, Alaska. The data were used to examine the interannual differences in the timing, duration, and magnitude of the spring phytoplankton blooms during each year and to relate these differences to interannual variations in weather patterns. Within any given year, a pre-bloom phase was characterized by low available light, low rates of primary production, low biomass, and predominantly small (<10 μm) diatoms. During the primary bloom, integrated production rates rose to 4 to 4.5 g C m^{-2} d^{-1}, and integrated biomass levels reached 415 to 972 mg chlorophyll m^{-2}. Primary blooms were usually dominated by large diatoms (*Thalassiosira* spp.), and in a single year (1989) by *Chaetoceros* spp. The primary blooms terminated upon nutrient depletion in the euphotic zone. Secondary blooms, triggered by nutrient resupply from below, occurred sporadically after the primary bloom and accounted for 4 to 31% of total spring production. The date of initiation and the duration of the primary bloom varied little from year to year (standard deviation 3 and 5 d, respectively). Seasonal production rates and biomass levels varied interannually by a factor of 2 to 3. In contrast, intra-annual variations of more than an order of magnitude, especially in biomass, occurred over periods as short as 10 d. These large variations over short time periods indicate the importance of synchronous timing between spring blooms and the production of larval fish and shellfish, which depend on an appropriate and adequate food supply for growth and survival. Parameters describing primary production (e.g. peak daily production, mean daily production, and total production during the primary bloom and the entire season) exhibited little interannual variation (coefficient of variation, CV = 10 to 19%), but a large degree of intra-annual variation (CV = 77 to 116%). Similarly, interannual variations in biomass (peak chlorophyll, mean chlorophyll) were also lower (CV = 20 to 33%) than intra-annual variations (CV = 85 to 120%).

Introduction

The subarctic spring bloom is a short period of rapid phytoplankton growth that may account for a large portion of annual primary production. Annual production rates in the Pacific subarctic ranged from less than 40 g C m^{-2} yr^{-1} in the open waters of the Gulf of Alaska (Anderson et al. 1977) to 300 to 400 g C m^{-2} yr^{-1} in coastal fjords and embayments (Hood and Zimmerman 1986, Williamson 1978). In both oceanic and coastal areas, the production associated with the spring bloom accounts for almost 50% of annual production. Similar production rates have been observed in Atlantic fjords (Wassman and Aadnesen 1984). In high-latitude ecosystems, the timing and duration of the spring bloom are critical to the recruitment success of larval fish and shellfish. The increased concentration of phytoplankton biomass typical of these blooms represents essential nutrition for higher trophic levels.

Changes in phytoplankton productivity, biomass, and species composition during the spring bloom are often associated with changes in environmental factors such as wind, sunlight, or water temperature. Similarly, interannual variations in the timing and magnitude of the bloom can in some cases be related to variations in environmental parameters from year to year.

This paper summarizes our 5 yr study of temporal patterns of environmental variability in Auke Bay and associated variations in spring phytoplankton blooms. Specifically, we examined inter- and intra-annual variations in available light, water temperature, wind events, surface mixing, and nutrient concentrations in relation to changes in phytoplankton productivity and biomass during spring blooms. We also tested the applicability of Sverdrup's (1953) critical depth model in Auke Bay, by comparing estimates of the depth of mixing with the depth of the euphotic zone throughout the month preceding each spring bloom.

Materials and methods

This research was conducted as part of the APPRISE (Association of Primary Production and Recruitment in a Subarctic Ecosystem) project, a 5 yr fisheries/oceanography study of Auke Bay, a semi-enclosed embayment in southeastern Alaska (Fig. 1), approximately 20 km northwest of Juneau. Data were collected between March and June of each year to provide a perspective on conditions preceding and following the spring bloom. Samples were taken twice weekly between 08.30 and 11.00 hrs.

The periods during which physical, chemical, and biological data were collected in Auke Bay are summarized in Table 1. Most of the water-column samples were taken at the Auke Bay Monitor (ABM) Station, slightly south of the center of the bay (Fig. 1). During some years, hydrographic data were also collected at a single station (Favorite Channel) outside of Auke Bay, to assess the applicability of Auke Bay data to other, more oceanic, areas.

Incident irradiance data were collected from a Biospherical Instruments quantum scalar irradiance sensor on the roof of the University of Alaska Fisheries Building, which is located near the northeast corner of the bay. Average daily wind velocities were obtained from a weather station at Juneau Airport (National Oceanic and Atmospheric Administration 1986–1989), about 3 km southeast of Auke Bay.

A profiling quantum scalar irradiance meter (Biospherical Instruments, Inc., QSP-200) was used to compile vertical irradiance profiles. Readings were taken every 2 m between the surface and 15 m. These data were fit to an exponential curve by a least-squares fit of the log-transformed data. The extinction coefficient (k) was calculated as the slope of the straight line and used to determine the depths of selected light levels.

A conductivity-temperature-depth (CTD) meter with internal memory (Applied Microsystems, Inc.) provided vertical distributions of temperature and salinity. The unit was lowered to a depth of 40 m, equilibrated for 1 min, and then retrieved at a speed of approx 10 cm s^{-1}. Once on deck, data in the CTD memory were sent to a printer and the temperature, salinity, and depth data were used to calculate water density between the surface and 40 m.

To estimate surface mixed-layer depths, we analyzed vertical salinity profiles and noted the depths ($\delta s_{0.1}$ and $\delta s_{0.2}$) at which ambient salinity levels were 0.1 and 0.2‰ greater than those measured at the surface. The lower boundary of an active mixing layer was inferred where the two δs depths were similar. Where $\delta s_{0.2}$ was much deeper than $\delta s_{0.1}$, mixing to $\delta s_{0.2}$ was assumed to have occurred within the last 1 to 2 d, followed by a restabilization of the water column.

The depth of the euphotic zone was taken as the compensation light depth (z_c), below which no net photosynthetic production occures (Parsons et al. 1984). The compensation irradiance level (I_c) was calculated from photosynthetron incubations (Ziemann et al. 1990b). The depth at which this light level occurred each day was then computed from daily irradiance and extinction coefficient data.

A 5-liter Niskin bottle (General Oceanics Model 1010-5) was used to collect water samples for dissolved nutrients and particulate constituents. Samples were collected at fixed depths (0, 2, 4, 6, 8, 10, 15, 20, 25, 30, 35 m) which extended below the photic zone (surface to 1% light level). Samples from each depth were stored in coolers in clean 4-liter polyethylene bottles until laboratory analysis. Subsamples to be analyzed for inorganic nutrients (nitrate + nitrite, ammonium, orthophosphate, and silicate) were first filtered through Whatman GF/C glass-fiber filters which had been pre-

Table 1. Summary of sampling schedule in Auke Bay, southeastern Alaska (58°22'N; 134°40'W), during 1985–1989. Samples were taken twice weekly at Auke Bay Monitoring Station and once a week in Favorite Channel between 08.30 and 11.00 hrs local time

Year	Sampling period	Station sampled
1985	18 March–27 May	Auke Bay Monitor
1986	17 March–24 June	Auke Bay Monitor
1987	16 March–25 June	Auke Bay Monitor and Favorite Channel
1988	14 March–6 June	Auke Bay Monitor and Favorite Channel
1989	14 March–14 June	Auke Bay Monitor

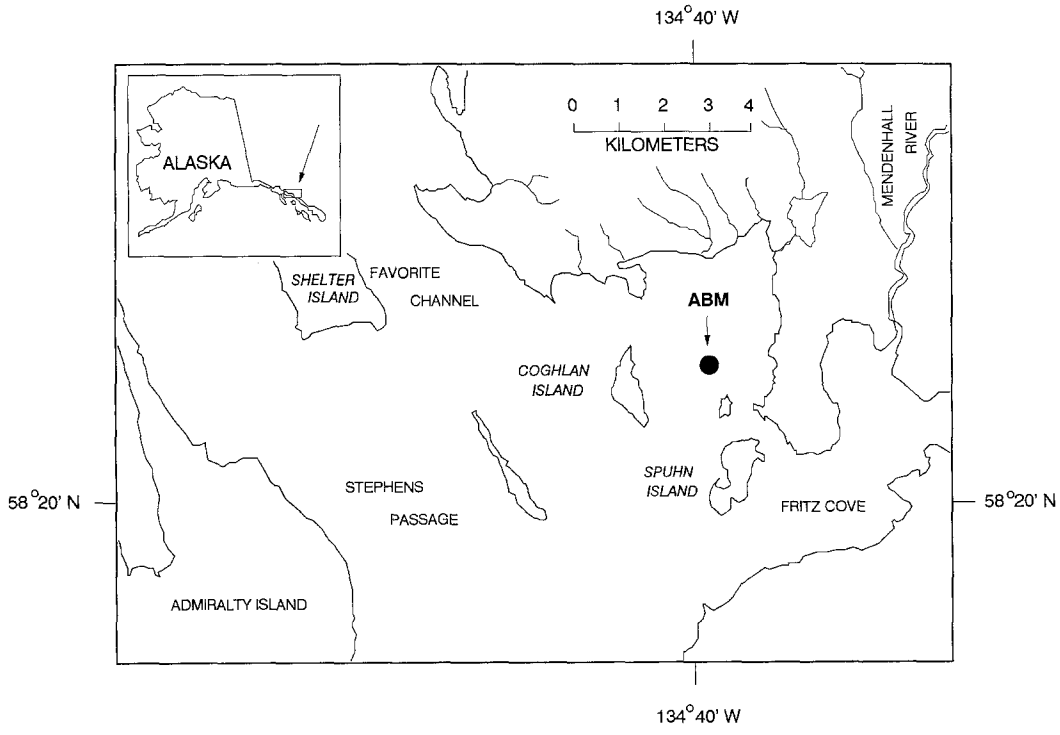

Fig. 1. Map of Auke Bay and vicinity. Auke Bay Monitor station (ABM), where most samples were taken, is shown near center of bay

rinsed with sample water to reduce the potential for contamination. These samples were analyzed using a Technicon AutoAnalyzer II system according to methods for automated analyses (general: Armstrong et al. 1967, Hager et al. 1968; nitrate + nitrite: Technicon Inc. 1977; ammonium: Solórzano 1969; phosphate: Murphy and Riley 1962; silicate: Strickland and Parsons 1972).

Chlorophyll and pheopigment concentrations were determined via the fluorometric method for acetone-extracted samples (Holm-Hansen et al. 1965, Strickland and Parsons 1972). Samples for pigment analysis were collected on 0.4 μm Nuclepore polycarbonate filters, extracted in the dark overnight at −5 °C, and measured with a Turner Designs fluorometer calibrated against pure chlorophyll *a* extract. Cell counts were made according to Utermöhl (1958) as described by Hasle (1978), using samples of preserved material from 2 m and from the chlorophyll maximum.

Measurements of primary productivity were made according to the ^{14}C method generally described by Strickland and Parsons (1972), with refinements taken from Berman and Williams (1972), Iverson et al. (1976), Lean and Burnison (1979), and Bienfang et al. (1984). Triplicate subsamples were drawn from samples from the surface and depths approximating selected light levels. These subsamples were inoculated with $NaH^{14}CO_3$ (12.5 μCi/ml specific activity) and incubated for 4 h between 10.00 and 14.00 hrs in a floating incubator; the incubator had neutral-density screens to simulate the light levels from which the samples were drawn. Zero time blanks were prepared by inoculating triplicates of a sample with the same amount of ^{14}C and immediately filtering the contents. At the end of the incubation, the samples were filtered onto 0.4 μm Nuclepore filters; the filters were placed in scintillation vials and acidified to drive off inorganic carbon. Ten ml of ACS scintillation fluor were then added, and the samples were counted on a Packard Tri-Carb liquid scintillation counter.

Results

The temporal patterns of spring bloom primary production and phytoplankton biomass showed strong similarities across all five years (Figs. 2 and 3, Table 2). Each spring could be divided into three periods: (1) an initial pre-bloom period during which biomass and production

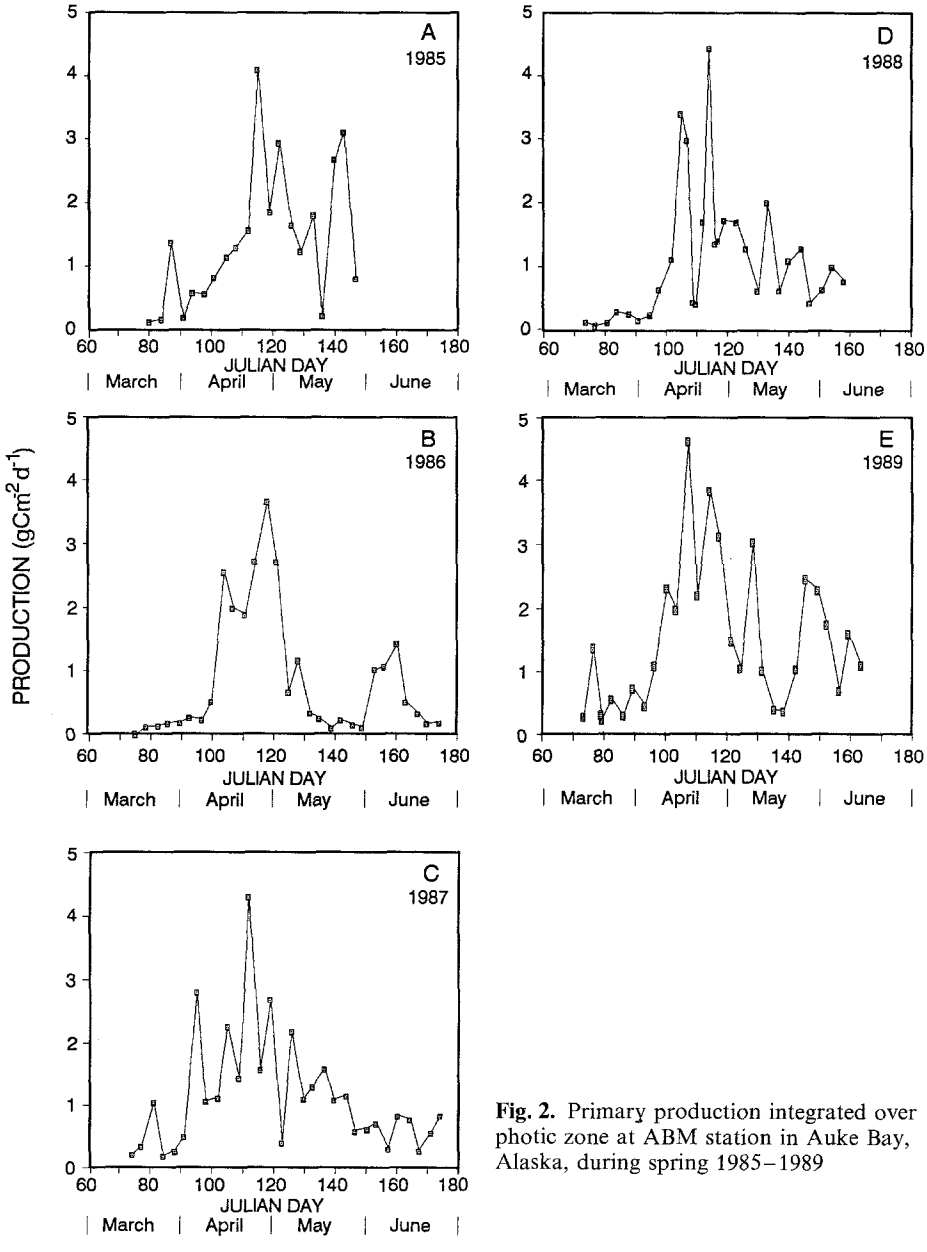

Fig. 2. Primary production integrated over photic zone at ABM station in Auke Bay, Alaska, during spring 1985–1989

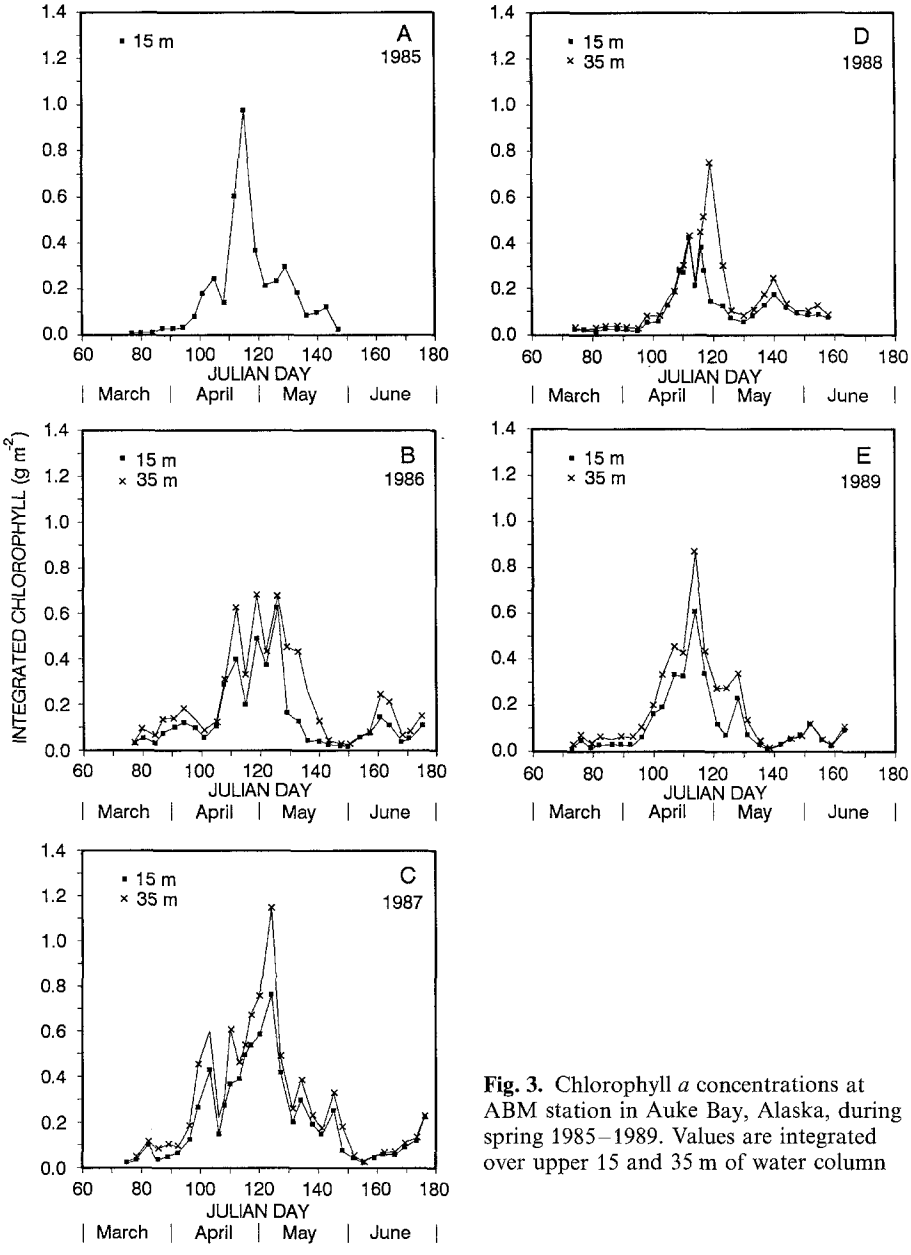

Fig. 3. Chlorophyll *a* concentrations at ABM station in Auke Bay, Alaska, during spring 1985–1989. Values are integrated over upper 15 and 35 m of water column

were low; (2) a primary bloom period during which production rates and biomass levels increased to a yearly maximum then decreased rapidly in response to nutrient depletion; (3) sporadic secondary blooms characterized by highly variable levels of production. The beginnings of primary and secondary blooms were defined as those sampling days on which specific production rates and biomass levels increased above pre-bloom levels.

Pre-bloom period

During the pre-bloom period (March through early April), total daily light levels (Fig. 4) were generally moderate to low ($<2\times10^{21}$ quanta cm^{-2} d^{-1}) because of short day lengths, low sun angles, and frequently overcast conditions. Throughout the spring, daily irradiance fluctuations due to variations in cloud cover were of a much greater magnitude than long-term seasonal increases. This is evidenced by the jagged distributions of Fig. 4. Winds were variable during early spring: passing low pressure systems often brought 1 to 5 d periods of high (>4.5 m s^{-1}) winds interspersed with 2 to 4 d periods of very light winds (<1 m s^{-1}). Pre-bloom water temperatures were low (3 to 5°C) and relatively constant, and nutrient concentrations were high (e.g. $NO_3\approx28\ \mu M$) throughout the water column. The water column was generally stable, but sporadic, short-lived mixing events extending from the surface to between 10 and 40 m were observed both before and after the beginning of the bloom (see Fig. 5).

Rates of primary production (Fig. 2) were generally low (<0.5 g C m^{-2} d^{-1}) prior to the primary bloom. Chlorophyll levels (Fig. 3) also remained relatively low

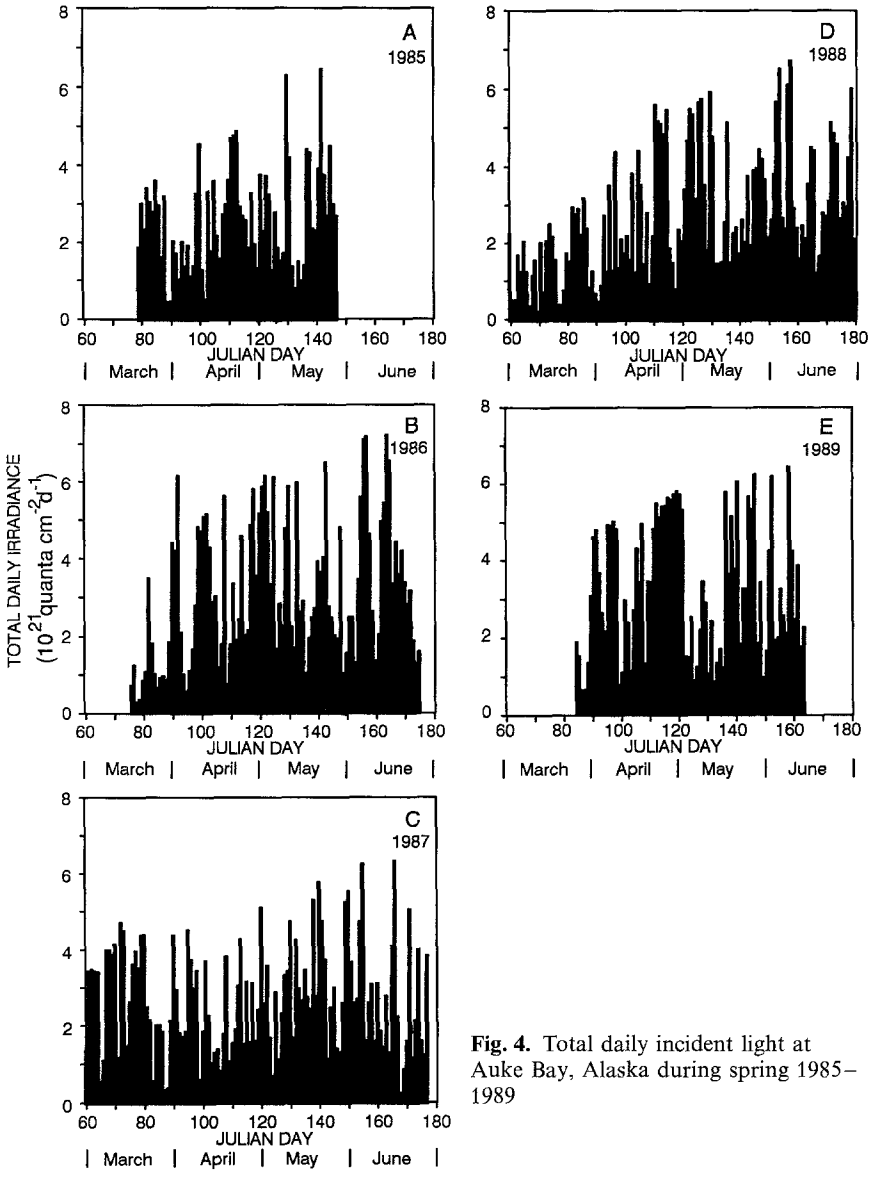

Fig. 4. Total daily incident light at Auke Bay, Alaska during spring 1985–1989

Table 2. Summary of primary production and biomass during spring blooms in Auke Bay, Alaska. Bloom dates were determined by changes in specific production and biomass relative to pre-bloom conditions

Parameter	1985	1986	1987	1988	1989
Primary bloom start date	8 Apr.	14 Apr.	6 Apr.	7 Apr.	6 Apr.
Primary bloom end date	16 May	12 May	11 May	5 May	1 May
Primary biomass peak date	25 Apr.	5 May	4 May	21 Apr.	24 Apr.
Nutrient depletion date	25 Apr.	5 May	4 May	21 Apr.	24 Apr.
Secondary bloom start date	16 May	5 June	11 May 21 May	16 May	4 May 18 May
Primary bloom duration (d)	38	28	35	28	25
start to peak	17	21	28	14	18
peak to end	21	7	7	14	7
Secondary bloom duration (d)					
1st secondary bloom	11	10	10	7	7
2nd (if any)			11		14
Total carbon production (g C m^{-2})					
total primary bloom	80.5	79.7	88.4	56.6	69.7
secondary bloom(s)	41.1	5.3	28.6	10.9	39.0
total spring period	131.7	128.7	140.4	95.8	131.5
Spring sampling duration (d)	70	98	101	84	90

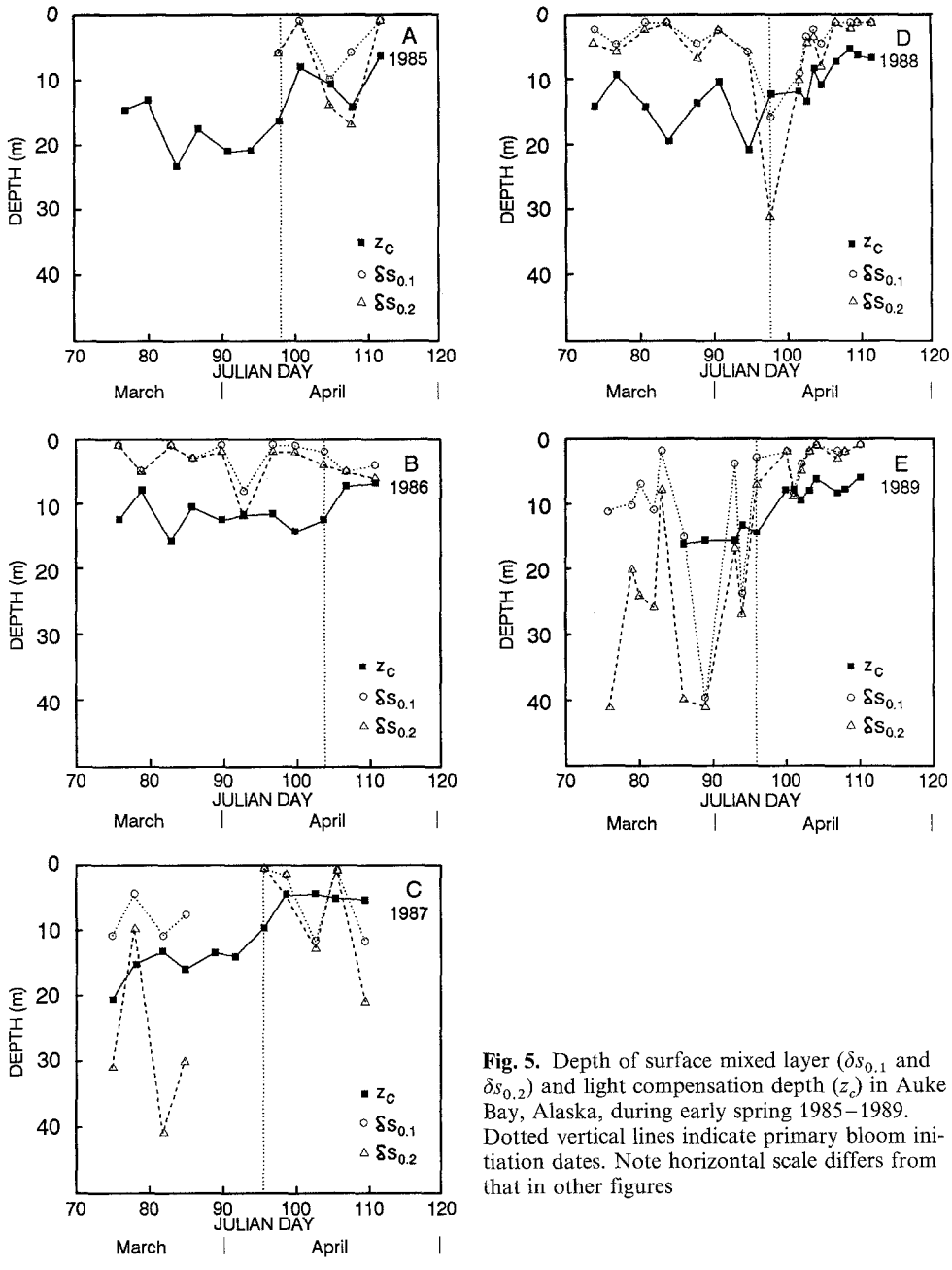

Fig. 5. Depth of surface mixed layer ($\delta s_{0.1}$ and $\delta s_{0.2}$) and light compensation depth (z_c) in Auke Bay, Alaska, during early spring 1985–1989. Dotted vertical lines indicate primary bloom initiation dates. Note horizontal scale differs from that in other figures

(<0.1 g m^{-2}) and uniform throughout the water column. Small diatoms (<10 μm) made up most of the pre-bloom algal population (Ziemann et al. 1990 b). During 3 out of the 5 years studied, short (3 to 4 d) bursts of higher (1 to 2 g C m^{-2} d^{-1}) production were observed in mid to late March, prior to bloom initiation. Only minor biomass increases were observed during these early events.

For each pre-bloom sampling date, the depth of the compensation light intensity, z_c, was compared to the depth of mixing indicated by δs depths. Fig. 5 shows z_c and δs depths from early March through mid-April (Julian Days 75 to 110) of each year. Table 3 summarizes the mean and range of these parameters that were observed during each pre-bloom period.

In 1985, the salinity record did not begin until 8 April (Julian Day 98), the first day of the primary bloom, so the degree of water column stability (and vertical mixing) is unknown. Compensation irradiance depths varied from 23 to 13 m prior to bloom initiation, and were generally deeper than during other years (primarily due to lower extinction coefficients).

In 1986, pre-bloom mixing only extended down to about 5 m, with the exception of a single 12 m mixing event measured on 3 April (Day 93, 11 d before the beginning of the bloom). In contrast, z_c averaged 12 m depth throughout this period and was never less than 8 m. Thus, in 1986, the euphotic zone depth was consistently below any surface mixing that occurred, including the event measured on 3 April.

Table 3. Compensation depth (z_c) and depth of surface mixed-layer (δs) in Auke Bay, Alaska, during 3 to 4 wk preceding spring bloom initiation. +: Surface mixed-layer generally shallower than compensation depth; −: surface mixed-layer generally extending below compensation depth; ?: insufficient data to determine relationship between mixed-layer and compensation depth; nd: no data

Parameter	1985	1986	1987	1988	1989
Sampling period (d)	21	28	21	24	20
Bloom start date	8 Apr.	14 Apr.	6 Apr.	7 Apr.	6 Apr.
z_c					
mean (m)	18	12	15	13	15[a]
range (m)	13–23	8–16	10–21	8–19	13–16[a]
$\delta s_{0.1}$					
mean (m)	nd	3	7[a]	4	13
range (m)	nd	1–8	1–11[a]	1–14	2–40
$\delta s_{0.2}$					
mean (m)	nd	4	23[a]		25
range (m)	nd	1–21	1–41[a]	1–28	7–41
Depth of mixing vs compensation depth	?	+	−(?)	+	−

[a] Based on less than complete data set for sampling period

Early in the 1987 pre-bloom period, the salinity structure showed evidence of intermittent deep mixing, with the $\delta s_{0.2}$ depth at 30 to 40 m. However the much shallower depth (10 m) of the $\delta s_{0.1}$ indicated that the water column had restabilized, with no active mixing occurring on sampling days. No salinity data are available for the days just preceding the primary bloom, but wind records (National Oceanic and Atmospheric Administration 1986–1989) show this to be a relatively calm period, with winds less than 5 m s^{-1}, when active mixing was unlikely to occur. We therefore assume that the mixed layer depth decreased rapidly to the shallow depths observed on 6 April. The pre-bloom compensation light depth gradually decreased from 21 to 10 m. Early in the pre-bloom period, the depth of mixing was generally far below the euphotic zone. However, on the day of primary bloom initiation, the depth of mixing was much shallower than the compensation light depth.

The pre-bloom salinity structure and z_c values observed during 1988 were similar to those observed during 1986: δs depths averaging 6 m indicated that the water column was generally stable. However, a deep mixing event occurred just prior to bloom initiation. The compensation depth ranged from 8 to 19 m, and, except for the mixing event on 7 April (Day 98), was below the mixing depth throughout the pre-bloom period.

In 1989, the salinity structure showed evidence of substantial vertical mixing on three occasions. Evidence of recent deep mixing ($\delta s_{0.2} = 40$ m) was observed on 17 March (Day 76). Active mixing to 40 and 24 m was observed on 30 March (Day 89) and 4 April (Day 94), respectively. During this year, irradiance data were not collected until 27 March, so the z_c could not be calculated for the early pre-bloom period. However, early spring irradiance data from the previous 4 yr and experimentally derived I_c values for the period prior to 27 March 1989 (Ziemann et al. 1990 a) suggest that z_c was less than 20 m. Thus, mixed-layer depths were probably much deeper than z_c during much of the pre-bloom period.

Primary bloom

Daily irradiance levels were generally higher during primary bloom periods than prior to the bloom (Fig. 4), the result of increasing sun angle, increased day length and more frequent and longer periods of clear skies. During 1986, 1988, and especially 1989, sustained (5 to 10 d) periods of high to moderate light levels occurred during the latter half of the bloom. Skies were generally cloudy during the 1987 bloom, with only a few isolated days of high irradiance. Sustained strong winds were observed only during the 1987 primary bloom, and coincided with 10 to 20 m mixing events. A mixing event of similar depth was observed during the 1985 primary bloom, but no wind data are available for that year. Water temperature generally did not begin its seasonal rise until late April or early May, reaching 6 to 10 °C by the end of the primary bloom. Nutrient concentrations in surface waters declined rapidly during the initial stages of the primary bloom, reaching minimum (virtually undetectable) levels at the time of the biomass peak in late April or early May (Table 2).

During 4 out of the 5 years studied (1985, 1987, 1988, and 1989), the primary bloom began on approximately the same date in early April (Table 2). During 1986, the initiation of the primary bloom was delayed by about 7 d. In contrast, the dates on which the primary bloom peaked and ended were more variable from one year to the next. Integrated production rates (surface to 1% light depth) during the primary bloom ranged from 1.8 to 4.5 g C m^{-2} d^{-1}. Short periods (<4 d) of overcast did not result in significant decreases in daily integrated production. However, a 9 d period of low light levels in late March of 1987 was of sufficient duration to cause a noticeable decrease in primary production rates.

Specific primary production rates (carbon uptake per unit of chlorophyll) peaked an average of 13 ± 5 d after bloom initiation; integrated primary production reached maximum levels 1 to 2 wk later. The integrated production peak usually occurred during the last week of April. The 1987 bloom provided an exception to this pattern, as variable irradiance conditions and wind-driven mixing apparently delayed the specific production peak until 17 d after the beginning of the bloom. Peak levels of integrated production were observed only 3 d later. Peak integrated production levels for all five years were similar, ranging between 3.7 and 4.6 g C m^{-2} d^{-1} (Fig. 2). During 4 of the 5 years, phytoplankton biomass increased rapidly from low pre-bloom levels to seasonal maximum values by late April or early May (Fig. 3). This pattern was not seen during 1986, when the main bloom peak was not well defined.

Peak biomass concentrations were quite variable among the five years. The highest 15 m integrated chlorophyll level was measured in 1985 and the lowest in 1988

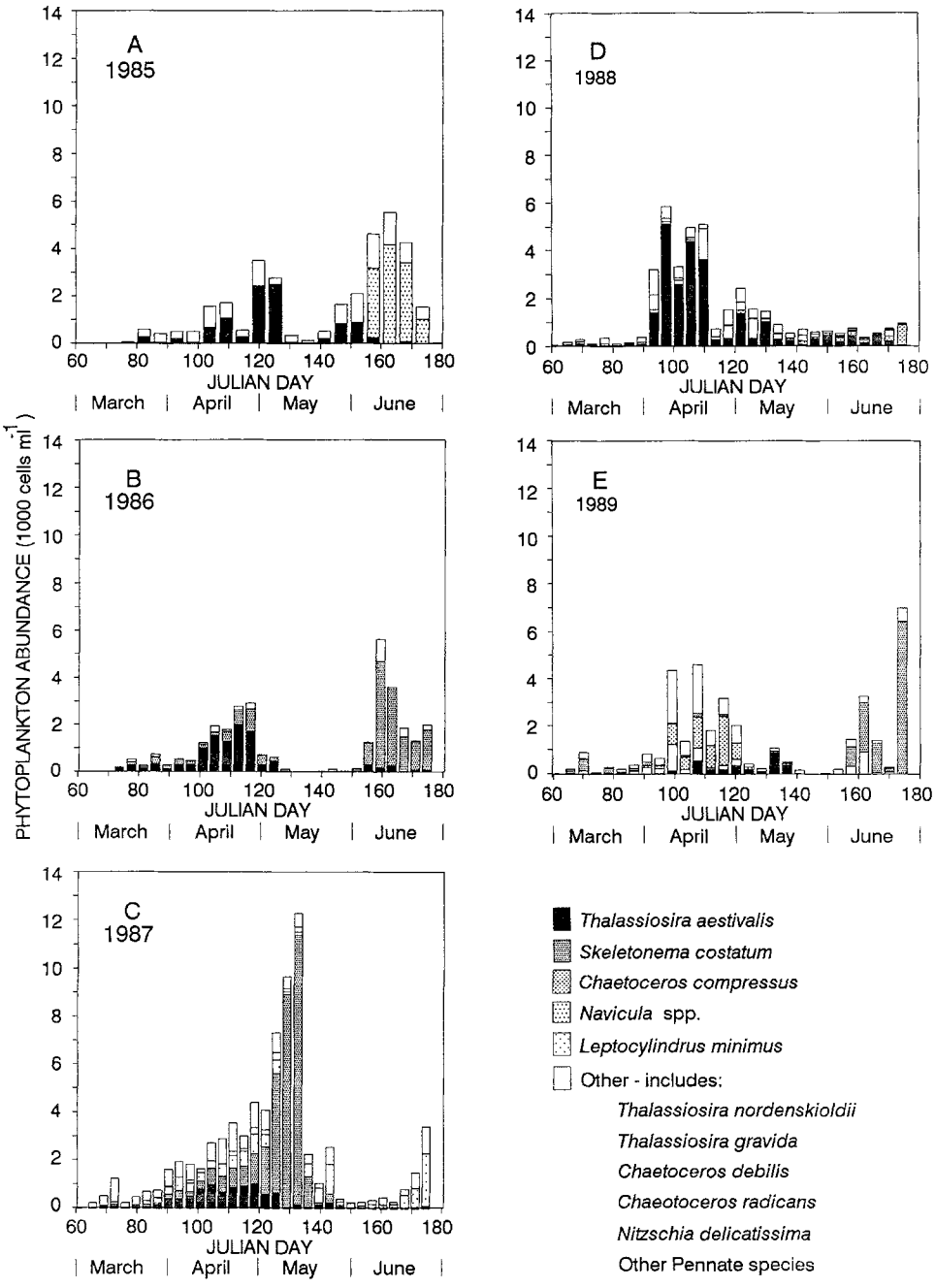

Fig. 6. Numerical abundance of major phytoplankton species from 2 m depth at ABM station in Auke Bay, Alaska, during spring 1985–1989

(972 and 415 mg m^{-2}, respectively). Chlorophyll concentrations >60 mg m^{-3} were common in the photic zone during the primary bloom in all five years.

Centric diatoms were the most common phytoplankton observed in Auke Bay during the spring bloom, with large (>100 μm) diatom chains dominant at the peak of the primary bloom. Net plankton (>10 μm) generally accounted for 60 to 100% of the production observed during primary blooms. Small cells (<2 μm) never accounted for more than 40% of total carbon uptake, generally reaching these levels only after the end of the primary bloom (Ziemann et al. 1990b).

During the 1985, 1986, and 1988 primary blooms, phytoplankton populations were dominated by long chains of *Thalassiosira aestivalis* (Fig. 6). A sustained, diverse phytoplankton population characterized the 1987 primary bloom. Only after the peak of the bloom did a single species, *Skeletonema costatum*, achieve dominance, increasing to a very high level of abundance. However, because of its small size and narrow depth distribution, the rise of this species to numerical dominance resulted in only a small increase in integrated chlorophyll. In 1989, as in 1987, high phytoplankton diversity was maintained over much of the spring period, but this diversity decreased during the peak of the bloom. Although similar species were observed during both years, in 1989 *Chaetoceros compressus* eventually gained dominance at the end of the bloom.

The latter part of the spring bloom was characterized by a rapid decline in productivity and biomass, resulting

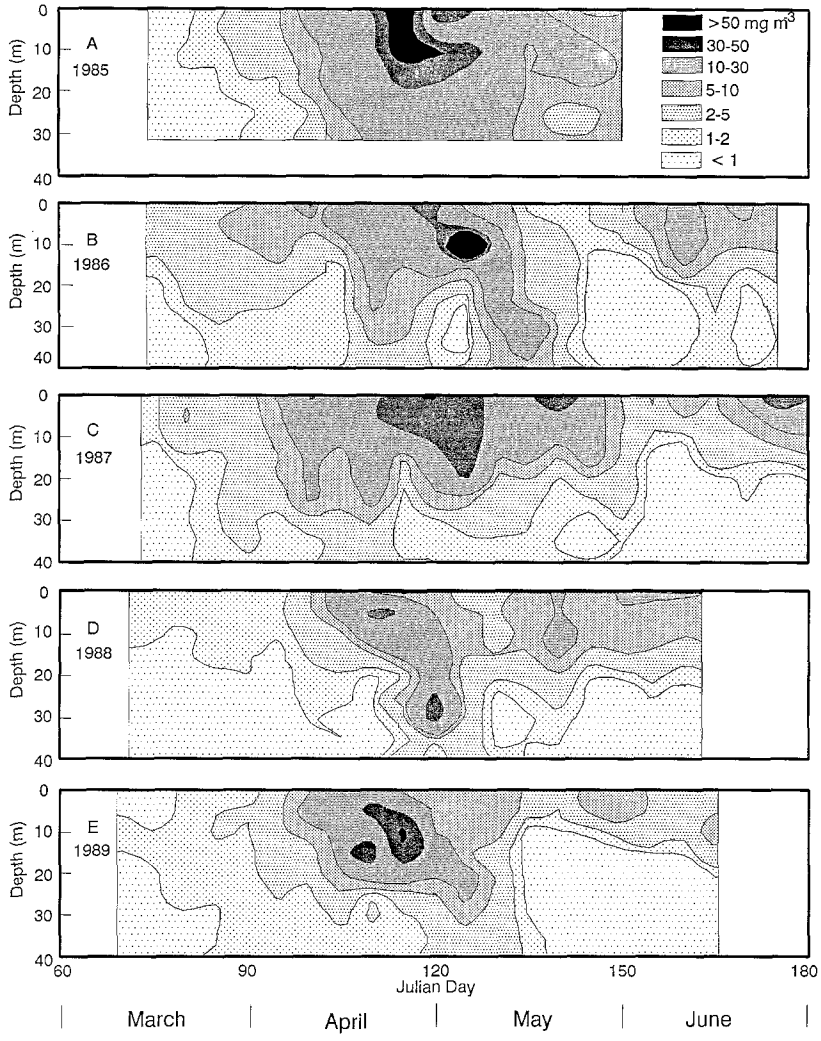

Fig. 7. Chlorophyll *a* concentrations (mg m^{-3}) in upper 40 m of water column at ABM Station in Auke Bay, Alaska, during spring 1985–1989

from almost total depletion of nutrients in the euphotic zone. At this point, much of the phytoplankton biomass began to sink through the water column. In some cases, this sedimentation could be observed as a well-defined layer of living, intact cells (Fig. 7). This layer is particularly visible in the chlorophyll contour plots for 1986 and 1988 B and D), in which the 10 mg m^{-3} chlorophyll contour lines can be traced from the surface layers to 35 m over a span of about 20 d.

Often, these sinking cells continued to contribute to the primary productivity of the Auke Bay system. In fact, during each year, between 10 and 50% of the spring primary production occurred as phytoplankton sank within the photic zone. Such deep productivity was most pronounced during 1985 and 1988, when the resulting layer of phytoplankton sank relatively slowly, and about 40 to 50% of total primary production took place during the sinking period. During 1986 and 1989, phytoplankton of the primary bloom also sank in distinct layers. However, these phytoplankton layers sank quite rapidly, and only minor post-peak production was observed. During 1987, no distinct sedimentation event was observed, and only about 10% of the seasonal primary production occurred after the bloom peak.

The decline in the primary bloom during most years was the result of sinking and sedimentation; grazing did not appear to play a major role. Sediment-trap data (Ziemann et al. 1990b) showed large pulses of chlorophyll flux as the phytoplankton layer passed the trap depth, but during this period there were no significant increases in pheopigment flux which would reflect fecal pellet production from grazing.

Secondary blooms

Secondary blooms were observed during May or June of each year, sometimes following the primary bloom by only 1 to 2 wk (Fig. 2). Although peak daily light levels were higher at this time of year than during the primary bloom, cloudy, low-irradiance days were also common. Strong winds were less frequent than during March or April, and no surface mixing extended deeper than 10 m. Surface water temperatures were variable, ranging from 8 to 14 °C. Although nutrients had been depleted from the euphotic zone during the primary bloom, their concentrations sporadically increased in the photic zone, reaching 25 to 50% of pre-bloom levels.

Integrated primary production increased substantially during most secondary blooms, reaching levels of 1.5 to 3.0 g C m^{-2} d^{-1}; 4 to 31% of all integrated seasonal production occurred during these events. The occurrence of secondary blooms frequently appeared to be a response to the resupply of nutrients to the photic zone after the end of the primary bloom; in some instances, however, secondary blooms occurred without any observed nutrient resupply.

Despite high production rates during many secondary blooms, biomass levels seldom reached one third of those measured during the main bloom (Figs. 3, 7). Grazing by herbivorous zooplankton, whose populations had increased rapidly in response to the primary bloom (Coyle and Paul 1990), nearly balanced the increased production. Between and following the secondary blooms, biomass levels were generally quite low, like those observed during the pre-bloom period.

Although *Thalassiosira aestivalis* dominated the Auke Bay primary bloom during 3 out of the 5 years, a wider variety of diatom species were abundant during secondary blooms. *Navicula* spp. dominated the 1985 secondary bloom. In 1986, *Skeletonema costatum* formed a small but noticeable component of the late primary bloom, and also dominated the secondary bloom. During 1987, the diverse primary bloom (which culminated in dominance by *S. costatum*) was immediately followed by a brief bloom of *T. nordenskjoldii*; *Leptocylindrus minimus* increased in abundance during a late secondary bloom. Similarly, in 1988, a rise in *Chaetoceros compressus* abundance on the last day of sampling may have marked the beginning of a late secondary bloom. Secondary blooms during 1989 were dominated by *T. aestivalis* and *S. costatum*.

Discussion

Many descriptions of spring bloom dynamics (Gieskes and Kraay 1975, Pingree et al. 1976, Hitchcock and Smayda 1977, Peinert et al. 1982) follow the critical depth model of the spring bloom first proposed by Sverdrup (1953). During the pre-bloom period, incident light and water column structure are assumed to be the dominant factors limiting phytoplankton growth. Low incident light results in a shallow critical depth, and uniform water temperature, salinity, and relatively constant winds produce a deep mixed layer. Increasing day length and total daily incident irradiation increase the critical depth for phytoplankton growth. At the same time, solar heating or fresh water input increases water-column stability, resulting in decreased mixed-layer depths. Eventually, the mixed-layer depth becomes shallower than the critical depth. At that point, net phytoplankton growth occurs, and the spring bloom begins. Thus, the initiation of the spring bloom should correspond with a time at which the depth of mixing becomes shallower than the critical depth.

During 1986 and 1988, the compensation light depth, z_c, which is shallower than the critical depth, was consistently below any surface mixing that occurred (Fig. 5). These data indicate that initiation of the primary bloom during these years was not dependent on the shallowing of a mixed-layer depth, contrary to the paradigm of the critical depth model. In 1989, mixing was much deeper than z_c during most of the pre-bloom period, but became shallower at the time of bloom initiation, in general agreement with the critical depth model. In 1985 and 1987, salinity data were not available on enough sampling dates to conclusively determine whether mixing depths were shallower or deeper than light compensation depths. Thus, although mixing patterns during 1989 were consistent with the critical depth model, the data for 1986 and 1988 clearly indicate that the model cannot reliably predict bloom initiation in Auke Bay.

The timing of the primary bloom initiation was remarkably similar for 4 of the 5 years studied (Table 2; 1985, 1987–1989). The interaction between mixed-layer depth and critical depth did not generally appear to control the initiation of the bloom. Other physico-chemical parameters apparently did not affect the initiation of the primary bloom: productivity rates did not correlate with increases or decreases in water temperature in the upper 10 m, and nutrient levels throughout the pre-bloom period were non-limiting (Kanda et al. 1989, Ziemann et al. 1990a).

Variations in cloud and wind conditions are believed to have been a predominant factor in initiation of the primary bloom. A period of 3 to 5 high-light days preceded the beginning of the primary bloom in several years, most notably 1986 and 1988. These high-light days triggered physiological changes [increases in photosynthetic maximum (P_{max}) and photosynthetic efficiency (alpha), Ziemann et al. 1990b; increases in nitrogen uptake rate, Kanda et al. 1989], which in turn resulted in increased production rates (Ziemann et al. 1990b). During 1986, overcast conditions lasted into the second week of April, apparently delaying the beginning of the bloom by 1 wk.

Given the similarity in light history that appeared to elicit a physiological response in this stratified system, and the often referenced "trigger" light intensity for net growth in mixed systems (Riley 1957, 1967, Pingree et al. 1976, Hitchcock and Smayda 1977, Townsend and Spinrad 1986), we speculate that physiological rather than physical processes may control bloom initiation. We observed large changes in the physiological rates of phytoplankton in response to changes in light level on a time scale of one to several days [photosynthetic parameters P_{max} and alpha, Ziemann et al. 1990b; nitrate uptake (maximum uptake rate and half-saturation light intensity), Kanda et al. 1989]. Sampling on this time scale is seldom feasible, and sampling frequencies on the order of once a week are more common (Gieskes and Kraay 1975, Winter et al. 1975, Hitchcock and Smayda 1977). A mixed layer can develop in less than one day, and return to stratified conditions with the same rapidity (Wroblewski and Richman 1987). Assuming constant mixed or stratified conditions for periods between sampling days may not be justified without supporting wind data. Although the Sverdrup (1953) model adequately describes the initiation of the spring bloom in well-mixed waters, it does not address the physiological changes we observed,

Table 4. Comparison of peak primary productivity (produc.) and biomass levels measured during spring blooms at various latitudes. diat: diatoms; dino: dinoflagellates; *Phaeo: Phaeocystis* spp. (Chrysophyta). nd: no data

Location	Lat. (°N)	Pre-bloom NO_3 (μM)	Peak bloom chl. conc (mg m^{-3})	Peak bloom biomass (mg chl m^{-2})	Peak bloom produc. (mg C m^{-2} d^{-1})	Total annual produc. (g C m^{-2} yr^{-1})	Sampling period	Dominant bloom algae	Source
Auke Bay (present study)	58	26–28	60–120	410–1 100	3 650–4 610	350	Mar.–June	diat	Ziemann et al. (1990b)
New York Bight	40	nd	5	nd	817	250	nd	nd	Dagg and Turner (1982)
Long Island Sound	40	3	9	30	nd	nd	Feb.–Dec.	diat/dino	Mandelli et al. (1970)
Narragansett Bay	41	nd	25	201.6	nd	nd	26 Feb.	diat	Hitchcock and Smayda (1977)
Georges Banks	42	nd	5	nd	2 500	375	nd	nd	Cohen et al. (1982), Dagg and Turner (1982)
Puget Sound	48	26	8	175	3 500	465	Apr.–June	nd	Winter et al. (1975)
Celtic Sea	50	6	10	nd	4 000	nd	Apr.–Dec.	diat	Pingree et al. (1976)
Belgian coast	51	20	20	nd	2 100	nd	Apr.–June	*Phaeo*	Lancelot and Mathot (1987)
North Sea – Holland	52	nd	10	nd	2 000	250	Feb.–July	diat	Gieskes and Kraay (1975)
Kiel Bight	54	12	nd	100–350	4 500–9 000	158	Feb.–May	diat	Smetacek (1985)
S.E. Bering Strait	56	14	20	500–700	nd	170	Mar.–June	diat	Sambrotto et al. (1986)
Tenakee Inlet	57	19	15	135	1 680	nd	Apr.–June	diat	Beattie (1984)
North Sea	58	nd	nd	500	8 930	nd	Mar.–June	nd	Radach et al. (1984)
W. Norway	60	8	12	55	2 000	230	Feb.–Oct.	nd	Wassmann and Aadnesen (1984)
Lindaspollene	60	7.5	12.5	328	nd	120	Mar.–Apr.	diat	Lannergren and Skjoldal (1975)
Bering Shelf	65	16	nd	200	2 700	324	Summer	diat	Sambrotto et al. (1984)

nor is it applicable to coastal areas that often do not exhibit mixed layers during the spring.

Instead, we suggest that the spring bloom may be viewed as an analog of an upwelling system. In such systems, changes in physiological rates control bloom progression (Jones et al. 1983, MacIsaac et al. 1985, Wilkerson and Dugdale 1987). Initial conditions of low light and high nutrients change (through the process of upwelling) to high light and high nutrients. A "shift-up" in nitrate uptake and carbon synthesis rates is observed several days after phytoplankton are exposed to elevated light conditions (MacIsaac et al. 1985, Wilkerson and Dugdale 1987). Higher rates prevail until cells deplete nutrients, sink, or are mixed below the photic zone; rates then "shift down" to pre-upwelling levels. We propose here that phytoplankton in subarctic waters undergo a process during the spring bloom analogous to that proposed for upwelling populations. After initial low-light and high-nutrient conditions, they experience an increase in the light field. Nitrate uptake and carbon fixation rates subsequently increase and remain elevated until a period of low light or nutrient depletion occurs. We intend to examine this process in subarctic systems in a subsequent publication.

Interannual differences in the duration, magnitude, and production of the primary bloom can be ascribed to variations in the physical conditions (primarily light and nutrient supply) that affect phytoplankton growth rates and nutrient uptake rates. The magnitude of both the integrated production rates and the peak chlorophyll biomass levels were unpredictably variable across the five years sampled. Years with continual high light levels and calm winds during the primary bloom (1985–1986, 1988–1989) had, in some instances, peak chlorophyll and primary productivity values similar to those of 1987, a year with variable light and higher wind conditions. Thus, the magnitude of the primary bloom was not dependent upon continual high light levels but some lower level which occurred during all five years.

The high production rates and biomass levels attained during the primary spring bloom in Auke Bay are the result of high initial nutrient concentrations and stable water-column conditions; regenerated nutrients are also important later during the bloom (Kanda et al. 1989). Early spring nitrate levels in Auke Bay are four to seven times as high as pre-bloom nitrate levels observed in North Atlantic subarctic regions, but are not atypical of other areas in the subarctic North Pacific (Table 4). Despite the large differences in initial nitrate supply between the North Atlantic and North Pacific, annual production in these areas varies only by a factor of 2 or 3. This may be due to the high degree of coupling and regeneration in systems with low initial nitrate concentrations. It may also result from the loss of nitrogen via sedimentation during the latter part of the primary bloom in systems such as Auke Bay, where initial nutrient levels are high.

The continued productivity of Auke Bay phytoplankton during sedimentation results in part from increases in the depth of light penetration as the bloom sinks. During the peak of the bloom, the depth of the 1% light level is as shallow as 8 m. As the bloom sinks, few cells remain in the overlying waters, and extinction coefficient values decrease substantially. Thus, the 1% light level travels downward with the chlorophyll layer, providing suffi-

cient light for continued production as the cells encounter new supplies of nutrients. In 1985 and 1988, when the water column was relatively stable, with little vertical mixing, there was more deep productivity. In 1987, strong winds apparently caused a water exchange between Auke Bay and the outside channel; the phytoplankton biomass was dispersed, and the 1987 bloom ended shortly after the biomass peak was reached.

The interannual variations in light and wind conditions affected both phytoplankton growth and uptake rates, and thus the duration of the primary bloom. Years with continual high light and calm winds had higher growth and uptake rates, which led to rapid increases to maximum biomass levels, rapid depletion of nutrients, and subsequent bloom declines. In 1987, the bloom took longer to reach maximum biomass than during other years. This was reflected in the longer time required for the phytoplankton population to deplete the nutrient supply (28 d compared with an average of 18 d), and the delayed end of the primary bloom.

A high degree of year-to-year variation was observed in the timing of the secondary blooms in Auke Bay. However, incident light was not a factor in their initiation; during May and June, light is of sufficient quantity so as to be non-limiting. Since no nutrients are left within the photic zone after the primary bloom, the initiation of secondary blooms may be in response to the addition of nutrients to that zone. Either regeneration through herbivore grazing or import by advective mechanisms must be invoked to account for the biomass increases during these periods. Summer blooms in Auke Bay have been described as being induced by wind-mixing (Iverson et al. 1974). Vertical mixing (sometimes associated with periods of strong winds) could have brought water from below 10 to 15 m into the surface layers and thus supplied nutrients to the photic zone. However, vertical mixing did not appear to be a source of nutrients to all secondary blooms, since during some blooms the water column remained generally unmixed and surface waters remained low in nutrients.

Based on nutrient profiles obtained during the 5 yr study (Ziemann et al. 1990a), and using NO_3 as an example, we found that the nitracline can become shallower several weeks after nutrient depletion by the primary bloom. This increased nutrient concentration was in some cases correlated with the secondary blooms. The upward shift of the nutracline indicates that deep nutrients are being transported upward, rather than being supplied by river input; the increase in nitrate rather than in ammonium levels suggests resupply rather than regeneration (via herbivore grazing) or rapid nitrification of ammonium within the photic zone.

The specific mechanisms by which nutrients are transported to the photic zone remain unclear. Since the water column often remained vertically stable throughout this period, wind-induced mixing appears not to be the sole driving force in initiating secondary blooms. High gradients in nutrient concentration (up to 4 μM NO_3 m^{-1}) below the photic zone, coupled with high eddy diffusion caused by turbulence/shear which develops as the tides flow in and out of the bay, may account for the high flux of nutrients into the surface layers. During all the nutrient shoaling events, the daily tidal range was >3 m (tides in Auke Bay range from 1 to 7 m). Similarly, shoaling internal waves may break and produce mixing across the pycnocline.

During the two years (1987 and 1988) in which nutrients were measured outside the bay, in Favorite Channel (Fig. 1), we found the same patterns (Ziemann et al. 1990a). The nitracline there also became shallower, but the resulting nitrate concentrations were two to three times higher than in the bay. This may indicate that the processes that import nutrients into the photic zone are stronger in the channel, perhaps because the channel is less protected than the bay. It is also possible that some "upwelling" events occur only outside the bay and the tidal exchange brings nutrient-rich water into the bay. As in the bay, the physical structure in the channel also seemed to remain stable near the surface.

Some of the secondary blooms were not associated with any detectable increase in nutrient concentrations at the surface. However, because our sampling frequency was only every 3 to 4 d, short nutrient spikes might have occurred and been taken up between sampling events. It is also possible that algae were advected into the bay from Favorite Channel, where nutrient upwelling events appear to be more common. However, our sampling frequency does not allow us to determine whether secondary blooms outside the bay preceded those in the bay.

The 5 yr data-base describing the timing, magnitude, and duration of the primary and secondary spring blooms in Auke Bay provides us with the unique opportunity to examine the inter- and intra-annual variations in these processes in a statistically rigorous manner. Table 5 presents the mean, standard deviation, and coefficient of variation (standard deviation $\div$ mean) for parameters describing the spring bloom in Auke Bay. The least amount of interannual variation was observed in parameters describing the timing of the primary bloom. As estimated by a period equal to ± 1 standard deviation, the bloom start-date, peak-date, and duration varied by 6, 12, and 10 d, respectively, over the 5 yr period. Thus, the time of year during which phytoplankton can provide an abundant supply of food for larval forms is, in Auke Bay at least, relatively constant. In temperate waters, fish spawn at a fixed season and the standard deviation of the peak spawning date is low – on the order of 7 d (Cushing 1969). Hatching dates of pollock and flathead sole in Auke Bay were also relatively consistent over the 1986–1989 period (Haldorson et al. 1990). The evolution of spawning at a relatively fixed time of year may be a response to a consistently available food supply.

The interannual variation in peak integrated biomass (CV = 37.1%) was almost four times greater than the variation in peak primary production (CV = 9.5%). The interannual variations in total secondary bloom production (CV = 65.5%) were very much greater than those of either the primary bloom (CV = 16.3%) or the total spring period (CV = 13.7%).

Year-to-year variations in biomass levels were small compared to the short-term changes observed during any one year. Maximum integrated biomass levels varied by

Table 5. Mean, standard deviation (SD) and coefficient of variation (CV = SD ÷ mean) for parameters describing timing, duration, and magnitude of spring bloom during 1985–1989 in Auke Bay, Alaska

	Mean	SD	CV (%)
Start date (Julian day)	98	3	3
Chlorophyll peak (Julian day)	118	6	5
Primary bloom duration (days)	31	5	16
Yearly mean integrated production (g C m^{-2} d^{-1})			
1985	1.4	1.1	77
1986	0.9	1.0	116
1987	1.2	0.9	75
1988	1.2	1.0	88
1989	1.5	1.2	78
between years	1.2	2.4	19
Peak primary production (g C m^{-2} d^{-1})	4.2	0.4	10
Total primary production (g C m^{-2})			
primary blooms	74.9	12.2	16
secondary blooms	24.9	16.3	66
total sampling period	125.6	17.2	14
Yearly mean integrated chlorophyll (mg chl m^{-2})			
1985	240	203	85
1986	145	154	104
1987	216	192	89
1988	124	109	88
1989	117	141	120
between years	168	56	33
Peak integrated chlorophyll level (mg chl m^{-2})	614	126	21

less than a factor of 2 over the five years studied (CV = 37%), and maximum chlorophyll concentrations varied by even less. In contrast, chlorophyll concentrations within any given year varied by a factor of at least 30 between the pre- and post-bloom periods and the bloom biomass peaks (CV = 84 to 120%). Furthermore, the time between order-of-magnitude concentration changes (increases or decreases) was often less than 10 d.

The magnitude of the bloom is not of paramount importance to the herbivorous zooplankton in the Auke Bay system, which depend on the primary bloom as the energy source for spring reproductive processes. Levels of particulate carbon produced by the primary bloom for each year exceeded levels required for copepod (*Pseudocalanus* sp.) reproduction (100 mg C m^{-3}, Corkett and McLaren 1978, Frost 1985) or for king crab (*Paralithodes camtschatica*) larval growth and survival (Paul et al. 1989). From the standpoint of a species whose larvae are dependent for growth and survival on an ample phytoplankton food supply of the appropriate size and concentration, short-term changes are probably more critical than relatively small interannual differences. This may be in contrast to the situation in lower latitudes, or in coupled systems, where seasonal changes in biomass are less extreme, and may be of the same magnitude as interannual variations.

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Literature cited

Anderson, G. C., Lam, R. K., Booth, B. C., Glass, J. M. (1977). A description and numerical analysis of the factors affecting the processes of production in the Gulf of Alaska: final report. Research Unit 58. In: Environmental Assessment of the Alaskan Continental Shelf, Annual Reports of Principal Investigators for the year ending March 1977. Vol. 7. National Oceanic and Atmospheric Administration, Anchorage, Alaska, p. 477–798

Armstrong, F. A. J., Stearns, C. R., Strickland, J. D. H. (1967). Measurement of upwelling and subsequent biological processes by means of the Technicon AutoAnalyzer and associated equipment. Deep-Sea Res. 14: 381–389

Beattie, W. D. (1984). Physical and chemical regulation of primary production: spring blooms in Tenakee Inlet, Alaska. M.S. thesis. University of Alaska, Juneau, Alaska

Berman, T., Williams, P. J. LeB. (1972). Notes on the methodology of the radiocarbon technique in studying algal productivity. Prog. Rep. Scripps Instn Oceanogr. (Univ. Calif. Inst. mar. Res. Fd Chain Res. Grp) 37–40

Bienfang, P. K., Szyper, J. P., Okamoto, M. Y., Noda, E. K. (1984). Temporal and spatial variability of phytoplankton in a subtropical ecosystem. Limnol. Oceanogr. 29: 527–539

Cohen, E. B., Grosslein, M. D., Sissenwine, M. P., Steimle, F., Wright, W. R. (1982). Energy budget of Georges Bank. Spec. Publs Can. Fish. aquat. Sciences 59: 95–107

Corkett, C. J., McLaren, I. A. (1978). The biology of *Pseudocalanus*. Adv. mar. Biol. 15: 1–231

Coyle, K. O., Paul, A. J. (1990). Interannual variations in zooplankton population and biomass during the spring bloom in an Alaskan subarctic environment. In: Ziemann, D. A., Fulton-Bennett, K. W. (eds.) APPRISE – Interannual variability and fisheries recruitment. The Oceanic Institute, Waimanalo, Hawaii, p. 179–228

Cushing, D. H. (1969). The regularity of the spawning season of some fishes. J. Cons. int. Explor. Mer 33: 81–92

Dagg, M. J., Turner, J. T. (1982). The impact of copepod grazing on the phytoplankton of Georges Bank and the New York Bight. Can. J. Fish. aquat. Sciences 39: 979–990

Forst, B. W. (1985). Food limitation of the planktonic marine copepods *Calanus pacificus* and *Pseudocalanus* sp. in a temperate fjord. Arch. Hydrobiol. (Beih. Ergebn. Limnol.) 2: 1–13

Gieskes, W. W., Kraay, G. W. (1975). The phytoplankton spring bloom in Dutch coastal waters of the North Sea. Neth. J. Sea Res. 9: 166–196

Hager, F. W., Gordon, L. I., Park, J. K. (1968). A practical manual for the use of the Technicon AutoAnalyzer in seawater nutrient analysis. Tech. Rep. Dep. Oceanogr. Ore. St. Univ., Corvallis 68-33: 1–33

Haldorson, L., Pritchett, M., Sterrit, D., Watts, J. (1990). Interannual variability in the recruitment potential of larval fishes in Auke Bay, Alaska. In: Ziemann, D. A., Fulton-Bennett, K. W. (eds.) APPRISE – Interannual variability and fisheries recruitment. The Oceanic Institute, Waimanalo, Hawaii, p. 319–356

Hasle, G. R. (1978). The inverted microscope method. Phytoplankton manual. Monogr. oceanogr. Methodol. (UNESCO) 6: 88–96

Hitchcock, G. L., Smayda, J. (1977). The importance of light in the initiation of the 1972–1973 winter-spring diatom bloom in Narragansett Bay. Limnol. Oceanogr. 22: 126–131

Holm-Hansen, O., Lorenzen, C. J., Holmes, P. E., Strickland, J. D. H. (1965). Fluorometric determination of chlorophyll. J. Cons. perm. int. Explor. Mer 30: 3–15

Hood, D. W., Zimmerman, S. T. (eds.) (1986). The Gulf of Alaska – physical environment and biological resources. U.S. Department of Commerce (NOAA) and U.S. Department of the Interior (Minerals Management Service), Juneau, Alaska

Iverson, R. L., Bittaker, H. F., Meyers, V. B. (1976). Loss of radiocarbon in direct use of Aquasol for liquid scintillation counting of solutions containing ^{14}C-$NaHCO_3$. Limnol. Oceanogr. 21: 756–758

Iverson, R. L., Curl, H. C., Jr., Connors, H. B., Jr., Kirk, D. K., Zakov, K. (1974). Summer phytoplankton blooms in Auke Bay, Alaska, driven by wind mixing of the water column. Limnol. Oceanogr. 19: 271–278

Jones, B. H., Brink, K. H., Dugdale, R. C., Stuart, D. W., Van Leer, J. C., Blasco, D., Kelly, J. C. (1983). Observation of a persistent upwelling center off Point Conception, California. In: Suess, E., Thiede, T. (eds.) Coastal upwelling: its sediment record. Plenum Press, New York, p. 37–60

Kanda, J., Ziemann, D. A. Conquest, L. D., Bienfang, P. K. (1989). Light-dependency of nitrate uptake by phytoplankton over the spring bloom in Auke Bay, Alaska. Mar. Biol. 103: 563–569

Lancelot, C., Mathot, S. (1987). Dynamics of a *Phaeocystis*-dominated spring bloom in Belgian coastal waters. I. Phytoplanktonic activities and related parameters. Mar. Ecol. Prog. Ser. 37: 239–248

Lännergren, C., Skjoldal, H. R. (1975). The spring phytoplankton bloom in Lindaspollene, a land-locked Norwegian fjord. Autotrophic and heterotrophic activities in relation to nutrients. Proc. 10th Eur. mar. Biol. Symp. 2: 363–391 [Persoone, G., Jaspers, E. (eds.) Universa Press, Wetteren, Belgium]

Lean, D. R. S., Burnison, B. K. (1979). An evaluation of errors in the ^{14}C method of primary product measurement. Limnol. Oceanogr. 24: 917–928

MacIsaac, J. J., Dugdale, R. C., Barber, R. T., Blasco, D., Packard, T. T. (1985). Primary production cycle in an upwelling center. Deep-Sea Res. 32: 503–529

Mandelli, E. F., Burkholder, P. R., Doheny, T. E., Brody, R. (1970). Studies of primary productivity in coastal waters of southern Long Island, New York. Mar. Biol. 7: 153–160

Murphy, J., Riley, J. P. (1962). A modified simple solution method for the determination of phosphate in natural waters. Analyt. chim. Acta 27: 31–36

National Oceanic and Atmospheric Administration (1986–1989). Local climatological data – monthly summary (for Juneau, Alaska). National Climatic Data Center, Asheville, North Carolina, USA

Parsons, T., Takahashi, M., Hargrave, B. (1984). Biological oceanographic processes. Pergamon Press, New York

Paul, A. J., Paul, J. M., Coyle, K. O. (1989). Energy sources for first-feeding zoeae of king crab *Paralithodes camtschatica* (Tilesius) (Decapoda, Lithodidae). J. exp. mar. Biol. Ecol. 130: 55–69

Peinert, R., Saure, A., Stegmann, P., Stienen, C., Haardt, H. (1982). Dynamics of primary production and sedimentation in a coastal ecosystem. Neth. J. Sea Res. 16: 276–289

Pingree, R. D., Holligan, P. M., Mardell, G. T., Head, R. N. (1976). The influence of physical stability on spring, summer and autumn phytoplankton bloom in the Celtic Sea. J. mar. biol. Ass. U.K. 56: 845–873

Radach, G., Berg, J., Heinemann, G., Krause, M. (1984). On the relation of primary production to grazing during the Fladen Ground Experiment 1976 (Flex '76). In: Fasham, M. J. R. (ed.) Flow of energy and materials in marine ecosystems. Theory and practice. Plenum Press, New York, p. 597–625

Riley, G. A. (1957). Phytoplankton of the North Central Sargasso Sea, 1950–1952. Limnol. Oceanogr. 2: 252–270

Riley, G. A. (1967). The plankton of estuaries. Publs Am. Ass. Advmt Sci 83: 316–326

Sambrotto, R. N., Goering, J. J., McRoy, C. P. (1984). Large yearly production of phytoplankton in the Western Bering Strait. Science, N.Y. 225: 1145–1150

Sambrotto, R. N., Niebauer, H. J., Goering, J. J., Iverson, R. L. (1986). Relationships among vertical mixing, nitrate uptake, and phytoplankton growth during the spring bloom in the southeast Bering Sea middle shelf. Contin. Shelf Res. 5: 161–198

Smetacek, V. (1985). The annual cycle of Kiel Bight plankton: a long term analysis. Estuaries 8: 145–157

Solórzano, L. (1969). Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr. 14: 799–801

Strickland, J. D. H., Parsons, T. R. (1972). A practical handbook of seawater analysis. 2nd ed. Bull. Fish. Res. Bd Can. 167: 1–310

Sverdrup, H. U. (1953). On conditions for the vernal blooming of phytoplankton. J. Cons. perm. int. Explor. Mer 18: 287–295

Technicon Inc. (1977). Nitrate and nitrite in water and seawater. Technicon, Inc., Tarrytown, New York (Indusrial Method No. 158)

Townsend, D. W., Spinrad, R. W. (1986). Early spring phytoplankton blooms in the Gulf of Maine. Contin. Shelf Res. 6: 151–529

Utermöhl, H. (1958). Zur Verfollkommnung der quantitativen Phytoplankton-Methodik. Mitt. int. Verein. theor. angew. Limnol. 9: 1–38

Wassman, P., Aadnesen, A. (1984). Hydrography, nutrients, suspended organic matter, and primary production in a shallow fjord system on the west coast of Norway. Sarsia 69: 139–153

Wilkerson, F. P., Dugdale, R. C. (1987). The use of large shipboard barrels and drifters to study the effects of coastal upwelling of phytoplankton nutrient dynamics. Limnol. Oceanogr. 32: 368–382

Williamson, R. S. (1978). Phytoplankton and productivity in Auke Bay, Alaska. NOAA/NMFS Auke Bay Laboratory, Juneau, Alaska (Manuscr. Rep., File No. 157).

Winter, D. F., Banse, K., Anderson, G. C. (1975). The dynamics of phytoplankton blooms in Puget Sound, a fjord in the northwestern United States. Mar. Biol. 29: 139–176

Wroblewski, J. S., Richman, J. C. (1987). The non-linear response of plankton to wind mixing events – implications for survival of larval northern anchovy. J. Plankton Res. 9: 103–123

Ziemann, D. A., Conquest, L. D., Fulton-Bennett, K. W., Bienfang, P. K. (1990a). Interannual variability in the physical environment of Auke Bay, Alaska. In: Ziemann, D. A., Fulton-Bennett, K. W. (eds.) APPRISE – Interannual variability and fisheries recruitment. The Oceanic Institute, Waimanalo, Hawaii, p. 99–128

Ziemann, D. A., Conquest, L. D., Fulton-Bennett, K. W., Bienfang, P. K: (1990b). Interannual variability in the Auke Bay Phytoplankton. In: Ziemann, D. A. Fulton-Bennett, K. W. (eds.) APPRISE – Interannual variability and fisheries recruitment. The Oceanic Institute, Waimanalo, Hawaii, p. 129–170