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I am submitting herewith a thesis written by Mary Evans Culver entitled "The Effects of Environmental Variation on the Sinking Rates of Marine Phytoplankton With an Emphasis on Light Intensity." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

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THE EFFECTS OF ENVIRONMENTAL VARIATION ON THE SINKING RATES
OF MARINE PHYTOPLANKTON WITH AN EMPHASIS
ON LIGHT INTENSITY

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ABSTRACT

The effects of light intensity on the sinking rates of phytoplankton were investigated using cultures of Chaetoceros gracilis and C. flexuosum in laboratory experiments and assemblages from the open ocean and marginal ice zone of the Greenland Sea in field experiments. A homogeneous sample method (SETCOL) was used to determine sinking rates of chlorophyll, biogenic silica, phaeophytin, particulate carbon and particulate nitrogen. For the experiments with diatom cultures, the light intensity under which the culture was grown was positively correlated with sinking rates as measured by chlorophyll and silica as well as with growth rates. Experiments conducted in the field indicated that variation in sinking may be associated with changes in water temperature, density, and nutrient concentrations. Environmental factors explaining variation in sinking rates support the hypothesis that buoyancy regulation is affected by physiological processes. Particulate matter sinking rates in the field were characteristic of passively sinking cells and were somewhat lower than rates previously reported for temperate, sub-polar, and polar regions.

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CHAPTER I

INTRODUCTION

The sinking of phytoplankton cells through the water column contributes to the vertical transfer of organic matter from the euphotic zone into the deep sea. Sediment traps placed below the euphotic zone have recorded a cycle in the supply of organic carbon to the aphotic region that corresponds to the seasonal cycle of primary production in surface waters. This pattern suggests that passive sinking of phytoplankton contributes to organic carbon flux below as well as within the euphotic zone. Evidence of this relationship exists in the Sargasso Sea (Deuser and Ross 1980, Deuser et al. 1981, 1983), the Panama Basin (Honjo 1982), regions of the Pacific Ocean (Betzer et al. 1984, Smith and Baldwin 1984, Knauer et al. 1979), and in some areas of the Arctic Ocean (Honjo et al. 1987).

Phytoplankton sink in various forms, such as aggregates, in fecal pellets, and as individual cells. The organic matter collected in sediment traps consists primarily of large ($> 32 \mu\text{m}$) particles including fecal pellets, marine snow aggregates, and calcareous and siliceous hard parts of larger organisms, which sink on the order of $50\text{-}100 \text{ m day}^{-1}$ (Silver and Alldredge 1981, Deuser and Ross 1980, Seuss 1980). An important mechanism for the transport of particulate organic matter out of the euphotic zone is the transformation of cells into fecal pellets or aggregates which sink at faster rates than individual cells (Smayda 1970, McCave 1975, Lal 1977, Silver and Alldredge 1981).

Increased phytoplankton biomass resulting from higher productivity could result in an increased amount of organic matter sinking out of the euphotic zone. Physiological responses to a change in environment could also change the buoyancy of a cell and affect its sinking rate. Comprehension of the factors controlling primary production in an area could lead to an understanding of the conditions influencing the settling of organic matter.

The Arctic Ocean is characterized by low temperatures, the presence of ice, and seasonal variations in light levels. These conditions dictate low standing stocks of primary producers (Smith et al. 1985) and low growth rates for most marine organisms (Eppley 1972). The melting and freezing of ice controls water temperature and salinity in polar regions. Surface water temperatures range from -1.5 to -1.8°C; surface salinity, from 28 to 33.5 per mil. As seawater loses heat to the atmosphere, crystals may form in the upper layers. These flat crystals consolidate into plates and spicules termed frazil ice. The plates aggregate to form pancake ice, and eventually, floes of ice are created. Thick (3 - 4 m) floes of ice are present year round covering approximately 70% of the Arctic Basin (Pickard 1979). Once formed, large masses of ice can stabilize surrounding water temperatures near freezing. The high specific heat of water prevents wide, rapid changes in temperatures.

The salinity of seawater is affected by ice formation because the salts are not frozen into the ice but are trapped in the crystalline structure. The salinity of the ice decreases with time as the brine

pockets drain, leaving nearly pure ice. In waters where freezing is occurring, the salinity increases. As salinity is the primary factor affecting density at low temperatures, increasing salinity results in increasing density. The newly formed dense, saline water sinks, vertically mixing the water column. If the depth of mixing exceeds critical depth, net primary production will be low (Sverdrup 1953). Conversely, melting ice forms a lens of low salinity water at the surface which stabilizes the upper layers. Phytoplankton production within this favorable light environment can increase the standing stock (McRoy and Goering 1974, Alexander 1980, Smith and Nelson 1985).

Ice and snow restrict the penetration of light, a potentially limiting factor for primary producers, by reflecting a substantial amount (80 to 99%) of incoming radiation (Maykut and Grenfell 1975). Incoming radiation also is affected by the low solar angle at high latitudes. As much as 40% of surface illumination can be reflected off of the sea surface independent of ice (Sverdrup et al. 1942). Considering these factors together, only a small fraction of the incident light penetrates ice-covered water. Additional light limitation results from seasonal extremes in polar regions. Near darkness occurs during winter months while near-continuous illumination is received in the summer. Annually the amount of light totals less than half that received in tropical latitudes (Pickard 1979). Low light levels create a net heat flux from the ocean to the atmosphere maintaining low seawater temperatures.

Low light, temperatures, and nutrient levels limit production in the Arctic. The limited circulation within the Arctic basin restricts nutrient input from surrounding areas. In the upper 10 m during summer, surface nitrate, phosphate, and silicate concentrations were reported to be 0.7, 0.2, and 3.5 μM respectively (Smith et al. 1985). Spring levels may be slightly higher. These nutrient concentrations would not be expected to support large standing stocks of primary producers (Smith et al. 1985). Conditions are more favorable for growth in the seas surrounding the Arctic basin where some interchange between water masses can occur.

The Fram Strait region of the Greenland Sea is an area of exchange between the Arctic and Atlantic Oceans. The East Greenland current flows south-westward, carrying Arctic water and ice along the east coast of Greenland. Approximately one-third of the total cap and pack ice is transported out of the Arctic by this current (Pickard 1979). The West Spitzbergen current carries warm ($3 - 4^{\circ}\text{C}$), saline (34.8 - 35 per mil) Atlantic water northward (Figure 1). The temperature difference between these currents forms a front, and their opposing motion generates transient eddies (Johannessen et al. 1983, Wadhams and Squire 1983). Water column stability, frontal structures, and ice-edge upwelling, each associated with highly productive areas, may occur within this area (Alexander and Niebauer 1981).

The movement of currents in the Fram Strait region favors an ice-melt year-round, allowing the formation of a low salinity region in the upper layers of the water column. The vertical stability combined with

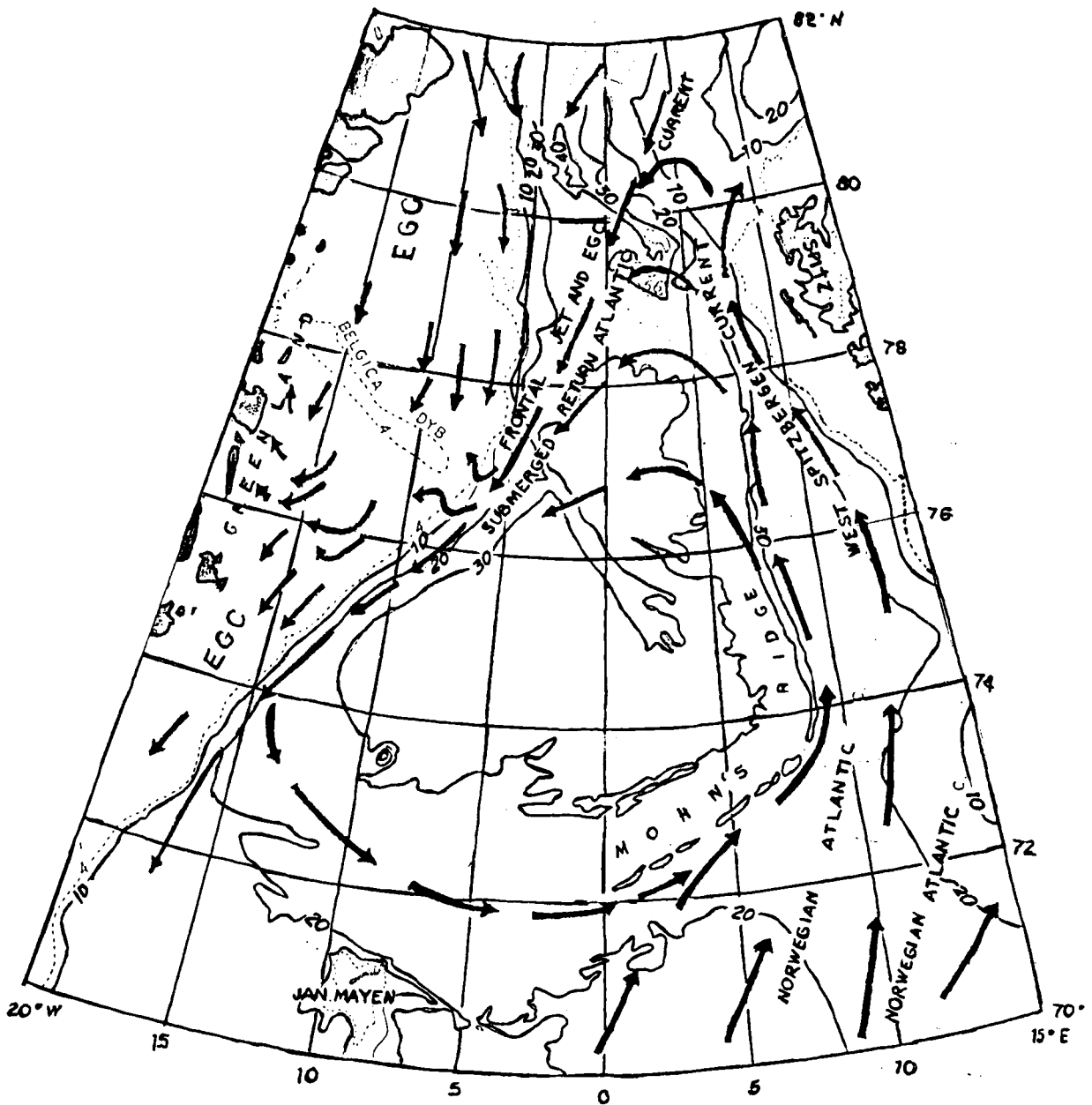


Figure 1. Current patterns in the Greenland-Norwegian Sea (modified from Paquette et al. 1985).

high light intensities, found during the short period from late spring to early summer in marginal ice zones, result in local areas of high productivity (McRoy and Goering 1974, Alexander 1980, Smith and Nelson 1985, Smith et al. 1987). Phytoplankton blooms in the Greenland Sea may ultimately be limited by the low level of nutrients found in Arctic water (Smith et al. 1985).

In stratified areas such as marginal ice zones, the factors which limit photosynthesis, light and nutrients, rarely coincide. At the surface where light is plentiful, nutrients generally are low; while in deeper waters, nutrients are higher, but light levels are low. The capacity of a cell to change its vertical placement within the water column by sinking could maximize conditions for photosynthesis. A cell with a high sinking rate potentially could increase its nutrient uptake by encountering areas of higher nutrient concentration while remaining within the euphotic zone. Cells with low sinking rates would remain, for better or worse, in the same conditions for a longer time period. Differential sinking and mortality rates affect the outcome of competition between algal species more directly than differences in growth rates under given light and nutrient conditions (Reynolds et al. 1982, Harrison et al. 1986).

If phytoplankton cells sank as inert particles, then Stokes' equation could be applied to describe the settling velocity. This equation bases the settling velocity on the difference in density between the liquid medium and the sinking body such that

$$v = \frac{2gr^2(p' - p)}{9n\phi}$$

Where v = velocity of the particle (cm sec^{-1}).

g = gravitational acceleration (cm sec^{-1})

r = radius of the particle (cm)

p' = density of the particle (g cm^{-3})

p = density of the medium (g cm^{-3})

n = viscosity of the medium (g cm-sec^{-1})

ϕ = form resistance of the particle (unitless)

However, experimental evidence indicates that this equation does not account for all the factors affecting sinking rates of phytoplankton. As cell size increases, the velocity does not increase as much as the equation predicts (Eppley et al. 1967b). For small marine and lacustrine particles, Stokes' equation can underestimate the settling velocity by an order of magnitude (Chase 1979, Kawana and Tanimoto 1976, 1979 in Hawley 1982). Surface coatings, solution electrolytes, and dissolved organic substances combine to affect the drag forces on the particles resulting in a settling velocity different from that expected (Chase 1979).

Low sinking rates appear to be associated with actively growing cells in nutrient-replete environments (e. g. Steele and Yentsch 1960, Eppley et al. 1967a, Titman and Kilham 1976, Bienfang et al. 1982, Bienfang 1984). The sinking of senescent cells is three to four times faster than actively growing cells (Smayda 1970). These findings indicate an association between buoyancy regulation and physiological

processes, and therefore, a connection to growth and photosynthetic processes (Steele and Yentsch 1960, Eppley et al. 1967a, Smayda 1970, Anderson and Sweeney 1978, Bienfang 1981a, 1985, Johnson and Smith 1986). If this is the case, environmental variations in nutrients, temperature, and light, which affect production, may also influence buoyancy.

Observations on cultures indicate that cells sink quickly when nutrients are depleted. Bienfang et al. (1982) studied the effect of nutrient limitation on the sinking rate of four diatom species in culture. They found the lowest sinking rates occurred when nutrients were not limiting growth. Silicate depletion caused a significantly higher settling rate. Depletion of nitrate or phosphate resulted in a decreased settling rate for three of the four species. A subsequent study using temperate and sub-tropical assemblages of species yielded a similar result. Silicate and phosphate concentrations were inversely related to sinking while nitrate concentration did not affect sinking (Bienfang and Harrison 1984). Harrison et al. (1986) also showed that cultures of natural assemblages had higher sinking rates under silicate-depleted conditions. From these experiments, the effect of nutrient concentrations does not appear to be simply related to sinking rates. The nutrient as well as the species of phytoplankton involved may affect the relationship between buoyancy and physiology.

The relationship between temperature and sinking is complicated by the fact that a change in temperature affects the density of the seawater as well as the physiology of the cell (Eppley 1972). In a

study using Antarctic assemblages, Johnson and Smith (1986) found significantly lower sinking rates at the pycnocline. However, density and viscosity variations in the seawater could account for only five percent of the variation in sinking rates. Physiological changes must also have occurred. Bienfang and Szyper (1982), working with Ditylum brightwelli, found that sinking rates remained fairly uniform over a range of salinities. Changes in temperature, given a constant salinity, resulted in a non-linear relationship. The minimum sinking rate occurred at 19.5°C. From 12°C to 19.5°C, the rate decreased linearly; from 19.5°C to 25°C, the rate increased linearly with a greater slope. The sinking rate responded to temperature in a manner similar to the response of growth rate to temperature for this species. This similarity supports the hypothesis that metabolic processes are involved in sinking rate variation. The effects of temperature may be a "second-order modifier" of sinking rates initially influenced by the physiological condition of the assemblage (Bienfang and Szyper 1982).

The amount of light an assemblage receives also appears to affect settling rates. As with nutrients, the relationship between light intensity and sinking is not simple and may be species-specific. Reviewing several experiments, Smayda (1970) concluded that light intensity and photoperiod clearly influence buoyancy. Two later studies showed that natural assemblages settled faster during evening hours than during daylight (Bienfang 1985, Johnson and Smith 1986). These findings are supported by culture experiments (Eppley et al. 1967a). In contrast, Skeletonema costatum and Ditylum brightwelli exhibited

lower sinking rates in the dark compared to experiments performed in the light (Steele and Yentsch 1960, Anderson and Sweeney 1977, 1978). The lowest sinking rates for Thalassiosira weissflogii and a subtropical assemblage occurred at one to three percent of full light intensity (Bienfang et al. 1983, Bienfang 1980). The latter studies suggest that slow growth in combination with low light results in physiological changes which lower sinking rates.

Low settling rates at light levels characteristic of the subsurface chlorophyll maximum (one to three percent of surface illumination) could aid in the maintenance of that layer (Bienfang 1980, 1985, Bienfang et al. 1983). The layer is created by a combination of factors. Shade adaptation causes an increase in chlorophyll a per cell. Cellular growth rates may be slightly higher because of increasing nutrient concentrations in deeper waters. A decreased settling rate coincident with that layer would result in an accumulation of cells which would then undergo the changes which increase chlorophyll.

Cellular responses to changes in light intensity include changes in photosynthetic pigment content, enzyme activity, cell volume, respiratory rate, and chemical composition (Falkowski 1980). Any or all of these factors can affect primary production, cell density, and therefore, the sinking rate of the cell. With light intensity and other environmental factors changing through the water column, a cell must constantly adjust to new conditions.

The set of experiments presented used cultures and natural assemblages to isolate the effect of changes in light intensity on sinking rates. Laboratory experiments with diatom cultures were used to provide control over temperature and nutrient conditions and to ascertain species-specific sinking responses to light intensity. Variations in growth rate were examined for similarities to sinking rate responses. A field study with natural assemblages expanded the varying factors to include light, temperature, salinity, and nutrients, as well as the number of species involved. These data were used to further examine environmental variations affecting sinking rates of small particulate matter.

CHAPTER II

METHODS AND MATERIALS

Sinking rate measurements

A homogeneous sample method, SETCOL (Bienfang 1981b), was used to estimate the sinking rates of both the unialgal cultures in the lab and the heterogeneous assemblages in the field studies. This method uses settling columns filled with a uniformly distributed sample. A sinking rate is calculated based on any change in the vertical distribution of biomass after a measured amount of time. Chlorophyll, phaeophytin, biogenic silica, particulate carbon, and particulate nitrogen were used as indicators of biomass.

The settling chambers are cylinders of clear Plexiglass fused at the bottom with a Plexiglass funnel (Figure 2). A clear Plexiglass water jacket surrounds the cylinder enabling circulating water to control the temperature. A lid fits into the top of the chamber to increase column stability.

For both lab and field experiments, the columns were filled with a seawater sample for which biomass concentrations were determined (b_{00}). The sample settled undisturbed for three hours. After that time, biomass determinations again were made on an aliquot of the original sample (b_{0t}) which was maintained outside of the column under the same environmental conditions. This control accounted for any change in the original sample resulting from processes other than sinking. The upper portion of the sample was drained through the side

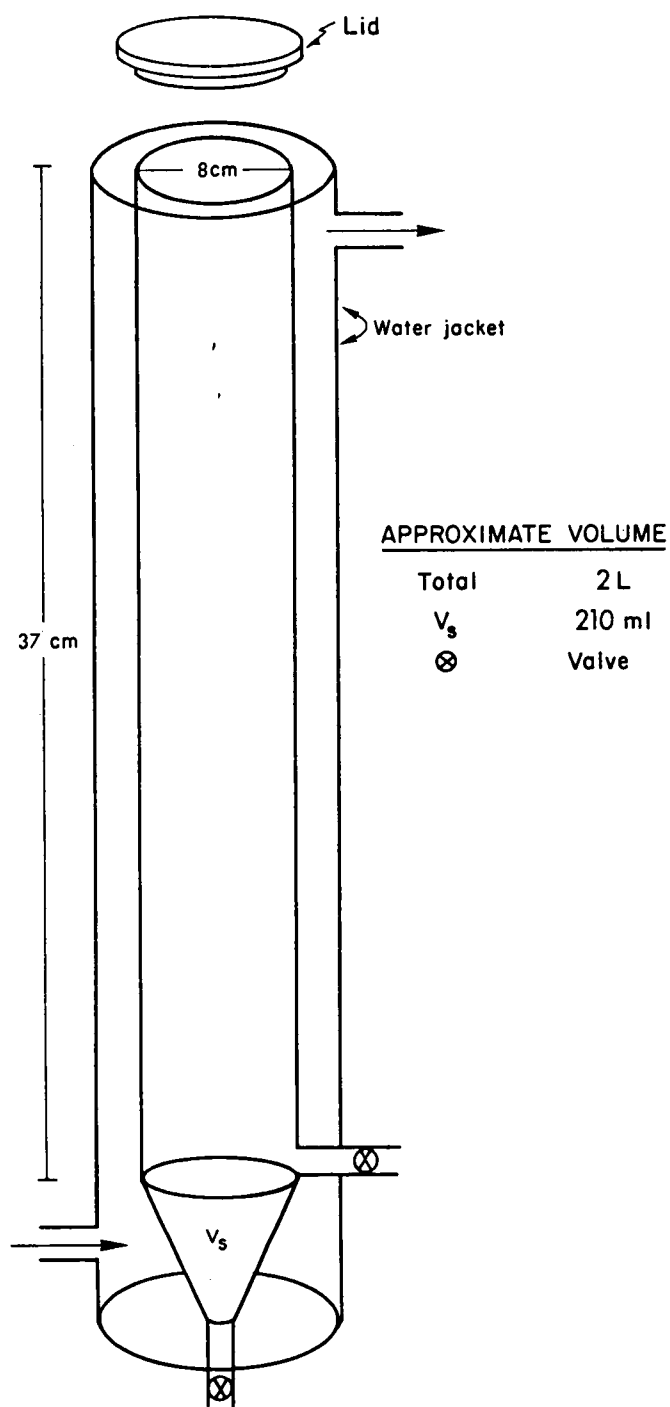


Figure 2. Settling column used to measure sinking rates of suspended particulates (modified from Bienfang 1981a).

valve of the chamber. The remaining volume (V_s) was agitated and decanted through the bottom valve. Biomass calculations were performed on the settled volume (b_s).

The total biomass (B_t) was determined using the total volume of the chamber (V_t) and an average of the biomass parameters over the time during which the experiment was conducted.

$$B_t = \frac{1}{2} (b_{oo} + b_{ot}) * V_t$$

The settled amount of biomass is calculated as:

$$B_s = V_s b_s - \frac{1}{2} (b_{oo} + b_{ot}) * V_s$$

The sinking rate (Ψ) is based upon the change in biomass of the settled region (B_s) compared to the initial total biomass (B_t), as well as the length of the column (l), and the time allowed for settling (t) such that:

$$\Psi = (B_s * l) / (B_t * t)$$

This equation produces sinking rates in distance time⁻¹. In this study all measurements were made in units of m day⁻¹.

Laboratory experiments

Cultures of Chaetoceros gracilis and C. flexuosum were individually cultured under a range of light intensities. C. gracilis is a single-cell centric diatom found in neritic temperate regions (Lebour 1978). It was maintained at approximately 27°C, under continuous illumination. C. flexuosum (clone AA63) was obtained from the Culture Collection of Marine Phytoplankton at Bigelow Laboratory for Ocean Sciences. Originally collected in the Antarctic, this species was kept under 24-hour illumination in an incubator at

approximately 2°C. Single-species cultures were chosen over an assemblage of phytoplankton in order to minimize any scatter resulting from differing responses by species to a varying factor.

Turbidostats were maintained in f/2 medium (Guillard and Ryther 1962). Daily monitoring of chlorophyll indicated that the cells remained in exponential phase of growth, a requirement to avoid any differences in sinking arising from aging of the culture.

Light intensity was varied using neutral-density screening over glass carboy containers. For C. gracilis the illumination ranged between seven and 100 $\mu\text{E m}^{-2} \text{ sec}^{-1}$. The range for C. flexuosum varied from 15 to 125 $\mu\text{E m}^{-2} \text{ sec}^{-1}$.

Each culture was maintained at the appropriate light intensity for a minimum of five generations before sinking experiments were conducted. This time period allowed the cells to achieve some degree of adaptation to the environmental conditions. For each light intensity, three to four replicate sinking experiments were conducted.

Growth rate constants for each culture were estimated from the daily chlorophyll measurements using a least-squares regression analysis (Sokal and Rohlf 1981). The specific growth-rate constant, k , was calculated using the regression line (Stanier et al. 1970).

Field experiments

Field experiments were conducted aboard the F. S. Polarstern during 19 May - 4 June 1987 as part of the Greenland Sea Project. Two locations in the Fram Strait region were sampled intensively

(Figure 3). Each transect crossed through a front in each of the areas. The East box, an open ocean area, consisted of stations between 74° 00' and 75° 15' North Latitude and 4° 10' and 9° 30' East Longitude. The West Box, 77° 20' to 78° 50' N and 5° 45' W to 3° 30' E, was sampled from 29 May through 4 June. The latter box, consisting of stations 118 - 179, was in a marginal ice zone.

Conductivity, temperature, and depth (CTD) measurements were collected using a Nell Brown instrument. Water samples were collected at depths using 10 l Niskin bottles.

Sinking rate experiments were conducted with samples collected from depths corresponding to 100%, 30%, and 5% of incident light. A secchi disk was used to determine the appropriate sampling depths. A total of thirty stations were sampled. The columns were placed on the upper deck of the ship under natural light. Gimbal frames kept the columns stable by counteracting the movement of the ship (Figure 4). The frames were shaded using neutral density filters so that settling occurred at a light level approximating that at which the samples were collected.

Biomass analysis

Chlorophyll a, a component of phytoplankton biomass, and phaeopigments, the degradation products of chlorophyll due to zooplankton grazing, were measured in duplicate by filtering a known sample volume (0.03 - 0.10 l) onto Gelman A/E (laboratory) or Whatman GF/F (field) glass-fiber filters and extracting in 90% acetone. For the culture experiments, the filters were ground by hand prior to

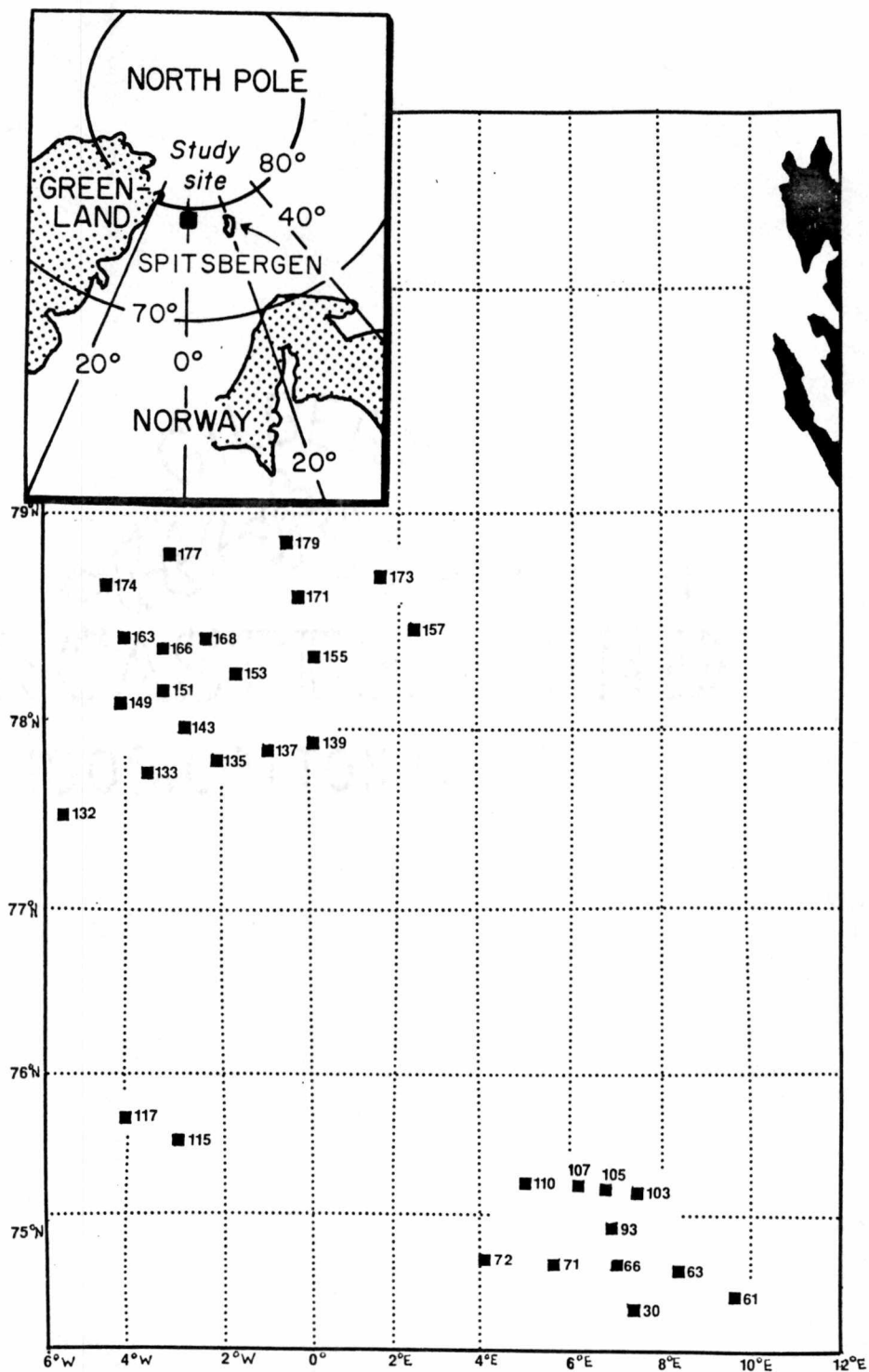


Figure 3. Map of Fram Strait showing station locations at which sinking rate experiments were conducted.

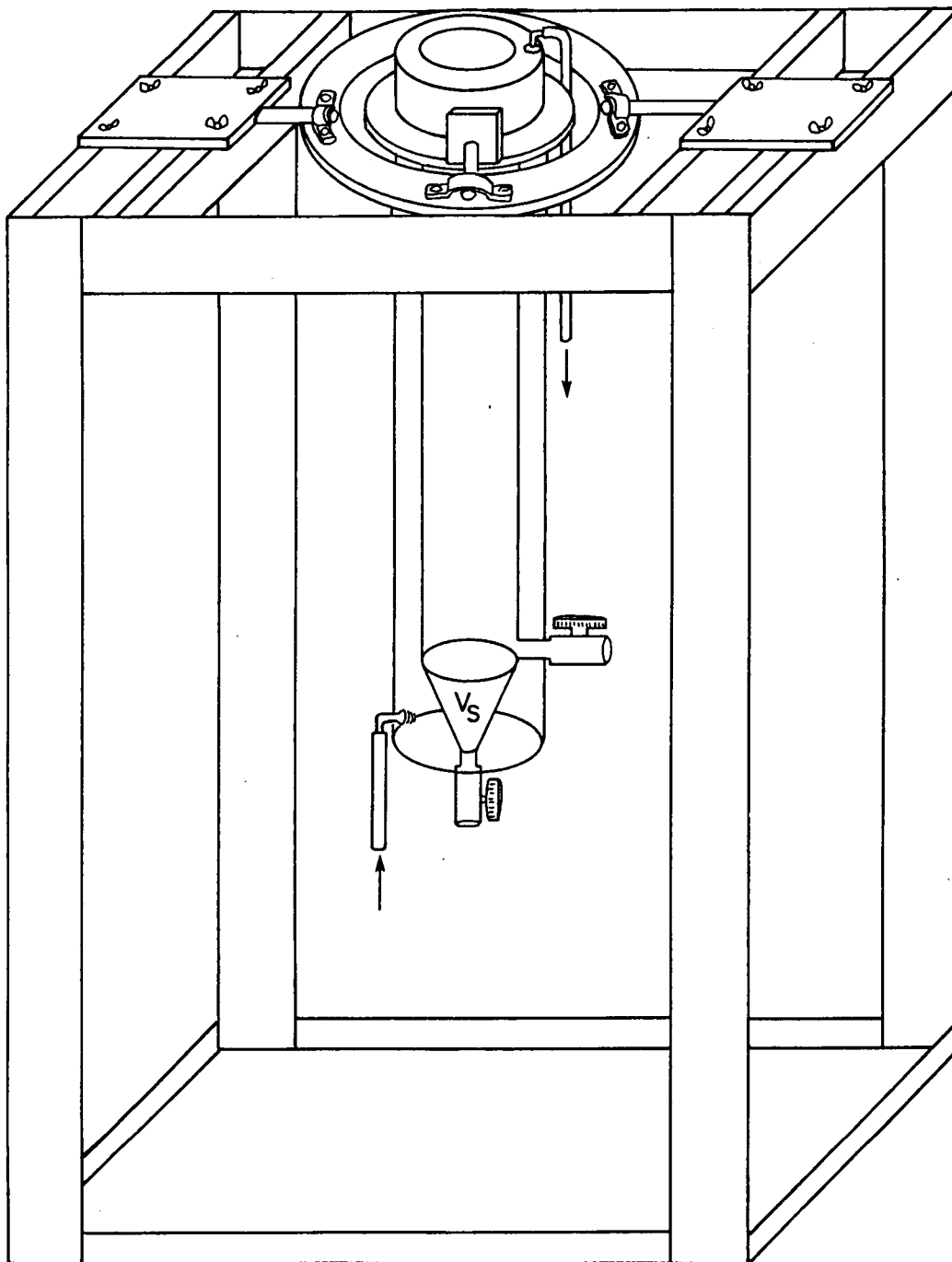


Figure 4. Settling column in gimbal apparatus.

extraction (Holm-Hansen et al. 1965). An ultrasonic processor (Heat-Systems-Ultrasonics, Inc., Model W-385) was used aboard ship to disrupt the cells. The filters were subject to sonication for 10 min at 70% maximum output while in an ice bath and in the dark (M. J. Perry pers. comm). Fluorescence was measured with a Turner Designs fluorometer before and after acidification with a few drops of 5% HCl. A purified chlorophyll a standard (Sigma) dissolved in 90% acetone was used to calibrate the fluorometer.

Particulate carbon and nitrogen measurements are indicative of elemental pools comprised of detritus, heterotrophs, and phytoplankton (Hunter and Laws 1981). These samples were collected by filtering a known volume of sample (0.03 - 0.10 l) onto a Gelman A/E or a Whatman GF/F glass- fiber filter which had been precombusted at 450°C for four hours. Filters were rinsed with 0.01 N HCl in filtered seawater, dried, and stored in combusted glass vials at 60°C. All samples were analyzed at the University of Tennessee with a Perkin - Elmer 240 B Carbon - Hydrogen - Nitrogen elemental analyzer. Second filters placed under the primary filters and processed identically served as blanks.

Biogenic silica analysis identifies organisms which assimilate silicic acid to form a test structure. Diatoms and silicoflagellates contribute to this parameter (Paasche 1980). A known volume of sample (0.03 - 0.10 l) was vacuum filtered onto a 0.6 μ m Nuclepore filter. The filters were dried and stored individually in sterile plastic Petri dishes at 60°C. Biogenic silica was converted to dissolved reactive silicate using a sodium hydroxide digestion method (Paasche 1973) and

measured on a Hitachi Model 100-20 spectrophotometer using a 1 cm cell (Parsons et al. 1984a). A solution of 100 μ M sodium silicofluoride was used to calibrate the spectrophotometer.

Statistical analysis

Statistical analysis of the data from culture experiments consisted of analysis of variance tests and correlation calculations. If the analysis of variance indicated a significant association between sinking rates and light intensity, the correlation coefficient was calculated to determine the degree of association.

For the experiments performed aboard ship, a stepwise-multiple regression (Statgraphics) was performed to see if variability in sinking rates could be explained by variability in the environment. A separate multiple regression was attempted for each biomass parameter for data collected in the open ocean and for that collected in the marginal ice zone. The environmental variables considered were water temperature, salinity, sigma-t, nitrate, silicate, and phosphate concentrations, and light level as a function of incident irradiance at the time of sampling.

CHAPTER III

RESULTS

Laboratory experiments

Sinking rates for Chaetoceros gracilis were low, from 0.007 m day^{-1} to 0.119 m day^{-1} as measured using chlorophyll. These low rates are typical of previously reported rates for C. gracilis of 0.15 m day^{-1} as measured using chlorophyll (Bienfang et al. 1982). Carbon-chlorophyll ratios averaged 27.5 with a range of 14.3 to 36.5. These values are representative of vigorously growing cells in nutrient-replete environments (Parsons et al. 1984b).

For C. gracilis, light intensity appears to significantly affect the sinking rate as measured by chlorophyll and biogenic silica. In each case, a log transformation of the light intensity measurements produces a significant linear association between light and sinking rates (Figures 5 and 6). Chlorophyll sinking rates and the log of light intensity have a correlation coefficient (r) of 0.75 ($p < 0.001$). The degree of association between sinking rates as measured by silica and the log of light intensity is less ($r = 0.50$) but is statistically significant ($p < 0.01$) showing a positive relationship.

The measurements using particulate carbon as a biomass indicator were more variable than those for chlorophyll or silica. Although not statistically significant, a trend toward increasing sinking rates with increasing light intensity was observed (Figure 7). Experiments in which high sinking rates were estimated also showed increased carbon-

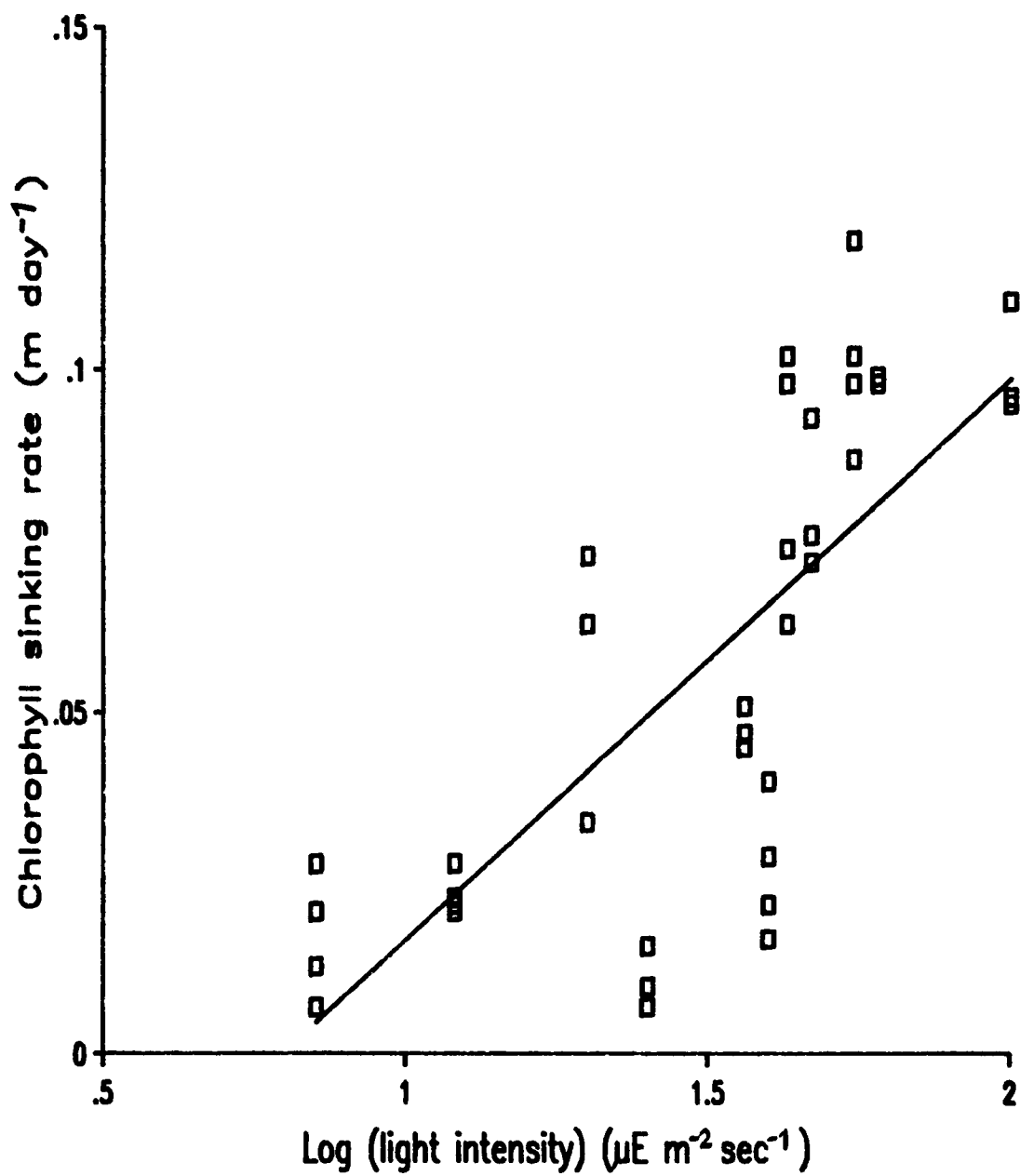


Figure 5. Relationship between chlorophyll sinking rates and the log of light intensity for C. gracilis ($r = 0.92$, $p < 0.001$).

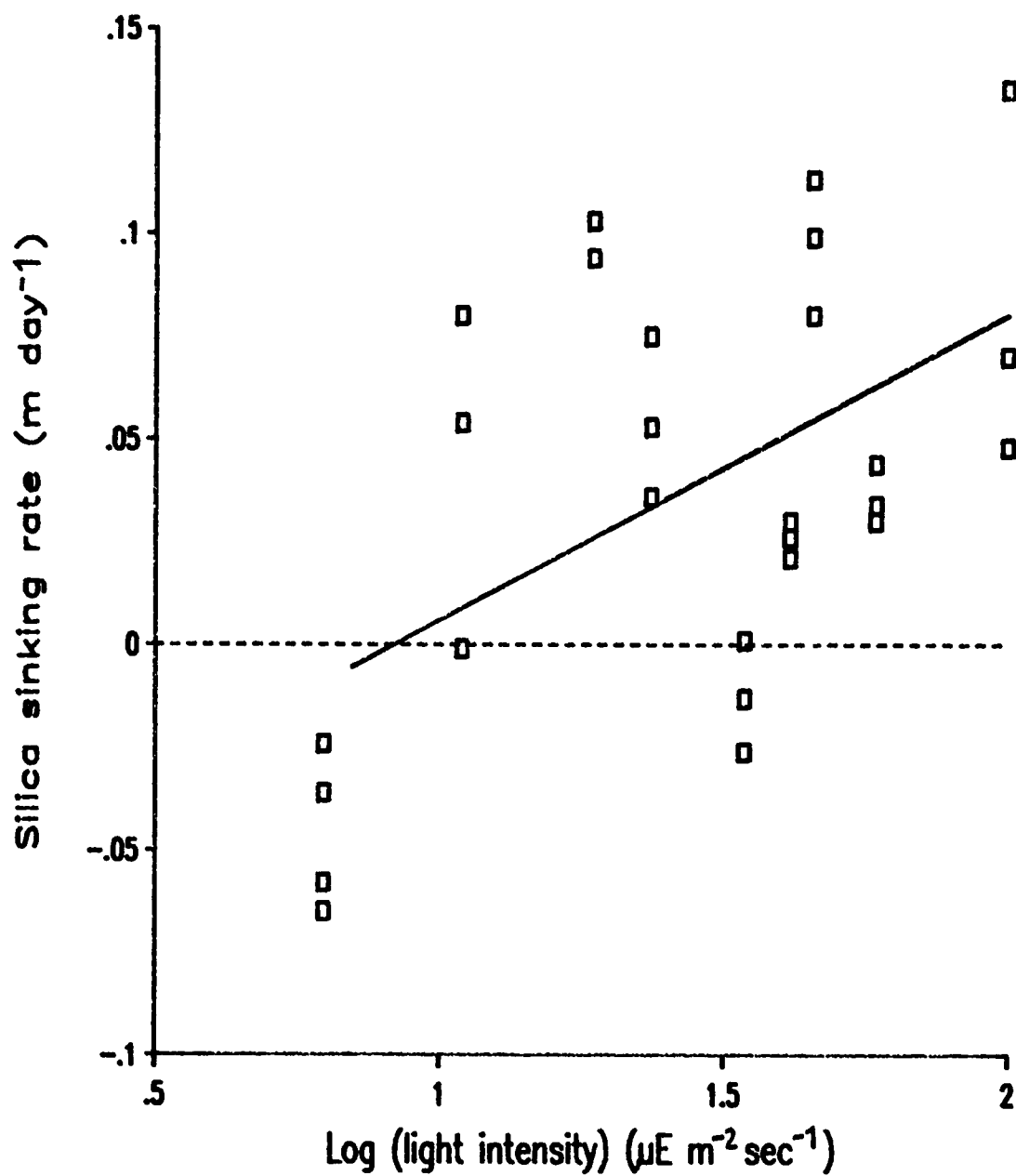


Figure 6. Relationship between silica sinking rates and the log of light intensity for *C. gracilis* ($r = 0.50$, $p < 0.001$)

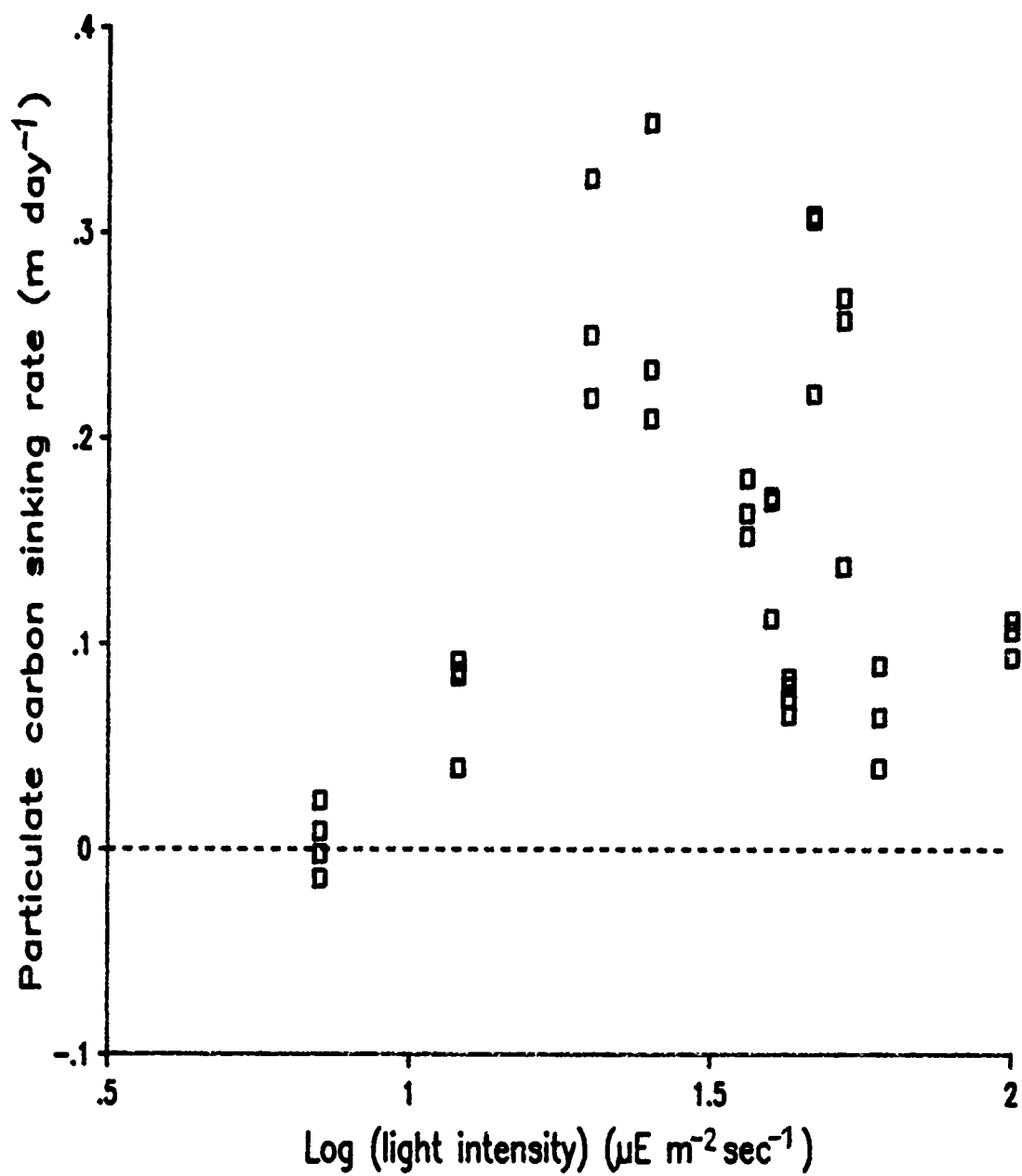


Figure 7. Relationship between particulate carbon sinking rates and the log of light intensity for *C. gracilis*.

chlorophyll ratios after sinking than were present prior to sinking. For example, the sample at $20 \mu\text{E m}^{-2} \text{ sec}^{-1}$ with $1.00 \text{ dbt day}^{-1}$ initially had a carbon-chlorophyll ratio of 28.7. The settled sample had a ratio of 44.5. This increase in non-chlorophyll related carbon can be attributed to the more rapid settling of detrital particles relative to viable cells. Detrital material would contribute to the faster sinking rates of particulate carbon compared to chlorophyll. Carbon sinking rates ranged from $-0.014 \text{ m day}^{-1}$ at $7 \mu\text{E m}^{-2} \text{ sec}^{-1}$ to 0.327 m day^{-1} for a sample at $20 \mu\text{E m}^{-2} \text{ sec}^{-1}$.

Growth rate also increased with light intensity (Figure 8). The relationship appears slightly curvilinear. Rapid changes occur in the middle of the light range and begin to level off as the species approaches its maximum growth rate at this temperature. As would be expected given this association, sinking rates are also correlated with growth rates (Figures 9 and 10). In this range, the relationship between these variables appears to be linear. The correlation coefficient for chlorophyll is 0.83 ($p < 0.001$); for silica, $r = 0.42$ ($p < 0.05$). Carbon measurements again were variable but showed a trend toward increasing sinking rates with increasing growth rate (Figure 11).

Several complications arose during the experiments with the Antarctic culture which make the results difficult to interpret. Twice while experiments were being conducted, the incubator failed and temperatures rose above those recommended for the maintenance of this species. At one point, a different culture batch was sent from Bigelow

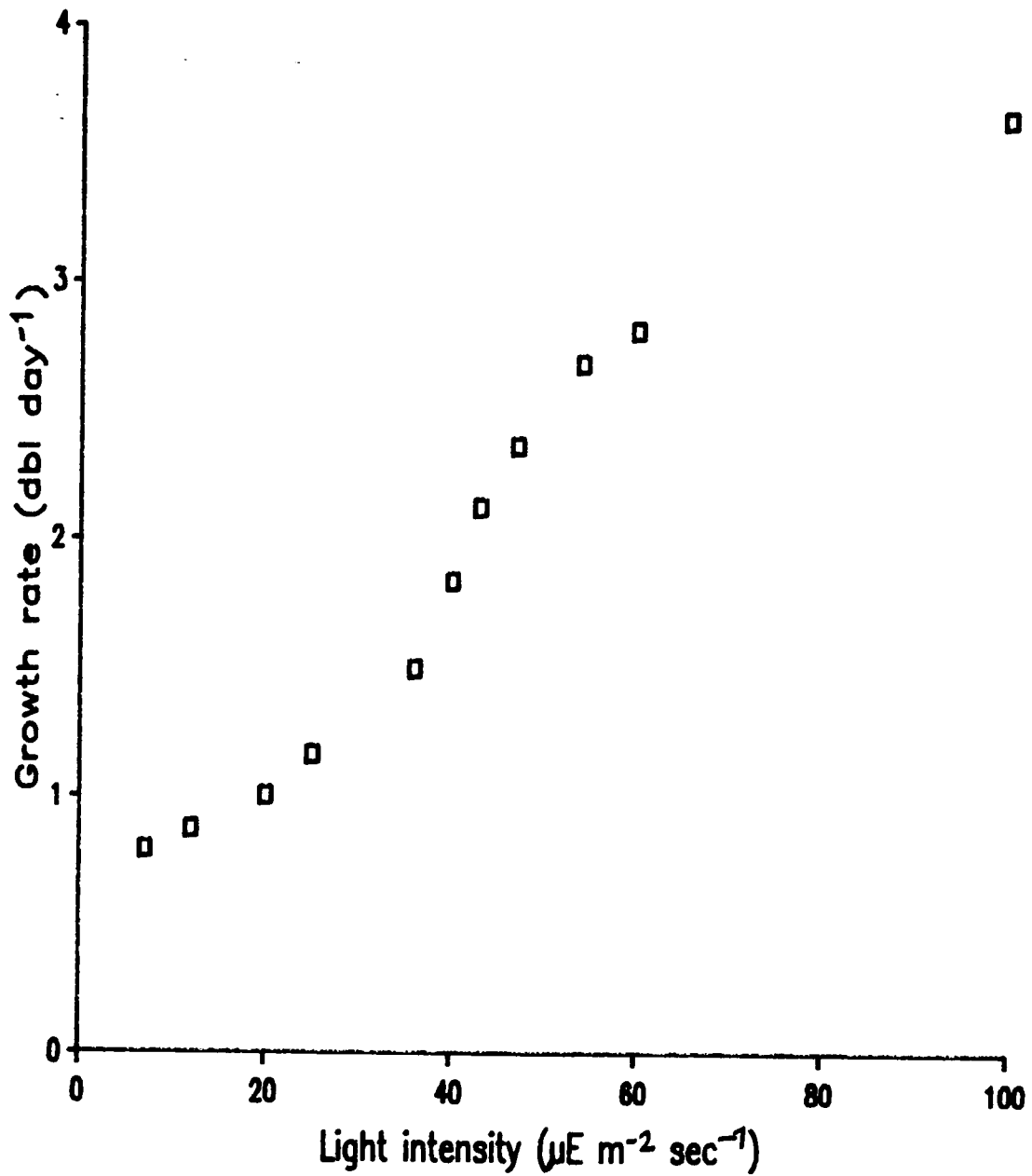


Figure 8. Relationship between the specific growth rate of C. gracilis and the light intensity under which it was grown ($r = 0.98$, $p < 0.001$).

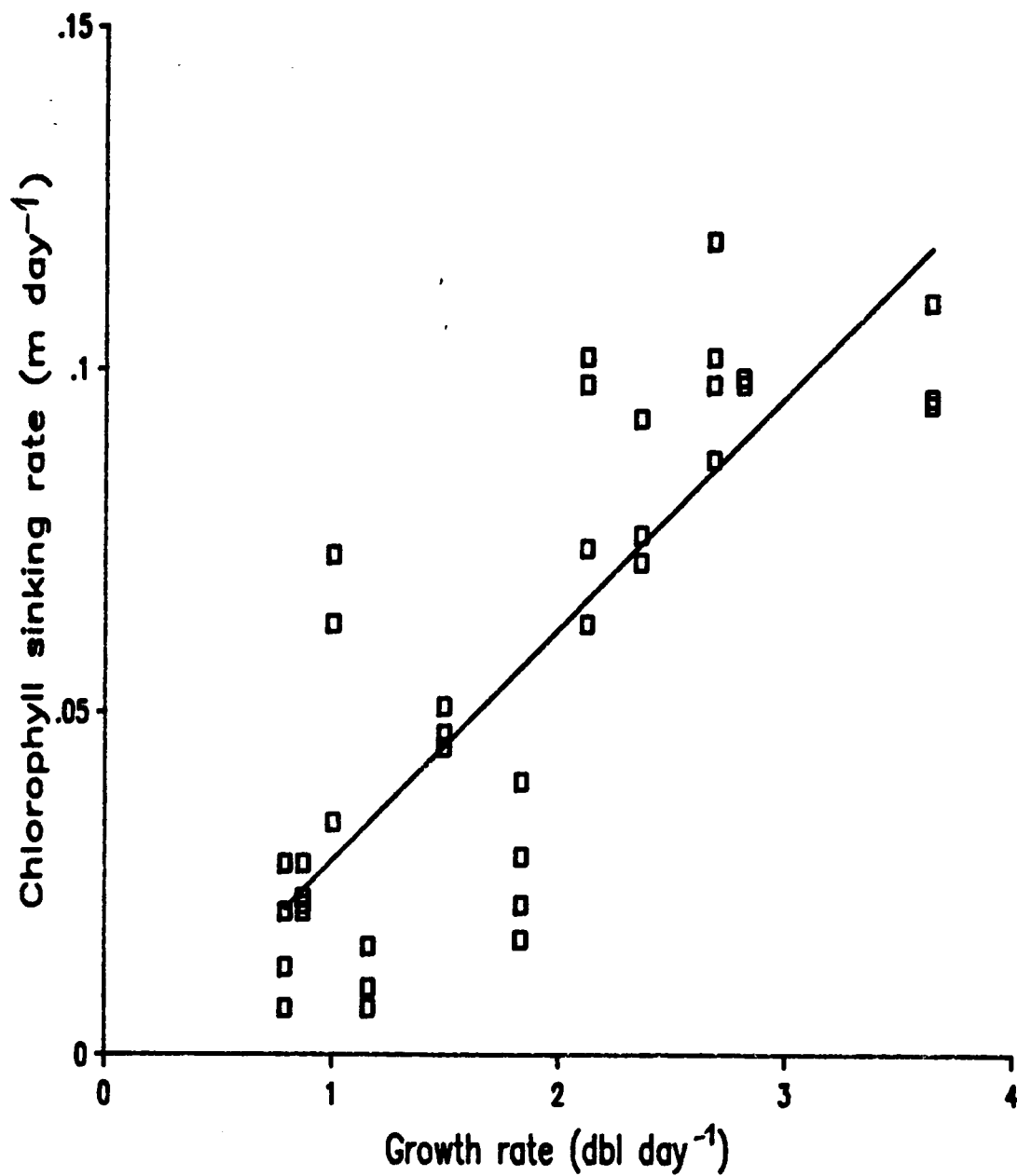


Figure 9. Relationship between chlorophyll sinking rates and growth rates for C. gracilis ($r = 0.82$, $p < 0.001$).

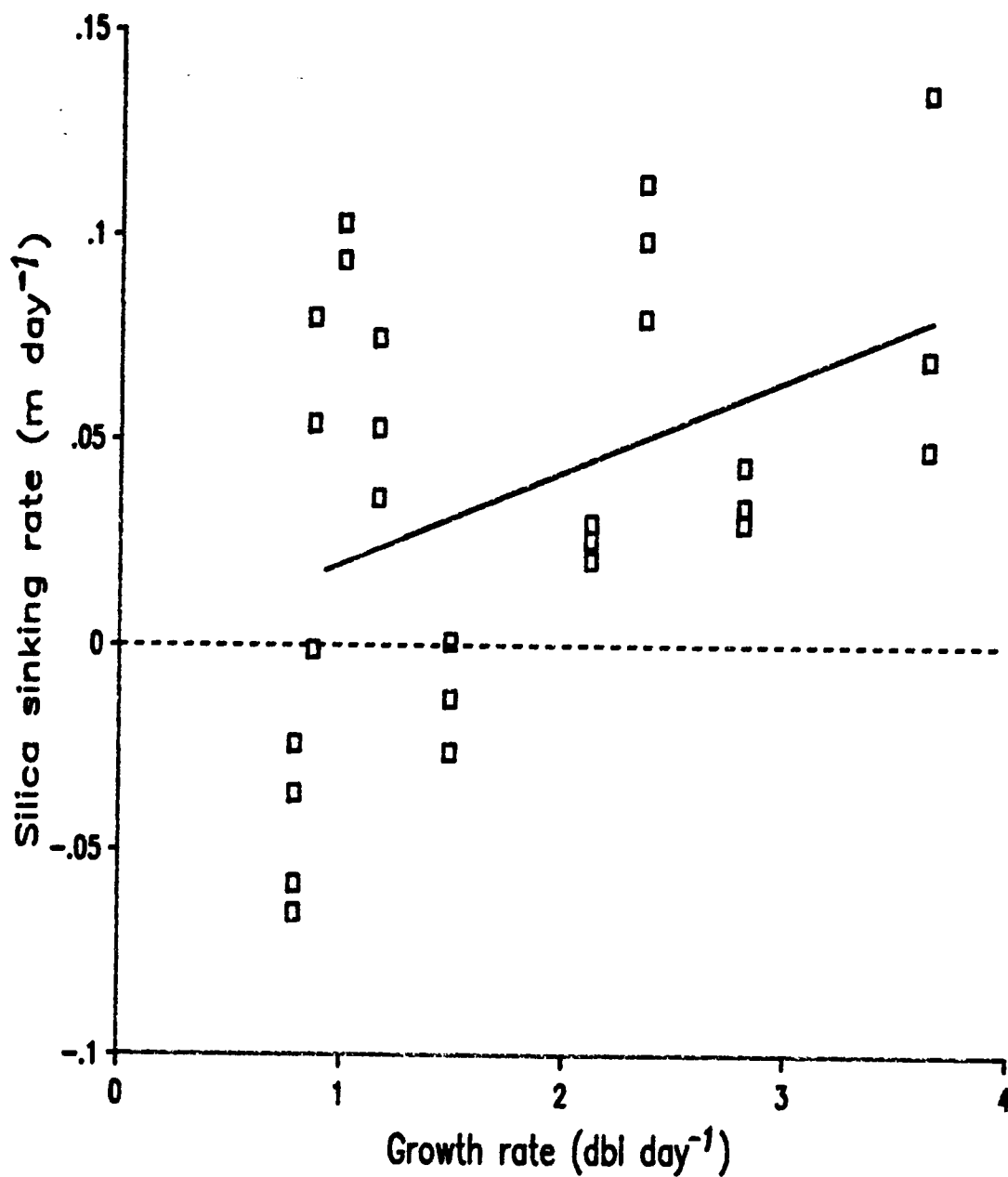


Figure 10. Relationship between silica sinking rates and growth rates for *C. gracilis* ($r = 0.38$, $p < 0.05$).

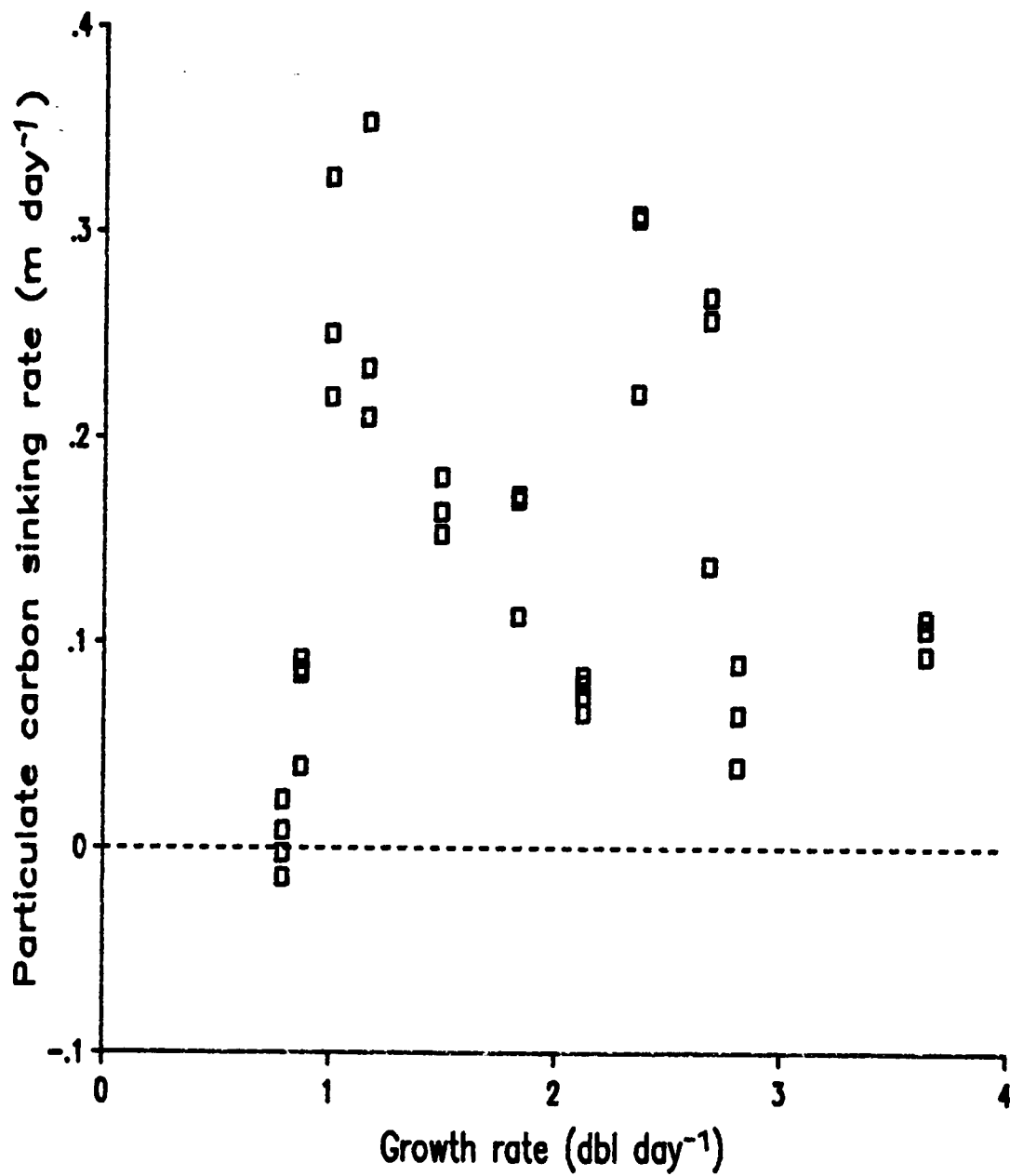


Figure 11. Relationship between particulate carbon sinking rates and growth rates for C. gracilis.

Laboratories. Although the same clone (AA63) was used, the new type may have a slightly different physiology. The clone types are identified separately in each of the figures.

The experiments with C. flexuosum produced results similar to those for C. gracilis, assuming clone types are comparable. The range of growth rate for this species was much smaller than for C. gracilis even though the light intensity range and variations were approximately the same. Temperature appears to prohibit rapid growth. Growth rates increase with light intensity and begin to level off as the maximum growth rate is approached (Figure 12).

Chlorophyll sinking rates are highly correlated with the log of light intensity ($r = 0.80$, $p < 0.001$) (Figure 13) as well as with growth rates ($r = 0.66$, $p < 0.001$) (Figure 14). Rates measured using silica are variable within experiments and between experiments such that no relationship is apparent between either light intensity or growth rate. Physiological differences due to inconsistent temperatures and clone types may account for some of the scatter. At the lower ends of the scales, particulate carbon rates showed an increase with light intensity and growth rates (Figures 15 and 16). The experiments conducted at the two highest light intensities had lower sinking rates measured using carbon than would be expected from the results using chlorophyll. The reasons for this discrepancy between these two measurements is unclear. Further experiments conducted at higher intensities could confirm whether these low rates are valid.

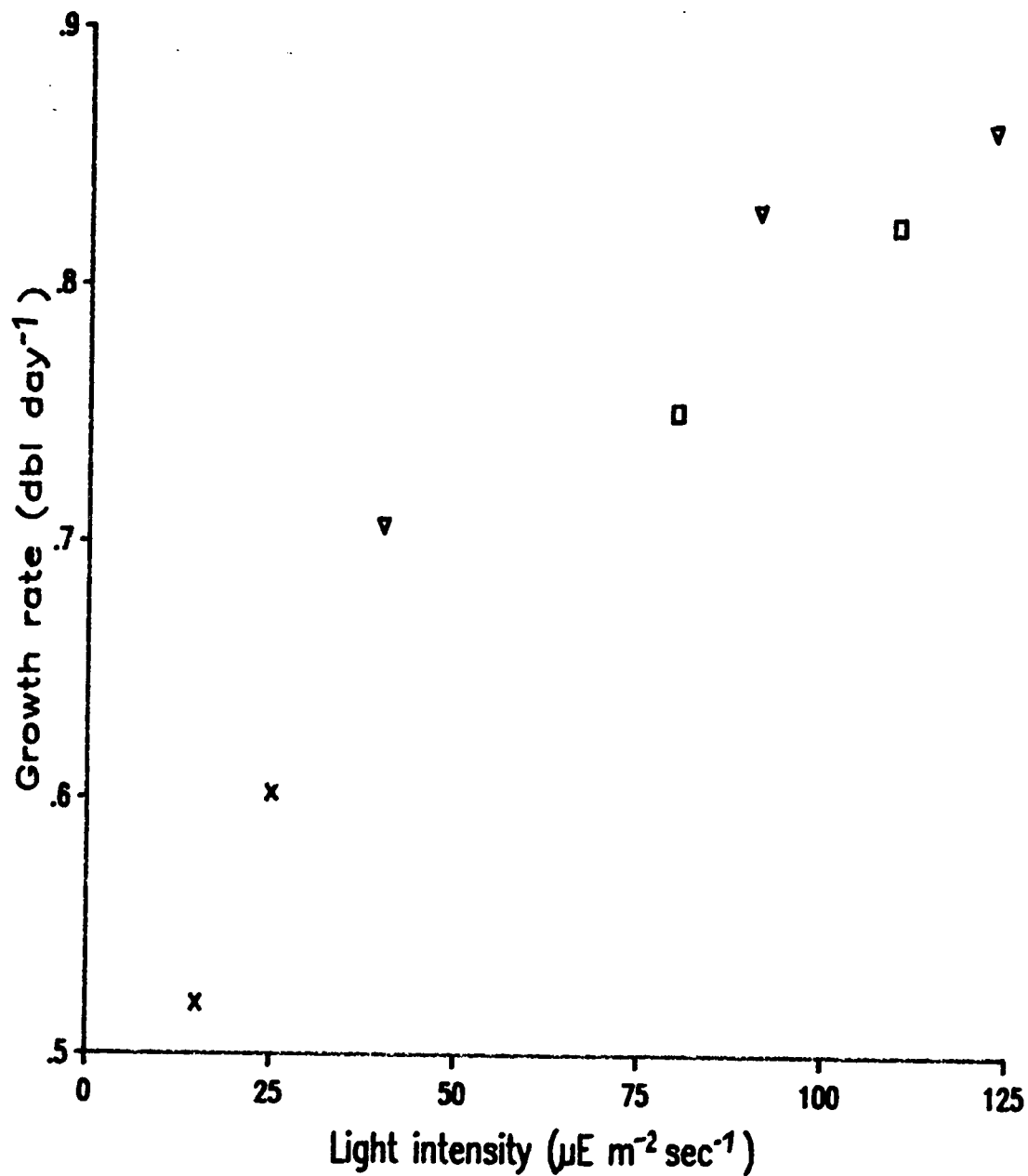


Figure 12. Relationship between growth rate and light intensity for C. flexuosum. Each symbol represents a different clone type.

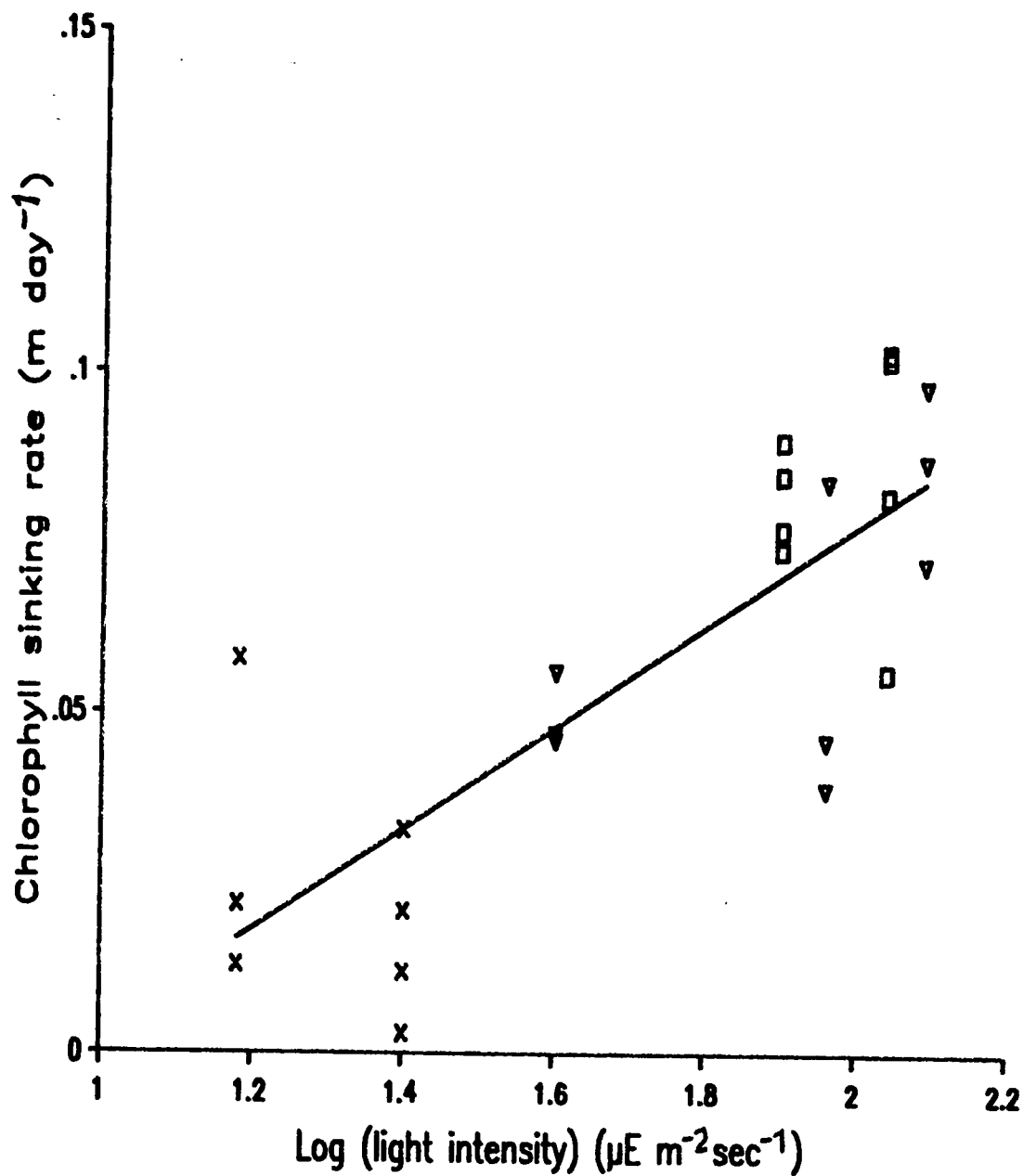


Figure 13. Relationship between chlorophyll sinking rates and the log of light intensity for *C. flexuosum* ($r = 0.80$, $p < 0.001$). Each symbol represents a different clone type.

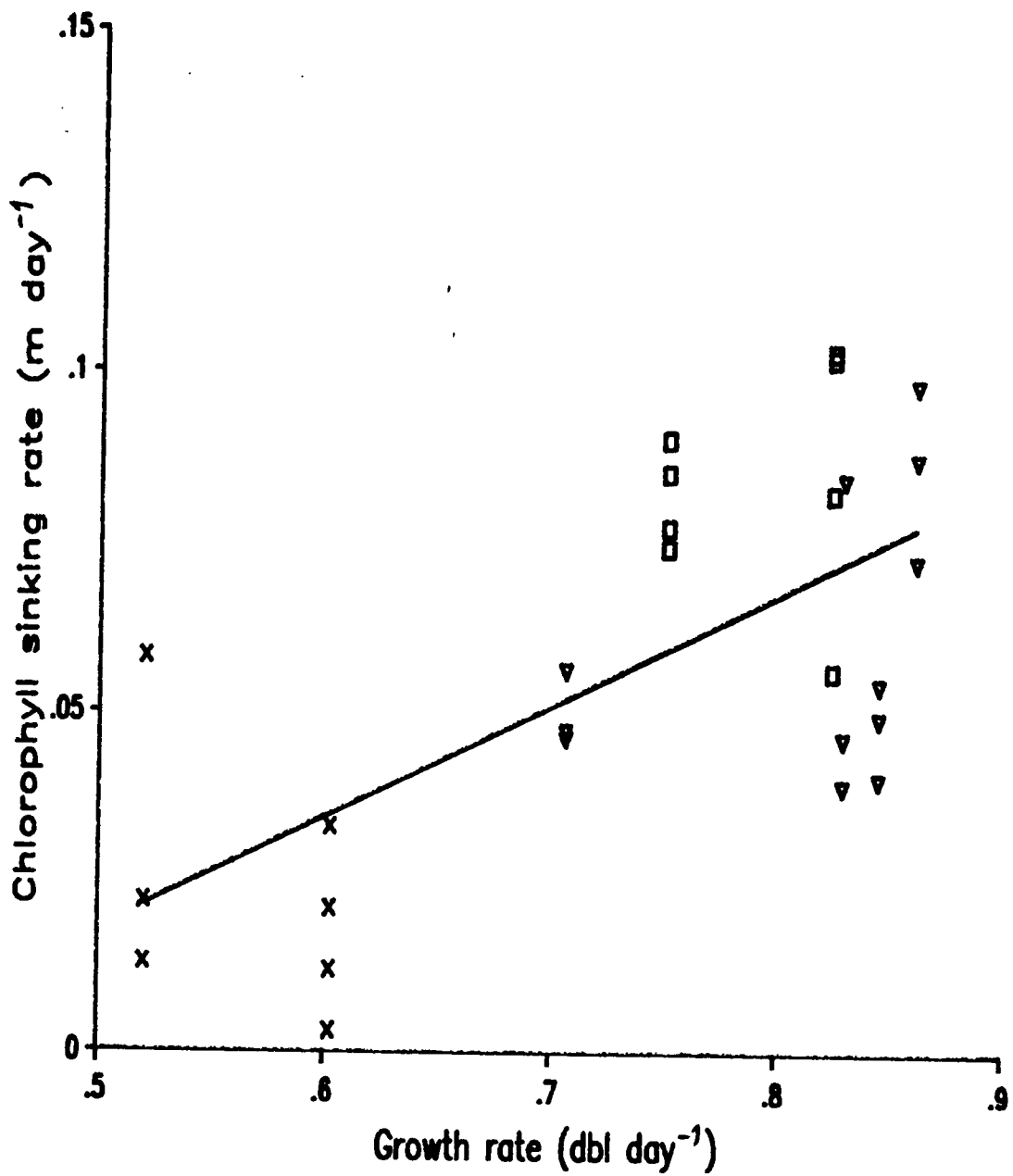


Figure 14. Relationship between chlorophyll sinking rates and growth rates for *C. flexuosum*. ($r = 0.66$, $p < 0.001$). Each symbol represents a different clone type.

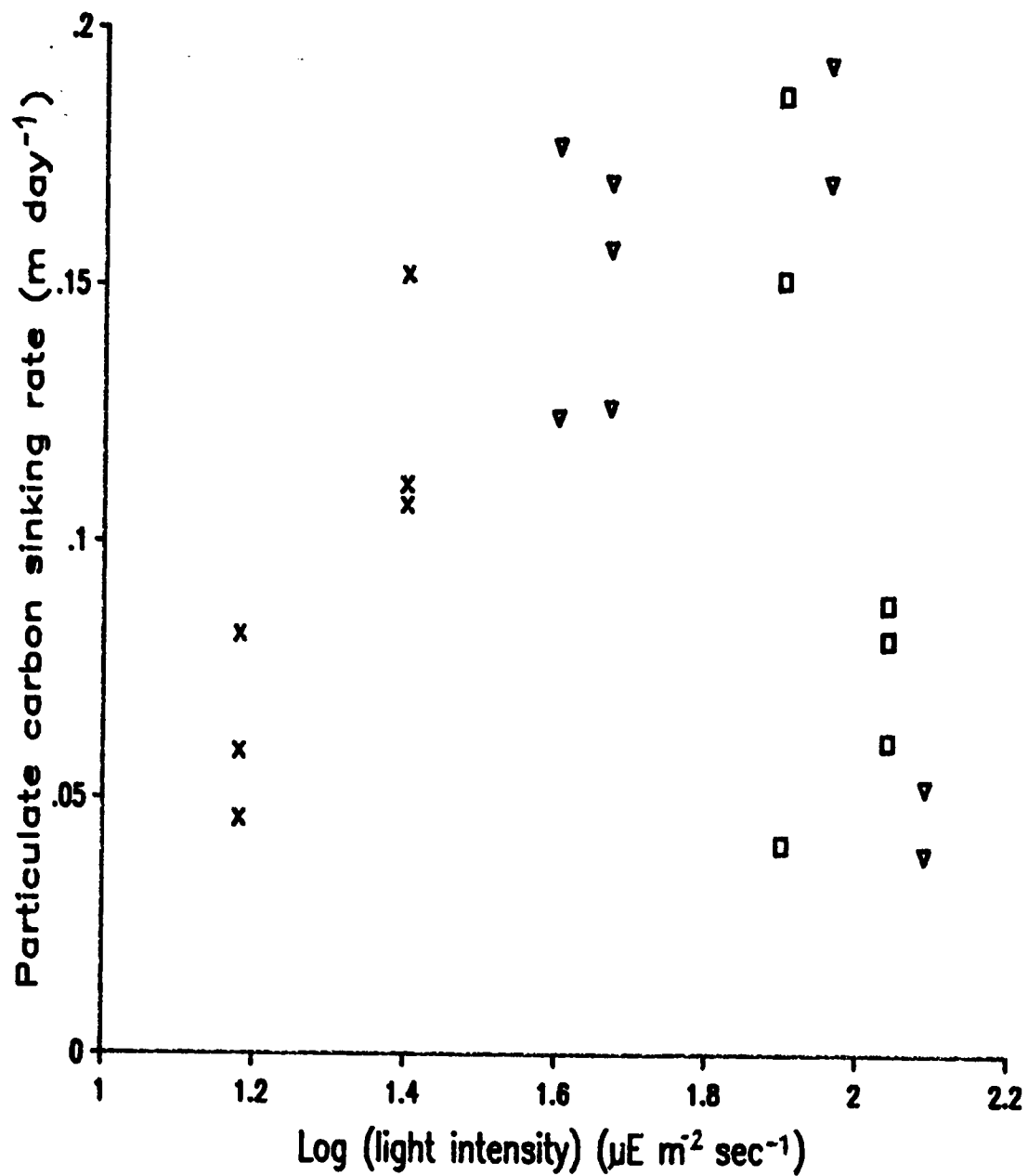


Figure 15. Relationship between particulate carbon sinking rates and the log of light intensity for *C. flexuosum*. Each symbol represents a different clone type.

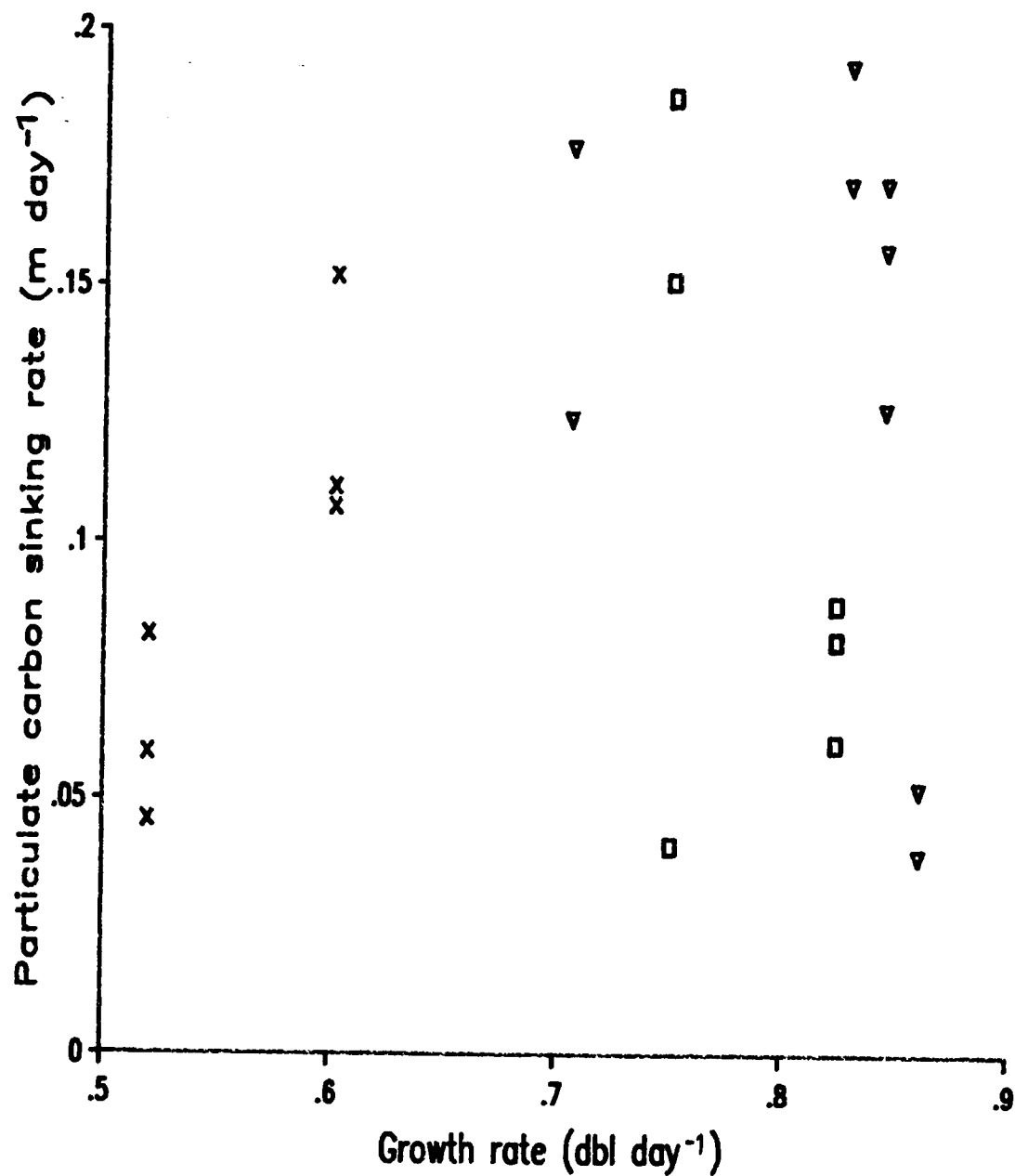


Figure 16. Relationship between particulate carbon sinking rates and growth rates for *C. flexuosum*. Each symbol represents a different clone type.

Field experiments

The open ocean area, in general, exhibited pre-bloom conditions (Table 1). Nutrient levels were high for the region (Smith et al. 1985) and probably were not limiting to phytoplankton growth. For depths within the euphotic zone, nitrate, silicate, and phosphate concentrations averaged 9.2, 3.8, and 0.67 μM respectively (G. Kattner, unpubl. data). There appeared to be a degree of vertical mixing throughout the euphotic zone (Figure 17). Any pycnocline was located below the one percent light level. A wide range of water temperatures was encountered between stations as the transects passed across a temperature front. Water temperatures also changed markedly with depth; temperatures decreasing as depth increased. Despite the varying temperatures, the ranges of salinity and sigma-t encountered were small. Daily integrated primary productivity averaged 400 $\text{mg C m}^{-2} \text{ day}^{-1}$ (M. E. M. Baumann, unpubl. data).

In the marginal ice zone, a pycnocline was usually present within the euphotic zone, indicating vertical stability in the upper layers (Figure 18). Again, the range of temperatures encountered varied as the transects passed across the marginal ice zone (Table 1). The melting ice in the area resulted in a wide range of values for salinity and density. Cold, less dense waters were found near the surface, probably the result of melting ice; deeper waters were generally more dense and warmer as is characteristic of Atlantic waters. Nutrient levels also varied widely. A Phaeocystis sp. bloom was present in several areas associated with decreased salinity and density. The

Table 1. Summary of various environmental parameters from the stations and depths at which sinking rate experiments were conducted.

Parameter	Area	
	Open Ocean	Marginal Ice Zone
Hydrographic Data		
Temperature ($^{\circ}\text{C}$)	-1.33 to 3.09	-1.73 to 2.28
Salinity (per mil)	34.67 to 35.06	33.21 to 34.97
Sigma-t	27.87 to 27.97	27.05 to 27.98
Nutrients (μM)		
Nitrate	7.0 to 11.4	1.2 to 11.9
Phosphate	0.49 to 0.79	0.27 to 0.91
Silicate	0.80 to 6.90	2.20 to 10.90
Particulates		
Chlorophyll <u>a</u> (mg m^{-3})	0.35 to 1.92	0.05 to 4.89
Phaeopigments (mg m^{-3})	0.16 to 0.75	0.11 to 1.19
Biogenic silica (μM)	0.58 to 2.44	0.55 to 2.52
Carbon (mg m^{-3})	51.40 to 322.46	27.11 to 563.75
Nitrogen (mg m^{-3})	5.07 to 120.07	1.43 to 94.08
Carbon-Nitrogen mole ratio	1.24 to 46.62	1.54 to 64.28
Silica-Carbon mole ratio	0.04 to 0.36	0.03 to 0.29
Integrated Primary Productivity		
($\text{mg C m}^{-2} \text{ day}^{-1}$)	112 to 964	195 to 1841

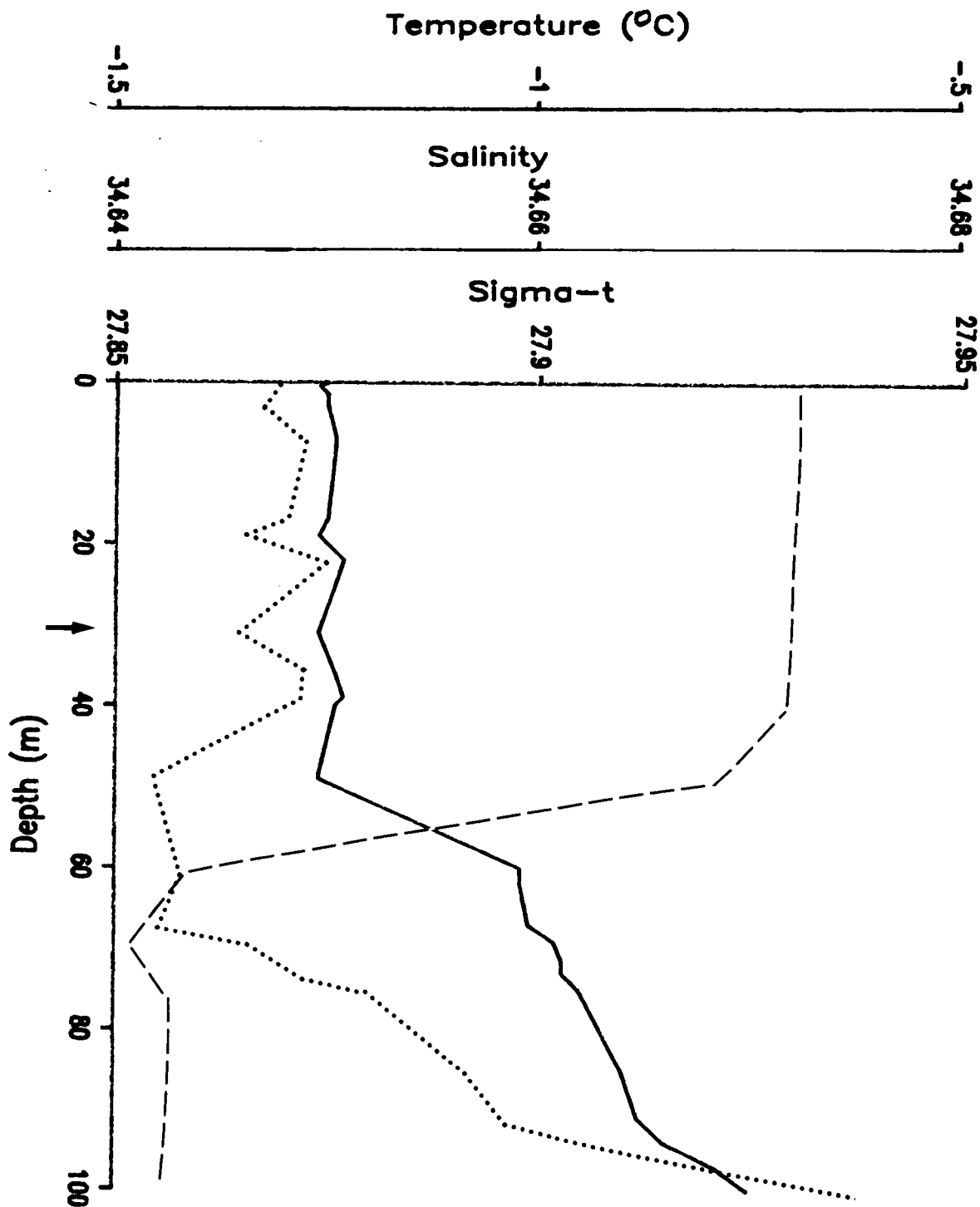


Figure 17. Depth profile for station 71 showing conditions representative of the open ocean area. Figure shows sigma-t (solid line), salinity (dotted line), and temperature (dashed line) within the first 100 m. The arrow along the depth axis marks the one percent light depth.

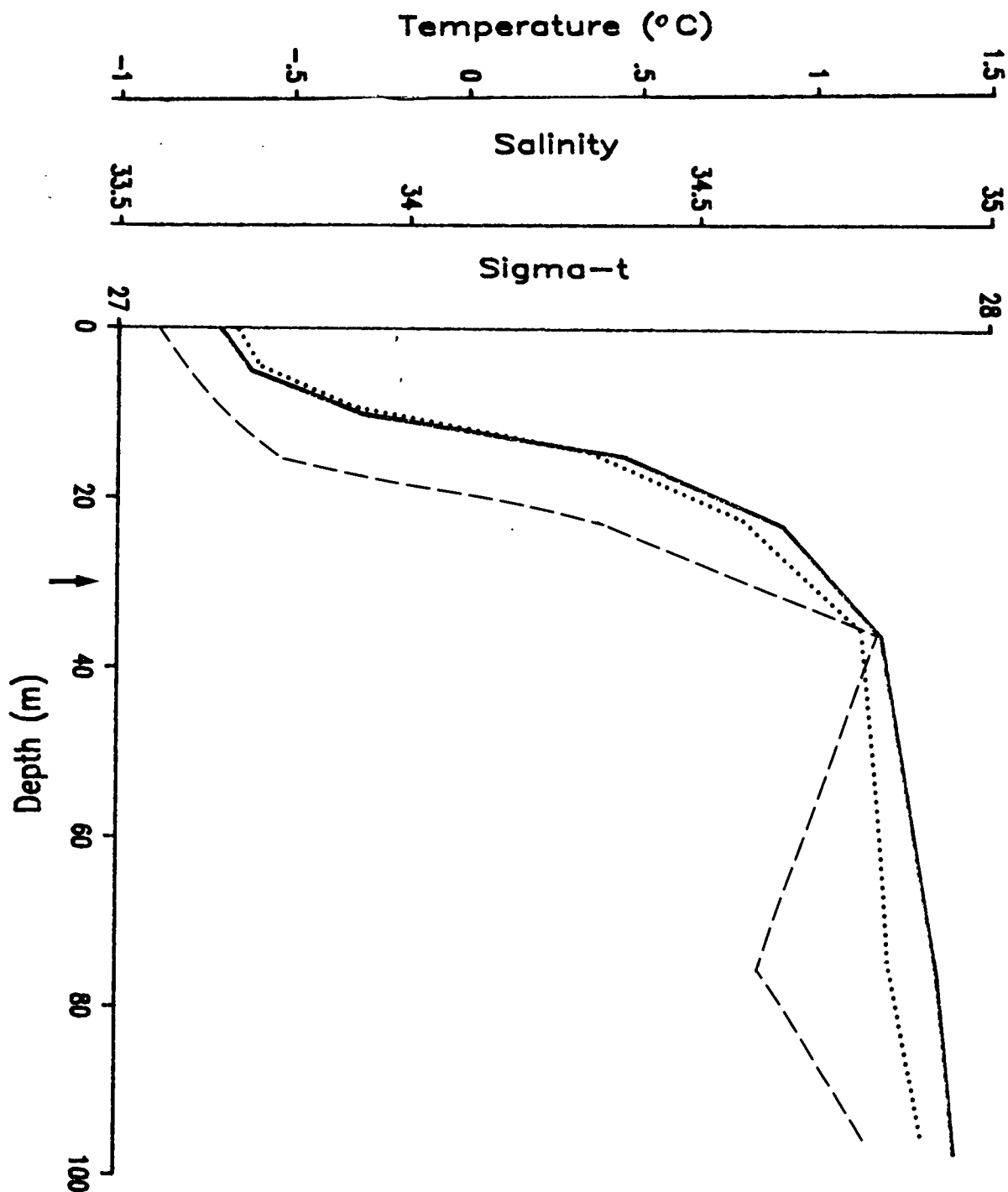


Figure 18. Depth profile for station 166 showing conditions representative of the marginal ice zone. Figure shows sigma-t (solid line), salinity (dotted line), and temperature (dashed line) within the first 100 m. The arrow along the depth axis marks the one percent light depth.

bloom regions were associated with the lowest nutrient levels encountered as well as the highest chlorophyll concentrations. Integrated daily primary production averaged $790 \text{ mg C m}^{-2} \text{ day}^{-1}$. In both areas biogenic silica concentrations were low (Table 1) suggesting that diatoms were not dominant organisms at this time. Silica-carbon ratios varied. A reasonable estimate of a biogenic silica-carbon ratio for a natural diatom assemblage consisting of a number of species is 0.12 (Nelson and Gordon 1982, Brezinski 1985). On several occasions the observed ratios were equal to or higher than this estimate. Diatoms were present in some areas but were in low concentrations.

Particulate carbon and chlorophyll a were significantly correlated ($p < 0.001$) (Figure 19). The carbon-chlorophyll content of the phytoplankton cells was 73.2, a value derived from the slope of the regression line. Although high, this value is within the range of samples from the world's oceans (Huntsman and Barber 1977). The positive y-intercept of 103 mg C m^{-3} indicates the presence of carbon which is not related to chlorophyll biomass. Microzooplankton and detrital material contribute to particulate carbon measurements.

Particulate carbon and nitrogen concentrations also were significantly correlated ($p < 0.001$) (Figure 20). The particulate carbon-nitrogen ratio, encompassing both living and detrital material, was calculated using average values for carbon and nitrogen and was 5.99. This figure is representative of vigorously growing cells which are not nutrient-limited (Parsons et al. 1984b).

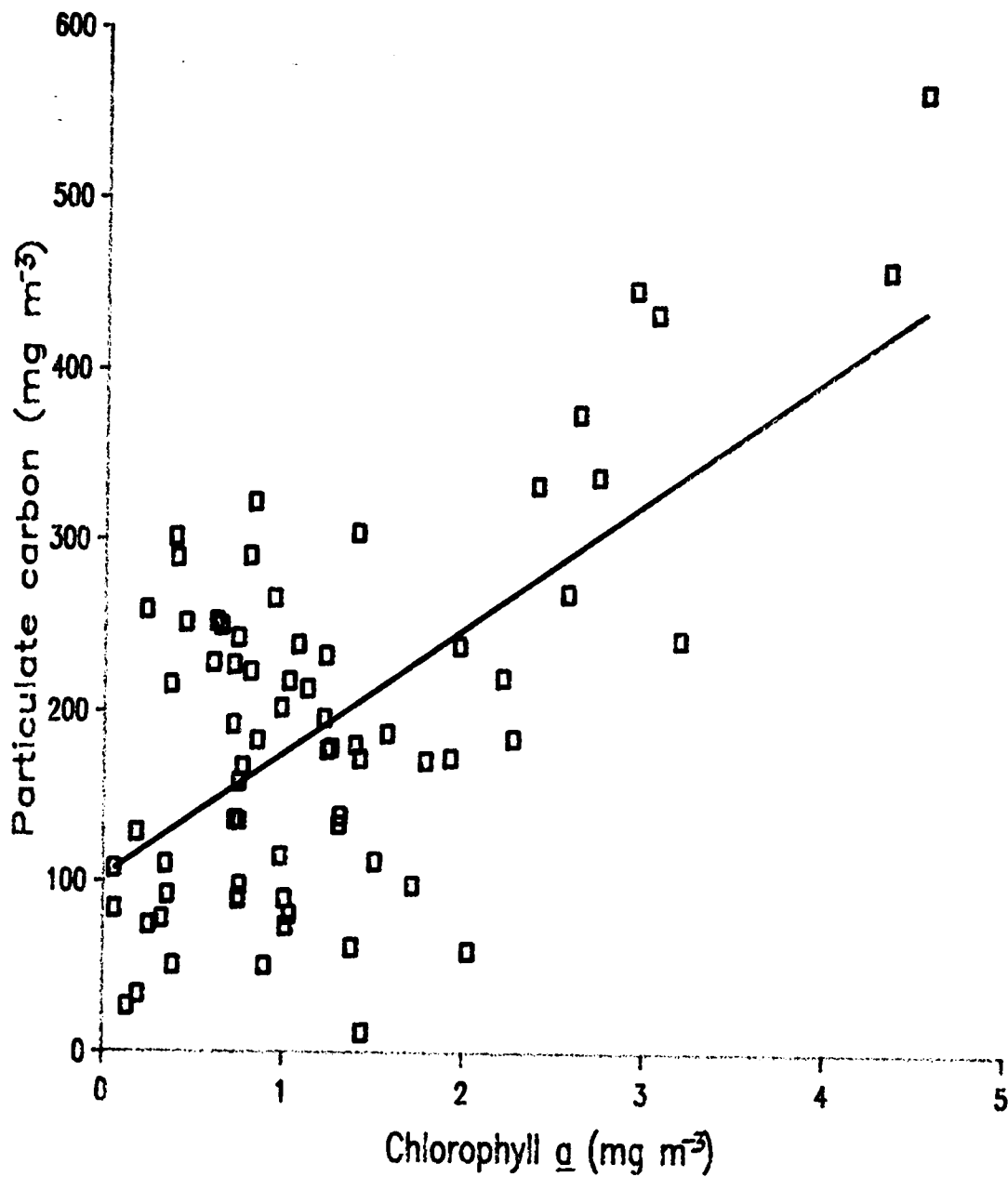


Figure 19. Relationship between chlorophyll a and particulate carbon. Figure shows data points and calculated regression line
 $PC = 73.2 \text{ chl } a + 103.2$ ($p < 0.001$).

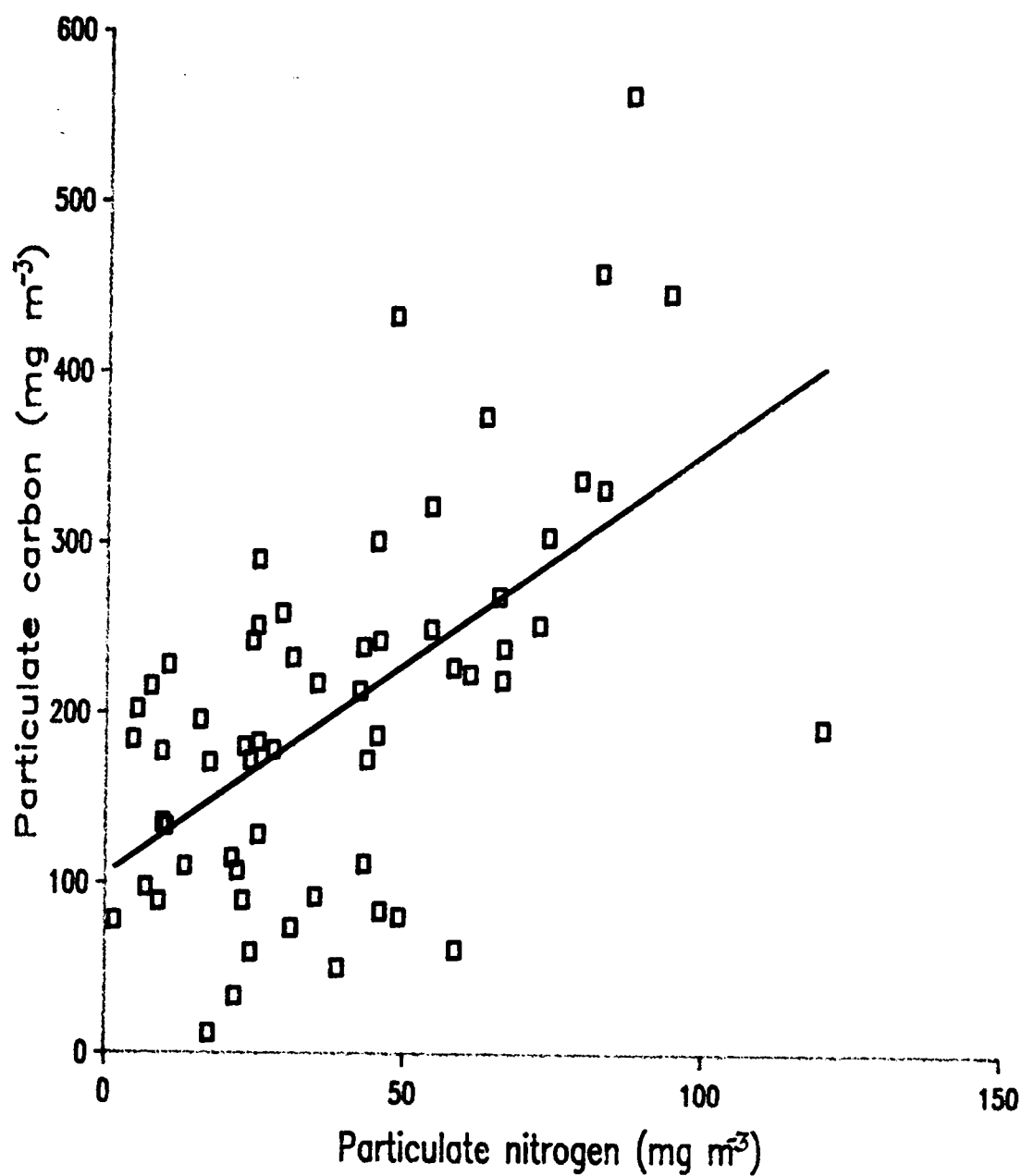


Figure 20. Relationship between particulate carbon and particulate nitrogen. Figure shows data points and calculated regression line $PC = 2.49 PN + 105.4$ ($p < 0.001$).

Growth rates for the assemblages were calculated using the productivity measurements for each sample. These values were converted into chlorophyll production using the carbon-chlorophyll ratio of cells estimated from the regression. This value was divided by the chlorophyll concentration and then divided by the natural log of two (0.69) to obtain the specific growth rate in doublings day⁻¹. Rates varied from 0.03 to 1.55 dbl day⁻¹ with an average value of 0.38 dbl day⁻¹. This average is lower than the calculated maximum growth rate at 0°C of 0.85 dbl day⁻¹ (Eppley 1972) and also lower than 0.71 dbl day⁻¹ calculated during the Summer, 1984 in Fram Strait (Smith et al. 1987).

Sinking rates varied within each experiment for each parameter. For example, at the surface of station 110, sinking rates as determined from changes in chlorophyll measured 0.17 m day⁻¹; for silica, 0.17; phaeopigments, 0.09; particulate carbon, 0.71; and particulate nitrogen, 0.89 m day⁻¹. A summary of the observed sinking rates for both locations is shown in Table 2. All of the values are included in Appendix B.

Table 2. Summary of sinking rates for field experiments by parameter in m day⁻¹

Biomass Indicator	Range	Mean	
Chlorophyll	-0.04 to 0.63	0.14	(n = 88)
Silica	-0.18 to 1.097	0.14	(n = 80)
Phaeopigments	-0.09 to 1.00	0.20	(n = 87)
Particulate Carbon	-0.20 to 1.69	0.55	(n = 63)
Particulate Nitrogen	-0.23 to 3.71	0.64	(n = 66)

Multiple regression analysis of the field data was complicated by the multi-collinearity of many of the environmental variables. Keeping the problems of multi-collinearity in mind, multiple regression analysis for the open ocean stations provided some insight into the environmental factors controlling sinking of suspended particulate matter. The factors affecting sinking differ for each parameter because each parameter measures different components of particulate matter. For sinking rates of chlorophyll, an indicator of living biomass, approximately 59% of the variation in sinking rates can be explained by changes in salinity and temperature ($p < 0.005$). The sinking rate is positively associated with salinity and negatively associated with temperature.

$$(1) \Psi_{chl} = 0.92(\text{salinity}) - 0.14(\text{temperature}) - 31.86$$

For diatoms and silicoflagellates, 61% of variation in sinking as measured by biogenic silica is explained by variation in sigma-t and phosphate concentrations ($p < 0.002$). Rates decrease as phosphate decreases; rates increase as sigma-t decreases.

$$(2) \Psi_{sil} = -4.28(\text{sigma-t}) + 1.26(\text{phosphate}) + 118.79$$

The best predictor variables for the sinking of particulate carbon are sigma-t, nitrate concentration, and temperature. The equation

$$(3) \Psi_{pc} = 13.9(\text{sigma-t}) + 0.52(\text{nitrate}) - 0.68(\text{temperature}) - 371.33$$

has a multiple coefficient of determination (R^2) of 0.54 ($p < 0.003$).

Analysis of data collected in the marginal ice zone showed less significant association between sinking rates and the environment. Sigma-t and temperature explained only 45% of the variation in the rates measured using particulate carbon ($p < 0.001$).

$$(4) \Psi_{pc} = 0.68(\text{sigma-t}) - 0.24(\text{temperature}) - 18.25$$

No one variable or combination of environmental variables significantly explained variation in phaeopigment or particulate nitrogen sinking rates in open ocean areas. No more than 25% of variation in silica, particulate nitrogen, and phaeopigment sinking rates in the marginal ice zone could be explained by environmental variations.

In the open ocean area where vertical mixing may distribute particulates evenly through the euphotic zone, the percentage of primary production lost from the euphotic zone in the form of small particulates can be estimated. These calculations were performed using data from stations where particulate carbon concentrations and sinking rates were uniform throughout the water column. A mean biomass estimate was used for each station. The following formulas were used (Bienfang 1984):

$$\text{Carbon flux} = (\text{carbon concentration}) * (\text{sinking rate of carbon})$$

$$\begin{array}{l} \text{\% of productivity} \\ \text{lost from euphotic} \\ \text{zone} \end{array} = \frac{\text{carbon flux}}{\text{integrated daily production}} * 100$$

The resulting percentages ranged from 16 to 37% with an average of 28% of daily phytoplankton production leaving the euphotic zone as small particulates ($n = 8$). The values at the higher end of this range are associated with high sinking rates. The carbon flux tends to increase as productivity increases (Figure 21).

In the open ocean area, growth rate and sinking rates were not significantly correlated ($r = 0.11$) (Figure 22). However, in the marginal ice zone, growth rate and sinking rates of chlorophyll were significantly correlated ($r = 0.30$, $p < 0.05$). Sinking rates tended to increase with increasing growth rates (Figure 23).

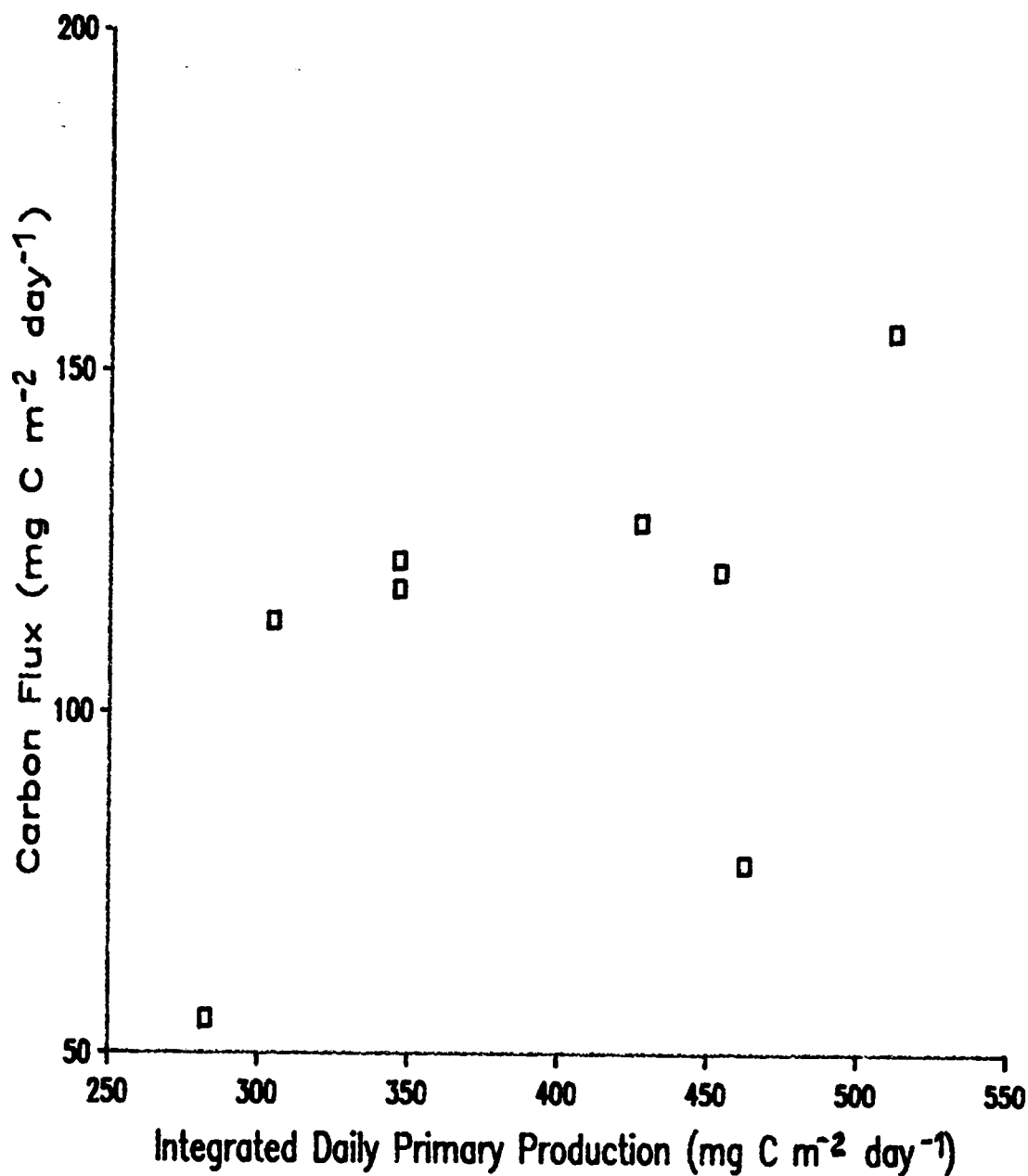


Figure 21. Relationship between integrated daily primary productivity and carbon flux for several stations in the open ocean area. Carbon flux tends to increase with productivity ($r = 0.51$).

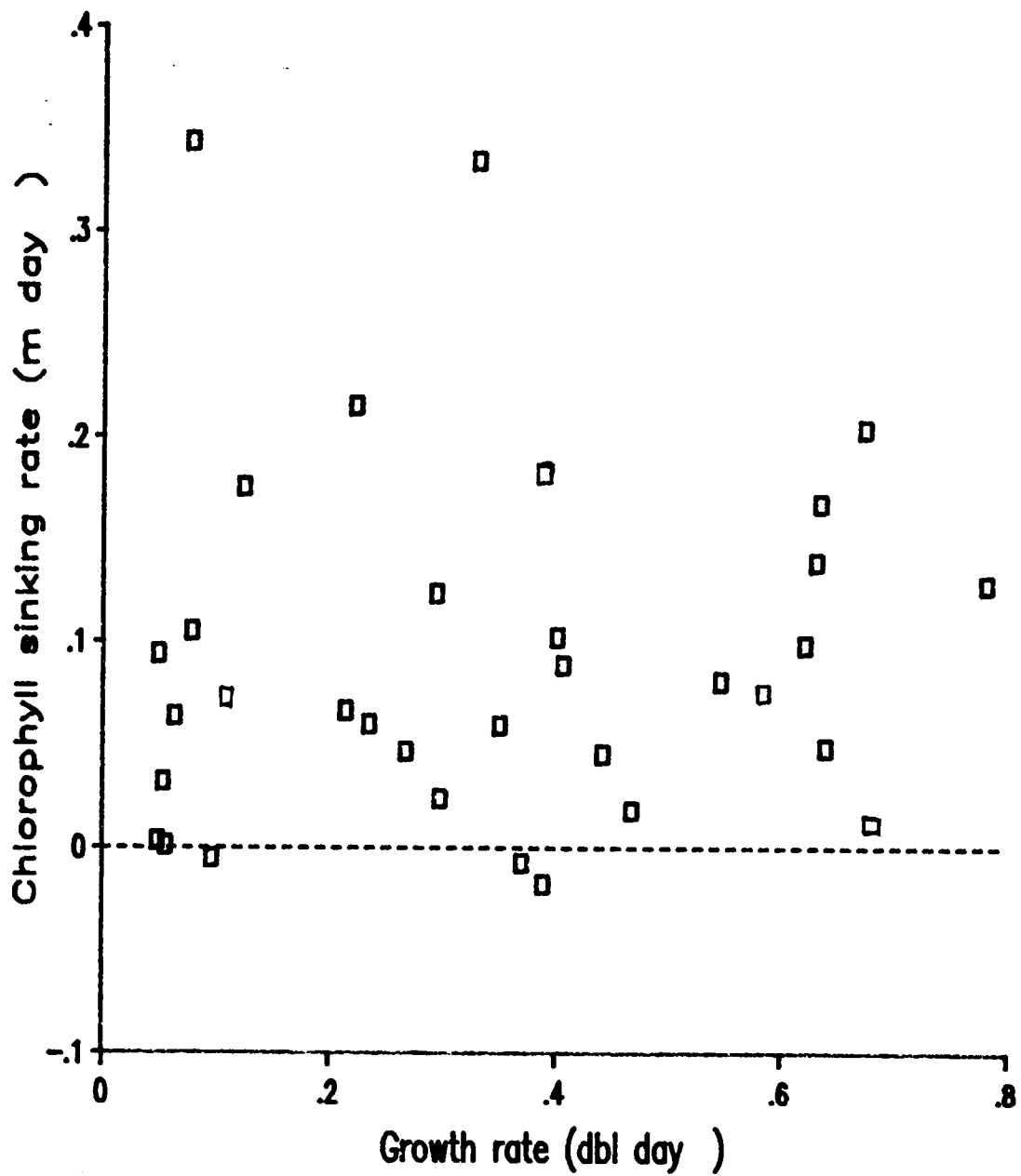


Figure 22. Relationship between chlorophyll sinking rates and growth rates for samples collected in the open ocean area.

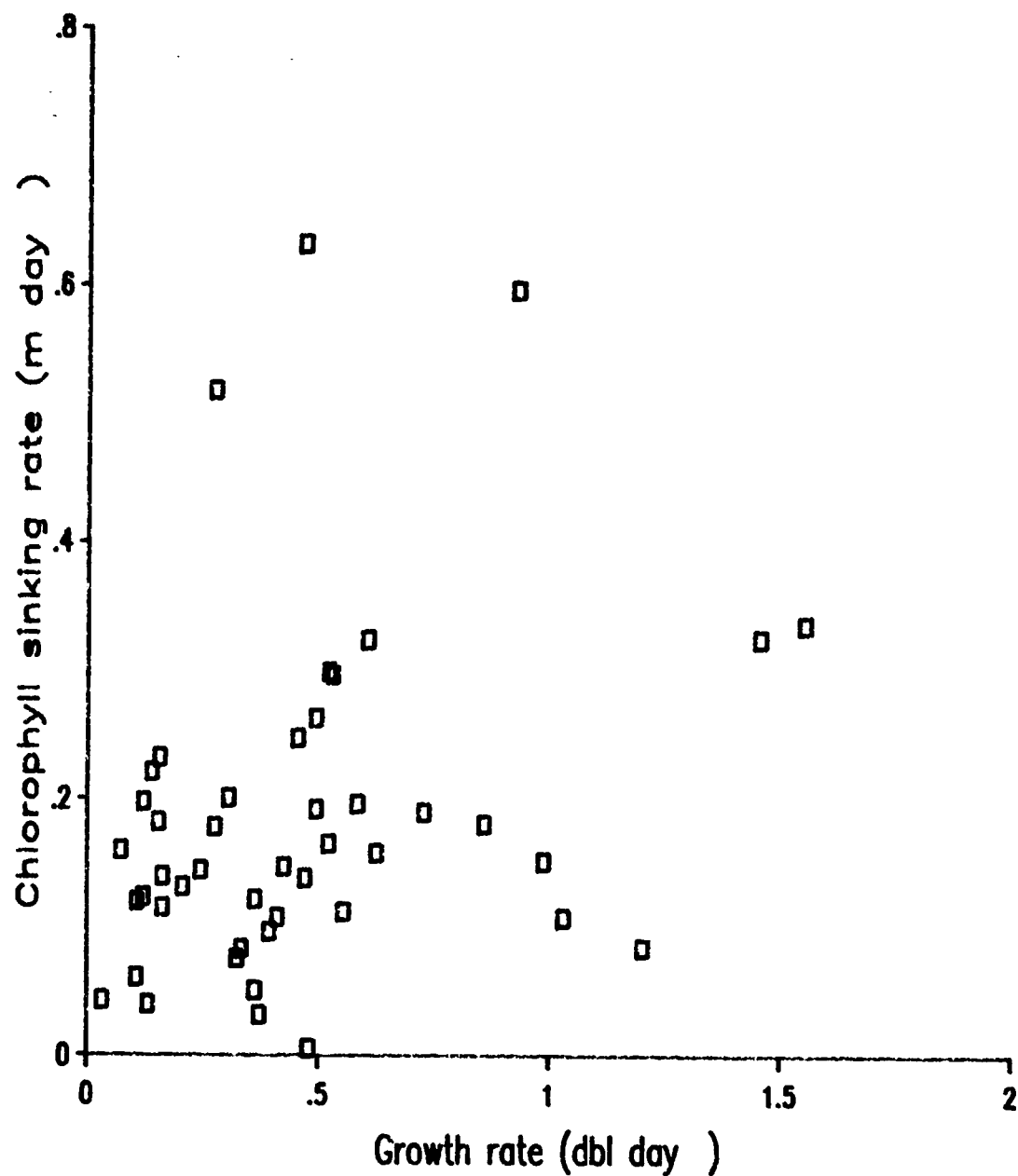


Figure 23. Relationship between chlorophyll sinking rates and growth rates for samples collected in the marginal ice zone ($r = 0.30$, $p < 0.05$).

CHAPTER IV

DISCUSSION

Laboratory experiments

Light intensity influences growth rates as well as sinking rates of laboratory cultures. Experiments with Chaetoceros gracilis and C. flexuosum show that an increase in light intensity results in an increase in both growth and sinking rates. The hypothesis that sinking of phytoplankton cells is associated with processes controlling photosynthesis (Anderson and Sweeney 1978, Bienfang 1981a, 1985, Johnson and Smith 1986) is supported by these results. The positive correlation found in this study agrees with several lab and field experiments which suggest that sinking rates are lower in dark light regimes than in bright (Steele and Yentsch 1960, Anderson and Sweeney, 1977, 1978, Bienfang 1980, Bienfang et al. 1983). During periods of high activity, a majority of the energy and resources of the cell may be devoted to production and less to buoyancy regulation. Another possibility is that the processes of photosynthesis change the composition or the drag forces on the cell which affect the cellular density or resistance to sinking in seawater.

Bienfang (1980) proposed that slow growth in combination with low light levels result in physiological changes which reduce sinking rates. These results support that hypothesis. If the response of these two species is representative of others, then phytoplankton adapted to low light conditions may sink slower and aid in the

maintenance of the chlorophyll maximum commonly found near the base of the euphotic zone.

Field experiments

Vertical stability was not evident in the open ocean area where small changes in sigma-t, if present, were located below the euphotic zone (Figure 17, p. 38). Productivity in this area averaged $400 \text{ mg C m}^{-2} \text{ day}^{-1}$. With the mixed-layer depth greater than that of the euphotic zone, available light could be a factor limiting primary production (Sverdrup 1953). The conditions in the open ocean area were characteristic of pre-bloom areas where high nutrient and light levels promote productivity, yet vertical mixing prohibits a rapid increase in the standing stock.

Daily integrated productivity values for the marginal ice zone varied from 195 to $1841 \text{ mg C m}^{-2} \text{ day}^{-1}$, and averaged $790 \text{ mg C m}^{-2} \text{ day}^{-1}$. This estimate is higher than that ($426 \text{ mg C m}^{-2} \text{ day}^{-1}$) reported for this area during the summer, 1984 (Smith et al. 1987). Surface nitrate concentrations averaged $1.6 \text{ } \mu\text{M}$ in 1984 (Smith et al. 1987), compared to $6.3 \text{ } \mu\text{M}$ during this study (Kattner, unpubl. data). Vertical stability was evident in both studies, as is typical of the polar front. High productivity rates during this cruise were most likely the result of greater nutrient availability and the high light intensities found in late spring.

Light limitation occurring as a result of deep vertical mixing can prevent high growth rates of phytoplankton (Sverdrup 1953, Eppley 1972). Estimated specific growth rates were slightly lower in areas

where vertical mixing occurred, averaging $0.32 \text{ db l day}^{-1}$ compared to $0.42 \text{ db l day}^{-1}$ in stratified areas. In both cases, the growth rates were lower than the predicted value of 0.85 for this temperature range (Eppley 1972).

Sinking rates were characteristic of passively sinking cells and are low compared to rates previously reported for polar areas. Sinking rates observed in the Greenland Sea marginal ice zone during summer 1984, and those recorded for a subtropical assemblage averaged 0.23 and 0.22 m day^{-1} respectively, as measured using chlorophyll (Bienfang and Harrison 1984, Johnson 1986). In both cases, the assemblages were dominated by small flagellates. Flagellate-dominated assemblages from subarctic assemblages had rates of 0.07 m day^{-1} (Bienfang 1984). The average sinking rate estimated in this study was 0.14 m day^{-1} , suggesting that this area may have been dominated by flagellates which sink slowly because of their small size and ability to move vertically. The presence of small species in addition to flagellates would also explain low sinking rates for particulate matter. Small species generally have a high surface area to volume ratio which results in lower settling rates because of high drag resistance (Smayda 1970). The limited amount of available light during this period would favor the growth of small cells over larger cells (Parsons and Takahashi 1973) and would favor flagellates rather than diatom-dominated communities (Parsons et al. 1978).

Each biomass parameter estimated the sinking rate of a different component of the particulate assemblage. Because of the presence of

detritus and microzooplankton, the components would not be expected to sink at the same rate or necessarily be controlled by the same factors. In each experiment, settling rates as measured by the different indicators varied widely. Sinking rates of particulate carbon and nitrogen, measuring both living and detrital material, were higher than any of the other biomass parameters. Chlorophyll, an indicator of living biomass, sank slowly. A comparison of these rates would indicate that the living components sank slowly while detritus sank relatively rapidly. A significant amount of detrital carbon is indicated by the positive y-intercept of the chlorophyll and particulate carbon regression (Figure 19, p. 41). Chlorophyll sinking more slowly than particulate carbon supports the idea that metabolic processes affect sinking rates.

Multiple regression analysis of sinking rates estimated by various parameters indicated several environmental factors contributing to variation in sinking rates. Light intensity at which samples were collected did not significantly contribute to variation in sinking rates. The partial regression coefficients of the equations in this study are specific to the area and time studied. The absolute values may not be as useful because of this restriction and because of substantial scatter in the data. However, the positive or negative relationship of the variable to sinking rates should be more widely applicable.

In all cases where a significant relationship was found, salinity or density, as measured by sigma-t, was an explanatory variable.

Substitution of the observed values for the density and viscosity of seawater into Stokes' equation approximates the effect of physical conditions on settling rates. These calculations indicate that changes in seawater characteristics do not account for all of the variation in observed settling rates. For chlorophyll sinking rates, if temperature is held constant, an increase in salinity results in increasing sinking rates (eq. 1, p. 44). Holding temperature and nitrate concentrations constant and increasing σ_t predicts an increase in particulate carbon settling rates (eqs. 3 and 4, pp. 44 and 45). Stokes' equation predicts a decrease in sinking rates as the density of the medium increases providing the cell density is not affected. Instead, a biological response maintains or increases the settling velocities. This relationship agrees with the culture experiments of Bienfang and Szyper (1982) in which Ditylum brightwelli maintained a steady sinking rate as salinity, and therefore seawater density, increased.

The importance of nutrient concentrations in explaining variation in particle sinking rates also supports the idea of a biological response. The concentration of phosphate or nitrate should not affect the physical properties of the liquid medium; therefore, they must be affecting the density of the cell. Phosphate concentration is a significant factor explaining variation in the sinking rates of biogenic silica (eq. 2, p. 44). Nitrate concentration is involved in the multiple regression for particulate carbon (eq. 3, p. 44). In both cases, the relationship between sinking and nutrient concentration is

positive, increasing nutrient concentrations result in increasing rates provided that the other variables in the equation are held constant.

Water temperature had a negative partial regression coefficient. This relationship occurred for particulate carbon sinking rates in both areas (eqs. 3 and 4, pp. 44 and 45), and for chlorophyll sinking rates in the open ocean (eq. 1, p. 44). Again, using Stokes' equation, the changes in viscosity and density of the medium as a result of water temperature differences do not account for the observed variation in settling rates.

Some variation in settling may be affected by the species composition of the phytoplankton assemblage. In the open ocean, transects were conducted across a temperature front, the Arctic front. The warm, saline, dense water originates from the Atlantic Ocean. The East Greenland Current carries cold, less dense water from the Arctic. The species composition of these water masses may be different and the assemblages on either side of the front would reflect that difference.

In the open ocean area, particle size analysis indicated a higher fraction of diatom-size particles near the cold water edge of the front and increasing concentrations of autotrophic microflagellates in concentration in warmer waters (M. Kahru, unpubl. data). This change in composition may be useful in explaining the relationship between temperature and sinking. Sinking rates determined from chlorophyll measurements should increase as temperature decreases, providing salinity remains constant (eq. 1, p. 44). In this area, salinity does not vary widely, from 34.67 to 35.06 per mil. A lower

sinking rate in the warm water area could be explained by a high percentage of microflagellates. Diatoms, which are larger and have less direct control over their vertical position, would have a higher sinking rate. Any effect of species composition on sinking rates of chlorophyll may also be reflected in particulate carbon measurements.

Another factor to consider when assessing the importance of environmental effects on sinking is the adaptation of the cells to the conditions under which they are sampled. The cells may not have been subjected to those conditions under which they were sampled for a substantial amount of time. Vertical currents, especially in the open ocean area, can distribute particles throughout the mixed layer. Consequently, the location at which they were sampled may or may not be representative of the conditions to which the cells were physiologically adapted. Samples in the ice zone may be more adapted to the conditions in which they were located because stratification prohibits a large amount of vertical mixing.

In the open ocean area where vertical mixing could evenly distribute particulates through the euphotic zone and where sinking rates did not vary through the euphotic zone, particulate carbon flux was approximated. Estimated carbon flux values increased with integrated primary production. Sediment traps record a cycle in carbon supply to depths below the euphotic zone which corresponds to primary production in surface waters (Knauer et al. 1979, Deuser and Ross 1980, Deuser et al. 1981, 1983, Honjo 1982, 1987, Betzer et al. 1984, Smith and Baldwin 1984). Although small suspended matter is only a fraction

of the total carbon flux (Smayda 1970, McCave 1975, Lal 1977, Silver and Alldredge 1981), it appears to follow the same seasonal pattern as larger particles such as fecal pellets and aggregates.

The percentage of daily integrated primary productivity sinking out of the euphotic zone in the form of small particulate matter ranged from 16 to 37% and averaged 28%. These estimates are higher than the 8 to 12% calculated by Johnson and Smith (1986) for Antarctic regions and the 13% calculated by Bienfang (1984) for subpolar areas. Above average sinking rates for particulate carbon occurred at these particular stations which may artificially inflate the calculated loss percentage. A substantial loss of production from the surface layers implies that new production is occurring to maintain the production cycle (Eppley and Peterson 1979). New production is also indicated by the high uptake rate of nitrate by phytoplankton (Keene, unpublished data). Production based on nitrate uptake indicates new production while regenerated production is based on ammonium uptake by primary producers (Eppley and Peterson 1979).

Sinking rates of chlorophyll tended to increase with estimated growth rates in stratified areas, exhibiting the same relationship as the culture experiments. If this is occurring, increased carbon flux during periods of high productivity may be a functional response as well as a numerical response. A greater amount of particulate matter sinks out of the euphotic zone not only because of the increased concentrations, but because the biomass may sink faster during periods of increased production. Direct growth rate measurements are necessary

to confirm this relationship for field assemblages. Sediment trap data for the area and time involved would also be useful.

CHAPTER V

CONCLUSIONS

1. The light intensity under which Chaetoceros gracilis and C. flexuosum were grown was positively correlated with both the growth rates and sinking rates of these species.

2. The light intensity from which assemblages in the Greenland Sea area were collected did not explain variation in the sinking rate of these assemblages.

3. In open ocean areas, 59% of the variation in sinking rates of chlorophyll could be attributed to changes in salinity and temperature.

4. In open ocean areas, 61% of the variation in sinking rates of silica could be attributed to changes in sigma-t and phosphate.

5. In open ocean areas, 54% of the variation in sinking rates of particulate carbon could be attributed to changes in sigma-t, nitrate, and temperature.

6. In the marginal ice zone, 45% of the variation in sinking rates of particulate carbon could be attributed to changes in sigma-t and temperature.

7. Changes in sinking rates as a result of environmental variations indicate a biological response in addition to the effects of physical factors.

8. A trend toward increasing sinking rates of chlorophyll with increasing growth rates in stratified areas implies that a functional response as well as a numerical response contributes to increased

particle flux from the euphotic zone during periods of high productivity.

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APPENDICES

APPENDIX A
LABORATORY DATA

Table A-1. Growth and sinking rate data for Chaetoceros gracilis.

Light intensity ($\mu\text{E m}^{-2} \text{sec}^{-1}$)	Growth rate (dbl day^{-1})	Sinking rate (m day^{-1})		
		Chlorophyll	Carbon	Silica
7	0.79	0.007	-0.014	-0.065
		0.013	-0.002	-0.058
		0.021	0.009	-0.036
		0.028	0.024	-0.024
12	0.87	0.021	0.040	-0.001
		0.022	0.085	0.054
		0.023	0.087	0.080
		0.028	0.092	*
20	1.00	0.034	0.220	0.094
		0.063	0.251	0.103
		0.073	0.327	0.103
25	1.16	0.007	0.210	0.036
		0.010	0.234	0.053
		0.016	0.354	0.075
36	1.49	0.045	0.153	-0.026
		0.047	0.164	-0.013
		0.051	0.181	0.001
40	1.83	0.017	0.113	*
		0.022	0.170	*
		0.029	0.172	*
		0.040	*	*
43	2.12	0.063	0.066	0.021
		0.074	0.074	0.026
		0.098	0.080	0.030
		0.102	0.084	*
47	2.36	0.072	0.222	0.080
		0.076	0.307	0.099
		0.093	0.309	0.113
53	2.68	0.087	0.138	*
		0.098	0.258	*
		0.102	0.269	*
		0.119	*	*
60	2.81	0.098	0.040	0.030
		0.099	0.065	0.034
		*	0.090	0.044
100	3.64	0.095	0.094	0.048
		0.096	0.107	0.070
		0.110	0.112	0.135

* Denotes missing values

Table A-2. Growth and sinking rate data for Chaetoceros flexuosum.

Clone type	Light intensity ($\mu\text{E m}^{-2} \text{sec}^{-1}$)	Growth rate (dbl day^{-1})	Sinking rate (m day^{-1})		
			Chlorophyll	Carbon	Silica
a	80	0.751	0.074	0.041	*
			0.077	0.151	*
			0.085	0.187	*
			0.090	*	*
a	110	0.824	0.056	0.061	*
			0.082	0.081	*
			0.102	0.081	*
			0.103	0.088	*
b	15	0.520	0.013	0.046	0.051
			0.022	0.059	0.057
			0.058	0.082	0.080
b	25	0.602	0.003	0.107	0.021
			0.012	0.111	0.052
			0.021	0.152	0.077
			0.033	*	*
c	40	0.706	0.046	0.124	0.017
			0.047	0.177	0.022
			0.056	*	0.030
c	47	0.845	0.040	0.126	0.026
			0.049	0.157	0.070
			0.054	0.170	0.086
c	91	0.829	0.039	0.170	0.018
			0.046	0.193	0.025
			0.084	*	0.040
c	123	0.861	0.072	0.039	0.036
			0.087	0.052	0.043
			0.098	*	0.052

* Denotes missing values

APPENDIX B
FIELD ASSEMBLAGE DATA

Table B-1. Station Data for Depths at Which Samples Were Collected for Sinking Rate Experiments.

Station	% Solar Constant	Chlorophyll (mg m ⁻³)	Temperature (°C)	Salinity (per mil)	Sigma-t	Nitrate (μM)
30	5	0.396	0.200	*	*	9.5
	1.5	0.383	0.200	*	*	9.4
	0.25	0.938	-0.060	*	*	9.8
61	5	0.799	3.000	*	*	11.2
	1.5	0.845	3.000	*	*	11.1
	0.25	0.824	3.000	*	*	11.0
63	8	0.750	2.400	*	*	10.5
	2.4	0.742	*	*	*	10.4
	0.4	0.746	*	*	*	10.3
66	5	1.224	1.400	*	*	9.3
	1.5	1.214	*	*	*	9.3
	0.25	1.234	*	*	*	9.2
72	7	1.375	-0.988	34.673	27.90	7.0
	2.1	1.502	-1.258	34.686	27.922	7.0
	0.35	1.025	-1.328	34.682	27.923	7.4
93	16	0.975	3.094	35.056	27.943	10.3
	4.8	1.019	3.086	35.056	27.944	10.3
	8	1.069	3.072	35.056	27.945	10.3
103	8	1.256	0.837	34.774	27.895	8.2
	2.4	1.416	0.841	34.775	27.896	8.3
	0.4	1.919	0.962	34.789	27.900	8.7
105	17	0.711	-0.036	34.684	27.873	8.0
	5.1	0.714	-0.045	34.684	27.874	8.0
	0.85	0.807	-0.084	34.687	27.878	8.6
107	9	0.745	0.478	34.747	27.896	9.1
	2.7	0.763	0.485	34.747	27.896	9.1
	0.45	0.742	0.459	34.752	27.901	9.4
110	7	0.976	-0.348	34.684	27.889	8.1
	2.1	1.001	-0.349	34.684	27.889	8.1
	0.35	1.009	-0.351	34.684	27.889	8.2
115	35	0.385	-0.965	34.722	27.946	9.5
	10.5	0.350	-0.999	34.722	27.946	9.5
	1.75	0.446	-1.116	34.726	27.955	9.5
117	11	0.644	-0.740	34.760	27.968	9.5
	3.3	0.615	-0.894	34.719	27.941	9.5
	0.55	0.738	-1.114	34.744	27.969	9.5
132	11	0.338	-1.710	33.677	27.120	7.7
	3.3	0.190	-1.720	33.865	27.276	8.2
	0.55	0.055	-1.718	33.980	27.369	9.1

Table B-1 (continued)

Station	% Solar Constant	Chlorophyll (mg m ⁻³)	Temperature (°C)	Salinity (per mil)	Sigma-t	Nitrate (μM)
133	18	0.241	-1.610	33.871	27.277	8.1
	5.4	0.179	-1.496	34.067	27.434	9.3
	0.9	0.058	0.024	34.539	27.754	11.9
135	15	1.730	0.130	34.131	27.420	9.3
	4.5	2.026	0.118	34.444	27.672	9.5
	0.75	1.835	0.619	34.759	27.897	10.6
137	10	0.723	0.152	34.126	27.414	9.8
	3.0	1.787	0.023	34.682	27.869	10.3
	0.5	1.300	0.279	34.802	27.952	11.4
139	9	1.307	0.253	34.297	27.547	9.7
	2.7	2.266	0.354	34.747	27.899	10.1
	0.45	1.709	0.421	34.817	27.942	11.0
143	15	1.564	0.051	34.699	27.881	9.2
	4.5	2.022	-0.549	34.715	27.923	9.1
	0.75	0.890	-0.611	34.714	27.925	10.0
149	9	0.321	-1.640	33.744	27.183	7.8
	4.5	0.246	-1.694	33.928	27.326	9.0
	0.45	0.131	-1.564	34.193	27.538	10.6
151	10	1.782	0.564	34.561	27.742	9.5
	3.0	2.566	0.591	34.594	27.766	9.8
	0.5	1.964	0.566	34.782	27.919	9.9
153	7	2.624	0.723	34.404	27.606	4.1
	2.1	3.060	0.713	34.379	27.586	5.4
	0.35	2.733	0.865	34.635	27.586	7.5
155	3	1.397	*	*	*	1.3
	0.9	2.938	0.728	34.207	27.450	1.2
	0.15	2.393	0.818	34.225	27.470	1.7
157	7	4.347	1.961	34.940	27.948	4.8
	2.1	4.547	1.950	34.927	27.938	5.2
	0.35	4.886	1.886	34.946	27.959	6.4
163	3	0.130	-1.717	33.210	26.745	5.0
	0.9	0.131	-1.531	33.609	27.063	8.6
	0.35	0.145	-1.725	33.892	27.297	8.8
168	20	1.555	-0.892	33.696	27.114	3.2
	6	3.192	-0.203	34.045	27.367	3.4
	1	1.604	0.662	34.570	27.742	6.4
171	9	1.151	0.443	34.119	27.393	6.1
	2.7	1.613	0.942	34.601	27.750	9.5
	0.45	0.297	1.407	34.853	27.920	11.8

Table B-1 (continued)

Station	% Solar Constant	Chlorophyll (mg m ⁻³)	Temperature (°C)	Salinity (per mil)	Sigma-t	Nitrate (μM)
173	4	1.387	2.277	34.966	27.950	7.3
	1.2	1.434	2.283	34.968	27.950	7.8
	0.2	1.544	1.750	34.961	27.980	9.2
174	21	0.115	-1.515	33.280	27.796	5.7
	6.3	0.225	-1.646	33.590	27.051	8.0
	1.05	0.601	-1.646	34.341	27.620	9.0
177	10	1.121	*	*	*	3.7
	3	0.624	-1.315	34.027	27.432	6.6
	0.5	0.365	*	*	*	9.4
179	6	2.028	*	*	*	2.7
	1.8	3.931	1.186	34.774	27.873	5.9
	0.3	1.581	*	*	*	7.6

* Denotes missing values

Table B-2. Sinking Rates Determined in Field Experiments for Each Biomass Parameter in m day^{-1}

Station	% Surface Intensity	Chlorophyll	Phaeo-pigments	Carbon	Nitrogen	Silica
30	100	0.10	0.10	0.29	*	0.06
	30	0.20	0.02	*	*	0.01
	5	0.06	0.22	0.25	*	-0.08
61	100	0.02	0.24	0.49	0.85	0.18
	30	0.06	0.23	1.02	0.14	0.08
	5	-0.01	0.10	0.08	-0.23	0.02
63	100	-0.01	0.16	0.36	0.96	0.09
	30	0.05	0.15	0.21	1.22	0.00
	5	0.03	0.08	0.07	0.84	0.60
66	100	-0.02	*	0.83	-0.15	0.03
	30	0.12	0.28	0.65	0.97	*
	5	0.00	0.49	0.33	1.24	0.32
72	100	0.10	0.02	1.11	0.20	-0.07
	30	0.33	0.34	1.42	1.23	-0.08
	5	0.34	0.20	1.63	0.55	-0.18
93	100	0.02	0.04	0.59	3.71	*
	30	0.06	0.34	0.34	0.41	*
	5	0.00	0.29	0.82	0.14	0.26
103	100	0.05	0.04	0.69	1.44	*
	30	0.09	0.26	0.16	0.80	0.08
	5	0.18	0.11	0.27	0.17	0.04
105	100	0.13	0.10	0.41	0.15	0.22
	30	0.22	0.13	0.45	0.04	0.38
	5	0.09	0.13	0.73	0.48	0.25
107	100	0.05	0.12	1.60	*	0.24
	30	0.08	0.00	0.72	*	*
	5	0.07	0.12	1.04	*	0.07
110	100	0.14	0.09	0.71	0.89	0.14
	30	0.17	0.10	1.49	1.98	0.17
	5	0.11	0.05	1.69	1.61	0.21
115	100	0.16	0.12	0.09	0.15	0.38
	30	0.18	0.08	*	0.16	0.07
	5	0.13	0.36	0.07	-0.03	0.36
117	100	0.01	0.17	0.29	0.30	0.36
	30	0.08	0.20	0.29	0.07	0.22
	5	0.07	0.24	0.36	0.50	0.47
132	100	0.14	0.03	0.56	0.88	0.13
	30	0.30	0.10	*	0.13	-0.13
	5	0.32	0.10	0.54	0.69	0.11

Table B-2 (continued)

Station	% Surface Intensity	Chlorophyll	Phaeo-pigments	Carbon	Nitrogen	Silica
133	100	0.09	0.08	*	0.30	*
	30	0.16	0.18	0.49	0.75	-0.17
	5	0.20	0.08	0.54	0.03	*
135	100	0.19	0.00	*	*	0.29
	30	0.12	-0.09	*	*	0.18
	5	0.12	-0.01	*	*	*
137	100	0.16	0.15	0.30	*	0.31
	30	0.11	0.38	*	1.33	0.01
	5	0.06	0.09	0.12	0.83	0.07
139	100	0.10	0.05	0.24	*	0.12
	30	0.14	0.28	0.52	*	-0.10
	5	0.22	0.04	0.63	*	-0.11
143	100	0.20	0.18	0.11	0.31	0.00
	30	0.03	0.41	1.11	0.61	-0.13
	5	0.23	0.75	1.06	0.26	0.00
149	100	0.60	0.50	0.43	*	0.18
	30	0.19	0.01	0.63	*	0.10
	5	0.25	-0.04	*	*	0.00
151	100	0.08	0.31	0.62	2.44	0.03
	30	0.05	0.11	0.48	0.07	-0.08
	5	0.12	0.16	0.88	0.15	0.06
153	100	0.08	1.00	*	*	0.68
	30	0.20	0.48	0.36	0.75	0.45
	5	0.16	0.09	-0.01	0.04	0.24
155	100	0.16	0.23	*	0.58	0.50
	30	0.20	0.36	0.15	0.14	0.49
	5	0.04	0.30	0.17	0.16	0.22
157	100	0.01	0.17	0.24	0.34	0.08
	30	0.11	0.33	0.18	0.68	0.04
	5	0.18	0.41	*	*	0.28
163	100	*	0.61	*	0.05	*
	30	0.32	0.16	*	0.19	*
	5	0.52	0.29	*	1.16	0.07
168	100	-0.04	0.01	*	0.44	0.10
	30	-0.01	-0.09	0.27	0.93	0.03
	5	0.10	-0.01	*	*	0.18
171	100	0.18	0.25	*	1.24	0.15
	30	0.63	*	*	0.03	-0.06
	5	*	0.37	*	1.10	0.22
173	100	0.11	0.27	-0.20	1.42	0.03
	30	0.18	0.35	*	1.94	0.06
	5	0.15	0.39	*	*	-0.02

Table B-2 (continued)

Station	% Surface Intensity	Chlorophyll	Phaeo-pigments	Carbon	Nitrogen	Silica
174	100	0.34	0.46	*	*	0.10
	30	0.30	0.34	0.54	0.20	-0.15
	5	0.04	*	0.62	0.73	0.08
177	100	0.08	0.07	*	*	0.14
	30	0.15	0.14	*	*	0.22
	5	0.14	0.16	0.64	0.62	-0.15
179	100	0.26	0.31	0.97	0.06	*
	30	0.13	-0.03	*	0.06	0.18
	5	0.12	0.21	*	*	-0.05

* Denotes missing values

VITA

Mary Evans Culver was born in Chapel Hill, North Carolina on February 3, 1963. She attended primary and secondary schools in Houston, Texas and Farragut, Tennessee, and graduated from The Webb School of Knoxville in May 1981. The following August, she entered Duke University and graduated cum laude in May 1985 with a Bachelor of Science degree in Zoology. In September 1985, she began graduate studies in The Graduate Program in Ecology at The University of Tennessee, working under graduate teaching assistantships or research assistantships until receiving a Master of Science degree in March 1988.