NUTRITION AND DISTRIBUTION OF THE ARCTIC CALANOID COPEPOD *PSEUDOCALANUS ACUSPES* DURING SPRING AND SUMMER IN RESOLUTE PASSAGE AND BARROW STRAIT, N.W.T., CANADA

by

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ABSTRACT

The distribution of the arctic calanoid copepod *Pseudocalanus acuspes* was examined during the summer (August) of 1990, and the spring (May) of 1991 in the waters of Barrow Strait and Resolute Passage, N.W.T. Water column particulates (chlorophyll a, phaeopigments, silicates, and CHN) were also concurrently described. Copepod incubations (ammonia/urea production and oxygen consumption translated to O:N ratios) and distribution information were used to describe aspects of the nutrition of *P. acuspes*.

A strong diel migration by *P. acuspes*, moving to the near underice surface at night, was detected during the month of May. During August, the bulk of the summer population remains near the sinking chlorophyll maximum (depths of 15-50m). Tidal current erosion and mixing are likely to be important in making epontic algae available for *P. acuspes*. Low O:N ratios (by atoms) measured during the summer and late spring (8.19-11.94) indicate high grazing rates on phytoplankton and probably an associated production of lipids. The O:N ratios are the lowest reported for arctic copepods.

Feeding selection experiments were conducted using the natural summer phytoplankton assemblage from Resolute Passage, N.W.T., in August, 1991. *P. acuspes* tended to positively select the diatoms *Nitzschia seriata,* a species of *Thalassiosira*, and one species of *Navicula*. It avoided a species of *Fragilaria*. The strength of the feeding selection was shown to be dependant on the extent of feeding (depletion of chlorophyll), and could be explained by selection for the largest "effective food parcel size". Feeding selection by *P. acuspes* is an important aspect of its natural feeding ecology.

ACKNOWLEDGMENTS

I would like to thank my supervisor, Dr. R.J. Conover, for all of his advice and assistance throughout this project. This study would not be possible were it not for the physical, mental, and academic support provided by Les Harris, Erica Head, Buster Welch, Tim Siferd, Henry Landry (and the whole gang at D.F.O. South Camp), and everyone in Biological Oceanography at B.I.O.

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I thank my parents for all of their love and support during my studies. A special big hug goes to my wife Rhonda for all of her love and emotional strength and for helping me survive a most trying spring field season in the arctic (polar bears and all).

PART I:

Distribution of the Arctic Calanoid Copepod *Pseudocalanus acuspes* and Characteristics of Water Column Particulates During Spring and Summer in the Canadian High Arctic

INTRODUCTION

The arctic marine environment possesses particularly challenging physical constraints which force the organisms living there to display highly adaptive behavioral and physiological characteristics. Life must be able to cope with long, cold winters, seasonally or permanently ice-covered seas, and lack of any significant light for up to four months of the year. It is truly a unique habitat.

The first annual potential nutrition in the arctic for the herbivorous zooplankton community appears during the initiation of epontic growth in the spring (Conover, 1988). The documentation of high levels of algae associated with the underside of the sea-ice (Apollonio, 1961 and 1965) initiated a proliferation of studies which have described the biological adaptations and physical factors which allow this potentially important food source to flourish (see reviews by Cota et al., 1991; Cota and Smith, 1991).

Recent zooplankton studies in the arctic focus on the role of spring epontic algae and summer phytoplankton in providing for the nutrition of the herbivorous copepod communities in the seasonally ice-covered seas (i.e., Conover et al., 1986b; Conover et al., 1988a; Head and Harris, 1985; Head et al., 1985; Head et al., 1988; Hirche et al., 1991; Runge and Ingram, 1991; Tremblay et al., 1989). Documentation of particular life-history and physiological strategies displayed by copepods, such as the

presence of annual or multiyear life-cycles and the ability to accumulate large overwintering reserves of lipids, has greatly enhanced our understanding of the arctic pelagic ecosystem (i.e., Conover, 1988; Conover and Corner, 1968; Grainger, 1959; Hirche, 1991; Longhurst et al., 1984).

This present study has the following objectives: to determine the vertical distribution of the arctic calanoid copepod *Pseudocalanus acuspes* (Giesbrecht) in relation to characteristics of the water column particulates during the spring and summer in Barrow Strait and Resolute Passage, N.W.T. (Fig. 1), to determine the metabolic condition of *P. acuspes* as indicated by oxygen consumption and nitrogenous excretion rates (O:N ratios by weight), and to examine feeding selection by *P. acuspes* when fed a natural phytoplankton assemblage from Resolute Passage, N.W.T. In this chapter, we will examine aspects of the nutrition and distribution of *P. acuspes*. The following chapter will examine feeding selection.

P. acuspes may be the most abundant and productive copepod in northern seas (Conover and Huntley, 1991). This copepod possesses an annual life cycle, with sexual maturity and the peak of reproduction occurring during the month of June and into July (at or just prior to ice break-up; Conover and Huntley, 1991; Conover et al., 1986a). *P. acuspes* develops relatively quickly and overwinters as copepodite stage III-V (CIII-CV) during which time

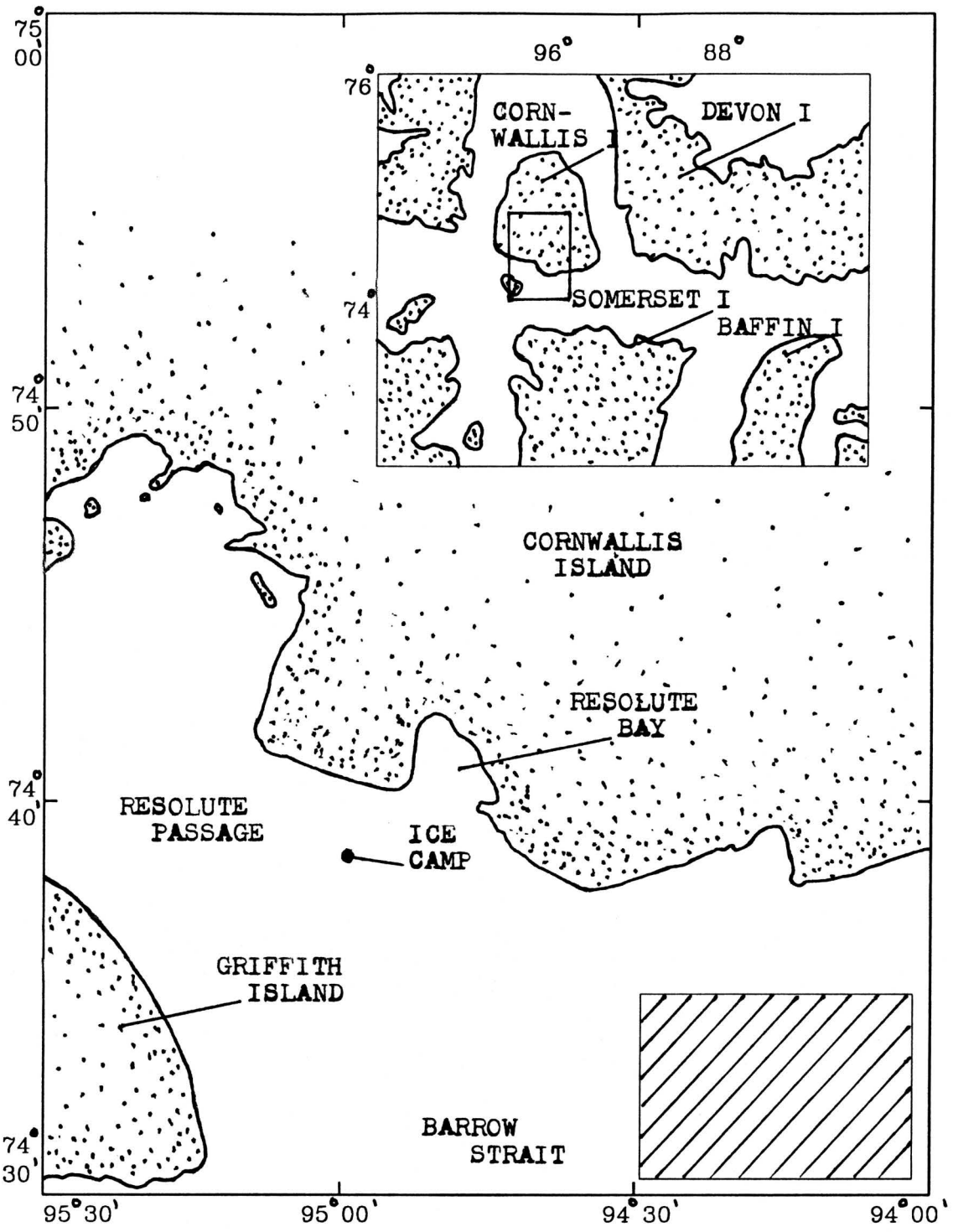


Figure 1. Map of the field site, showing the area of the summer, 1990, sampling stations in Barrow Strait (hatched rectangle), and spring, 1991, ice camp location in Resolute Passage. Insert shows relationship within the arctic archipelago (Northwest Territories, Canada).

development is apparently arrested (Conover et al., 1986a). Few adult females and males survive through to the following spring. This annual life cycle of *Pseudocalanus acuspes* in the Resolute Bay area is in contrast to its more southernly counterparts (*Pseudocalanus acuspes* and other *Pseudocalanus* species) which show multiple generations annually (McLaren et al., 1989).

Typically, Barrow Strait is covered from the end of November through to the end of June with land-fast ice. Breakup occurs in July, leaving a short "ice-free" season during August and September (Markham, 1981). Ice builds rapidly reaching 9/10ths concentrations by the middle of October and thicknesses of up to 1.95m before melting begins in May (Prinsenberg and Bennett, 1987).

The sun first appears over the horizon in the middle of February, and by the end of April does not again dip below until the end of August. The sun disappears again for the year by the beginning of November (Resolute Airport Station RF-1 Summaries, Environment Canada).

Water mass transportation through the Canadian arctic archipelago is generally from west to east, spilling into Baffin Bay (Prinsenberg and Bennett, 1987). Three distinct surface water masses of arctic origin, whose depth varies from 15m in the north to 60m in the south (depth and mixing varying as tidal current strength), can be identified in Barrow Strait (Prinsenberg and Bennett, 1987). From Peel

Sound in the south, warmer, moderately saline water enters the strait, while slightly cooler, less saline surface water enters from the west through Viscount Melville Sound. Both these water masses are identifiable as Canadian Basin surface water (Melling et al., 1984; Prinsenberg and Bennett, 1989). Surface water travelling into Barrow Strait from the north along both sides of Cornwallis Island, is also of Canadian Basin surface water origin, but due to cooling and turbulent mixing with subsurface water, is cooler and saltier (Prinsenberg and Bennett, 1989).

Subsurface waters entering Barrow Strait also possess separate and distinct characteristics: cool, salty water from the north, warmer (0.2-0.4°C) water from the west, and warmer, fresher water from the south. The water entering from Peel Sound in the south, being the least dense, remains along the southern shore of the strait as it flows towards Baffin Bay (overriding the heavier subsurface waters from the west and north; Prinsenberg and Bennett, 1987).

As this present study was conducted along the northern side of Barrow Strait and into Resolute Passage (Fig. 1), the area will typically have the shallowest surface mixed layer (as low as 15m), as well being the most saline and coolest of any waters which pass through the strait (Prinsenberg and Bennett, 1987 and 1989).

MATERIALS AND METHODS

This study was conducted during three field seasons from Resolute Bay, N.W.T., over a one year period from the summer of 1990 through the summer of 1991.

Summer, 1990:

Two separate cruises were conducted in the waters of Barrow Strait (Fig. 1) from August 8-10 and August 20-21, 1990, using the R.V. Ogac (Dept. of Fisheries and Oceans, Canada). These cruises concentrated on establishing the vertical distribution of *Pseudocalanus acuspes* in relation to various particulate characteristics of the water column (chlorophyll a/ phaeopigment, silicate, and carbon/ hydrogen/ nitrogen (CHN) content). A plankton pumping system (Fig. 2) was developed by this author and R.J. Conover (Bedford Institute of Oceanography; see also Miller and Judkins, 1981; Taggart and Leggett, 1984) to allow replicate sampling at discrete depths.

The plankton pumping system was powered by a Gorman-Rupp® self-priming centrifugal pump (model 13D-19) located on the deck of the ship. 100m of 3" plastic suction hose, divided into 5m sections connected by couplings, was attached to the intake end of the pump. At the intake, an L-shaped piece of aluminum piping with a $0.5m^2$ fin was attached, along with a weight and a Benthos® depth recorder (0-100m range) to estimate sampling depth. On the output end of the pump, ball valves allowed water to be shunted

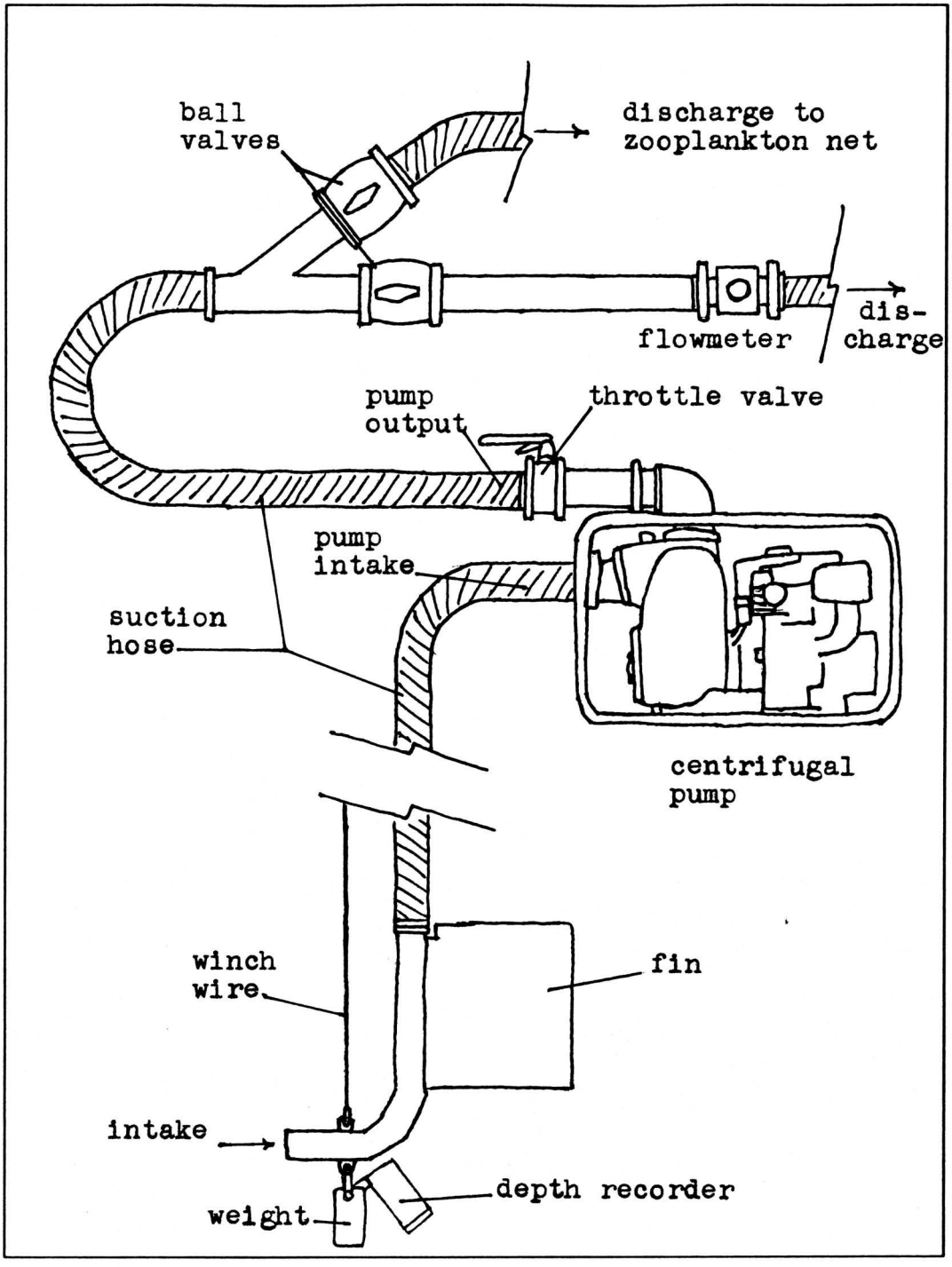


Figure 2. General diagram of the plankton pumping system used during the summer of 1990 in Barrow Strait, N.W.T.

through a turbine flowmeter (Neptune 3" Trident®) for periodic estimation of flow rates; water used for sampling by-passed the meter. Water was discharged into a 100μm mesh net for zooplankton collections immediately after sampling for particulates. Pumping flow rate was maintained at approximately 8 Ls^{-1}.

During the first cruise, August 8-10, one vertical diel series was conducted using the plankton pump system. Preserved zooplankton, particulate chlorophyll a/ phaeopigment, particulate silicate, and particulate CHN samples were taken at four discrete depths (usually 2m, 10m, 50m, and 80m; three replicates at each depth). This sampling was conducted every six hours until three complete sets of vertical profiles were obtained (the first profile set starting at 19:30hr, August 8, the second at 01:30hr, August 9, and the last at 08:00hr, August 9). Because of required maintenance on the pump, further sampling using the pump system (i.e., for a complete diel series) was not practical during this cruise. Instead, particulate sampling was continued using 5L Niskin bottles following the same protocol. The fourth profile set for particulates started at 14:00hr (August 9), the fifth at 21:00hr (August 9), and the sixth at 02:00hr (August 10). No preserved zooplankton samples were taken for the fourth, fifth, and sixth vertical profile sets.

Two pairs of oblique hauls from 0-100m were done

using a 100μm mesh zooplankton net after we could no longer use the plankton pump system on this first cruise. The first set was done at 23:00hr, August 9 (during the fourth profile set), and the second set at 03:30hr, August 10 (during the fifth profile set). This oblique haul information was converted to an average number of *P. acuspes* per cubic metre for each developmental stage. We can then compare these numbers with the numbers calculated from the pump samples from the corresponding times the previous evening (profiles #1 and #2, respectively). This helped us determine how the copepod concentrations measured at discrete depths using the pump compare with the average concentration in the top 100m of the water column (i.e., are the copepods concentrated at some other depth not sampled by the pump?). The depth of the water column at this sampling area was always between 100m and 120m, so the net samples closely represent the average in the water column.

During the second cruise, August 20-21, another vertical diel series was conducted using the plankton pump, except this time sampling was conducted at about 12hr intervals (the first profile set started at 13:30hr, August 20, the second at 01:30hr, August 21, and the third at 14:00hr, August 21). The sampling protocol followed was as previously outlined for the first three vertical profile sets initiated on August 8.

In between sampling periods with the pump, oblique

hauls from 100m depth were taken, using a 0.5m diameter 100μm mesh net, for incubation experiments (oxygen utilization and ammonia/urea excretion measurements) with *Pseudocalanus acuspes*. Copepodite stages IV, V and adult females (CIV-CVIf) were sorted from the zooplankton assemblage immediately after capture, and experiments initiated at 21:00hr (August 20), 09:30hr (August 21), and 21:00hr (August 21) respectively.

Spring, 1991:

An ice camp was established in Resolute Passage, N.W.T. (Fig. 1), from April 30 to May 22, 1991, during which time two vertical diel series were conducted. Sampling was similar to that done the previous summer, except that a 0.5m diameter, 100μm mesh net (without closing mechanism), for zooplankton samples, and 5L Niskin bottles, for water particulates, were used.

The first vertical diel series was conducted on May 7-8. Water samples for particulate chlorophyll a/ phaeopigment, particulate silicate, and particulate CHN were taken every 12hr over a 36hr period, for a total of 3 complete vertical profile sets. No preserved zooplankton samples were taken at this time. The first set was sampled at four discrete depths (0m, 2m, 6m, and 25m) with three replicates each. The second and third sets were sampled at five discrete depths (with the addition of a sample at 12m) with no replicates. The first profile set was started at

21:30 hr (May 7), the second at 09:30hr (May 8), and the third at 21:30hr (May 8). After each of the last two profiles, a vertical net haul from 5m depth was taken and *Pseudocalanus acuspes* copepodite stages V, adult males, and adult females (CV, CVIm, and CVIf) immediately sorted from the samples for incubation experiments.

The second diel series was conducted on May 15-16. Oblique hauls with the zooplankton net were taken at four depth intervals (0-5m, 0-10m, 0-15m, and 0-25m) every eight hours over 24hr for collection of preserved samples (for a total of four complete profiles). Two replicates were taken at each depth. Sampling for the first profile began at 10:00hr (May 15), for the second at 18:00hr (May 15), for the third at 02:00hr (May 16), and for the four at 10:00hr (May 16). Concurrent with the collection of the zooplankton samples, particulate profiles were again taken at four discrete depths (0m, 2m, 6m, and 25m) with three replicates at each depth.

A CTD cast was done for each vertical profile done during the spring using a Seabird Seacat Profiler® (SBE19, courtesy of S. Narayanan, Dept. of Fisheries and Oceans, St. John's, Newfoundland). The data was processed using the instrument's associated software.

On the evening of May 17th (19:00hr) and the morning of May 18th (07:00hr) *Pseudocalanus acuspes* incubation experiments were initiated, again using stages CV, adult

males (CVIm), and adult females (CVIf) captured within 5m below the ice.

Summer, 1991:

Most of the activities for this field season were concentrated on a series of feeding selection experiments, the results of which are presented in the next chapter. However, in order to supplement the information from the incubation experiments (oxygen utilization and ammonia/urea excretion measurements) for *Pseudocalanus acuspes* from the previous summer, two further experiments were conducted. The copepods were captured in Resolute Passage, again using a 0.5m diameter, 100μm mesh net, and stages CIV and adult females (CVIf) sorted from the zooplankton assemblage at the laboratory facilities provided at the Department of Fisheries and Oceans (Central and Arctic Region, Winnipeg, Manitoba) in Resolute Bay. All experiments began within 3hr after the zooplankton samples were collected. The first incubation experiment began at 14:00hr (August 3, 1991), and the second one at 15:30hr (August 12, 1991).

Laboratory procedures:

For particulate chlorophyll a/ phaeopigment determination, 100ml (200ml in the spring) of sample water was filtered through a Whatman GF/F® glass fibre filter and immediately frozen at -20°C until later processing in the laboratory facilities at Resolute Bay (Scotia Fundy Region, Dartmouth, Nova Scotia). Chlorophyll and phaeopigment

samples were processed fluorometrically according to Parsons et al. (1984) using a Philips PU8625® UV/visible specrophotometer. During the summer of 1990, 90% acetone was used as the pigment extraction solvent, while 95% methanol was used during the following spring and summer, 1991. All samples were processed within two weeks of collection.

For particulate silicate determination, 100ml (200ml in the spring) of sample water was filtered through a cellulose fibre filter (1.0µm nominal pore size). For particulate CHN determination, 200ml (400ml in the spring) of sample water was filtered through a baked (450°C for 1hr) Whatman GF/F® glass fibre filter. Both sets of samples were frozen at -20°C until they could be processed later at the Bedford Institute of Oceanography in Dartmouth, Nova Scotia. Silicate samples were processed according to Paasche (1980). A Perkin Elmer 2400 CHN Elemental Analyser® was used for CHN determination after the filtrates were dried at 60°C over 24hr. The CHN content data was then converted to C:N ratios (by weight). All samples were processed within three months of collection.

For *Pseudocalanus acuspes* incubation experiments, the animals were sorted according to stage and placed in 300ml reagent bottles (approximately 50 individuals per bottle; at least 3 controls and 3 experimental treatments were run concurrently). The bottles were incubated in the

dark at temperatures between -1.0°C and 1.0°C for 24-36hr. Oxygen content (µg-at O_2L^{-1}) was determined for each bottle by Winkler titration according to Levy et al. (1977), using 60ml oxygen bottles. From each experimental treatment and control bottle one 20ml aliquot was removed for ammonia determination (µg-at NL^{-1}) and four 20ml aliquots removed for urea determination (µg-at NL^{-1}) according to Parsons et al. (1984). From this data, O:N ratios (by atoms) were calculated, using only ammonia excretion, only urea excretion, and with both urea and ammonia excretion taken into account.

Zooplankton samples were preserved in a 1% formalin solution and sorted at the Bedford Institute of Oceanography within the following year. The animals were counted according to copepodite stage and the adults were sexed using Corkett and McLaren (1978) and Frost (1989).

Plots of vertical profiles of *P. acuspes*, particulates, temperature, salinity, as well as the T-S plots were produced using the Sigmaplot® software package.

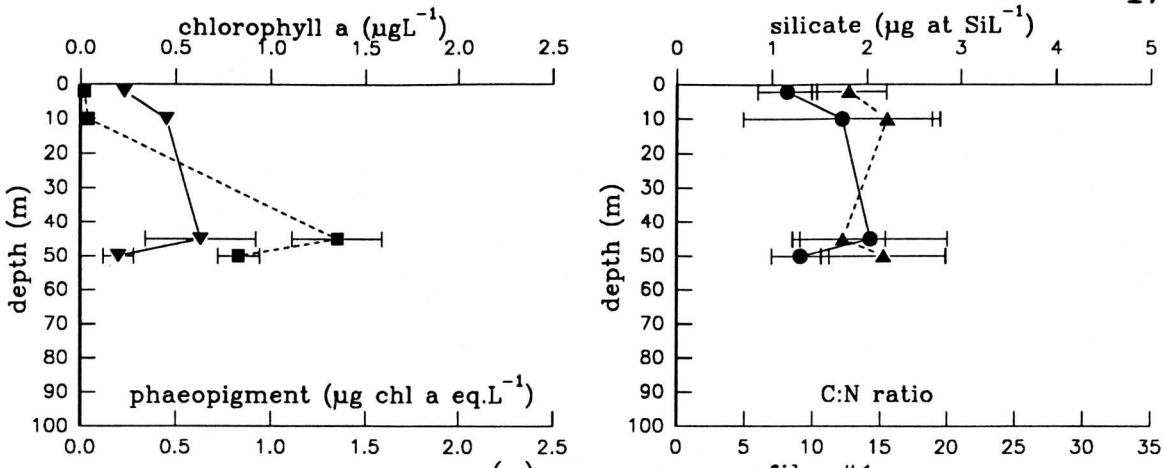
RESULTS

Summer, 1990:

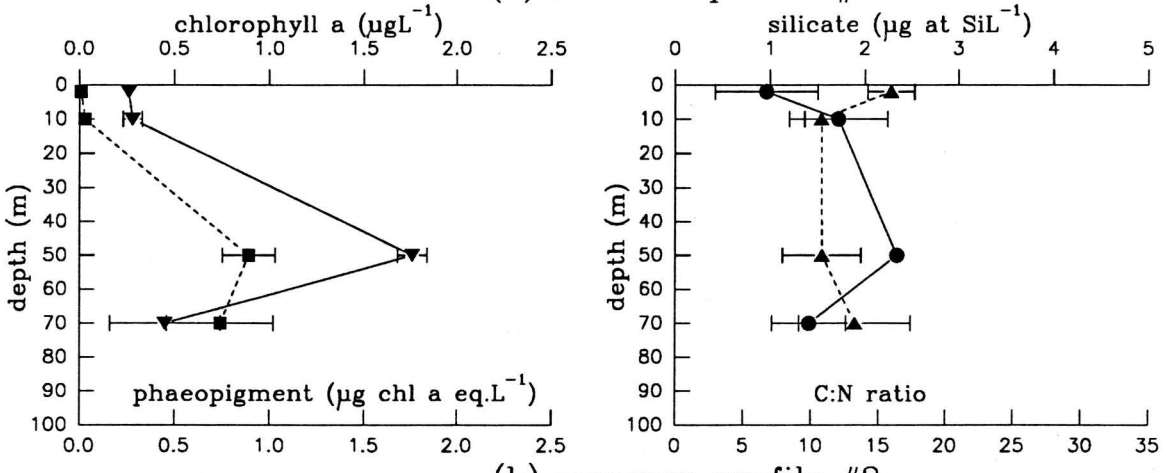
When we examine the profile of particulates in early August (Figs. 3a and 3b), it is evident that the bulk of the algal community lies between 10m and 50m (as indicated by the chlorophyll a and silicate profiles). The lack of sampling between 10m and 40m prohibits an accurate description of the vertical structure of the particulates, but the chlorophyll maximum most likely lies between 20m and 30m during this time of the year (Harold Welch, pers. comm.; see Fig. 16 in the following chapter for an example of typical summer profiles).

The profiles of the particulate C:N ratios (by weight) do not show any clear trend. Most values lie between 10 and 15, an indication of algae in a post-bloom condition (Banse, 1974). Late August ratios (Fig. 5) do not show any significant change over the early August values (Figs. 3a-b). The apparently poor condition of the phytoplankton community persists throughout our sampling period.

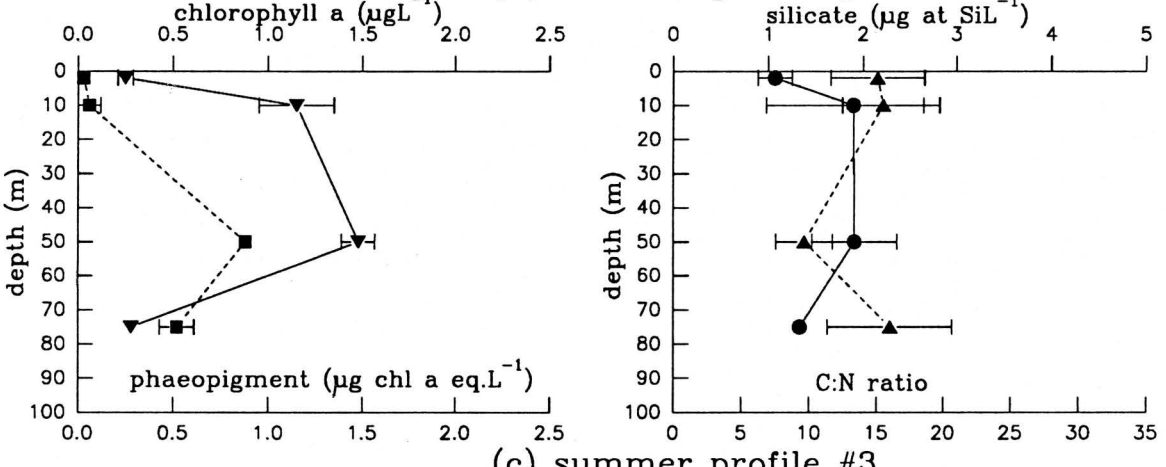
The predominant copepodite stages in early August in Barrow Strait are CI and CII (Figs. 4a-c), i.e. offspring of the present year's breeding efforts. There are relatively few CIII's and CIV's (Figs. 4a-c), marking the separation of the new generation from the previous year's crop. Most CIII's and CIV's found at this time of the year are likely



(a) summer profile #1

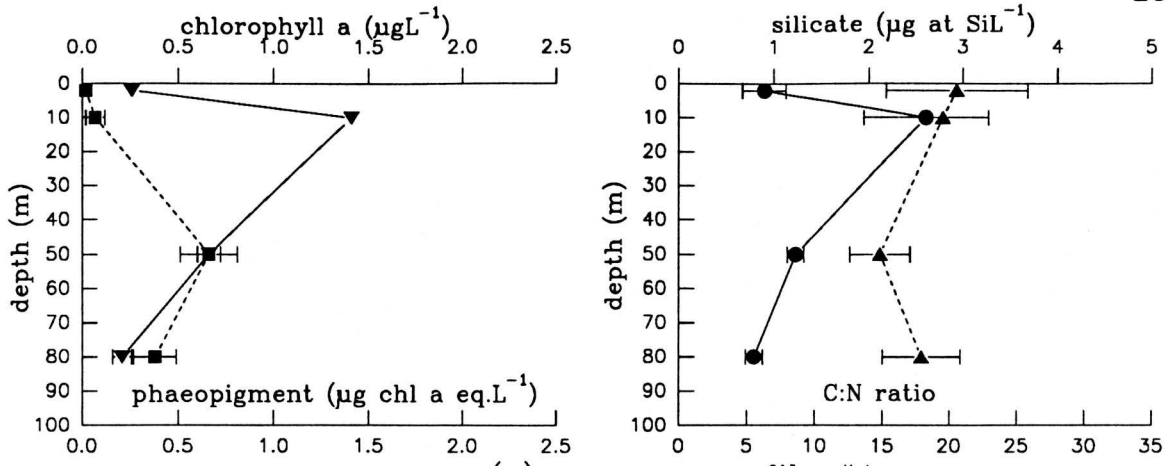


(b) summer profile #2

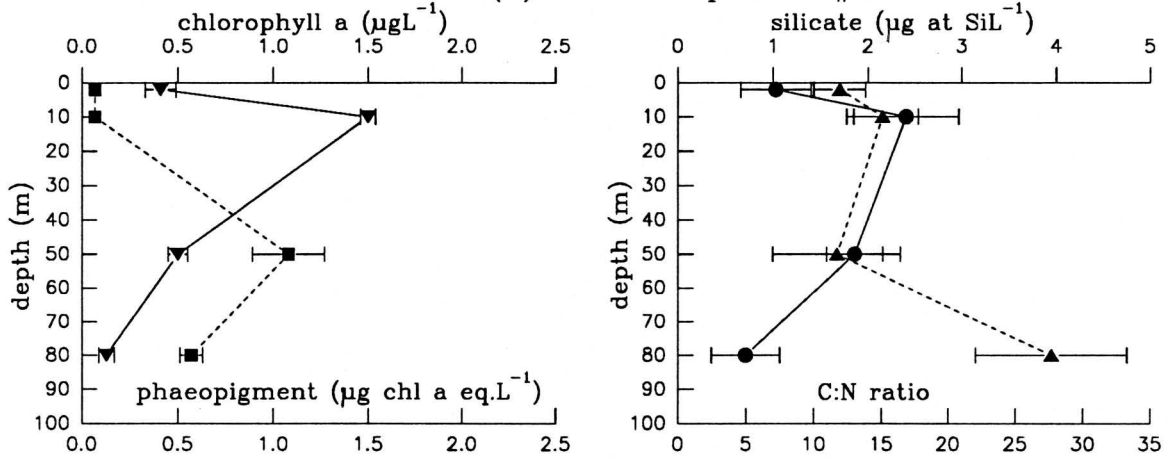


(c) summer profile #3

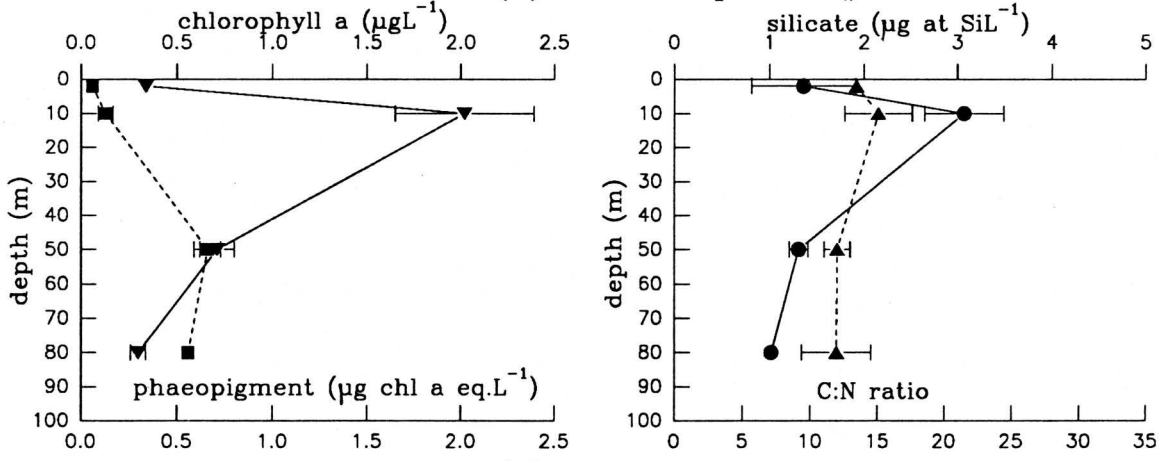
Figure 3a. Summer profiles of particulate chlorophyll a (µgL^{-1}), phaeopigments (µg chl a eq.L^{-1}), silicate (µg at SiL^{-1}), and C:N ratios (by weight) in Barrow Strait, N.W.T. Profile #1 samples collected 19:30–23:00hr (Aug. 8/90), profile #2 01:30–04:00hr (Aug. 9/90), and profile #3 08:00–10:30hr (Aug. 9/90). Chlorophyll a (solid line) and phaeopigment (dashed line) profiles are shown on left graphs. Silicate (solid line) and C:N ratio (dashed line) profiles are shown on right graphs. Error bars represent the standard deviation of replicate samples.



(a) summer profile #4



(b) summer profile #5



(c) summer profile #6

Figure 3b. Summer profiles of particulate chlorophyll a (µgL^{-1}), phaeopigments (µg chl a eq.L^{-1}), silicate (µg at SiL^{-1}), and C:N ratios (by weight) in Barrow Strait, N.W.T. Profile #4 samples collected 14:00–17:00hr (Aug. 9/90), profile #5 21:00–23:30hr (Aug. 9/90), and profile #6 02:00–04:00hr (Aug. 10/90). Graphic elements are as defined in Figure 3a.

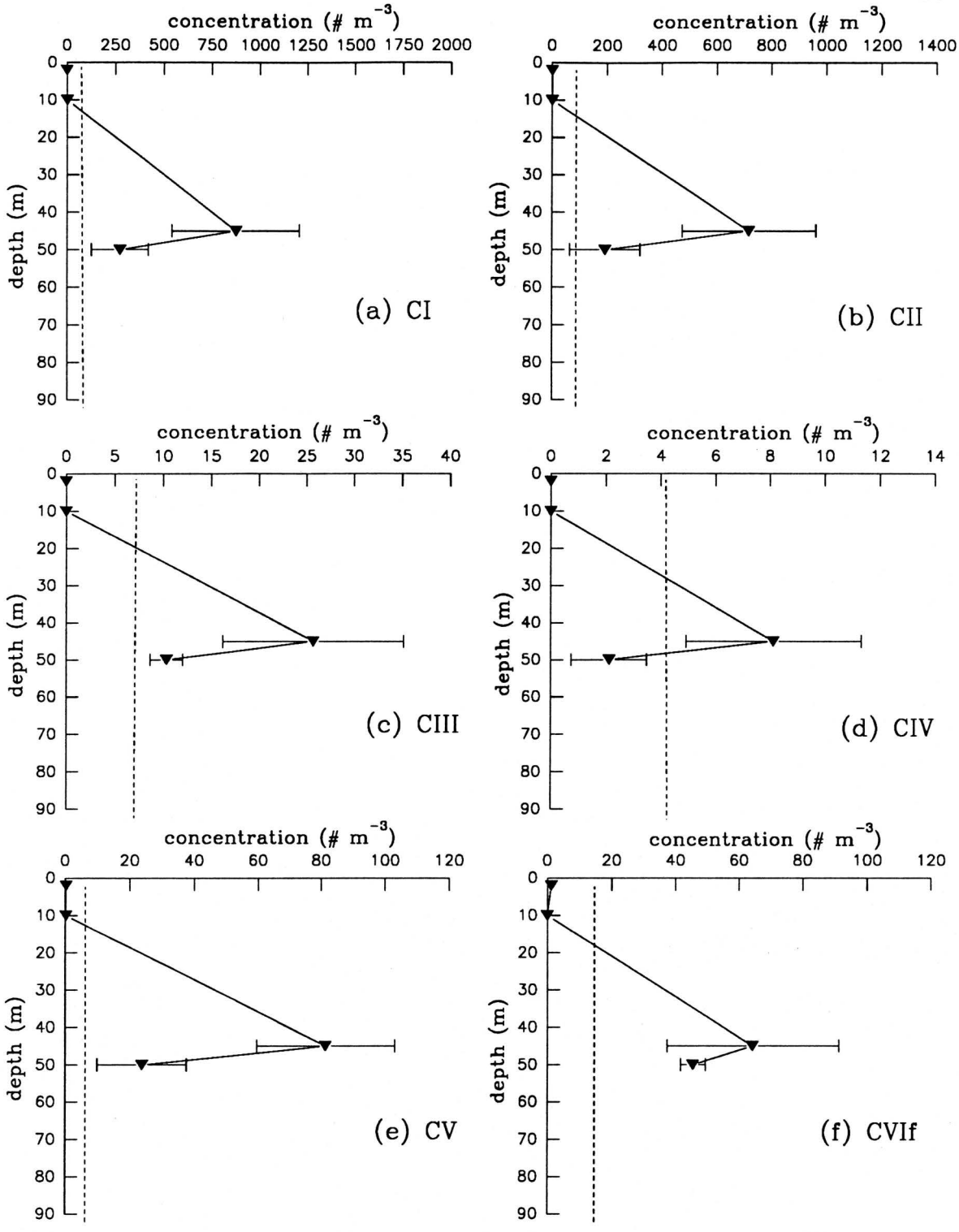


Figure 4a. Summer profile of *Pseudocalanus acuspes* copepodite stages (CI–CVIf) in Barrow Strait, N.W.T. Samples collected from 19:30–23:00 hr (Aug. 8/90). Please note horizontal scale changes. This profile corresponds to profile #1 on Figure 3a. Error bars represent the standard deviation of replicate samples. Dashed line is average concentration (0–100m; # m^{-3}) determined by oblique net haul.

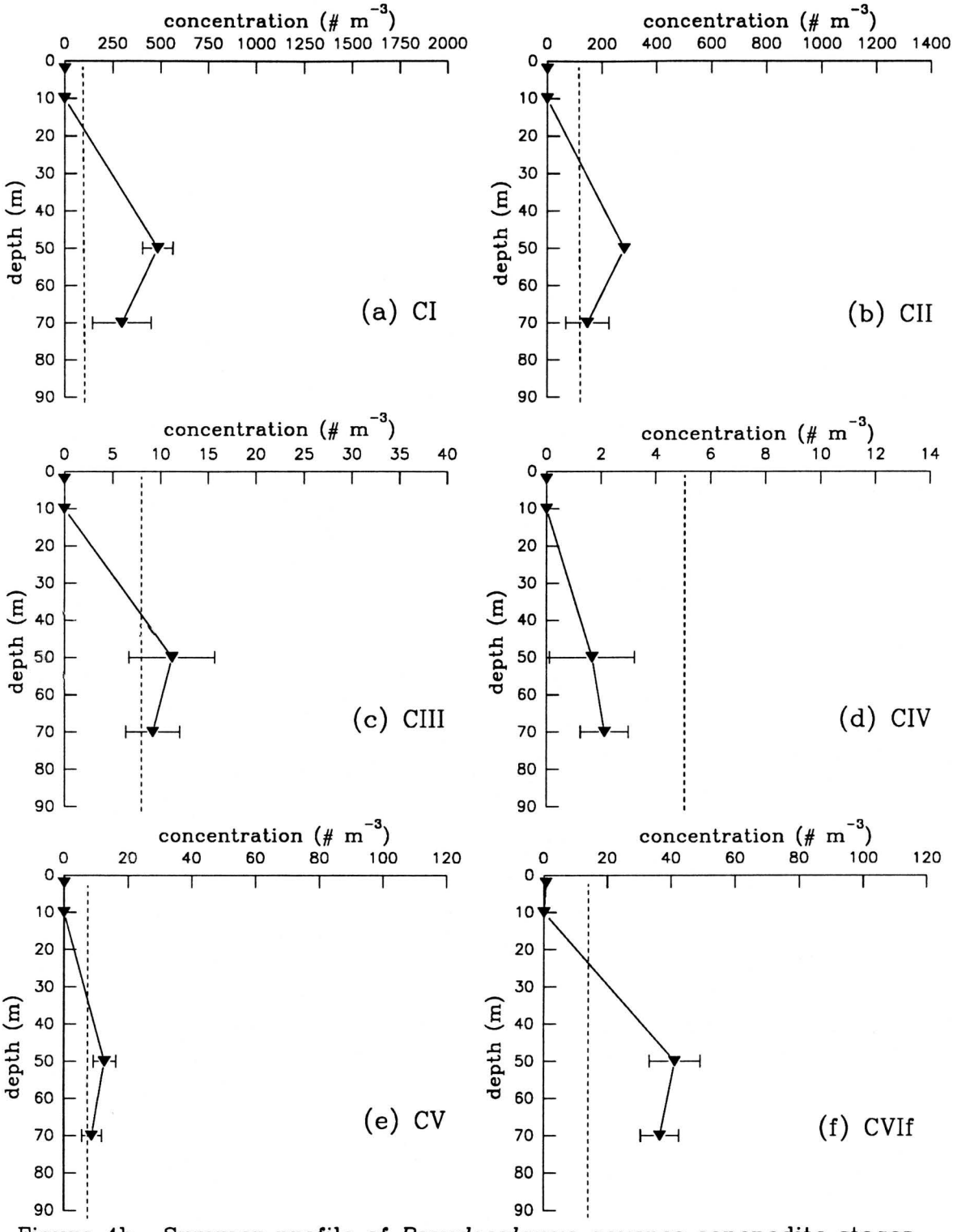


Figure 4b. Summer profile of *Pseudocalanus acuspes* copepodite stages (CI–CVIf) in Barrow Strait, N.W.T. Samples collected from 01:30–04:00 hr (Aug. 9/90). Please note horizontal scale changes. This profile corresponds to profile #2 on Figure 3a. Dashed line is average concentration (0–100m; # m^{-3}). determined by oblique net haul.

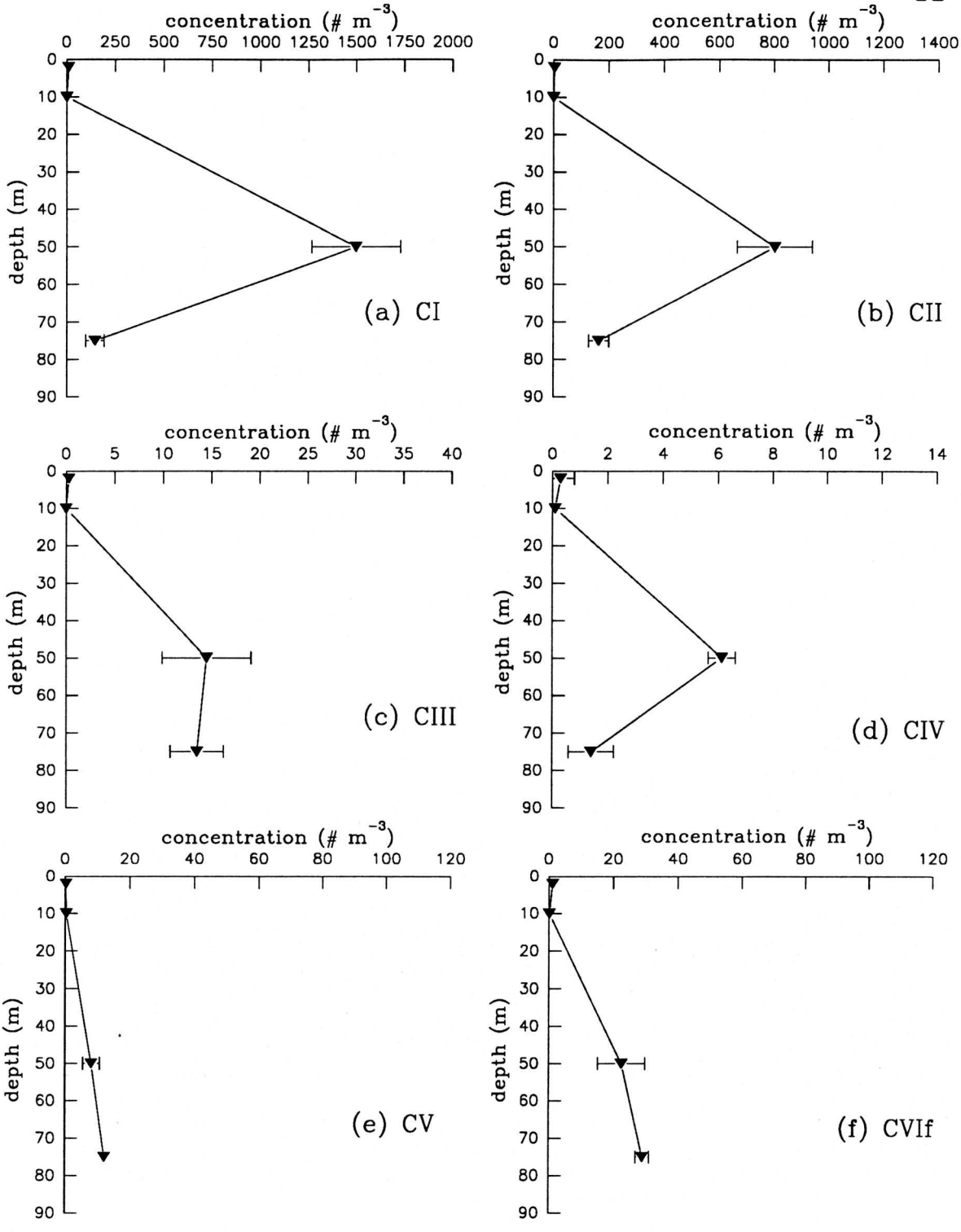
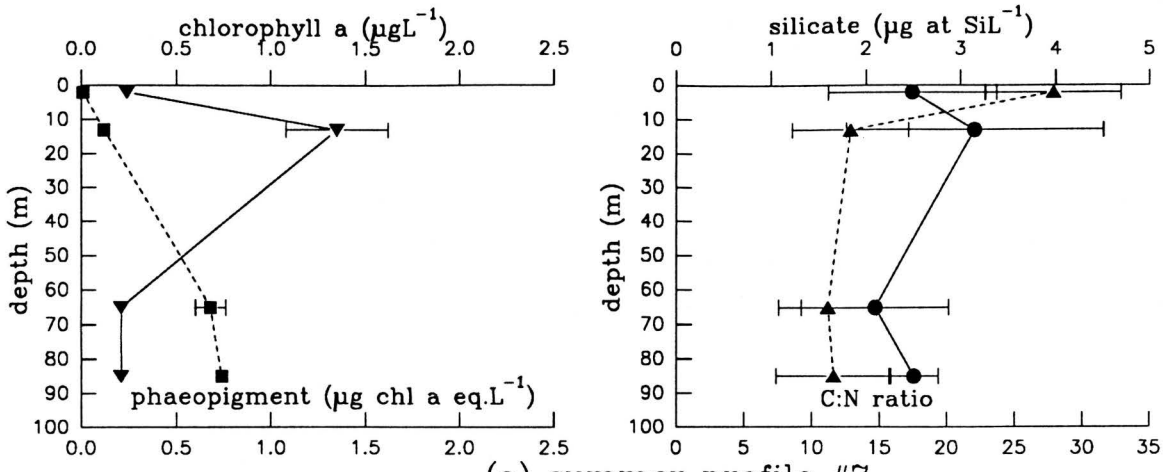
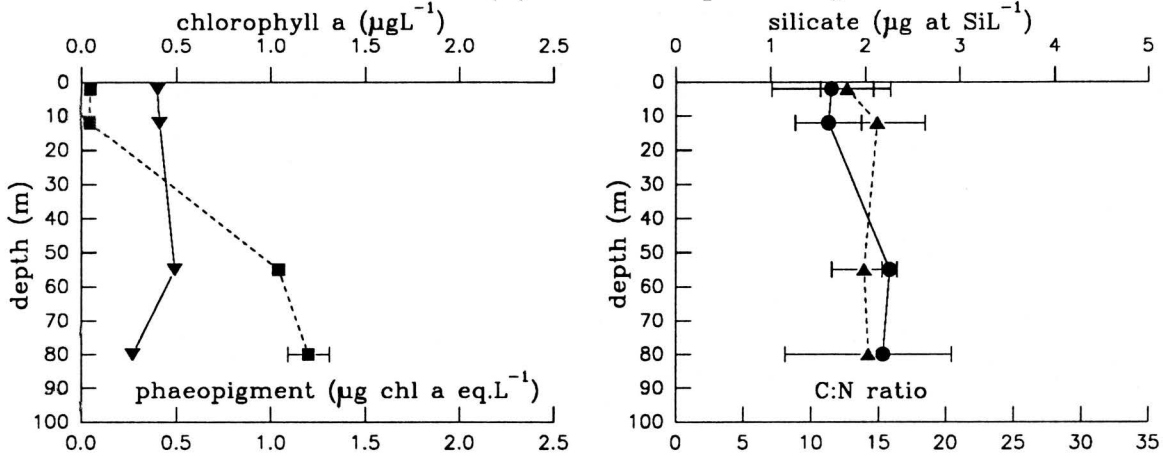


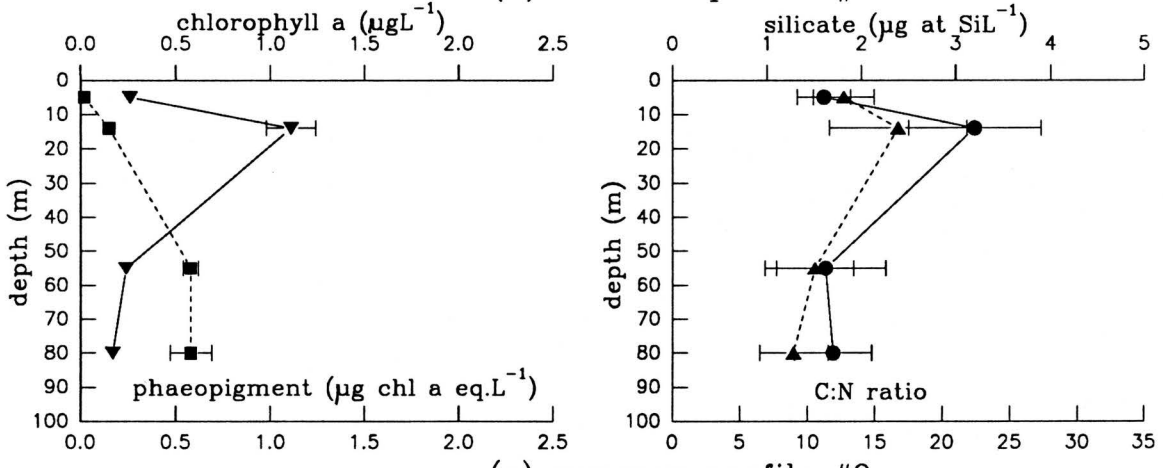
Figure 4c. Summer profile of *Pseudocalanus acuspes* copepodite stages (CI–CVIf) in Barrow Strait, N.W.T. Samples collected from 08:00–10:30 hr (Aug. 9/90). Please note horizontal scale changes. This profile corresponds to profile #3 on Figure 3a.



(a) summer profile #7



(b) summer profile #8



(c) summer profile #9

Figure 5. Summer profiles of particulate chlorophyll a (µgL^{-1}), phaeopigments (µg chl a eq.L^{-1}), silicate (µg at SiL^{-1}), and C:N ratios (by weight) in Barrow Strait, N.W.T. Profile #7 samples collected 13:30–16:30hr (Aug. 20/90), profile #8 01:30–04:00hr (Aug. 21/90), and profile #9 14:00–16:30hr (Aug. 21/90). Graphic elements are as defined in Figure 3a.

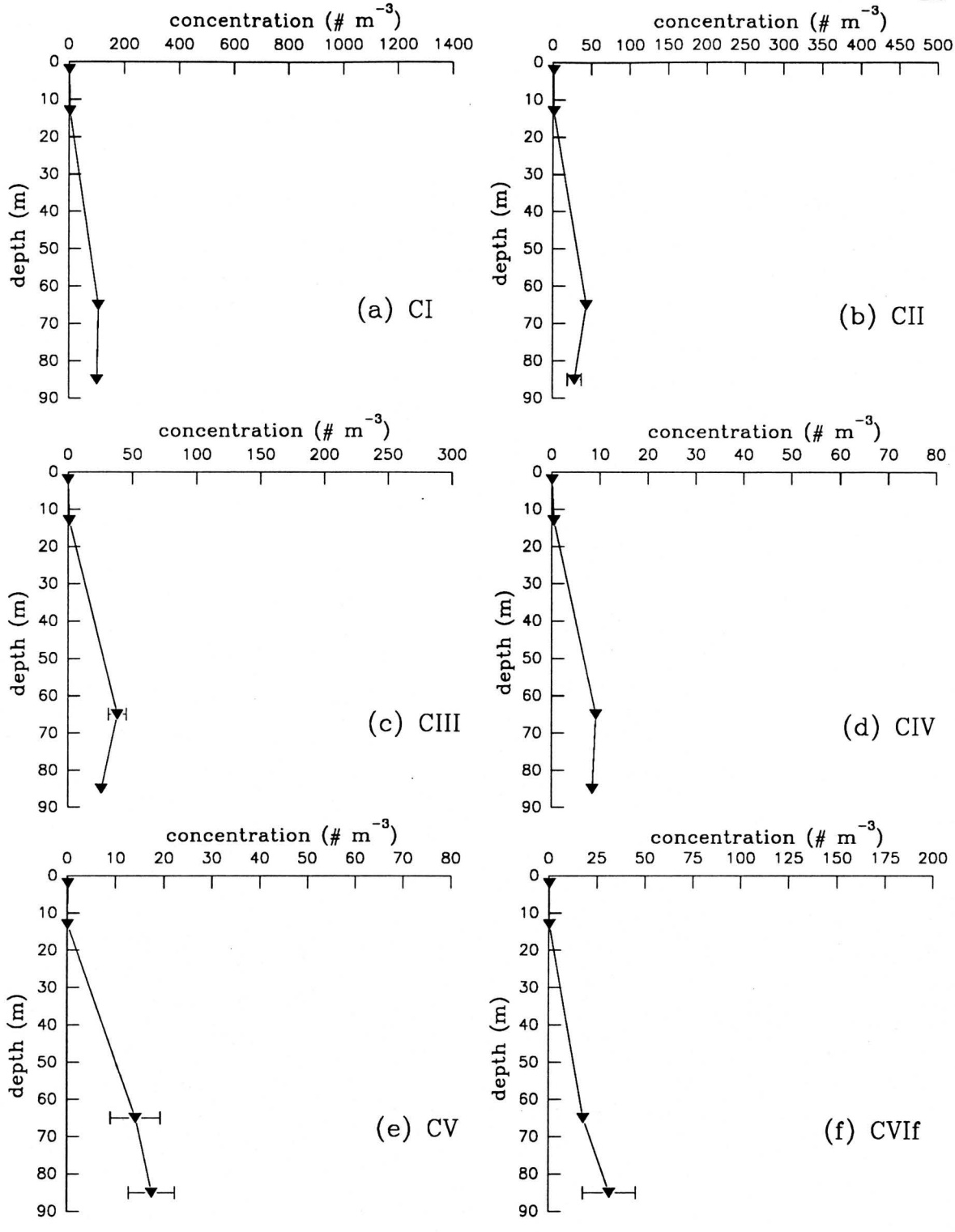


Figure 6a. Summer profile of *Pseudocalanus acuspes* copepodite stages (CI–CVIf) in Barrow Strait, N.W.T. Samples collected from 13:30–16:30 hr (Aug. 29/90). Please note horizontal scale changes. This profile corresponds to profile #7 on Figure 5. Error bars represents the standard deviation of replicate samples.

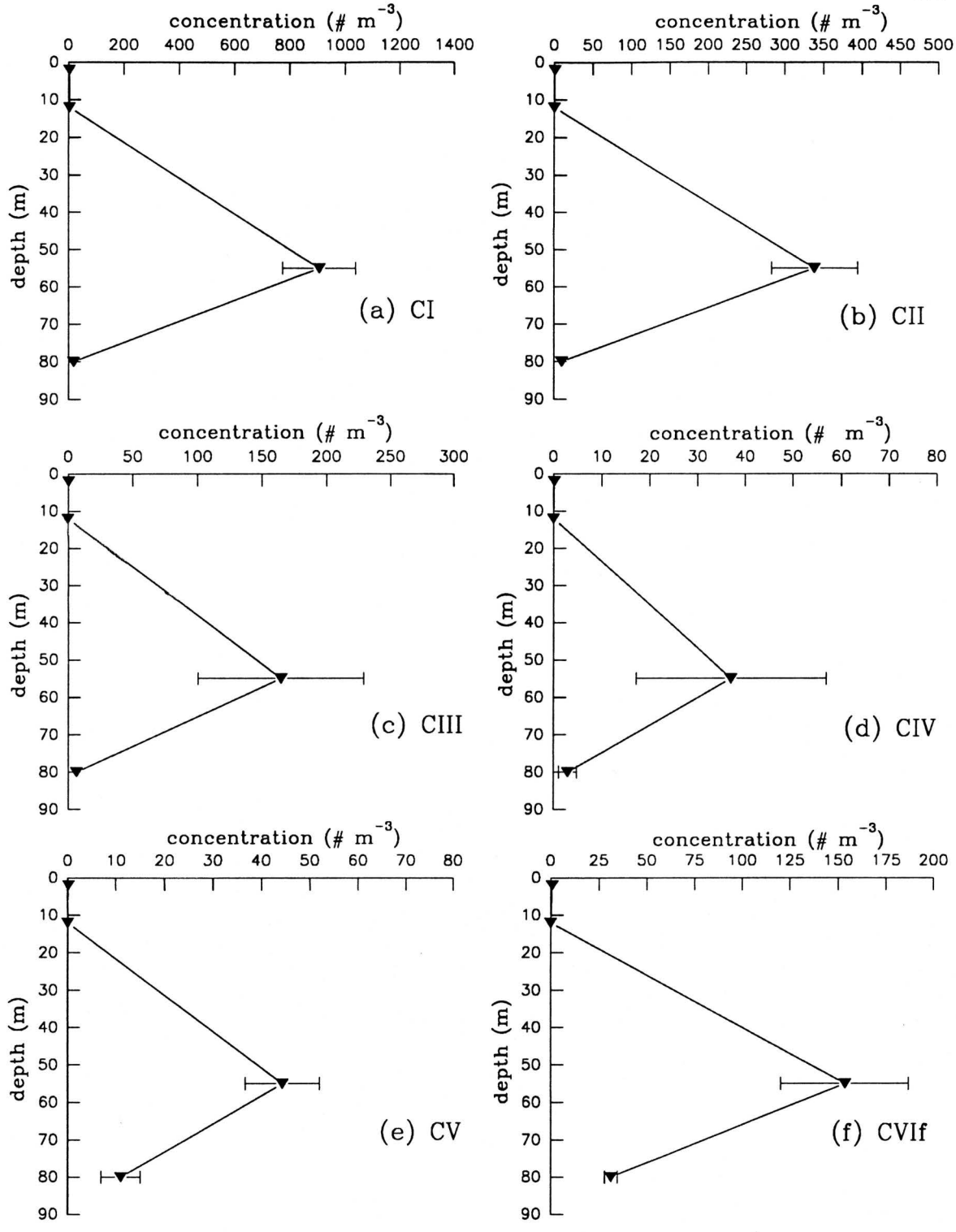


Figure 6b. Summer profile of *Pseudocalanus acuspes* copepodite stages (CI–CVIf) in Barrow Strait, N.W.T. Samples collected from 01:30–04:00 hr (Aug. 21/90). Please note horizontal scale changes. This profile corresponds to profile #8 on Figure 5.

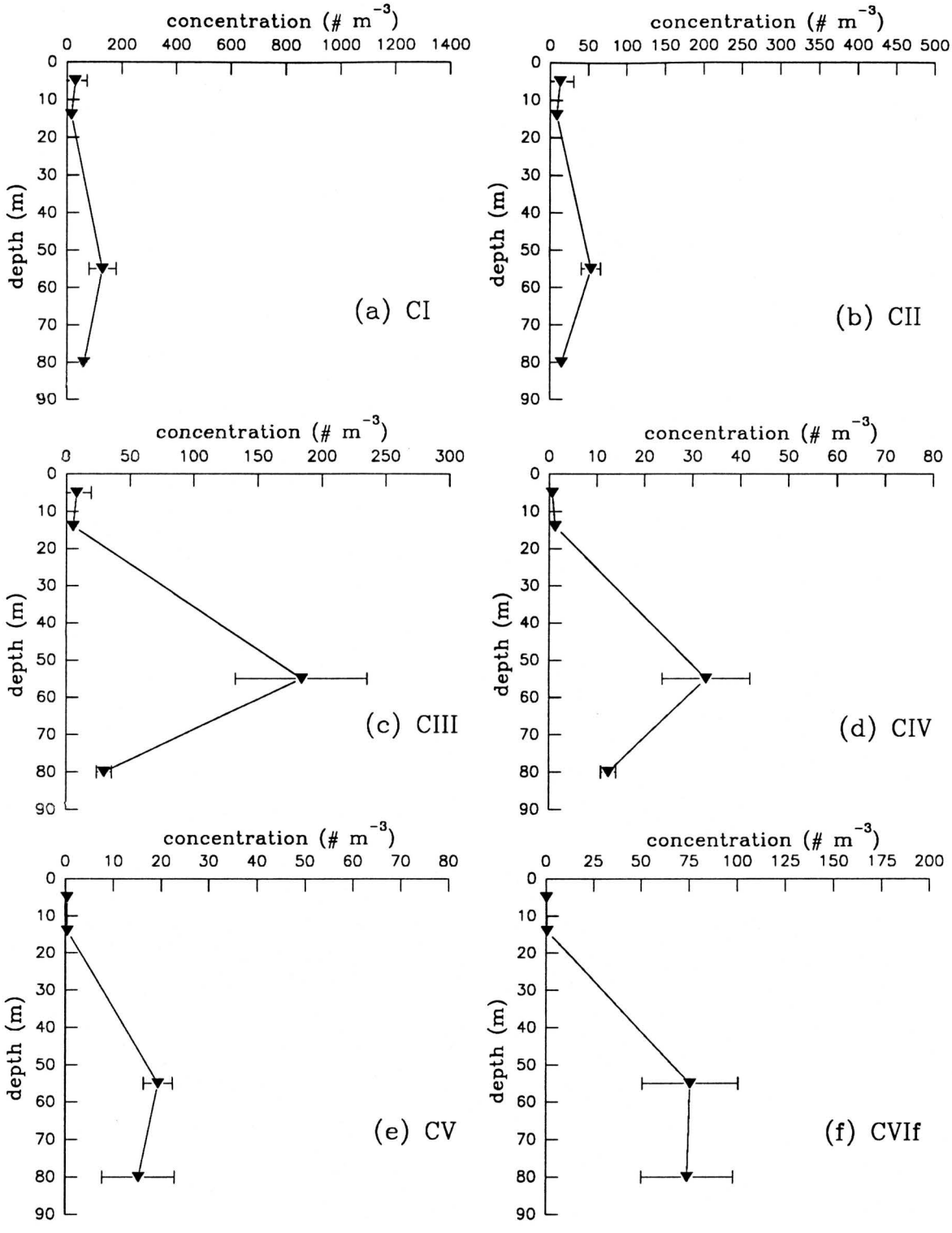


Figure 6c. Summer profile of *Pseudocalanus acuspes* copepodite stages (CI–CVIf) in Barrow Strait, N.W.T. Samples collected from 14:00–16:30 hr (Aug. 21/90). Please note horizontal scale changes. This profile correspond to profile #9 on Figure 5.

part of the new cohort. The number of copepodites again increases from CIV through CV and adult females (CIVf; Figs. 4a-c). There were no adult males (CVIm) found in any of the August zooplankton samples (Figs. 4 and 6). The adult male is a non-feeding, short-lived stage in the *P. acuspes* life-cycle (Corkett and McLaren, 1978), and all males from the previous year's cohort should have disappeared from the water column by this time.

Using the zooplankton pump samples (Figs. 4a-c), it was not possible to make any definite statements regarding diel migration in *P. acuspes*. Evidently, CI and CII stages are concentrated below 10m but above 50m depth in the water column. There is some indication that these two developmental stages also migrate to shallower depths during the evening (10-30m) and descend to slightly greater depths during the day (see large peaks at 50m in Figure 4c and lack of peaks in Figure 4b). There were too few individuals of CIII and CIV sampled to make any statements regarding their vertical distribution. CV and adult females (CVIf) may also be following a similar pattern to CI and CII, but once again, we have too few sampling points to make any definite statements.

If we take the amount of phaeopigment relative to chlorophyll a as an index of the grazing activity on algae (Shuman and Lorenzen, 1975), then it is also evident that the herbivorous zooplankton community feeds most heavily in

the early evening (see the large peak in phaeopigment levels at 50m depth in profiles #1 and #5, Figs. 3a-b, sampled from 19:30-23:30hr on two consecutive days). This feeding behaviour might be related to the copepods migrating below the chlorophyll maximum during the day then moving back into the highest concentrations of algae in the evening, which is consistent with our observations on vertical distribution. Regardless of the mechanism, a diel pattern in grazing activity by *P. acuspes* is indicated.

In late August, we can clearly see the decrease in the number of CI's and CII's, with a corresponding increase in CIII's as the current year's cohort develops (Figs. 6a-c). The CIV's do not show a substantial increase and the number of CV's have decreased over the previous series (August 8-9). There is still a significant number of adult females (CVIf) in our deep samples, most either carrying egg sacks or spent and in poor condition by this time of the year as indicated by the lack of oil reserves (pers. observ.).

There was not clean evidence for varying vertical distribution or diel migration by *P. acuspes* during this second summer profiling series (Figs. 6a-c). Instead, the copepods seem to be generally concentrated in the mid regions of the water column. By late August all stages of *P. acuspes* are largely absent in the top 15m of the water column even though it appears that there are still

significant amounts of algae present (Fig. 5). However, the summer phytoplankton bloom would still be sinking out of the water column and the chlorophyll maximum should be around 30-40m by this time of the year (Harold Welch, unpubl. data; Fig. 16), enabling the copepods to remain relatively deep in the water column and still have access to a source of food.

The incubation experiments to measure the oxygen utilization and nitrogenous excretion of *Pseudocalanus acuspes* during late August were most satisfying (Table 1). Stages CIV, CV, and adult females (CVIf) were pooled in the experiments and demonstrated a low total (ammonia+urea) O:N ratio (by atoms; mean range of 8.19-11.94). This is probably indicative of continuous feeding by the copepods on a bloom at high rates (Conover and Corner, 1968), and supports the above comments regarding their distribution and access to a significant algal source. As an O:N ratio of 3-16 is indicative of pure protein catabolism (Mayzaud and Conover, 1988), lipid stores do not appear to be utilized by the copepods at this time. Some adult female (CVIf) *P. acuspes* might be metabolizing their own body proteins to a certain extent as their lipid reserves were reduced (pers. observ.), which also would result in the low O:N ratios in absence of high levels of algae grazing (Mayzaud and Conover, 1988). Large lipid stores were clearly visible in CIV and CV individuals also used in the experiments (pers. observ.), so body proteins should not be metabolized in

INCUBATION EXPERIMENT #1:				
	mean	standard deviation	n	copepodite stages used:
NH_4^+ O:N	45.21	10.02	8	CIV, CV, and CVIf
Urea O:N	10.44	4.96	9	
NH_4^++Urea O:N	8.19	3.23	9	

INCUBATION EXPERIMENT #2:				
	mean	standard deviation	n	copepodite stages used:
NH_4^+ O:N	37.57	12.06	9	CIV, CV, and CVIf
Urea O:N	11.97	5.56	6	
NH_4^++Urea O:N	8.64	3.01	6	

INCUBATION EXPERIMENT #3:				
	mean	standard deviation	n	copepodite stages used:
NH_4^+ O:N	23.93	1.84	9	CIV, CV, and CVIf
Urea O:N	26.33	11.86	8	
NH_4^++Urea O:N	11.94	2.42	8	

Table 1. Calculated O:N ratios (by atoms) for summer, 1990, *Pseudocalanus acuspes* incubation experiments (NH_4^+ and urea production, oxygen consumption). Incubation experiment #1 initiated at 21:00 hr (August 20, 1990), experiment #2 at 09:30 hr (August 21, 1990), and experiment #3 at 21:00 hr (August 21, 1990).

large quantities by these stages. It is somewhat surprising that the copepods seem to demonstrate a high degree of reliance on the phytoplankton for its source of energy despite the apparently poor quality of the algae (Mayzaud and Conover, 1988).

It is also evident from the incubation experiments with *P. acuspes* (Table 1) that urea contributes a significant amount of the nitrogenous waste products excreted by the copepod. Ammonia excretion ranged from 0.001-0.006 μg-at N animal^{-1} day^{-1}, while urea excretion ranged from 0.003-0.016 μg-at N animal^{-1} day^{-1}.

Spring, 1991:

From vertical profiles of temperature and salinity, and T-S plots (Figs. 7a-c), periodicity in degree of vertical mixing is indicated (a straight T-S line indicating complete mixing; Pickard and Emery, 1982). Figure 7b, profiled at 09:30 hr on May 8, shows nearly complete vertical mixing and corresponds to a period between slack tides during a period of moderate change in water heights (1.3-0.6m height change; Canadian Tide and Current Tables 1991, Arctic Region, Dept. of Fisheries and Oceans). T-S plots 12hr earlier and later (Figs. 7a and 7c) show stronger vertical stratification and the emergence of two distinct water masses (the surface mixed layer and the subsurface layer, particularly evident on Fig. 7a). Figures 7a and 7c correspond to nearly slack tides during small tidal exchanges (0.3m-0.4m height difference).

The extent of the mixing is directly proportional to the strength of the tidally dominated currents in Resolute Passage (Canadian Tide and Current Tables 1991, Arctic Region, Dept. of Fisheries and Oceans, Canada; Prinsenberg and Bennett, 1987). Eddy diffusivities and nutrient fluxes are known to vary with the tidal cycle and the associated turbulent energy and velocity shears under the ice (Cota et al., 1987).

In this diel series, there seems to be no relationship between the vertical particulate profiles

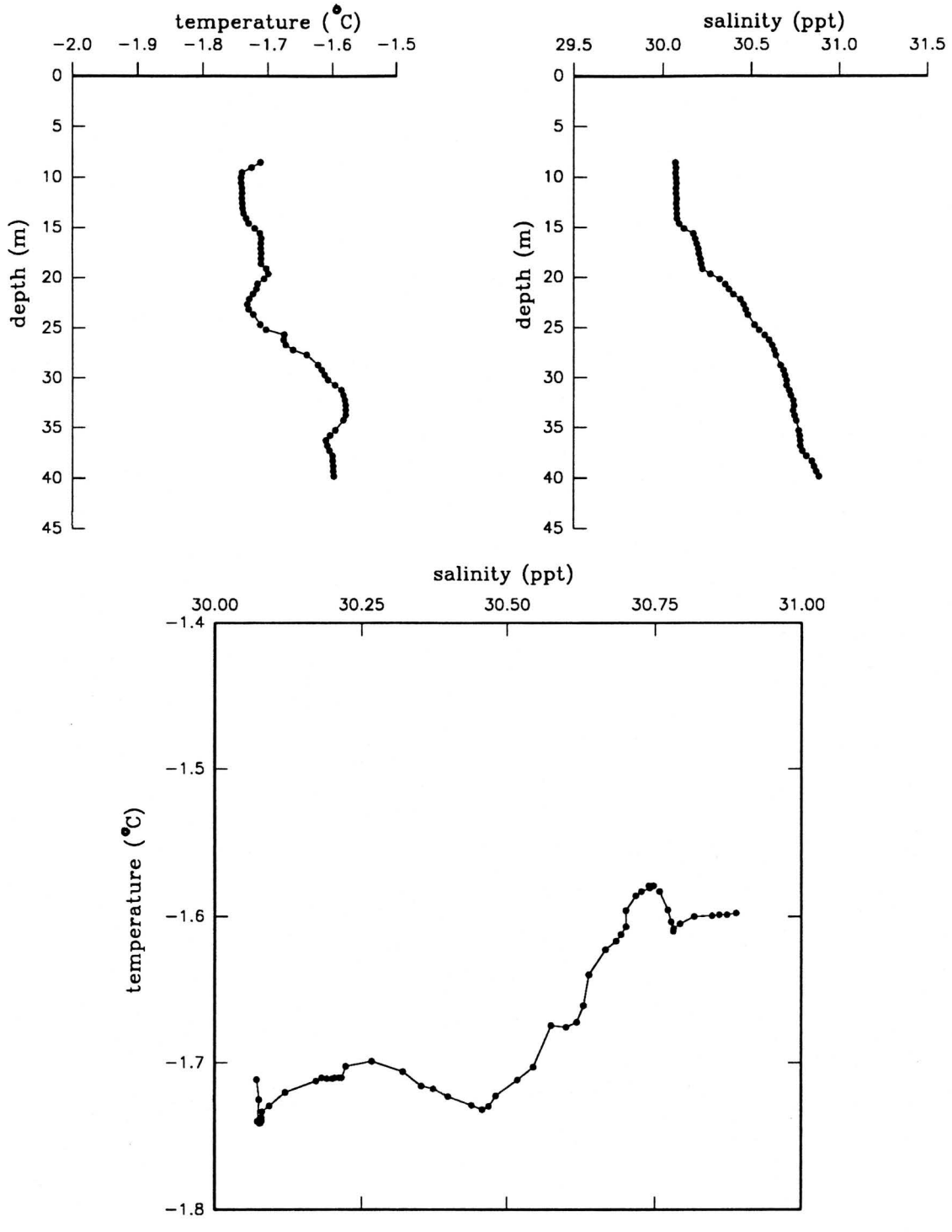


Figure 7a. Results of CTD cast at 21:30 hr (May 7/91) for spring profile #1 showing temperature (°C) and salinity (ppt) plots with depth, as well as the corresponding T–S plot.

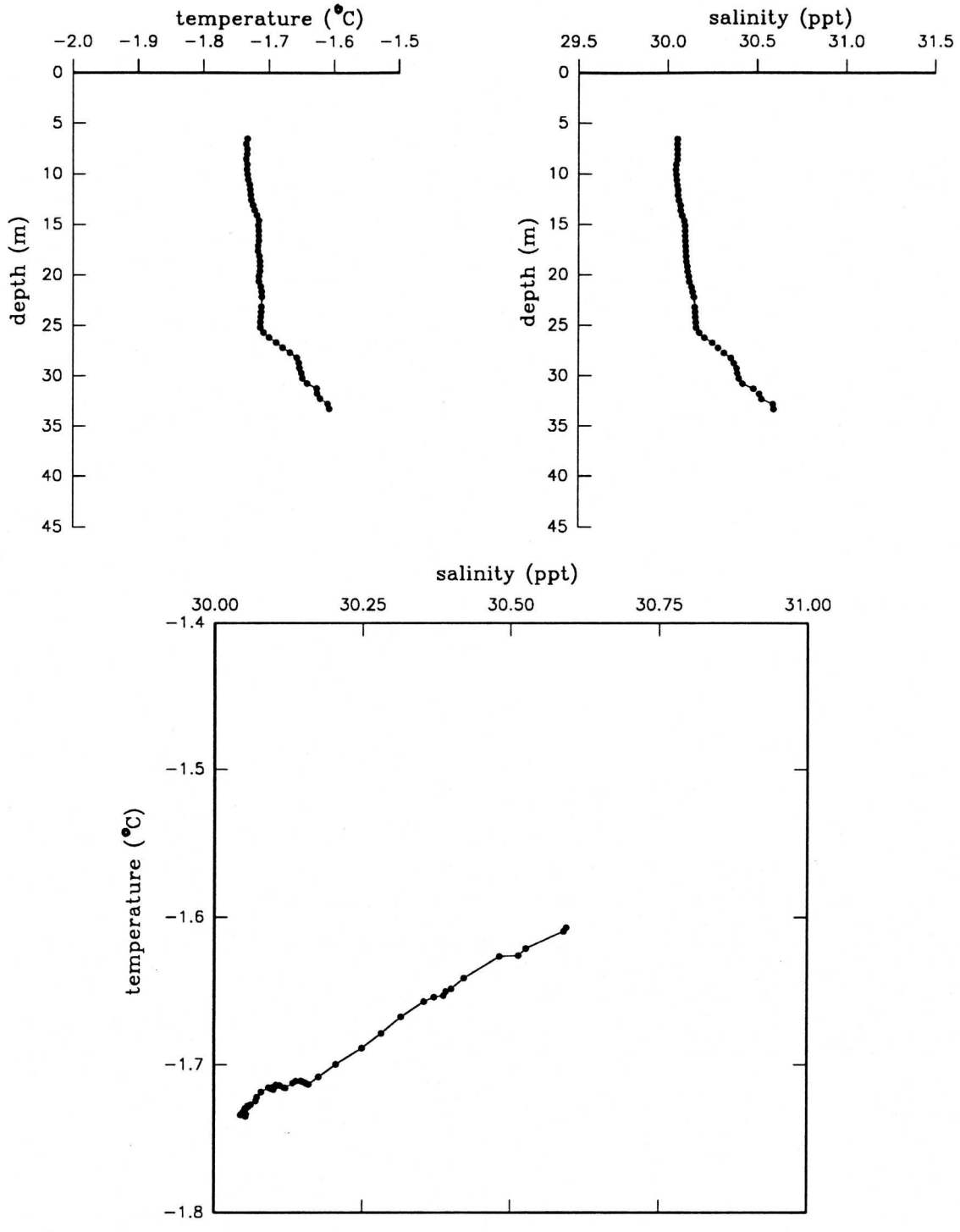


Figure 7b. Results of CTD cast at 09:30 hr (May 8/91) for spring profile #2 showing temperature (°C) and salinity (ppt) plots with depth, as well as the corresponding T–S plot.

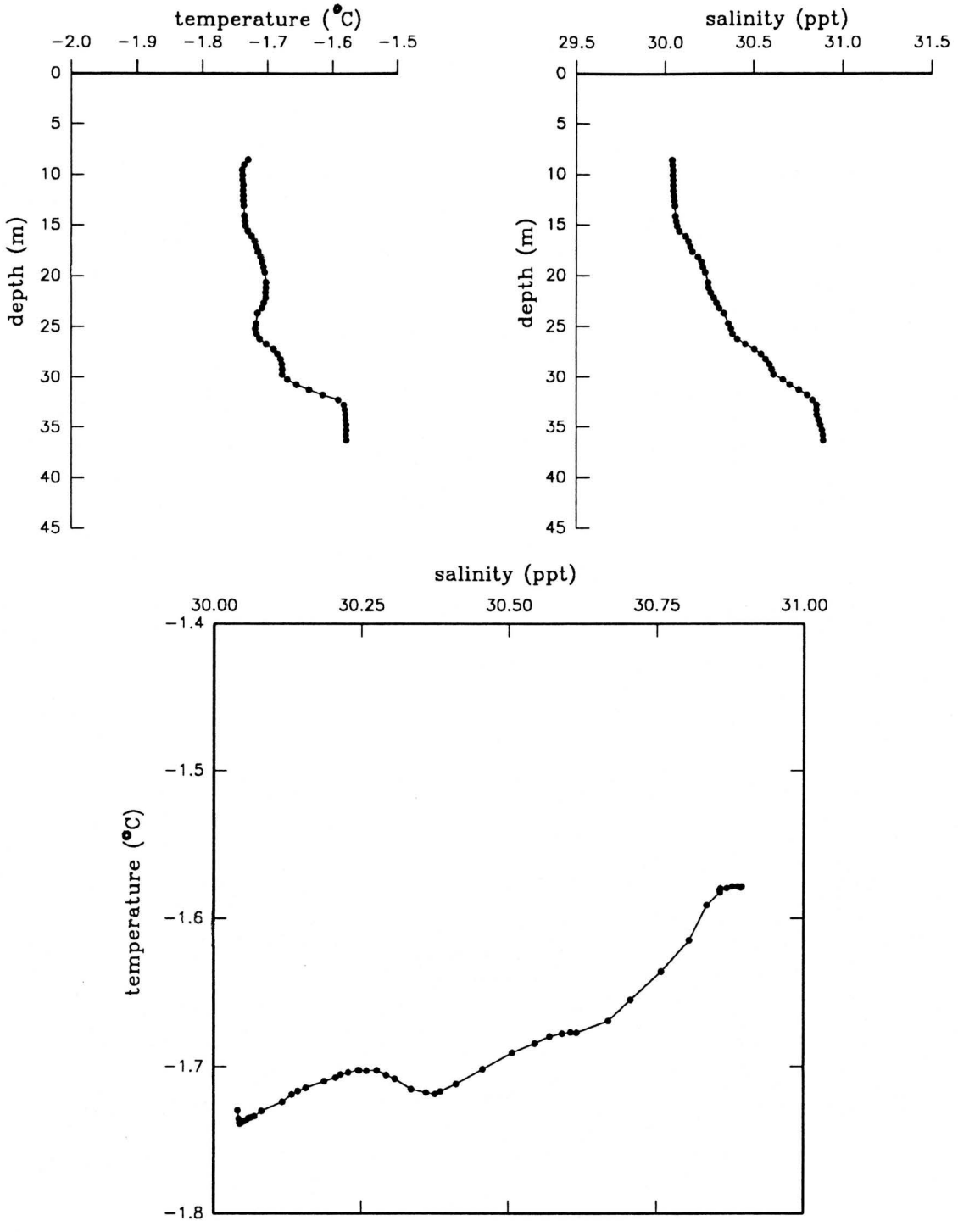


Figure 7c. Results of CTD cast at 21:30 hr (May 8/91) for spring profile #3 showing temperature (°C) and salinity (ppt) plots with depth, as well as the corresponding T–S plot.

(chlorophyll a and silicate levels in particular; Fig. 8) and the extent of vertical mixing. Thus, we did not detect any measurable tidal erosion of epontic algae (chlorophyll peaks) or indication of enhanced *P. acuspes* grazing activity (phaeopigment peaks) as a result of tidal activity.

There was little algae present in the water column by the second week in May (peaking at slightly above 0.4µg chl a L^{-1}; Fig. 8). The highest concentrations are immediately below the ice, within the upper 6m. There is also a moderate amount of phaeopigment relative to chlorophyll a (at least 75% of the chlorophyll a levels), indicating that some grazing by the herbivorous zooplankton community is occurring. Not surprisingly, the silicate profiles mimic the chlorophyll a profiles, as the algal community in the water column at this time of the year is believed to be dominated by diatoms of epontic origin which have eroded from the ice surface (Conover et al., 1986b; Conover et al., 1990).

Furthermore, most of the water column particulate material is of only moderate quality (C:N ratio between 8-10; Fig. 7; Banse, 1974). Epontic algae is physiologically highly sensitive to removal from the ice, where it is highly adapted and restricted to that particular physical environment and light regime (Conover et al., 1988b; Cota, 1985; Cota et al., 1990). However, particulate C:N ratios (by weight) are comparable to those measured directly for

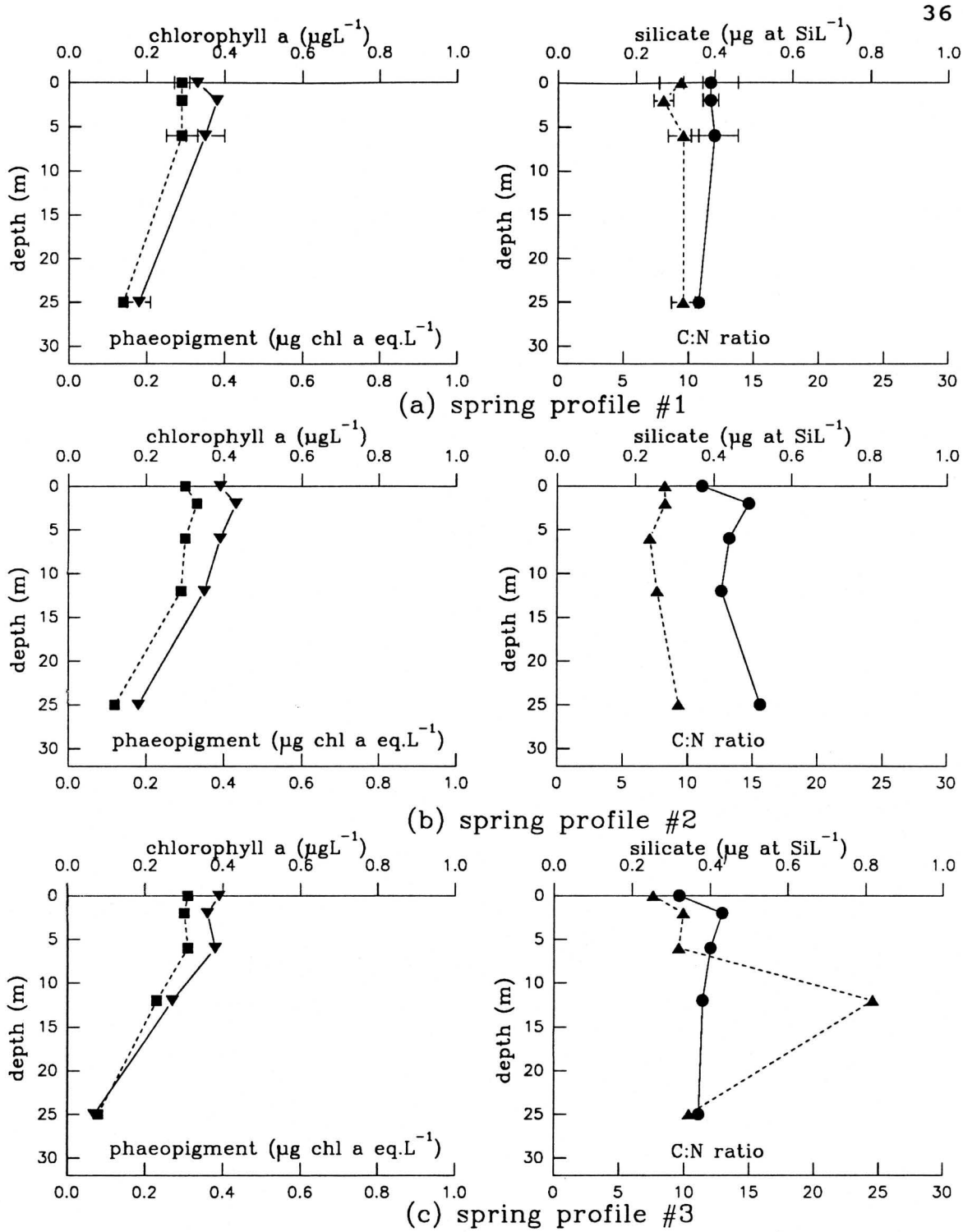


Figure 8. Spring profiles of particulate chlorophyll a (µgL^{-1}), phaeopigments (µg chl a eq.L^{-1}), silicate (µg at SiL^{-1}), and C:N ratios (by weight) in Resolute Passage, N.W.T. Profile #1 samples collected 21:30–00:30hr (May 7–8/91), profile #2 09:30–11:00hr (May 8/91), and profile #3 21:30–23:00hr (May 8/91). No replicates were taken for profiles #2 and #3. Graphic elements are as defined in Figure 3a.

the epontic algae community throughout the month of May during this study (ranging from 8.7-9.5; unpubl. data).

From the results of the first *Pseudocalanus acuspes* incubation experiment of spring, 1991 (May 9; Table 3, incubation experiment #4), it is evident from the high O:N value (40.48) that the copepods are partially relying on their own energy reserves (lipids) and not yet fully dependant on the available algae (equal amounts of lipid and protein metabolism corresponding to O:N ratio values between 50 and 60; Mayzaud and Conover, 1988). During this experiment, ammonia excretion ranged 0.004-0.005 μg-at N $animal^{-1}day^{-1}$ and urea excretion ranged 0.001-0.005 μg-at N $animal^{-1}day^{-1}$.

During the second diel series (May 15-16), the T-S plots (Figs. 9a-d) demonstrate little variability in vertical mixing, as all profiles show a significant amount. The CTD for profile #4 (Fig. 9a) was cast at a time when slack high tide was approaching during a tidal range of 0.4m to 1.4m (Canadian Tide and Current Tables 1991, Arctic Region, Dept. of Fisheries and Oceans, Canada). The cast presented on Figure 9b was near slack tide during the start of the largest tidal exchange for the month of May (0-1.9m). Figure 9c also represents a CTD cast done during a large tidal exchange (1.9-0.4m). The periodicity in the tidal forcing and subsequent mixing over this particular profiling series is not reflected in our CTD profiles. However, a

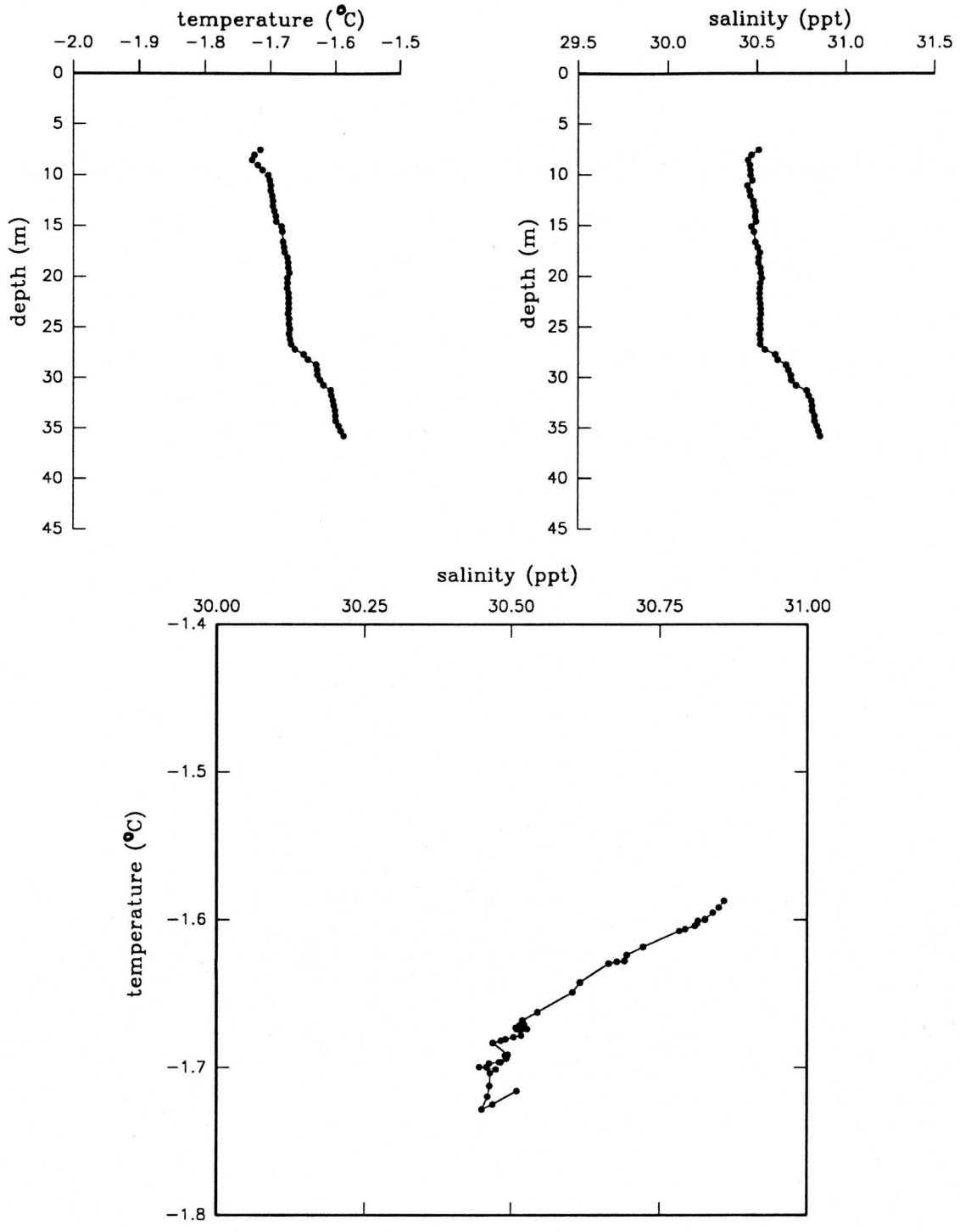


Figure 9a. Results of CTD cast at 12:30 hr (May 15/91) for spring profile #4 showing temperature (°C) and salinity (ppt) plots with depth, as well as the corresponding T−S plot.

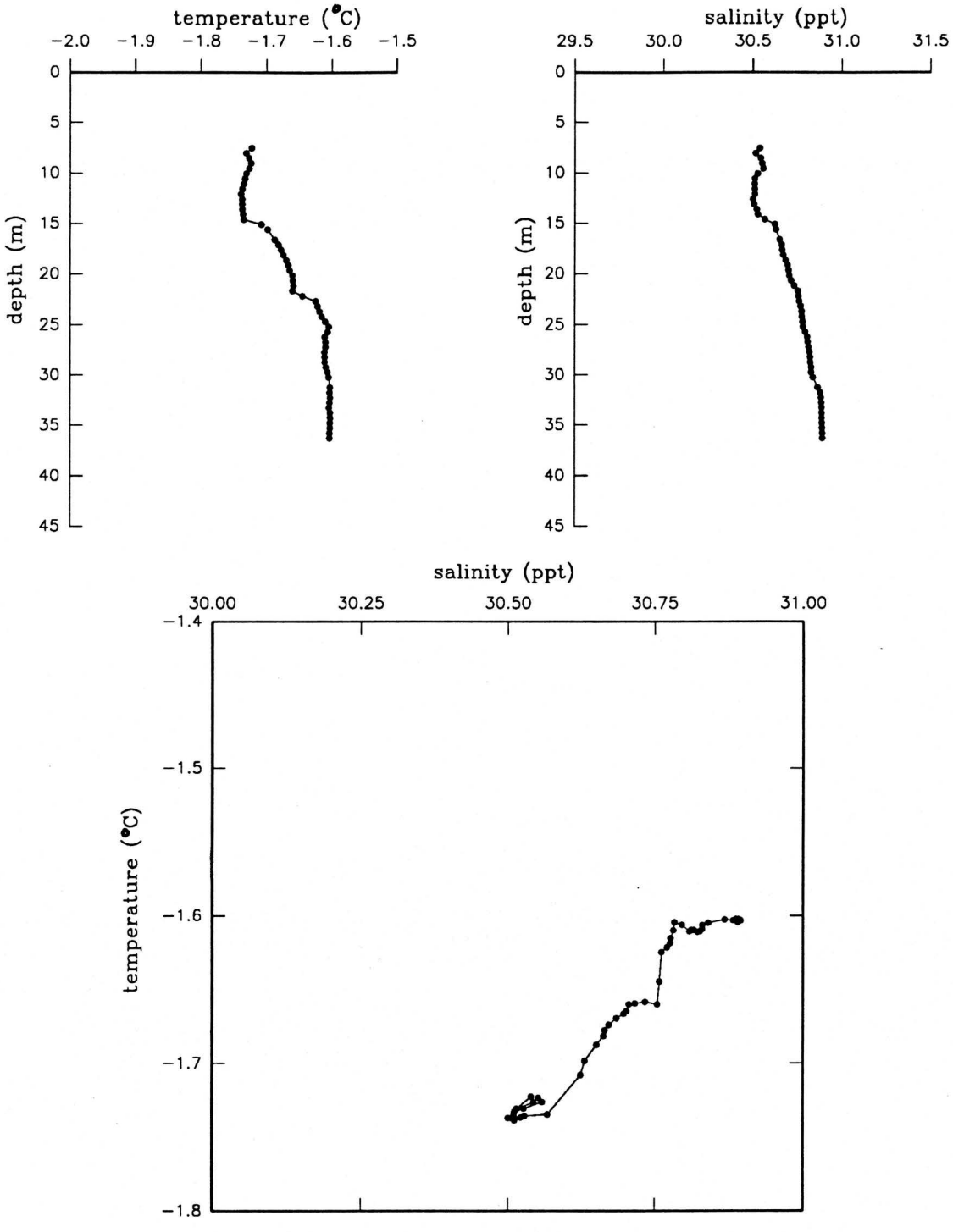


Figure 9b. Results of CTD cast at 20:30 hr (May 15/91) for spring profile #5 showing temperature (°C) and salinity (ppt) plots with depth, as well as the corresponding T–S plot.

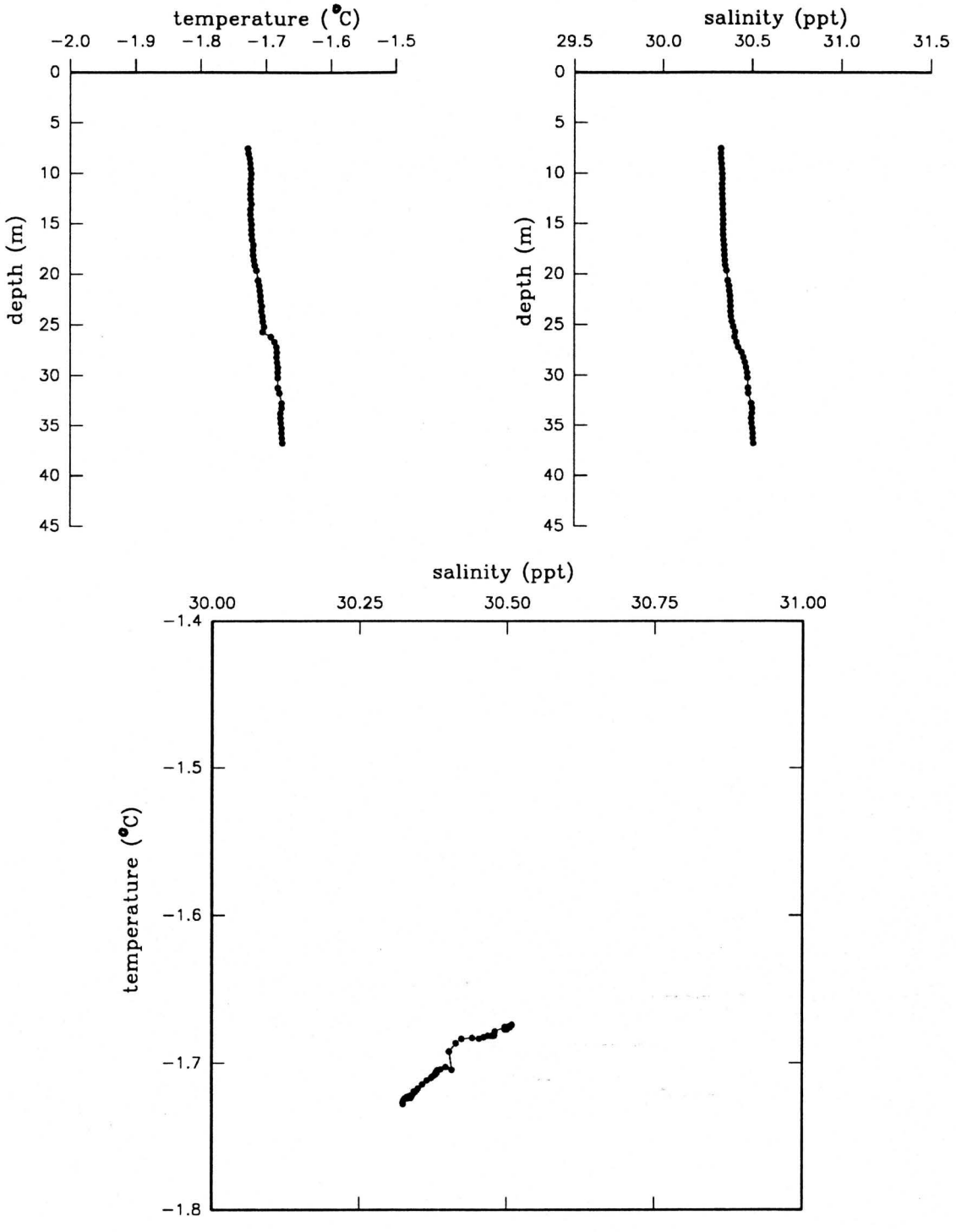


Figure 9c. Results of CTD cast at 04:30 hr (May 16/91) for spring profile #6 showing temperature (°C) and salinity (ppt) plots with depth, as well as the corresponding T–S plot.

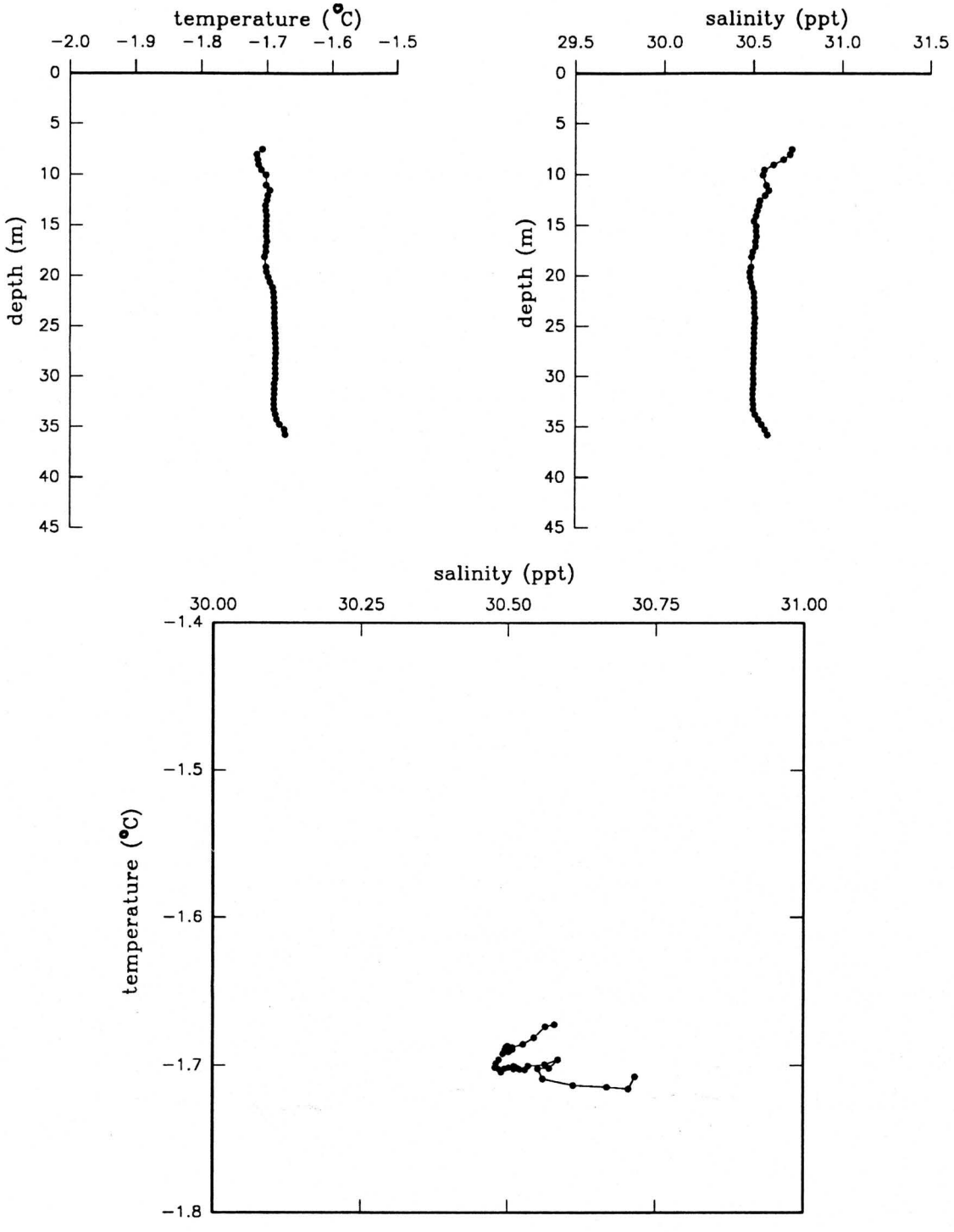


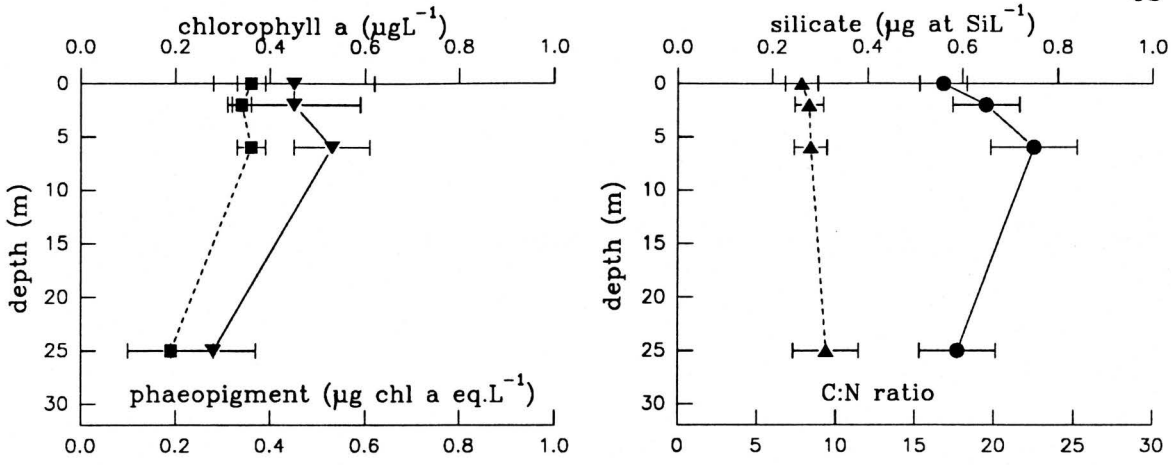
Figure 9d. Results of CTD cast at 12:00 hr (May 16/91) for spring profile #7 showing temperature (°C) and salinity (ppt) plots with depth, as well as the corresponding T–S plot.

general high degree of vertical mixing is indicated during this period of monthly maximum tidal exchanges.

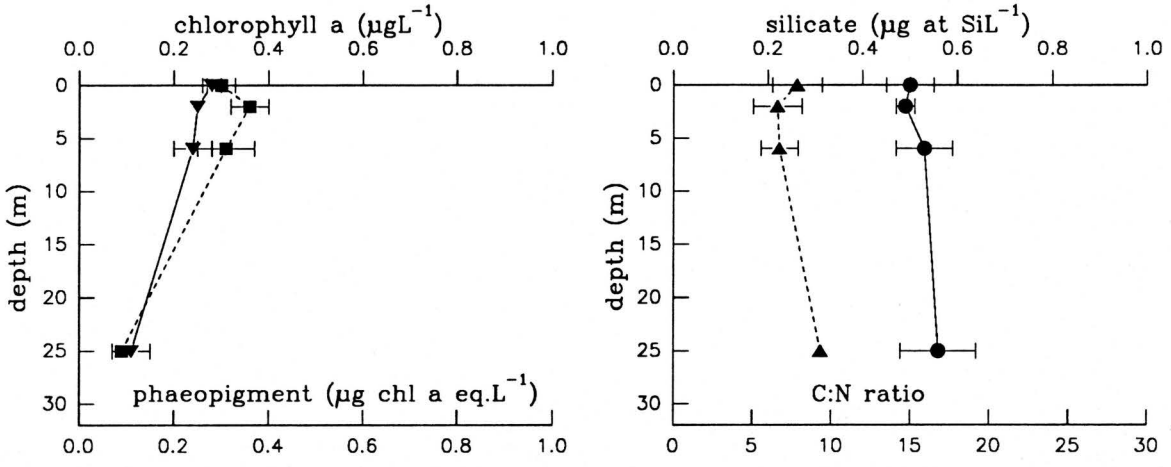
The particulate profiles presented on Figures 10a and 10b again show that there is still very little algae in the water column at this time of the year (chlorophyll a levels rarely above 0.4µg chl aL^{-1}), and concentrations are highest near the underice surface, as predicted. There is an increase in the diatom concentration in the upper water column during the first and last profiles, as indicated by chlorophyll and silicate levels (corresponding to profiles #4 and #7), probably as a result of decreased zooplankton grazing activity. In fact, the phaeopigment levels are nearly double the chlorophyll a levels during the two evening profiles (profiles #5 and #6), indicating a higher level of grazing by zooplankton at those times. Note that high levels of herbivore grazing correspond to periods with the greatest tidal exchanges and thus strongest currents.

The dominant developmental stage in late May in Resolute Passage is CV, closely followed by adult females (CVIf), adult males (CVIm), and CIV's (Figs. 11a-d; Table 2). There were no CI's found in the zooplankton samples at this time of the year, and few CII's and CIII's.

There is no clear trend in the vertical distribution of CII's and CIII's, our information being incomplete due to the low number of individuals counted in the samples (Figs. 11a-d; usually less then ten individuals counted). All

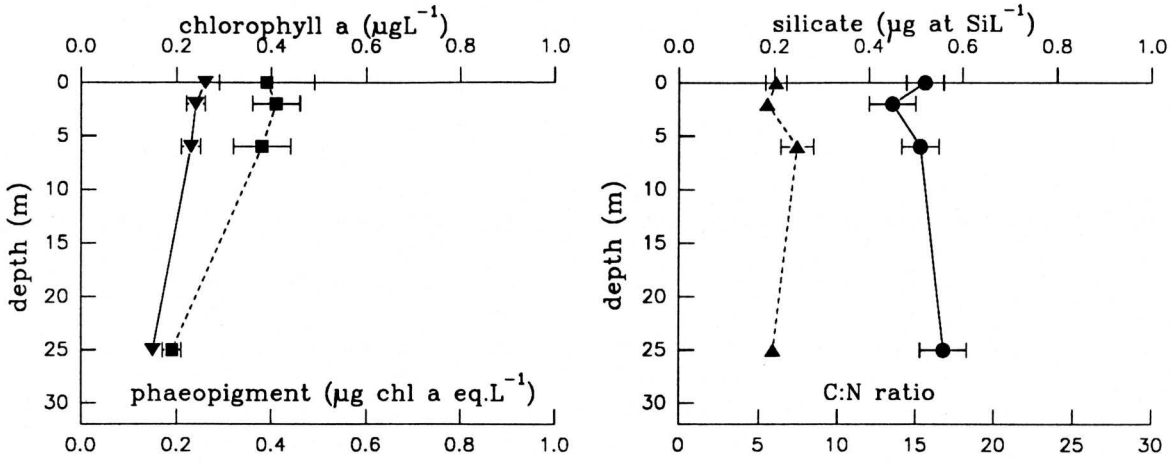


(a) spring profile #4

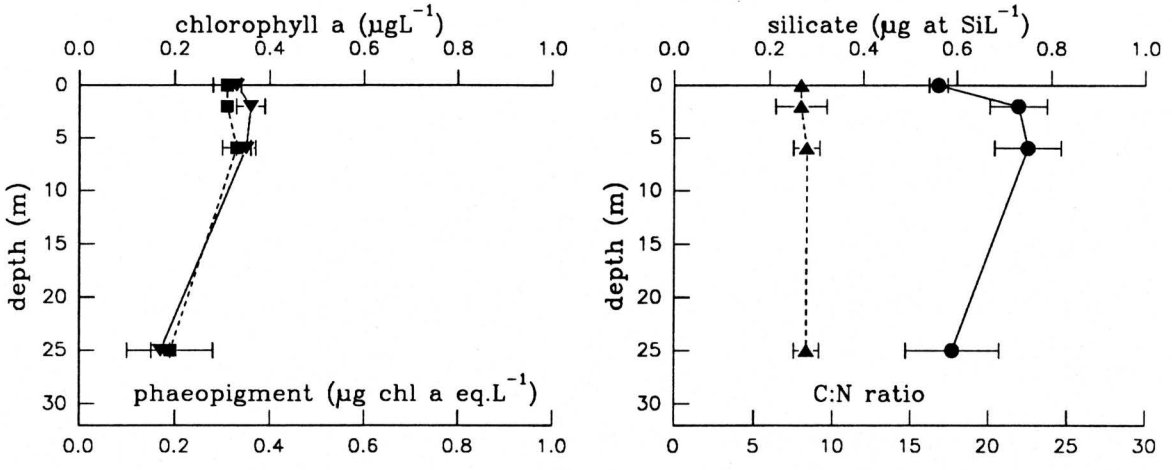


(b) spring profile #5

Figure 10a. Spring profiles of particulate chlorophyll a (μgL^{-1}), phaeopigments (µg chl a eq.L^{-1}), silicate (µg at SiL^{-1}), and C:N ratios (by weight) in Resolute Passage, N.W.T. Profile #4 samples collected 11:00–12:30hr (May 15/91), and profile #5 18:30–20:30hr (May 15/91). Graphic elements are as defined in Figure 3a.



(a) spring profile #6



(b) spring profile #7

Figure 10b. Spring profiles of particulate chlorophyll a (μgL^{-1}), phaeopigments (μg chl a eq.L^{-1}), silicate (μg at SiL^{-1}), and C:N ratios (by weight) in Resolute Passage, N.W.T. Profile #6 samples collected 03:00–04:30hr (May 16/91), and profile #7 10:30–12:00hr (May 16/91). Graphic elements are as defined in Figure 3a.

other stages, particularly CIV's and CV's, show a strong diel migration to the upper areas of the water column during the night. The migration of the adult males (CVIm) to the lowest interval sampled (15-25m) at the onset of day (Fig. 11d), is nicely demonstrated in the series. Table 2 supports the movement of the copepods to the underice surface during the night (evident in 0-5m net hauls), particularly in the late stages (CIV-CVIf). The water column depth at this station was approximately 40m, so there was some room for the copepods to move below our lowest sampling depth; however, it is likely that during the day *P. acuspes* would be found only in deeper waters more offshore.

Pseudocalanus acuspes is present in the upper region of the water column during the two night profiles #5 and #6 (Figs. 11a-11d, Table 2) during the largest tidal exchange of the month and during which time we have an indication from the high phaeopigment measurements of elevated grazing activity (Figs. 10a and 10b). It appears that in this case the erosion of the epontic algae by the tidal currents, and mixing to below the underice surface, is important in the nutrition of the copepod. It also appears that when the copepods were no longer present near the underice surface and not grazing at such high levels, the algae concentrations were allowed to build up slightly in the upper regions (Figs. 10a and 10b, profiles #4 and #7). Low O:N ratios (by atoms) from incubation experiments #5 and #6

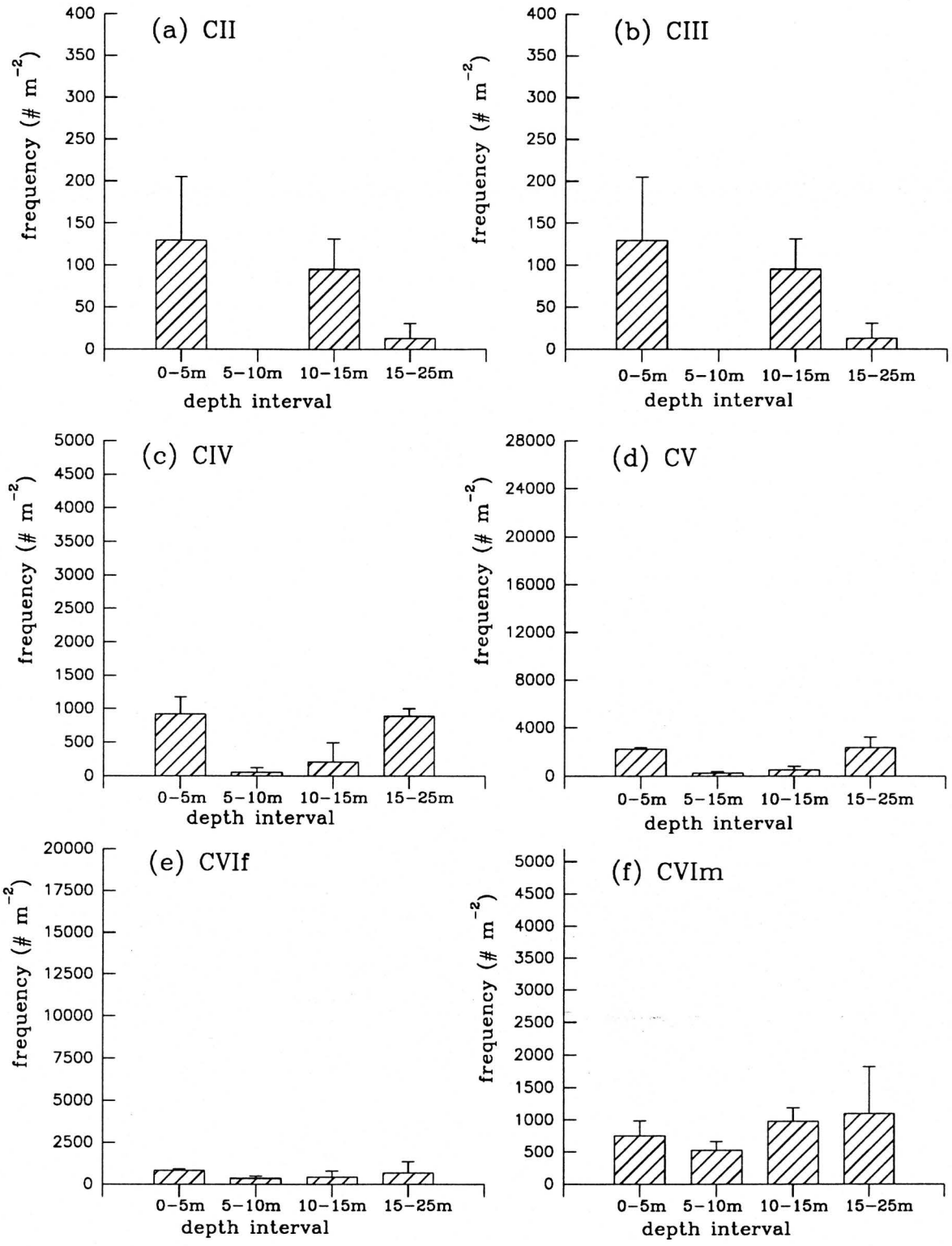


Figure 11a. Spring profile of *Pseudocalanus acuspes* copepodite stages (CII–CVIf; CI in only trace numbers) in Resolute Passage, N.W.T. Samples collected from 10:00–11:00 hr on May 15, 1991. Please note vertical scale changes. This profile corresponds to profile #4 on Figure 10a. Standard deviation represented by error bars.

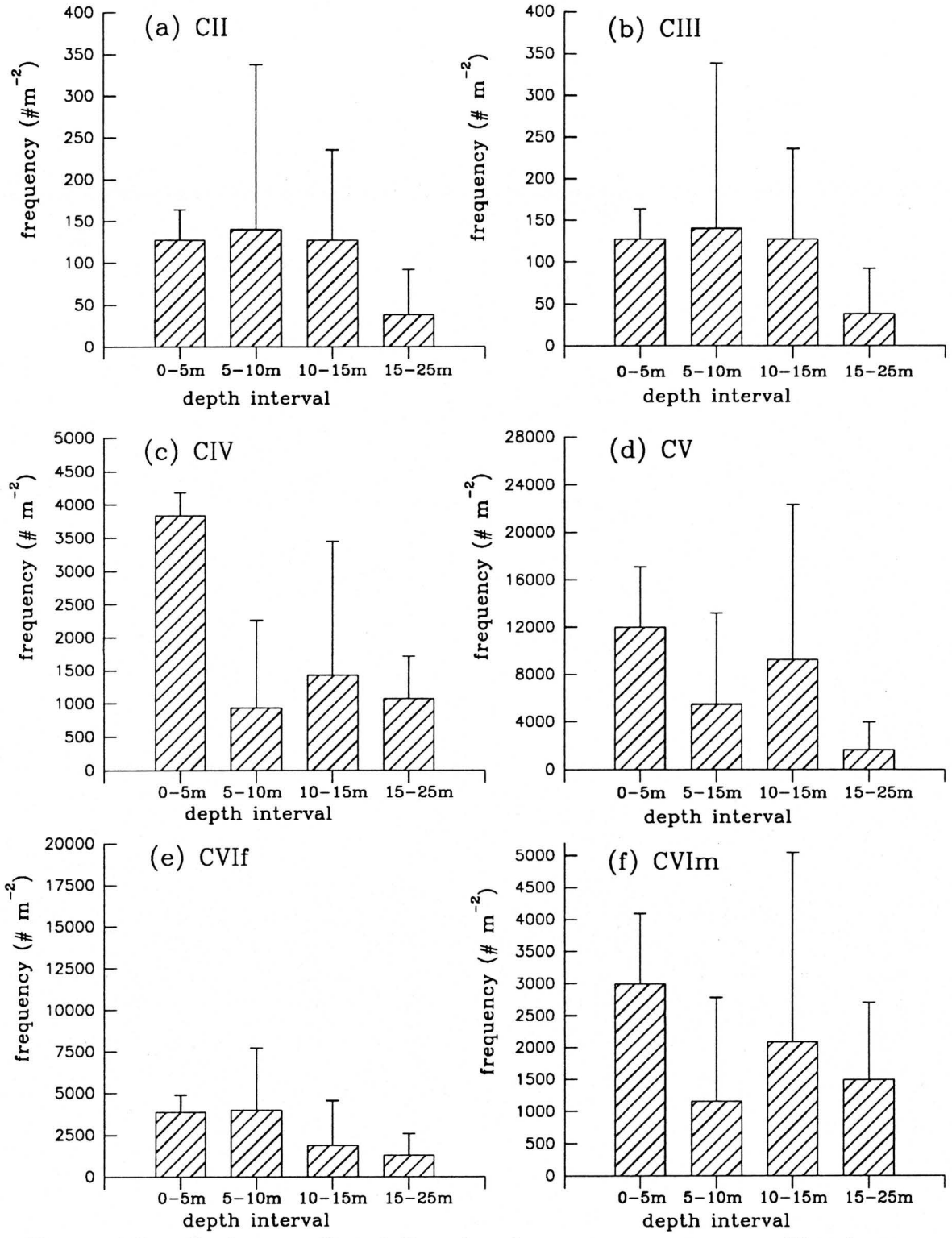


Figure 11b. Spring profile of *Pseudocalanus acuspes* copepodite stages (CII–CVIf; CI in only trace numbers) in Resolute Passage, N.W.T. Samples collected from 18:00–18:30 hr on May 15, 1991. Please note vertical scale changes. This profile corresponds to profile #5 on Figure 10a.

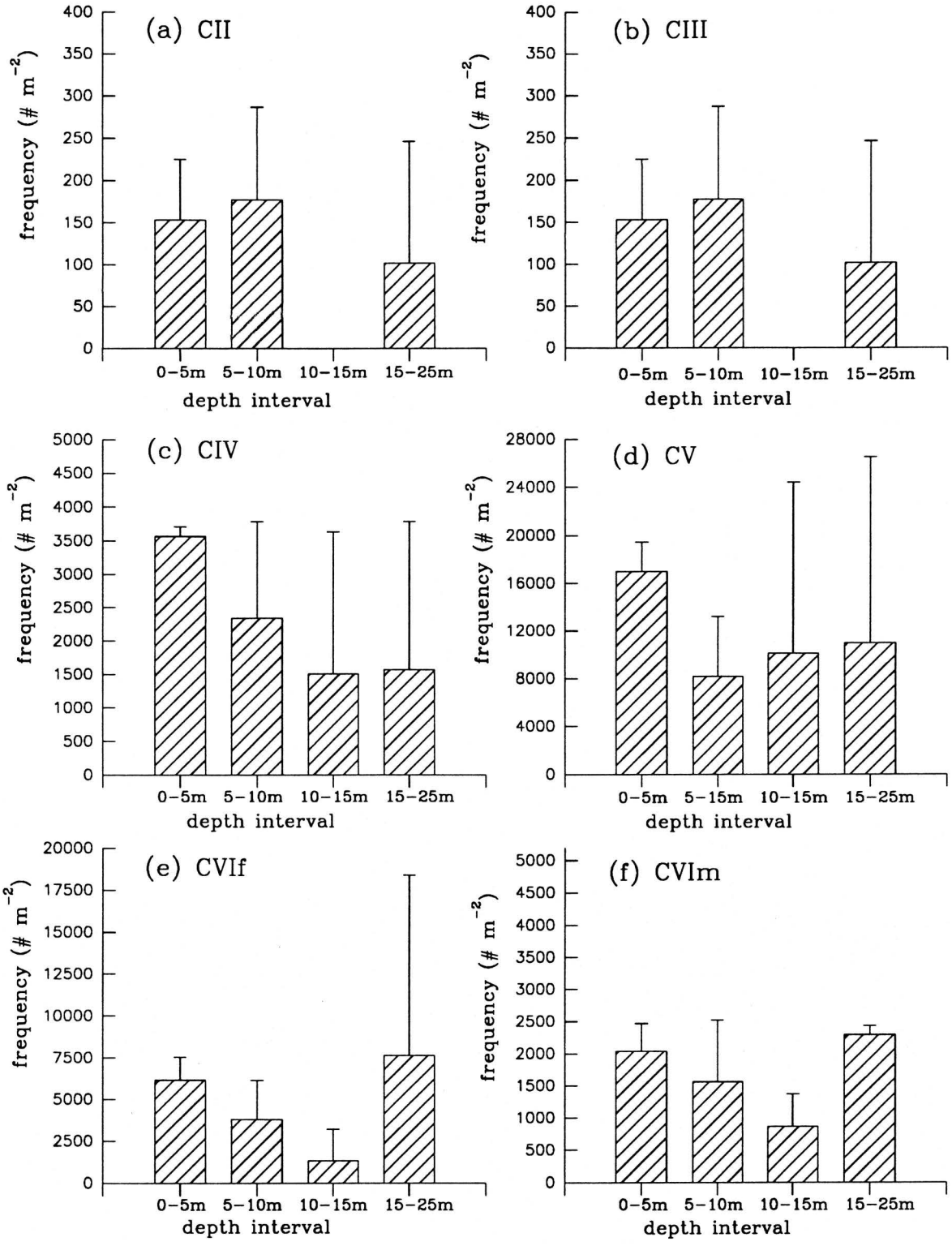


Figure 11c. Spring profile of *Pseudocalanus acuspes* copepodite stages (CII–CVIf; CI in only trace numbers) in Resolute Passage, N.W.T. Samples collected from 02:00–03:00 hr on May 16, 1991. Please note vertical scale changes. This profile corresponds to profile #6 on Figure 10b.

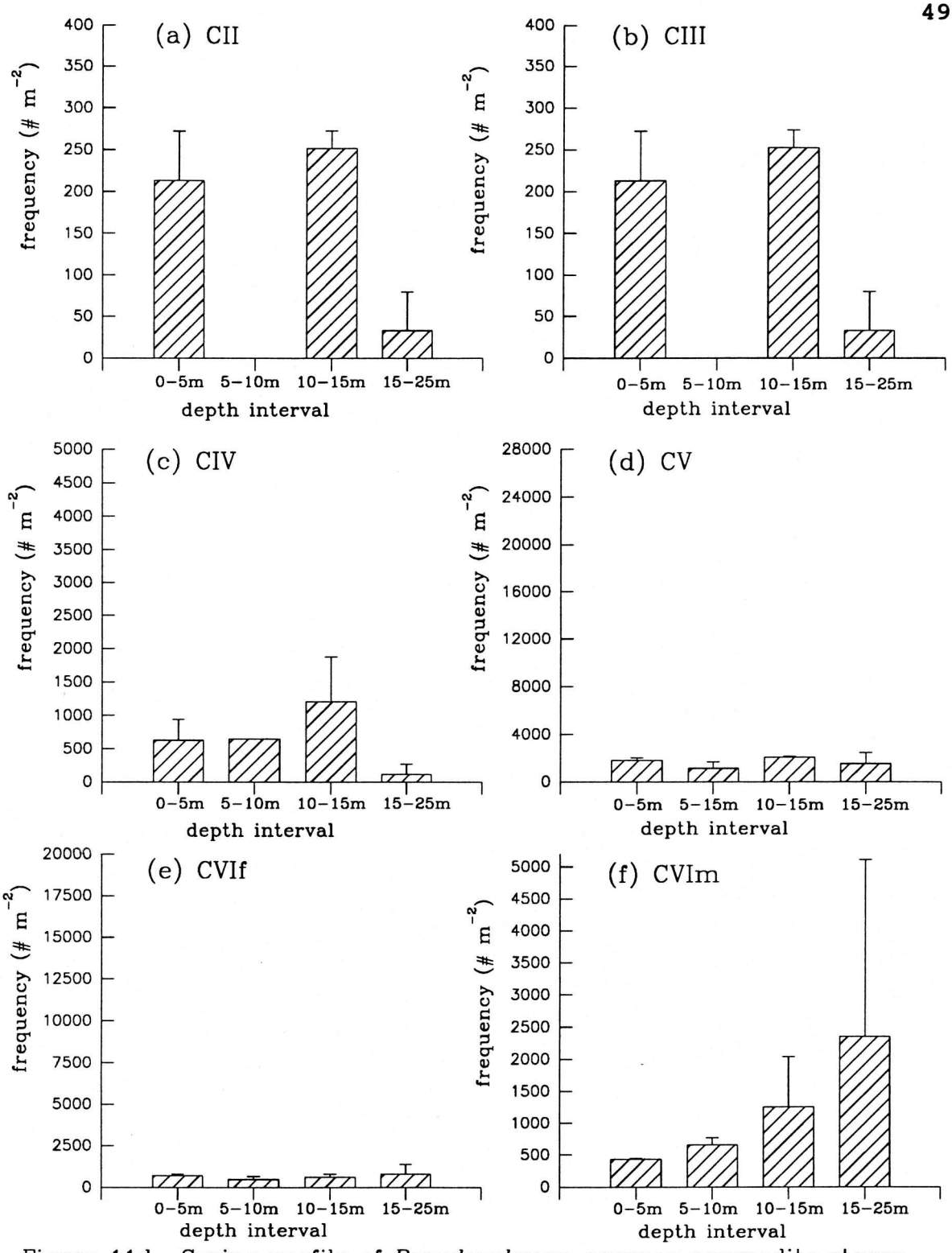


Figure 11d. Spring profile of *Pseudocalanus acuspes* copepodite stages (CII–CVIf; CI in only trace numbers) in Resolute Passage, N.W.T. Samples collected from 10:00–10:30 hr on May 16, 1991. Please note vertical scale changes. This profile corresponds to profile #7 on Figure 10b.

		Spring Profile # (0-5m oblique net hauls)			
		1 (day)	2 (night)	3 (night)	4 (day)
Stage CII Frequency (# m^{-2})	$\bar{x}$	1.30×10^{2}	1.28×10^{2}	1.53×10^{2}	2.13×10^{2}
	s.d.	0.75×10^{2}	0.36×10^{2}	0.72×10^{2}	0.59×10^{2}
Stage CIII Frequency (# m^{-2})	$\bar{x}$	4.31×10^{2}	6.88×10^{2}	6.62×10^{2}	3.25×10^{2}
	s.d.	1.41×10^{2}	3.25×10^{2}	0.72×10^{2}	1.71×10^{2}
Stage CIV Frequency (# m^{-2})	$\bar{x}$	1.00×10^{3}	3.83×10^{3}	3.57×10^{3}	6.28×10^{2}
	s.d.	0.26×10^{3}	0.34×10^{3}	0.14×10^{3}	3.11×10^{2}
Stage CV Frequency (# m^{-2})	$\bar{x}$	2.24×10^{3}	1.20×10^{4}	1.69×10^{4}	1.79×10^{3}
	s.d.	0.11×10^{3}	0.51×10^{4}	0.23×10^{4}	0.23×10^{3}
Stage CVIf Frequency (# m^{-2})	$\bar{x}$	8.33×10^{2}	3.86×10^{3}	6.16×10^{3}	6.97×10^{2}
	s.d.	0.83×10^{2}	1.03×10^{3}	1.37×10^{3}	0.96×10^{2}
Stage CVIm Frequency (# m^{-2})	$\bar{x}$	7.52×10^{2}	2.99×10^{3}	2.04×10^{3}	4.36×10^{2}
	s.d.	2.34×10^{2}	1.10×10^{3}	0.43×10^{3}	0.15×10^{2}

Table 2. Mean frequencies ($\bar{x}$) of *Pseudocalanus acuspes* copepodite stages (CII-CVIm) counted from the 0-5m oblique net hauls during the spring, 1991. Profile #1 sampled 10:00-11:00hr (May 15/91), profile #2 18:00-18:30hr (May 15/91), profile #3 02:00-03:00hr (May 16/91), and profile #4 10:00-10:30hr (May 16/91). This data corresponds to plotted data on Figures 11a-d (s.d.=standard deviation).

INCUBATION EXPERIMENT #4:				
	mean	standard deviation	n	copepodite stages used:
NH_4^+ O:N	42.78	7.89	3	CV, CVIm, and CVIf
Urea O:N	127.23	92.89	4	
NH_4^++Urea O:N	40.48	7.03	5	

INCUBATION EXPERIMENT #5:				
	mean	standard deviation	n	copepodite stages used:
NH_4^+ O:N	21.43	0.021	2	CV, CVIm, and CVIf
Urea O:N	15.64	10.44	2	
NH_4^++Urea O:N	8.53	3.63	2	

INCUBATION EXPERIMENT #6:				
	mean	standard deviation	n	copepodite stages used:
NH_4^+ O:N	16.35	9.33	3	CV, CVIm, and CVIf
Urea O:N	28.93	13.36	3	
NH_4^++Urea O:N	10.33	5.55	3	

Table 3. Calculated O:N ratios (by atoms) for spring, 1991, *Pseudocalanus acuspes* incubation experiments (NH_4^+ and urea production, oxygen consumption). Incubation experiment #4 initiated at 00:30 hr (May 9, 1991), experiment #5 at 19:00 hr (May 17, 1991), and experiment #6 at 07:00 hr (May 18, 1991).

with *Pseudocalanus acuspes*, conducted on May 17 and 18 (8.53-10.33; Table 3), indicate that stages CV, adult females (CVIf) and adult males (CVIm) are feeding on algae at high levels (low total O:N ratios). This is in contrast to the results found earlier in May (incubation experiment #4), demonstrating that the transition from utilization of oil reserves as an energy substrate to relying largely on the algae as an energy source has been made. Lipid reserves were highly visible in all copepods used for these experiments, so individual body proteins could not account for the low O:N ratios observed. Ammonia excretion ranged from 0.006-0.018 μg-at N $animal^{-1}day^{-1}$ and urea excretion from 0.004-0.023 μg-at N $animal^{-1}day^{-1}$. Thus, urea is still a significant waste product of *P. acuspes*.

Summer, 1991:

O:N ratios (by atoms) obtained for *Pseudocalanus acuspes* during the last summer field season (Table 4) agree well with the values found in 1991. This time, stages CIV and adult females (CVIf) were separated in the experiments. The low O:N ratio measured for CIV's would indicate feeding on algae at high rates (Conover and Corner, 1968) as individual lipid reserves were extensive (pers. observ.). Starvation and catabolism of body proteins would be highly unlikely. I cannot be this assured concerning adult females (CVIf) because, as noted previously, their lipid reserves were not as extensive (pers. observ.).

Again, urea was excreted as a waste product in similar or, in most cases, greater amounts, than ammonia (ammonia excretion ranged from 0.002-0.004 µg-at N $animal^{-1}day^{-1}$ and urea from 0.004-0.011 µg-at N $animal^{-1}day^{-1}$).

INCUBATION EXPERIMENT #7:				
	mean	standard deviation	n	copepodite stages used:
NH_4^+ O:N	81.40	16.36	6	CVIf
Urea O:N	37.63	16.31	6	
NH_4^++Urea O:N	25.19	8.38	6	

INCUBATION EXPERIMENT #8a:				
	mean	standard deviation	n	copepodite stages used:
NH_4^+ O:N	37.16	9.65	6	CIV
Urea O:N	18.04	8.83	5	
NH_4^++Urea O:N	11.40	3.29	5	

INCUBATION EXPERIMENT #8b				
	mean	standard deviation	n	copepodite stages used:
NH_4^+ O:N	40.92	12.00	3	CVIf
Urea O:N	16.99	9.68	3	
NH_4^++Urea O:N	11.36	4.42	3	

Table 4. Calculated O:N ratios (by atoms) for summer, 1991, *Pseudocalanus acuspes* incubation experiments (NH_4^+ and urea production, oxygen consumption). Incubation experiment #7 initiated at 14:00 hr (August 3, 1991), experiments #8a and #8b at 15:30 hr (August 12, 1991).

DISCUSSION

First, a few comments should be made regarding the use of methanol instead of the more widely used acetone as a solvent in the estimation of chlorophyll a and phaeopigment concentrations. Various authors have investigated the applicability of methanol as a useful pigment extractor in fluorometric and spectrophotometric methodology, with emphasis on the interactions of the solvent with the chlorophyll pigments. The method of estimating phaeopigments using the difference in sample absorption before and after acidification presents some difficulties. Marker (1972 and 1977) demonstrated that the absorption of phaeophytin a was lower in an acidic 95% methanol solution than at neutrality. It was further complicated with an increased interference with chlorophyll b and irreversible alterations in phaeophytin b absorption. The problems associated with the presence of chlorophyll b and degradation products was ignored because of a dominance of diatoms, which do not contain chlorophyll b, in the phytoplankton community at Resolute (pers. observ.). Tett et al. (1977) gave corrected equations for the determination of chlorophyll a and phaeophytin a in 95% methanol, but the coefficients were highly dependant on the final pH after acidification. Neutralization of the samples before reading the acidified fluorescence was not attempted here, but the error associated with phaeopigment underestimation (and the

corresponding overestimation of chlorophyll a) is usually restricted to 5% when there is little chlorophyll b present (Marker, 1972 and 1977). However, pigment extraction in 90% acetone was said to be less complete (Jacobsen and Hakumat, 1980) and there was increased interference when chlorophyll c was present, such as would occur in my study (Trees et al., 1985). It is often difficult to say which pigment solvent, acetone or methanol, would be the solvent of choice.

The zooplankton pump used in this study (Fig. 2) did not give results which were as satisfying as we had hoped. Plankton pumps have been recently used in preference to more traditional oceanographic methods (water bottles and nets) for various reasons: reliability of volume filtered, absolute resolution for vertical stratification, ease of taking time replicates, ability to do long-term small scale distributions, and elimination of problems associated with using fine nets to collect small organisms (Harris et al., 1986).

Due to time constraints, and the desirability to obtain replicate samples for each depth, only four discrete depths were selected for sampling with the pump during the summer of 1990 (Figs. 3-6). Unfortunately, this resulted in a lack of resolution between 10 and 40 meters. Although the ability to take time replicates and the avoidance of net clogging problems was useful during the summer, the more

traditional collection methods with zooplankton nets and water bottles might have provided much more useful information.

The extent of diel vertical migration by *P. acuspes* during the summer months is unclear in this study (Figs. 4a-c and 6a-c). A diel pattern is suggested for the early stages (CI and CII). Longhurst et al. (1984) reported that by the month of August in arctic waters, any diel patterns was absent in copepods and ontogenetic migrations dominated. The bulk of zooplankton may already have descended to overwintering depths by this time (Longhurst et al., 1984). Two other dominant calanoid copepods in Barrow Strait, N.W.T., (*Calanus glacialis* and *Calanus hyperboreus*) usually do not display diel migration during the summer months in other regions of the arctic, although some stages are known to migrate weakly (i.e. *C. glacialis* adult females; Bamstedt, 1984; Head and Harris, 1985; Kosobokova, 1978; Sameoto, 1984). Continuous feeding on phytoplankton during the summer and later descent to depth for overwintering seems to be the general rule for most arctic copepods, including *P. acuspes* (Bamstedt, 1984; Conover and Huntley, 1991).

Our results indicate that throughout the month of August most *P. acuspes* remain near the depth of the summer phytoplankton bloom as it sinks out of the water column. This is supported not only by the information on

distribution, but also by low O:N ratios suggesting considerable feeding (8.19-11.94, Tables 1 and 4). The lack of a consistent diel vertical migration, but with the bulk of the zooplankton biomass remaining at the same depth as the chlorophyll maximum has also been documented by Hansen et al. (1990). Here, only relatively few *P. acuspes* CV's and adult females (CVIf) descended and remained below the sinking chlorophyll maxima (>50m) by the end of August (Figs. 6a-c). Most adult females probably do not survive winter, based on their poor condition and low lipid content noted from visual examinations (see Results). Only a few individuals have been taken in January (Les Harris, pers. comm.). Low O:N ratios for adult females (11.36-25.19; Table 4) might reflect utilization of their own body proteins for energy in absence of sufficient oil reserves.

Existence of strong diel vertical migration by *Pseudocalanus acuspes* in the spring (Table 2) should not be surprising. Although the sun never sinks below the horizon from late April to August, there is a strong diurnal periodicity in the surface irradiation levels during the month of May in the Resolute Bay area. Nighttime minima are 5% or less of daytime maxima (Resolute Airport Station RF-1 Annual Summaries, Environment Canada).

Some caution should be exercised when interpreting the vertical distributional profiles for the spring of 1991 (Figs. 10a-d; Table 2). The evening samples which showed

higher concentrations of animals in the near underice zone also corresponded to periods of stronger tides. Although a heavy weight was used on the cable and on the cod end of the zooplankton net to decrease wire angle and reduce horizontal fishing, the night profiles probably sampled somewhat more water than the corresponding day profiles. However, this relatively small error could not account for the large differences seen in the frequencies. Diel migration was still thought to be very real.

Runge and Ingram (1988 and 1991) reported diel migration by the spring population of *Pseudocalanus minutus* in southeastern Hudson Bay. The nighttime migration to the underice surface was correlated with utilization of the ice algae by the copepods during the epontic bloom. Similar observations have been made in the past regarding *Pseudocalanus acuspes* in the Resolute Bay area. Conover et al. (1986b) reported dense congregations ($>10^6 m^{-3}$) of *P. acuspes* under the fast ice during the May, 1984, and also noted diel migration to the near ice zone at night. I also encountered large swarms near the underice surface at night.

Conover et al. (1986b) and Conover et al. (1988a) also examined the role of tidal currents in eroding epontic algae so that it would become available for consumption by *P. acupes*. Conover et al. (1986b) attempted to correlate particulate pigment concentrations, copepod gut pigment levels, and tidal current speeds. Although the relationship

was not simple, there was some pattern evident. Similar results were obtained by Conover et al. (1988a) but in 1986 a relatively consistent diel migration pattern was observed, which was not shown in the earlier study (Conover et al., 1986b). In these studies, the authors were not able to determine whether the copepods were feeding directly on attached algae or after it was eroded.

Here, although we have not come much closer to answering the last question, the important role of epontic algal erosion is supported. The particulate profiles of May 15-16, 1991 (Figs. 10a and 10b), indicate that there was increased grazing activity during the evening profiles, correlated with higher concentrations of *P. acuspes* near the underice zone and increased tidal currents (Figs. 11a-d; Table 2). I also measured high gut pigment levels in the copepods during this time, with individual levels reaching as high as 2.5ng ind^{-1}. (stages CIV-adults; unpubl. data). High grazing activity is also supported by the low O:N ratios at that time (8.53-10.33; Table 3). The currents at this time were generated by spring tides (1.9m height difference; Canadian Tide and Current Tables 1991, Arctic Region, Dept. of Fisheries and Oceans). Feeding directly on the attached algae would not have been possible, as tidal current speeds typically reach 0.25-0.50m sec^{-1}, far greater than the maximum swimming speeds of *Pseudocalanus acuspes* (Conover et al., 1986b; Conover et al., 1988a). It should

also be noted that when the copepods were near the underice surface in the early evening, tidal currents would already be present, and the initiation of the feeding response would be in the presence of these currents. Thus, from our results it appears that *P. acuspes* feeds primarily on the epontic algae as it is eroded off the ice surface.

The idea of the underice surface representing a second benthos has been discussed in the past, as it is a relatively stable structure which allows for the growth of large concentrations of highly-adapted epontic algae and an enriched feeding environment for zooplankton (Conover et al., 1990). The epontic algal community represents an incredibly rich potential food source for *Pseudocalanus acuspes*. Measurements of the chlorophyll levels in the bottom few centimetres of the fast ice near our ice camp during the month of May, 1991, ranged from 20-160 mg chl a m^{-2} (algal concentrations decaying exponentially with increasing thickness of snow cover on the ice; data courtesy of Glenn Cota, University of Tennessee). These chlorophyll concentrations are consistent with previous observations (Welch et al., 1988). Furthermore, recent studies of the epontic community in Resolute Passage, N.W.T., have indicated that as much as 65% of production could be exported from the ice during the growth season, preceding the decline of the algal bloom in late May (Smith et al., 1988). This represents production rates of 20-463 mgC $m^{-2}d^{-1}$

of potential food source for herbivorous copepods in Resolute Passage (Smith et al., 1988).

The O:N ratio (respiration and nitrogen excretion by atoms) is believed to be a good indicator of the type of energy source being used by copepods. A value of 6-16 is indicative of primarily protein being used as a substrate, typical when feeding on an algal bloom, while a higher value (upwards of 200) is indicative of lipid and/or carbohydrate respiration; intermediate values are typical of mixed metabolism with several sources of energy and materials being used (Conover and Corner, 1968; Mayzaud and Conover, 1988). Because the effects of body mass and habitat temperature are negligible, the index is truly universal (Ikeda, 1985). It has been used quite successfully in the past to follow the life-history strategy of temperate and arctic copepods, particularly during the transition from summer feeding to overwintering state and from overwintering state to spring feeding (i.e., Bedo et al., 1990; Conover and Corner, 1968; Head and Harris, 1985; Schneider, 1990).

This study has reported the lowest O:N ratio measurements reported in the literature for *Pseudocalanus acuspes* in the area. Bedo et al. (1990) reported early May measurements of 57 (standard deviation of 14) and late May measurements of 26 (s.d.=9), corresponding in season to our values of 40.5 (s.d.=7.0) and 8.5-10.3 (s.d.=3.6-5.6). However, much of the difference can be attributed to the

significant contribution of urea, which was not measured in earlier studies, to the nitrogenous excretion of *P. acuspes*. In fact, urea can be produced in up to two or three times the levels of ammonia (ammonia at 0.001-0.018 µg-at N $animal^{-1}day^{-1}$ and urea at 0.001-0.023 µg-at N $animal^{-1}day^{-1}$; Tables 1, 3, and 4).

Harrison et al. (1985) measured high concentrations of urea in the Canadian arctic (<0.03 to >2.00 mg-at N m^{-3}), accounting for >50% of the total dissolved nitrogen in the mixed layer. Excretion measurements with the copepods *Calanus finmarchicus, C. hyperboreus, C. glacialis,* and *Metridia* sp. indicated that they supplied only 3% of the urea-N but 40% of the ammonia-N required by primary producers, urea accounting for only 0-11% of the nitrogen excreted. Harrison et al. (1985) were unable to explain the source of urea in the water column, but hypothesized that a significant contribution might have been made by bird guano and marine mammals. Our study suggests significant contribution to total urea-N could be made by *P. acuspes*.

In conclusion, it is evident that *Pseudocalanus acuspes* utilizes both the summer phytoplankton and the spring epontic algae extensively. The copepod positions itself in the water column to take full advantage of this food source during both seasons. In fact, we have every indication that *P. acuspes* is, by the middle of May and through the month of August, relying extensively on the

algal community for its present energy requirements and to build up the large lipid reserves for survival through the oncoming winter. This work further challenges past views of the arctic environment being a dilute, highly oligotrophic environment (i.e., McLaren, 1964; Nansen, 1902).

PART II:

Feeding Selection in the Arctic Calanoid Copepod *Pseudocalanus acuspes* Using a Natural Summer Phytoplankton Assemblage From Resolute Passage, N.W.T., Canada.

INTRODUCTION

The oceanic regime represents a continuously transient and often dilute environment for the planktonic organism. Each species must be able to respond and adapt to that changing environment if it is to be a successful member of the pelagic community. One of the primary questions is that of optimization. Are members of the planktonic community able to select food sources which will give them the greatest chance for survival? How does optimal utilization of the resources vary between species and over time? Furthermore, is a species able to effectively optimize a food source that itself is continuously changing in response to a varying environment? Of primary concern is to establish whether or not feeding selection occurs in the natural environment. If the answer to this question is yes, it would then be appropriate to investigate when and under what conditions pelagic community members select particular food. A further extension would be to describe the physical, chemical, and physiological mechanisms which determine how selection operates.

This study will focus on the step in the pelagic food chain between phytoplankton and herbivorous zooplankton. Gathering detailed information can be difficult largely due to methodological and logistic restrictions associated with working with such small organisms which live in a large, expansive environment.

Numerous researchers have, however, investigated selective feeding behaviour in filter-feeding copepods and their ability to discriminate between various algae and particulates in the laboratory.

Selective feeding by copepods had been viewed as a passive, mechanical size-selection based on the dimensions of the algae and of the copepod's filtering appendages (i.e., Boyd, 1976; Frost, 1977). However, further laboratory studies found feeding selection which was difficult to explain with the simple passive mechanical model, and had to invoke explanations involving post-capture rejection and active manipulation of setae spaces (e.g., Donaghay and Small, 1979). The first cinematographic account of filter-feeding by a calanoid copepod (Alcaraz et al., 1980) indicated the combined use of mechanical and chemical reception with filtering mechanics that operated in a viscous, low Reynold's number (Re) flow (Reynold's number being the ratio of inertial forces to viscous forces). It is now generally accepted that copepods can use their filtering appendages as both "paddles and rakes", depending on the relative frequencies in question, the presence/absence of adjacent appendages, and the size of the filtering appendages (with a Re of about 0.1; Cheer and Koehl, 1987). Thus, it is evident that copepods are physically able to capture a wide size range of particles by operating either in the viscous or partially inertial world.

There is potential for particle selection far beyond that of a simple mechanical or passive nature based on the size of the particulate food.

Numerous laboratory studies have further investigated this selective ability. Huntley et al. (1983) noted that *Calanus pacificus* was able to select a species of *Thalassiosira* over a similarly sized artificial bead; furthermore, the copepod seemed to prefer one species of dinoflagellate over another, despite their being of a similar size. DeMott (1988) demonstrated that the freshwater calanoid *Eudiaptomus* and the marine copepods *Temora longicornis* and *Pseudocalanus* sp. all showed optimal selection based on the quality of food when they chose living algae over algae-flavoured spheres, and both were chosen over untreated spheres. However, "tasting" of the particulates necessitated by quality selection seems to largely occur after capture, mechanoreception being of primary importance in long-distance detection (DeMott and Watson, 1991).

It appears that when feeding selection does occur in filter-feeding copepods, it optimizes the animal's nitrogenous ingestion rate by selecting the faster growing, healthier algae cells over those of poorer quality; i.e., ingestion can be correlated with N intake (Libourel-Houde and Roman, 1987; Coules et al., 1988). Conover et al. (1988b) noted that living, healthy ice algae were

preferentially ingested over dead algae for arctic populations of *Pseudocalanus acuspes*, *Calanus glacialis*, and *Metridia longa*; this in turn was reflected in the respiration and nitrogenous excretion rates for *P. acuspes*. Such chemically mediated selection has obvious positive ramifications for survival. In fact, laboratory selection studies do seem to follow optimal foraging predictions, copepod behaviour being influenced by both particle quality and the abundance of alternative foods (DeMott, 1989).

It is becoming increasingly evident that feeding selection studies can lead to drastic changes in our perceptions of trophic roles in the natural environment. For example, Kerfoot and Kirk (1991) showed that cladocerans and daphnids showed no taste discrimination (i.e., they acted as general detritivores), while various calanoid copepods showed a high degree of selection for algae and higher quality detritus. This later study has suggested a new trophic classification for cladocerans and daphnids. While I do not expect all investigations to produce such dramatic results, there is need to extrapolate laboratory feeding selection studies meaningfully into natural situations.

Few studies have examined selection in the field and its implications for community structure and survivorship. The majority of recent past work which assessed feeding on natural phytoplankton assemblages was restricted to the use

of electronic particle counters. These can only examine size selection and have proven difficult to interpret. An erroneous preference for larger-sized particles can be mistakenly indicated by the addition of smaller particles from the breakup of larger ones (Poulet and Chanut, 1975); nor can selection at the level of specific food species be examined. Opportunistic feeding has been shown to occur for five species of neritic copepods, including *Pseudocalanus acuspes*, in Bedford Basin, Nova Scotia; they nonselectively consumed the algae in the size class that was most abundant (Poulet, 1978). This behaviour results in the copepods eating the algae that are actively growing (log phase) and consequently more nutritious. The different developmental stages of *Pseudocalanus minutus* (probably *P. acuspes*) have been demonstrated to size-partition the natural particulate community (Poulet, 1977). Such intraspecific separation of feeding niches has obvious developmental advantages. Harris (1982), in another Coulter Counter experiment, noted that *Pseudocalanus* and *Calanus* chose the largest cells over the smallest when feeding on a natural phytoplankton assemblage.

Particle size counts to explore selective feeding in the natural environment have limited use. Size class information alone yields few satisfying results, yet researchers have been reluctant to adopt other methods of examining the phytoplankton community, such as direct visual counts. Barthel (1988) examined selective feeding in three

Calanus species on different phytoplankton assemblages in the Greenland Sea. Visual examination to compare ingestions of diatoms, ciliates, and flagellates seemed to indicate that the largest, dominant algae was eaten most of the time, but there was no clear trend. The study was not species specific. Although more laborious, researchers must be able to assess the composition of the phytoplankton community at the species level in order to provide truly useful information.

This study restricted itself to examining the extent of selective feeding behaviour in a herbivorous arctic marine calanoid copepod, *Pseudocalanus acuspes*, using a natural summer phytoplankton community. Specific taxonomical distinctions were made when documenting feeding on the particulate assemblage. Experimental conditions closely approximated the natural environment, and the results were extrapolated to the conditions experienced naturally by the copepod.

MATERIALS AND METHODS

From late July through to late August, 1991, a series of eight feeding selection experiments were conducted in laboratory facilities in Resolute Bay, N.W.T., Canada (Department of Fisheries and Oceans, Central and Arctic Region, Winnipeg, Manitoba). Zooplankton and high concentrations of naturally occurring phytoplankton were collected from the waters of Resolute Passage, N.W.T. (Fig. 12), using a 100μm mesh, 0.5m diameter net hauled obliquely from 80m depth. A high degree of clogging occurred due to the dominance of colonial, filamentous diatoms (pers. observ.). Collection of phytoplankton using water bottles was not attempted because of the difficulty in obtaining large volumes of algae in high concentrations. Within 12hr after capture, adult female *Pseudocalanus acuspes* (Copepoda, Calanoida) were separated from the plankton mixture and placed in 500ml clear polycarbonate bottles filled with ambient seawater. The copepods were kept in a water bath maintained at temperatures between -1.0°C and +1.0°C until the commencement of each feeding selection experiment. Different individuals of *P. acuspes* were used for each experiment, and copepods were not kept in the laboratory for longer than one week after collection.

Within 2hr after the collection of the net phytoplankton samples from Resolute Passage, the assemblage was passed through a 355μm mesh screen to remove most of the

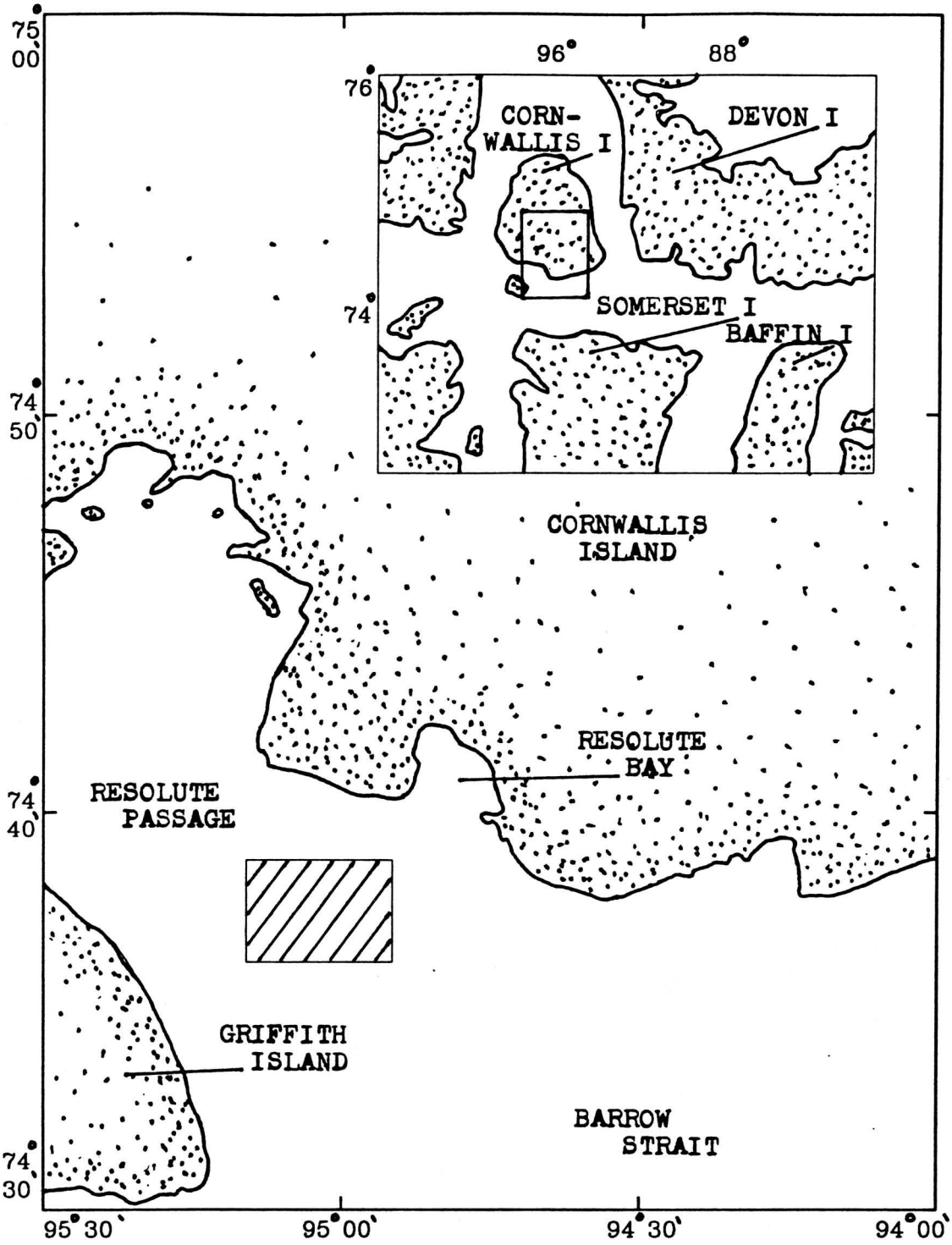


Figure 12. Map of the field site, showing the area where plankton collections were made during the summer of 1991 (hatched rectangle) land the location of Resolute Passage within the Canadian arctic archipelago (see insert).

fauna present. The microzooplankton that remained appeared to be dominated by copepod nauplii. Protists and other invertebrate eggs and larval stages (bivalves, gastropods, polychaetes, and echionoderms) do not contribute substantially to the total microzooplankton carbon (approximately 14%) in the waters adjacent to the plankton collection site (Paranjape, 1988). Feeding selection experiments were conducted using 50-60 adult female *Pseudocalanus acuspes* in 250ml clear polycarbonate bottles incubated on a rotating wheel (2 r.p.m.) for 12-24 hrs in low ambient light ($<100\mu Em^{-2}$). The extent of feeding, as measured by the depletion of chlorophyll a, was affected by the duration of the experiment and, to a certain extent, by the initial chlorophyll a concentration (Table 6). At no time after the collection of the copepods were they kept in concentrations exceeding 240 ind.L^{-1}, so that there would be no accessory problems associated with overcrowding (Corkett and McLaren, 1978).

Particulate carbon/ hydrogen/ nitrogen content (CHN) and chlorophyll a/ phaeopigment samples were taken of the feeding incubation water at the commencement of each experiment and from each bottle (controls and treatments) at the experiments' terminations. No CHN samples were taken from experimental treatments, but were taken from initial and control feeding water samples.

50ml of water was filtered through a Whatman GF/F®

glass fibre filter for fluorometric determination of particulate chlorophyll a/ phaeopigment using a Philips PU8625® UV/visible spectrophotometer according to Parsons et al. (1984). 95% methanol was used as a pigment-extraction solvent. 100ml of water was filtered through a baked (450°C for 1hr) Whatman GF/F® glass fibre filter for particulate CHN determination. The samples were analyzed with a Perkin Elmer 2400 CHN Elemental Analyser® after drying in an oven at 60°C for 24hr and cooled in a desiccator. All chlorophyll a/ phaeopigment and CHN filtrates were frozen at -20°C immediately after collection and kept frozen until processing. Pigment samples were processed in the laboratory facilities at Resolute Bay within 2 weeks, and all CHN samples were processed at the Bedford Institute of Oceanography in Dartmouth, Nova Scotia, 2-3 months later.

Initial, final treatment, and control water samples were retained for each feeding selection experiment (20ml for initials and controls, and 100ml for experimental treatments) and preserved with a combination of formalin and Lugol's solution to a final concentration of 1% by volume each (Parsons et al., 1984). Diatom cell and colony counts were obtained at the Bedford Institute of Oceanography in Dartmouth, Nova Scotia, following the inverted microscope technique after Lund et al. (1958) and Sournia (1978). To detect any unexpected effect of the incubation procedure on the diatom counts, initial samples were processed from only

3 of the experiments (experiments #1, #4, and #8) due to time constraints. 25ml sedimentation chambers were used and all counts were made no sooner than 24hr and no later than 72hr after the samples were placed in the chambers. Diatoms were identified to genus (in one case to species) and, if necessary, further separated into size categories. Medlin and Priddle (1990) and Lebour (1930) were used to aid in identifications and for description terminology.

Raw diatom cell and colony counts for each identified species were converted to a proportion of the total and then arcsine root transformed before statistical tests were conducted (Zar, 1984). For colonial diatoms only the colony counts were used so that assumptions of independence were not violated in the statistical analysis. Individual t-statistics for differences between proportion means for each diatom species and each experiment (controls vs. experimental treatments; controls vs. initials and initials vs. experimental treatment for three of the experiments) were calculated using the Systat^{R} statistical software package. Plots of diatom proportional differences and the associated regressions were produced using the Sigmaplot^{R} software package. A feeding preference index ($\hat{\alpha}$) was also calculated for each diatom species after Manly et al. (1972) as reported in Chesson (1983). The index was calculated individually for each experiment and then averaged over all feeding experiments.

RESULTS

Five species of diatoms were selected to examine the variety of selective feeding responses by *Pseudocalanus acuspes* when offered the mixture of algae present in a natural phytoplankton assemblage (Table 5). Data for six other diatom species are presented in the appendices. The four pennates (*Navicula* sp.A, *Navicula* sp.B, *Fragilaria* sp.A, and *Nitzschia seriata*) and one centrate (*Thalassiosira* sp.A) all form colonial chains which make them highly susceptible to capture by *P. acuspes*. Even the range of individual cell lengths (27-90μm) and widths (3-20μm) is within the documented size limits of cells known to effectively captured by various species of *Pseudocalanus* (Corkett and McLaren, 1978).

Chlorophyll a depletions range from 1.66μgL^{-1} to 20.65μgL^{-1}, dependant in part by the duration of the experiment (Table 6). There seems to be an added effect of varying levels of copepod feeding activity. Feeding history and previous acclimation to a particular environment has been shown to have a significant effect on ingestion rates of copepods (Mayzaud and Poulet, 1978). If this is a factor in our experiments, then a pattern of chlorophyll a depletion should appear according to the use of "fresh" copepods (just collected from the field) versus "older" copepods (kept in the laboratory). "Fresh" samples were used in experiments #1, #3, and #6, while the animals used

Species:	Characteristics:
Navicula sp.A	-cells 31-34μm long by 6μm deep, forming long ribbon-like chains. -cells boxy and contact adjacent cells along their full length.
Navicula sp.B	-same as *Navicula* sp.A, except cells 40-45μm long by 6μm deep.
Fragilaria sp.A	-cells 75-90μm long by 3μm deep, found in chains (often broken in samples). -lanceolate, fusiform cells with no discernable internal structures.
Nitzschia seriata	-cells 60-90μm long by 6-9μm wide, linear with rounded apices. -cells united in stiff, hair-like chains.
Thalassiosira sp.A	-cells 27-30μm in diameter by 18-20μm deep. -cells form long chains and are connected by a thick and rigid thread.

Table 5. Characteristics of the diatoms found in the summer phytoplankton assemblage in Resolute Passage, N.W.T., and chosen for examination to indicate degree of feeding selection behaviour in *Pseudocalanus acuspes*.

	Experiment #							
	1	2	3	4	5	6	7	8
Control chl a (μgL^{-1}) x	9.97	23.32	35.73	12.47	17.12	12.47	12.94	7.21
s.d.	0.58	1.14	3.41	0.62	0.74	0.47	1.18	0.14
Final chl a (μgL^{-1}) x	8.31	2.67	24.41	3.79	7.41	10.68	9.46	4.37
s.d.	3.12	1.67	1.22	0.84	0.80	0.86	1.24	0.36
Control-Final chl a (μgL^{-1})	1.66	20.65	11.32	8.68	9.71	1.79	3.48	2.84
standard error (diff. of means)	1.88	1.11	1.61	0.57	0.59	0.55	0.89	0.22
Duration of Experiment (hours)	19.50	28.75	24.00	27.00	21.25	10.50	10.25	10.00

Table 6. Control and final chlorophyll a (μgL^{-1}) levels of the eight feeding selection experiments, showing the extent of depletion (s.d.=standard deviation; standard error calculated according to Zar,1984).

in the other experiments were maintained in the laboratory for up to one week before being used. If we examine Table 6 with this in mind, a clear pattern is not evident (i.e., pigment depletion in experiments #1, #3, and #6 was not distinct from that of the other experiments). Thus, the time copepods were maintained in the laboratory before use did not seem to have an effect.

Initial chlorophyll a values were, in most cases, only slightly lower than the control values, with the exception of the second and third experiment: chlorophyll a initial-control differences were -0.88, -8.73, -5.36, -0.65, 0.15, -1.02, -2.15, -1.12μgL^{-1} for experiments #1-8 respectively. Only experiment #2 had statistically significant "growth" of algae in the controls over the course of the experiment (t-test, 2-tailed, $p<0.05$). Control chlorophyll a concentrations among experiments varied widely due to the difficulty in accurately predicting concentration when starting experiments.

C:N ratios for the phytoplankton in the initials and controls ranged from 7.3-11.5 (standard deviations ranged from 0.6-3.4). The values appear to be randomly scattered throughout the experiments; thus variations in the quality of the food could not account for any differences seen between experiments, but may account for some of the variance within experiments.

It is difficult to visualize from Table 7 any clear

pattern in the strengths of the differences between either the various experiments or different diatom species. One question that should be explored is whether differences between the experimental treatments and the controls depend on the extent of chlorophyll a depletion during feeding. Is the extent of feeding selection dependant on how much we allow *Pseudocalanus acuspes* to eat (affected by varying satiation times, ingestion rates, and/or total consumption)?

Plots of the colony proportional differences (experimental treatment mean minus control mean) versus the extent of chlorophyll a depletion (μgL^{-1}; control mean minus experimental treatment mean) for each of the feeding selection experiments using the untransformed data are shown on Figures 13a-e. The plots with the untransformed data points visually indicate the actual sizes of the proportional differences for each of the diatom species in question, and the variances involved. Quantification of the relationship between algal-colony proportional differences and the extent of chlorophyll a depletion is done with linear regression (Figs. 14a-e). Experiments were excluded from the regression plots if the experimental and control variances were not shown to be statistically homogeneous for that particular diatom species (Zar,1984).

For *Navicula* sp.A (Fig. 14a), the regression equation was not significant, demonstrating that chlorophyll depletion had no effect in the experiments. In fact, the

	Experiment #							
	1	2	3	4	5	6	7	8
Navicula sp.A t	* 4.17	0.12	0.98	2.52	0.13	0.94	1.04	1.71
p	0.014	0.909	0.399	0.053	0.899	0.389	0.338	0.147
df	4	5	3	5	5	5	6	5
Navicula sp.B t	1.26	-	2.35	-	1.15	1.52	0.35	0.58
p	0.277	-	0.100	-	0.302	0.189	0.736	0.585
df	4	-	3	-	5	5	6	5
Fragilaria sp.A t	* 4.31	* 2.89	* 4.17	2.54	0.49	0.82	0.85	* 5.15
p	0.013	0.034	0.025	0.052	0.643	0.449	0.429	0.004
df	4	5	3	5	5	5	6	5
Nitzschia seriata t	* 3.03	* 5.92	2.92	-	* 7.63	2.40	1.62	* 5.85
p	0.039	0.002	0.061	-	0.001	0.062	0.156	0.002
df	4	5	3	-	5	5	6	5
Thalassio-sira sp.A t	1.65	* 16.38	* 5.22	* 8.13	* 5.12	* 5.17	* 2.96	1.32
p	0.175	0.000	0.014	0.000	0.007	0.004	0.025	0.245
df	4	4	3	5	4	5	6	5

Table 7. Experimental results for individual diatom species showing t-statistic values ($\alpha(2)$) and probabilities (p) of correctly accepting the null hypothesis of no difference between experimental and control means (df= degrees of freedom; *=significance at p=0.05 level).

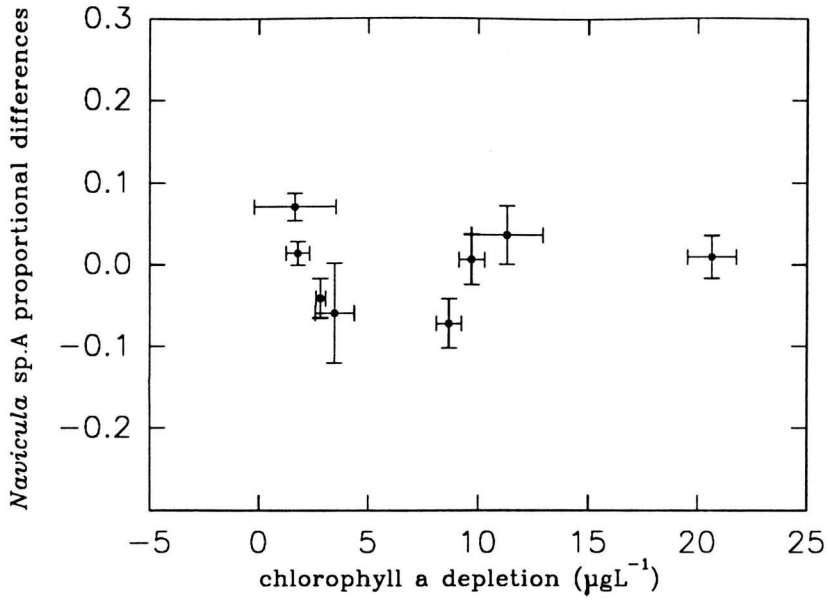


Figure 13a. *Navicula* sp.A proportional differences (experimental treatment mean−control mean) versus the extent of chlorophyll a depletion (μgL^{-1}; control mean−experimental treatment mean) for each of the feeding selection experiments. The length of each error bar represents the standard error for the difference between means (Zar, 1984). Data points were not included if the experimental and control variances were shown not to be equal (Zar,1984).

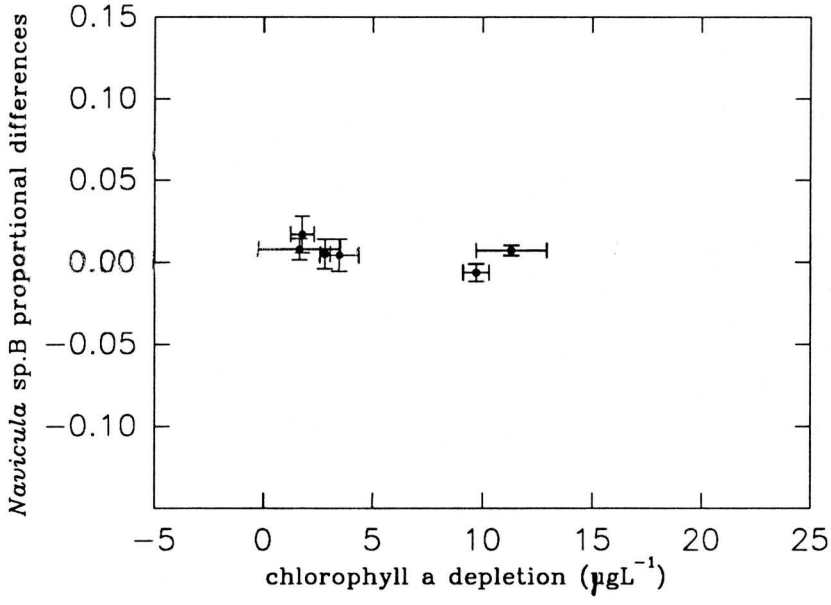


Figure 13b. *Navicula* sp.B proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 13a. Note the change in the vertical scale.

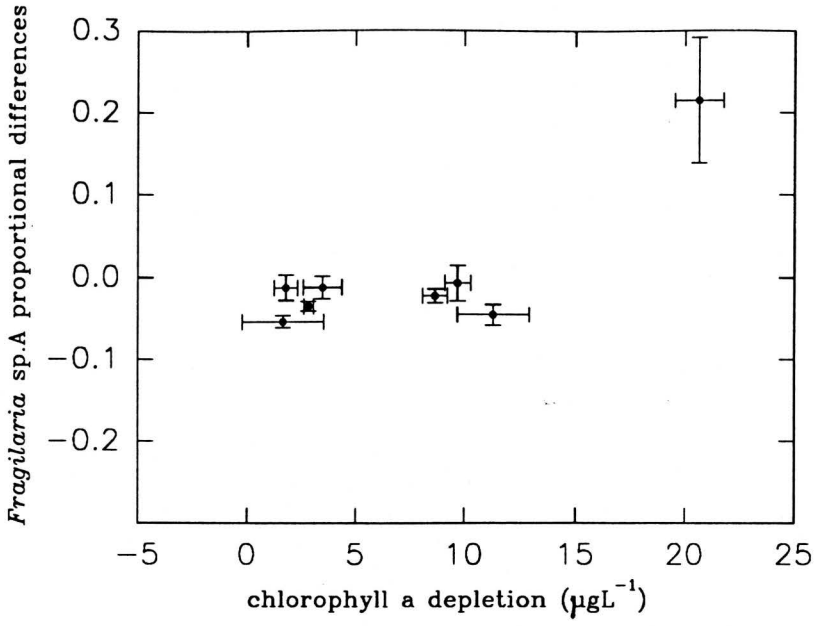


Figure 13c. *Fragilaria* sp.A proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 13a. Note the change in the vertical scale.

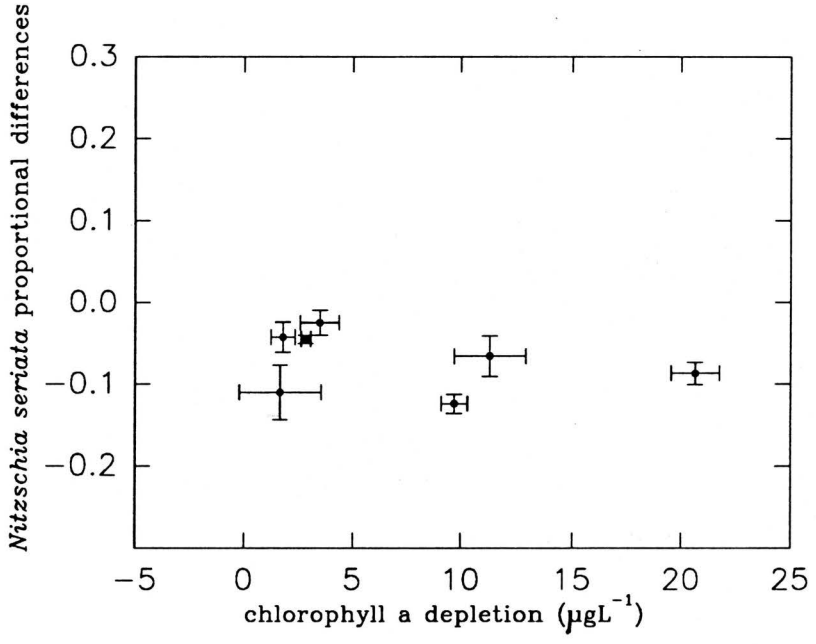


Figure 13d. *Nitzschia seriata* proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 13a. Note the change in the vertical scale.

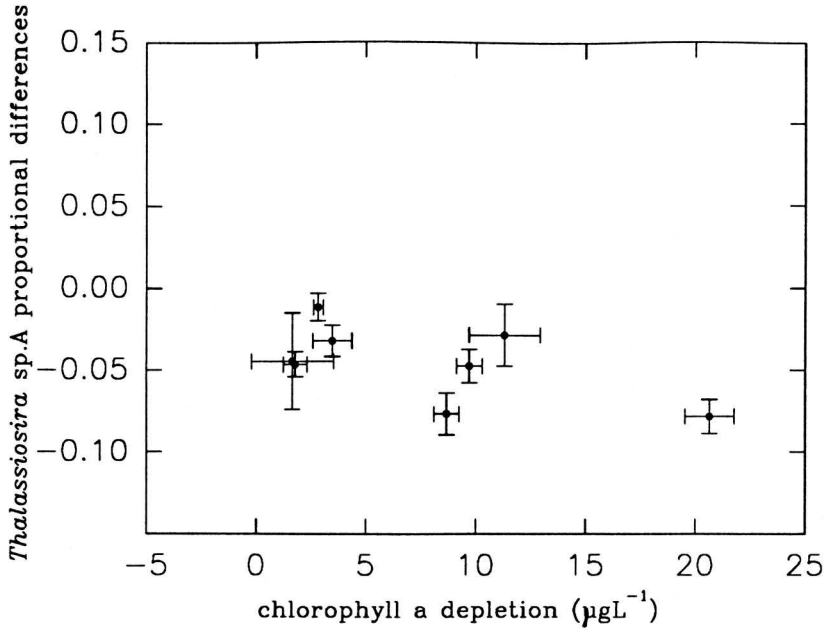


Figure 13e. *Thalassiosira* sp.A proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 13a. Note the change in the vertical scale.

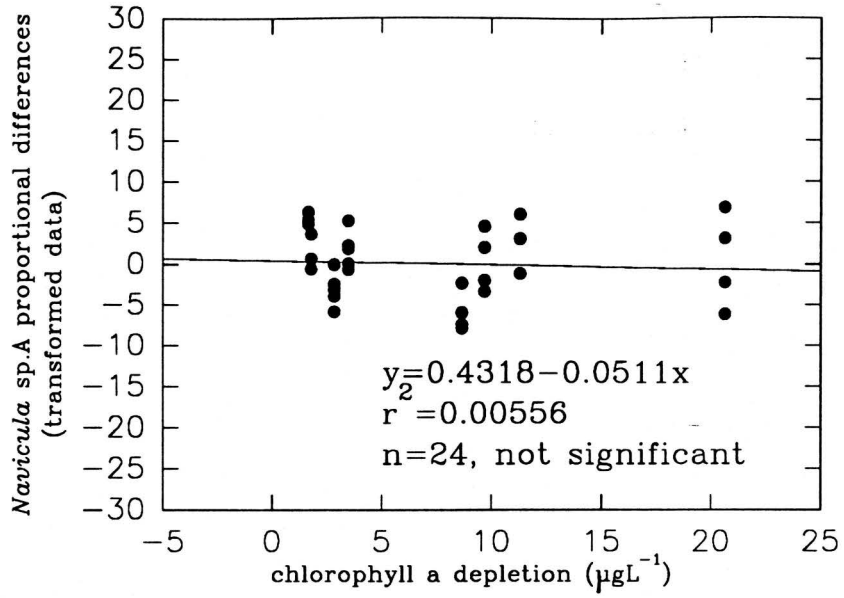


Figure 14a. *Navicula* sp.A proportional differences (arcsine root transformed data; experimental treatment−control mean) versus the extent of chlorophyll a depletion (μgL^{-1}; control mean−experimental treatment mean) for each of the feeding selection experiments. Regression line through the points is shown. Data points were not included if the experimental and control variances were shown not to be equal (Zar,1984).

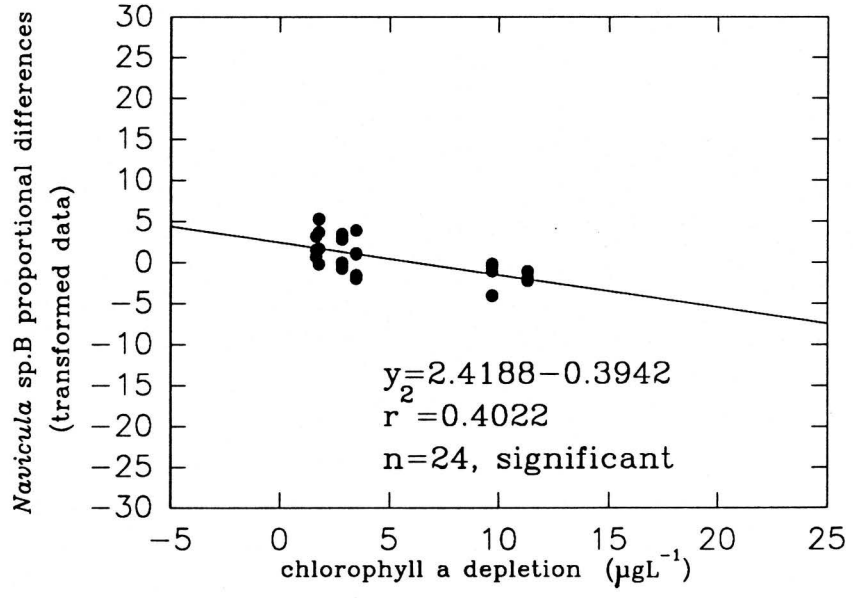


Figure 14b. *Navicula* sp.B proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 14a.

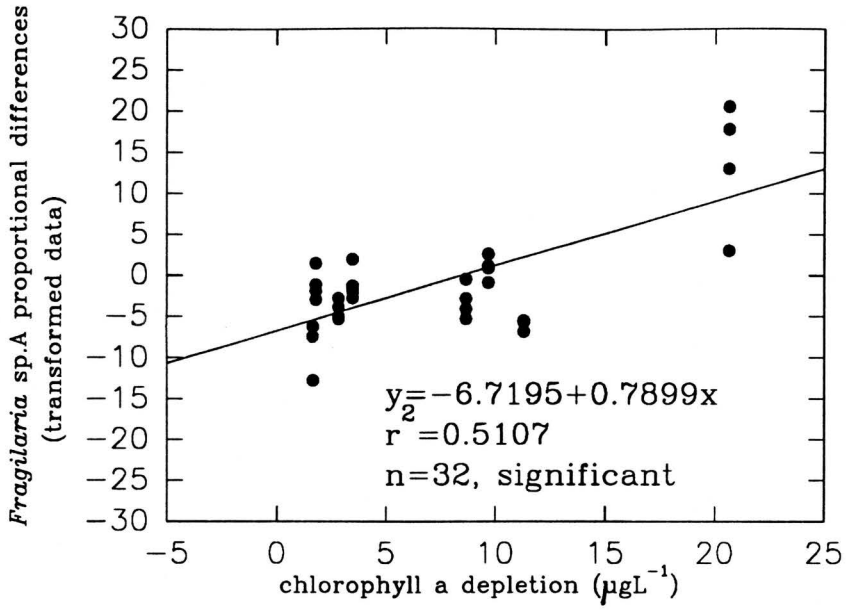


Figure 14c. *Fragilaria* sp.A proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 14a.

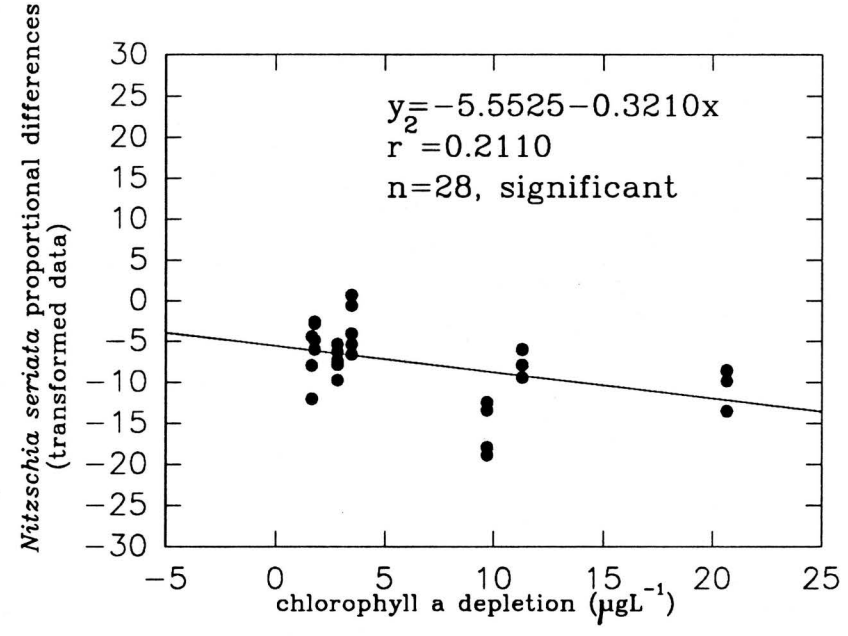


Figure 14d. *Nitzschia seriata* proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 14a.

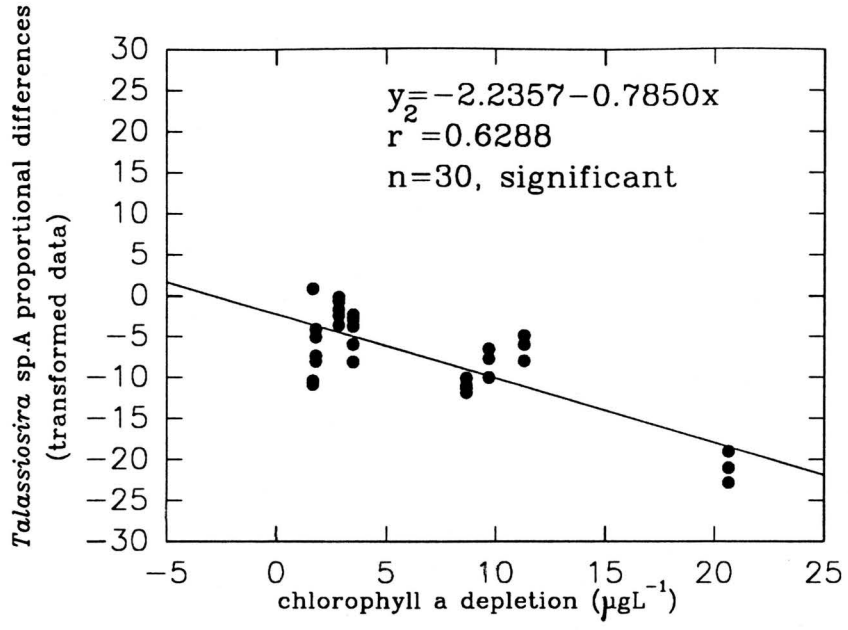


Figure 14e. *Thalassiosira* sp.A proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 14a.

points show a general scattering around the zero point for proportional differences between the experimental treatments and controls. In other words, *Pseudocalanus acuspes* seems to eat *Navicula* sp.A in the proportion that it is found in the incubation bottles, but with a high degree of variance within experiments. The plot for *Navicula* sp.B (Fig. 14b) illustrates a significant regression line that explains approximately 40% of the variance (r^2=0.4022). The negative slope (increasing proportion of algal cells in the controls than in the experiments) represents an increase in selection for that species of algae by the copepod as chlorophyll depletion increases. Figure 14c shows a significant positive relationship between chlorophyll a depletion and the proportional differences in the experiments with *Fragilaria* sp.A (explaining about 51% of the variance; r^2=0.5107). Contrary to *Navicula* sp.B, *Fragilaria* sp.A seems to be increasingly avoided as a food source (towards a higher proportion of algal cells in the experimental treatments over the controls) as *P. acuspes* is allowed to consume more algae. The final two species of diatoms (*Nitzschia seriata* (Fig. 14d) and *Thalassiosira* sp.A (Fig. 14e)) are both selected for by *P. acuspes* when feeding on the natural phytoplankton assemblage (almost always a higher proportion of the algae in the controls than in the experimental treatments) and this positive selection increases with chlorophyll depletion (significant negative

slopes; explaining 21% (r^2=0.2110) and 63% (r^2=0.6288) of the variance respectively).

Note that all of the regression equations (Figs. 14a-14e) have a y-intercept that is noticeably different from zero. To help explain why there would be a difference between the experiments and controls when there is no chlorophyll a depletion (i.e., no feeding), we must compare the initial values with both the experimental treatments and the controls. For *Navicula* sp.B (Fig. 14b), it seems that the proportion increased in the experimental treatments over the controls when there was little or no feeding (i.e., y-intercept appears to "work" against the direction of selection). For *Fragilaria* sp.A (Fig. 14c), the proportion seemed to decrease in the experimental treatments over the controls when there was little or no feeding. For *Nitzschia seriata* (Fig. 14d) and *Thalassiosira* sp.A (Fig. 14e) the y-intercept appears to "work" in the direction of selection, as the diatom proportions tend to decrease in both the controls and the experimental treatments. This could have the result of increasing the apparent slope of the regression if this "effect" is enhanced by the extent of chlorophyll a depletion (the "effect" here being an inexplicable change in the diatom community within the incubation bottles during the course of the experiments). Therefore, we might be mistakenly led to believe that the relationship between the extent of feeding and selection is

stronger than it really is. However, when the initials are examined for experiments #1, #4, and #8 for these diatoms, it is evident that the effect is relatively constant over the range of chlorophyll a depletions from 1.66μgL^{-1} to 8.68μgL^{-1}. Thus there is no indication that this "effect" would significantly alter the apparent selection indicated by the slopes, but would only cause translation of the lines up or down.

From Figures 14(a-e), we can see that, in most cases, a significant part of the variance in the t-test from Table 7 can be attributed to the amount of algae that *Pseudocalanus acuspes* consumes during the course of the experiment. Feeding selection seems to depend on the amount of algae the copepods are allowed to eat.

At this point in our study, it would be satisfying to be able to quantify the selection response by the copepod (i.e., a rank order of diatom preference) by, for example, comparisons between regression equation slopes; i.e., the diatom *Thalassiosira* sp.A seems to be more strongly selected for than *Nitzschia seriata*, on the basis of the larger negative slope (Figs. 14d and 14e).

However, the experiments were only designed to test for the presence of selection in an environment that attempts to duplicate natural conditions. It was paramount to establish the importance of feeding selection by *P. acuspes* when presented with a natural phytoplankton

assemblage. Caution should be exercised when inferring comparative selection strengths from the available data. More controlled experimental conditions, with careful consideration of particle sizes, abundances, condition or physiological state, and availability are required for strong food preference statements.

In this study we do have information on the approximate sizes of the various diatom species. As an index of relative cell biomass, approximate cell volumes were calculated for each diatom species. The following values were obtained: *Navicula* sp.A =$1.11 \times 10^3 \mu m^3$-$1.22 \times 10^3 \mu m^3$, *Navicula* sp.B =$1.44 \times 10^3 \mu m^3$-$1.62 \times 10^3 \mu m^3$, *Fragilaria* sp.A =$0.68 \times 10^3 \mu m^3$-$0.81 \times 10^3 \mu m^3$, *Nitzschia seriata* =$2.16 \times 10^3 \mu m^3$-$7.29 \times 10^3 \mu m^3$, and *Thalassiosira* sp.A =$10.31 \times 10^3 \mu m^3$-$14.14 \times 10^3 \mu m^3$. The average colony sizes were also calculated for each species (pooled for all eight experiments) using the experimental controls. The average number of cells per colony for *Navicula* sp.A =9.7 (standard deviation=5.2), for *Navicula* sp.B =9.3 (s.d.=4.2), for *Fragilaria* sp.A =1.0 (s.d.=0.1), for *Nitzschia seriata* =1.8 (s.d.=0.3), and for *Thalassiosira* sp.A =1.7 (s.d.=0.6). We can now take the approximate cell volumes and multiply that by the average number of cells per colony and get a measure of their relative "effective food parcel size". The following results were obtained: *Navicula* sp.A =$10.8 \times 10^3 \mu m^3$-$11.8 \times 10^3 \mu m^3$, *Navicula* sp.B =$13.3 \times 10^3 \mu m^3$-$15.1 \times 10^3 \mu m^3$, *Fragilaria* sp.A

=0.68x10^{3}μm^3-0.81x10^{3}μm^3, *Nitzschia seriata* =3.89x10^{3}μm^3-13.1x10^{3}μm^3, and *Thalassiosira* sp.A =17.5x10^{3}μm^3-24.0x10^{3}μm^3.

As some indication of how particle size might be reflected in the feeding selection, without considerations of abundances, the slope of the significant regression lines (Figs. 14b-e) are related to "effective food particle size" (Fig. 15). Even though we are limited to four points on the graph, there is a strong negative relationship indicated between the slope of the regression lines and the size of the diatom food parcel. Thus, feeding selection depends on the amount of algae (chlorophyll a) eaten by *Pseudocalanus acuspes* (Figs. 14a-e), and this relationship can in turn be related to the size of the diatoms (Fig. 15). Size is an important factor in our experiments: the larger the food parcel size, the stronger the detected selection.

The average feeding preference measure ($\hat{\alpha}$) for the individual diatom species over the course of the feeding selection experiments (Table 8) indicates the overall selection. The index can be interpreted as "the proportion of the diet which would consist of type *i* if all food types were present in equal numbers in the environment" (Chesson, 1983). Thus, random feeding is indicated by a preference index of 0.20, as we are considering five diatom species. A value of 1.00 indicates complete selection for a particular species, while a value of 0.00 indicates complete avoidance. Overall, both *Navicula* sp.A and *Navicula* sp.B seem to be

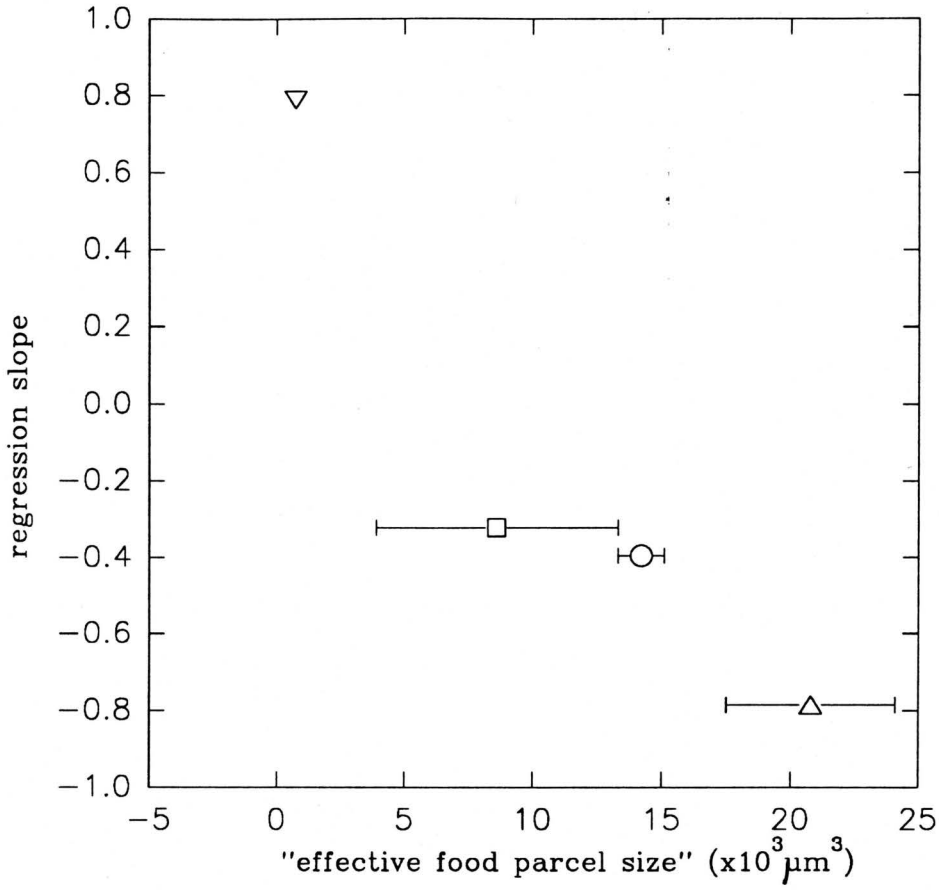


Figure 15. "Effective food parcel size" for *Navicula* sp.B (hollow circle), *Fragilaria* sp.A (hollow triangle down), *Nitzschia seriata* (hollow square), and *Thalassiosira* sp.A (hollow triangle up) versus the slope of the regression line (from chlorophyll a depletion versus colony proportional differences; Figures 14b–e). See text for calculation of "effective food parcel size". Error bars represent the range of size.

Species:	Preference Measure:		
		s.d.	n
Navicula sp.A	0.12	0.06	8
Navicula sp.B	0.12	0.04	6
Fragilaria sp.A	0.23	0.09	8
Nitzschia seriata	0.27	0.04	7
Thalassiosira sp.A	0.35	0.11	8

Table 8. Average preference measure for individual diatom species over the course of the feeding selection experiments. Index ($\hat{\alpha}$) is after Manly et al. (1972) as reported in Chesson (1983). A value of 0.20 indicates random feeding, while a value of 1.0 indicates complete selection and a value of 0.00 indicates complete avoidance (n= number of experiments considered; s.d.= standard deviation).

avoided slightly as a food source. Overall, *Fragilaria* sp.A is randomly eaten roughly in the proportion that it is found in the feeding environment (with a significant amount of variance). Both *Nitzschia seriata* and *Thalassiosira* sp.A seem to be preferred by *Pseudocalanus acuspes*.

However, these overall averages (Table 8) do not show the tendency for selection to change with increasing consumption (Fig. 14a-e). Selection appears to be highly dependant on diatom depletion, which would reflect the feeding rates and/or duration of exposure to the feeding environment. Moreover, the apparent "effect" discussed earlier whereby their is a change in the colony proportions due to the experimental treatment even when no grazing was evident is not taken into account during calculation of the preference measure. The index simply measures overall differences in numbers between controls and experimental treatments.

DISCUSSION

The results indicate that a significant level of feeding selection can indeed occur in *Pseudocalanus acuspes* when it grazes on a natural phytoplankton assemblage (Figs. 14a-e; Table 8). At this point, however, a few areas of possible concern should be addressed.

Harbison and McAlister (1980) discussed the experimental artifacts which can lead to erroneous conclusions in feeding selection studies. Although they were concerned with studies that used particle counters, a few comments should be made regarding the breakage of colony chains into smaller pieces by the copepods as they feed. There is the possibility that a feeding encounter by *P. acuspes* on a diatom chain might result in a broken remnant of that chain being left behind. This would not register as a feeding encounter when the proportion of total colonies for that particular diatom species are taken into account. This would then register as either no selection or avoidance by the copepod. We would not only lose the ability to accurately detect selection for that particular species, but might erroneously conclude that there is positive selection for other species of diatoms simply because sloppy feeding did not proportionally decrease the colony numbers of the first species relative to the others.

We can easily address this problem by examining the average numbers of cells per colony (square root

transformed) in the experimental treatments and compare them with the controls. When this is done, we find that for *Navicula* sp.B and *Fragilaria* sp.A there is no difference in the number of cells per colony between the experimental treatments and the controls (t-test, $p>>0.05$ in all experiments). However, there are significant differences (t-test, $p<0.05$) for *Navicula* sp.A (all 8 experiments), *Nitzschia seriata* (2 out of 7 experiments), and *Thalassiosira* sp.A (5 out of 8 experiments). Thus, at this point it seems that sloppy feeding could possibly complicate interpretation of the results.

We can take this process one step further to see how well the colony proportions (arcsine root transformed) correlate with the number of cells per colony (square root transformed) for *Navicula* sp.A, *Nitzschia seriata*, and *Thalassiosira* sp.A. Significant ($p<0.10$) positive correlations occur for *Nitzschia seriata* (4 out of 5 experiments) and *Thalassiosira* sp.A (all 6 experiments), indicating that the colony proportions used to indicate feeding selection mimic a decrease in the number of cells per colony in the experimental treatments. Thus, for at least those two species, there was sloppy feeding but it was reflected in the colony proportions, and this would not complicate our interpretation of the experiments. However, *Navicula* sp.A showed only one significant positive correlation between the colony proportions and the number of

cells per colony in the eight experiments (experiment #7). The correlation coefficients are completely scattered among experiments, being both positive and negative. Furthermore, when the coefficients are compared to the colony proportional differences between experimental treatments and controls for each experiment (Fig. 13a), there is no discernable pattern. This does not pose a problem for interpretation, but reinforces our conclusion of non-selective feeding behaviour by *Pseudocalanus acuspes* on the diatom *Navicula* sp.A.

The ability of a copepod to be selective in its feeding may be dependant on the animal's preconditioning. Mayzaud and Poulet (1978) demonstrated that in the natural environment of Bedford Basin, Nova Scotia, a linear relationship existed between copepod ingestion rates and particulate matter content that never demonstrated saturation, perhaps indicating an acclimation over periods of days or weeks. This was related to the quantity and quality of the particulate food. Donaghay and Small (1979) noted that the copepod *Acartia tonsa* showed optimal selection for *Thalassiosira* cells, but that this ability was severely hampered when the animal was placed in a new phytoplankton assemblage to which it was not conditioned.

The experiments reported here took *Pseudocalanus acuspes* individuals and placed them in experimental bottles with the ambient phytoplankton assemblage within a few days

after capture. The copepods would probably still be "conditioned" to this algae mixture. Lack of preconditioning to the phytoplankton, however, would only result in decreased selective behaviour by the copepods, rather than increased selection as a copepod becomes "familiar" with an algal assemblage (Donaghay and Small, 1979). If some preconditioning was lost in our experiments, feeding selection by *P. acuspes* in their natural environment would be expected to be stronger than detected here.

Although I had to manipulate the concentration of phytoplankton in the feeding water used in each experiment, the concentrations are well within realistic values for Resolute Passage, N.W.T., during the summer (with the possible exception of experiments #2 and #3; H. Welch, pers. comm.). H. Welch (Freshwater Institute, Dept. of Fisheries and Oceans, Winnipeg, Manitoba) and his colleagues carried out several vertical profiles of chlorophyll a from the waters adjacent to Resolute Bay during the summer of 1991. Four representative profiles were selected to illustrate a typical summer seasonal pattern of chlorophyll a (Fig. 16). Summer phytoplankton blooms typically begin in mid July and can reach peaks exceeding 10µg chl a L^{-1} (H. Welch, pers. comm.). By early August, the algae begin sinking out of the water column, though it is still readily available to *Pseudocalanus acuspes*. In fact, it is evident that by early in August, the copepods have largely descended to deeper

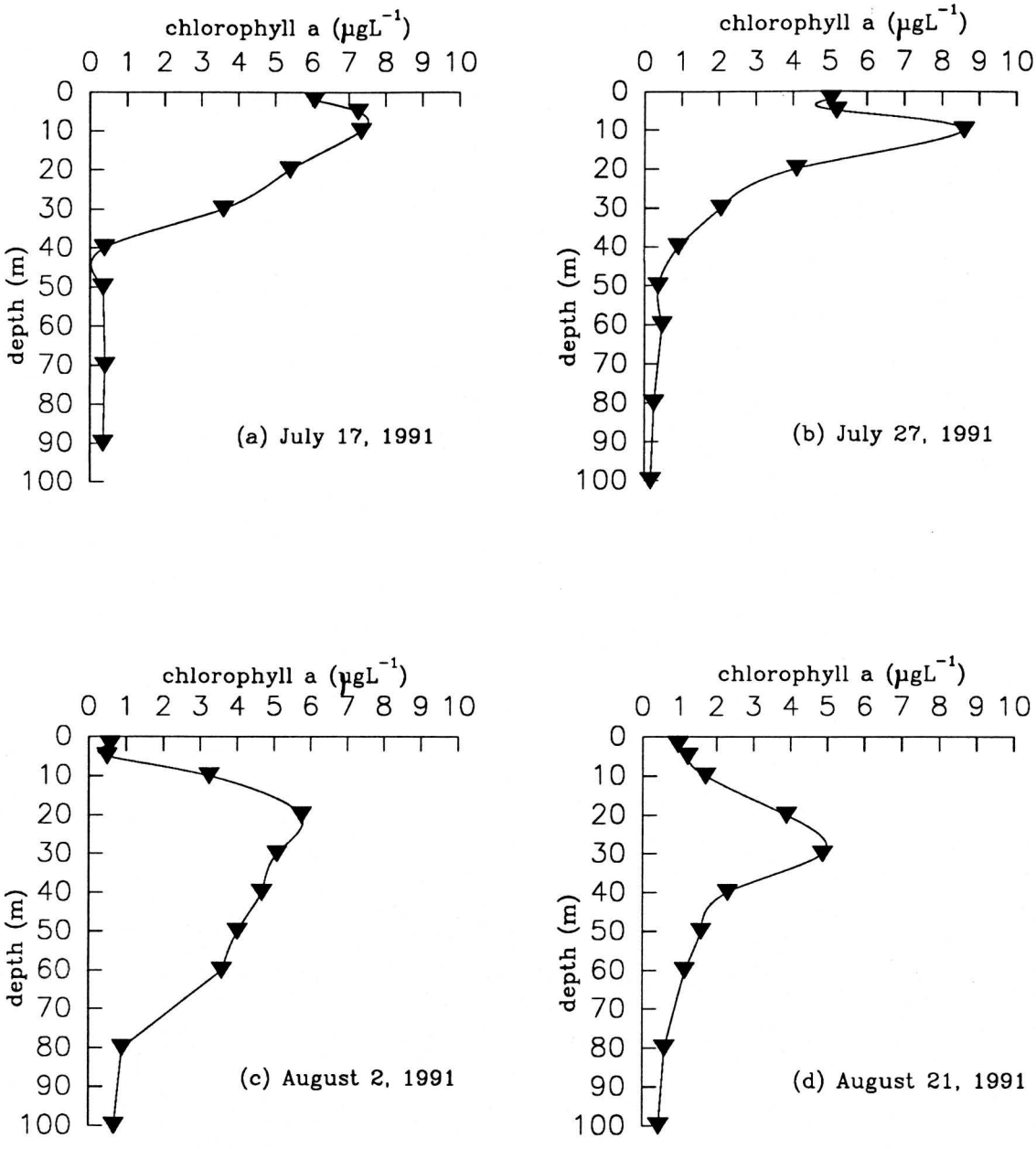


Figure 16. Typical vertical profiles of particulate chlorophyll a (μgL^{-1}) during the summer (July–August) in the waters of Resolute Passage, N.W.T., and adjacent Barrow Strait. Dates of profiles are shown on each plot. Data courtesy of H. Welch, Freshwater Institute, Department of Fisheries and Oceans, Winnipeg, Manitoba, Canada.

water where they can presumably take advantage of the sinking algal bloom (see previous chapter).

Even though two (and possibly three) of the experiments began with phytoplankton concentrations higher than might be expected in the field, it should not be of serious concern. DeMott (1989) found that for the freshwater copepod *Eudiaptomus,* selectivity did not change with food concentration, but was most strongly influenced by particle quality and the abundance of alternative foods. The independence between degree of feeding selection and food concentration is not unexpected for animals in a well-nourished state. *Pseudocalanus acuspes* in the waters of Resolute Passage during the month of August shows no signs of being severely limited by food, as supported by the low O:N ratios (by atoms) measured in incubation experiments, and its ability to accumulate large lipid reserves (see previous chapter).

Now that we have established that feeding selection can occur when a copepod feeds on a natural phytoplankton assemblage, it would be advantageous to know what characteristic or condition of diatoms *Pseudocalanus acuspes* is selecting for or avoiding. We can superficially examine is diatom size. The calculations of "effective food parcel size" presented at the end of the results seem to indicate that the animals are selecting for size to a certain extent (Fig. 15). The smallest food parcel size, *Fragilaria* sp.A,

was avoided during feeding. The species selected for are all in the larger size ranges. Thus, by concentrating its feeding endeavours on the largest food parcels, *P. acuspes* might be able to more efficiently control its energy expenditures. However, one should not quantify the selection between diatoms here. As noted in the introduction, feeding selection is likely a complicated response related to food quality and the abundance of alternative foods (DeMott, 1989). More controlled experimental conditions are needed to more fully examine specific factors effecting selection.

The increase in selection with the extent of chlorophyll depletion in our experiments (Fig. 14a-e) is understandable as one expects the copepods to be more selective while satiated in an abundant food supply ("pickier" when not hungry). Furthermore, the ability of the copepods to make a significant impact on the algae concentrations such that selection is detectable could be a factor in our experiments. As selection seems to change with the extent of feeding for *Pseudocalanus acuspes*, it should be accounted for in future experiments.

In conclusion, the arctic calanoid copepod *Pseudocalanus acuspes* selects particular species of diatoms over others when presented with a natural summer phytoplankton assemblage under experimental conditions which closely mimic the natural environment. The presence of

significant feeding selection by the copepod in the waters of Resolute Passage, N.W.T., is strongly suggested in this study. It would be desirable to examine in the future what impact this selective behaviour might have on the phytoplankton community. For example, what is the effect on the structure and succession of the algae? A closer examination of the features of the diatoms for which the copepods are selecting would also be desirable. Nonetheless, we know that feeding selection can occur and that this is a behavioral response which likely significantly enhances the ability of *Pseudocalanus acuspes* to survive in the arctic environment.

APPENDICES

The following pages outline feeding studies of diatom species examined in Part II of this study, but not discussed in the text.

Species:	Characteristics:
Navicula sp.C	-same as *Navicula* sp.A, except cells 18-20μm long by 6μm deep.
Navicula sp.D	-same as *Navicula* sp.A, except cells 25-27μm long by 6μm deep.
Thalassiosira sp.B	-same as *Thalassiosira* sp.A, except cells 22-25μm in diameter by 12-15μm deep.
Thalassiosira sp.C	-same as *Thalassiosira* sp.A, except cells 39-42μm in diameter by 15-18μm deep.
Coscinodiscus sp.A	-large circular pill-box cells, 200-250μm in diameter by 125μm deep.
Chaetoceros sp.A	-cells 36-39μm by 36-39μm (not including spines) with a typically hourglass shape. -cells form long chains.

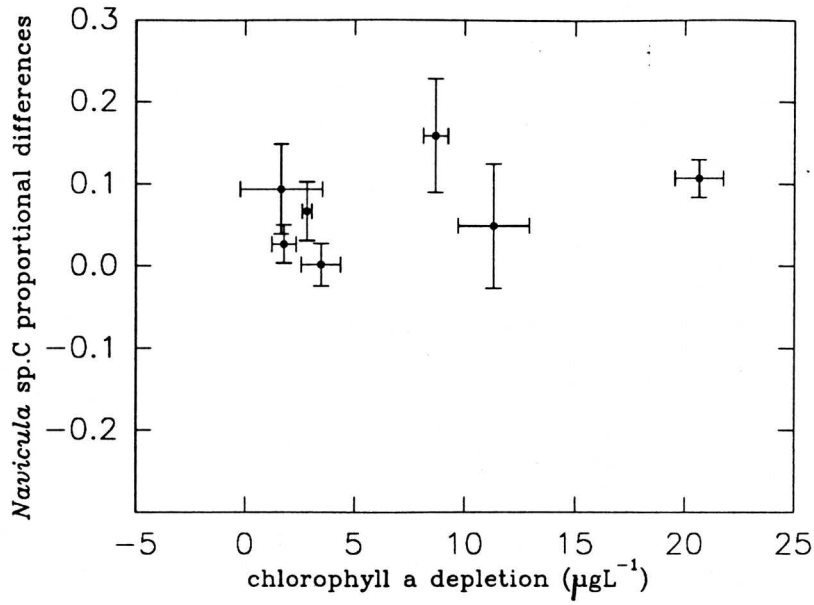
Appendix A. Characteristics of the diatoms found in the summer phytoplankton assemblage in Resolute Passage, N.W.T., and chosen for examination to indicate degree of feeding selection behaviour in *Pseudocalanus acuspes*.

	Experiment #							
	1	2	3	4	5	6	7	8
Navicula sp.C		*						
t	1.68	5.08	0.63	2.36	-	1.14	0.05	1.89
p	0.169	0.004	0.575	0.065	-	0.306	0.960	0.117
df	4	5	3	5	-	5	6	5
Navicula sp.D			*	*				*
t	1.47	1.94	3.74	2.84	-	1.63	2.32	4.29
p	0.216	0.110	0.033	0.036	-	0.163	0.060	0.008
df	4	5	3	5	-	5	6	5
Thalassio-sira sp.B		*	*	*	*		*	*
t	0.98	6.20	4.61	7.64	24.59	2.05	4.65	3.70
p	0.383	0.003	0.019	0.002	0.000	0.095	0.004	0.014
df	4	4	3	4	5	5	6	5

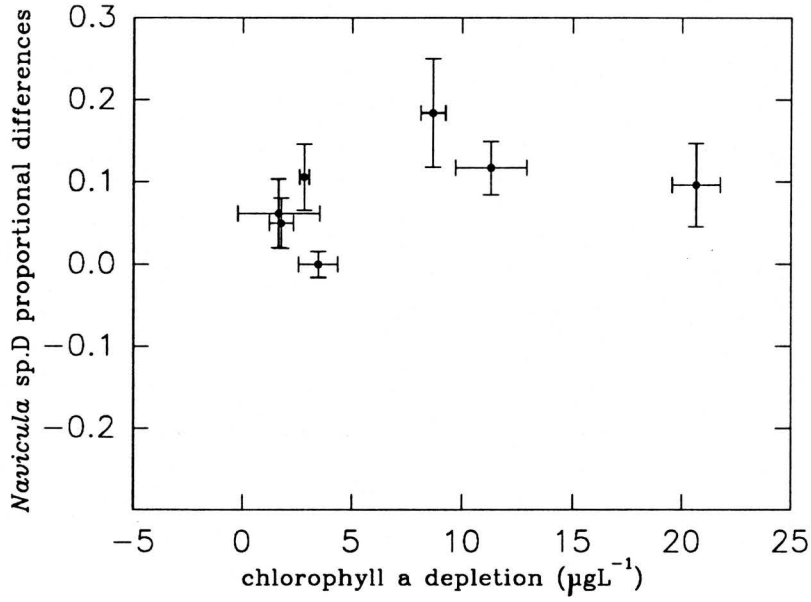
Appendix B1. Experimental results for individual diatom species showing t-statistic values ($\alpha(2)$) and probabilities (p) of correctly accepting the null hypothesis of no difference between experimental and control means (df= degrees of freedom; *=significance at the p=0.05 level).

		Experiment #							
		1	2	3	4	5	6	7	8
Thalassio-sira sp.C			*		*				
	t	0.27	7.73	-	7.41	-	0.14	1.26	-
	p	0.807	0.005	-	0.005	-	0.898	0.262	-
	df	3	3	-	3	-	4	5	-
Coscino-discus sp.A					*	*		*	
	t	0.07	-	2.09	7.47	3.51	2.28	3.10	0.26
	p	0.947	-	0.128	0.001	0.025	0.071	0.021	0.804
	df	4	-	3	5	4	5	6	5
Chaeto-ceros sp.A									
	t	-	-	1.43	-	0.85	-	1.53	1.50
	p	-	-	0.249	-	0.457	-	0.177	0.193
	df	-	-	3	-	3	-	6	5

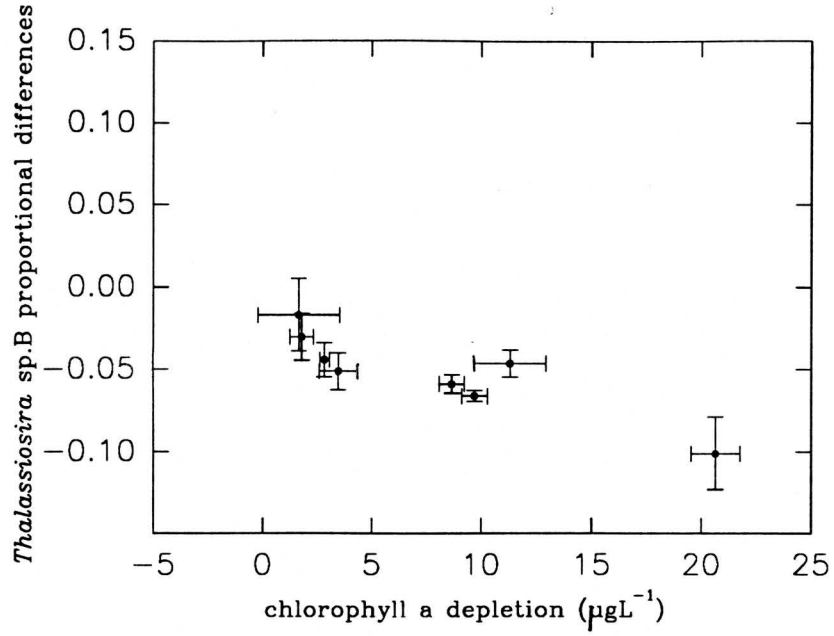
Appendix B2. Experimental results for individual diatom species showing t-statistic values ($\alpha(2)$) and probabilities (p) of correctly accepting the null hypothesis of no difference between experimental and control means (df= degrees of freedom; *=significance at the p=0.05 level).



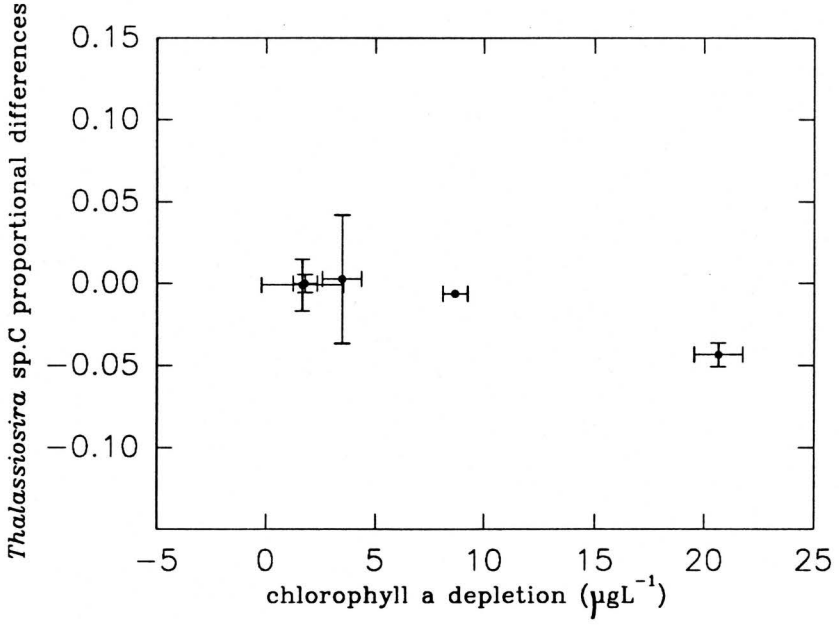
Appendix C1. *Navicula* sp.C proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 13a. Note the change in the vertical scale.



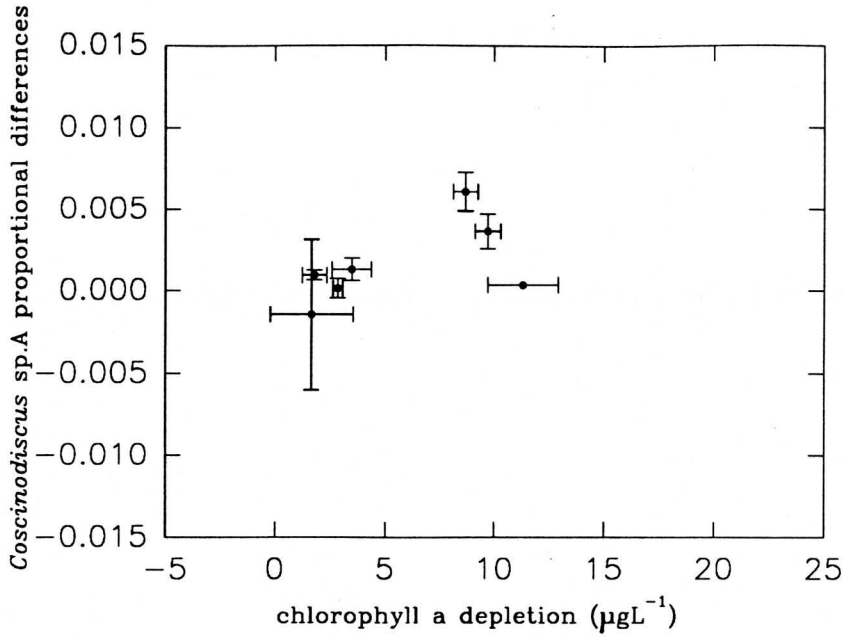
Appendix C2. *Navicula* sp.D proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 13a. Note the change in the vertical scale.



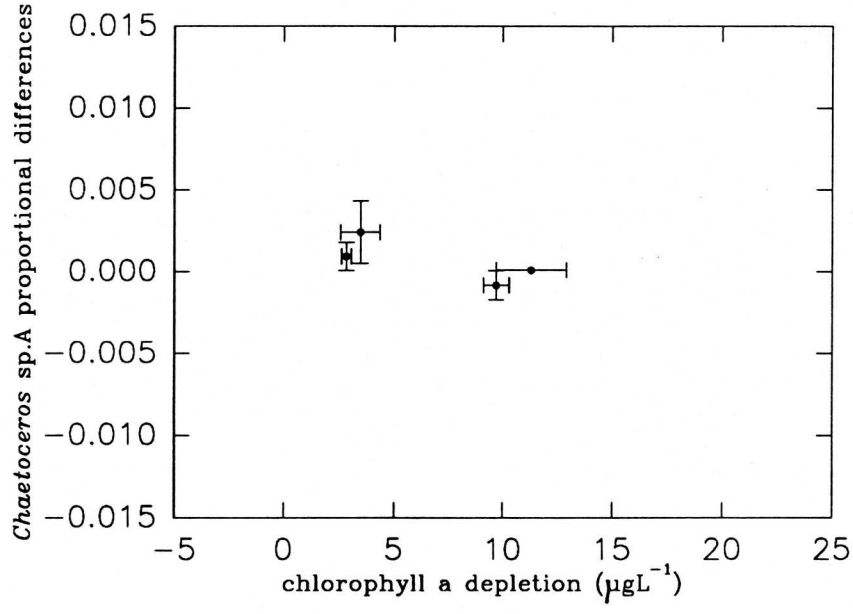
Appendix C3. *Thalassiosira* sp.B proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 13a. Note the change in the vertical scale.



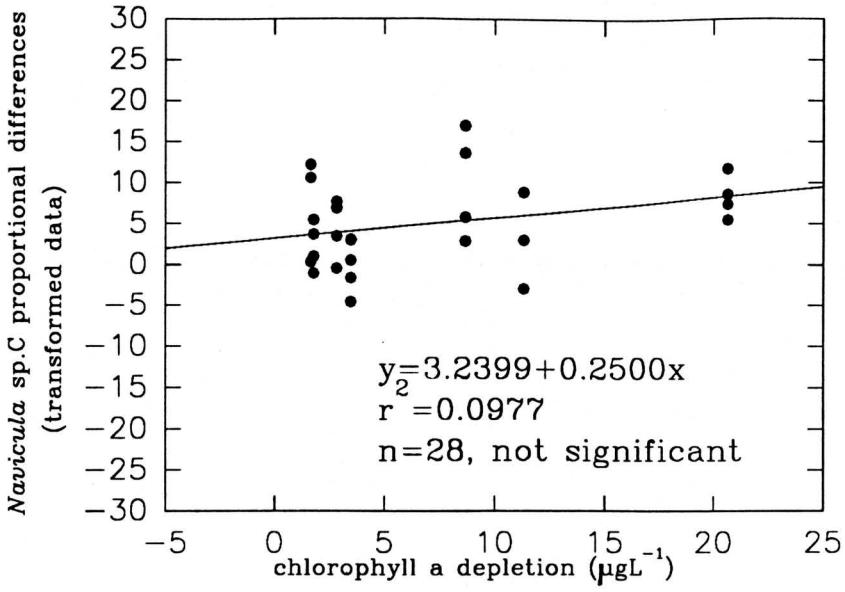
Appendix C4. *Thalassiosira* sp.C proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 13a. Note the change in the vertical scale.



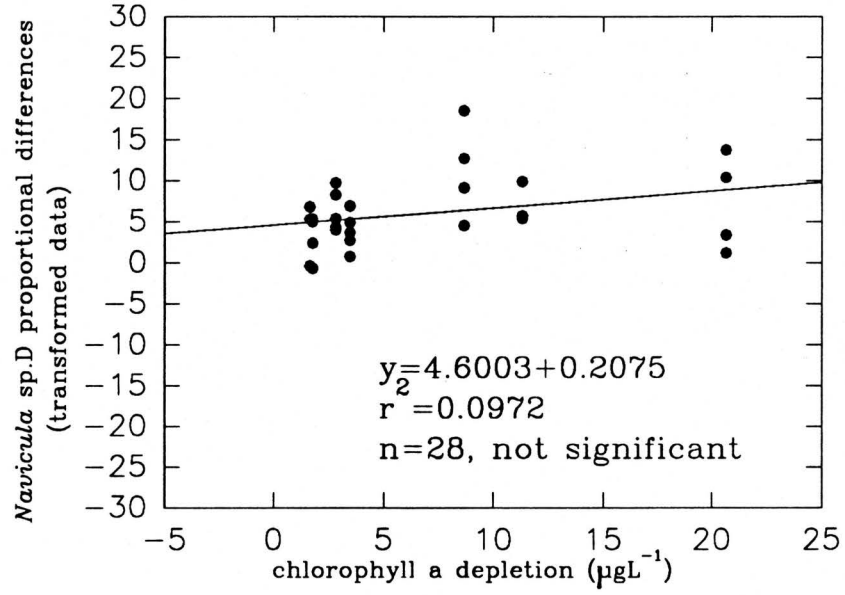
Appendix C5. *Coscinodiscus* sp.A proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 13a. Note the change in the vertical scale.



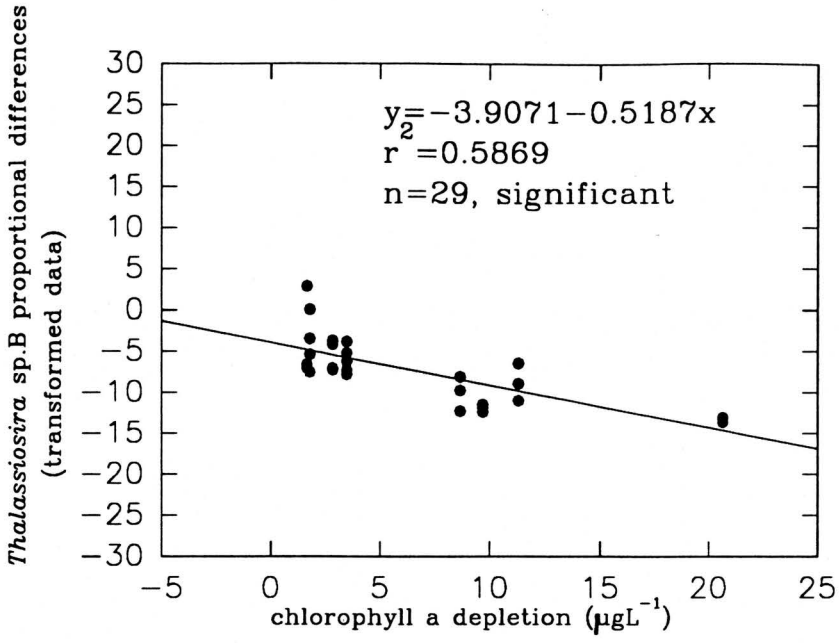
Appendix C6. *Chaetoceros* sp.A proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 13a. Note the change in the vertical scale.



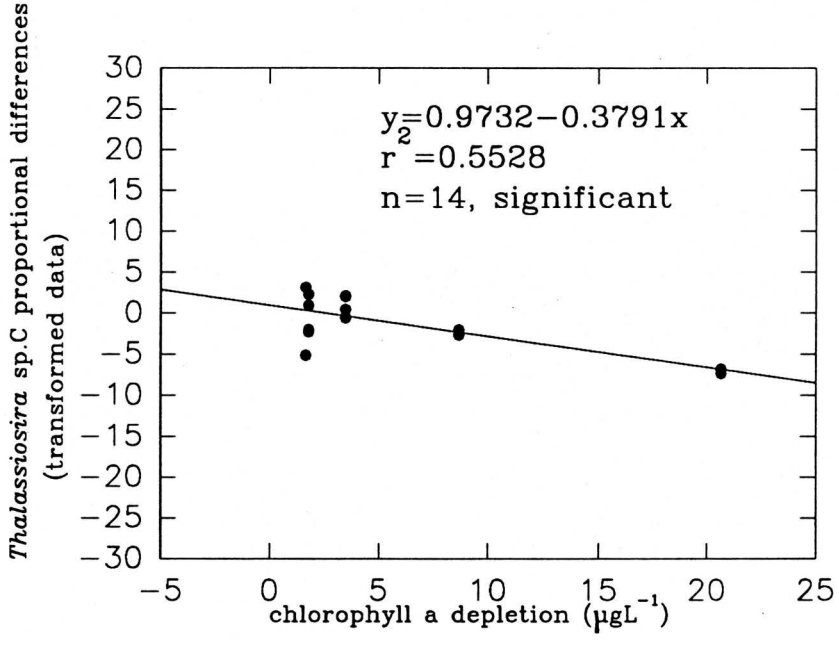
Appendix D1. *Navicula* sp.C proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 14a.



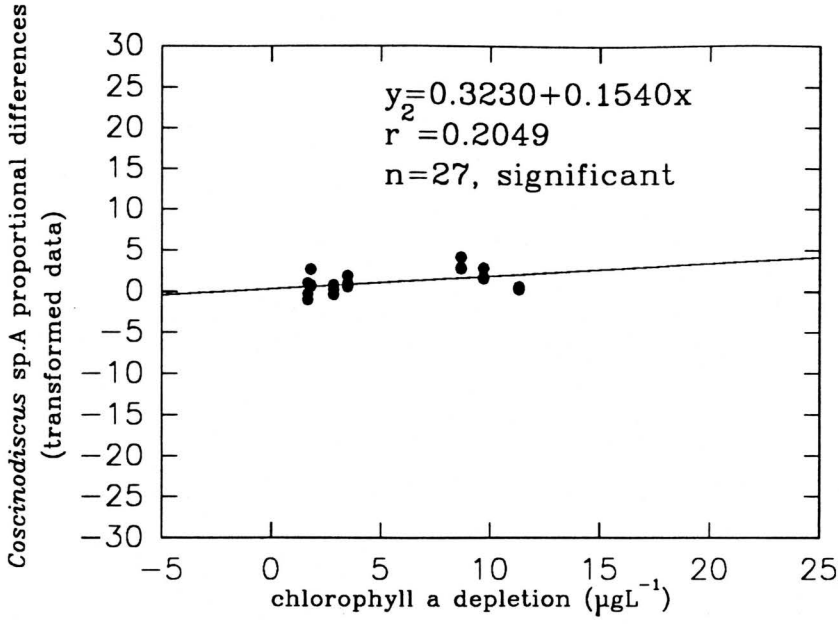
Appendix D2. *Navicula* sp.D proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 14a.



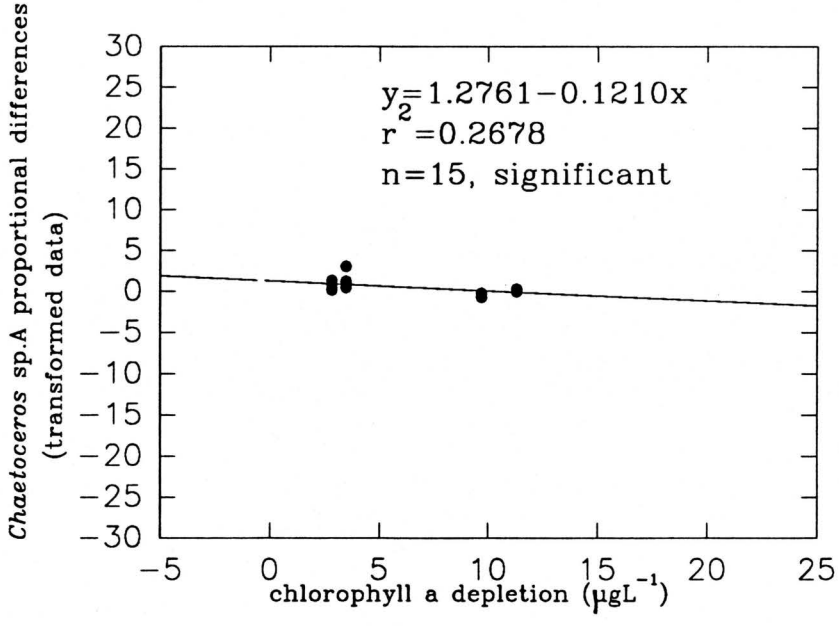
Appendix D3. *Thalassiosira* sp.B proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 14a.



Appendix D4. *Thalassiosira* sp.C proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 14a.



Appendix D5. *Coscinodiscus* sp.A proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 14a.



Appendix D6. *Chaetoceros* sp.A proportional differences versus the extent of chlorophyll a depletion for each of the feeding selection experiments. Graphic elements are as defined in Figure 14a.

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