Exxon Valdez Oil Spill
Restoration Project Annual Report

Sound Ecosystem Analysis: Phytoplankton and Nutrients
Restoration Project 97320G

This annual report has been prepared for peer review as part of the Exxon Valdez Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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Sound Ecosystem Analysis: Phytoplankton and Nutrients

Restoration Project 97320G
Annual Report

Study History: The project was initiated as Restoration Project 94320G. A "Draft Final Report" was produced as an annual report in 1995, 1996 and 1997 under the title "SOUND ECOSYSTEM ANALYSIS: Phytoplankton and Nutrients" and continues under the present grant number. Papers were presented at the AAAS Arctic Science Conference, AGU/ASLO Ocean Sciences meeting and The Oceanography Society meeting.

Abstract: In 1997 we collected 636 water samples for analysis which were from cruise BE705 (5-12 May 97) and daily collections (April through June) from a location (same place as 1995 and 1996) in Elrington Passage near AFK Hatchery. Measurements included chlorophyll, nutrients, particulate carbon and nitrogen, species composition, CTD, and dissolved oxygen from 6 depths in the upper water column. This is the third consecutive year for a spring cruise to study the spatial distributions of phytoplankton and nutrients. The data indicate the presence of a re-occurring front located about 30 km inside Hinchinbrook entrance that partitions biological processes into inner and outer regions. The front is an upwwelling zone with moderate sustained phytoplankton biomass (chlorophyll).

This is also the third data set for a daily time series in Elrington Passage for phytoplankton and nutrients that fully includes the spring bloom. Here the spring phytoplankton increase is strongly influenced by light and mixing. The decline of phytoplankton biomass is a result of nutrient depletion and grazing. The spring phytoplankton cycle begins with a bloom dominated by diatoms, particularly *Skeletonema costatum*, followed by a low biomass of flagellates and succeeded by another low biomass of diatoms. The timing of the spring increase in phytoplankton, as measured by chlorophyll, based on the data collected here and historical work back to 1971, is remarkably similar with the peak occurring on or about 28 April. The only exceptions to this were in 1993 and 1977. This fact indicates that solar angle, rather than mixing, determines the initiation of the bloom in most years. Estimated primary productivity in 1997 was 46% lower than 1996 and 36% lower than 1995. Overall, the data indicate a robust, healthy foundation for the pelagic ecosystem in Prince William Sound. A detailed analysis of the phytoplankton community for 1995 and 1996 is included as an attachment.

Key Words: Exxon Valdez, phytoplankton, nutrients, primary productivity, algae

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INTRODUCTION:

The project seeks to determine the driving force of ecosystem variability from a bottom-up perspective. In this component our hypothesis is that the timing, quantity and species composition of the plant community, that is, the phytoplankton, is a major determinant of variability in upper trophic levels, a bottom-up scenario of ecosystem forcing.

The Sound Ecosystem Assessment program (SEA) aims to understand and predict restoration of populations of pink salmon and herring in Prince William Sound. Fundamental to this goal is the understanding of controls of ecosystem processes that nourish the food web at its primary level. Restoration of marine populations that have been damaged by human activity is usually limited to a few options that focus on controlling loss rate processes, i.e. harvest level, predator control, etc., or minor habitat modification. Pink salmon and herring offer a spectrum of strategies since a large portion of salmon are protected in hatcheries in their early life and herring are completely wild subject to the variance of nature. What then is the role of the annual cycle of primary production in the success of these upper trophic level species? Does the magnitude of the phytoplankton production determine the strength of a year class? Is the phytoplankton species composition an important determinant of the grazing zooplankton community? Does any of this matter or is there always enough food at the right time of the year so that predator populations are determined by the uppermost consumer on the food web? All are questions that are being examined in this study.

One central SEA hypothesis concerns the impact of circulation and physical conditions on the restoration of fish stocks (the Lake-River Hypothesis). This proposes that the circulation of Prince William Sound alternates irregularly between years of strong through-flow, river-like conditions, and relatively stagnant, lake-like conditions. The consequence is a high biomass of large zooplankton (copepods) in 'lake' years that are the major food for target fish (salmon, herring) and their predators (termed 'middle-out' food web control by Cooney and associates). In alternate 'river' years, the large zooplankton are sparse and predation on the target fish species predominates (top-down control).

While middle-out or top-down are principal hypotheses being tested by SEA research, the possibility of bottom-up control, where the production of upper trophic level species is modulated by variations in light- and nutrient-driven phytoplankton production. In this hypothesis, the production and/or composition of the zooplankton community is determined by variations in phytoplankton primary production and by the species composition of the phytoplankton community. For example, a phytoplankton community dominated by large diatoms can support a high biomass of large oceanic copepods, whereas a phytoplankton population dominated by smaller flagellates results in a reduced number of larger copepods, or in a shift to a zooplankton community dominated by smaller neritic copepod species. Variations in the timing of phytoplankton populations have been previously suggested to be a control of ecosystem events in Prince William Sound (McRoy 1988). A further complication in the interrelationship is that the large zooplankton are one year old when they become major prey for fishes (Cooney, personal communication) so their abundance must be determined by the events of the previous year and their specific biomass by the production cycle of the present year.

In this component, we provide the nutrient and phytoplankton data that are essential to evaluate the influence of phytoplankton dynamics on the food web and to test the bottom-up hypothesis. We will characterize the interannual spatial and temporal variation in nutrient and phytoplankton fields. We will evaluate the role of phytoplankton production in zooplankton recruitment and growth (especially for *Neocalanus* and *Pseudocalanus*). In a general sense we will provide an answer to the question "Is it food?".

A central tenet of the Lake/River Hypothesis is the variable advection of Gulf of Alaska waters into Prince William Sound. This advection affects not only zooplankton populations, but also the Prince William Sound phytoplankton populations and production. Strong advection may confound the effects of in situ primary production in the Sound. To test the hypotheses further, we use satellite-derived sea-surface temperatures to examine the movement of Gulf of Alaska surface waters into Prince William Sound.

OBJECTIVES:

This study is designed to investigate the distribution, amount, and type of phytoplankton growth and the major inorganic nutrient fields associated with the growth processes. Our hypothesis is that variations in the phytoplankton production and populations are transferred to the zooplankton and that such variations are a function of oceanographic conditions that control the supply of inorganic nutrients and light. The objectives for 1997 were:

1. Analysis of phytoplankton community ecology in Prince William Sound.
2. Determination of basin-wide patterns of temperature, salinity nutrients and chlorophyll from ship-board observations.
3. Determination of temporal patterns of temperature, salinity, nutrients and chlorophyll in western Prince William Sound from a station near AFK Hatchery.
4. Determination of the linking between phytoplankton and upper trophic levels.

METHODS:

Phytoplankton Biomass, Spatial and Temporal Patterns

Phytoplankton biomass is measured using the standard chlorophyll techniques (Parsons et al., 1984) on a Turner Designs Fluorometer. Samples were collected at specific 309 time/space locations on cruises and at a shore-based station. Data allow mapping the areal pattern and description of the water column profile.

Phytoplankton Primary Production

The biomass pattern provides a picture of what is present, but it does not provide information on the phytoplankton dynamics. We can estimate production using dissolved oxygen and nutrient data. Productivity data are also available in our historical database (McRoy, unpublished data; Goering et al. 1973b). Methods used involved uptake of ^{14}C by phytoplankton in containers under neutral density filters (Strickland and Parsons, 1972; Parsons et al., 1984).

Phytoplankton Community Composition

The composition of the phytoplankton community can be as important as the total primary production in determining zooplankton species and abundance. We collected 50 ml aliquots from water samples and preserved them in Lugol's solution for species identification. Identifications and cell counts were done using an inverted microscopy method (Sournia 1978). On low (20x) magnification, all visible cells in two transects are counted. On high (40x) magnification, fields are counted until a total of 300 cells is reached. For cell volume calculations and calculation of carbon content, cells identified to genus were grouped according to the maximum cell dimension. At least 20 cells of each species for size class were measured. The procedure is labor intensive and only a portion of the samples collected can be counted.

Nutrient Fields

Phytoplankton require the major inorganic nutrients (nitrogen, phosphorus and silica) for growth. General oceanographic circulation and land run-off supply nutrients. Since phytoplankton also require light, the problem is understanding how the nutrients are supplied to the illuminated zone of the sea. We routinely collected water samples for quantitative nutrient analysis. In the field, water samples were collected with Niskin Bottles at standard depths over the upper 100 m (deeper if necessary). A small aliquot (250 ml) was filtered and frozen for later chemical analysis. Chemical determination of the quantity of dissolved nitrogen (as nitrate, nitrite and ammonium), phosphate and silicate were measured using prescribed Continuous Flow Analysis methods with an Alpkem Auto-Analyzer in our laboratory in Fairbanks.

Personnel

The following people have contributed to sample and data collection and analysis:

P. Simpson	Graduate Student
A. Ward	Graduate Student
K. Tamburello	Graduate Student
J. Cameron	Senior Technician
S. McCullough	Field Technician
P. Cassidy	Field Technician

RESULTS:

Samples were collected to document the time series of events in the annual phytoplankton/nutrient cycle as well as to examine spatial variations in Prince William Sound. These data are collected in conjunction with other SEA projects and are supplied to the SEA data base after appropriate analysis and verification.

Sample Collection

We collected water samples for analysis from two types of platforms in Prince William Sound. In 1997 a single cruises on board chartered vessel in May permitted regional sampling from the standard SEA ocean stations. The second sample site is a station in Elrington Passage (60°01'N, 148°00'W) near the AFK Hatchery on Evans Island in the southwestern corner of the sound. We used this shore facility to collect daily samples from mid-April until late June. The station was visited daily by skiff and all samples were collected from a 5 liter Niskin bottle lowered repeatedly to each sample depth with a hand winch. These data provide temporal continuity to the ship-board sampling.

The field season began in April and ended in June. In 1997 we collected 636 samples from 1 cruise and a time series station. An decrease of 42% over 1996 (Tables 1 and 2). The chartered vessel provided areal coverage of the Sound for oceanographic and biological parameters (Figure 1). The time series began on 01 April 97 and ended on 15 June 97.

The Phytoplankton-Nutrient Component database includes dissolved nutrients (nitrate+nitrite, ammonia, phosphate, and silicate), dissolved oxygen, CTD (salinity, temperature, depth), chlorophyll a, and particulate carbon (PC) and nitrogen (PN) from all sampling

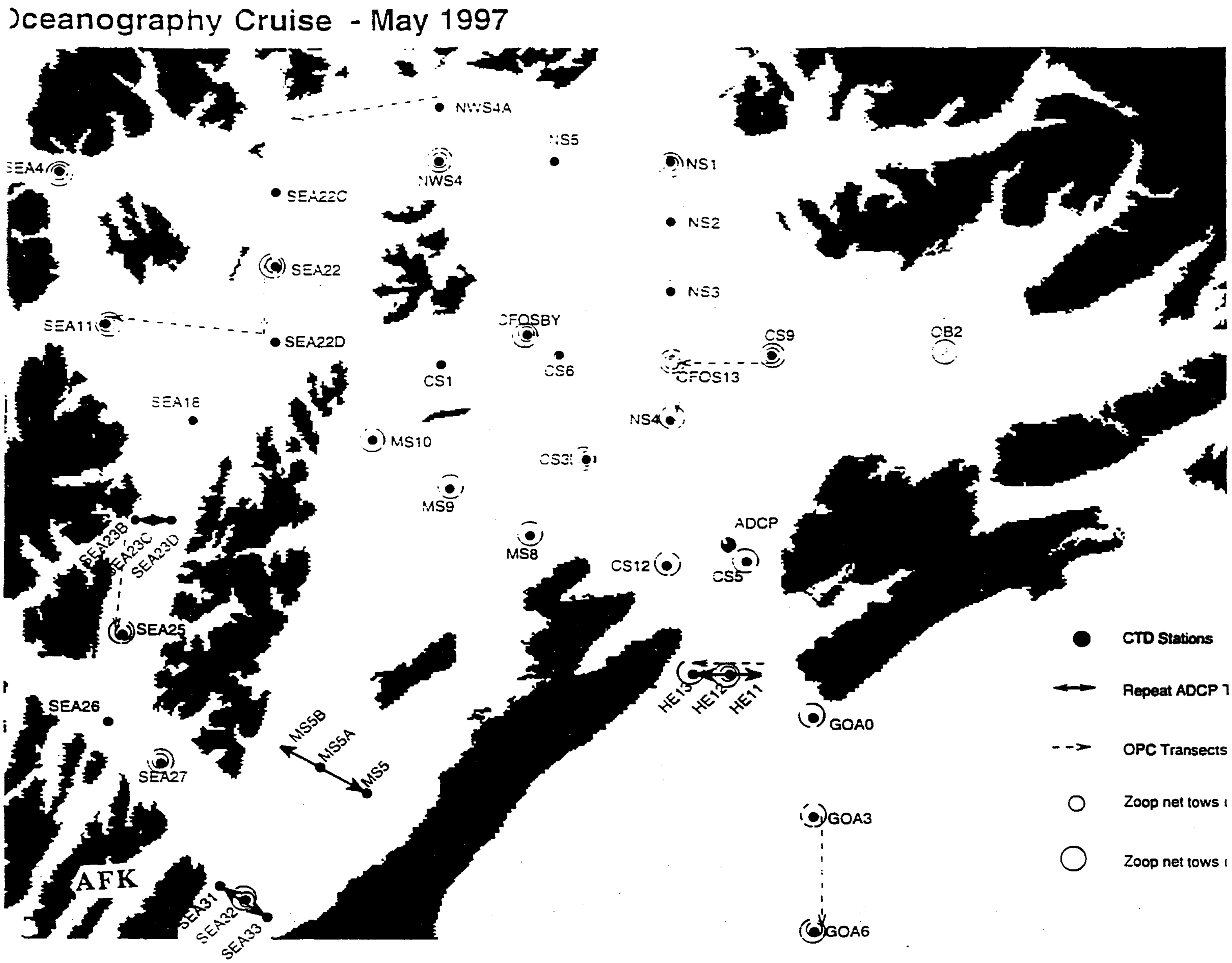


Figure 1. SEA 1997 station locations for phytoplankton and nutrient sample collection.

platforms. In addition selected representative samples for phytoplankton identification and enumeration were processed.

Phytoplankton Time Series Measurements in Prince William Sound

The temporal pattern of the spring phytoplankton increase was similar in all 3 years (Figure 2). In 1997 the bloom began on day 93 and terminated by day 137. Chlorophyll levels in 1997 were only about half those reached in 1995 and 1996 but the duration of the bloom was about 10 days longer in 1997.

The peak biomass, as measured by chlorophyll concentration, in 1997 occurred on day 107 which was very close to the peak in 1996. The 1995 peak occurred on day 117 which is close to the mean for all phytoplankton time series measurements for the Sound (Figure 3). The mean from all current and historical measurements is day 118 (28 April). This is also the mean date for peak occurrence for 1985-89 in Auke Bay in Southeast Alaska (Ziemann et al. 1990). With 2 exceptions there is a remarkable coincidence of peak chlorophyll around day 118 for 11 years from 1971 to present. The exceptions are 1995 (data source: CFOS buoy) when the peak occurred about 2 weeks earlier on day 95 and 1977 (data source: Alexander and Chapman 1980) when the bloom maximum occurred around day 165. The first exception is a result of unusually calm spring conditions as supported by the ancillary hydrographic data collected by the buoy instrumentation. The data from 1980 are for Port Valdez and can not be readily explained but it may simply be a plotting error on the figure.

The cluster of peak biomass values around day 118 (28 April) in 11 of the 13 years for which there are data is an indication of the forces that control phytoplankton production. A coincidence of dates suggests that in most years sun angle is a primary physical mechanism controlling production and that this even dominates over mixing processes, or the lack thereof, as seen in 1995.

A detailed analysis of the 1995 and 1996 phytoplankton data written by Alison Ward as a thesis for the degree of Master of Science at the University of Alaska Fairbanks is included with this report as Attachment A. The 1997 data set is in the process of analysis.

Primary Production

As stated in the methods section, direct measurements of primary production were not made during this study but the growth rate of the phytoplankton during the spring bloom can be determined from the time course of nitrate+ntrite depletion (Figure 4) and by invoking the Redfield ratio of 6.6 for Carbon to Nitrogen. The results are overall primary production rates of 2.33, 2.75 and 1.49 $gCm^{-2}\ d^{-1}$ for 1995, 1996 and 1997 respectively, a nearly two-fold difference between the highest and lowest value. These rates fall well within the values for the spring bloom measured by Goering et al (1973a and 1973b) in Port Valdez and Valdez Arm using direct ^{14}C uptake. The total production can be twice these values if the f ratio is less than 0.5 as would be expected for the region.

Spatial Measurements:

Biological data collected during the single cruise in May 1997 further illustrates the high temporal variability of Prince William Sound. Nitrate throughout the central sound was more depleted in May 1997 and chlorophyll concentrations were an order of magnitude higher than in

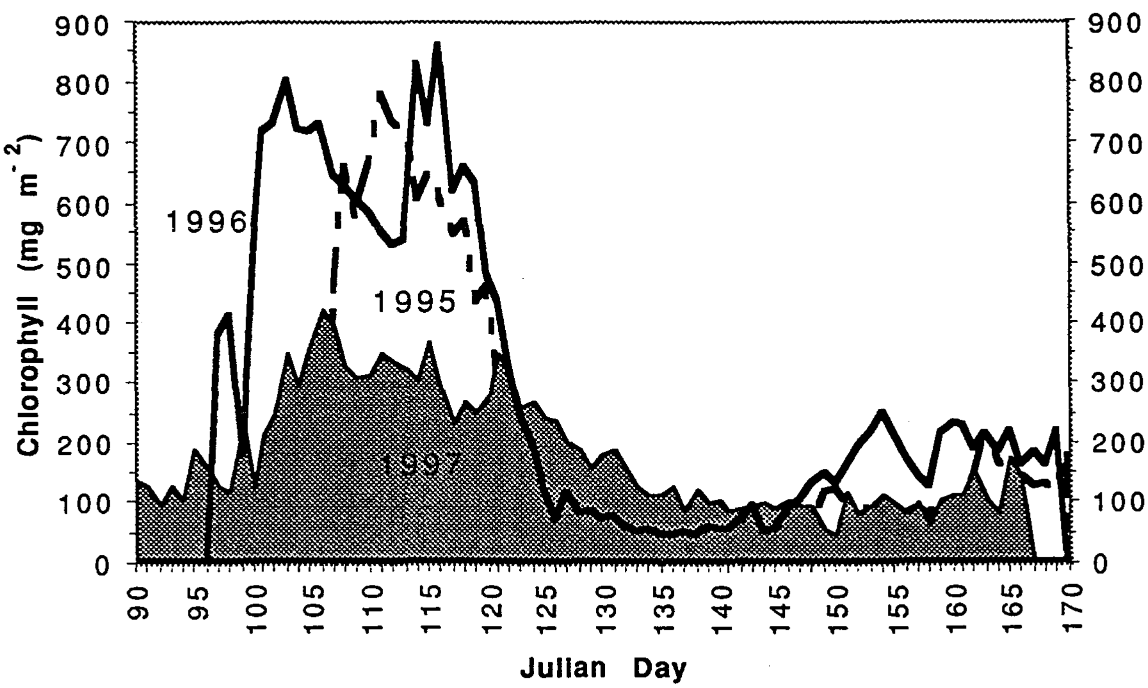


Figure 2. **Integrated Chlorophyll a (upper 50 m) for the spring time series in Elrington Passage in 1995, 1996 and 1997.**

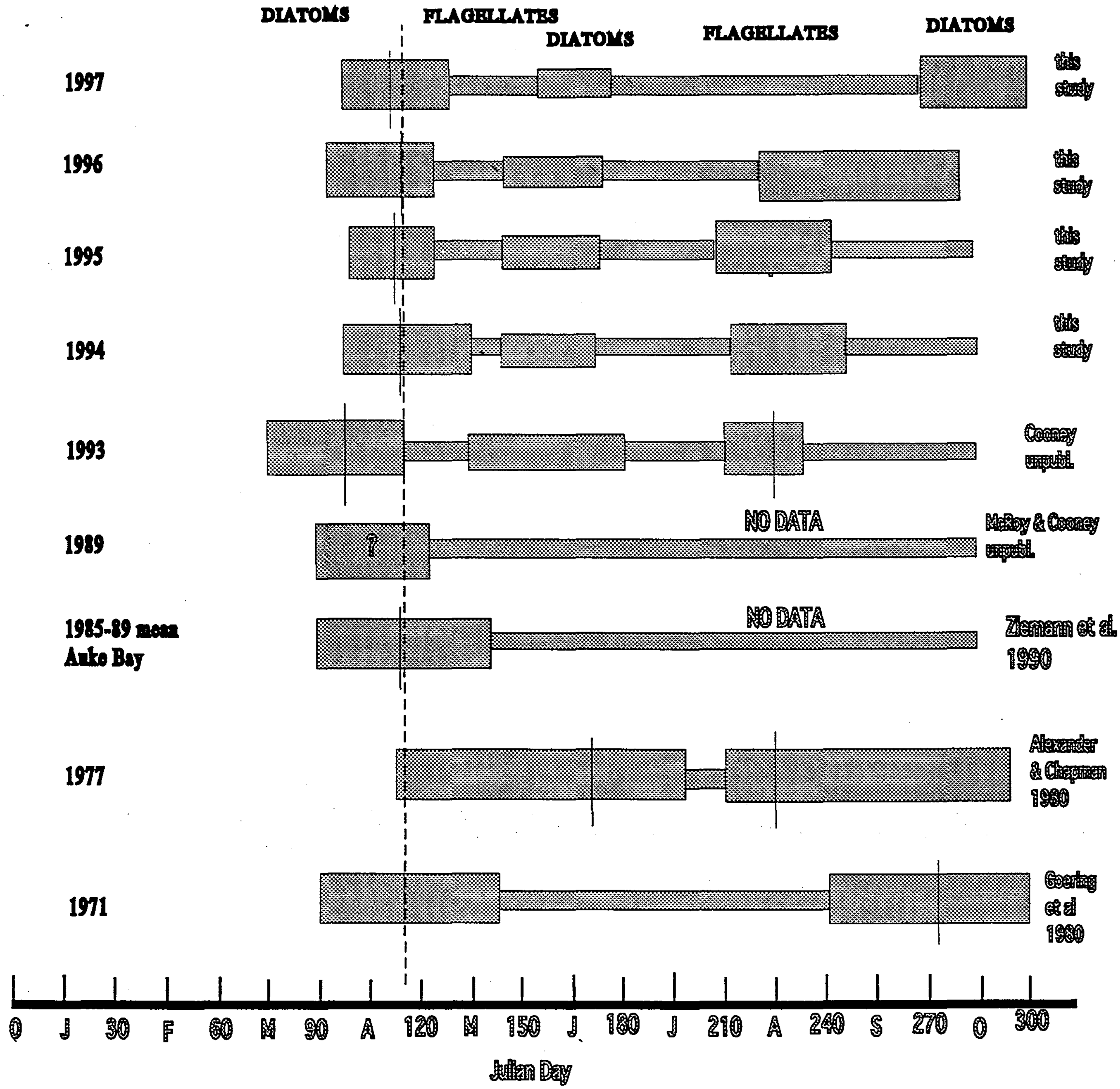


Figure 3. Comparison of timing of phytoplankton spring bloom for all known studies of Prince William Sound. Data from the Apprise Project time series in Auke Bay in Southeast Alaska for 1985-89 are also included. The vertical bars indicate the day of the peak biomass; the average for all studies is day 118 (dashed line).

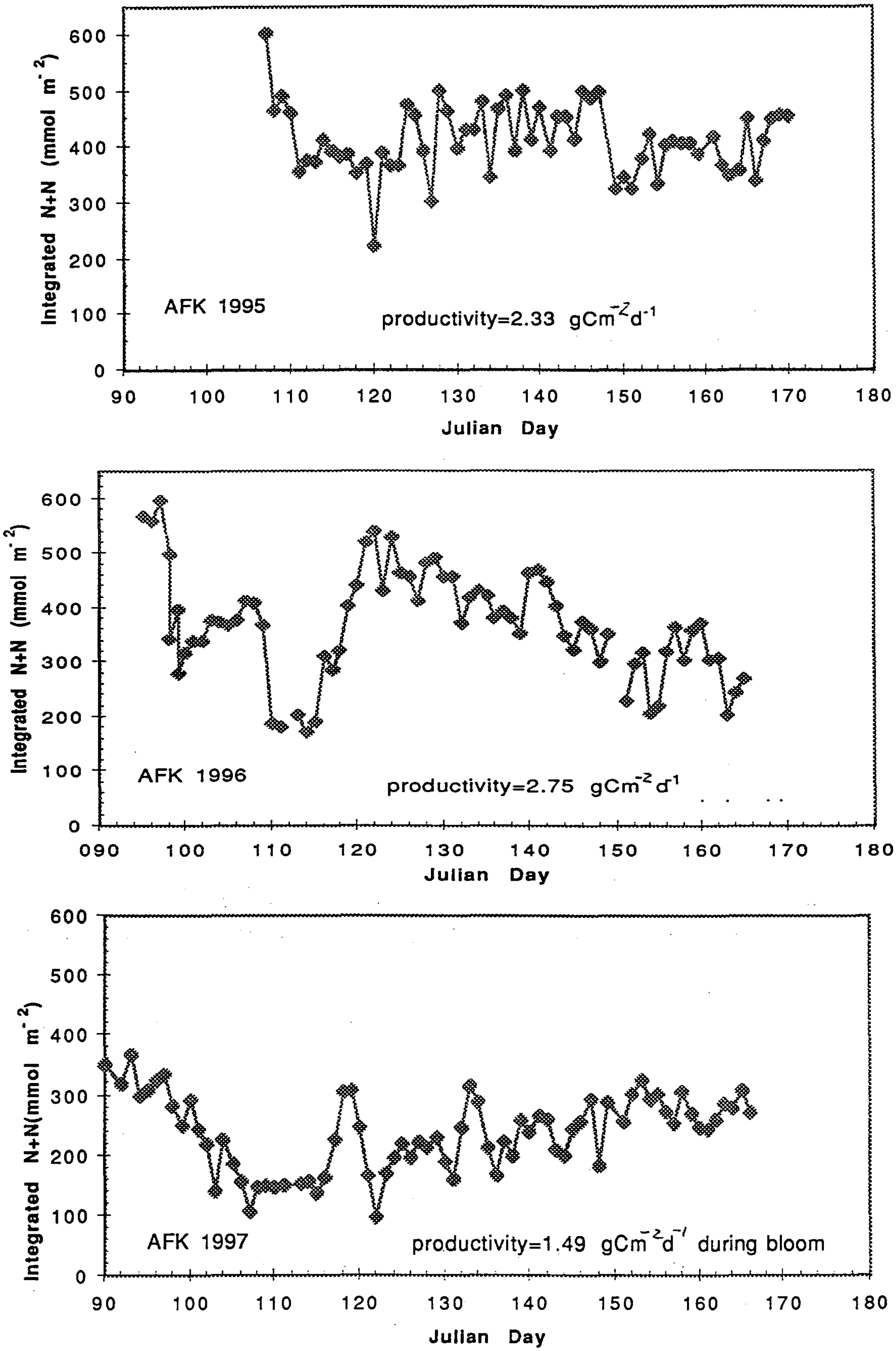


Figure 4. Time series of integrated (upper 50 m) nitrate+nitrite content of thewater column in 1995, 1996, and 1997 with estimated primary production rate.

May of previous years. Despite such high variability, several apparent fronts and upwelling zones consistently appear every year. The central sound in spring is characterized by a front centered 30 km north of Hinchinbrook Entrance (Figure 5). North of this front the phytoplankton bloom early and fast, depleting the surface nutrients and disappearing within a few weeks. South of this front the phytoplankton bloom begins later and lasts longer than in the north, possibly a result of higher vertical mixing rates in this region. This front disappears in the summer to be replaced by an upwelling zone which supplies deep nutrients that supports a moderate phytoplankton community at that location.

Montague Strait is characterized by 2 sets of fronts, one in the south associated with Knight Island Passage and one in the north where Montague Strait enters the central sound. Chlorophyll concentrations within Montague Strait vary from year to year much like they do in the central sound, and the location of the peak chlorophyll concentration changes from month to month, but the location of the peak chlorophyll concentrations each month has been the same every year (Figure 6). These consistent patterns in the face of the recognized high temporal variability within Prince William Sound implies a similar pattern in the physical environment. The consistent spatial pattern of chlorophyll peaks implies consistent large scale circulation patterns within the sound, while variability in chlorophyll concentrations, nutrient depletion and bloom timing imply variability in smaller time scale events such as wind driven mixing. Under conditions such as these it may be sufficient to use the density structure and circulation pattern of a "typical" year and annual wind records to adequately model the biology of lower trophic levels in Prince William Sound. However, such a tactic may result in dramatic errors in years with atypical circulation patterns such as we might expect as a result of El Nîno.

Discussion

The general pattern of the time course of phytoplankton biomass is a rapid spring increase followed by an equally sharp decline after about 3 weeks. The increase begins in early April and the decline occurs in early of May. The high biomass of the spring bloom, consisting of a dominant diatom flora, is followed by a short period of very low biomass characterized by a flagellate community. A small increase of biomass and diatoms can again occur for a few weeks in June. While our field work did not include daily sampling beyond mid June, past research in Prince William Sound and other coastal embayments around the Gulf of Alaska have documented fall increases in phytoplankton (Goering et al 1973b). A large flagellate population is often observed in August (Alexander and Chapman 1980) and the CFOS buoy recorded such chlorophyll increases in 1993, 1994, 1995, and 1996. In addition the CFOS buoy indicated an fall (October) phytoplankton increase in 1997. The later phytoplankton increase was most likely a diatom community (Goering et al. 1973b).

The pattern of the phytoplankton cycle indicates the classic response of increasing light and stratification in spring followed by nutrient limitation. This pattern has been reported for previous studies of Prince William Sound (Goering et al., 1973a, 1973b). The time series data indicate that nutrient limitation is a significant factor in terminating the bloom. The nutrient-nutrient plot of silicate vs. nitrate shows that the diatoms are able to utilize silicate below the threshold level required for growth (Paasche 1980). The condition must also be a powerful force in species succession. The end of the bloom period is also influenced by zooplankton grazing since the increase in zooplankton directly follows the decrease in phytoplankton. It is likely that both nutrient limitation and grazing lead to the decrease in phytoplankton biomass. These forces

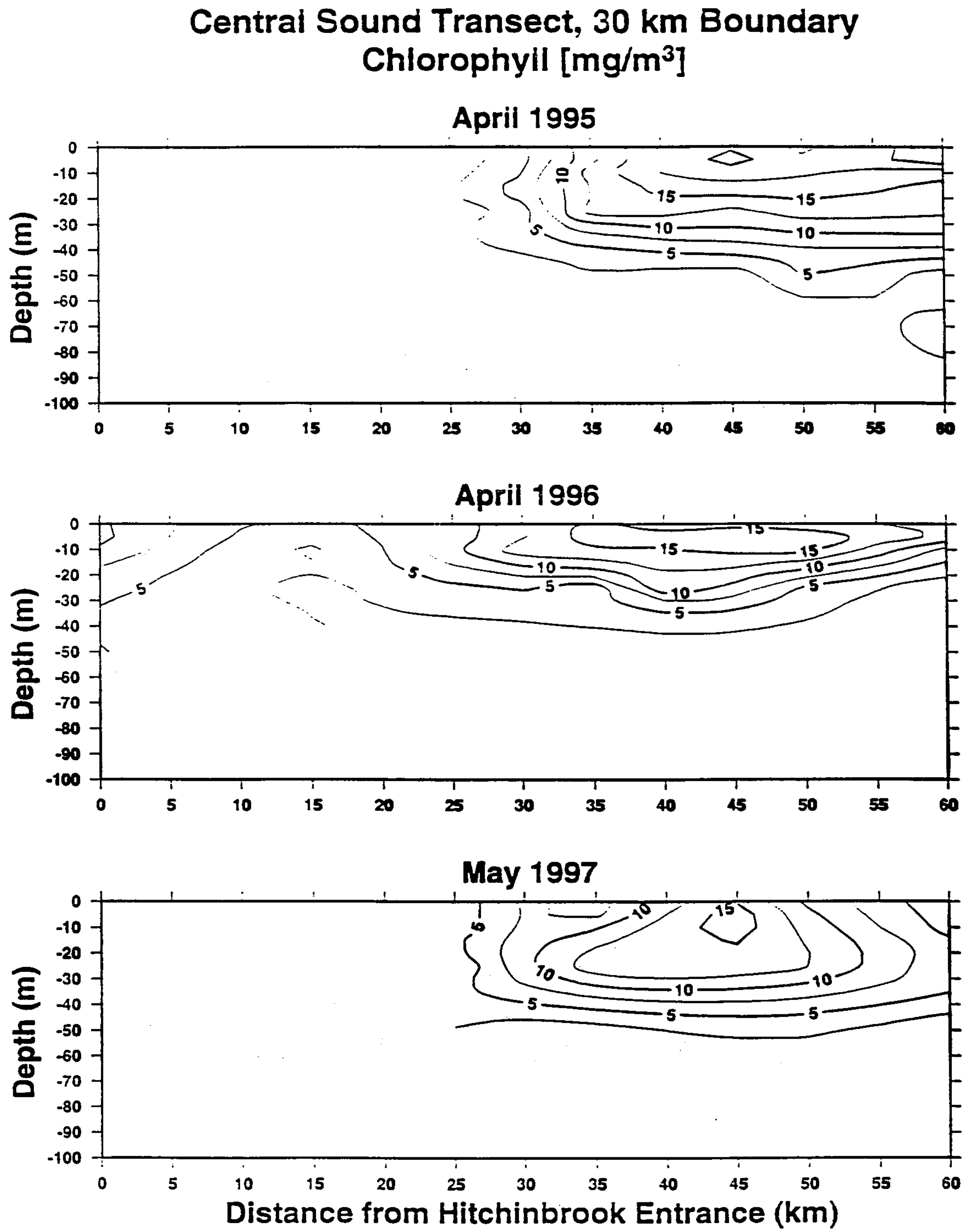
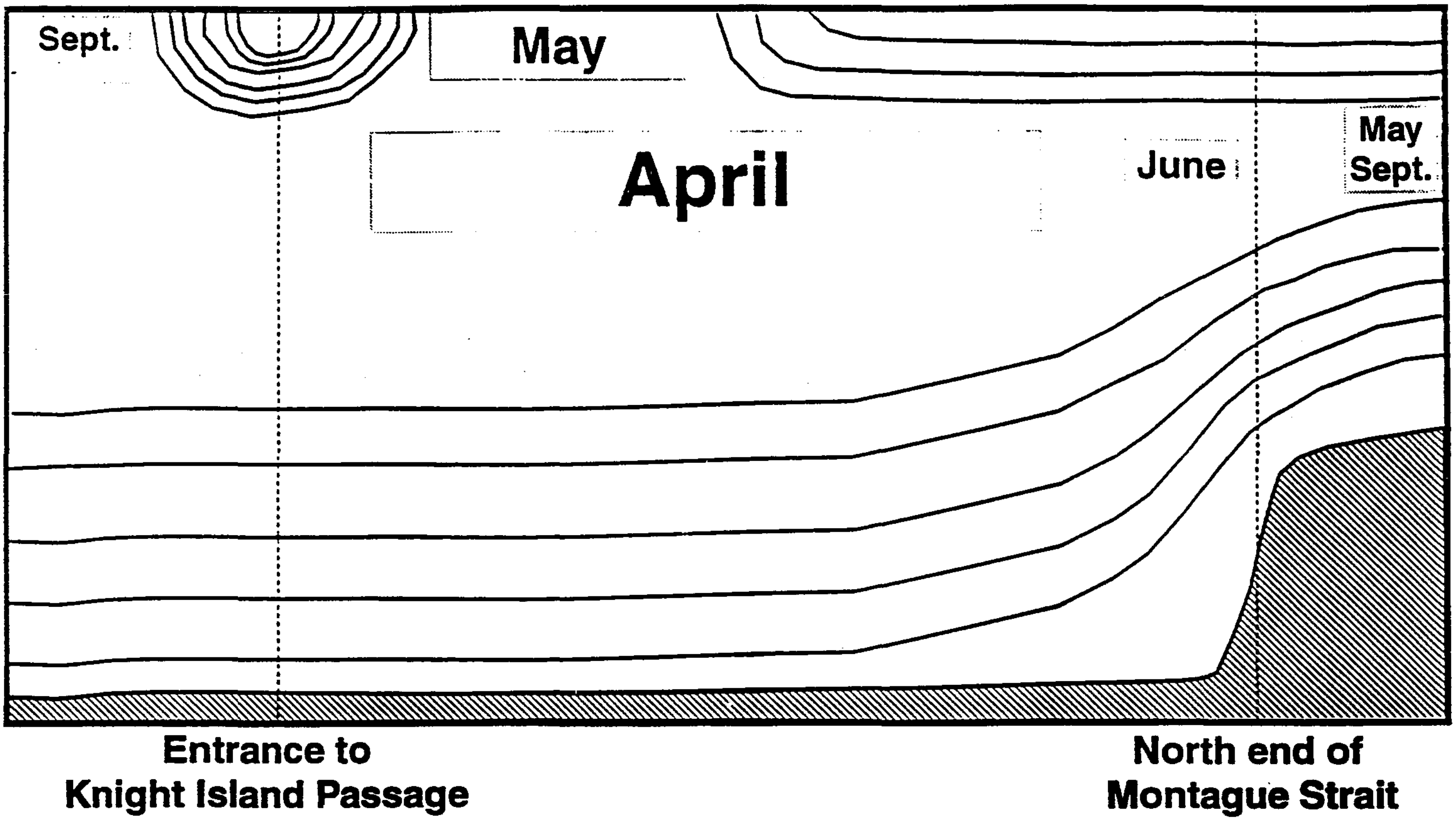


Figure 5. Transects from Hinchinbrook Entrance to the central region of Prince William Sound showing the 30 km front in chlorophyll (mg m^{-3}) in spring of 1995, 1996 and 1997.

Location of chlorophyll maximum in Montague Strait each month.



Contours represent salinity.
May includes 3 years data, other months represent 2 years data

Figure 6. Variability of the location of the chlorophyll maximum by month for the years studied.

can also have a major impact on the composition of the phytoplankton community. Horner et al. (1973) report a detailed list of phytoplankton species for Port Valdez that can also be used for comparison

Alexander and Chapman (1980) report that the phytoplankton community consisted of 97% diatoms in April but by July it was 95 % microflagellates. We found that the diatom abundance in April 1995 and 1996 was over 55%, with remainder consisting of flagellates. The presence of abundant flagellates is indicative of a mechanism for channeling dissolved organic matter (DOM) that is excreted by phytoplankton through a microbial loop. Such a mechanism retains energy in the food web that might otherwise be lost through excreted DOM. The process is relatively inefficient since at least 3 trophic levels are probably involved (Azam et al. 1983).

The diatoms present in April and May are expected to be prime food for the large zooplankton, and hence a major energy source for upper trophic level species. On the other hand the picoplankton are a poor food source for these zooplankton but contribute to a microbial food web that can eventually provide energy to the larger consumers.

Do phytoplankton drive the food web? We have compiled a table of features of the Prince William sound ecosystem for the three years of the study to quantitatively and qualitatively compare the basis of the food web with production of upper trophic level target species (Table 3). In all features compared there appears to be a direct relationship between the quantity and quality of primary production and the production of pink salmon and herring. This finding though somewhat preliminary will certainly warrant discussion and further documentation during the synthesis of the SEA Project. It is at least positive evidence that the food ecosystem is driven by bottom up processes.

Conclusions:

1. A well-defined spring bloom of phytoplankton occurs in Prince William Sound. The timing of the bloom depends on light but the lack of mixing in a given year can predominate. The average peak of the phytoplankton biomass for all studies of Prince William Sound is day 118 (28 April).
2. Phytoplankton bloom community consists of at least 55% diatoms in 1995, 1996, and 1997, followed by a post-bloom period of 3 weeks consisting of more than 80% flagellates. A resurgence of diatoms occurred after the post-bloom period but attained only 33% of their former abundance.
3. Primary production was highest (2.75 $gCm^{-2}\ d^{-1}$) in 1996 and lowest (1.49 $gCm^{-2}\ d^{-1}$) in 1997. Productivity was ultimately silica limited.
4. A physical front located about 30 km inside Hitchinbrook Entrance is an upwelling feature and separates the central sound into biological regions that have different timings of biological events.
5. Evidence is accumulating that during the years studied there is a direct relationship between nutrient supply, primary production and upper trophic level production.

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Simpson, E.P. and C.P. McRoy. 1997. The architecture of the Prince William Sound ecosystem: I. Variability of chlorophyll and nutrient fields. Arctic Division, AAAS Meeting, Valdez AK, September 1997.

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Table 1. Summary of data collection, including number of samples collected, and sampling days for 1995, 1996 and 1997 at AFK Station SB2.

Data Collection	**1995**	**1996**	**1997**	**Totals all years**
Sampling Dates (Julian)	107 - 170	97 - 169	91-166	91-170
Sampling Depths	0, 5, 10, 25, 50, 75	0, 5, 10, 25, 50, 75	0, 5, 10, 25, 50, 75	0, 5, 10, 25, 50, 75
No. Sampling Days	64	73	73	210
CTD Casts	63	73	73	210
Secchi Depth Measurements	63	73	73	210
Chlorophyll *a* Concentration Measurements	372	437	435	1244
Size Fractionation Measurements	0	68	219	287
Nitrate + Nitrite Concentration Measurements	372	438	435	1245
Silicate Concentration Measurements	369	438	435	1242
Phosphate Concentration Measurements	372	438	435	1245
Species Composition and Abundance Measurements	73	80	110	263
Autotrophic Carbon Biomass Measurements	68	80	110	258

Table 2. Summary of sample collection for 1995, 1996 and 1997 from oceanographic cruises.

Data Collection	**1995**	**1996**	**1997**	**Totals all years**
No. Cruises	5	3	1	9
No. Stations	153	112	29	294
Chlorophyll *a* Concentration Measurements	918	672	174	1764
Size Fractionation Samples	329	0	0	329
Nitrate + Nitrite Concentration Measurements	918	672	174	1764
Silicate Concentration Measurements	918	672	174	1764
Phosphate Concentration Measurements	918	672	174	1764
Species Composition and Abundance Samples	760	672	174	1764

Table 3. Interannual comparison of features that provide evidence supporting a bottom-up hypothesis.

FEATURE	1995	1996	1997
Initial N+N Content of Water Column (mmole m-2)	604	597	368
Silicate / N+N Ratio	1.55	1.55	3.00
Maximum Phytoplankton Biomass (mg Chl *a* m^{-2})	723	863	423
Year Day of Maximum Biomass	113	116	106
Dominant Diatom Species	*Thalassiosira sp.* *Skeletonema sp.* *Chaetoceros sp.*	*Skeletonema sp.*	*Thalassiosira* sp
Carbon / Chlorophyll Ratio	12 +/- 3	22 +/-6	(30) preliminary
Estimated Primary Production During Bloom (g C m^{-2} d^{-1})	2.33	2.75	1.49
Zooplankton, maximum settled volume (ml) (R.T. Cooney data)	5.61	6.21	4.97
Wild Pink Returns (ln total) (M. Willette data)	14.987	15.316	should be low
Herring Growth, fork length of 0 class (mm) in Oct., Zaikof Bay (K. Stokesbury data)	78.19+/_14.77	93.49+/-8.49	75.94+/-7.54

ATTACHMENT A

A TEMPORAL STUDY OF THE PHYTOPLANKTON SPRING BLOOM IN PRINCE WILLIAM SOUND, ALASKA

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTERS OF SCIENCE

By

Alison Emmett Ward, B.A.

Fairbanks, Alaska

August 1997

A TEMPORAL STUDY OF THE PHYTOPLANKTON SPRING BLOOM IN PRINCE WILLIAM SOUND, ALASKA

By

Alison Emmett Ward

RECOMMENDED:

Advisory Committee Chair

Department Head

APPROVED:

Dean School of Fisheries and Ocean Sciences

Dean of the Graduate School

7 - 7 - 97

Date

ABSTRACT

The phytoplankton bloom in southwest Prince William Sound, Alaska began in early April, declined by May and had a small recovery in June 1995 and 1996. Phytoplankton bloom was nutrient-limited in April and phytoplankton biomass was controlled by zooplankton grazing in May. The bloom consisted of 80 % microplankton; the post bloom was predominantly flagellates, followed by a small diatom recovery. A seasonal succession in the diatom community occurred from *Skeletonema costatum*, *Thalassiosira* spp. and *Chaetoceros* spp. in April to *Rhizosolenia fragilissima* in June. There was little vertical variation in species composition. More than twice as much organic carbon due to phytoplankton was present in 1996 as in 1995. In 1995, *Thalassiosira* spp. was 73-80 % of diatom carbon and in 1996 *Skeletonema costatum* made up 58-78 %. The timing of the bloom, cell abundance and patterns of succession resembled other marine environments of similar latitude.

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ACKNOWLEDGMENTS

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INTRODUCTION

On 28 March 1989, the *Exxon Valdez* oil tanker spilled 11 million gallons of crude oil into the estuarine waters of Prince William Sound (PWS), Alaska. This event precipitated the question of how such a widespread pollutant would affect the long-term health of Prince William Sound. In order to address this question from a broad perspective, the Sound Ecosystem Assessment (SEA) Project was initiated in the spring of 1994. SEA originated as an interdisciplinary, multifaceted study designed to evaluate Prince William Sound from an ecosystem perspective to determine the factors that constrain the restoration of commercially important fish stocks (especially pink salmon and herring) in the region of the spill (Cooney 1996). The Phytoplankton and Nutrient Component SEA, of which this study is an integral part, was designed to assess the health of the sound temporally and spatially from the base of the food-chain. It provides four years of supporting field data to modeling components and establishes a database of biological and chemical information for future reference. The data presented here are the results of a collaborative effort of a group of marine scientists and technicians led by Dr. C. Peter McRoy at the Institute of Marine Science, University of Alaska, Fairbanks.

This thesis, one sub-set of the Phytoplankton and Nutrient Component of SEA, is an analysis of the seasonal and interannual dynamics of the phytoplankton community in 1995 and 1996. This study involved collecting and analyzing a series of daily observations on the phytoplankton and nutrients in the springs of two consecutive years. I proposed that an assessment of the phytoplankton community in the sound would be a basis for inferences about on the transfer of energy to higher trophic levels, i.e. a test of the bottom-up driven ecosystem hypothesis. I planned to accomplish this by means of a temporal understanding of the phytoplankton biomass, species composition, size structure and limiting nutrient availability. From these results I asked questions such as: is phytoplankton standing stock controlled from the bottom-up? What is the species succession during the bloom? Does succession vary temporally and how does standing stock translate into organic carbon? How pronounced is interannual variability in the phytoplankton dynamics and how could this affect upper trophic levels?

Few phytoplankton community studies had been conducted in Prince William Sound before or after the oil spill. In Port Valdez and Valdez Arm, a fjord in northeast Prince William Sound used heavily by oil tanker traffic and vulnerable to crude oil pollution, four phytoplankton studies were conducted in the late 1960s and 1970s. Alexander and Nauman (1969), in September 1969, found low cell abundance, low chlorophyll *a* concentration and a phytoplankton community dominated by dinoflagellates, primarily *Ceratium* spp. In Galena Bay off Valdez Arm, AK during 1971-1972, Goering et al. (1973) used chlorophyll *a* analysis and net phytoplankton tows to investigate a spring diatom bloom, dominated by *Biddulphis aurita* and *Chaetoceros debilis*. This bloom began in March and declined by May due to nutrient depletion. Horner et al. (1973) studied Port Valdez from 1971-1972 and reported a spring diatom bloom dominated by *Thalassiosira* spp., *Chaetoceros* spp, and *Skeletonema costatum*, followed by a succession to a lower abundance of small flagellates and dinoflagellates in late summer, fall and winter. A classic spring diatom bloom beginning in late March followed by microflagellate dominance by July was also found by Alexander and Chapman (1980) in Port Valdez from 1976-1978.

Since 1978, studies of phytoplankton species composition in Alaskan waters have been conducted in geographically close regions like the Bering Sea (Goering and Iverson 1978; Goering and Iverson 1982; Kocur 1982), Auke Bay in Southeast Alaska (Ziemann et al. 1990; Ziemann et al. 1991), and Boca de Quadra, Southeast Alaska (VTN Consolidated, Inc. 1980), but not within Prince William Sound.

This study was based in Elrington Passage, a major channel connecting the sound with the Gulf of Alaska, in southwest Prince William Sound. Elrington Passage was one of the heavily oiled regions in 1989 (Galt et al. 1991). At this location I carried out and analyzed a daily series of phytoplankton observations never before conducted in this region. This level of detail is unprecedented for any type of study of Prince William Sound. This study augments the concurrent biological (McRoy and Eslinger 1995; McRoy et al. 1996 and 1997; Eslinger 1997) research, begun in September 1994, targeting the regional distribution of phytoplankton within Prince William Sound.

METHODS

The data sets are a contribution to the SEA project and will be subjected to several analyses in addition to this thesis. I chose to study the phytoplankton bloom through a detailed analysis of the species composition at a location in southwest Prince William Sound in conjunction with supporting physical and chemical oceanographic data obtained during the SEA study. The following methods describe the collection of phytoplankton and chlorophyll *a* samples, and analyses of water samples for species composition, autotrophic biomass, and nutrient concentrations; also included are methods for measuring water transparency, temperature and salinity.

1. Sampling Dates and Study Site

Oceanographic data were collected daily from 17 April to 19 June, 1995 (Julian days 107-170) and from 6 April to 17 June, 1996 (Julian days 97-169) at a station in Prince William Sound, Alaska (Figure 1). Prince William Sound is located on the coast of South-central Alaska and lies adjacent to the Gulf of Alaska in the Pacific Ocean. The station was located in southwest Prince William Sound in Elrington Passage between Bettle Island and Elrington Island (60º 02.4'N, 148º 00.6'W). The sampling station was in the middle of the passage and had a bottom depth of 140 m. During sampling, sea conditions varied from flat calm (glassy) to rough depending on the wind speed and direction.

The circulation of Prince William Sound is complicated and influenced by fresh water input and the Alaska Coastal Current in the Gulf of Alaska (Muench and Schmidt 1975; Niebauer et al. 1994). Prince William Sound is diluted by freshwater input from precipitation and glacial and snow melt, making it a cold-water estuarine region with a

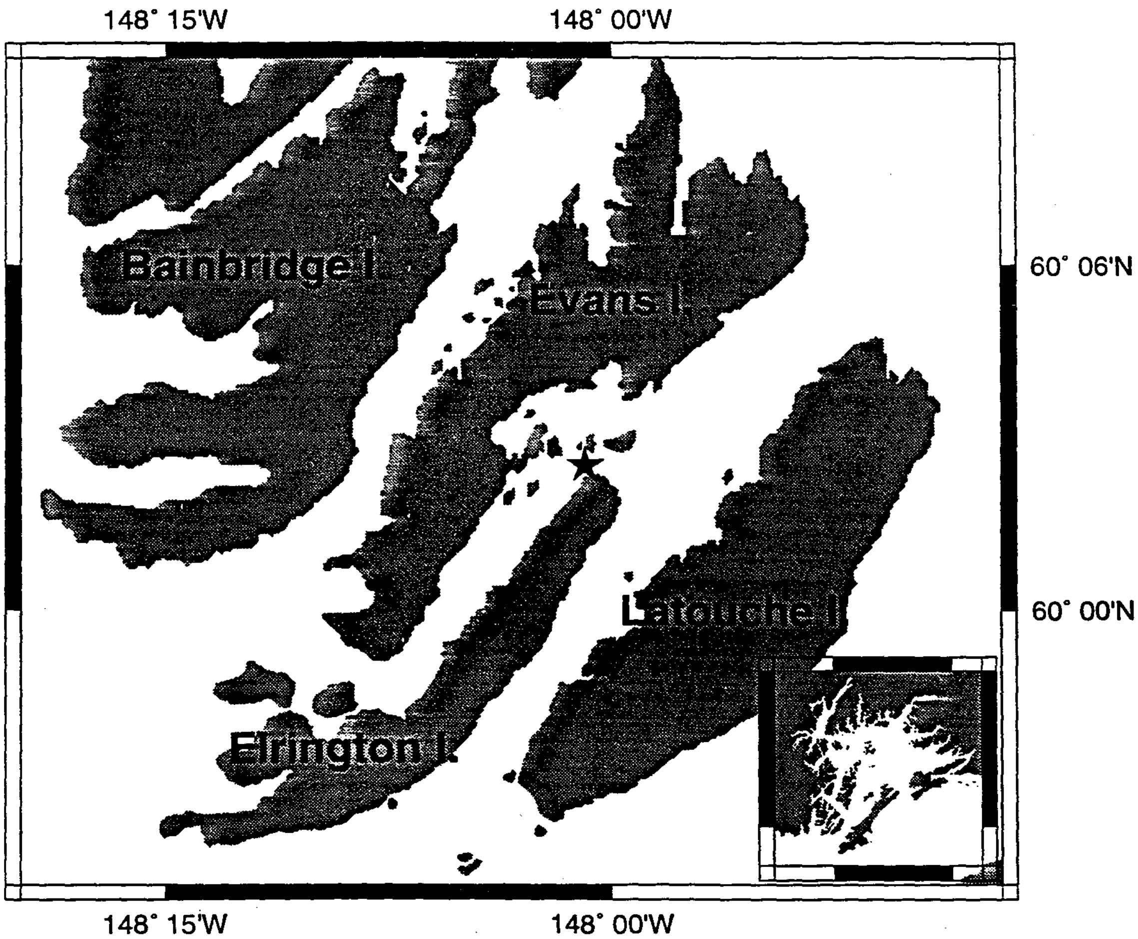

Figure 1. Prince William Sound showing the location of the sampling site (star) between Evans Island and Elrington Island.

fluctuating pattern of circulation (Niebauer et al. 1994). In general, geostrophic flows enter through Hinchinbrook Entrance and exit the sound through Montague Strait in the southwest, or flow back out Hinchinbrook Entrance, depending on fresh water input, winds and tides (Niebauer et al. 1994; Vaughan et al. 1997). An upwelling cyclonic gyre exists in the central sound in summer and fall (Muench and Schmidt 1975; Vaughan et al. 1997). The current flow in southwest Prince William Sound and Elrington Passage, the region of detailed biological studies, varies directionally and seasonally. Currents flow southwest into the Gulf of Alaska in April, northeast into Latouche Passage in May and southwest again into the Gulf of Alaska by October (Niebauer et al. 1994). Prince William Sound is also influenced by strong tidal currents that drive vertical mixing in shallow water (Muench and Schmidt 1975).

2. Sample Collection

Water samples for biological and chemical analyses and CTD (conductivity, temperature and depth) measurements were collected daily in Elrington Passage from April to June from a small skiff. Water samples were processed at the Armin F. Koernig Hatchery (AFK), a pink salmon hatchery operated by Prince William Sound Aquaculture Corporation, in Port San Juan immediately following collection.

2.1. Field Procedures

We collected hydrographic data (temperature, salinity and transparency), biological samples (chlorophyll and phytoplankton) and water samples for nutrient analysis during the hours of 0800-1000 using a 5 L Niskin bottle and SeaCat Sea-Bird Electronics, Inc. CTD (Model 19-03) attached to a hand-operated winch. One CTD cast was lowered to 80 m each sampling day. Data were collected from the downcast and filtered and processed to 1 m averages. Additional bottle casts were deployed to collect water at 0, 5, 10, 25, 50 and 75 m. Approximately 4 L of water from each depth were collected and stored in dark plastic bottles until processing. After water collection, a Secchi disk was lowered to depth of disappearance as an estimate of water transparency.

2.2 Nutrients

Water samples for chemical analysis were processed within one hour of collection. A sample of 100 mL was filtered through Gelman A/E glass fiber filters, stored in acid-washed plastic bottles and frozen. Later at the University of Alaska Fairbanks, samples were analyzed for nitrate+nitrite (N+N), silicate, and phosphate using CFA techniques on an Alpkem 305 auto analyzer within 3-6 months after collection.

2.3 Phytoplankton Community Measurements

2.3.1 Chlorophyll *a*

Water samples for chlorophyll *a* analysis were processed at the AFK laboratory after collection. Chlorophyll *a* was measured by filtering 250-1,000 mL (depending on standing stock) of seawater through Gelman 25 mm glass fiber filters, extracting the chlorophyll in 10 mL of 90 % acetone and measuring the fluorescence of the supernatant after 10 minutes of centrifugation. Fluorescence was measured with a Turner Designs fluorometer, calibrated with spinach before each field season using a Hitachi spectrophotometer (Model 100-40) (Strickland and Parsons 1977; Parsons et al. 1984).

2.3.2 Size fractionation

Water was filtered through three mesh sizes to collect the cells in different size ranges and determine the percentage of chlorophyll *a* contributed by each size fraction. The filter mesh sizes were chosen to roughly determine what proportion of the bloom was composed of picoplankton (0.2-3.0 µm), nanoplankton 2-20 µm (Tomas 1993), microplankton (>20 µm) and chains of cells (>100 µm). Filtration sizes were secondarily based on the availability of the smallest Nitex netting (5 µm).

Size fractionation of phytoplankton was done only on water from the depth of the chlorophyll maximum after determination of chlorophyll *a* content at the 6 depths. Techniques were based on the methods of Ray et al. 1989. After thoroughly mixing 2 L of water, a 500 mL sub-sample was removed and processed for chlorophyll *a* without pre-filtration. The remaining 1500 mL were filtered through 100 μm Nitex netting. A 500 mL portion of this water was immediately removed and set aside for the 100 μm fraction. The remaining liter was filtered through 20 μm Nitex netting and 500 mL set aside for the <20 μm portion. The last 500 mL were filtered through 5 μm Nitex netting and set aside for the <5 μm portion (Ray et al. 1989). Chlorophyll concentrations in four categories (≥100 μm, 100-20 μm, 20-5 μm, and <5 μm) were calculated following fluorescence measurements.

2.3.3 Species identification and enumeration

Phytoplankton identification and enumeration were conducted on samples from the spring bloom and two post-bloom periods at 5 depths (0, 5, 10, 25 and 50 m) for 1995 and 1996 using an inverted microscope technique (Utermohl 1931). Although samples were collected daily, only a subset of these collections were analyzed. based on the chlorophyll *a* time series, to represent the seasonal succession. For 1995, samples were analyzed on Julian days 108 to 119, 131, 133, 135, 162, 164 and 166. In 1996, days 102 to 120 (even days only), as well as 136, 138, 140, 159, 161 and 163, were analyzed. The first series of days covers the primary bloom, from pre-bloom until the chlorophyll biomass distinctly fells. The second series was selected from the time of minimum chlorophyll *a* . The third subset was selected from mid-June, when the chlorophyll biomass increased slightly.

In the field, 50 mL of sea-water were preserved with 1 mL of Lugol's solution and stored in the dark until analysis. In the laboratory at UAF, a subsample of 25-50 mL of water was settled in the dark at room temperature in a settling chamber according to

Utermohl (1931) for a minimum of 24 hours. Water was slowly poured down the side of the cylinder to prevent convection currents. Using a Zeiss Telaval 31 Inverted Microscope, live cells (at the time of preservation) $\geq$ 15 µm were counted and identified within a rectangular field using 200 x magnification on two transacts (one horizontal, one vertical) across the diameter of the settling chamber. All cells within a chain were counted separately. If at least 300 cells were not enumerated, additional transacts were counted. In addition, cells < 15 µm were counted at 400 x magnification across the same horizontal transact until a minimum of 300 cells were totaled. Cells $\leq$ 2 µm, the size limit for accurate identification using a light microscope, were not identified or counted. These enumeration techniques are based on the compilation of several published phytoplankton sampling approaches (Utermohl 1931; Lund et al. 1958; Venrick 1978; Sandgren and Robinson 1984). This technique enabled me to achieve 95 ± 10 % confidence for samples in April and June (Lund et al. 1958). In May, when cell abundance was extremely low, additional transacts were enumerated until at least 100 cells on 200 x magnification were enumerated. For these samples the error increased to ± 20 % (Lund et al. 1958). All fields viewed were counted and recorded for abundance calculations. Diatoms were identified to the lowest possible taxon (usually genus) while nano-plankton (2-20 µm) were identified to genus or class. Phytoplankton identification was based on comparison with several taxonomic guides (Gemeinhardt 1930; Schiller 1933; Cupp 1943; Hustedt 1959; Brunel 1962; Vinyard 1979; Yamaji 1986; Tomas 1993; Tomas 1996)

2.3.4 Carbon biomass

Phytoplankton with the greatest numerical abundance were measured for biomass determination using cell dimension techniques (Kovala and Larrance 1966). Phytoplankton that could only be identified to genus were placed in size categories. For each dominant species or size category, length and width were measured to the nearest 1 μm. Average dimensions were calculated from the measurements of 20 cells and used for volume calculations. Cell depth measurements (Table 3) were estimated from equations specific for each cell type (F. Reid, personnel communication). Cell volume was calculated by using the geometric shapes and volume equations from Kovala and Larrance (1966). Cell carbon was estimated from cell volume calculations using separate equations for diatoms and other non-diatom phytoplankton (Strathmann 1967).

RESULTS

The following results are a compilation and analysis of data sets that describe the phytoplankton spring bloom on a daily basis for two years from one location in southwest Prince William Sound (Table 1). Additional information on the physical and chemical oceanography that influence the biology are also presented. In 1995, Julian days 148 and 160 were not sampled due to rough weather conditions. In 1996, no days were missed but on day 99 at 25 m, the chlorophyll *a* sample was lost. In 1996, not enough water was collected for size fractionation analysis on days 97, 98, 123, 126, and 137.

The spring chlorophyll time series in both years exhibits three distinct events; a bloom of high biomass, followed by a period of very low biomass, and then a period of increase. This pattern allowed the data to be separated into three periods to study phytoplankton succession: (1) spring bloom, the period of highest chlorophyll, (2) post-bloom, the period of lowest chlorophyll following the spring bloom, and (3) the recovery, when chlorophyll biomass increased again from the lowest levels.

1. Hydrography

The waters were cold and isothermal throughout the water column during the bloom in 1995 and 1996 (Figure 2). In 1995, from April through early May temperatures remained between 4-5 °C. Surface warming was not apparent until day 121.

Stratification was weak and occurred earlier in 1995, around day 115, due to freshening at the surface from precipitation (Figure 3). In 1995, the salinity averaged 31.2 at 5 m and density profiles mirrored salinity. Density remained between 24.2-25.2 sigma-t. In 1996, temperatures were the same as 1995 and mixing extended down to 80 m prior to day 110. Fresh water input was lower in 1996 (Figure 3) and salinity averaged 31.6 at

Table 1. Summary of data collection, sampling days and periods of the phytoplankton cycle from spring 1995 and 1996 in Elrington Passage, Prince William Sound.

Data Collection	1995	1996
Sampling Period (Julian days)	107-170	97-169
Spring Bloom Period (Julian days)	107-123	97-126
Post Bloom Period (Julian days)	124-145	127-145
Recovery Period (Julian days)	146-170	146-169
Sampling Depths (m)	0, 5, 10, 25, 50, 75	0, 5, 10, 25, 50, 75
Total Sampling Days	64	73
CTD Casts	63	73
Secchi Depth Measurements	63	73
Chlorophyll *a* Measurements	372	437
Size fractionation Measurements	0	68
N+N Measurements	372	438
Silicate Measurements	369	438
Phosphate Measurements	372	438
Species Composition/Abundance Measurements	73	80
Autotrophic Biomass Measurements	68	80

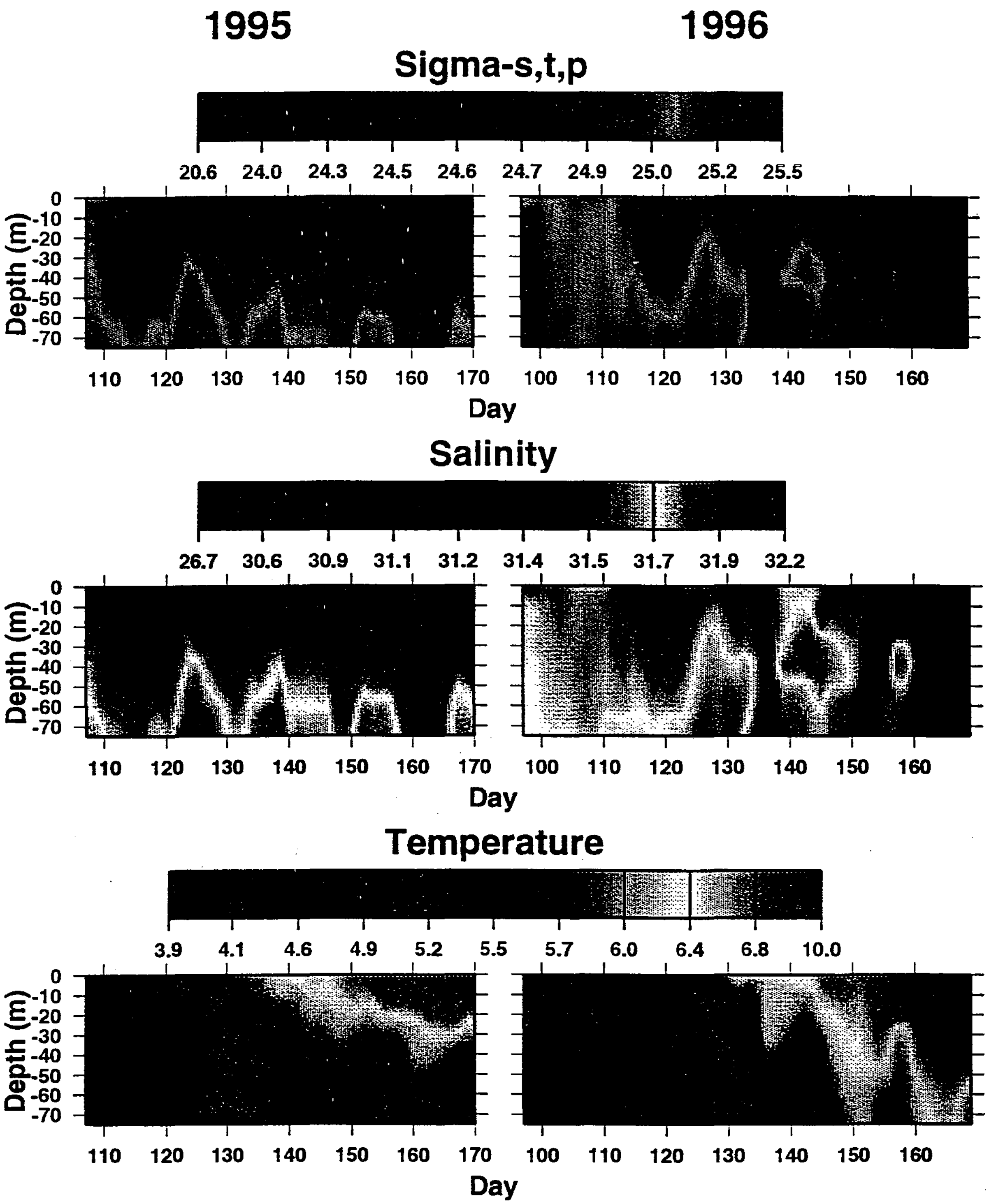

Figure 2. Vertical profiles of temperature (°C), salinity and sigma-t for the upper 75 m of the water column in spring 1995 and 1996.

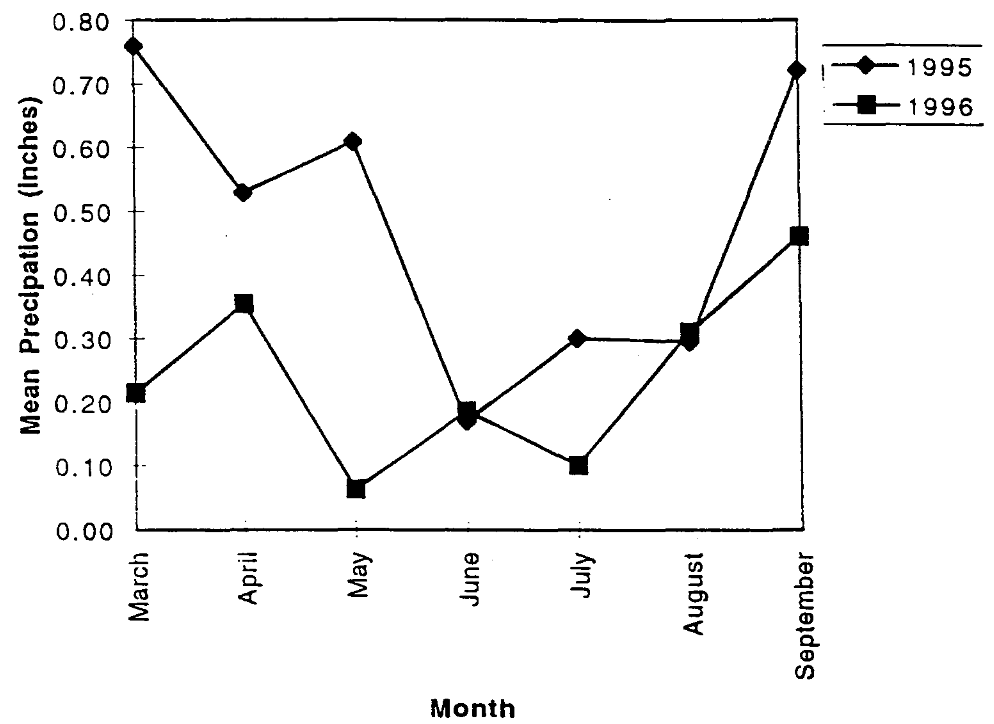

Figure 3. Monthly mean precipitation from rain and melted snow collected at AFK Hatchery from March-September 1995 and 1996 (unpublished data).

5 m. After day 111, stratification was weak in April and the density of the water remained between 24.8-25.2.

During the post-bloom, stronger stratification was achieved as solar heating and fresh water runoff increased in both years (Figure 2). In 1995, the surface waters warmed to 6.8°C by day 143. A strong pycnocline was formed in the upper water column due to heavy fresh water input. Surface salinity fell to 29 after day 130. In 1996, intense solar input increased water temperatures to 7 °C by day 144. Salinity ranged from 31.2-31.8 in the upper 75 m during the post-bloom. Salinity and density remained higher in 1996 than 1995, probably due to reduced precipitation (Figure 3) and increased evaporation. In 1996, deep mixing to 75 m (days 135-139) occurred during this period. A salty intrusion (31.7-31.9 psu) was detected on day 140 between 20 and 60 m and lasted for several days.

Following day 145, surface waters gained their greatest stability and temperature in both years. In 1995, surface temperature reached a maximum of 9°C as the surface salinity dropped to 26.7 psu. Strong stratification and a pycnocline formation caused by both heating and fresh water remained throughout the month of June. In 1996, surface temperature rose to 10°C by day 163 and warm waters penetrated to 75 m. Freshening occurred in the surface waters after day 150, probably due to snow and glacial melt, but the minimum salinity in June reached only 30. Solar radiation warmed the surface waters but only had a small effect on stability. In June the water column was less stable in 1996 than 1995 and stratification in the upper 25 m was interspersed with deep mixing events on days 153 and 162. Another high salinity intrusion (31.7-31.9) at mid depths was seen on day 158 and lasted two days.

Throughout the year increases in salinity and density every 15 days corresponded to the spring tides. This was especially pronounced in the 1995 salinity and density series (Figure 2). In both 1995 and 1996, the spring tides ranged between -2 and 13 ft. The maximum spring tides occurred around days 120, 135, 150 and 165. These days had between 31.7-31.9 salinity and 25-25.2 sigma-t below 30 m. In 1996, tidal influences were less apparent in the salinity and density data but slight increases in both were observed. Maximum spring tides occurred around days 110, 125, 140 and 155. Slight increases in density and salinity corresponded to spring tides.

2. Nutrient Time Series

In 1995 and 1996, nutrient concentrations were high preceding the spring bloom then decreased in surface waters as production increased (Figure 4). In 1995, concentrations of all nutrients were highest around day 107 and a nutricline was apparent throughout the bloom. In the upper 75 m, concentrations of N+N, silicate and phosphate ranged from 10-15, 15-25, and 1-2 μM, respectively. As the bloom progressed, nutrients were depleted in the surface waters but remained high below 50 m. By day 120 concentrations of N+N, silicate and phosphate in the upper 10 m had dropped to levels of 1.5-2.5, 3-4.5 and 0.3-0.8 μM, respectively. Following day 120, all nutrient concentrations remained low but detectable in the surface waters. In 1996, a similar pattern emerged, but concentrations of all nutrients were lower throughout the bloom, especially at depth. On day 97, N+N, silicate and phosphate in the upper 75 m ranged from 10-11.5, 16-17 and 1.2-1.5 μM, respectively. As the month of April passed, all the nutrient concentrations were reduced at the surface especially around days 104 and 117. No nutrients were completely assimilated by plankton but ratios of N+N:silicate were very low. Nutrients were replenished by mixing events around days 109-111.

During the post-bloom of both years nutrients were replenished from depth. Low nutrient concentrations did not exist below 25 m. In 1995, all nutrient concentrations

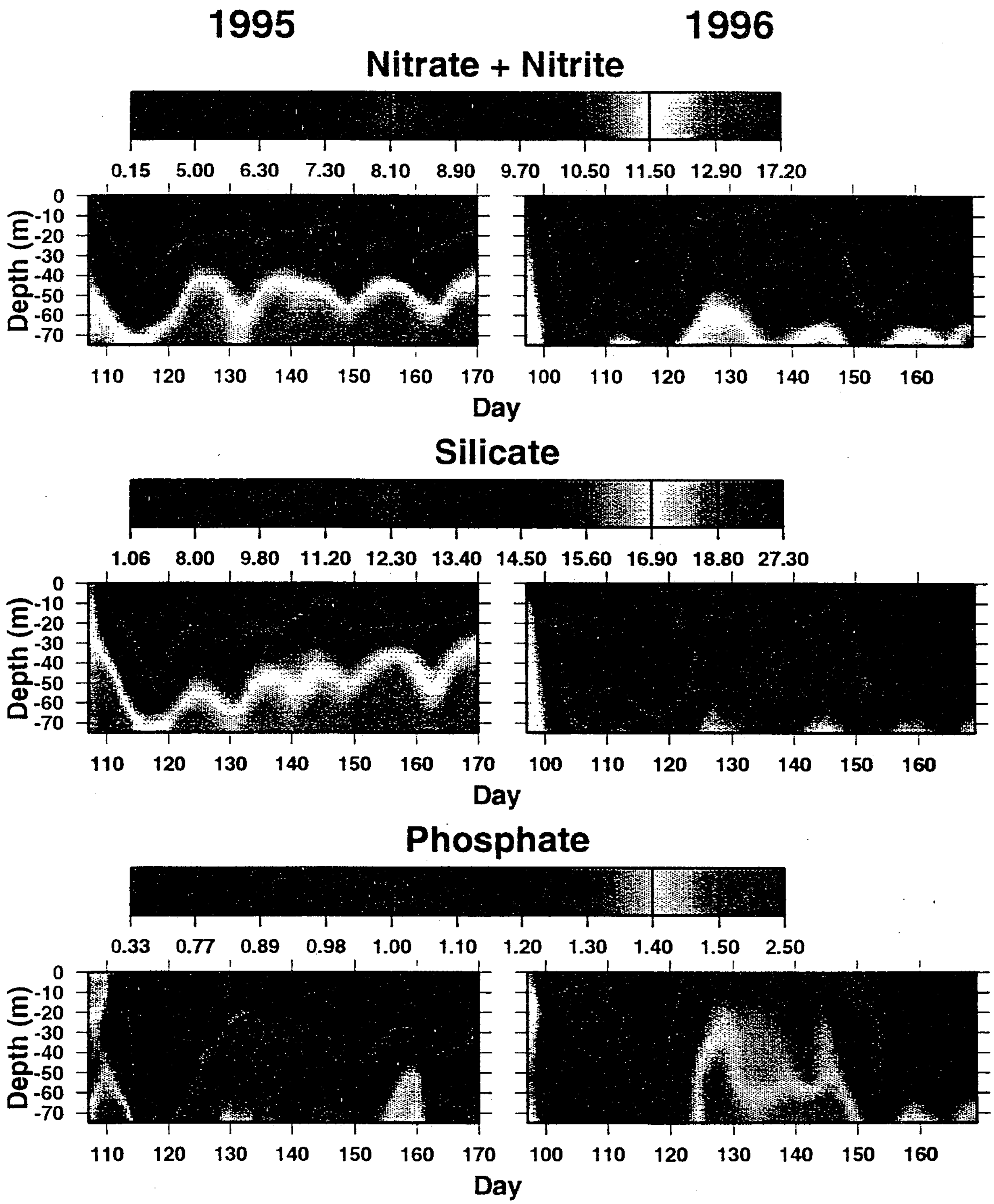

Figure 4. Vertical profiles of N+N (μM), silicate (μM), and phosphate (μM) concentrations for the upper 75 m of the water column in 1995 and 1996.

were high. Only around days 138-143 did all the nutrients show a slight decline in the upper 10 m. Nutrients remained highest below 50 m, with maximum N+N, silicate and phosphate concentrations of 16, 25 and 2 μM, respectively. In 1996, all nutrients were also replenished in the upper layers. Only two times in the post-bloom, around days 131 and 141 had decreased concentrations. Maximum values, at depth and at the surface, were lower in 1996. Below 50 m maximum N+N, silicate and phosphate concentrations reached 14, 17 and 2.4 μM, respectively. Higher concentrations of phosphate existed below 10 m in 1996.

During the recovery period, nutrients in the surface waters decreased again, but concentrations below 25 m remained high. In 1995, all nutrient concentrations remained low in surface waters and high below 25 m. The highest N+N concentrations during the recovery appeared in June at 75 m. In 1996, all surface nutrients were reduced in the upper 25 m throughout the recovery period. Concentrations were highest below 25 m but considerably lower than in 1995.

Similar to the salinity and density, the nutrients increased at depth in response to mixing from spring tides. This was most apparent in the silicate and N+N data (Figure 4). In 1995, nutrients increased at depth after days 120, 135, 150 and 165, when spring tides occurred. In 1996, silicate and N+N increased below 50 m after days 110, 125, 140 and 155, the maxima of the spring tidal cycle.

3. Phytoplankton Community

3.1 Chlorophyll Time Series

During the spring bloom chlorophyll extended below 50 m, and the highest concentrations of chlorophyll were present at this time during both 1995 and 1996 (Figure 5). In 1995, the chlorophyll levels were between 2 and 19 mg/m^3 in the upper 25 m and between 1 and 13 mg/m^3 below 25 m. The peak concentration occurred as a short

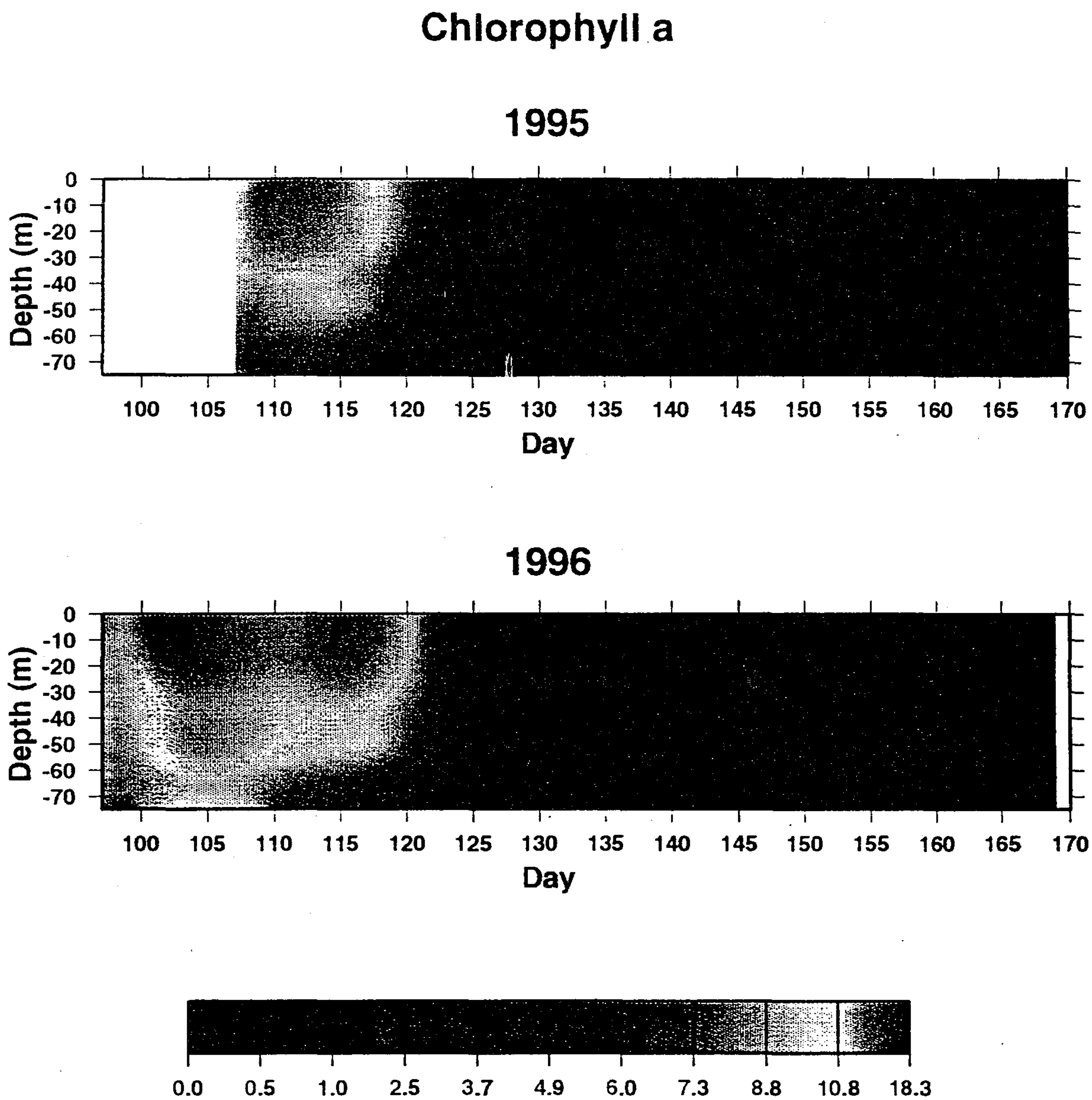

Figure 5. Vertical profiles of chlorophyll *a* (mg/m^3) for the upper 75 m of the water column in spring 1995 and 1996.

pulse between days 111-114 in the upper 25 m. In 1996 chlorophyll levels were higher, variations with depth were less, and the length of the bloom increased. High levels of chlorophyll were present between days 97 and 121. In the upper 25 m, chlorophyll ranged from 2-20 mg/m^3; at 50 m and below the range was 0.5-16 mg/m^3. There were two distinct periods of high concentration between days 100 and 104 and 114 and 116; both periods had high levels of chlorophyll below 25 m.

During the post-bloom, chlorophyll concentration was uniformly low throughout the water column in both years. In 1995, chlorophyll ranged from 0.15-4 mg/m^3 in the water column. Low concentrations (< 4 mg/m^3) occurred in the upper 10 m on days 125-127 and 138; chlorophyll levels below 50 m were ≤ 2 mg/m^3. In 1996, chlorophyll ranged from 0.2-3.2 mg/m^3. Highest relative concentrations were in the upper 25 m.

Following day 145 in both years, chlorophyll increased above 25 m (Figure 5). In 1995, chlorophyll recovered to 7 mg/m^3 as stratification strengthened. Concentrations between 0.5-7 mg/m^3 remained until day 170 in the upper 50 m. Small transitory increases in chlorophyll occurred in 1996 above 25 m. Chlorophyll increased to highs around 5 mg/m^3 on days 153-154, 160-163, 165 and 169. Levels remained low below 25 m except on day 154 where 6.3 mg/m^3 was measured at 50 m.

Depth-integrated chlorophyll was highest during the spring bloom in 1995 and 1996 (Figure 6A). In 1995, the spring bloom had already begun on day 107 (17 Apr), reached its highest integrated chlorophyll concentrations on day 110 and decreased to low levels by day 123. Chlorophyll ranged from 157-780 mg/m^2 and averaged 541 mg/m^2. In 1996, the bloom appeared between days 97-126, with two peaks in biomass occurring at different times throughout the bloom. On day 103 (12 Apr), integrated chlorophyll reached 804 mg/m^2 and on day 116 (25 Apr) it peaked at 863 mg/m^2. Chlorophyll ranged from 72-863 mg/m^2 and averaged 545 mg/m^2. The concentrations are similar to those in 1995.

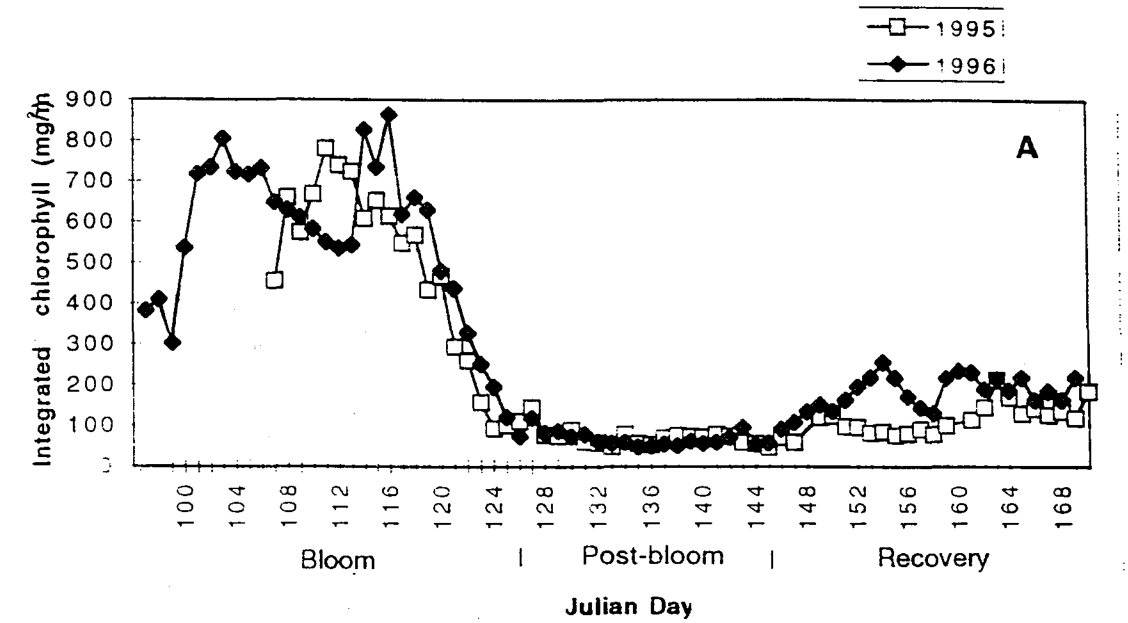

Figure 6. Chlorophyll *a* integrated over the upper 50 m of the water column (A) and Secchi depth (m) (B) from spring 1995 and 1996.

During the post-bloom period in both years, integrated chlorophyll levels were low (Figure 6A). In 1995, concentrations ranged from 47-144 mg/m^2 and the mean was 75 mg/m^2. In 1996, concentrations were approximately the same as in the previous year, ranging between 46-118 mg/m^2 with a mean concentration of 66 mg/m^2. Daily chlorophyll levels fluctuated only slightly during this period.

A slight increase in the integrated chlorophyll concentration occurred after day 145 in both years (Figure 6A). Chlorophyll concentrations increased to a maximum of 213 mg/m^2 by day 163 in 1995. Levels remained higher than during the post-bloom period until the last day of sample collection. In 1996, chlorophyll concentrations increased to higher levels. Chlorophyll stayed higher than post-bloom concentrations, ranging between 91-254 mg/m^2. Concentrations were at least 30 % higher in 1996 than 1995 during the first 10 days of June.

Secchi depths showed reduced water transparency in April and June when chlorophyll was high and increased transparency in May when chlorophyll was low (Figure 6B). During the spring bloom Secchi depths ranged from 4-6.5 m in 1995 and 3-9 m in 1996. During the post-bloom depths ranged from 6.5-11.5 m in 1995 and from 8.5-13 m in 1996. During the recovery period Secchi depths increased slightly both years ranging from 5-8 m in 1995 and 6.5-9 m in 1996. The depths in 1995 were slightly greater during periods of higher chlorophyll. In 1996 during the post-bloom the depths were greater for the same quantity of chlorophyll. This probably was a result of measurement error. The depth of disappearance of the Secchi depth is difficult to determine under rough weather conditions. Overcast skies, heavy rain and rough waters made visibility poor and measurements less accurate in 1995. In 1996, calm waters, clear skies and greater light intensity enabled the disk to be seen at deeper depths.

3.2 Size Structure

The phytoplankton community was partitioned into size fractions in 1996 to assess the biomass contributed by picoplankton, nanoplankton and microplankton (Figures 7A and 7B). In this year, the maximum chlorophyll *a* content over the study period ranged from 1.1-19.4 mg/m^3. The sample depth for size fractionation was chosen from the highest daily chlorophyll value, and ranged from 0-75 m with a median of 5 m for the study period.

During the spring bloom the phytoplankton community was dominated by microplankton (cells >20 μm). The mean chlorophyll concentrations for each size fraction were 3.9 mg/m^3 for microplankton $\geq$100 μm, 7.0 mg/m^3 for microplankton <100 μm and 1.5 mg/m^3 for nanoplankton (5-20 μm). Over the bloom, at least 85 % of the chlorophyll was contributed by cells greater than 5 μm, with the largest portion (80 %) from microplankton.

During the post-bloom the lowest levels of chlorophyll occurred and picoplankton dominated the community. The total chlorophyll biomass ranged from 1.1-6.1 mg/m^3. In the post-bloom, a shift in the community structure from microplankton and nanoplankton to picoplankton occurred. Up to day 138, microplankton and nanoplankton accounted for greater than 60 % of the chlorophyll but picoplankton accounted for 20-100 % of the total chlorophyll during the post-bloom. From days 138 to 145, greater than 60 % of the chlorophyll was contributed by picoplankton.

As the season progressed the phytoplankton community structure shifted from picoplankton back to microplankton with increased chlorophyll *a* (Figure 7). In this recovery period, chlorophyll concentrations were about 30 % of previous bloom levels. Nanoplankton consisted of 0-31 % of the chlorophyll and picoplankton dominated with greater than 50 % until day 154. Following day 154, microplankton increased and

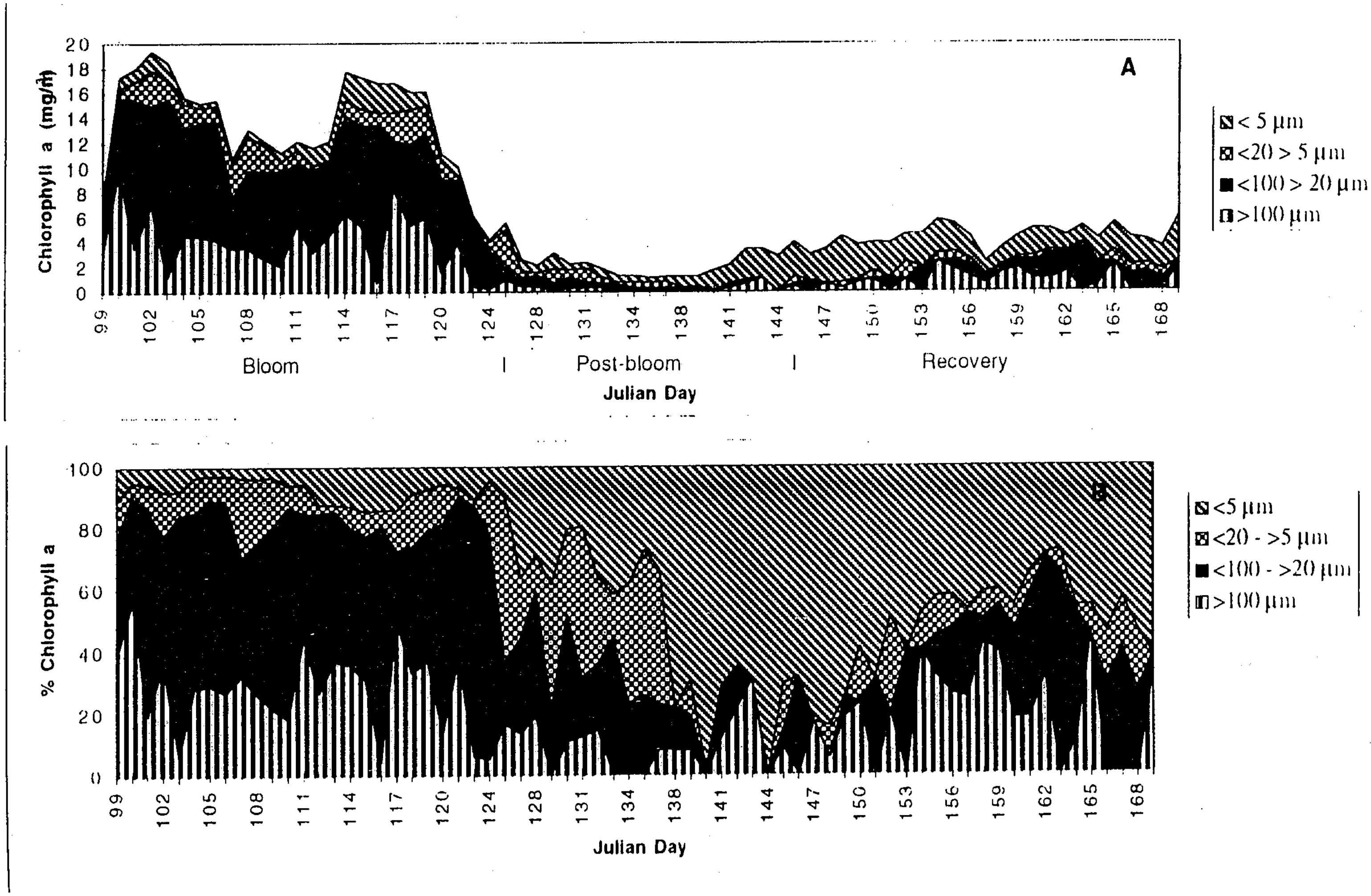

Figure 7. Chlorophyll *a* time series divided into size fractions (<5 µm, >5<20 µm, >20<100 µm and >100 µm) from the chlorophyll maximum during 1996; chlorophyll *a* by size fraction (A) and % of chlorophyll contributed by each size fraction (B).

regained over 50 % of the chlorophyll. Large algae >100 µm reappeared and contributed as much as 45 % of the chlorophyll by day 165.

A delay occurred in the succession to picoplankton after chlorophyll levels declined in early May (Figure 7). The chlorophyll concentrations decreased to 6.2 mg/m^3 on day 122 and fell to a low of 1.1 mg/m^3 by day 135, but the shift to picoplankton lagged the decline by approximately 12 days. Plankton ≥100 µm disappeared around day 133 while microplankton < 100 µm comprised at least 20 % of the biomass until day 136.

3.3 Species Composition

3.3.1 Species descriptions

The phytoplankton community in both years was composed of a few species of chain forming diatoms and single-celled flagellates (Table 2). A detailed list of phytoplankton and their abundance per day and depth sampled for 1995 and 1996 is given in Appendices 1 and 2. Due to orientation on the settling plate, weak silicification, poor preservation, lack of distinguishing features and/or the limitations of inverted light microscopy, many of the cells could only be identified to genus. The flagellates, single celled flagellated eukaryotic nano- and picoplankton, were from two algal divisions, Chromophyta and Chlorophyta. The most abundant were spherical cells <10 µm that closely resembled *Phaeocystis* spp., but no colonies were seen. These cells were identified only as flagellates and placed into size categories because verification was not possible without higher magnification. A few flagellates from the class Dinophyceae, including *Ceratium* spp., were encountered but their abundance was very low in comparison with other phytoplankton.

The major constituents of the diatom community in 1995 and 1996 were *Skeletonema costatum*, *Thalassiosira* spp., *Chaetoceros* spp., *Pseudo-nitzschia* spp., *Leptocylindus* spp. and *Rhizosolenia fragilissima*. *Skeletonema costatum* is a small diatom that is united in chains by external silica structures. The chains vary in length

Table 2. Species list of diatom and flagellate taxa and their size ranges in the upper 50 m from spring 1995 and 1996

Diatoms	Size Range (LxW) µm	Flagellates	Size Range (LxW) µm
Asterionella glacialis	10x5-20x5	*Ceratium furca*	80x75
Biddulphia sp.	15x15	*Ceratium* spp.	20x12-90x90
Chaetoceros spp.	2.5x2.5-40x30	*Dinophysis* spp.	50x45
Chaetoceros deciprens	25x15-25x20	*Distephanus speculum*	20x20-25x25
Cocconeis sp.	40x20	*Ebria tripartita*	15x15-30x30
Coscinodiscus sp.	135-190	*Oxytoxum* spp.	20x10-40x15
Eucampia spp.	30x25-55x25	*Peridinium* spp.	20x15-65x50
Fragilariopsis sp.	10x2-15x2.5		
Grammatophora sp.	40x2.5-35x20	Unidentified flagellate	5-17.5
Leptocylindrus danicus	20x10-85x10	Unidentified silicoflagellate	no data
Leptocylindrus minimus	20x2.5-35x2	Unidentified dinoflagellate	15x10-60x20
Leptocylindrus spp.	35x5-40x7		
Licmophora glacialis			
Navicula spp.	20x5-80x5		
Pseudo-nitzschia spp.	30x2-65x2		
Rhizosolenia fragilissima	15x5-35x5		
Rhizosolenia stolterforthii	45x8-60x10		
Rhizosolenia spp.	25x14-500x15		
Skeletonema costatum	7.5x5-17.5x5		
Stephanopyxis nipponica	30x20-60x20		
Thalassiosira spp.	10x7-55x15		
Thalassionema nitzschioides	25x5-45x5		
Unidentified centric diatom	10x15-45x35		
Unidentified pennate diatom	20x5-45x7		
Unidentified diatom	15x10-130x15		

from a few cells to more than 10. *Thalassiosira* spp. are larger centric diatoms with a width of 10 μm to 55 μm. Like *Skeletonema*, they also form long chains connected by organic threads (Tomas 1996). Since this species frequently appears in girdle view and is difficult to identify in this orientation, cells were placed in three size categories (<25, 25-44, ≥45) for identification purposes. *Chaetoceros* spp. are diverse centric chain-forming diatoms varying in length from 2.5 μm to 40 μm and often having long, coarse setae. Due to their great diversity only one species, *C. decipiens*, could be identified to species level with high precision. All others were placed into size categories. *Pseudo-nitzschia* spp. are narrow elongate pennate diatoms that are multi-celled chains or solitary. Their length is as great as 30 times their width (2 μm) and they have the smallest cell volume of any phytoplankton in this study. *Leptocylindrus minimus* and *Leptocylindrus danicus* are cylindrical chain forming diatoms that appear like adjacent rectangles in girdle view. The two species were differentiated based on diameter and appearance. *L. danicus* is larger, averaging 11.5 μm in width, often appearing singly or in chains of two or three cells. *L. minimus* is smaller, having an average width of 2.5 μm, and more cells per chain. *Rhizosolenia fragilissima*, also known as *Dactyliosolen fragilissimus* (Tomas 1996), is a cylindrical centric diatom that averaged 22 x 5 μm (l x w) and formed chains by uniting the valve surfaces of two cells. They often appeared in chains of only a few cells.

3.3.2 Distribution and abundance

3.3.2.1 Total diatoms and flagellates

In both 1995 and 1996 during the spring bloom diatoms and flagellates were present at all depths (Figures 8 and 9). Cell numbers remained high throughout the bloom and started to decline by the end of the bloom at all depths. The highest

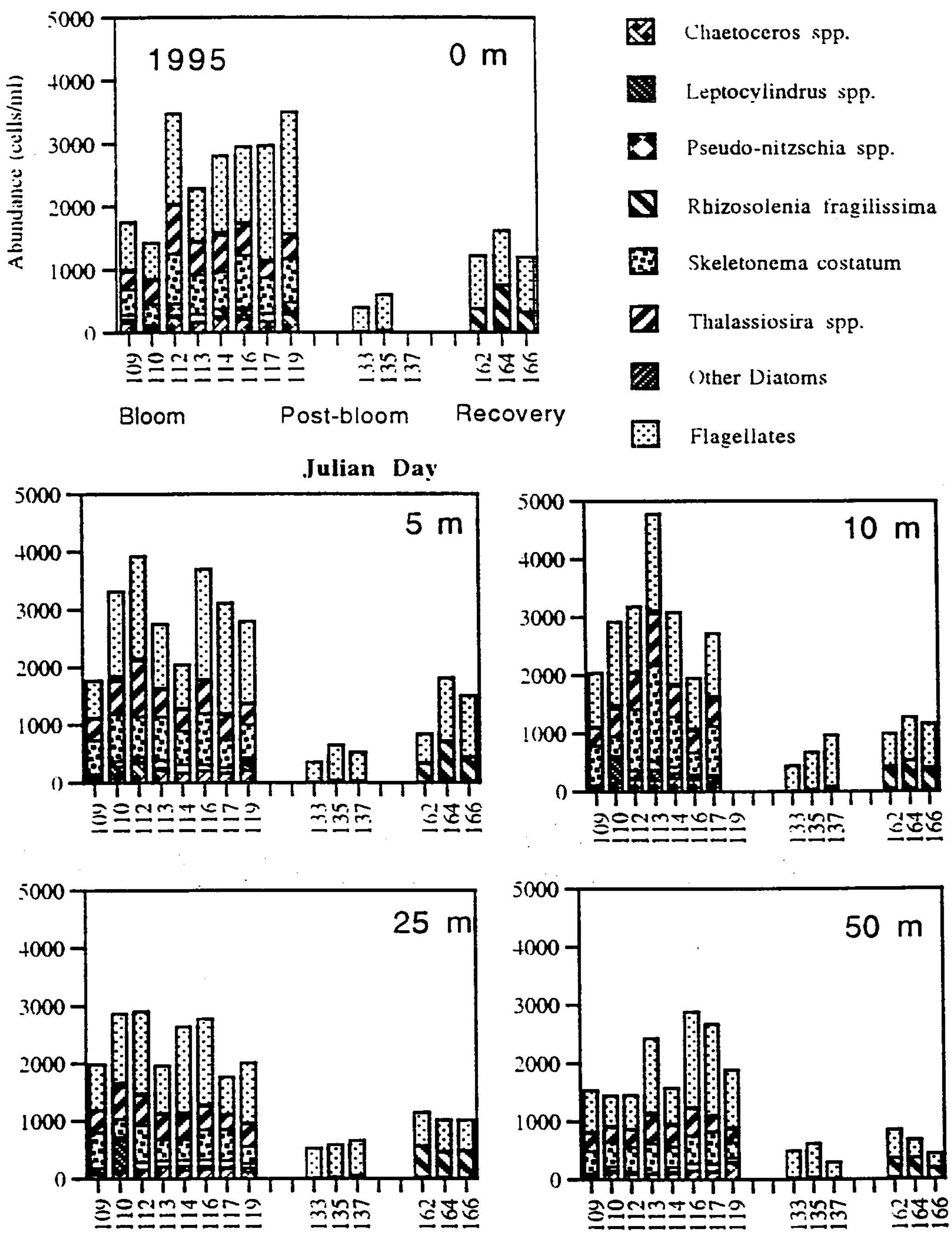

Figure 8. Abundance of major diatoms and flagellates from five depths in the upper 50 m from spring 1995.

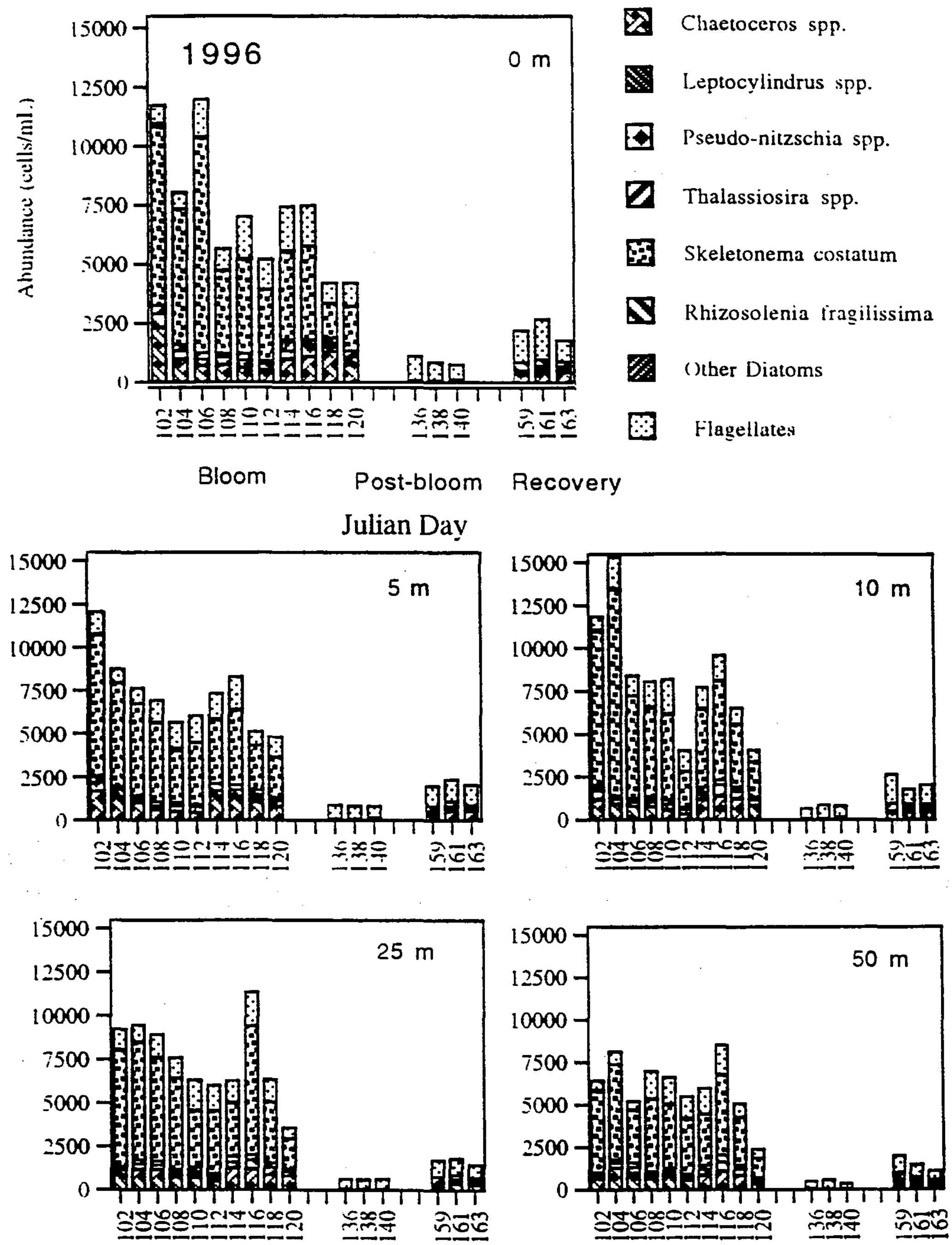

Figure 9. Abundance of major diatoms and flagellates from five depths in the upper 50 m from spring 1996.

abundance of cells was within the upper 10 m and the lowest abundance was at 50 m. In 1995, diatom abundance ranged from 813-3,110 cells/mL within the top 50 m. Flagellates appeared in high abundance and ranged from 525 cells/mL at 50 m to 1,900 cells/mL at the surface. Flagellates were the most numerous phytoplankton constituting as much as 61 % of the total abundance, and a mean of 45 % of the total for all depths. In 1996, diatom abundance was approximately three times as great as 1995. Diatom abundance ranged from 1,872-13,500 cells/mL in the upper 50 m. However, flagellate abundance remained about the same in 1996 as in 1995. Flagellates peaked at 2,021 cells/mL on day 110 at 10 m. During the bloom their lowest abundance of 481 cells/mL occurred at 50 m on day 106. At this time, they accounted for $\leq$ 25 % of the total phytoplankton abundance. In both years, dinoflagellates (Dinophyceae) and silicoflagellates, mainly *Distephanus speculum*, were less than 1 % of total cell abundance.

During the post-bloom and recovery periods flagellates were more abundant than diatoms at all depths and abundance was low (Figures 8 and 9). In 1995, flagellates composed greater than 90 % of the phytoplankton abundance and ranged from 283-880 cells/mL throughout the upper 50 m during periods of low chlorophyll. Abundance increased slightly (250-1,088 cells/mL) during the recovery period and flagellates composed about 60 % of the community. In 1996, more than 80 % of the post-bloom phytoplankton was composed of flagellates. At this time the lowest flagellate abundance at 50 m was 300 cells/mL and the highest abundance (1,014 cells/mL) was at the surface. Day to day variations at all depths were slight. In June of 1996, abundance increased but flagellates composed an average of 53 % of the phytoplankton over 50 m. Flagellate abundance over the upper 50 m ranged from 494-1,689 cells/mL.

3.3.2.2 Diatom species and genera

In both years, centric diatoms were the most common phytoplankton during the bloom at all depths, but interannual differences in abundance were large. In 1995 and 1996, *Chaetoceros* spp., *Skeletonema costatum*, *Thalassiosira* spp., and *Leptocylindrus* spp. were most abundant throughout the upper 50 m (Figures 8 and 9). Species composition remained the same with depth but diatom abundance decreased with depth below 10 m. In 1995, total diatom abundance ranged from a low of 813 cells/mL at 50 m on day 109 to a maximum of 3,110 cells/mL at 10 m on day 113. *Skeletonema costatum* and *Thalassiosira* spp. averaged over 37 % and 30 %, respectively, of the total diatom abundance during the bloom at all depths (Figure 10). *Chaetoceros* spp. was always present at all depths and constituted between 5-31 % of the total diatoms. *Leptocylindrus* spp. appeared inconsistently, composing only a small portion of the bloom. In 1996, the same species and genera reappeared but the smaller diatoms tripled in abundance while the larger species declined (Figure 9). *Skeletonema costatum* represented greater than 72 % of the total diatom abundance throughout the water column ranging from 1,150-12,072 cells/mL (Figure 11). *Chaetoceros* spp. increased at all depths and reached a maximum of 2,311 cells/mL at the surface on day 102. In this year the abundance of *Thalassiosira* spp. and *Leptocylindrus* spp. was lower than in 1995. These genera composed < 9 % and < 2 % , respectively, of the diatom population. For both years, other diatoms, in order of abundance, that were $\leq$5 % of the total diatom numbers were *Fragilariopsis* spp. , *Asterionella glacialis*, *Navicula* spp., *Eucampia* spp., *Stephanopyxis nipponica* and *Rhizosolenia stolterforthii* (Appendices 1 and 2).

During the post-bloom, diatom abundance was lower in both 1995 and 1996 (Figures 8 and 9). In 1995, less than 100 cells/mL existed at all depths in mid May. Only small variations in cell abundance occurred with depth. The small diatoms, *Pseudo* -

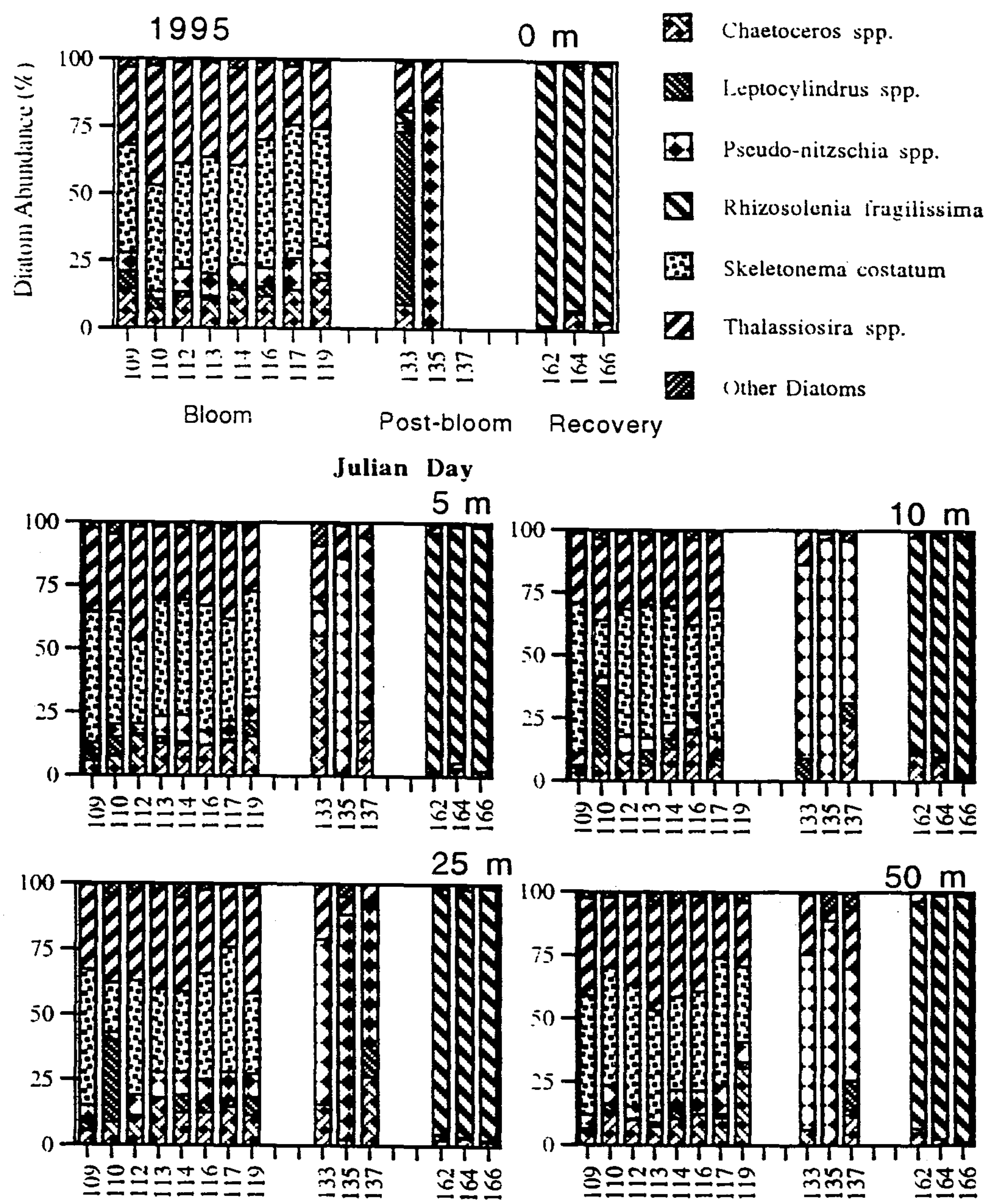

Figure 10. Diatom species composition (% total diatoms) from five depths in the upper 50 m from spring 1995.

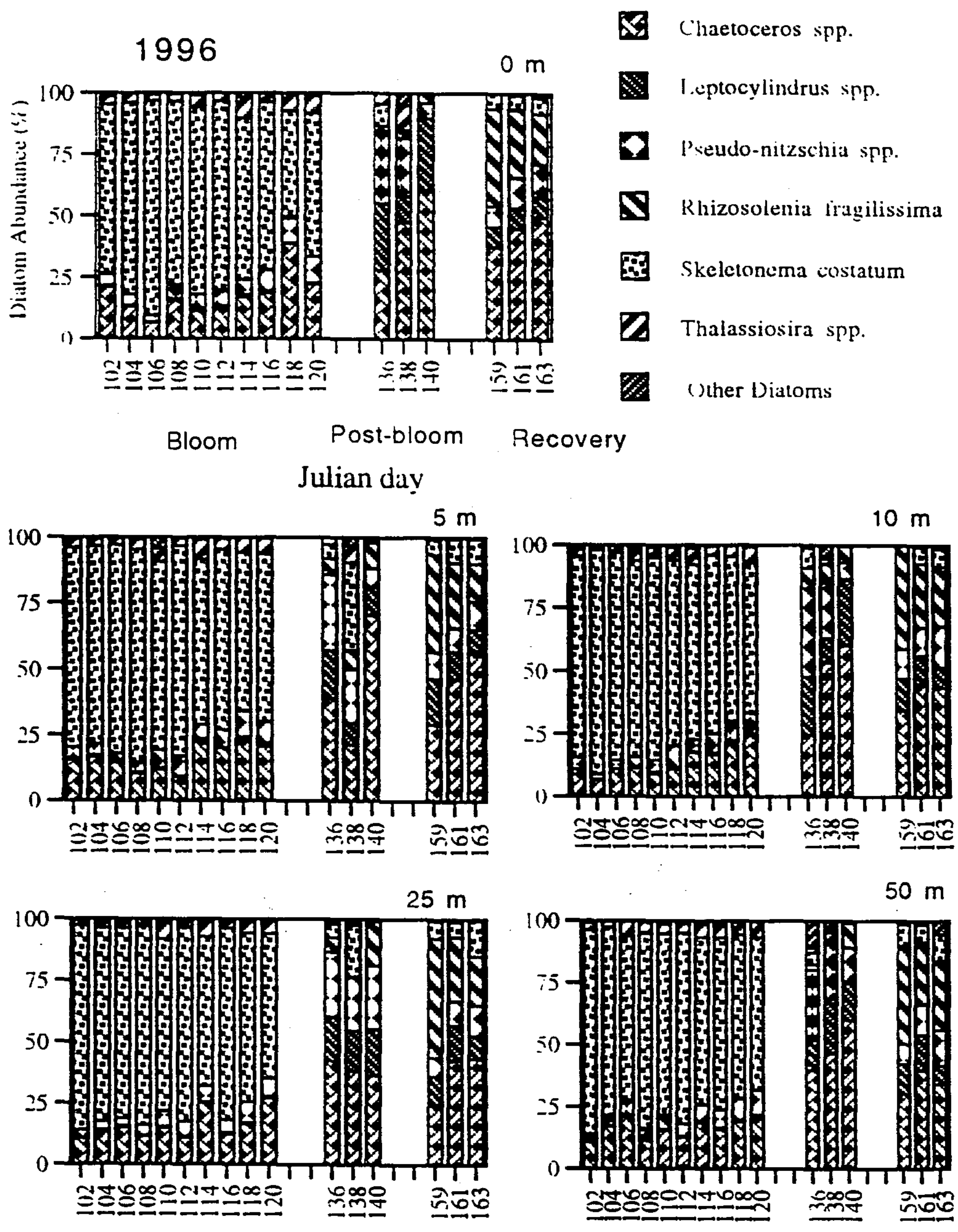

Figure 11. Diatom species composition (% total diatoms) from five depths in the upper 50 m from spring 1996.

nitzschia spp. and *Chaetoceros* spp., dominated the community and the proportion of *Thalassiosira* spp. decreased (Figure 10). In the 1996 post-bloom period, less than 150 cells/mL were observed and lowest abundance was at 50 m. *Chaetoceros* spp. numerically dominated at all depths. *Pseudo-nitzschia* spp. and *Leptocylindrus* spp., present during the bloom in low abundance, were still present accounting for as much as 35 % of the diatom abundance (Figure 11). *Skeletonema costatum* abundance declined and was zero at several depths around day 138. *Rhizosolenia fragilissima*, not present during the bloom, first appeared in low abundance at this time in 1996 but not 1995.

In June, the diatom abundance recovered slightly and a shift in species composition occurred (Figures 8 and 9). In 1995, total diatom abundance increased to about 30 % of the bloom abundance. This phytoplankton community was composed almost entirely of *Rhizosolenia fragilissima* at all depths (Figure 10). *Chaetoceros* spp. was the second most abundant diatom with <10 % of the abundance. *Skeletonema costatum* was absent at this time. In June of 1996, diatoms resurged during the post-bloom period with abundances ranging from 560 cells/mL at 50 m to 1,088 cells/mL at 5 m (Figure 9). *Rhizosolenia fragilissima* returned in 1996, constituting 25-48 % of the diatom community, and was co-dominant with *Chaetoceros* spp. (Figure 11). *Pseudo-nitzschia* spp. and *Leptocylindrus* spp. were the third most abundant diatoms. *Skeletonema costatum* was present but averaged only 6 % of the abundance in the upper 50 m.

3.3.3 Integrated abundance

Abundances of phytoplankton were integrated with depth to calculate what potential food was available to herbivores in the upper water column during the spring bloom. Values were integrated for the upper 50 m because the majority of phytoplankton existed in this region.

The spring bloom in the upper 50 m was composed of the same flagellates and diatom species each year, but 1996 had a greater abundance of diatoms (Figures 12 and 13). In 1995, flagellates were approximately 50 % of the integrated phytoplankton abundance with a mean abundance of 5.6×10^{10} (cells/m^2) during April. Diatoms composed the remainder of the phytoplankton. Total cell abundance fluctuated only slightly from day to day. Of the diatoms in 1995, *Skeletonema costatum* had the highest abundance, ranging from 28-52 % of the total diatom abundance. It averaged 2.8×10^{10} (cells/m^2). *Thalassiosira* spp. was the second most abundant, averaging 33 % of the integrated abundance. *Chaetoceros* spp., *Leptocylindrus* spp. and *Pseudo-nitzschia* spp. composed between 6-13 %, 0.5-22 % and 4-9 %, respectively, of total diatom abundance. In 1996, diatom abundance increased by two- to three-fold, while flagellates remained about the same, and total cell abundance varied greatly throughout the bloom. *Skeletonema costatum* dominated the diatom component with a mean of 2.3×10^{11} (cells/m^2) over the 10 sampling days in April, constituting > 60 % of the diatom abundance. *Chaetoceros* spp. had a higher percentage of the abundance (11-24 %) in 1996 than 1995 and greater than four times as many cells. *Thalassiosira* spp. composed only 4.2 % of abundance with a mean of 1.2×10^{10} (cells/m^2). This was 45 % lower than the 1995 spring bloom abundance. *Pseudo-nitzschia* spp. increased but remained between 4-9 % in 1996.

During the post-bloom, a low abundance of flagellates dominated and interannual differences were small (Figures 12 and 13). Flagellate abundance ranged from 2.3-3.1 x 10^{10} (cells/m^2) for both years. They constituted over 92 % of the total abundance. In 1995, of the few diatoms remaining, *Pseudo-nitzschia* spp. was dominant. *Chaetoceros* spp., and *Thalassiosira* spp. were also present in small numbers. In 1996, *Chaetoceros* spp. was dominant and *Pseudo-nitzschia* spp. and *Leptocylindrus* spp. made up the majority of the remaining 55 % of the diatom community.

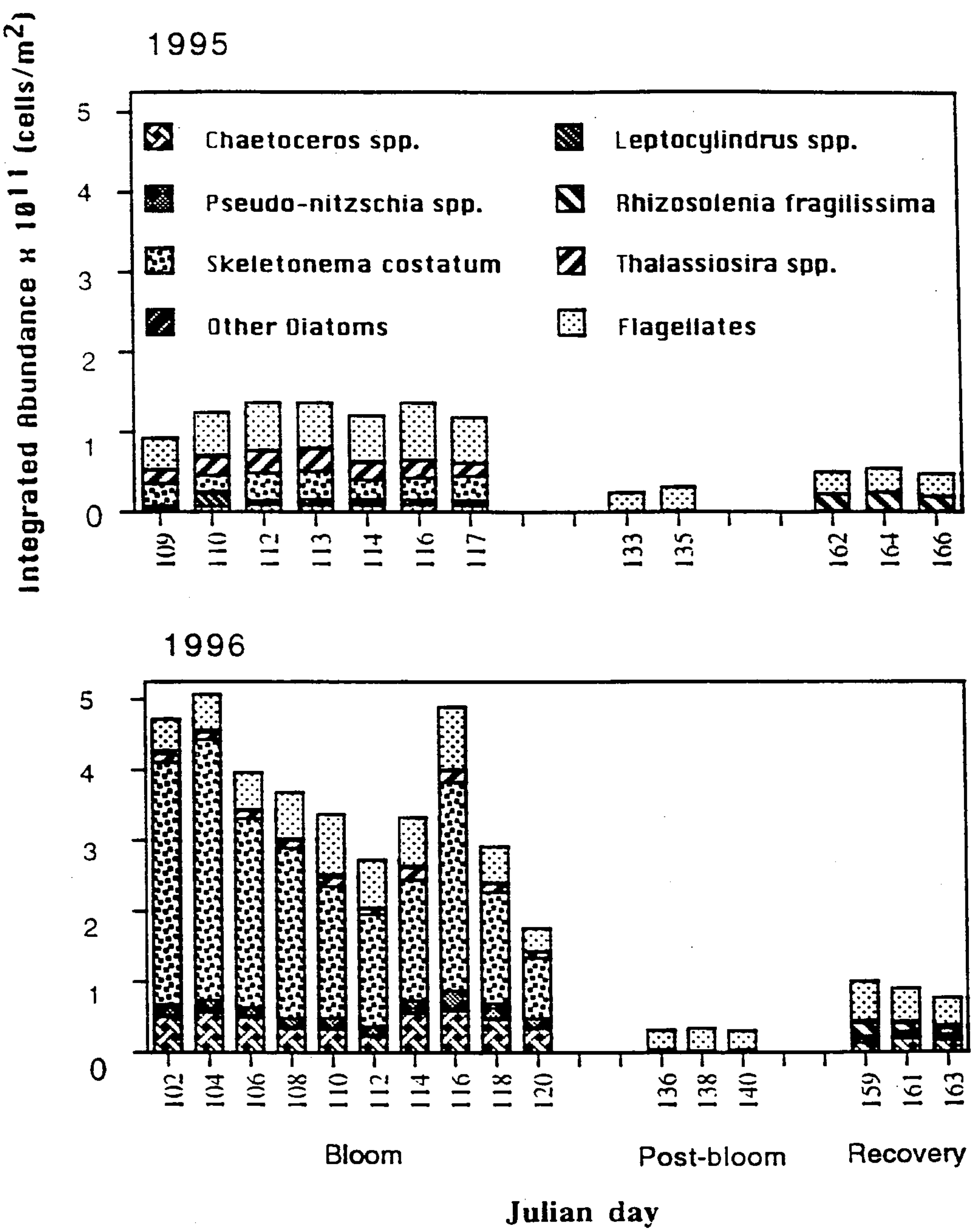

Figure 12. Diatom and flagellate abundance integrated over the upper 50 m from spring 1995 and 1996.

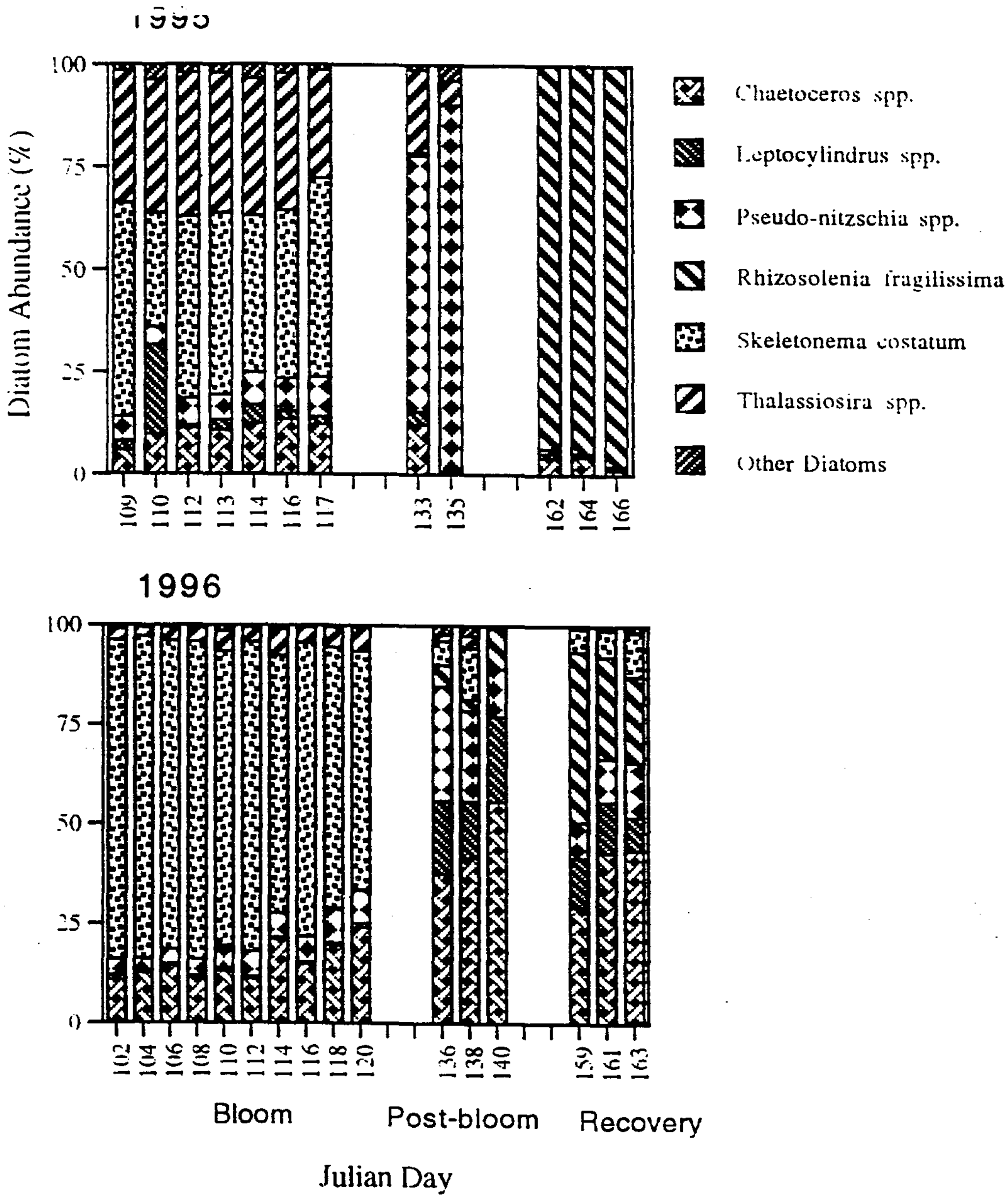

Figure 13. Diatom species composition (% total diatoms integrated over 50 m) from spring 1995 and 1996.

During the recovery period of both years diatom abundance increased, flagellates remained a large constituent, and a succession in the diatom community occurred (Figures 12 and 13). In 1995, flagellate abundance equaled post-bloom levels. Diatoms increased and a previously unseen species, *Rhizosolenia fragilissima*, was the major constituent with > 93 % of the abundance and a mean of 2.1×10^{10} (cells/m^2). In 1996, diatoms and flagellates also increased but the diatom community had greater diversity. *Rhizosolenia fragilissima* averaged only 30 % of the abundance. The other major diatoms were *Chaetoceros* spp. (38.5 %), *Leptocylindrus* spp. (17 %), *Pseudo-nitzschia* spp. (11 %) and *Skeletonema costatum* (7.8 %).

3.4 Carbon Content

Carbon biomass was calculated from cell volume to get a perspective on the phytoplankton standing stock in terms of available organic carbon (Table 3). Abundance studies alone can misrepresent the available plant resources in terms of trophic interactions and energy transfer. There is the potential to overemphasize large numbers of small cells that, due to their small cell volume and equivalent small carbon biomass, contribute minimally to the available pool of energy. In this study only the most abundant species or genera were converted into carbon. Carbon biomass was calculated only for the dominant species of diatoms and flagellates, determined from the abundance measurements. Carbon estimates were calculated from cell volume and converted into mg carbon/m^3. The same dominant phytoplankton were present in 1995 and 1996.

3.4.1 Carbon biomass by time and depth

Estimated carbon biomass was highest during the spring bloom, had approximately the same proportion of diatoms and flagellates throughout the water column, and had great interannual variability compared to later in the season (Figures 14 and 15). In both years, species composition remained the same with depth but biomass

Table 3. Cell shape, volume equations, measurements, cell volumes and cell carbon estimates for major phytoplankton taxa.

Phytoplankton taxa	Cell Shape	Volume Equation	Mean Diameter (µm) A	Mean Height (µm) (B or C)	Thickness Equation	Thickness (µm) (B or C)	Cell Volume (um^3)	Carbon (pg/cell)
Chaetoceros <25 µm	flattened cylinder	V= BC(A-B +pi/4(B))	4.60	9.90	B=2/3A	3.08	120.21	14.28
Chaetoceros 25-44 µm	flattened cylinder	V= BC(A-B +pi/4(B))	10.25	25.25	B=2/3A	6.83	1514.90	97.44
Chaetoceros deciprens	flattened cylinder	V= BC(A-B +pi/4(B))	24.65	19.90	B=2/3A	13.27	5576.71	261.67
Fragilariopsis spp. <25 µm	rectangular box	V= BC(A-B +pi/4(B))	14.25	2.43	B=2C	4.86	112.80	13.60
Leptocylindrus danicus	rectangular box	V=ABC	47.35	11.50	C=1/2B	5.75	3131.02	168.94
Leptocylindrus minimus	rectangular box	V=ABC	26.75	2.75	C=1/2B	1.38	101.15	12.52
Pseudo-nitzschia 25-44 µm	ellipsoid	V=pi/6 (ABC)	33.90	2.15	C=1/2B	1.07	41.36	6.36
Pseudo-nitzschia ≥45 µm	ellipsoid	V=pi/6 (ABC)	52.30	2.50	C=1/2B	1.25	85.60	11.04
Rhizosolenia fragilissima	right circular cylinder	V=pi/4 (A·B)	22.40	5.00			1970.41	118.93
Skeletonema costatum	right circular cylinder	V=pi/4 (A·B)	12.88	4.15			540.72	44.63
Thalassiosira <25 µm	right circular cylinder	V=pi/4 (A·B)	18.88	10.35			2897.57	159.30
Thalassiosira 25-44 µm	right circular cylinder	V=pi/4 (A·B)	29.25	10.50			7055.55	312.74
Thalassiosira ≥45 µm	right circular cylinder	V=pi/4 (A·B)	48.83	14.90			27902.92	886.75
Unidentified flagellates <10 µm	sphere	V=pi/6 (A^3)	5.75				99.54	18.63
Unidentified flagellates ≥ 10 µm	sphere	V=pi/6 (A^3)	13.44				1269.70	168.97

Note: Mean diameter and height were calculated from measurements of 20 cells.
Shapes and equations were modified versions from the work of Kovala and Larrance (1966).
Carbon was calculated from two equations (Strathmann, 1967) :

Diatoms : $\log C = -0.422 + 0.758 (\log V)$

Other phytoplankton: $\log C = -0.460 + 0.866 (\log V)$

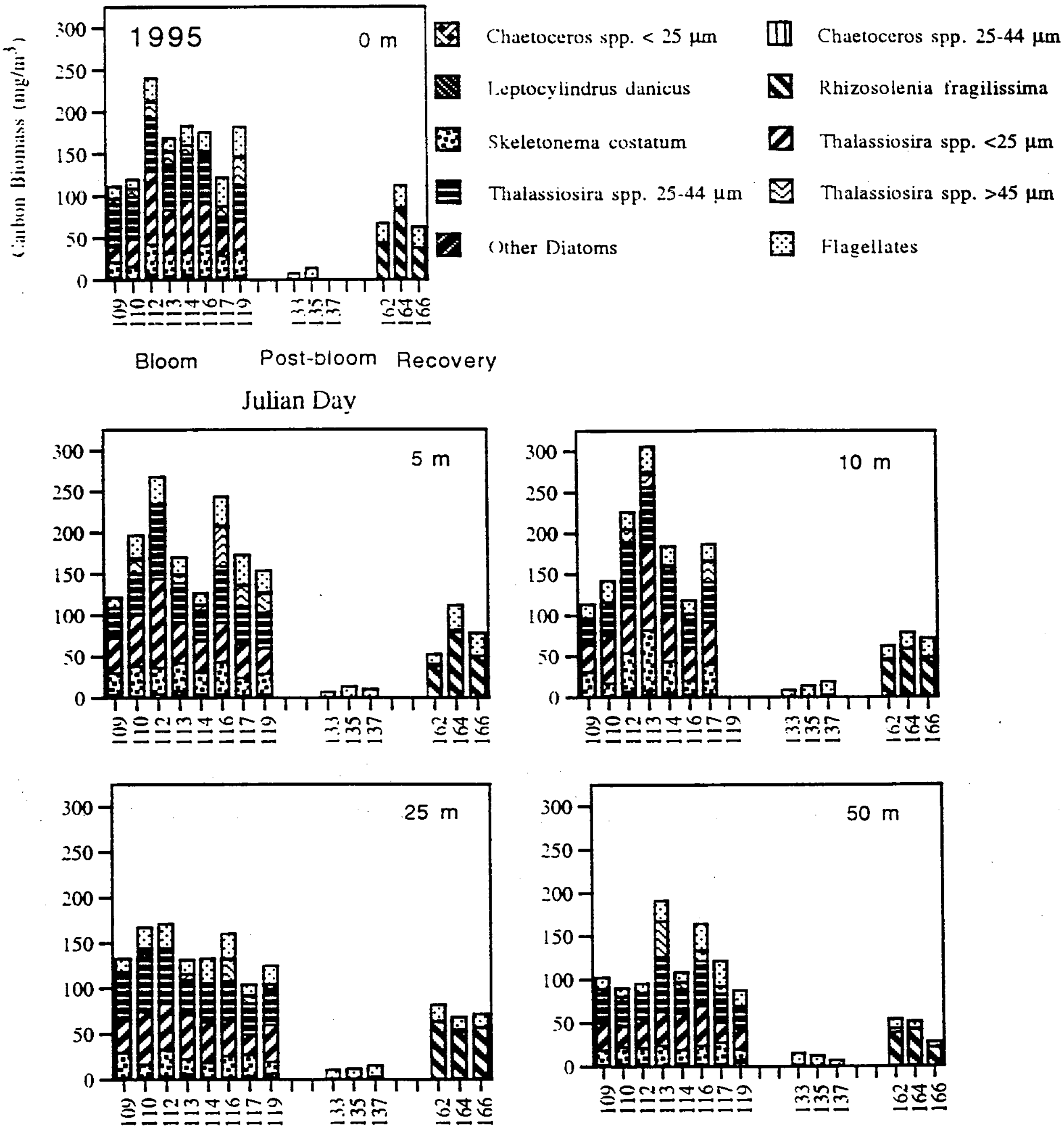

Figure 14. Estimated carbon for major diatoms and flagellates from five depths in the upper 50 m from spring 1995.

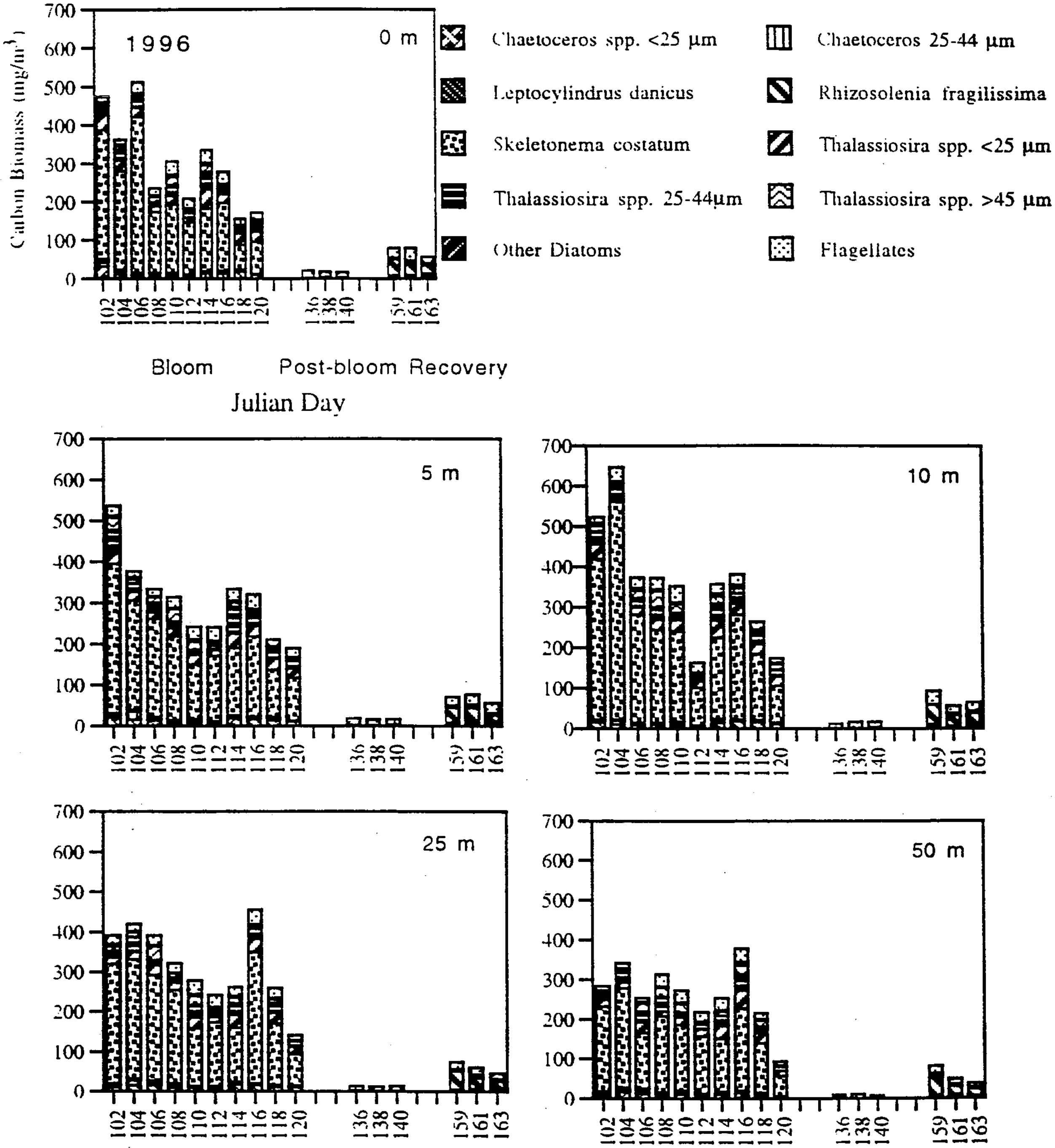

Figure 15. Estimated carbon for major diatoms and flagellates from five depths in the upper 50 m from spring 1996.

decreased below 10 m. In 1995, total autotrophic carbon ranged from 88 mg/m^3 at 50 m to 306 mg/m^3 at 10 m. At all depths the major constituent of the carbon was *Thalassiosira* spp. from the smallest (<25 μm) and middle (25-44 μm) size classes. *Skeletonema costatum* was the second dominant diatom and averaged 17-23 % of the total diatom carbon biomass over all depths. Flagellate carbon was present in small amounts at all depths throughout the bloom in 1995, with a mean ranging from 18 mg/m^3 at 50 m to 25 mg/m^3 at 10 m. In 1996, the same species constituted the bulk of the carbon at all depths, but *Skeletonema costatum* biomass increased and *Thalassiosira* spp. decreased. The total autotrophic carbon increased from 94 mg/m^3 on day 120 at 50 m to 647 mg/m^3 at 10 m on day 104. In 1996, the contribution by all three size classes of *Thalassiosira* spp. approximately equaled the contribution of *Skeletonema costatum* from the previous year. In contrast, in 1996, *Skeletonema costatum* averaged 68-73 % of the total diatom carbon over the upper 50 m. Chaetoceros spp. <25 μm had a greater biomass in 1996 but only accounted for < 7 % of the total diatom carbon. Flagellate carbon was present at all depths in the same proportions as 1995; the mean ranged from 21-24 mg/m^3.

In the post-bloom of each year, carbon was low throughout the water column when flagellates composed the majority of the biomass (Figures 14 and 15). In 1995, flagellate carbon ranged from 6-16 mg/m^3 and showed no decrease with depth except on day 137. Diatom carbon constituted < 15 % of the total. Small *Thalassiosira* spp. were the main constituent of this biomass. In 1996, flagellate carbon ranged from 6-19 mg/m^3. Diatom carbon was < 23 % of total carbon and was composed of a small proportion of several genera (see Section 3.4.2).

In the recovery period, diatom carbon increased at all depths and a late season bloomer, *Rhizosolenia fragilissima*, composed the majority of the biomass (Figures 14 and 15). Flagellate biomass remained unchanged throughout this period. In 1995, total carbon recovered to reach highs of 112 mg/m^3 at both the surface and 5 m on day 164. About 75 % of this carbon originated from diatoms other than *Skeletonema costatum*. At all depths, >94 % of the total mean carbon was from *Rhizosolenia fragilissima*. Flagellate carbon decreased with depth and averaged < 25 mg/m^3 during June. In 1996, total carbon ranged from 38-93 mg/m^3, but the biomass did not have a two-fold difference from 1995, as seen in the bloom period. On a daily basis, total biomass was often lower in 1996 than 1995 during this period. *Rhizosolenia fragilissima* accounted for 60-70 % of the diatom carbon throughout the 50 m layer. The other major contributors to the diatom carbon biomass were *Chaetoceros* spp., *Leptocylindrus danicus* and *Skeletonema costatum*. Flagellate carbon increased from low levels in the post-bloom period and remained below 33 mg/m^3.

3.4.2 Integrated carbon

The phytoplankton, in terms of carbon potentially available to zooplankton in the upper water column, were integrated for the upper 50 m (Figure 16). During the bloom integrated carbon throughout the water column was highest in both years, but the 1996 values were two to three times those of 1995. Each year the same genera were responsible for this biomass but there were differences in dominance between years. In 1995, total carbon varied < 30 % between days 109-117. On day 113 (23 Apr) the highest carbon occurred (9,400 mgC/m^2). The mean was 7,600 mgC/m^2. During the bloom, diatoms were 84-88 % of the total carbon. *Thalassiosira* spp., from three size classes, made up 73-80 % of the diatom carbon (Figure 17). *Skeletonema costatum* had the second largest biomass, comprising 14-24 % of the diatom biomass. *Chaetoceros* spp. and *Leptocylindrus* spp. composed less than 2 % and 3.8 %, respectively, of the carbon. *Pseudo-nitzschia* spp., due to small cell volume (41 μm^3), constituted only 0.30-0.82 % of the diatom carbon. Flagellates averaged only 7.5 % of the total carbon during the bloom. In 1996, the mean carbon biomass (15,500 mgC/m^2) was approximately twice

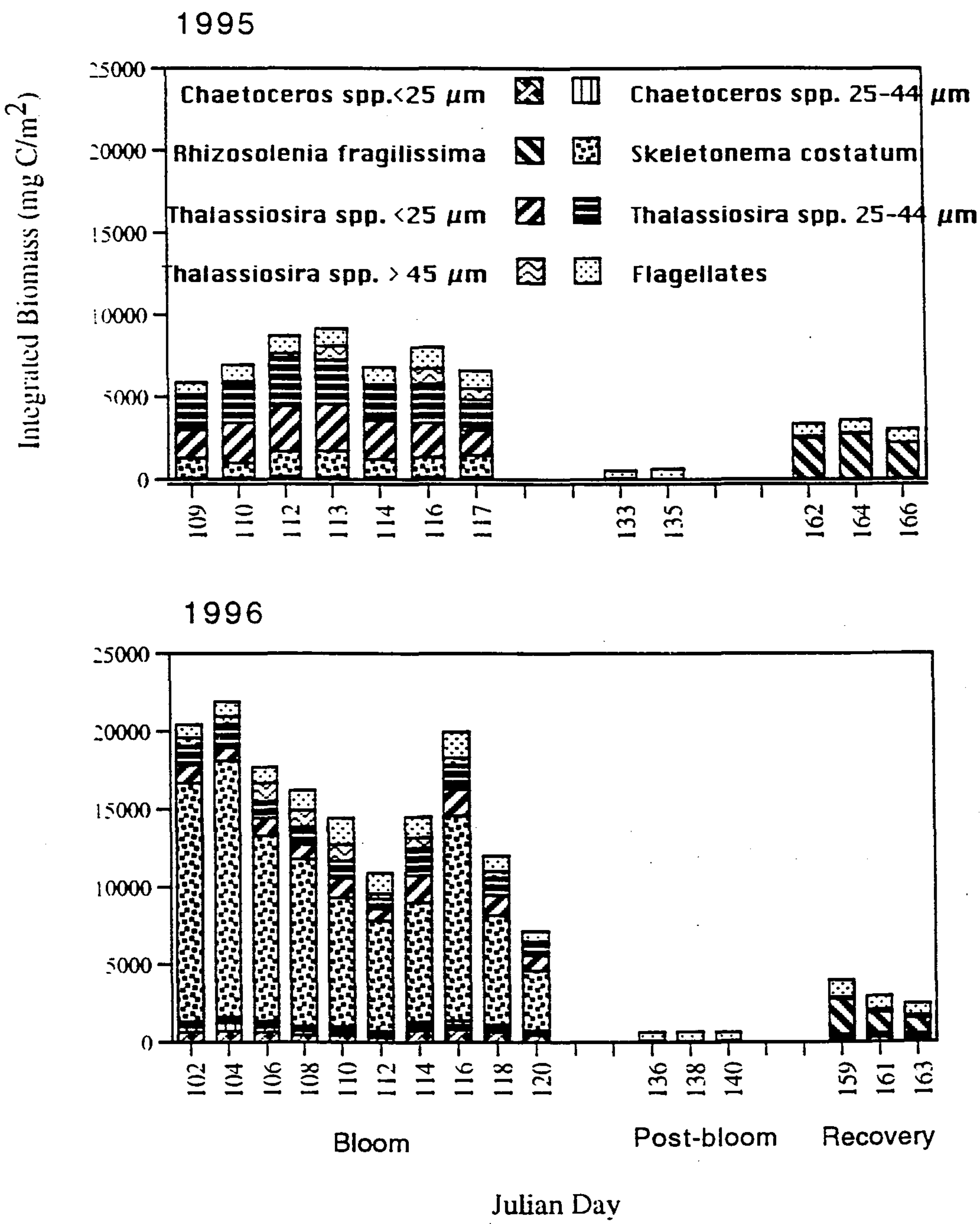

Figure 16. Estimated carbon for diatoms and flagellates integrated over the upper 50 m from spring 1995 and 1996.

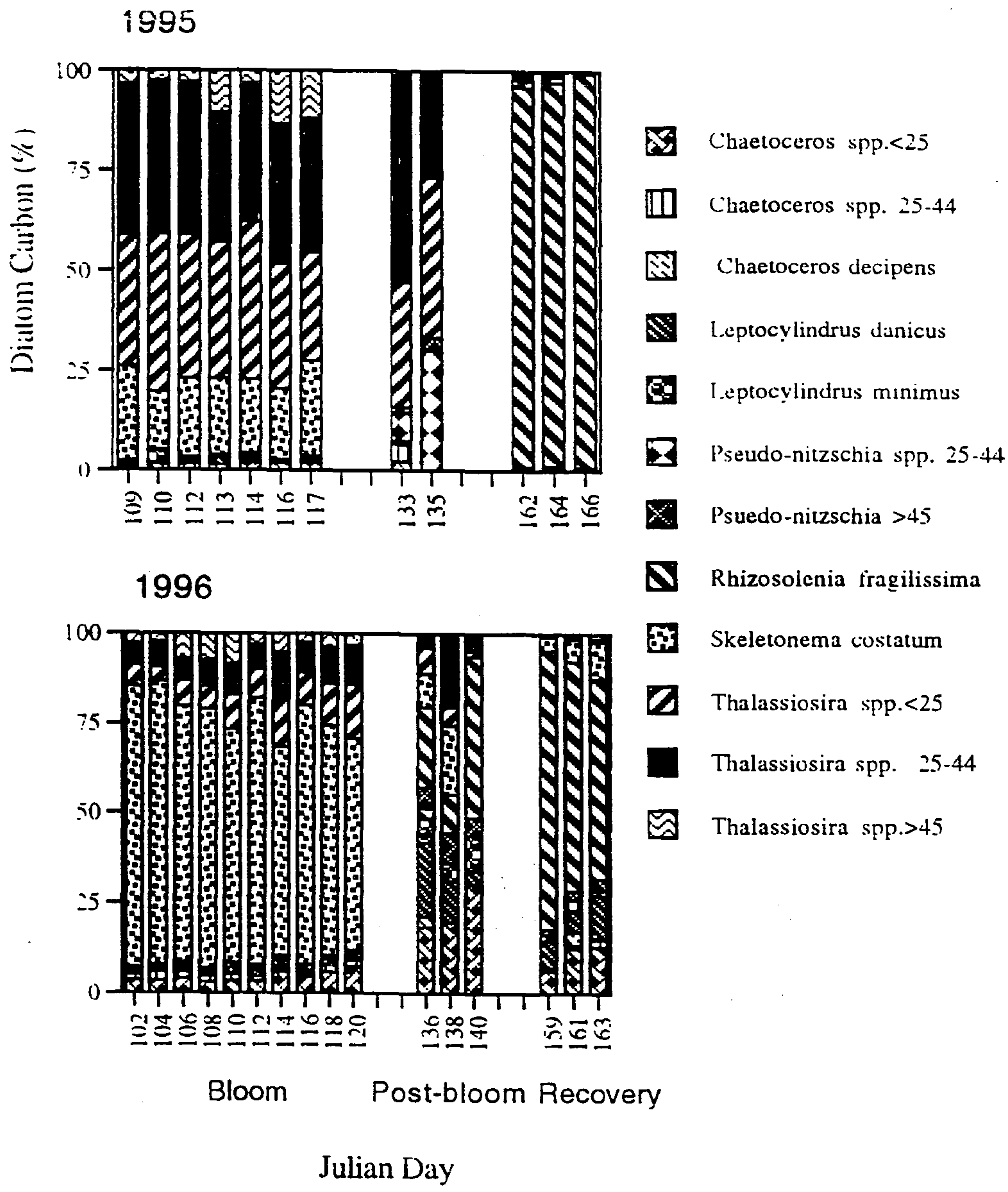

Figure 17. Estimated carbon (% total diatom carbon integrated over 50 m) of major diatoms from spring 1995 and 1996.

as large as 1995 and the peak biomass was 22,000 mgC/m^2. Diatoms were 88-96 % of the total autotrophic biomass. *Skeletonema costatum,* not *Thalassiosira* spp., was the primary constituent in 1996; it contributed 58-78 % of diatom carbon, while *Thalassiosira* spp., on average, constituted only 22 %. *Chaetoceros* spp., dominated by the small cells < 25 µm, had less than 9 % of the diatom carbon. *Pseudo-nitzschia* spp. constituted only 0.8-2 % of the diatom carbon. Flagellates averaged 13.8 % of the total autotrophic carbon during the bloom.

During the post-bloom, carbon fell to its lowest levels. Flagellate carbon dominated and only a few taxa contributed to the small amount of diatom carbon (Figure 16). In 1995, the mean biomass was 600 mgC/m^2. Diatom carbon consisted of < 8 % of the total. This biomass was almost all from *Thalassiosira* spp. (66-84 %), *Pseudo-nitzschia* spp. (7-30 %) and *Chaetoceros* spp. (0-7 %). *Rhizosolenia fragilissima* did not appear at this time in 1995. In 1996, the mean post-bloom phytoplankton biomass, 700 mgC/m^2, was slightly higher than 1995. Again most of the carbon originated from flagellates and < 18 % was from diatoms. *Chaetoceros* spp. (<25µm), *Leptocylindrus* spp., *Rhizosolenia fragilissima, Skeletonema costatum* and *Thalassiosira* spp., in nearly equal proportions, were the main constituents. *Pseudo-nitzschia* made up <9 % of the diatom biomass.

During the recovery period the diatom carbon increased and a shift in the community composition occurred (Figure 17). Diatoms recovered and composed greater than 50 % of the biomass. In contrast to the spring bloom period, the recovery period in 1995 had a greater biomass than 1996. In 1995, the mean total biomass was 3,300 mgC/m^2 and daily fluctuations were small (Figure 16). A shift in species composition from *Thalassiosira* spp. and *Skeletonema costatum* to *Rhizosolenia fragilissima* occurred late in the bloom. *Rhizosolenia fragilissima* averaged 96.5 %, of the diatom carbon; on day 164, it reached 2,700 mgC/m^2. *Thalassiosira* spp., *Chaetoceros* spp. and

Leptocylindrus danicus amounted to less than 140 mgC/m^2 during the recovery. *Skeletonema costatum* was not present at this time in 1995. In 1996, the mean total, 3,100 mgC/m^2, was lower than 1995 and was only composed of 70 % diatoms. *Rhizosolenia fragilissima*, after first appearing in the post-bloom, averaged 66 % of the diatom carbon in the recovery period. The remaining carbon was comprised primarily of *Chaetoceros* spp., *Leptocylindrus* spp., *Skeletonema costatum*, *Pseudo-nitzschia* spp., *Thalassiosira* spp. and *Fragilariopsis* spp.

3.5 Community Interactions

3.5.1 Physics, nutrients and chlorophyll relationships

Daily inorganic nutrient concentrations were compared with chlorophyll *a* concentrations and physical data to determine how the phytoplankton interacted within the marine environment of southwest Prince William Sound (Figure 18). Chlorophyll *a* concentrations from all days and depths were compared with corresponding nutrient concentrations for 1995 and 1996. Scatter diagrams show negative or no correlation between chlorophyll concentrations and nutrients in both years. In 1995, chlorophyll *a* vs N+N and silicate had a weak negative correlation. Chlorophyll *a* vs phosphate showed no relationship (r=0.03). In 1996, stronger negative relationships between all nutrients and chlorophyll existed.

During the spring bloom when chlorophyll profiles were compared to nutrient profiles similarities were apparent (Figures 4 and 5). In 1995, high patches of chlorophyll, for example around day 111, corresponded to low nutrient patches ranging from 5-7 μM of N+N and 8-12 μM of silicate in the upper 10 m. Nutrient decline was most evident above 50 m and fell to between 0.15-3 μM N+N and 1-5 μM silicate at 5 m and above after days 121-126. In 1996, N+N, silicate and phosphate concentrations decreased at the same time and depth as chlorophyll increased. Nutrients remained high

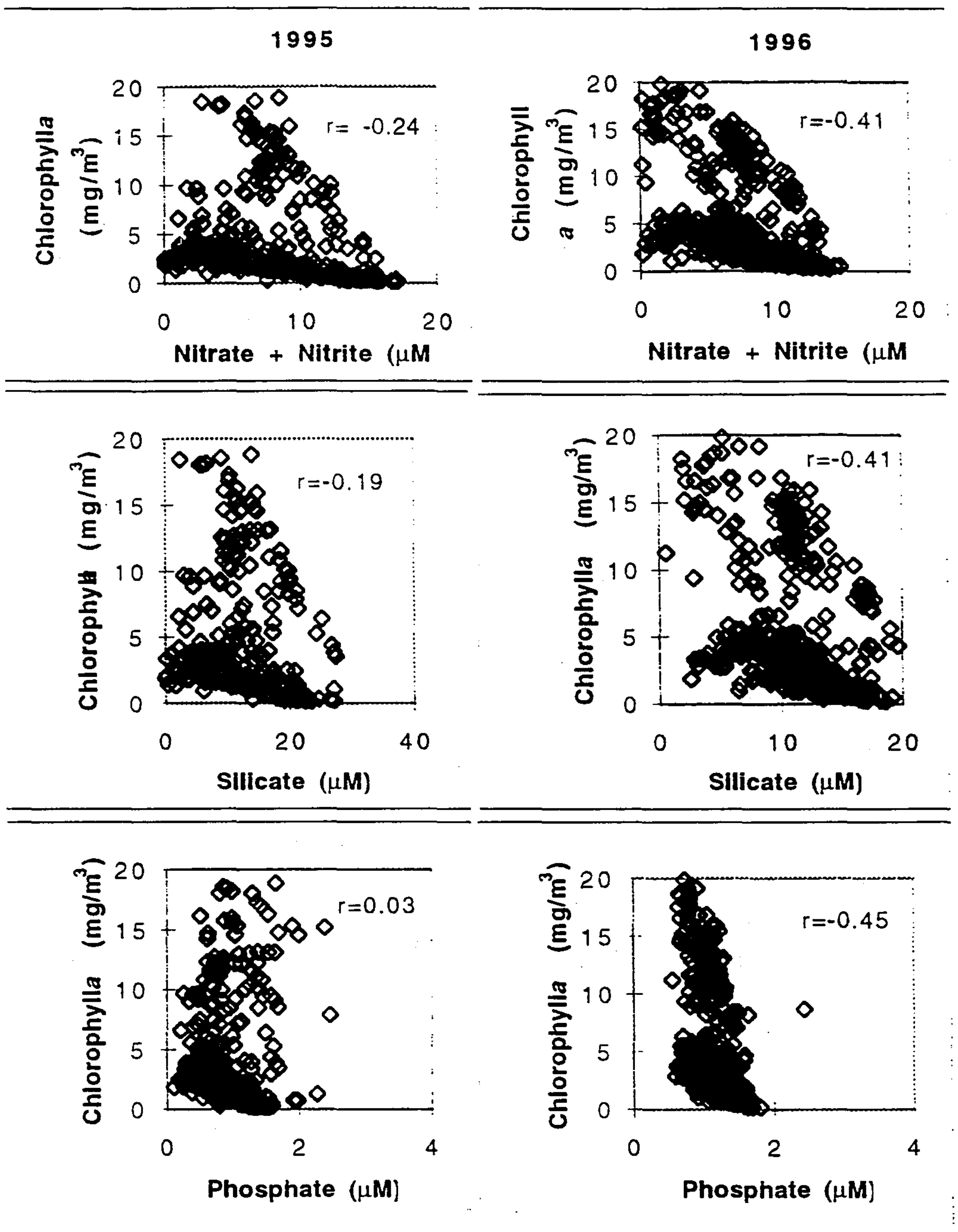

Figure 18. Chlorophyll *a* (mg/m^3) vs. nutrient (μM) concentration from spring 1995 and 1996.

throughout the upper 75 m until day 100. As chlorophyll increased to 15-20 mg/m^3 in the upper 25 m after day 101, nutrient concentrations decreased to close to zero at the surface. After day 104, chlorophyll levels remained between 10-15 mg/m^3 and N+N, silicate and phosphate remained between 5-9 µM, 8-15 µM and 1-1.25 µM, respectively, throughout most of the water column. As the chlorophyll biomass increased again around day 114, nutrients decreased showing highest values only below 50 m.

During the post-bloom and recovery periods, thermal stratification started to occur and chlorophyll decreased. A negative correlation existed between temperature and chlorophyll ($r = -0.494$ in 1995 and $r = -0.565$ in 1996). After day 128 in 1995 and 1996, chlorophyll declined to its lowest levels and was vertically uniform throughout the post-bloom. Nutrients remained low in surface waters but increased with depth as standing stock diminished. In 1995, accompanied by strong stratification, chlorophyll rebounded in the upper 25 m during the recovery period to values between 1-7 mg/m^3. At the same time, nutrient concentrations fell again to near depletion in the upper 5 m. In 1996, chlorophyll increased between 2-7 mg/m^3 in the upper few meters after day 146 of the recovery. As in 1995, the phytoplankton biomass rebounded as N+N, silicate and phosphate levels (µM) were reduced to 0.15-3, 1-10 and 0.5-1 µM, respectively, in the upper 10 m.

3.5.2 Chlorophyll and carbon relationships

Carbon to chlorophyll ratios and chlorophyll per cell were calculated to access physiological condition of the phytoplankton community (Table 4 and 5). High carbon/chlorophyll ratios (e.g. 60) and low chlorophyll/cell ratios (e.g. 0.1 pg/cell) often indicate nutrient limitation (Darley 1982). Carbon was not estimated for phytoplankton < 2 µm and numerically minor constituents.

Table 4. Mean, range, standard deviation and number of observations of chlorophyll *a* (pg/cell) in the upper 50 m from spring 1995 and 1996.

	1995				1996			
Period	Mean	Range	SD	n	Mean	Range	SD	n
Bloom	5.3	2.6-10.3	1.7	39	2.0	1.0-3.5	0.5	50
Post-bloom	2.6	1.1-3.1	0.5	14	1.6	0.9-2.2	0.3	15
Recovery	3.0	2.7-3.8	0.4	15	2.4	1.5-3.5	0.6	15

Table 5. Mean, range, standard deviation and number of observations of estimated carbon/chlorophyll *a* (mg/mg) in the upper 50 m from spring 1995 and 1996.

	1995				1996			
Period	Mean	Range	SD	n	Mean	Range	SD	n
Bloom	12	8-20	3	39	22	11-43	6	50
Post-bloom	15	6-20	3	14	14	10-20	3	15
Recovery	21	16-27	3	15	15	9-22	4	15

Relationships between calculated autotrophic and chlorophyll *a* of the same day and depth showed strong associations (Figure 19). Diatom carbon in 1995 and 1996 was positively correlated with chlorophyll concentrations ($r = 0.86$ in 1995, $r = 0.91$ in 1996). Flagellate carbon was not as significantly correlated with chlorophyll. The regression of carbon vs. chlorophyll *a* is statistically significant ($p = <0.0001$). A least squares regression of total phytoplankton carbon on chlorophyll *a* concentration can explain 75 % in 1995 and 83 % in 1996 of the variability in phytoplankton carbon. The slopes of the least squares line differ between years and show interannual variability between phytoplankton carbon and chlorophyll concentration, a reflection of species abundance and composition.

Carbon to chlorophyll ratios and chlorophyll per cell ratios had interannual variability (Tables 4 and 5). In 1995, chlorophyll *a* ranged from 1.1 to 10.3 pg/cell throughout the season. Highest chlorophyll/cell ratios occurred in the first few days of the spring bloom and lowest occurred during the post-bloom. Carbon/chlorophyll ranged from 6-27 throughout the sampling season in 1995. Ratios were low in the bloom and post-bloom periods and increased to between 16 and 27 during the recovery. In 1996, mean chlorophyll/cell ratios were lower. Ratios ranged from 0.9-3.5 pg/cell throughout all periods. Cell ratios remained approximately the same between the bloom and recovery. Lowest chlorophyll/cell ratios occurred during the post-bloom. In contrast to chlorophyll/cell ratios, carbon/chlorophyll ratios were higher in 1996. They ranged from 9-43 throughout the study period. The highest ratios occurred at the beginning of the bloom at all depths. Lower ratios, between 10 and 22, occurred in the post bloom and recovery periods.

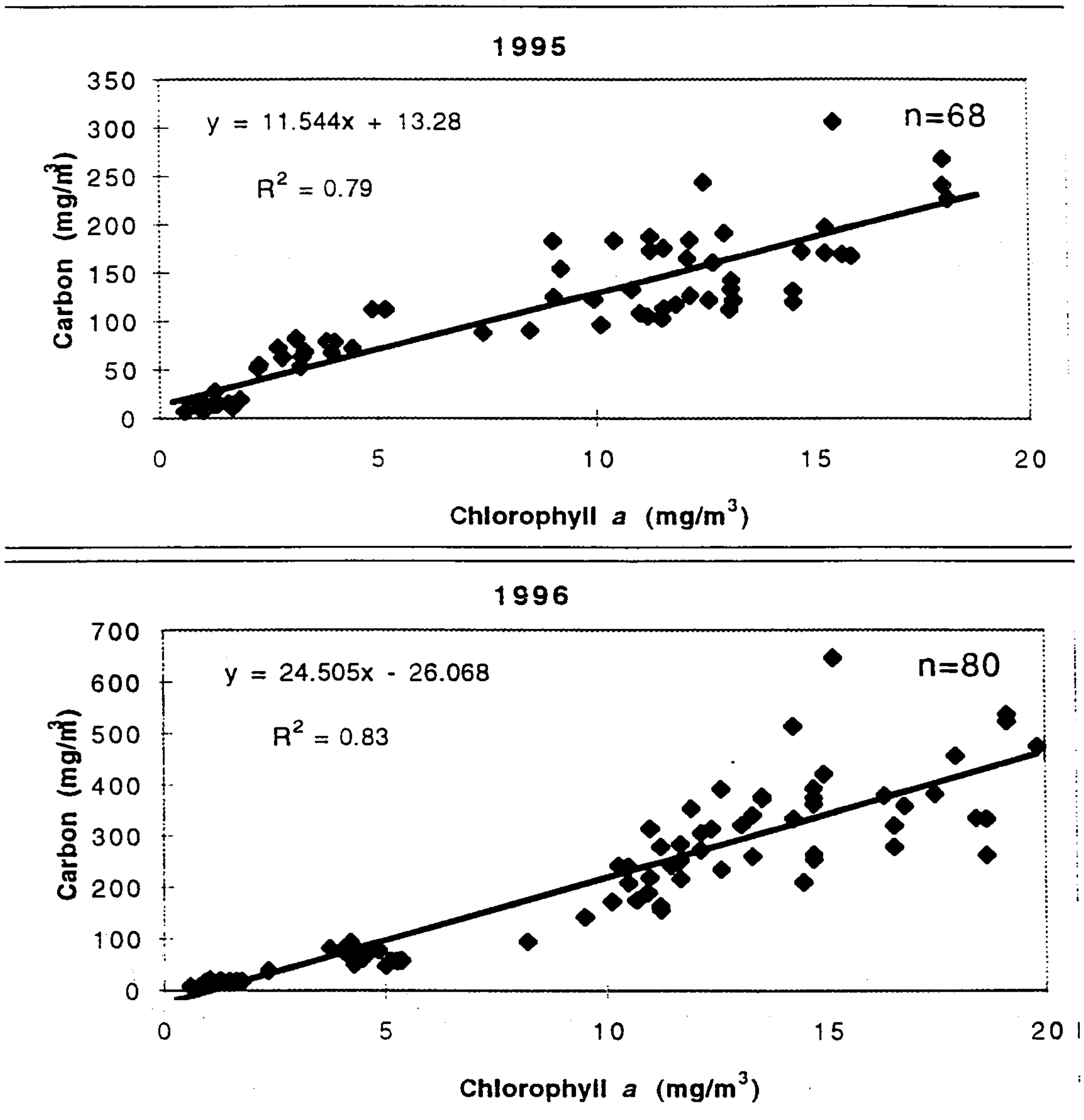

Figure 19. Estimated autotrophic carbon (mg/m^3) vs. chlorophyll *a* (mg/m^3) for the upper 50 m from spring 1995 and 1996.

DISCUSSION

1. Temporal Pattern of the Phytoplankton Bloom

In high latitudes, the timing of the spring bloom is due to a combination of atmospheric and oceanic events. It is believed that the timing of the bloom is a function of warming air temperatures, reduced wind stress, decreased deep mixing events, increased solar radiation, intensity and duration, and stratification of the water column (Lalli and Parsons 1993). The physical oceanographic conditions that can affect the timing of the bloom in Prince William Sound were originally described by Sverdrup (1953) for the Norwegian Sea. He theorized that in the spring in high latitudes, as solar heating increased and mixing decreased, the mixed layer depth rose above the critical depth and net photosynthesis exceeded net respiration throughout the water column, enabling the phytoplankton to bloom in nutrient-rich waters. In Prince William Sound, these physical events are coupled with local hydrography to initiate the bloom within a short window of time. Local features such as the narrow, shallow basin of Elrington Passage, high precipitation rates, the tidal cycle and terrestrial run-off can also affect the timing.

The timing of the spring bloom in southwest Prince William Sound reported here is similar to that found during other studies of Prince William Sound (Goering et al. 1973; McRoy et al. 1996; Eslinger 1997) and northern subarctic marine waters (VTN Consolidated, Inc. 1980; Goering and Iverson 1982; Ziemann et al. 1991) (Table 6). In 1995 and 1996, the phytoplankton bloom started in early to mid April, had peaked by late April and declined to low levels by the first week of May. A slight, secondary recovery of the bloom occurred in June. In accordance with this study, monthly research cruises in Prince William Sound in 1995 and 1996 recorded highest chlorophyll concentrations in

Table 6. Comparison of the timing of the spring bloom and chlorophyll concentrations at other regions in Prince William Sound and northern regions.

Location	Latitude (°N)	Timing of peak bloom (Julian day)	Max. chlor conc. (mg/m^3)	Study period	Reference
Southwest PWS	60	107-123	2-19	Apr-June 1995	present study
Southwest PWS	60	97-126	2-20	Apr-June 1996	present study
Port Valdez, AK	61	75-135	0-10	May 1971 - Apr 1972	Goering et al. 1973
Central PWS	60.5	95-115	nd	Mar-July 1993	McRoy et al. 1996
Central PWS	60.5	95-130	nd	Mar-July 1994	McRoy et al. 1996
Central PWS	60.5	95-125	nd	Mar-July 1996	Eslinger 1997
Auke Bay, AK	58	90-120	1->50	Mar-June 1985-1989	Ziemann et al. 1991
Auke Bay, AK	58	91-120	nd	Mar-June 1968	Schell 1971
Boca de Quadra, AK	55	86-89	1-53	Mar-July 1980	VTN Consolidated Inc. 1980
Bering Sea	57	118-132	nd	Mar-June 1981	Goering & Iverson 1982
Bering Sea ice edge	58	116-133	0-35	Apr-May 1988	Niebauer et al. 1995
Gulf of Alaska Station P	50	122-244	0.20-0.50	Jan-Dec 1959-1970	Sambrotto & Lorenzen 1986

April (McRoy et al. 1996; McRoy et al. 1997). The C-LAB (Communications-Linked Automated Buoy), a moored buoy equipped with a fluorometer, stationed in the central region of Prince William Sound east of Naked Island, was deployed in 1991 to collect continuous biological and physical oceanographic data. The fluorescence data from C-LAB support these results: highest chlorophyll occurred between days 95-125 for years 1993, 1994 and 1996 (McRoy et al. 1996; Eslinger 1997). Following a nadir in chlorophyll, an increase occurred after day 150 in agreement with these field site measurements.

In Port Valdez, a fjord in northern Prince William Sound Goering et al. (1973) found high levels of productivity and chlorophyll in mid-April followed by low levels in May, 1971. In southeastern Alaska in Auke Bay, the spring bloom lasted from early April to the first week of May (Ziemann et al. 1991). In the southern Bering Sea, the peak of the spring bloom lags the peak biomass in Prince William Sound by approximately three weeks (Goering and Iverson 1982), but blooms in the marginal ice zone begin as early as the last week of April due to salinity-driven stratification and high nutrients (Niebauer et al. 1995). In the Gulf of Alaska, at the Coastal Ocean Weather Station P, chlorophyll *a* concentration remains low (< 0.50 mg/m^3) throughout the year but primary productivity peaks in early July (Sambrotto and Lorenzen 1986).

2. Temporal and Vertical Patterns of Succession

2.1 Phytoplankton Biomass

The magnitude of the spring bloom is a function of nutrient content and supply and stratification within the marine environment. In 1995, fresh water dilution lowered the salinity, decreased density at the surface and increased stratification. Under such conditions, phytoplankton were maintained in the euphotic zone and biomass increased as a distinct peak that declined as nutrients were depleted. Nitrate+nitrite concentrations decreased to < 2 μM in the upper surface waters after day 121. Half-saturation constants for nitrate in neritic diatoms range from 0.4-5.1 μM (Valiela 1984). Therefore, diatom growth was limited by low concentrations of nitrate+nitrite in the surface waters at the end of the spring bloom.

In 1995, due to our late arrival in the field (day 107), it is likely that we missed the early portion of the bloom. However, looking at the magnitude of the bloom by day 111, the limited nutrient supply, and comparing the timing with the 1994 and 1996 chlorophyll data from the C-LAB (McRoy et al. 1996; Eslinger 1997), I maintain that we arrived in time to measure the majority of the biomass.

In 1996, the phytoplankton chlorophyll biomass pattern was slightly different. The magnitude was slightly greater and the bloom duration of the bloom was longer than 1995. The salinity of the water column was greater and freshwater dilution was less. Consequently, stabilization of the water column was reduced. Therefore, weak stratification events (around days 105 and 120) promoting increases in phytoplankton stocks were interspersed with mixing events, allowing the nutrient supply to replenished from depth and lengthening the bloom period. Around day 118, chlorophyll concentrations reached maximum levels and nitrate+nitrite concentrations were reduced to < 2 μM in the upper 10 m. Again the phytoplankton growth was likely controlled from the bottom up by nitrate+nitrite concentrations as in 1995. Similar chlorophyll levels, nutrient concentrations and higher-salinities were also detected throughout Prince William Sound in April 1996 (McRoy et al. 1997; Vaughan et al. 1997).

In both years, silicate concentrations were low in surface waters in April which may also have affected the length of the diatom bloom. Ratios of Nitrate+nitrite:silicate were around 5:10 instead of the modified Redfield ratio of 16:50 (nitrate:silicate) (Broecker and Peng 1982) for optimal nutrient conditions. Also concentrations of silicate in the upper surface waters were lower than nutrient half saturation constants for some diatoms (k_s=0.5-5.0 μM) (Lalli and Parsons 1993). As a result, Prince William Sound may be silicate-limited even though small amounts of the nutrient are usually present at all times. This hypothesis is also supported by weak silicification of diatoms and formation of resting spores, most frequently by *Chaetoceros diadema*, found throughout the study.

In 1995 and 1996, chlorophyll remained very low throughout the month of May while inorganic nutrients were present, suggesting other controls on the phytoplankton community. During the time of lowest chlorophyll (days 124-149), nitrate+nitrite, silicate and phosphate were available in the water column (Figure 4). This suggests that nutrients had been replenished by tidal and wind mixing but chlorophyll biomass remained low, possibly due to grazing control from zooplankton. In addition, ammonia concentrations, not examined in this study, probably increased due to zooplankton excretion and other forms of regeneration. The ammonia would preferentially be removed by phytoplankton, reducing the uptake of nitrate+nitrite and leaving higher concentrations of the "new" nitrogen in the water column.

I speculate that copepods of the genus *Neocalanus*, whose life cycle includes ontogenetic migrations (Fulton 1973; Miller and Clemons 1988), found to be present at this station (Cooney and Coyle 1996), graze heavily during the post-bloom accumulating lipids and keeping phytoplankton standing stocks, but not productivity, at minimal levels. Zooplankton data from the same site showed high settled volumes during the post-bloom but low volumes during the bloom (Figure 20). The zooplankton included the *Neocalanus* copepods (Cooney and Coyle 1996). There exists a negative correlation in 1995 ($r = -0.83$) and 1996 ($r = -0.51$) between zooplankton settled volume and integrated chlorophyll *a* in the bloom and post-bloom periods. This suggests grazing control by zooplankton.

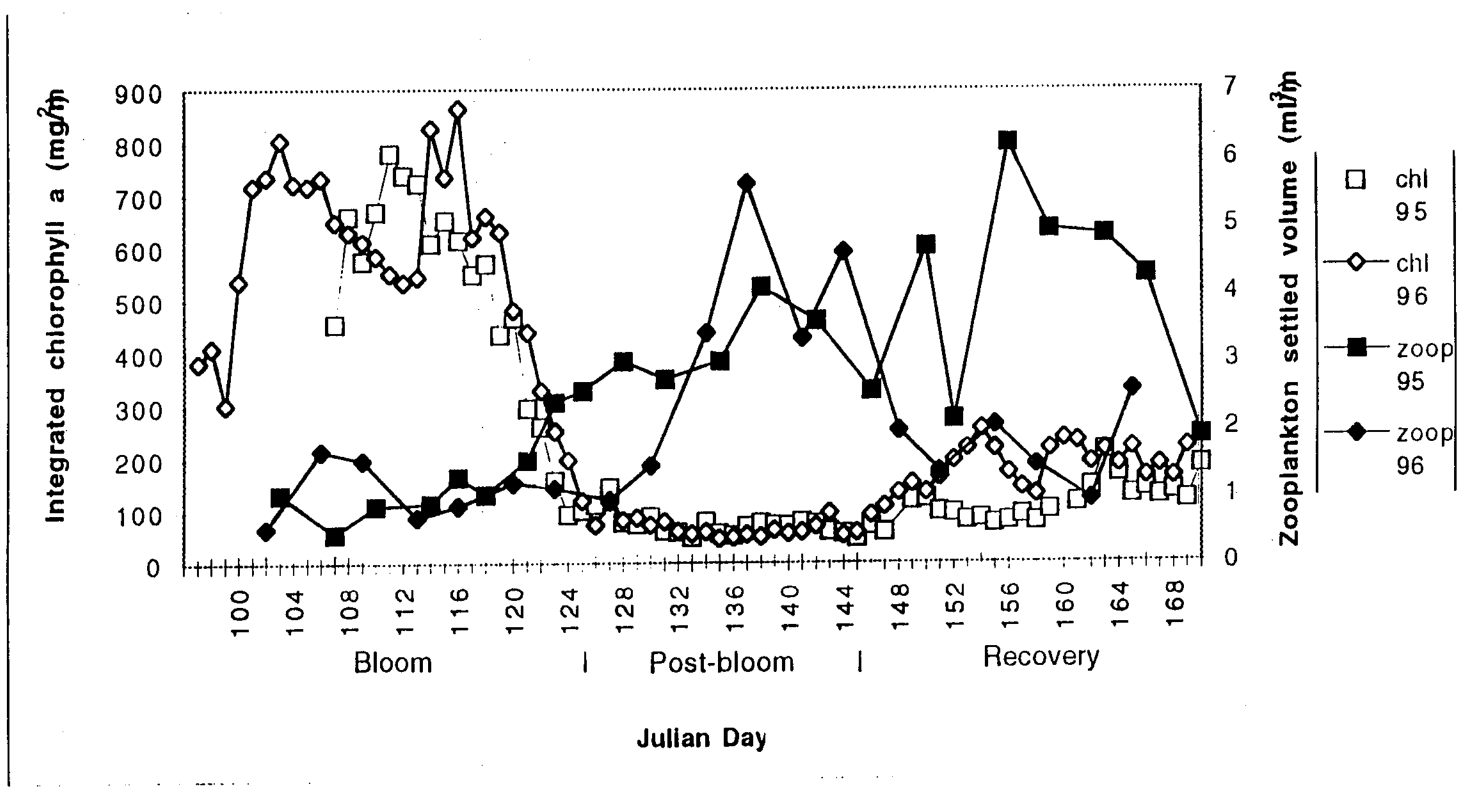

Figure 20. Depth-integrated chlorophyll *a* and zooplankton settled volume (Eslinger 1997) from spring 1995 and 1996.

Another piece of evidence that supports top-down control during the post-bloom period is the 12 day lag in the change of the phytoplankton community size structure as chlorophyll *a* was diminished (Figure 7B). Larger cells persisted until around day 136, suggesting grazing control on microalgae rather than nutrient driven succession in the early days of the decline. *Neocalanus* spp. are known to graze on *Thalassiosira weissflogii*, a centric diatom with a similar diameter to the species found in this study, in the subarctic Pacific Ocean (Frost et al. 1983) and therefore probably fed on the major constituents in Prince William Sound. In both years, chlorophyll reappears after day 146 due to the release of top-down control as the large copepods, *Neocalanus plumchrus* and *Neocalanus flemingeri*, descend to depth in late May (Cooney and Coyle 1996).

The phytoplankton increased after day 146 but remained a fraction of the April biomass. This pattern was a result of a combination of reduced grazing, increased water stability and decreased nutrient concentrations. Large copepods were now mostly absent from surface waters. However, other zooplankton, especially the small copepod *Pseudocalanus* spp., which can feed at low prey density on the same sizes of diatoms as *Neocalanus* (Frost et al. 1983; Valiela 1984), still were present in high biomass (Cooney and Coyle 1996), cropping a smaller proportion of the phytoplankton stocks. By June, the waters were stratified and the nutrient-rich deeper layers were restricted from mixing into surface waters. Nutrient concentrations in the photic zone were lower than in early April and were rapidly depleted by primary producers. These effects restricted the growth of the algae in early summer.

Vertical distribution of chlorophyll fluctuated throughout the season but displayed little interannual variability. During the bloom in both years, the highest chlorophyll concentration was in the upper 25 m. However, substantial concentrations (up to 15 mg/m^3) of chlorophyll were measured at 75 m. The chlorophyll concentrations extended into deep layers because vertical mixing occurred in April and the stability of the water column was weak. This was especially apparent in 1996 when strong stratification did not develop until after the bloom had subsided in May. Cells can survive below the 1 % light depth as long as they spend a portion of the day conducting sufficient photosynthesis to exceed losses from respiration within the photic zone (Round 1981). Thus, phytoplankton sampled below the compensation depth likely survived because they were continuously mixed in and out of the euphotic zone during the bloom period. During May, all depths had low chlorophyll levels. By June, due to solar heating and freshwater additions, the waters stratified and mixing below 25 m was restricted. At this time, the majority of the phytoplankton was confined to the upper 25 m.

2.2 Species Succession

In northern temperate waters the seasonal succession of phytoplankton is well documented (Valiela 1984). During periods of high nutrients, the spring bloom is composed of chain-forming diatoms, with high chlorophyll per cell, followed by flagellate dominance plus sparse numbers of diatoms tolerant of low nutrient conditions. In Prince William Sound, the size fractionation studies were the first to confirm this succession. The succession sequence was from high amounts of microplankton during the bloom to low picoplankton biomass, followed by a slight recovery of the microplankton, nanoplankton and picoplankton biomass. The fractionation results were in agreement with results from Boca de Quadra in southeast Alaska, where the researchers found a shift from netplankton (> 5 µm) dominance in March to ultraplankton (< 5 µm) by May and July (VTN Consolidated, Inc. 1980).

During the spring bloom, the same species returned annually. There was substantial interannual variability in abundance and carbon biomass, but not chlorophyll. In both years *Thalassiosira* spp., *Skeletonema costatum*, and *Chaetoceros* spp. were major constituents but different species dominated each year and interannual abundance and carbon biomass varied among species. In 1995, *Skeletonema costatum* dominated the abundance but *Thalassiosira* spp. dominated the carbon biomass. This was due to the larger cell volume of *Thalassiosira*. These diatoms have 4-50 times the volume of the smaller *Skeletonema* cells (Table 3). In contrast to total carbon biomass, the chlorophyll concentration was similar between years, so the chlorophyll per cell was higher in 1995. This may be attributed to different factors. *Thalassiosira* spp. was more abundant in 1995 than 1996. *Thalassiosira* spp. have large cell volumes and therefore, under optimal conditions, potentially should have greater amounts of chlorophyll per cell than smaller diatoms. *Thalassiosira fluviatilis* and *T. allenii*, two species < 35 µm in diameter, contained 1.37-6.63 pg chlorophyll/cell (Perry et al. 1981) and 30-58 pg chlorophyll/cell (Redalje and Laws 1983), respectively, under different light and nutrient conditions. *Skeletonema costatum*, under the same high light conditions as *T. fluviatilis*, has 0.58 pg chlorophyll/cell (Perry et al. 1981). Consequently, 1996 had approximately the same amount of chlorophyll because *Thalassiosira* spp. was less abundant than in 1995, and *Skeletonema costatum*, with low amounts of chlorophyll/cell, occurred in highest abundance.

In 1996, *Skeletonema costatum* dominated both abundance and biomass. *Thalassiosira* spp. and *Chaetoceros* spp. were insignificant in comparison. There were at least two to three times the cell abundance and carbon in 1996 than in 1995, but chlorophyll levels were only slightly higher. There is not a fixed relationship between total chlorophyll and total carbon (Darley 1982). Chlorophyll may have been approximately the same because the predominant species only has one to two chloroplasts per cell (Tomas 1996), a small volume, and a low amount of chlorophyll per cell (Perry et al. 1981; Darley 1982). This hypothesis is also supported by the carbon to chlorophyll ratio. From laboratory studies, *Skeletonema costatum* is known to have a carbon to chlorophyll ratio of 26 if not nutrient limited (Darley 1977). In 1996, in Prince

William Sound, when most of the carbon was derived from *Skeletonema costatum* the carbon to chlorophyll ratio averaged 22 throughout the bloom above 50 m (Table 5).

A second factor that may have contributed to the chlorophyll levels was the response by phytoplankton to different amounts of light each year. High light intensity inhibits photosynthesis and the production of plant pigments (Darley 1982; Valiela 1984). Cells grown in high light intensity have less chlorophyll/cell (Darley 1982). Results from cloud cover data collected daily at the AFK Hatchery revealed that 1996 had a slightly greater number of days with < 50 % cloud cover during the bloom than did 1995 (Table 7). The interannual difference in cloud cover was greater during the post-bloom and recovery periods. The higher frequency of partly cloudy days may have inhibited the production of chlorophyll in algal cells due to greater light intensity at the surface.

Table 7. Number of days having < 50 % cloud cover, median cloud cover during each period, and number of days observed from April-June 1995 and 1996 at AFK Hatchery (unpublished data).

	1995			1996		
Period	< 50 % cloud cover	Median cloud cover (%)	n	< 50 % cloud cover	Median cloud cover (%)	n
Bloom	11	100	27	13	90	29
Post-bloom	4	100	21	10	17.5	18
Recovery	4	50	25	8	95	25

The response to light and species composition could have caused the differences in the chlorophyll/cell in Prince William Sound. The findings in the current study are in agreement with results from in Auke Bay, Alaska by Ziemann et al. (1991) who found depth-integrated chlorophyll levels lower than peak depth-integrated chlorophyll levels when the abundance of *Skeletonema costatum* reached a maximum of approximately 11,000 cells/mL. They reasoned that this was due to the small size of the species and narrow depth distribution. However this explanation is unconvincing and I hypothesize that the low chlorophyll values were due to the low amounts of chlorophyll/cell in *Skeletonema costatum*.

As the spring bloom progressed, the pattern of phytoplankton succession from flagellate dominance to a mixed different diatom and flagellate community occurred each year from May to June. In May, almost all of the carbon was of flagellate origin in the periods of lowest chlorophyll. As alluded to previously, grazers appeared to harvest the large diatoms as fast as cells replicated. The flagellates and smaller diatoms, like the long narrow *Pseudo-nitzschia* spp., were all that remained in the water.

Most of the flagellates were < 5 μm and may have been an unsuitable size of food for large copepods. *Phaeocystis* sp., a possible major constituent of the flagellate community, has been found unsuitable as food for *Calanus* sp. and *Pseudocalanus* sp. copepods (Bautista et al. 1992). By June, the large *Neocalanus* copepods had left the surface waters (Cooney and Coyle 1996) and large cells again appeared in the water. At this time, *Rhizosolenia fragilissima*, a diatom species not seen in April, became the primary constituent in terms of carbon biomass in both years due to its large cell volume. In 1995, it contributed almost all of the diatom biomass but in 1996 a few previous community constituents, e.g. *Chaetoceros* spp. and *Skeletonema costatum*, persisted in the warmer temperatures and low nutrient conditions and occurred in low numbers.

The major diatom species present in April and June were those adapted to surviving in high latitude coastal waters (Valiela 1984). The dominant diatom genera and species in both years at the peak of the bloom were *Skeletonema costatum*, *Thalassiosira* spp., *Chaetoceros* spp., and *Pseudo-nitzschia* spp. All are characteristically found in the early stages of the bloom when nutrients concentrations are high. These diatoms are species that can bloom after sedimentation and resuspension and survive in turbid waters (Round 1981). Their dominance of the community is probably a result of rapid uptake of nutrients, high nutrient affinity, cold temperature tolerances and rapid growth.

Skeletonema costatum is found worldwide (Round 1981). It can survive in a broad range of light and temperature conditions, absorb organic material as a nutrient source and, in contrast with other colonial cells, decrease its sinking rate by forming long chains. From laboratory studies, *Skeletonema costatum* was found to have a lower half saturation constant for silicate than *Thalassiosira pseudonana* and *T. decipiens* (Paasche 1973). This may have enabled it to survive longer in low silicate conditions. These adaptations of *Skeletonema costatum* could have given it a competitive edge over *Thalassiosira* spp., especially in 1996 when silicate concentrations were lower and water column stratification was weaker. *Thalassiosira* spp. has a greater diameter and is likewise denser than *Skeletonema costatum*, so it is more likely to sink out of the photic zone as stratification increases and viscosity decreases due to warming. This factor may also have contributed to its lower abundance in 1996.

In June as the microplankton returned, around day 160, there was a shift in succession to *Rhizosolenia fragilissima* in both years. This genus is typically found in late stages of blooms (Round 1981; Valiela 1984). It has the ability to survive under low nutrient conditions in stratified waters (Valiela 1984) and it has been found to have endosymbiotic relationships with nitrogen fixing cyanobacteria in oceanic waters (Paerl 1995). These adaptations could enable *Rhizosolenia fragilissima* to outcomplete *Skeletonema costatum* when environmental conditions were less favorable.

The phytoplankton abundance, carbon biomass and species composition did not change substantially over the upper 50 m. During the bloom, when substantial chlorophyll concentrations extended down to 75 m, large numbers of phytoplankton were also found at depths below the euphotic zone. At this time, the same species in similar proportions were located at all depths. Only 50 m had lower abundance of algae. These features of the distribution can be attributed to vertical mixing. Sinking of cells is probably a minor factor because the settling of cells from nutrient-rich surface waters is insignificant compared to the turbulent mixing. Even in June when the surface waters were fairly well-stratified (especially in 1995) minor mixing events, due to tidal currents and geostrophic flows presumably submerged live cells as deep as 50 m.

The species composition and abundance of the phytoplankton community in Prince William Sound discussed here are similar to those in Alaska coastal and oceanic regions (Horner et al. 1973; Iverson et al. 1974; VTN Consolidated, Inc. 1980; Kocur 1982; Ziemann et al. 1991). In Valdez Narrows, Horner et al. (1973) found the abundant species in late April to be *Thalassiosira* spp., *Chaetoceros* spp. and *Phaeocystis pouchetii* at the surface. It is possible, based on the similarity in appearance, that what they have identified as *P. pouchetii* may be the same as a flagellate that I could not clearly identify and therefore have labeled "unidentified flagellate". No colonial *Phaeocystis* was observed in either year in Prince William Sound. *Skeletonema costatum* did not appear until November in Valdez Narrows but did appear in April at other Port Valdez study sites (Horner et al. 1973). These results support my findings, except for a greater abundance and earlier appearance of *Skeletonema costatum* in the southwest Prince William Sound study site. However, Horner et al. (1973) only sampled one day at one depth in late April, and the bloom was probably already in decline.

In Auke Bay, Alaska, a time series of diatom species composition from 2 m was collected from 1985-1989 (Ziemann et al. 1991). Like Prince William Sound, the same species returned annually in different proportions to compose the bloom. Two periods during spring and early summer (one around day 100 and the second around day 160) showed peak abundance of different diatoms. Cell abundance ranged from 0-12,000 cells/mL with *Skeletonema costatum* being the major constituent of the phytoplankton after the peak of the bloom. The timing, not the abundance, contrasts with this study. In Prince William Sound, *Skeletonema costatum* occurs in highest abundance during the height of the bloom. In Auke Bay, *Thalassiosira aestivalis* was the dominant plankton during the primary spring bloom (Ziemann et al. 1991). Similar to 1996 in Prince William Sound, Auke Bay in 1987 was a year with high abundance of *Skeletonema costatum* (approximately 11,000 cells/mL) in the spring. This demonstrates how one small chain-forming diatom species can dominate the cell counts in some years but not others. My findings show a succession to *Rhizosolenia fragilissima* in early June. This was not seen in either the Auke Bay (Ziemann et al. 1991) or the Port Valdez studies (Horner et al. 1973).

3. Relationship to Upper Trophic Levels

3.1 Food Availability

When determining food availability for trophic transfer it is necessary to consider organic carbon and species composition in the waters and not just chlorophyll concentrations or cell abundance. In both years, the highest amounts of diatom carbon available to herbivores were present in April. This phytoplankton bloom may have triggered some over-wintering, deep water zooplankton to migrate to upper waters to feed in late April (Cooney and Coyle 1996). Due to the slow reproductive rates of zooplankton in comparison to algae, the phytoplankton escaped predation early in the season. In 1995 and 1996, most of the carbon originated as chain forming diatoms, *Thalassiosira* spp. and *Skeletonema costatum*. These genera are known to be heavily grazed upon by zooplankton (Round 1981; Valiela 1984; Nejstgaard et al. 1995). However, in 1996 there was a two- to three-fold increase in carbon biomass during the bloom. Since zooplankton are known to increase fecundity and therefore increase density in response to food density (Valiela 1984), 1996 should have been a more fruitful year for secondary producers. Consequently, since copepods including, *Neocalanus* spp. and *Pseudo-calanus* spp., are known to be a major prey for pollock (Cooney and Coyle 1996), salmon (Willette et al. 1995) and Pacific herring (Foy et al. 1997) in Prince William Sound and schools of these forage fish are found in high densities in southwest Prince William Sound (Willette et al. 1995; Stokesbury et al. 1997), 1996 might have been a better year for fisheries recruitment.

The *Exxon Valdez* oil spill occurred March 24, 1989 during the onset of the phytoplankton bloom. Since crude oil affects light transparency and cell respiration (Round 1981) phytoplankton growth may have been hampered or some phytoplankton may have died rapidly from pollutant effects. Data collected two weeks after the spill in Prince William Sound, showed higher concentrations of chlorophyll *a* in the southeast than the southwest (McRoy and Eslinger 1995), where the oil had drifted covering the western region (Galt et al. 1991). These chlorophyll concentrations were lower than levels in either 1995 or 1996, possibly due to oil pollution. In 1989 in southwest Prince William Sound, lower levels of organic carbon biomass would have limited zooplankton production. This loss would have transferred to the 1989 year class of pink salmon, herring and pollock reducing larval survival and recruitment.

4. Future Research

To better understand the phytoplankton and nutrient dynamics of Prince William Sound additional research needs to be conducted. Two to three additional years of data need to be collected to document interannual variability. The addition of a fluorometer attached to the CTD would give more information about the vertical distribution of phytoplankton biomass. A time series of productivity data and ammonium concentrations would help elucidate the controls on the phytoplankton community. The deployment of a sediment trap could determine how much primary productivity is lost to the benthos due to sinking. Lengthening the study period to include late summer and fall would allow for determination of any fall bloom and the major constituents of that bloom

Additional species composition work needs to be conducted. I would suggest sampling more days from only one depth in the upper 10 m throughout the spring, summer and fall to document changes in species succession. Epi-fluorescence techniques could be applied to determine the abundance and carbon biomass of bacteria, mixotrophs, and heterotrophic phytoplankton. A study of the micro-zooplankton (ciliate) abundance would be beneficial in understanding the grazing controls on the phytoplankton community throughout the year.

CONCLUSIONS

- The bloom began in early April, declined by May and exhibited a small recovery in June.
- The phytoplankton biomass was likely nutrient controlled from the bottom up in April, followed by top-down grazing control in May.
- The bloom consisted of 80 % microplankton: the post bloom was predominantly picoplankton followed by a small diatom recovery.
- High levels of phytoplankton biomass and abundance extended down to 50 m with little variation in species composition.
- A seasonal succession of the diatom community occurred from *Skeletonema costatum*, *Thalassiosira* spp. and *Chaetoceros* spp. in April to *Rhizosolenia fragilissima* in June.
- In 1995, *Thalassiosira* spp. contributed 73-80 % of the diatom carbon, and in 1996 *Skeletonema costatum* made up 58-78 % of the carbon during the bloom.
- Flagellate carbon was the main constituent in the post-bloom of both years while *Rhizosolenia fragilissima* composed the majority of the carbon biomass during the recovery.
- More than twice as much organic carbon was present in 1996 than 1995.
- 1996 had a greater biomass of organic carbon and therefore a potentially greater food supply for zooplankton.
- The timing of the bloom and the temporal and vertical patterns of the phytoplankton succession in southwest Prince William Sound in 1995 and 1996 resembled other marine environments of similar latitude.

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APPENDIX 1

0 m Phytoplankton (cells/ml)	April									May			June		
	Julian Day 1995														
	108	109	110	112	113	114	116	117	119	133	135	137	162	164	166
Asterionella glacialis	0	19	21	13	17	40	20	23	7	0	0		0	0	0
Biddulphia sp.	0	0	0	0	0	0	0	0	0	0	0		0	0	0
Chaetoceros spp.	129	145	60	235	148	227	206	164	280	1	0	-	2	49	10
Cocconeis sp.	0	0	0	0	0	0	0	0	0	0	0	-	0	1	0
Coscinodiscus spp.	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0
Eucampia spp.	0	8	0	0	0	5	3	0	4	0	0	-	0	0	0
Fragilariopsis sp.	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0
Grammatophora sp.	0	4	0	0	0	0	0	0	0	0	0	-	0	0	0
Leptocylindrus danicus	0	5	0	21	12	15	3	0	8	0	0	-	1	2	0
Leptocylindrus minimus	320	64	31	37	20	23	61	0	35	5	0	-	0	4	0
Licmophora sp.	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0
Navicula spp.	0	0	0	0	0	0	0	0	0	0	0	-	0	0	1
Pseudo-nitzschia spp.	52	67	24	181	121	127	121	133	156	0	29	-	3	2	1
Rhizosolenia fragilissima	0	0	0	0	0	0	0	0	0	0	0	-	364	686	314
Skeletonema costatum	238	399	335	794	624	582	831	568	686	0	0	-	0	0	0
Stephanopyxis nipponica	0	0	0	3	1	0	0	0	5	0	0	-	0	0	0
Thalassionema nitzschioides	0	0	0	0	0	9	0	3	0	0	0	-	0	0	0
Thalassiosira spp.	593	288	377	769	509	576	501	249	386	1	5	-	2	12	1
Unidentified centric	0	0	0	0	0	0	0	0	0	0	0	-	0	0	3
Unidentified diatoms	31	0	0	0	0	0	0	0	0	0	0	-	0	0	3
Unidentified pennate	0	0	1	10	0	0	0	5	0	0	0	-	0	0	0
Ceratium spp.	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0
Dinophysis spp.	0	0	0	0	0	0	0	0	0	0	0	-	0	1	2
Distephanus speculum	0	0	0	0	0	0	0	0	0	0	0	-	3	4	2
Ebria tripartita	0	0	0	0	0	0	0	0	0	0	0	-	1	2	2
Peridinium spp.	0	0	0	0	0	0	0	0	1	0	0	-	0	1	0
Unidentified dinoflagellates	0	0	0	3	0	5	1	6	17	0	1	-	3	0	0
Unidentified flagellates	2489	756	565	1430	840	1210	1198	1805	1901	385	565	-	832	847	858
Unidentified silicoflagellates	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0

Julian Day

5 m Phytoplankton (cells/mL)	April 108	109	110	112	113	114	116	117	119	May 133	135	137	June 162	164	166
Asterionella glacialis	0	29	85	17	28	19	18	15	15	0	0	0	0	0	0
Biddulphia sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaetoceros spp	593	67	143	337	212	156	216	158	214	7	0	5	3	25	0
Cocconeis sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Coscinodiscus sp.	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Eucampia spp.	0	0	3	0	0	5	3	1	0	0	0	0	0	0	0
Fragilariopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatophora sp.	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0
Leptocylindrus danicus	0	18	1	0	32	15	0	0	4	0	0	0	0	0	1
Leptocylindrus minimus	589	24	138	17	43	17	0	16	82	0	0	0	0	0	9
Leptocylindrus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Licmophora sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Navicula spp.	0	0	0	8	0	0	0	0	0	0	0	0	1	0	2
Pseudo-nitzschia spp.	117	56	96	89	133	137	99	88	129	1	29	17	5	14	1
Rhizosolenia fragilissima	0	0	0	0	0	0	0	0	0	1	0	0	321	664	425
Skeletonema costatum	362	583	814	707	752	586	885	481	572	0	0	0	0	0	0
Stephanopyxis nipponica	4	0	0	4	0	5	0	0	0	1	0	0	0	0	0
Thalassionema nitzschioides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalassiosira spp.	731	372	569	965	471	364	568	434	356	2	4	1	12	12	1
Unidentified centric	0	0	0	5	0	0	0	0	0	0	0	0	0	0	5
Unidentified diatoms	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified pennate	3	0	4	5	0	0	0	4	0	0	0	0	1	0	0
Ceratium spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Dinophysis spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Distephanus speculum	0	0	0	0	0	0	0	0	0	0	0	0	3	1	3
Ebria tripartita	0	0	0	0	0	0	0	0	0	0	0	0	1	1	6
Peridinium spp.	0	0	0	0	0	0	4	3	0	0	0	1	0	0	0
Unidentified dinoflagellates	9	0	0	7	0	0	24	15	20	1	2	0	1	0	0
Unidentified flagellates	2231	639	1459	1747	1106	752	1880	1900	1402	340	609	502	491	1087	1049
Unidentified silicoflagellates	10	0	0	17	0	0	0	0	0	0	0	0	0	0	0

10 m Phytoplankton (cells/mL)	Julian Day														
	April									May			June		
	108	109	110	112	113	114	116	117	119	133	135	137	162	164	166
Asterionella glacialis	32	12	36	13	45	25	38	6	-	0	0	0	0	0	0
Biddulphia sp.	0	0	0	0	0	0	0	0		0	0	0	0	0	0
Chaetoceros spp.	85	57	159	220	196	238	207	145		0	0	23	46	44	5
Cocconeis sp.	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
Coscinodiscus spp.	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
Eucampia spp.	3	0	4	4	5	3	0	0	-	0	0	0	0	0	0
Fragilariopsis sp.	0	0	0	0	0	0	0	0	-	0	0	4	0	0	0
Grammatophora sp.	0	3	0	0	0	0	0	0	-	0	0	0	0	0	0
Leptocylindrus danicus	7	0	0	23	34	9	0	0	-	0	0	6	0	2	1
Leptocylindrus minimus	195	11	404	7	183	78	17	28	-	1	0	0	1	5	5
Leptocylindrus spp.	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
Licmophora sp.	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
Navicula spp.	0	0	0	0	0	0	0	0	-	0	0	0	0	2	1
Pseudo-nitzschia spp.	115	52	56	139	150	116	73	112	-	11	41	59	6	2	0
Rhizosolenia fragilissima	3	0	0	0	0	0	0	4	-	0	0	0	369	480	400
Skeletonema costatum	449	668	332	1047	1645	856	375	832	-	0	0	0	0	0	0
Stephanopyxis nipponica	0	3	4	4	1	0	0	3	-	0	0	0	0	0	0
Thalassionema nitzschioides	0	0	8	0	0	4	0	0	-	0	0	0	0	0	0
Thalassiosira spp.	389	307	479	621	884	529	369	505	-	2	1	0	11	3	3
Unidentified centric	0	0	0	5	0	0	0	0	-	0	0	0	0	0	8
Unidentified diatoms	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
Unidentified pennate	0	0	4	3	0	0	4	0	-	0	1	0	1	0	0
Ceratium spp.	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
Dinophysis spp.	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
Distephanus speculum	0	0	0	0	0	0	0	0	-	0	0	0	3	3	3
Ebria tripartita	0	0	0	0	0	0	0	0	-	0	0	0	4	3	4
Peridinium spp.	0	0	0	0	0	0	0	0	-	0	0	1	0	1	0
Unidentified dinoflagellates	0	0	7	0	20	0	1	11	-	2	1	0	0	0	0
Unidentified flagellates	1573	933	1422	1119	1645	1234	869	1066	-	432	638	881	557	734	731
Unidentified silicoflagellates	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0

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25 m Phytoplankton (cells/mL)	Julian Day														
	April									May			June		
	108	109	110	112	113	114	116	117	119	133	135	137	162	164	166
Asterionella glacialis	44	5	52	32	17	49	22	12	13	0	0	0	0	0	0
Biddulphia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaetoceros spp.	51	65	145	156	203	145	160	167	112	2	1	17	13	13	8
Cocconeis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coscinodiscus spp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucampia spp.	0	0	0	4	0	0	0	0	1	0	0	0	0	0	0
Fragilariopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatophora sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Leptocylindrus danicus	13	4	0	0	15	0	0	4	22	0	0	8	0	3	3
Leptocylindrus minimus	87	34	518	7	4	75	48	25	43	0	0	0	10	0	0
Leptocylindrus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Licmophora sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Navicula spp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pseudo-nitzschia spp.	79	81	53	117	111	99	115	120	86	8	22	35	3	0	0
Rhizosolenia fragilissima	0	0	0	1	0	0	0	0	0	0	0	0	528	436	469
Skeletonema costatum	563	618	316	647	363	356	524	533	297	0	0	0	0	0	0
Stephanopyxis nipponica	1	3	8	3	0	4	3	0	0	0	1	0	0	0	0
Thalassionema nitzschioides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalassiosira spp.	556	386	567	512	436	413	412	258	387	3	2	4	8	10	3
Unidentified centric	0	0	0	0	5	1	0	0	0	0	0	0	0	0	3
Unidentifed diatoms	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified pennate	0	0	3	0	0	5	6	0	0	0	0	0	1	0	0
Ceratium spp.	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Dinophysis spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Distephanus speculum	0	0	0	0	0	0	0	0	0	0	0	0	5	1	1
Ebria tripartita	0	0	0	0	0	0	0	0	0	0	0	0	7	1	1
Peridinium spp.	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
Unidentified dinoflagellates	0	0	19	1	3	7	5	12	0	5	0	0	5	1	0
Unidentified flagellates	1480	791	1185	1425	820	1485	1477	642	1049	513	562	598	568	551	528
Unidentified silicoflagellates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

50 m Phytoplankton (cells/mL)	Julian Day														
	April									May			June		
	108	109	110	112	113	114	116	117	119	133	135	137	162	164	166
Asterionella glacialis	26	14	21	15	39	34	15	22	19	0	0	0	0	0	0
Biddulphia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaetoceros spp.	128	41	124	87	85	102	151	123	277	2	0	1	17	9	2
Cocconeis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coscinodiscus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucampia spp.	3	0	0	0	0	0	0	0	5	0	0	0	0	0	0
Fragilariopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatophora sp.	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptocylindrus danicus	0	5	7	8	0	12	0	5	21	0	0	1	0	0	0
Leptocylindrus minimus	8	11	26	3	0	30	0	10	0	0	0	0	1	0	0
Leptocylindrus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Licmophora sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Navicula spp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Pseudo-nitzschia spp.	54	46	66	43	18	78	116	127	71	17	31	4	6	0	1
Rhizosolenia fragilissima	0	0	0	0	0	0	0	0	0	0	0	0	324	349	179
Skeletonema costatum	330	379	424	417	510	352	485	557	267	0	0	0	0	0	0
Stephanopyxis nipponica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalassionema nitzschioides	12	0	0	0	0	0	0	3	1	0	0	0	0	0	0
Thalassiosira spp.	266	314	251	305	493	361	466	260	229	6	1	2	13	6	0
Unidentified centric	0	0	0	0	1	1	3	0	0	0	0	0	0	0	3
Unidentified diatoms	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0
Unidentified pennate	3	0	0	0	1	0	0	0	0	0	2	0	1	0	0
Ceratium spp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Dinophysis spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Distephanus speculum	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Ebria tripartita	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Peridinium spp.	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Unidentified dinoflagellates	4	10	1	1	10	0	21	3	18	2	0	0	1	0	0
Unidentified flagellates	682	705	525	576	1269	609	1629	1565	960	466	576	284	475	312	249
Unidentified silicoflagellates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 2

0 m Phytoplankton (cells/mL)	Julian Day 1996															
	April										May			June		
	102	104	106	108	110	112	114	116	118	120	136	138	140	159	161	163
Asterionella glacialis	0	0	13	5	14	0	31	3	0	14	0	3	0	0	0	12
Biddulphia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaetoceros deciprens	0	0	0	0	10	0	0	5	0	0	0	0	0	0	0	4
Chaetoceros spp.	2311	953	686	735	596	502	955	1063	1300	724	21	39	80	320	440	438
Cocconeis sp.	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucampia spp.	0	4	9	0	3	0	4	6	0	0	0	0	0	1	0	0
Fragilariopsis sp.	168	0	39	4	25	0	52	8	0	22	0	0	0	0	5	0
Grammatophora sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptocylindrus danicus	54	26	13	8	26	23	19	0	0	0	1	3	5	26	21	36
Leptocylindrus minimus	0	19	15	23	0	5	28	49	12	15	20	6	33	45	61	34
Licmophora glacialis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Navicula spp.	5	4	4	8	5	4	1	3	0	0	0	1	0	0	0	0
Pseudo-nitzschia spp.	529	321	269	281	306	241	331	498	338	347	24	19	8	71	123	120
Rhizosolenia fragilissima	3	9	2	1	0	1	8	5	25	0	0	3	5	339	270	181
Rhizosolenia stolterforthii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Skeletonema costatum	7553	5741	9086	3521	3988	3024	3665	3950	1442	1880	7	0	0	51	58	59
Stephanopyxis nipponica	0	0	2	5	0	0	5	0	0	0	0	0	0	0	0	0
Thalassionema nitzschioides	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Thalassiosira spp.	351	273	260	146	258	132	476	194	244	231	3	8	0	0	1	3
Unidentified centric	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified pennate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratium furca	0	0	0	0	0	0	0	0	0	0	0	0	1	1	3	0
Ceratium spp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Distephanus speculum	0	0	2	0	1	0	1	0	0	0	0	0	0	0	9	3
Ebria tripartita	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
Peridinium spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
Unidentified dinoflagellates	0	9	0	0	0	12	12	5	17	9	4	7	2	8	8	5
Unidentified flagellates	729	666	1504	899	1771	1262	1834	1691	816	944	1014	776	632	1349	1688	876

5 m Phytoplankton (cells/mL)	April 102	104	106	108	110	112	114	116	118	120	May 136	138	140	June 159	161	163
Asterionella glacialis	0	0	0	0	0	4	0	18	0	0	0	1	0	0	0	0
Biddulphia sp.	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0
Chaetoceros deciprens	0	0	0	0	5	0	5	0	1	0	0	0	0	0	0	0
Chaetoceros spp.	1653	1321	977	585	478	408	1358	1268	1021	757	37	10	103	234	504	502
Cocconeis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucampia spp.	0	0	0	0	10	3	1	5	3	6	0	0	0	6	0	0
Fragilariopsis sp.	39	58	13	44	165	6	56	0	0	10	0	0	0	0	0	0
Grammatophora sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptocylindrus danicus	29	26	22	14	19	17	12	0	0	0	3	0	0	28	27	25
Leptocylindrus minimus	0	11	19	12	18	0	5	30	26	45	14	4	15	111	85	45
Licmophora glacialis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Navicula spp.	8	4	2	3	3	1	1	0	0	3	0	0	2	0	0	0
Pseudo-nitzschia spp.	502	359	202	209	278	336	311	425	423	303	27	10	10	80	101	94
Rhizosolenia fragilissima	0	0	0	4	4	4	10	19	9	1	6	3	14	300	269	124
Rhizosolenia stolterforthii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Skeletonema costatum	8147	5968	5339	4561	2981	3578	3675	4379	2592	2331	5	16	0	43	98	84
Stephanopyxis nipponica	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Thalassionema nitzschioides	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Thalassiosira spp.	384	211	189	214	207	130	431	274	248	213	3	3	1	1	5	4
Unidentified centric	5	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Unidentified pennate	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ceratium furca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ceratium spp.	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0
Distephanus speculum	3	0	0	0	1	0	0	0	0	0	0	0	1	1	0	4
Ebria tripartita	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Peridinium spp.	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified dinoflagellates	30	6	0	0	0	0	3	8	5	31	5	3	6	7	3	3
Unidentified flagellates	1228	754	880	1291	1472	1538	1461	1859	795	1104	773	773	646	1149	1256	1140

10 m Phytoplankton (cells/mL)	Julian Day															
	April										May			June		
	102	104	106	108	110	112	114	116	118	120	136	138	140	159	161	163
Asterionella glacialis	0	0	0	10	12	5	34	17	5	22	0	1	0	1	5	6
Biddulphia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaetoceros deciprens	0	0	15	0	0	0	14	0	0	0	1	0	0	0	0	0
Chaetoceros spp.	1172	887	768	746	555	305	1110	1349	1197	821	16	25	98	323	407	399
Cocconeis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucampia spp.	0	0	0	0	0	4	3	3	3	0	0	0	0	1	0	3
Fragilariopsis sp.	145	47	0	90	39	13	41	22	4	0	0	2	0	0	0	0
Grammatophora sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptocylindrus danicus	8	17	0	18	28	9	18	4	0	0	0	1	1	41	4	41
Leptocylindrus minimus	5	4	13	3	12	8	9	43	39	28	17	4	43	79	103	34
Licmophora glacialis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Navicula spp.	8	4	6	5	1	1	3	0	0	0	0	0	0	0	0	0
Pseudo-nitzschia spp.	504	301	232	270	290	241	318	616	423	271	25	11	11	111	105	152
Rhizosolenia fragilissima	0	2	0	0	1	3	0	4	9	12	6	4	10	389	234	219
Rhizosolenia stolterforthii	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
Skeletonema costatum	8891	12072	5967	5156	4977	2091	4520	5775	3642	2037	6	0	0	0	61	65
Stephanopyxis nipponica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalassionema nitzschioides	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	3
Thalassiosira spp.	349	155	213	302	261	147	416	274	247	218	1	1	1	0	0	1
Unidentified centric	0	4	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified pennate	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratium furca	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Ceratium spp.	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Distephanus speculum	3	2	0	0	0	0	3	0	0	0	0	0	0	0	0	5
Ebria tripartita	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Peridinium spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified dinoflagellates	0	9	0	1	3	4	10	13	1	5	1	2	6	10	8	9
Unidentified flagellates	757	1815	1184	1437	2021	1200	1216	1462	948	633	573	807	626	1671	866	1101

25 m Phytoplankton (cells/mL)	Julian Day															
	April										May			June		
	102	104	106	108	110	112	114	116	118	120	136	138	140	159	161	163
Asterionella glacialis	13	0	4	19	5	4	23	12	27	15	0	0	0	3	5	0
Biddulphia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaetoceros deciprens	6	0	4	0	0	0	0	0	0	0	0	0	0	0	14	0
Chaetoceros spp.	838	1154	1139	735	675	487	1263	1172	833	794	41	20	19	194	360	310
Cocconeis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucampia spp.	1	0	0	0	6	0	0	8	0	0	1	0	0	0	0	1
Fragilariopsis sp.	44	75	41	3	71	12	32	25	8	0	0	0	0	0	0	0
Grammatophora sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptocylindrus danicus	6	28	26	22	15	23	18	3	0	0	4	2	0	19	9	23
Leptocylindrus minimus	6	0	23	0	13	5	5	41	22	27	14	7	10	70	116	44
Licmophora glacialis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Navicula spp.	5	3	5	1	3	3	1	0	0	0	0	0	0	0	1	0
Pseudo-nitzschia spp.	280	300	231	266	290	274	318	494	434	214	25	11	13	61	88	89
Rhizosolenia fragilissima	1	3	4	8	1	5	5	4	5	9	6	0	9	382	229	143
Rhizosolenia stolterforthii	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Skeletonema costatum	6720	6710	5922	5226	3232	3594	3052	7369	3484	1735	5	11	0	56	55	104
Stephanopyxis nipponica	3	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Thalassionema nitzschioides	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0
Thalassiosira spp.	167	250	235	173	296	141	311	305	249	164	1	1	1	4	3	3
Unidentified centric	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified pennate	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ceratium furca	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Ceratium spp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Distephanus speculum	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	1
Ebria tripartita	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Peridinium spp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified dinoflagellates	0	0	1	0	5	4	1	9	9	4	1	3	3	7	6	5
Unidentified flagellates	1124	935	1295	1141	1716	1477	1269	1917	1266	611	528	546	575	934	919	718

50 m Phytoplankton (cells/mL)	Julian Day															
	April										May			June		
	102	104	106	108	110	112	114	116	118	120	136	138	140	159	161	163
Asterionella glacialis	0	0	0	6	9	0	0	5	0	8	6	0	0	1	0	0
Biddulphia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaetoceros deciprens	0	0	4	0	0	0	0	10	0	0	0	0	0	0	0	0
Chaetoceros spp.	622	1259	973	598	782	533	824	1059	810	383	24	12	14	305	283	191
Cocconeis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucampia spp.	0	1	3	0	0	5	1	0	3	0	0	0	0	0	0	3
Fragilariopsis sp.	61	13	15	15	67	49	6	30	17	0	0	0	0	13	0	28
Grammatophora sp.	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptocylindrus danicus	18	14	30	13	22	9	32	10	0	0	4	0	0	22	27	10
Leptocylindrus minimus	0	10	0	31	4	13	4	31	32	26	3	6	4	101	74	31
Licmophora glacialis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Navicula spp.	1	4	1	4	1	0	0	0	3	0	0	0	0	0	0	0
Pseudo-nitzschia spp.	172	301	287	201	287	208	293	501	371	185	17	7	3	81	89	81
Rhizosolenia fragilissima	0	1	10	1	9	3	6	5	9	1	1	0	2	402	177	155
Rhizosolenia stolterforthii	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Skeletonema costatum	4810	5619	3122	4271	3708	3250	3010	4664	2816	1149	3	0	0	86	51	60
Stephanopyxis nipponica	0	3	0	0	1	0	3	3	0	0	0	0	0	0	3	0
Thalassionema nitzschioides	0	0	0	15	0	5	0	0	0	0	0	0	0	0	5	0
Thalassiosira spp.	176	182	280	223	187	156	289	436	226	120	1	0	0	1	4	0
Unidentified centric	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified pennate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratium furca	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Ceratium spp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Distephanus speculum	0	0	0	0	3	0	0	0	0	0	0	0	0	1	1	4
Ebria tripartita	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Peridinium spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified dinoflagellates	0	0	0	3	0	3	6	6	9	3	1	2	1	8	0	8
Unidentified flagellates	546	702	481	1576	1548	1262	1502	1761	783	501	410	542	301	959	722	494

APPENDIX 3

Abundance Calculations

1). The dimensions of the settling chamber were determined using a Mitutoya caliper.

Diameter = 25.5 mm

Radius = 12.75 mm

Area of the settling chamber = 510.7 mm^2

2). A rectangular box in the eyepiece of the inverted microscope (field of view) was used when counting phytoplankton cells. Using a micrometer, the dimensions of the field of view were determined to equal 0.44 mm (L) x 0.31 mm (W) on 200 x magnification and 0.220 mm (L) x 0.155 mm (W) on 400 x magnification. The area inside the field of view equaled 0.1364 mm^2 on 200 x and 0.0341 mm^2 on 400 x.

3). Area of each transact sampled was determined:

200 x: Total sample area = (# of fields viewed) * .1364 mm^2

400 x: Total sample area = (# of fields viewed) * .0341 mm^2

4). Total abundance for the entire sample was calculated by using the equation:

$$\text{Abundance (cells/mL)} = \frac{(\text{area settling chamber / total sample area}) * \text{\# of cells counted}}{\text{settled sample volume (mL)}}$$